THE ECOLOGY OF THE PLANKTON OFF LA JOLLA, CALIFORNIA, IN THE PERIOD APRIL THROUGH SEPTEMBER, 1967

EDITED BY
J. D. H. STRICKLAND

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY • LOS ANGELES • LONDON
1970

BULLETIN OF THE SCRIPPS INSTITUTION OF OCEANOGRAPHY
OF THE UNIVERSITY OF CALIFORNIA
LA JOLLA, CALIFORNIA

Volume 17
Approved for publication March 20, 1970
Issued November 16, 1970
Price, $4.00

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY AND LOS ANGELES
CALIFORNIA

UNIVERSITY OF CALIFORNIA PRESS, LTD.
LONDON, ENGLAND

ISBN: 0-520-09362-3
LIBRARY OF CONGRESS CATALOG CARD NUMBER: 79-631069
[CONTRIBUTION FROM THE SCRIPPS INSTITUTION OF OCEANOGRAPHY, NEW SERIES]

CONTENTS

THE ECOLOGY OF THE PLANKTON OFF LA JOLLA, CALIFORNIA, IN THE PERIOD APRIL THROUGH SEPTEMBER, 1967

EDITED BY
J. D. H. STRICKLAND

PART I

GENERAL INTRODUCTION, HYDROGRAPHY, AND CHEMISTRY

BY
J. D. H. STRICKLAND, LUCIA SOLÓRZANO, and R. W. EPPLEY

ABSTRACT

Weekly observations of nearshore plankton and related hydrographic variables were made from mid-April to mid-September, 1967, at three stations, 1.4, 4.6, and 12.1 km offshore, just north of La Jolla. Daily water-temperature measurements were obtained from the Navy Electronic Laboratory Oceanographic Research (NEL) Tower and the Scripps Institution of Oceanography pier. The amount of incoming solar radiation was measured at the Scripps Institution of Oceanography.

At each weekly station, measurements were made of temperature, salinity, submarine light attenuation, phytoplankton, microzooplankton, chlorophyll *a*, phosphate, nitrate, and silicate, the last four using automated methods of analysis. In addition, an estimate was obtained of the total amount of particulate and dissolved organic carbon, nitrogen, and phosphorus over the "plant pigment depth."

The thermocline sharpened as the surface waters warmed progressively throughout the period under study, and "upwelling," indicated by a shoaling of the thermocline, occurred periodically over the whole region. Because there was a close correlation among each of the three plant nutrients and temperature, "upwelling," which was roughly predictable from local wind patterns and more widespread meteorological conditions, caused layers of high nutrient concentration to move nearer the sea surface at these times. The shoaling of the "trophocline" was the feature probably most responsible for qualitative and quantitative changes of productivity.

Although the amount of detritus in the water appeared to depend on the level of primary production, the production had little effect on the amount of dissolved organic material except perhaps at the station closest to the coast, where the plant-cell concentration was densest.

GENERAL INTRODUCTION

THE NEARSHORE plankton ecology has never been studied off the Scripps Institution of Oceanography by an interdisciplinary approach measuring biomass changes simultaneously in all size ranges of the plankton and relating these changes to the hydrographic environment and to the primary productivity of the region. An attempt was made to do so in 1967 through weekly observations from mid-April to mid-September made by the Food Chain Research Group of the Institute of Marine Resources (IMR).

Complete data accumulated during the investigation is found in two reports: University of California, Institute of Marine Resources (1968*a* and *b*). Copies of these two data records are on file at Scripps Institution of Oceanography.

Some of the more interesting findings of the 5-month survey are considered in the seven papers composing the present work. In addition to the hydrography, inorganic nutrient chemistry, and dissolved and particulate organic chemistry presented in this paper (Part I), the other units are: Part II, Vitamin B_{12}, thiamine, and biotin (Carlucci); Part III, Estimates of phytoplankton crop size, growth rate, and primary production (Eppley, Reid, and Strickland); Part IV, Relationships of phytoplankton species distribution to the depth distribution of nitrate (Eppley); Part V, Phytoplankton taxonomy and standing crop (Reid, Fuglister, and Jordan); Part VI, Numerical abundance and estimated biomass of microzooplankton (Beers and Stewart); and Part VII, Production of the planktonic copepod, *Calanus helgolandicus* (Mullin and Brooks).

The time of year for the investigation was chosen in the hope that we would see the development and decay of a red tide. This phenomenon, which has occurred in the area on numerous occasions, has been described by many authors and a summary, together with some recent investigations, is to be found in a paper by Holmes *et al.* (1967). Unfortunately, a major red-tide condition never developed in the area during 1967, although a small bloom of the dinoflagellate, *Gonyaulax polyedra,* lasting for less than a week, was noted in early September. Weekly flights over the coast from Point Loma to Oceanside failed to detect discolored water at any other time except that attributable to diatoms in the vicinity of Point La Jolla during the last week in June.

A preliminary study over a 9×15 km rectangular grid in the same general area on four successive days in September, 1965 (University of California, Institute of Marine Resources, 1966) had revealed that, even in so brief a period, significant changes in the hydrographic and biological variables occurred and that at least semiweekly observations should therefore be attempted. Logistical reasons, however, compelled us to limit observations to once a week.

The earlier survey indicated that conditions were more stable and reproducible well north of the La Jolla Canyon than south of it, but the desirability of having deep water at a nearshore location close to the Scripps Institution pier prompted us to locate only a little north of La Jolla. This earlier work had also shown a sharp seaward gradient of water quality and standing stock of plants and animals. The station pattern chosen for the current study is given in figure I-1. Station 3 was the longest distance offshore that could be managed with the daily ship-time available. Stations 1, 2, and 3 were occupied routinely throughout the 5-month period. Stations 4 and 5 were bathythermograph (BT) stations taken for only part of the period.

Previous hydrographic measurements in the immediate area of the coast have been limited largely to the routine observations of temperature taken at the Scripps Institution pier and the more extensive series of temperature and other physical measurements recorded from the NEL Tower near the entrance to Mission Bay (see, e.g., LaFond, 1966).

Early studies of the general oceanography of the area are summarized by McEwan (1916) and, based on later work from the Scripps Institution (e.g., Fleming, 1941), a general picture has emerged of the current system and temperature and salinity structure which is well described by Reid *et al.* (1958). The

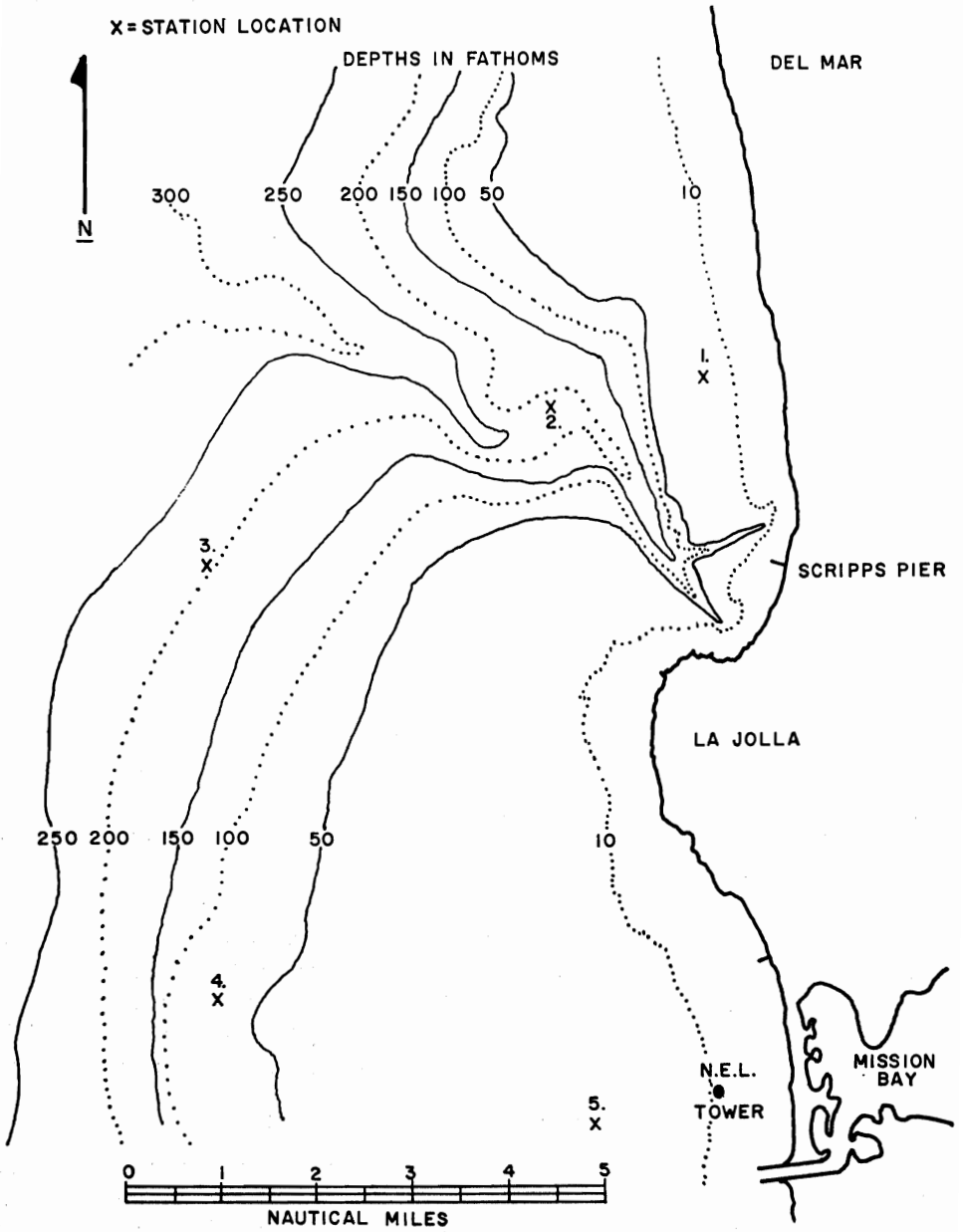

Fig. I-1. Location of stations 1–5, the NEL Tower and the Scripps Institution of Oceanography pier.

conditions off southern California have been summarized by Stevenson (1959) although there is little information in his work about the San Diego area.

The offshore south-flowing California Current of cool, low-salinity water has a subsurface nearshore counter current that at certain times of the year may affect the surface (the Davidson Current in winter). Close to San Diego the prevailing direction of surface movement is again southward but there is a large tidal component. It causes surface velocities of several tenths of a knot which move the water clockwise, northward at the time of the high tide and southward at low tide (see, e.g., Gaul and Stewart, 1960). Tidal movement and possible interactions with bottom topography have been suggested to cause local invasions of cold water (Stevenson and Gorsline, 1956). The oscillation of thermal gradients in the sea near San Diego has also been attributed to tidal motion (Cairns, 1967, 1968) although there is a significant contribution from wind transport as described by Cairns and LaFond (1966). Arthur (1960) demonstrated the rapid changes to be expected from internal waves near the Scripps Institution pier and documented at least one wind-driven invasion of warm offshore water to the depth of 50 m in the La Jolla Canyon.

In the present study, the major emphasis was to obtain data about the chemical environment, as we were primarily concerned with plankton nutrition. The limited amount of hydrographic data collected at the same time confirms the observation of previous workers and augments the routine observations collected at the Scripps Institution pier and at the NEL Tower over the same period.

Acknowledgments

This research was supported in full by the United States Atomic Energy Commission, Contract No. AT(11-1) GEN 10, P.A. 20.

We thank many colleagues and assistants who helped in various phases of the work, in particular C. R. Stearns for instrument support and O. Holm-Hansen, I. H. Ji, H. A. Kobayashi, and P. M. Williams for assistance with the analytical program. R. J. Linn maintained weekly aerial reconnaissance looking for visual evidence of high plankton crops. J. Cairns kindly made available water temperatures and wind data collected at the NEL Tower. Finally, the thanks of the entire group go to J. J. Mehling and C. W. Clampitt, Jr., the captains of the 60-ft vessel used during this study. Their cooperation and skill greatly facilitated the operation.

FIELD PROGRAM AND METHODOLOGY

Stations 2 and 3 were marked by bottom-moored buoys. Station 1 was located by a direct fix and by depth and the ship was anchored while on this station. The BT stations, 4 and 5, were located by radar fixes and were geographically determined with the least precision.

The routine at stations 2 and 3 was to steam to the buoy and make hydrographic observations consisting of a BT lowering and a Nansen-bottle cast for temperature and salinity measurements at depths of 75, 100, 125, 150, and 175 m. These observations generally required about 20 minutes. Note was taken of the drift during this time and the ship was next brought upwind from the buoy to a distance that would allow drift back past the buoy again about halfway through the next

operation, which was made with the profiling hose and which required about 60 minutes. Drift rates of more than half a knot were sometimes encountered but, in general, the midpoint positions of stations were within 100 or 200 m of the marker buoys. The profiling hose, with submersible pump, depth transducer, and thermistor-thermometer, was lowered slowly in two steps to 100 m. At station 1 the profile was to 21 m in a single step. The upper part of the profile at stations 2 and 3 was through the "pigment layer" while the second step was from the bottom of this layer to 100 m. The "pigment layer" is defined as that interval extending from the surface to a depth at which the *in vivo* fluorometer showed only insignificant amounts of fluorescing material representative of chlorophyll-containing particles. At station 1 this layer would have extended below the base of the weekly 21-m profile to near the bottom and has been taken as a standard 25 m throughout the study. At both stations 2 and 3 the pigment layer varied in depth from week to week, ranging from approximately 30 to 60 m and averaging 50 m. On more than one-third of the sampling dates at station 2 the pigment layer was more than 33 percent deeper than the depth of the euphotic zone as estimated at 3× the Secchi-disk depth. At station 3 a magnitude of that difference was observed on only one occasion.

Water was taken during profiling for the continuous analysis of chlorophyll, nitrate, silicate, and phosphate and for the batch analysis of other constituents. Salinities and temperatures at 25 m and 50 m were generally measured using the pump assembly. The continuous thermistor-temperature–depth profile to 100 m could be used to augment the data from the bathythermograph. The final operation at each station was a cast of 8-l plastic Van Dorn bottles to obtain water for photosynthetic rate measurements (Eppley *et al.*, Part III, below).

Water from the profiling hose was used for various analyses and the excess filtered for plankton. Salinities were measured by a Hytec inductive salinometer calibrated with Copenhagen water. Nitrate, silicate and phosphate were measured using the Technicon Autoanalyzer[R] adapted as described by Strickland and Parsons (1968) and chlorophyll was continuously recorded as fluorescence by the method of Lorenzen (1966). The chlorophyll profiles were generally calibrated by taking a sample from the hose effluent at the depth of the maximum fluorescence and by determining the absolute amount of chlorophyll by filtration and extraction. Subsequently we discovered that this procedure could lead to a significant error as the ratio $\frac{\text{fluorescence}}{\text{chlorophyll } a}$ varied with depth and the calibration was therefore sensitive to the exact depth at which standards were taken. The data given here indicate the general structure of the chlorophyll profiles and are sufficiently precise for making productivity estimates (see later) but they may be considerably in error at certain depths. At depths well below the euphotic zone the fluorescence was found to be attributable largely to phaeopigments.

The remaining water from the pump system was filtered through fine netting to catch microzooplankton (Beers and Stewart, Part VI, below), and a small fraction was diverted into a 5-gal polyethylene container at a constant rate such that about 10 l of water had accumulated by the time a profile segment was completed. This

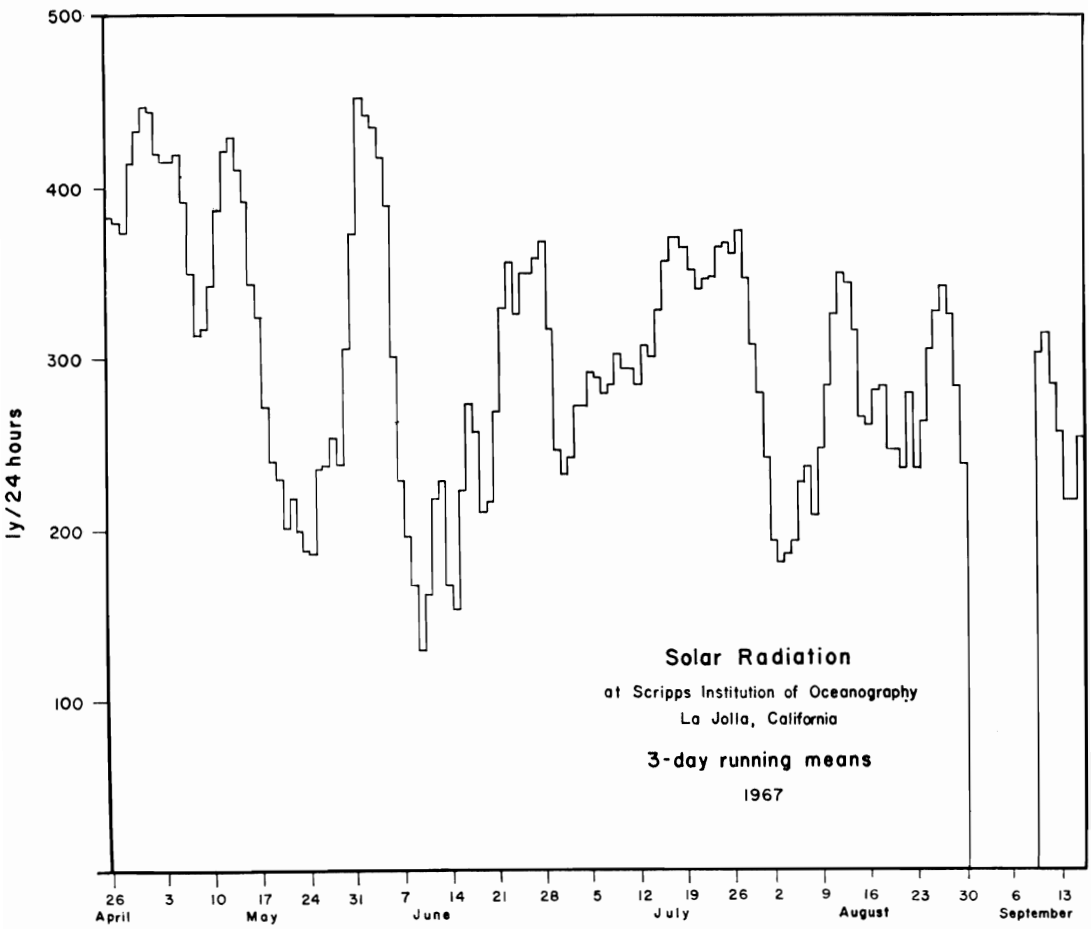

Fig. I-2. Total solar radiation at the Scripps Institution of Oceanography.

subsample was used for floristic analysis and an aliquot taken to determine the mean quantity of chlorophyll *a* by filtration, extraction, and fluorometry (Strickland and Parsons, 1968). The water was also used for the determination of total particulate carbon, nitrogen, and phosphorus collected by filtration through Whatman GF/C glass filters, and the filtrates were analyzed for dissolved organic carbon, nitrogen, and phosphorus. Methods for these determinations are described in detail by Strickland and Parsons (1968).

Solar radiation was measured at the Scripps Institution where the cloud cover would have been very similar to the area under study. A bimetallic actinograph (Kahl Scientific Instrument Corporation) was used to get daily records and was calibrated under noonday sun against an Eppley pyranometer. The depth profile of downwelling radiation was estimated at each station from Secchi depth measurements, assuming an intensity of 1 percent surface radiation occurred at three times and about 20 percent at one times the Secchi-disk depth. This assumption was an extreme oversimplification and was particularly in error when the plant cells occupied subsurface layers of high concentration in which the Secchi disk

was obscured. A more precise profile was therefore measured whenever possible using a submarine photometer fitted with a green filter and cosine collector.

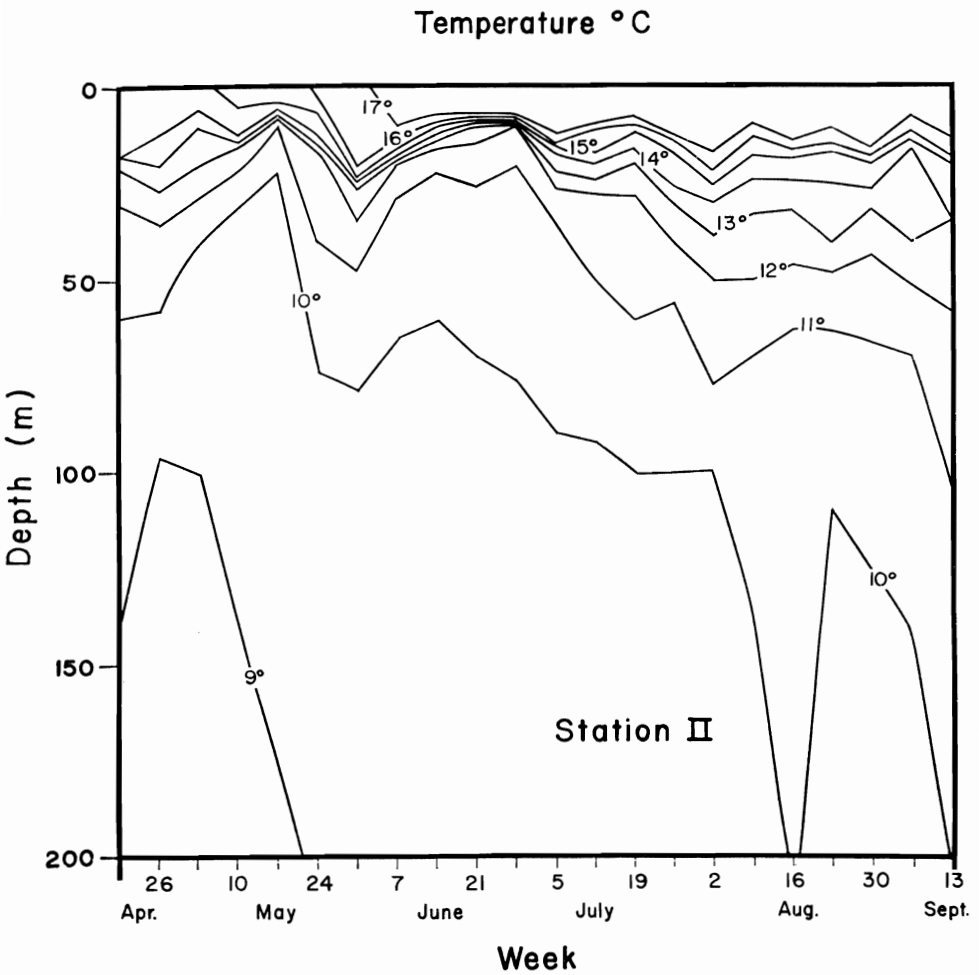

Fig. I-3. Isotherms at station 2, April–September, 1967.

RESULTS AND DISCUSSION

Radiation

Figure I-2 shows the 3-day running means of total radiant energy at the Scripps Institution. The photosynthetically active portion of this radiant energy would be about 50 percent. There was little seasonal change in daily radiation over the period, the greater radiation at the solstice being offset by the increase of cloud cover characteristic of that period. Maximum and minimum values occurred within a week of each other in June (460 and 130 cal/cm^2/day) and clearly reflected the effect of clouds and fog. The mean of about 300 cal/cm^2/day is representative of high summer values in more northern latitudes and we would not expect any light limitation of phytoplankton growth at the surface. No correlation was apparent between productivity and the amount of incoming radiation.

The euphotic depth was assumed to be the depth where incoming radiation in the visible part of the spectrum was attenuated to 1 percent of its surface value. This assumption is open to criticism. At best it is approximate and is probably an underestimate of the true euphotic depth. The values varied from week to week, ranging from as little as 12 m at station 1 to over 60 m at station 3. The euphotic

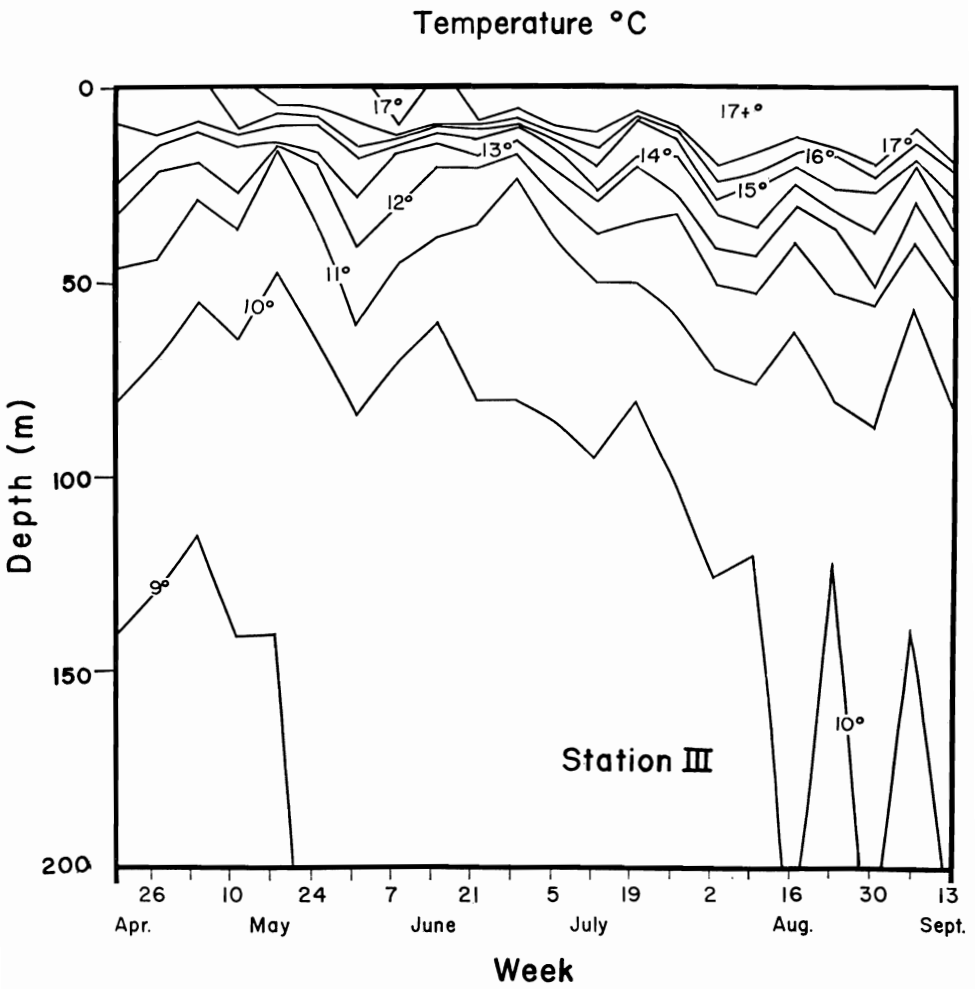

Fig. I-4. Isotherms at station 3, April–September, 1967.

depth for eight transects is shown in figures I-6 and I-7. Nearly every week the water clarity increased as one went seaward from the coast.

Hydrography

Except during periods of upwelling, salinity changes in the surface and subsurface waters were not pronounced. Salinities increased from about 33.5 percent at the surface to 34.2 percent at 175 m. The variation at a given depth was small over the entire 21 weeks and most of the density changes in the water are attributable to temperature variations.

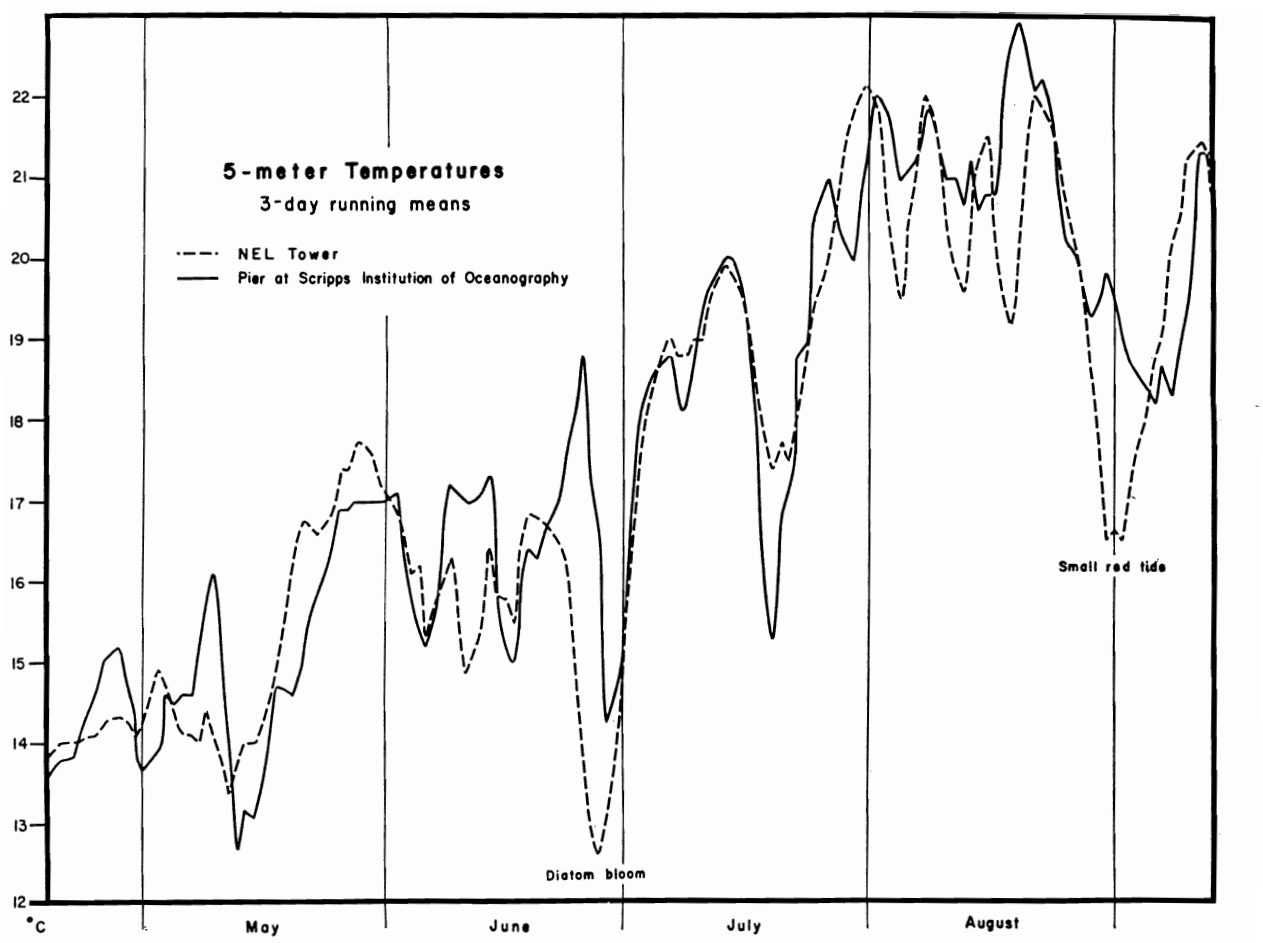

Fig. I-5. Three-day running mean temperatures at 5-m depth at NEL Tower and the Scripps Institution of Oceanography.

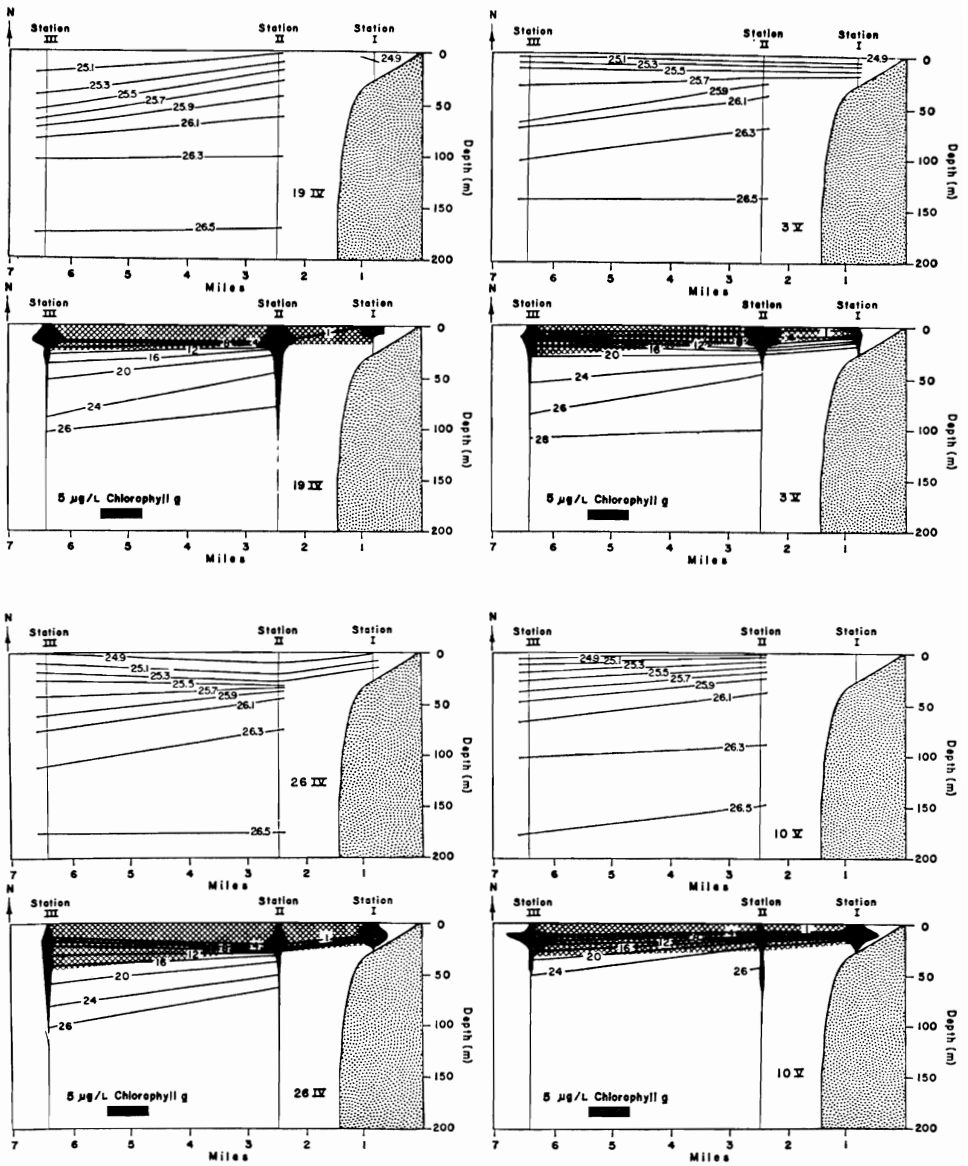

Fig. I-6. δ_t and NO_3^- isolines of a transect through stations 1–3 showing also chlorophyll and the euphotic depth. Selected dates in April–May, 1967.

Isotherms at stations 2 and 3 are plotted in figures I-3 and I-4. Changes in the temperature at 5-m depth at the NEL Tower are shown in figure I-5 as 3-day running means. Similar data are also shown in figure I-5 from the Scripps Institution pier (University of California, 1968). Data for station 1 and stations 4 and 5 are not being reported separately but showed the same trends as seen at the other locations.

Finally, the σ_t isopleths for a transect perpendicular to the coast were drawn for each week. Of these, four in April and May, at the commencement of the program,

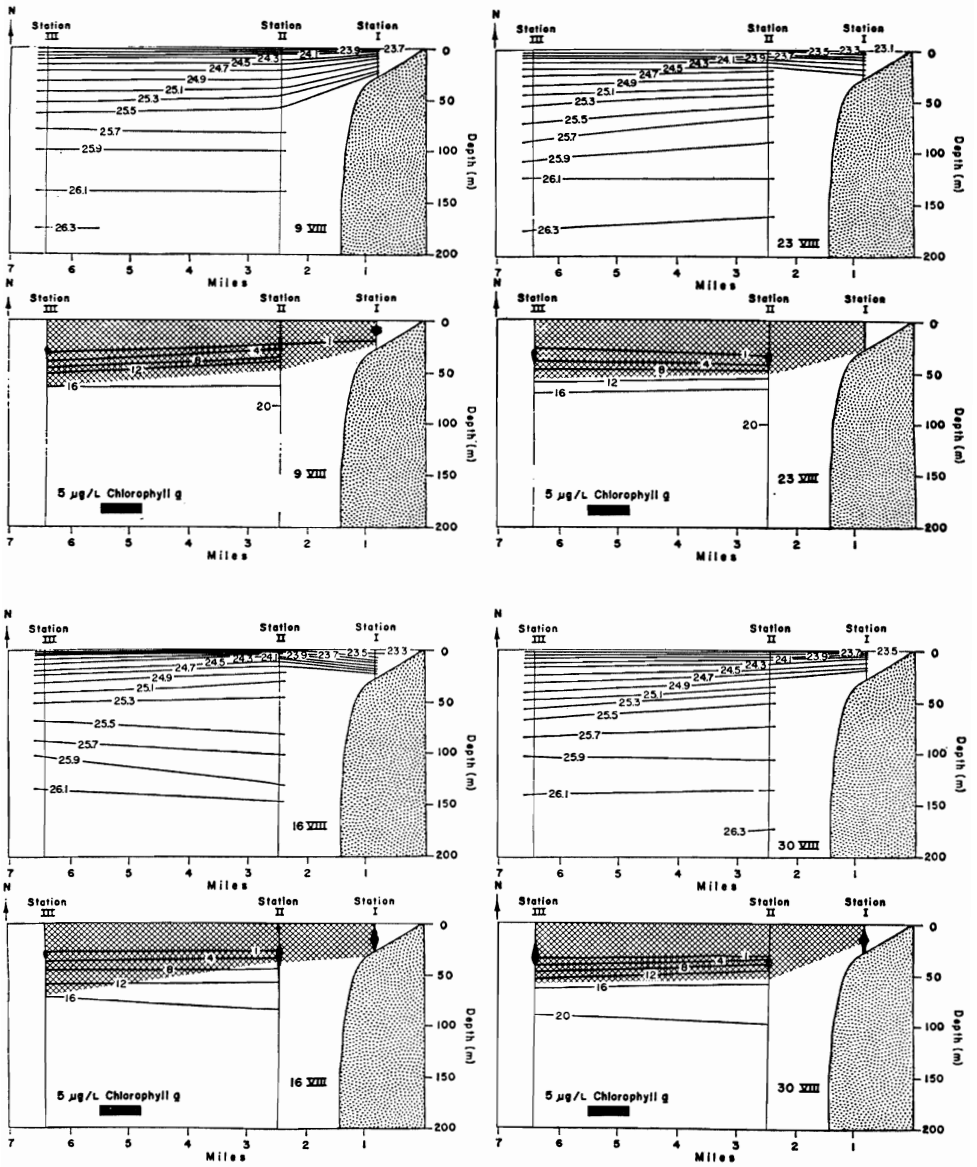

Fig. I-7. δ_t and NO_3^- isolines of a transect through stations 1–3 showing also chlorophyll and the euphotic depth. Selected dates in August, 1967.

and four in August, near the end of the program, are shown in figures I-6 and I-7. The crowding of the σ_t isopleths largely reflects the thermocline which is seen to be relatively weak in April and very sharp and near the surface in August. It is doubtful if the slope of σ_t lines shoreward has any significance for upwelling as variations are well within the limits to be expected from the passage of internal waves at the three stations during the time the transect was being measured (cf. Arthur, 1960).

An inspection of figures I-3, I-4, and I-5 shows that the depth at which one encountered cooler water shoals and the thermocline sharpened over the entire region (Mission Bay to Torrey Pines Park and offshore for about 7–8 miles) several times during the 21 weeks of the program. The peak of these "upwelling" periods occurred during the weeks in which measurements were made on 10 and 17 May, 28 June, 19 July, and 30 August. Less marked disturbances were seen at the end of April and in early June. For at least two periods, the first half of July and for most of August, conditions were very stable. During the upwelling periods in May and June the surface salinity showed a marked increase.

The influx of cold or warm water into the region (see fig. I-5) was remarkably coincident at the two points where near-continuous measurements had been made. Except for one or two brief periods the 5-m temperatures at the Scripps Institution pier and at the NEL Tower near Mission Bay fluctuated together and were as close to each other, numerically, as one could expect, considering the effects of topography on internal wave structures.

Cairns and LaFond (1966) have shown a good relationship between the west-northwest to east-southeast component of the wind along the coast (called positive) and the isotherm depth at the NEL Tower. The relationship between this wind vector and the thermocline depth is not as good in our data as has been found in other years, although the main upwelling periods are reflected by the wind patterns.

It may be that values at the NEL Tower are too local always to reflect the main wind forces responsible for water movement. At the other extreme, one can examine meteorological patterns for the entire northwest Pacific which show the gross wind patterns off the California coast. This meteorological data is conveniently obtainable as surface pressure analyses produced by Fleet Numerical Weather Central at Monterey and delivered to the Bureau of Commercial Fisheries at La Jolla. Inspection of these data showed a good correlation between upwelling and persistent northwest winds blowing a few days earlier. Thus, winds peaking between 9 and 13 May were probably responsible for upwelling in the period 10 to 17 May, winds from 26 to 30 May for the upwelling in early June, and the persistent northwesterlies in the second half of June can be related to the upwelling at the end of that month. There was weak evidence to suggest that the 19 July period originated from a wind pattern during 12 to 16 July but there was no explanation for the large disturbance at the end of August. The latter showed up well from the wind vector measured at the NEL Tower and was thus presumably of purely local origin.

Dissolved Inorganic Nutrients

Phosphorus (reactive phosphate) is not thought to be limiting to phytoplankton growth in the area under study and is not discussed in detail. Surface values never decreased below about 0.25 μg at/l and the concentration of this element increased, coincident with the increase of nitrate and silicate. Values of around 2 μg at/l were found at 100 m at the beginning of the period and 1–1.5 μg at/l at the end of the period. At station 1 bottom values were quite variable, ranging from over 1 μg at/l to as little as 0.5 μg at/l in August and September.

The use of an autoanlyzer profiling hose assembly reveals a considerable amount of fine structure in nutrient profiles. An example is given in figure I-8 showing the phosphate, nitrate, and silicate profiles for station 3 on 19 July, together with the *in situ* temperature.

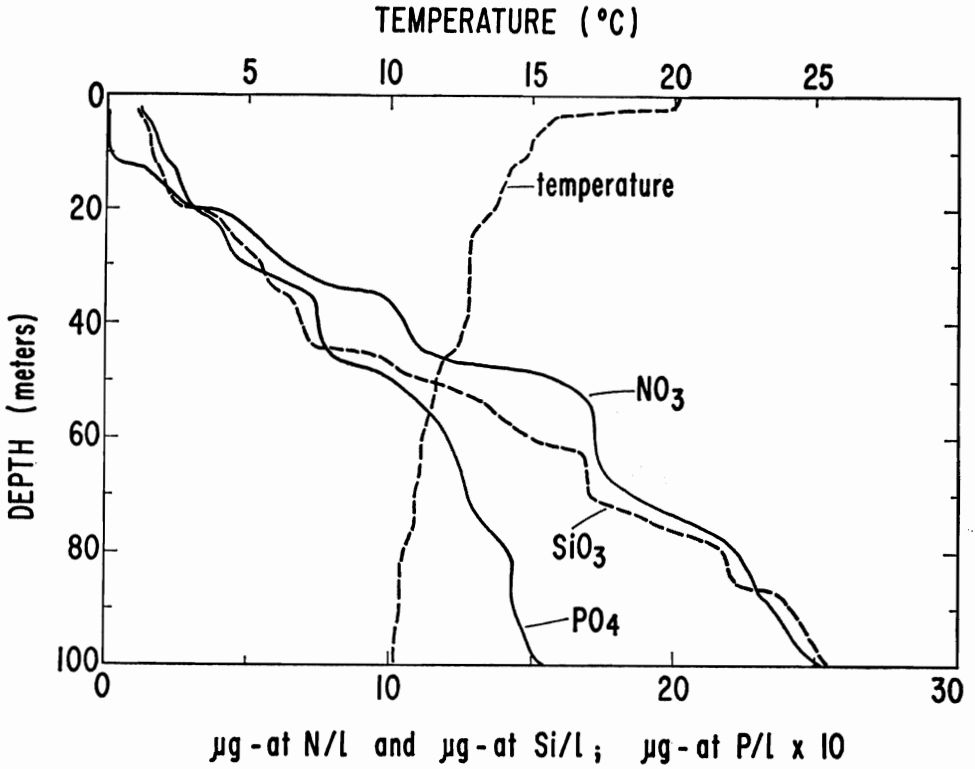

Fig. I-8. Profile of phosphate, nitrate, and silicate concentrations and temperature at station 3, 19 July 1967.

Inflections indicate layering and may result from uneven local rates of utilization, incomplete mixing, or the passage of internal waves during the time of measurement (Holm-Hansen *et al.*, 1966). The first explanation would seem to be the least likely, unless diatoms always constituted a constant fraction of the total plant crop, as generally changes in the silicate and nitrate curves closely paralleled each other. One of the few exceptions is shown in figure I-8 between 55 and 70 m where there is a wide difference in the inflections of the silicate and nitrate curves. The reason for this divergence is obscure but we may be seeing the effects of lateral interdigitation of water masses.

The relationship between silicate and nitrate is summarized in figure I-9, showing data for the three stations on three separate dates during the investigation. Nearly all the other data fell on these curves, within the limits of experimental error, irrespective of the date or depths of samples.

There was sometimes appreciably more silicate relative to nitrate in the waters of the inshore station, especially near the surface (see figure I-9). This increase

presumably reflects the rate of dissolution of silica relative to nitrification because the diatom populations were not noticeably low at station 1. As the deeper samples at station 1 had a more "normal" ratio than those nearer the surface, the influence of the bottom is not suspect. On the average, 3 μg at Si/l remains in surface waters after all nitrate has been utilized. The net loss of 100 parts by

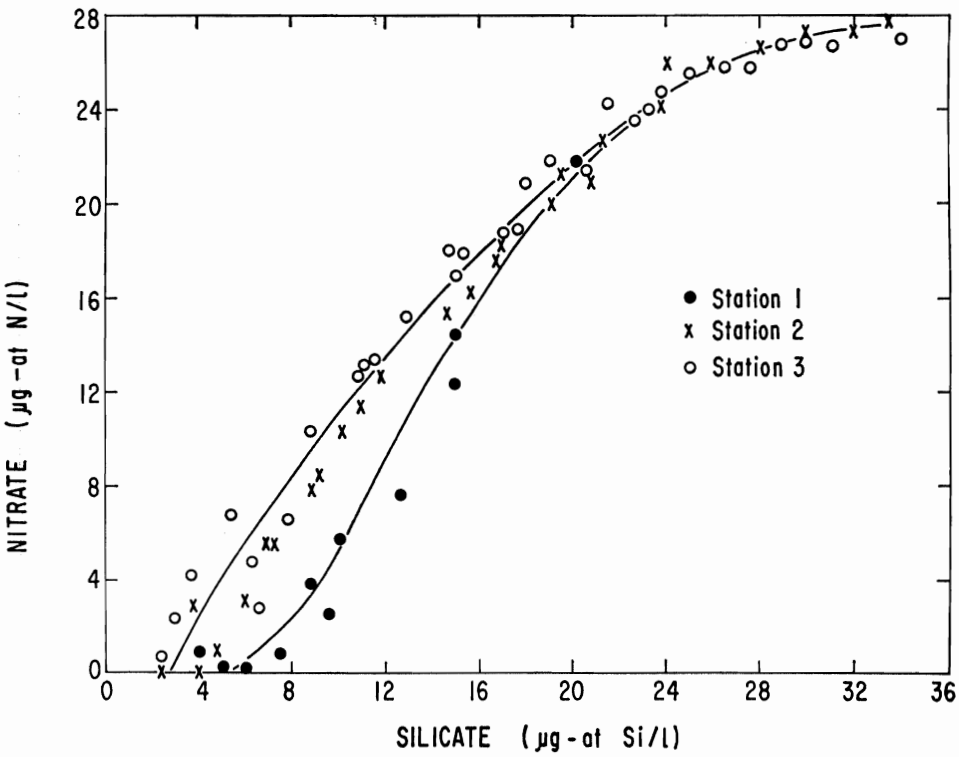

Fig. I-9. Silicate-nitrate relationships.

weight of nitrate-nitrogen from near the surface corresponds to a loss of about 140 parts by weight of silicon. In deeper waters the nitrogen-to-silicon ratio progressively decreased, probably reflecting the relative rates of dissolution of silica compared with nitrification.

The ratio of decrease in nitrate concentration to decrease in phosphate concentration in the lower parts of the water column was almost exactly 15:1 by atoms, which is what one would expect from the production of plankton having the "classical" N:P ratio (e.g., Redfield *et al.*, 1963; Holm-Hansen *et al.*, 1966). Nearer the surface the ratios were more erratic and generally somewhat higher (20:1).

The most striking feature of the nutrient data was the very close correlation between temperature and nitrate (or silicate and phosphate) concentrations. This affinity had been suspected ever since Armstrong and LaFond (1966) showed that the temporal variations of nitrate and silicate at a fixed depth at the NEL Tower followed almost exactly the changes attributable to internal waves

as measured by temperature. The relationship is shown by the solid lines in figure I-10 for data obtained on 3 May. Values for samples taken near the surface at station 1 lay on a different curve from those taken at stations 2 and 3. Nearly all the data obtained during the early weeks of the program, certainly until mid-July, lay near the solid line curve in figure I-10 so that, from a knowledge

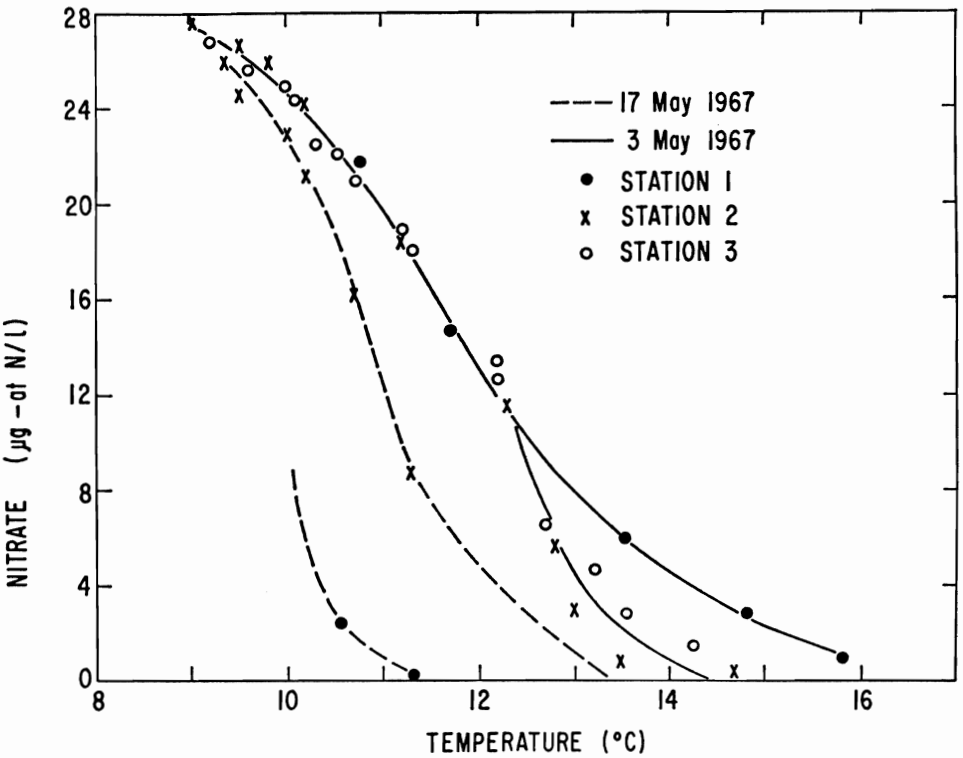

Fig. I-10. Nitrate-temperature relationships in May, 1967.

of the temperature (between 10°C and 13°C), one could predict nutrient concentrations almost to within experimental accuracy, irrespective of how deep in the water column a given temperature was encountered.

The relationship between nutrient depletion and the heating of the water column cannot be expected to be exact and must depend upon the amount and activity of the plankton in the water. It is therefore surprising that so good a relationship should exist from week to week considering the fluctuations in the site and activity of the phytoplankton crop (Eppley *et al.*, Part III, below). As the season progressed the T-NO_3 and T-SiO_3 curves changed very little in slope but there was progressively less nutrient at a given temperature (see fig. I-11). Although there were small weekly variations the only abrupt change was found on 17 May when there were very high phytoplankton crops at stations 1 and 2. The T-NO_3 curve for station 3 was "normal" that week but the data for stations 1 and 2 were greatly displaced (see dashed curve in fig. I-10). At 11°C at station 2 there was 8 μg at N/l less than the value to be expected from the data taken

during other weeks in the same month. At station 1 the deficit was some 20 μg at N/l. These amounts of nitrogen must have been consumed by the plant crops that were present in concentrations of 10 to 20 μg of chlorophyll *a*/l during the week of 17 May at stations 1 and 2.

The total amount of nitrate and silicate in the top 100_m of the water column

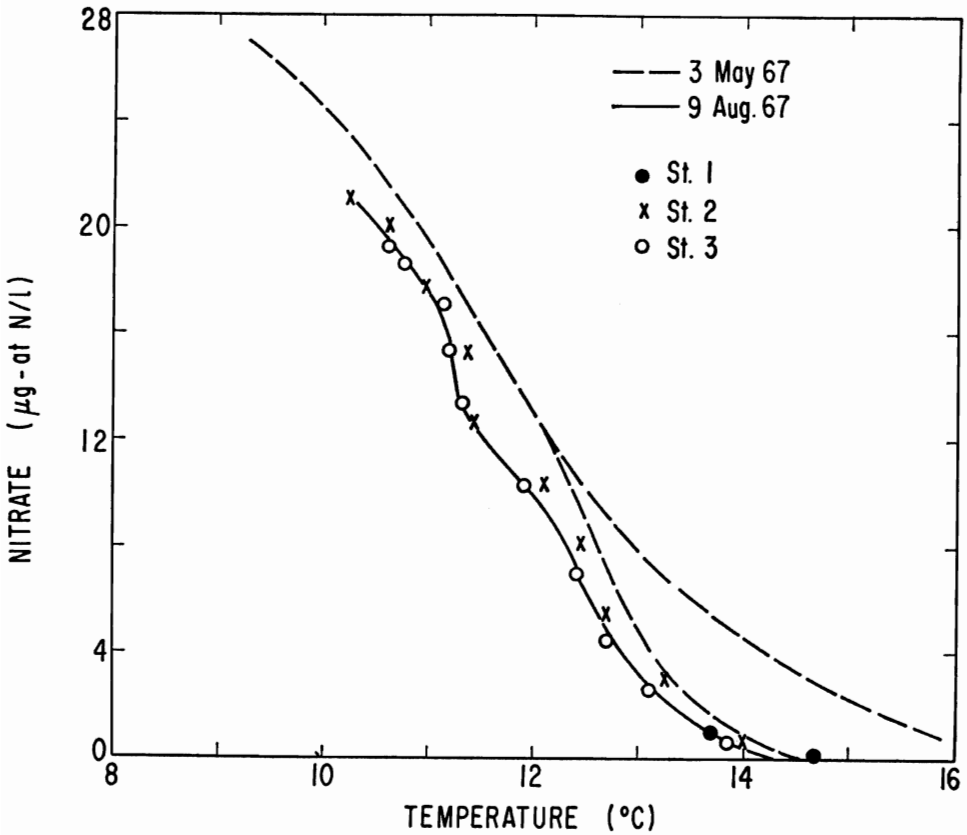

Fig. I-11. Nitrate-temperature relationships in August, 1967.

increased to a maximum of about 30 g NO_3-N/m^2 and 65 g Si/m^2 by mid-May at both stations 2 and 3. The quantity then decreased linearly and by approximately the same amount at both stations until, by early September, it was reduced to 10 g NO_3-N/m^2 and 20 g Si/m^2. Such decrease could only be used to calculate net production of phytoplankton if the vertical transport of nutrients at the same time could be calculated and if one could also assume that the waters off La Jolla in September had had the same nutrient content in May (wherever their location at that time) as did the La Jolla water that month. Such an assumption is clearly untenable. The measured productivities over 16 weeks added up to values very close to the measured decrease in nitrate stock over the same period. Presumably, however, the summed productivities should have been very much larger to allow for upward transport and the recycling of nitrogen compounds via ammonia.

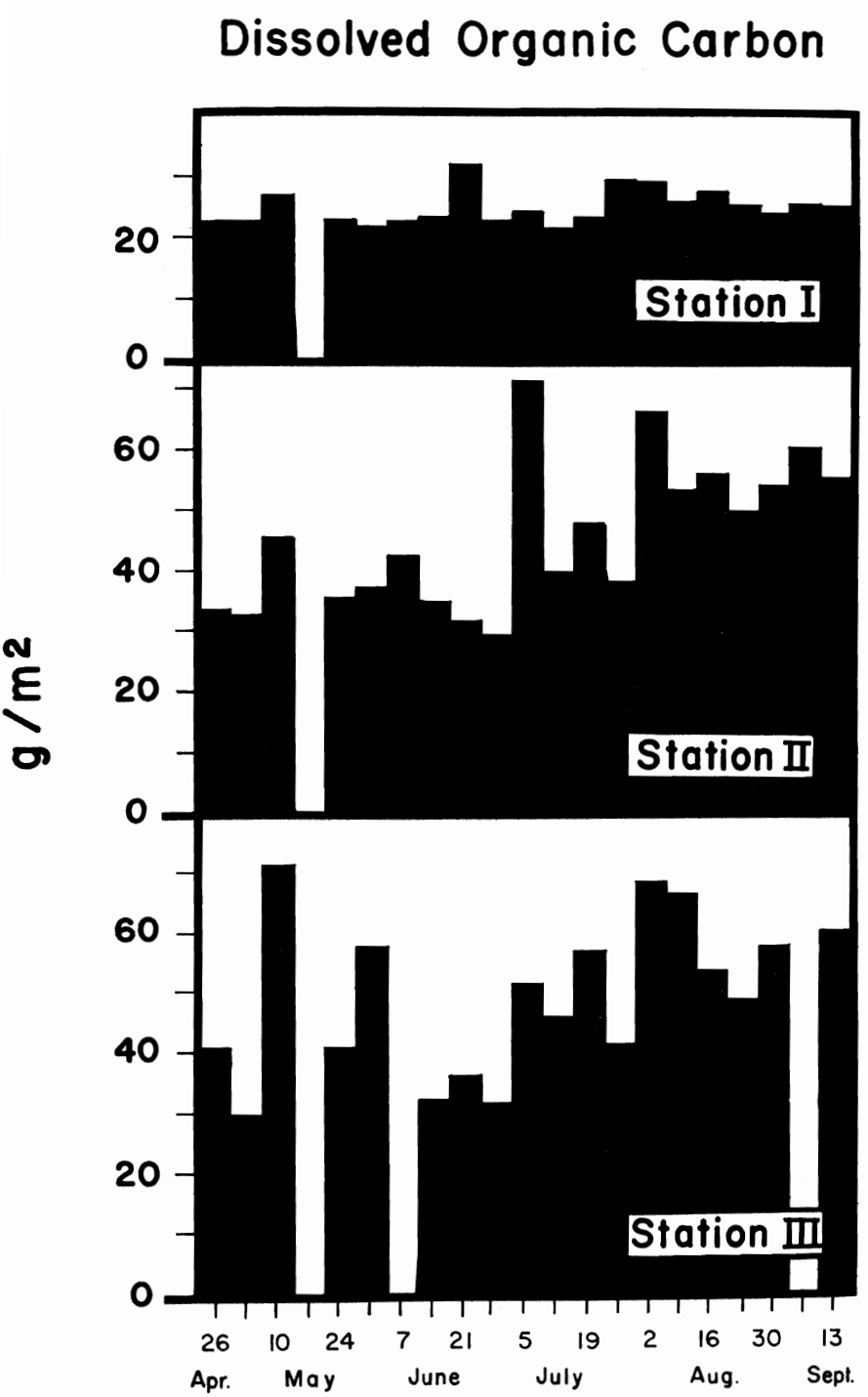

Fig. I-12. Total dissolved organic carbon in the pigment layer, April–September, 1967.

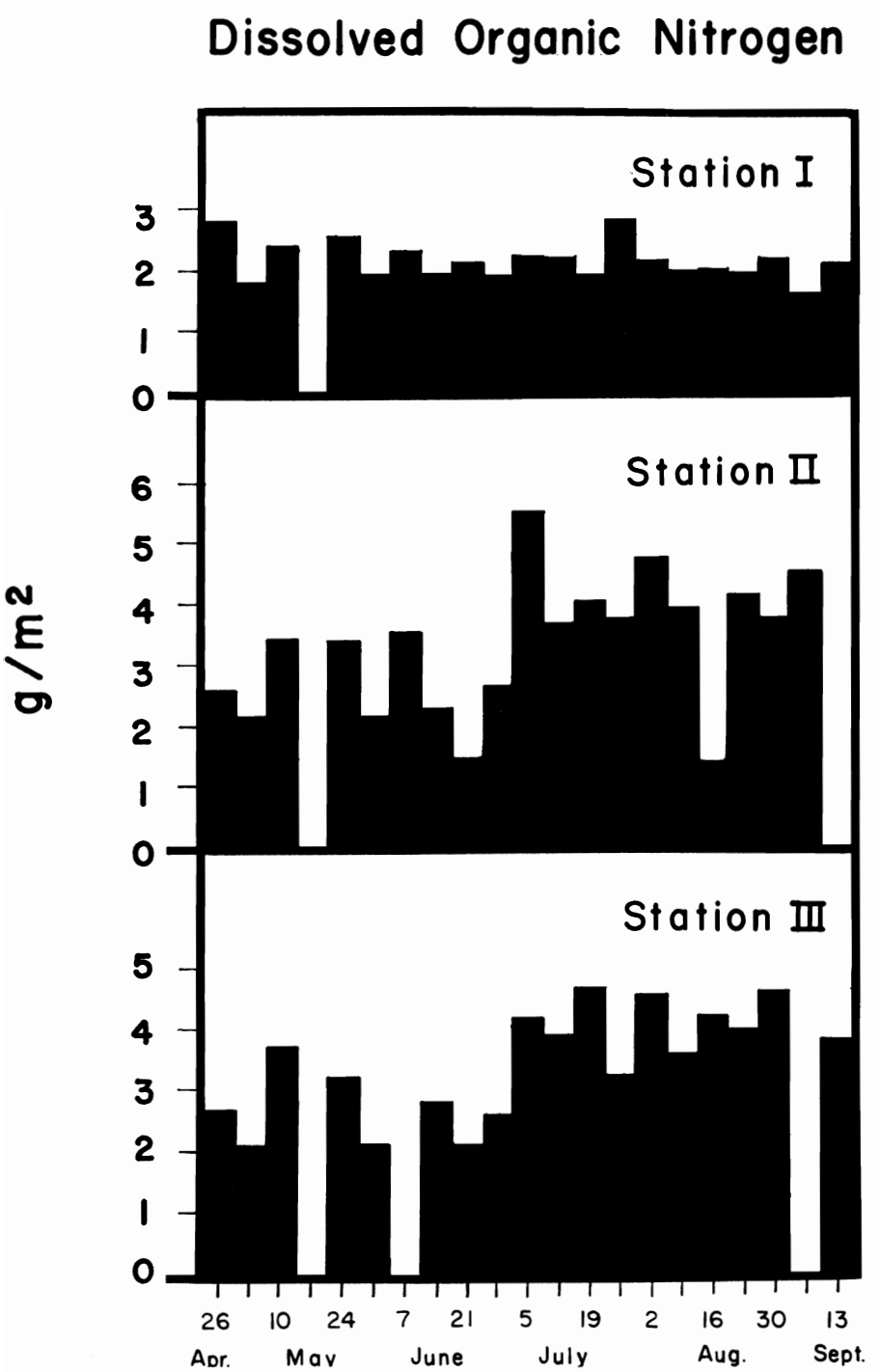

Fig. I-13. Total dissolved organic nitrogen in the pigment layer, April–September, 1967.

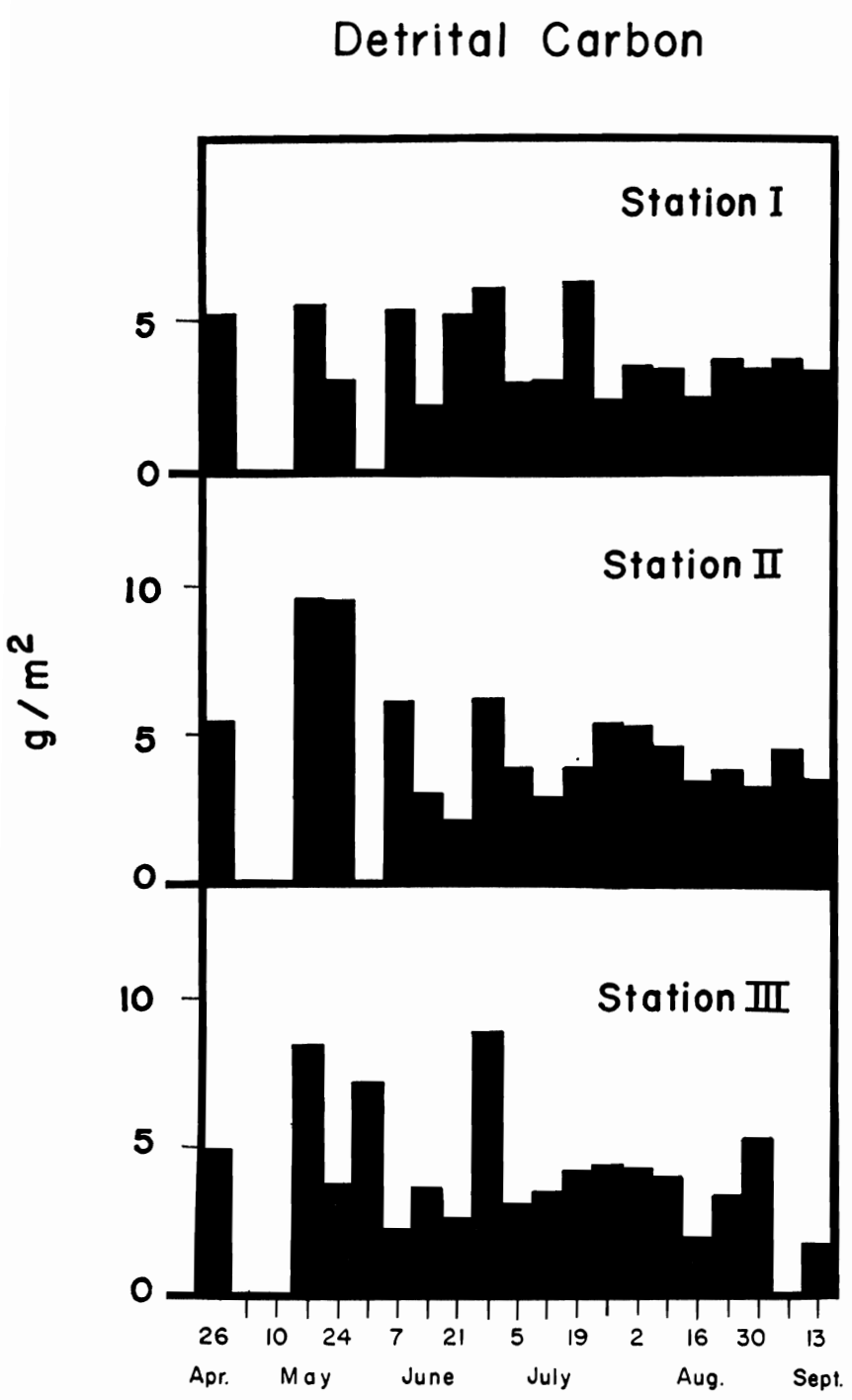

Fig. I-14. Detrital carbon in the pigment layer, April–September, 1967.

Dissolved and Particulate Organic Matter and Detritus

The total amount of dissolved organic carbon (DOC) over the pigment-layer depth changed very little from week to week (fig. I-12). Average concentrations varied only in the range 0.71–1.43 mg C/l (cf. Holmes *et al.*, 1967).

The dissolved organic nitrogen (DON) was a little more variable. The amount in the pigment layer is given in figure I-13. Concentrations varied between 1.7 and 8 μg at N/l and contrasted with amount/m^2 were nearly always higher at station 1 than further offshore.

A similar pattern was found with dissolved organic phosphorus (DOP). Average concentrations ranged between 0.2 and 0.5 μg at P/l and decreased progressively from station 1 to station 3.

The ratio by weight of dissolved organic carbon to nitrogen to phosphorus averaged about 100:8:1, which agrees with previously reported data obtained from the same general area (Holm-Hansen *et al.*, 1966). The amount of dissolved organic material corresponds to about 1 month of the total production of plants in the same area.

Coefficients of correlation were calculated between productivity and the concentration of DOC, DOP, and DON at each station. Significant values at the 5-percent probability level (r exceeding 0.4 for 18 degrees of freedom) were found only for DOC at station 1. At station 3 the value was significant between productivity and DOC the following week and for DOP at station 3 after a delay of two weeks. These last two relationships are not very convincing, especially considering that the same body of water is not being measured each week, and we may be witnessing spurious correlations or displaced correlations (e.g., effects of zooplankton activity).

The average particulate carbon in the pigment layer varied between about 50 and 500 μg C/l. The ratio of carbon to nitrogen varied between 100:10 and 100:20 by weight, with a mean of 100:15, and was not significantly different between stations.

The amount of particulate detritus (reported as carbon) could be calculated by subtracting from the total particulate carbon an estimate of the carbon held as standing stock of phytoplankton. (Details of the latter estimate are given by Eppley, Part III, below.) Resulting detrital carbon values include contributions from bacteria and microzooplankton but these values are not thought to be very significant. The total amount of detrital matter in the pigment layer is shown in figure I-14. There was a strong correlation between the amount of detritus and the amount of plant crop and productivity measured the same day ($r = 0.64$, $p < .01$). Detritus always exceeded living matter in abundance and corresponded to a few days of total production. This implies a turnover rate for detritus in the upper layers which cannot much exceed 1 or 2 weeks even assuming a most efficient utilization of the plants by animals.

REFERENCES

ARMSTRONG, F. A. J., and E. C. LAFOND

1966. Chemical nutrient concentrations and their relationship to internal waves and turbidity off southern California. Limnol. Oceanogr., 11:538–547.

ARTHUR, R. S.

1960. Variations in sea temperature off La Jolla. J. Geophys. Res., 65:4081–4086.

CAIRNS, J. L.

1967. Asymmetry of internal tidal waves in shallow coastal waters. J. Geophys. Res., 72: 3563–3565.

1968. Thermocline strength fluctuations in coastal waters. J. Geophys. Res., 73:2591–2595.

CAIRNS, J. L., and E. C. LAFOND

1966. Periodic motions of the seasonal thermocline along the southern California coast. J. Geophys. Res., 71:3903–3915.

FLEMING, R. H.

1941. Character of the currents off southern California. Proc. Sixth Pacific Sci. Congr., 3:149–160.

GAUL, R. D., and H. B. STEWART, JR.

1960. Nearshore ocean currents off San Diego, California. J. Geophys. Res., 65:1543–1556.

HOLMES, R. W., P. M. WILLIAMS, and R. W. EPPLEY

1967. Red water in La Jolla Bay, 1964–1966. Limnol. Oceanogr., 12:503–512.

HOLM-HANSEN, O., J. D. H. STRICKLAND, and P. M. WILLIAMS

1966. A detailed analysis of biologically important substances in a profile off southern California. Limnol. Oceanogr., 11:548–561.

LAFOND, E. C.

1966. The U. S. Navy Electronic Laboratory Oceanographic Research Tower: Its development and utilization. NEL Res. Develop. Rep. 1342. San Diego. 161 pp.

LORENZEN, C. J.

1966. A method for the continuous measurement of *in vivo* chlorophyll concentration. Deep-Sea Res., 13:223–227.

MCEWAN, G. F.

1916. Summary and interpretation of the hydrographic observations made by the Scripps Institution for Biological Research of the University of California, 1908–1915. Univ. of California. Publ. Zoology V (15):255–356.

REDFIELD, A. C., B. H. KETCHUM, and F. A. RICHARDS

1963. The influence of organisms on the composition of seawater. *In* M. N. Hill, ed., The sea. Vol. 2. New York and London: Interscience. Pp. 26–77.

REID, JR., J. L., G. I. RODEN, and J. G. SYLLIE

1958. Studies of the California Current System. California Cooperative Oceanic Fisheries Investigations (CALCOFI). Progr. Rep. July 1956–Jan. 1958. Pp. 293–324.

STEVENSON, R. E.

1959. Oceanographic survey of the continental shelf area of southern California. State of California Water Pollution Control Board. Publ. 20. 560 pp.

STEVENSON, R. E., and D. S. GORSLINE

1956. A shoreward movement of cool subsurface water. Trans. Am. Geophys. Union, 37:553–557.

STRICKLAND, J. D. H., and T. R. PARSONS

1968. A practical handbook of seawater analysis. Bull. Fish. Res. Board. Can. No. 167. Ottawa: Queens Printer. 311 pp.

UNIVERSITY OF CALIFORNIA

1968. Daily surface water temperatures and salinities at shore stations, 1967. California, Oregon and Washington coasts. Preliminary Unofficial Report. May 27. Scripps Institution of Oceanography.

UNIVERSITY OF CALIFORNIA, INSTITUTE OF MARINE RESOURCES

1966. Research on the marine food chain: progress report, Jan. 1965–Dec. 1965. Part IV.

Data record and comments cruise FCRG 65/2 and some miscellaneous data concerning the red tide off La Jolla during 1965. Unpubl. MS (IMR Ref. 65-30).

1968*a*. Research on the marine food chain; progress report, Jan. 1967–June 1968. Part III. Data record, coastal plankton survey, 1967. Section I. Chemistry and productivity. Unpubl. MS (SIO Ref. 68-20; IMR Ref. 68-8).

1968*b*. Research on the marine food chain; progress report, Jan. 1967–June 1968. Part IV. Data record, coastal plankton survey, 1967. Section II. The plankton. Unpubl. MS (SIO Ref. 68-38; IMR Ref. 69-3).

THE ECOLOGY OF THE PLANKTON OFF LA JOLLA, CALIFORNIA, IN THE PERIOD APRIL THROUGH SEPTEMBER, 1967

EDITED BY

J. D. H. STRICKLAND

PART II

VITAMIN B_{12}, THIAMINE, AND BIOTIN

BY

A. F. CARLUCCI

ABSTRACT

Dissolved vitamin B_{12}, thiamine, and biotin concentrations in the pigment layer of three near-shore locations were determined weekly. Average vitamin concentrations throughout this period were generally higher than in central Pacific waters. Ranges of vitamin concentrations found were: B_{12}, 0.4–6.5 ng/l, with most samples containing more than 1.5 ng/l; thiamine, 2–25 ng/l, 5–10 ng/l being found in most samples; and biotin, 0.1–125 ng/l with many samples containing greater than 0.5 ng/l. Vitamins were generally present in highest amounts at station 1 (1.4 km from shore) and least concentrations at station 3 (12.1 km from shore). Certain abrupt changes in vitamin concentrations appeared to be related to water movement (advection). There was no statistical evidence obtained to show that the concentration of vitamins limited the production of phytoplankton over the studied area as a whole, although individual species of phytoplankton may have been affected. In one instance vitamin B_{12} utilization could be correlated with a sudden growth of *Gonyaulax polyedra*.

INTRODUCTION

As a part of a comprehensive study of the effects of various physical, chemical, and biological factors in the ecology of coastal plankton (cf. Strickland *et al.*, Part I, above) the occurrence and distribution of dissolved vitamin B_{12}, thiamine, and biotin in the coastal waters off La Jolla, California, were studied during the period of 19 April to 13 September, 1967. The relationships between vitamins and other parameters, mainly phytoplankton, of the waters are discussed.

ACKNOWLEDGMENTS

This work was supported in part by the Marine Life Research Program, Scripps Institution of Oceanography's component of the California Cooperative Oceanic Fisheries Investigation, a project sponsored by the State of California, and, in part, by the United States Atomic Energy Commission, Contract No. AT(11-1)-GEN 10, P.A. 20.

I would like to thank Miss Peggy M. McNally who assisted with some of the vitamin assays and compilation of the data. The assistance of Dr. M. M. Mullin in statistical treatment of the data is gratefully acknowledged.

MATERIALS AND METHODS

Station locations, water depths, and methods of collection for each sample are given by Strickland *et al.* (Part I, above). Briefly, the water samples from sta-

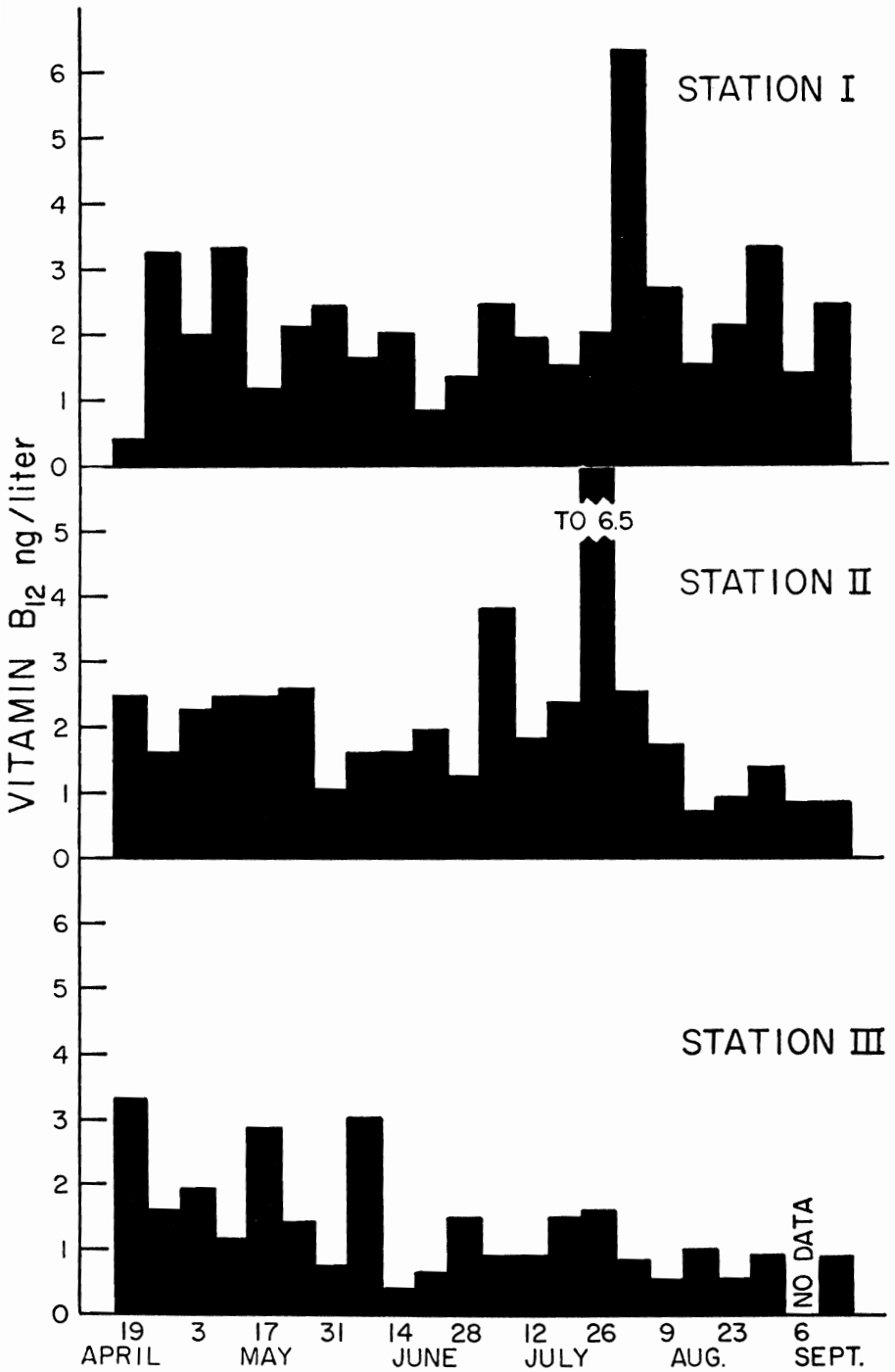

Fig. II-1. The concentrations of dissolved vitamin B_{12} in the pigment layers of stations 1, 2, and 3 at weekly intervals, April–September, 1967.

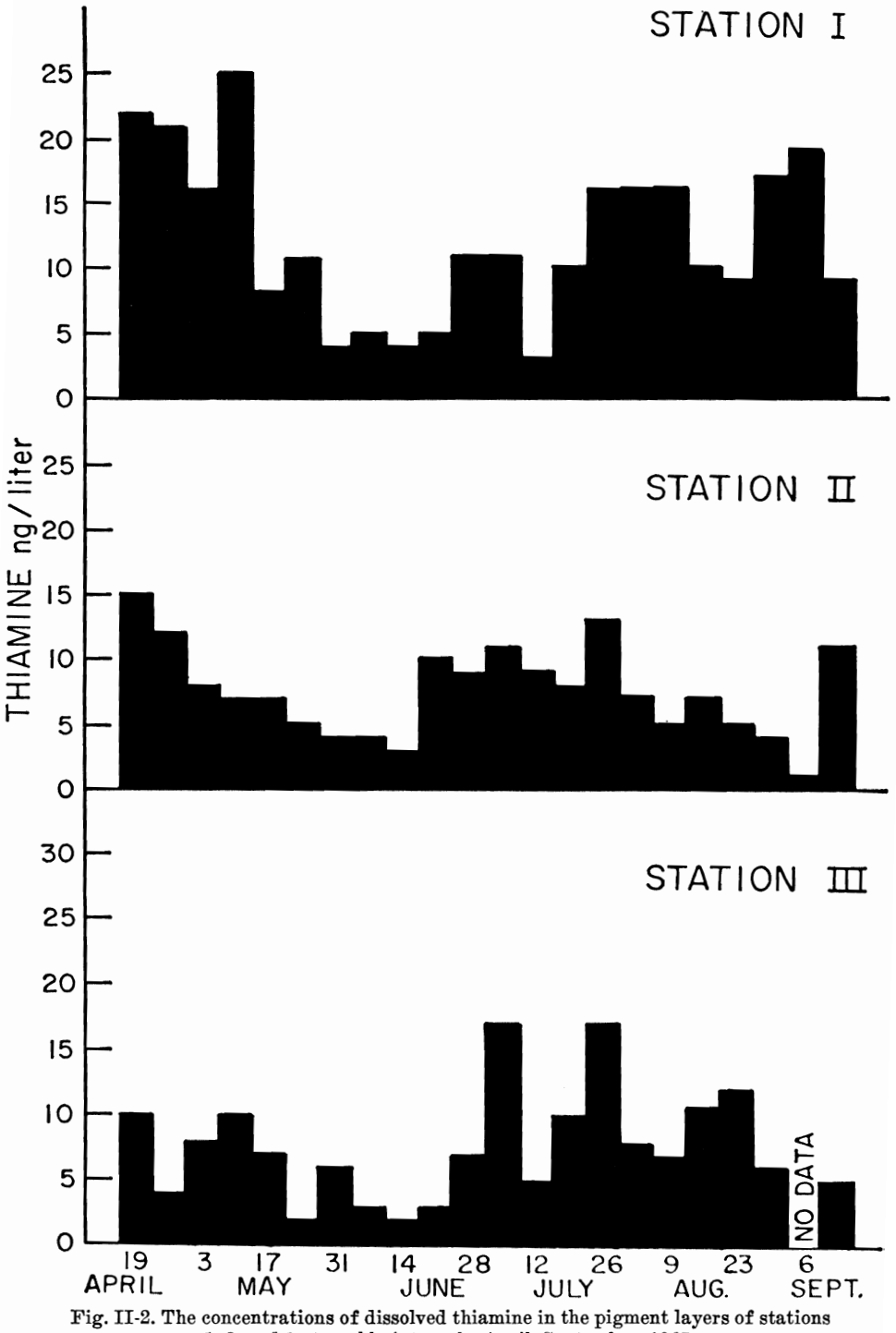

Fig. II-2. The concentrations of dissolved thiamine in the pigment layers of stations 1, 2, and 3 at weekly intervals, April–September, 1967.

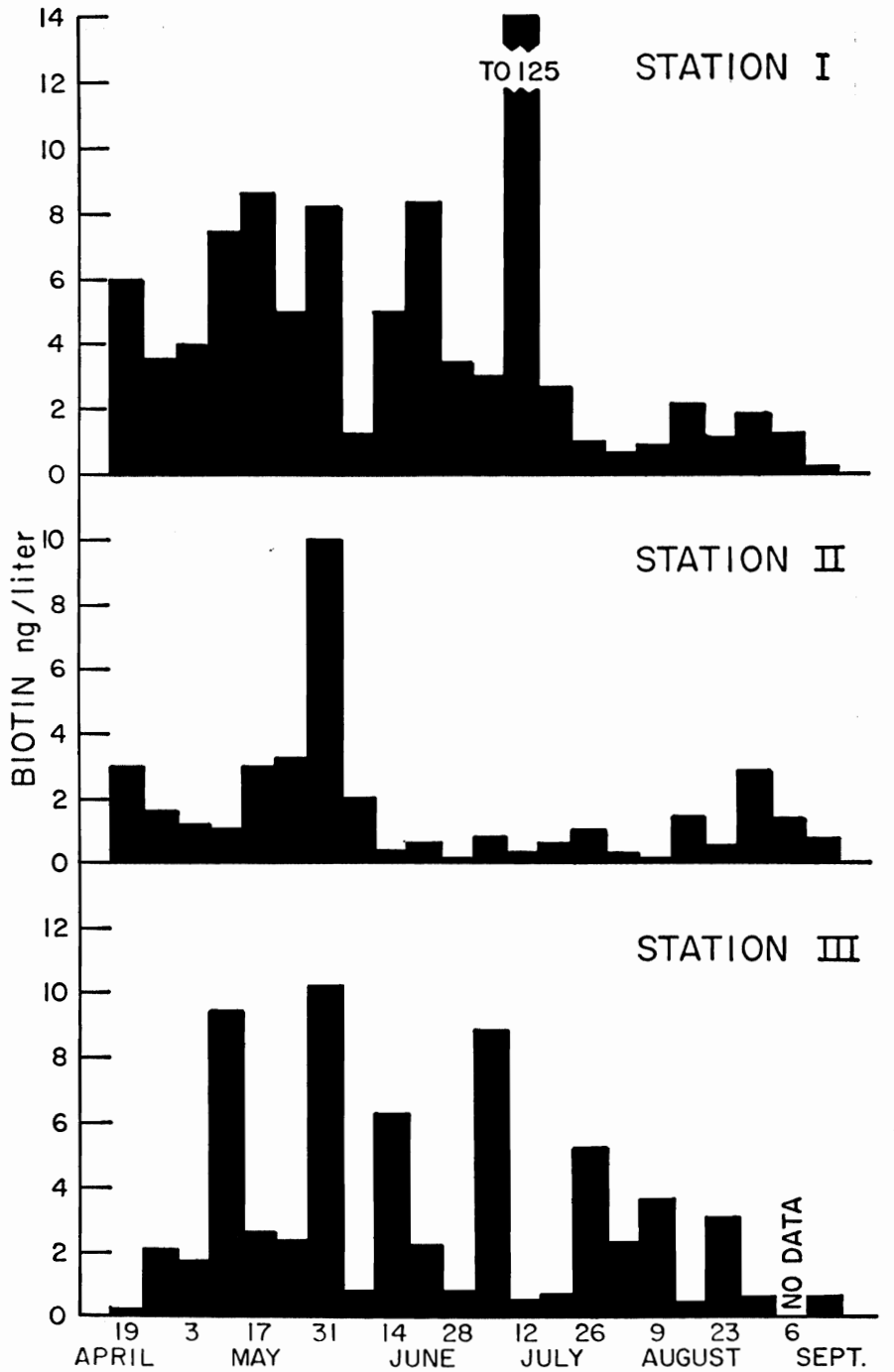

Fig. II-3. The concentrations of dissolved biotin in the pigment layers of stations 1, 2, and 3 at weekly intervals, April–September, 1967.

tion 1 were integrated over the upper 25 m; those at stations 2 and 3 were integrated from waters throughout the "pigment layer." The pigment layer is defined as the water column from the surface to a depth where fluorescence indicative of chlorophyll-containing material is minimal. At stations 2 and 3 these depths varied between 30 and 60 m, averaging 50 m. All samples were frozen immediately at –20°C. The vitamin concentrations were determined ashore using assay procedures described by Carlucci and Silbernagel (1966*a*, 1966*b*, 1967).

TABLE II-1

AVERAGE VITAMIN CONCENTRATIONS IN PACIFIC OCEAN WATERS
(Unit of measurement; mg/l)

Water	Vitamin B_{12}	Thiamine	Biotin
SIO pier [a]	2.9	15	3.8
Coastal [b]			
Station 1	2.2	12	3.4
Station 2	2.0	8	1.6
Station 3	1.3	8	3.0
Central Pacific [c]	0.1	8	1.3

[a] Carlucci, unpublished.
[b] Average of vitamin concentrations obtained in present study.
[c] Average of vitamin concentrations from four discrete depths (0, 15, 30, and 60 m) at two stations in central Pacific Ocean.

RESULTS AND DISCUSSION

The weekly distribution of vitamin B_{12}, thiamine, and biotin at each station is given in figures II-1, II-2, and II-3, respectively. At no time did vitamin concentrations fall below detectable levels. There were seasonal and weekly changes, some of which were quite marked. Vitamin B_{12} concentrations were, in general, higher in waters of stations 1 and 2 than in those of station 3 (table II-1). Thiamine concentrations were high throughout the sampling period; station 1 had, in general, higher levels of this vitamin than stations 2 and 3. Biotin was present in moderate amounts in all samples except those from station 2 taken during the summer months.

Vitamin B_{12} concentrations in water from station 1 decreased from mid-May to mid-June. Subsequent samples showed a trend of vitamin B_{12} increase. The sample of 2 August had over 6 ng/l of vitamin B_{12}. This high concentration of vitamin was probably brought to station 1 by advection of vitamin-rich waters. A number of oceanic phytoplankters were found in the samples collected on this date (Reid *et al.*, Part V, below). At stations 2 and 3 there was little seasonal change in vitamin B_{12} concentrations except for a few sampling periods. After 14 June, vitamin B_{12} concentrations at station 3 were relatively constant at low levels. In less productive waters of the Sargasso Sea, Menzel and Spaeth (1962) found a seasonal variation of vitamin B_{12} with a minimum in the summer months.

Thiamine concentrations in waters from the three stations declined from mid-May to mid-June (late spring). After late June, waters at stations 1 and 3 showed a general increase in thiamine content. Station 2 showed a second period of decreasing vitamin concentrations beginning about 2 August and continuing to 6 September.

Biotin concentrations were low in waters of all three stations toward the end of the sampling period. Generally high amounts of biotin were found at station 1 through June with the maximum, 125 ng/l, occurring on July 12. At station 2 higher than average levels were found in April and May. Levels at station 3 oscillated from high to low several times during the program and no clear trend was established.

Carlucci and Silbernagel (1966*a*, 1966*b*, 1967) frequently assayed surface-water samples taken off the SIO pier during development of assay methodology for vitamin B_{12}, thiamine, and biotin. The concentrations of vitamins found then were similar to those reported in this study, that is, vitamin B_{12}, 0.3–3.5 ng/l; thiamine, 5–20 ng/l; and biotin, 0.5–4 ng/l (table II-1).

Water samples collected at discrete depths in the open ocean and assayed with the same methods generally had lower concentrations of dissolved vitamins (Carlucci and Silbernagel, 1966*c;* see University of California, 1967) than these near-shore waters. Many samples collected in late July–early September in the central Pacific (north-south transect, 155°W) showed less than 0.5 ng B_{12}/l, 10 ng/l thiamine, and 1.5 ng biotin/l; often vitamins were not detectable throughout the water column. Average values are given, for comparison with coastal values, in table II-1.

There was evidence of upwelling on several occasions during the programs as judged by nutrient and temperature data (Strickland *et al.*, Part I, above). In a few of the samples from station 1, it is possible that upwelled water brought up vitamins from the bottom sediments where vitamins may have been produced (Burkholder and Burkholder, 1956, 1958). In a deepwater column upwelling is probably not important in influencing vitamin concentrations in upper waters since concentrations of vitamins below 200–500 m are low (Daisley and Fisher, 1958; Carlucci and Silbernagel, 1966*c*).

In addition to providing a measure of vitamin concentrations the assay methods used in this study determined seawater inhibitions to the test algae. Inhibition was determined from recoveries of internal standards in 1:2 dilutions of the samples. Many (~30 percent) of the samples were somewhat toxic to the algae. Waters were especially inhibitory to *Cyclotella nana,* the B_{12}-assay alga, during May and June and only sporadically toxic throughout the rest of the sampling period. With *Monochrysis lutheri* and *Amphidinium carterae,* the thiamine- and biotin-assay algae, respectively, few samples were inhibitory for the first half of the sampling program. From late June on, a majority of the samples were toxic. The nature of the factor(s) of seawater causing toxicity is not known, although the subject of inhibition has received considerable attention (Johnston, 1963*a*, 1963*b;* Provasoli, 1963; Carlucci and Silbernagel, 1966*d;* Droop, 1968).

Although data on vitamin-requiring algae have appeared recently (Provasoli, 1963; Strickland, 1965; Thomas, 1968), the vitamin requirements of many of the phytoplankters studied in this investigation are not known (Reid *et al.*, Part V, below). One needs to know the relative biomass of vitamin-requirers in order to study uptake of vitamin from seawater. It is also important for this purpose to know the biomass of those organisms that produce vitamins during their growth.

Lack of such information prevented detailed study of relationships between plankton-crop changes and vitamin concentrations.

The sampling program was suboptimal in two respects. First, the time interval between samples was too long in terms of rates of phytoplankton growth, that is, one week between samples vs. a doubling time of 2–3 days. Second, no information was collected on the depth distributions of individual phytoplankton species or of vitamin concentrations.

Bacteria are thought to be the major producers of vitamins in the sea (Provasoli, 1963; Burkholder and Burkholder, 1956, 1958), but recent evidence obtained in our laboratories indicates that, under certain conditions, algae produce vitamins during their growth. The relative importance of bacteria and algae in contributing to the total amount of vitamins in seawater is not known and it is difficult to envisage a sampling program that would provide an adequate picture of vitamin metabolism.

If vitamins limited the growth of phytoplankton during the period of study, then concentration of phytoplankton might be correlated with concentration of vitamins in the euphotic zone. This correlation could conceivably be either positive (high vitamin concentrations supporting abundant phytoplankton) or negative (large phytoplankton crops having reduced the concentration of vitamins over some time period). The correlation coefficient between mean concentration of all phytoplankton per m^3 (data from University of California, Institute of Marine Resources, 1968) and the mean concentration of each vitamin in the pigment layer was calculated for each station separately and all stations combined over the whole period of study. For the combined data from all stations, the only significant correlation was between phytoplankton concentration and concentration of thiamine ($r = 0.44$, $p < 0.005$). There was a significant, positive correlation between phytoplankton and thiamine at station 1 ($r = 0.57$, $p < 0.01$); a positive, but nonsignificant correlation at station 2; and a negative, but nonsignificant, correlation at station 3. It is apparent that the strong correlation obtained in station 1 accounted for the positive correlations obtained for the combined three stations, since these relationships were insignificant with stations 2 and 3.

Somewhat unexpectedly, there was not a significant correlation between the concentration of thiamine and that of *Coccolithus huxleyi* which requires thiamine for growth (Provasoli, 1963) and which was one of the most important species during the study in terms of its contribution to total biomass of phytoplankton (Reid *et al.*, Part V, below). The only other significant correlation was between the concentration of phytoplankton and that of vitamin B_{12} at station 3 ($r = 0.57, p < 0.01$).

Positive correlations were found between the net primary production of phytoplankton per unit surface area (data from fig. III-4 of Eppley *et al.*, Part III, below) and the concentrations of both vitamin B_{12} ($r = 0.47$, $p < 0.005$) and thiamine ($r = 0.35$, $p < 0.01$) for the combined data of all stations. There were significant positive correlations between production and thiamine at station 1, and between production and B_{12} at stations 2 and 3. These correlations were similar in pattern to those between the abundance of phytoplankton per m^3 and the vitamin concentration, so that the effect of vitamins in stimulating production

independent of the size of the plant crop is not clear. In order to test this, correlation coefficients were calculated between the concentration of each vitamin and the mean specific growth rate for the pigment layer, that is, the mean net primary production per unit plant biomass where both biomass and production are calculated per unit of surface area (data from figs. III–1 and III–4 of Eppley *et al.*, Part III, below). The only correlation was a positive one between the concentration of B_{12} and the mean specific growth rate at station 3. This correlation is of doubtful significance ($p \sim 0.05$), especially because the same data on concentration of vitamins were used in three tests for correlation, so only tests of $p < 0.02$ should be accepted as significant. There thus is no evidence that the concentration of vitamins limited the production of phytoplankton over the studied area as a whole, although, of course, individual species of phytoplankton may have been affected.

Gonyaulax polyedra, a B_{12}-requiring dinoflagellate and a predominant organism in some red tides, was present in many of the samples, sometimes in moderate numbers. On 6 September *G. polyedra* was by far the predominant phytoplankter at stations 1 and 2. The preceding week it was only sparsely present. During the same period vitamin B_{12} decreased markedly at stations 1 and 2, indicating possible utilization by *G. polyedra.* On 13 September the *G. polyedra* population was down and vitamins increased, probably as a result of water movement (advection) and decomposition by-products. It is possible that the importance of vitamins in the marine ecology of nearshore waters may be in the initiation of blooms. Once a mixed crop of organisms develops, vitamins are produced and their concentrations probably do not greatly affect the kinds and numbers of organisms that predominate.

REFERENCES

BURKHOLDER, P. R., and L. M. BURKHOLDER

1956. Vitamin B_{12} in suspended solids and marsh muds collected along the coast of Georgia. Limnol. Oceanogr., 1:202–208.

1958. Studies on B vitamins in relation to productivity of the Bahia Fosforescente, Puerto Rico. Bull. Mar. Sci. Gulf Carib., 8:201–223.

CARLUCCI, A. F., and S. B. SILBERNAGEL

1966*a*. Bioassay of seawater. I. A ^{14}C uptake method for the determination of concentrations of vitamin B_{12} in seawater. Can. J. Microbiol., 2:175–183.

1966*b*. Bioassay of seawater. II. Methods for the determination of concentrations of dissolved vitamin B_1 in seawater. Can. J. Microbiol., 12:1079–1089.

1966*c*. Bioassay of seawater. III. Distribution of vitamin B_{12} in the northeast Pacific Ocean. Limnol. Oceanogr., 11:642–646.

1966*d*. Effect of different seawaters on the development of biochemically deficient mutants of *Serratia marinorubra*. Appl. Microbiol., 13:663–668.

1967. Bioassay of seawater. IV. The determination of dissolved biotin in seawater using ^{14}C uptake by cells of *Amphidinium carteri*. Can. J. Microbiol., 13:979–986.

DAISLEY, K. W., and L. R. FISHER

1958. Vertical distribution of vitamin B_{12} in the sea. J. Mar. Biol. Ass. U.K., 37:683–686.

DROOP, M. R.

1968. Vitamin B_{12} and marine ecology. IV. The kinetics of uptake, growth, and inhibition in *Monochrysis lutheri*. J. Mar. Biol. Ass. U.K., 48:689–733.

JOHNSTON, R.

1963*a*. Antimetabolites as an aid to the study of phytoplankton nutrition. J. Mar. Biol. Ass. U.K., 43:409–425.

1963*b*. Seawater, the natural medium of phytoplankton. I. General features. J. Mar. Biol. Ass. U.K., 43:427–456.

MENZEL, D. W., and J. P. SPAETH

1962. Occurrence of vitamin B_{12} in the Sargasso Sea. Limnol. Oceanogr., 7:151–154.

PROVASOLI, L.

1963. Organic regulation of phytoplankton fertility. *In* M. N. Hill, ed., The sea. Vol. 2. New York and London: Interscience. Pp. 165–219.

STRICKLAND, J. D. H.

1965. Production of organic matter in the primary stages of the food chain. *In* J. P. Riley and G. Skirrow, eds., Chemical oceanography. Vol. 1. New York: Academic. Pp. 477–610.

THOMAS, W. H.

1968. Nutrient requirements and utilization: Algae. *In* P. L. Altman and D. S. Ditmar, eds., Metabolism. Fed. Amer. Soc. Exper. Biol. Bethesda, Md. Pp. 210–228.

UNIVERSITY OF CALIFORNIA

1967. Scripps Institution of Oceanography. Data report, Ursa Major Expedition. SIO Ref. 67-5.

UNIVERSITY OF CALIFORNIA, INSTITUTE OF MARINE RESOURCES

1968. Research on the marine food chain; progress report, Jan. 1967–June 1968. Part IV. Data record, coastal plankton survey, 1967. Section II. The plankton. Unpubl. MS (SIO Ref. 68-38; IMR Ref. 69-3).

THE ECOLOGY OF THE PLANKTON OFF LA JOLLA, CALIFORNIA, IN THE PERIOD APRIL THROUGH SEPTEMBER, 1967

EDITED BY

J. D. H. STRICKLAND

PART III

ESTIMATES OF PHYTOPLANKTON CROP SIZE, GROWTH RATE, AND PRIMARY PRODUCTION

BY

R. W. EPPLEY, F. M. H. REID, and J. D. H. STRICKLAND

ABSTRACT

Phytoplankton crop size varied extensively over the period of study, increasing after upwelling and decreasing abruptly with incursions of nutrient-poor water. Two independent estimates of crop size were undertaken: (1) from cell counts of groups of species ranked according to cell volume and converted to cell carbon using a mathematical relationship between cell volume and carbon content; (2) from continuous chlorophyll fluorescence profiles converted to cell carbon using experimentally determined carbon/chlorophyll ratios. The two methods agreed as well as could be expected (correlation coefficient ($r = 0.71$, $p < .01$). Heterotrophic phytoplankton species, such as *Peridinium depressum*, accounted for about 5 to 10 percent of the crop, and their biomass was related to the total phytoplankton standing stock ($r = 0.59$, $p < .01$). Primary production, dependent upon crop size, was estimated from measurements of photosynthesis carried out each week and from a calculation of specific growth rate based upon temperature, irradiance, and cell chlorophyll concentration.

Crop size and primary production were highest during periods of upwelling and lower during periods of nitrate depletion in the mixed layer. Photosynthetic rates calculated per weight of chlorophyll and growth rates gave no evidence of nutrient deficiency during nitrate depletion, however, and nutrient enrichments had little effect on the measured rates of photosynthesis. In fact, rates in the nitrate-depleted mixed layer averaged about 6 gC/g chl. *a*·hr with about 3 gC/g chl. *a*·hr below the thermocline where nitrate was present. These results probably represent short-term physiological adaptation of the phytoplankton to prevailing light intensity.

Some differences were noted among the three stations routinely occupied. The seawardmost station showed the lowest average crop, carbon/chlorophyll *a* ratio, and primary production but the highest average chlorophyll *a* concentration per plant cell, specific growth rate, and the greatest euphotic depth.

INTRODUCTION

THIS ACCOUNT REPRESENTS part of a study of coastal plankton ecology carried out by the Food Chain Research Group of the Institute of Marine Resources, University of California. A general introduction and description of the study is given by Strickland *et al.*, Part I, above.

ACKNOWLEDGMENTS

This research was supported in full by the United States Atomic Energy Commission, Contract No. AT(11-1)GEN 10, P.A. 20.

We thank Mr. J. B. Jordan for help with phytoplankton counting and Miss

Lucia Solórzano and Mr. J. L. Coatsworth for analytical assistance. Miss Elizabeth Fuglister provided the programs for computer processing of data.

METHODS

Phytoplankton Crop Estimation from Cell Volume

The carbon content of a cell of measured volume has been calculated using two regression equations, both obtained from new data on living cells in this laboratory, from Mullin *et al.* (1966) and from Strathmann (1967). For diatoms we used:

$$\log C = 0.76 \log V - 0.29$$

and for all other cells:

$$\log C = 0.94 \log V - 0.60$$

as described in our data record (University of California, Institute of Marine Resources, 1968), where C is grams of carbon and V is milliliters cell volume. Integrated samples were taken with a submersible pump-profiling hose system through the pigment layer (Strickland *et al.*, Part I, above). Phytoplankton cells in these samples were counted and measured as described by Reid *et al.*, Part V, below.

Crop Estimation from Chlorophyll *a* and Carbon/Chlorophyll *a* Ratios

Water from the profiling hose was passed through a fluorometer to give continuous depth records of chlorophyll *a* fluorescence (Lorenzen, 1966), as described in Strickland *et al.*, Part I, above.

Carbon/chlorophyll ratios were obtained by incubating, under natural light and at sea-surface temperature, samples of seawater inoculated with $^{14}CO_3^{2-}$ and in some experiments with nutrients sufficient for several days growth. Subsamples were removed after 24 and 48 hours for determining carbon assimilation by the phytoplankton. Specific growth rate was calculated from the 24- and 48-hour values and the initial carbon content of the phytoplankton was computed as that which would give the observed 24-hour carbon increase at the calculated specific growth rate (see Eppley, 1968, for a detailed description of the experiments). Subsamples were also taken at 0, 24, and 48 hours for chlorophyll *a* analysis by fluorescence of 90 percent acetone extracts (Yentsch and Menzel, 1963; Holm-Hansen *et al.*, 1965). The initial chlorophyll *a* values were used, with the estimates of initial phytoplankton carbon, to compute carbon/chlorophyll *a* ratios. These ratios were used with the chlorophyll *a* profiles to compute the total phytoplankton crop. This crop estimate is hereafter called "crop from fluorometer." The ratio was 33 when nitrate was ≥ 1 μM and 98 otherwise (Eppley, 1968).

Phytoplankton Photosynthetic Rates

Rates of phytoplankton photosynthesis were computed from 24-hour carbon assimilation (see above), chlorophyll *a*, and submarine light based on the following assumptions: (1) Photosynthetic rate measurements made on only one station each week, averaged over the period of study, are representative. (2) Chlorophyll *a* was accurately measured in the fluorometer profiles. (3) Photosynthetic rate per unit chlorophyll *a* was proportional to irradiance (400–700 nm) between 1 percent and 20 percent of surface irradiance, was negligible below 1 percent and constant above 20 percent of surface irradiance. (4) The phytoplankton community

was stratified physiologically into an upper and a lower layer, from the surface to the depth at which 1 μM nitrate was encountered and from that depth to the 1 percent depth of light level, respectively (see table III-1). Irradiance (downwelling) profiles were prepared using submarine photometer data, or that lacking, 3× the Secchi depth was taken as the depth of 1 percent light, the surface as 100

TABLE III-1

SUMMARY OF PHOTOSYNTHETIC RATES PER UNIT CHLOROPHYLL *a*
SEASONAL AVERAGE
(Data from Eppley [1968])

Character of seawater samples	Rate as g carbon/g chlorophyll *a* per day[a] and, in parentheses, per daylight hour	
	Per initial chlorophyll *a* content	Per average chlorophyll *a* content[b]
Nitrate undetectable (shallow samples)		
a) Nutrients not added before incubation.....	146 ± 44, n = 7 (10.4)	91 ± 19 (6.5)
b) Nutrients added prior to incubation.....	190 ± 84, n = 19 (13.5)	96 ± 27 (6.8)
Nitrate present (light saturated rate of deeper samples).	33 ± 18, n = 11 (2.4)	40 ± 19 (2.9)

[a] Based upon 24-hour incubation of samples.
[b] Average of initial and 24-hour chlorophyll *a* concentrations.
± Values are standard deviations from the mean.

percent and the level of 20 percent light was read off semilog graph paper, assuming a constant attenuance coefficient. The calculated photosynthetic rates were then plotted vs. depth and integrated graphically to give production as gC/m^2·day.

GROWTH RATES

Specific growth rate was calculated, as crop doublings/day as follows:

$$\mu = \text{doublings/day} = \frac{3.32}{t} \log_{10} \left[\frac{P_0 + \delta P}{P_0} \right] \tag{1}$$

where t is in days, 3.32 is $\log_2 10$, P_0 is the initial crop size in gC/m^2, and δP is the daily increment in crop size (net carbon assimilation) as gC/m^2· day.

Specific growth rates were also calculated from an equation (Eppley and Sloan, 1966) where specific growth rate (μ) is considered to depend upon temperature, day length, irradiance (400–700 nm) and light absorption by cell chlorophyll *a*.

$$\mu = \frac{t_1 \, (10^{0.036T - 0.28}) \, I \, (1 - 10^{-100(chl)}) \, (12.6\, I + 0.18)}{0.015 + I \, (1 - 10^{-100(chl)}) \, (12.6\, I + 0.18)} \tag{2}$$

where t_1 is the hours of daylight expressed as a fraction of the 24-hour day, T is temperature in °C, I is the incident irradiance as langlies/min, and *chl* is chlorophyll *a* in units g/ml cell volume. Photosynthetically active irradiance was computed very approximately as ly/min from depth profiles, recorded as percentage of surface light, and 0.5 times the total solar radiation values recorded ashore by a bimetallic actinograph. Values of chlorophyll per unit cell volume were cal-

culated for each station and week and averaged values at each station were used in the specific growth rate calculations. Since the variation with depth of the chlorophyll per cell volume parameter was not measured, a comparison of the μ values of equation (2) with μ calculated from photosynthesis and standing stock is not justified. Rather, the theoretical specific growth rate, calculated as above, was used with crop data (from fluorometer) to calculate production at several depths and this value, when integrated over depth, should be comparable with the values obtained more directly from photosynthetic rate measurements.

Equation (2) can be only approximate because of oversimplified assumptions. Since, however, this study is the first one to include a detailed estimate of phytoplankton cell volume in natural communities, along with the other requisite data, it seemed worthwhile to carry out a few calculations. They serve primarily as an internal check on methodology rather than as a verification or test of the equation. Equation (2) fits well the data for several phytoplankton cultures grown in continuous light and for the green flagellate, *Dunaliella tertiolecta,* grown with light-dark cycles (Eppley and Coatsworth, 1966), but it underestimated the maximum growth rates of diatoms occurring at intermediate day lengths (Castenholz, 1964; Paasche, 1968). The entire problem of spectral energy distribution is ignored in this simplified approach.

RESULTS AND DICUSSION

Phytoplankton Crop

Histograms of the standing stock of phytoplankton, as cell carbon, are given in figure III-1 to show temporal variation at each of the three stations. The crop was high at stations 1 and 2 in May during a period of vigorous upwelling. The peak in early September at station 1 represents a small dinoflagellate bloom, composed chiefly of *Gonyaulax polyedra.* The standing stock in figure III-1 was computed from cell volumes and cell counts. "Crop from fluorometer" estimates showed the same trends but were, on the average, about 15 percent lower (table III-2). Some of the difference is due to including colorless dinoflagellates, such as *Peridinium depressum,* in the crop as estimated from cell volume (table III-2). The remaining difference is probably due to low estimates of chlorophyll *a* owing to variation in chlorophyll *a* fluorescence with depth. Linear regression equations were computed for the variation in (1) heterotrophic phytoplankton standing crop with total crop (based on cell volume):

$$\text{Heterotrophs} = 0.22\ (\text{total crop}) - 0.29\ (r = 0.59, p < 0.01)$$

and (2) "crop from fluorometer" vs. the total crop:

$$\text{"Crop from fluorometer"} = 0.69\ (\text{total crop}) + 0.52\ (r = 0.71, p < 0.01)$$

All crop units are mg carbon/m^3. The heterotrophic phytoplankton were considered to be *Peridinium depressum,* the most abundant heterotrophic alga, *P. conicum, P. divergens, P. excentricum, P. globulus, P. oceanicum, P. pellucidum, P. steinii, Phalocroma cuneus,* and *Phal. ovum.*

Crop size was responsive to increased nutrients in the euphotic zone as a result of upwelling. The crop at station 1 showed the most dramatic changes in time with crop increases lagging a week behind increases in nutrients (fig. III-2). The effect

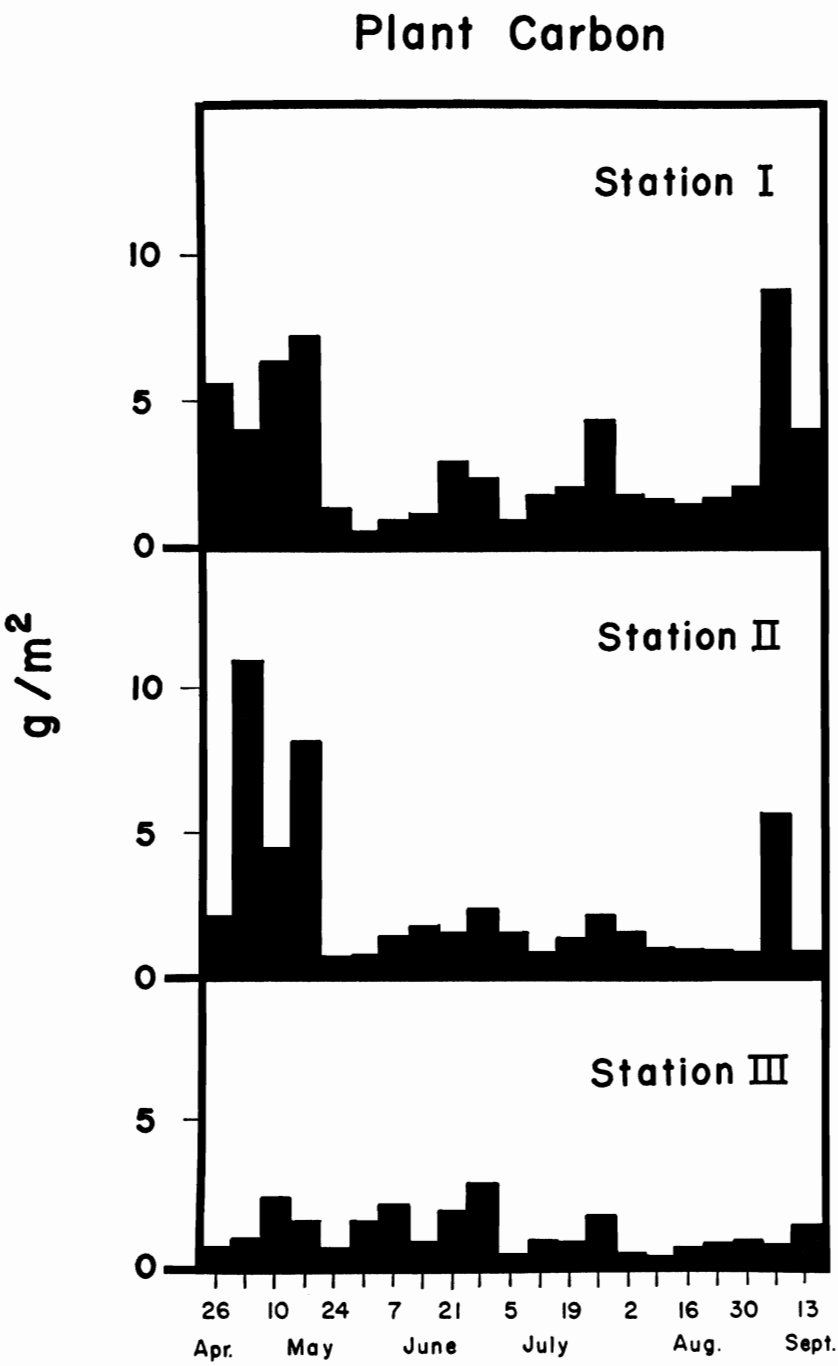

Fig. III-1. Variation with time of the total crop of phytoplankton, as carbon (from cell volume), at stations 1, 2, and 3. The abscissa is marked off by weeks with the date indicated every other week.

may be most apparent at station 1 because of less intense grazing by herbivores at this shallow (25 m) station.

Changes in certain other constituents took place as crop size changed. Particulate organic carbon varied directly with crop size, as noted in Strickland *et al.* (Part I, above), although the concentration of dissolved organic carbon (DOC)

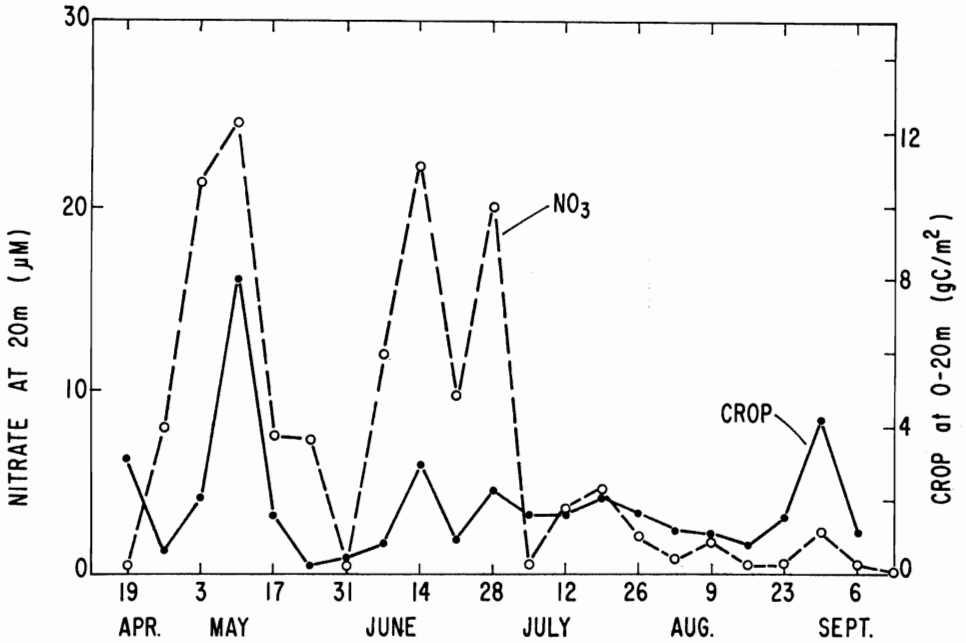

Fig. III-2. Variation in nitrate concentration at the 20-m depth at station 1 and the phytoplankton crop at station 1. Crop data are offset 1 week (moved 1 week earlier) to dramatize the lag in the response of the crop to earlier nitrate enrichment.

did not. Lack of a relationship between DOC and crop size may be due to saprophytic, colorless phytoplankton (*P. depressum* and others) rapidly utilizing any organic substances released by the photosynthetic species. The direct relationship between the quantity of these heterotrophs and total phytoplankton crop is consistent with the idea that the heterotrophs were using photosynthetic products for growth.

Depth Distribution of the Crop

Four examples of chlorophyll *a* distribution with depth are shown in figure III-3, as calculated from continuous profiles of chlorophyll fluorescence. Curves such as figure III-3, *a*, were typical with the chlorophyll *a* maximum near the thermocline and with a secondary plateau just beneath the peak. The very sharp chlorophyll maximum of figure III-3, *b*, was noted during a heavy diatom bloom with most of the crop consisting of one species, *Leptocylindrus danicus*. Another atypical trace, with many small peaks, is shown in figure III-3, *c*. The crop consisted primarily of seven diatom species varying in abundance from 3 to 12 μg C/liter in the integrated samples used for species enumeration. Figure III-3, *d*, is also atypical in that chlorophyll fluorescence was uniform with depth. In this case

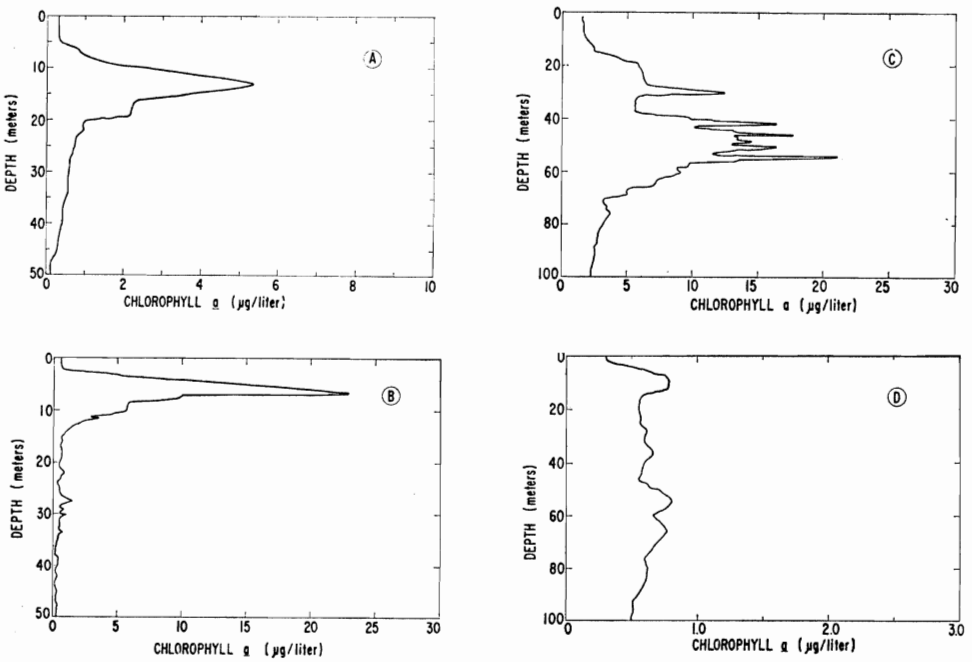

Fig. III-3. Some examples of chlorophyll *a* depth profiles. (*a*) 10 May, 1967, station 3; (*b*) 17 May, 1967, station 2; (*c*) 5 May, 1967, station 2; (*d*) 24 May, 1967, station 2.

the standing stock was very low and *Coccolithus huxleyi* was the predominant organism.

Photosynthetic Rates

The data of table III-1 indicate differences in carbon assimilation rate per weight of chlorophyll *a* between phytoplankton above and below the trophocline (judged as the depth where nitrate concentration reached 1 μM). The difference in rate may imply a controlling action of nutrients on photosynthesis but may result also from depth stratification of phytoplankton in layers with different average irradiance at different stations. Similar differences in photosynthetic rate are noted in cultures of the same organism grown with high or low irradiance (e.g., Myers, 1946).

Primary Production

Variation in phytoplankton production, as grams carbon/m^2 and day, are shown in figure III-4. Since production rates were calculated from the standing stocks the two parameters will be related closely except where the bulk of the crop was encountered either very shallow or very deep in the euphotic zone. Independent estimates of production, based on crop size and calculated specific growth rate using equation (2), paralleled those of figure III-4. They were generally lower for the reason mentioned under "Methods," but not as much lower as we expected (table III-3). This observation and the knowledge that "crops from fluorometer" estimates were low lead us to believe that the data of figure III-4 underestimate phytoplankton production by about 10 percent.

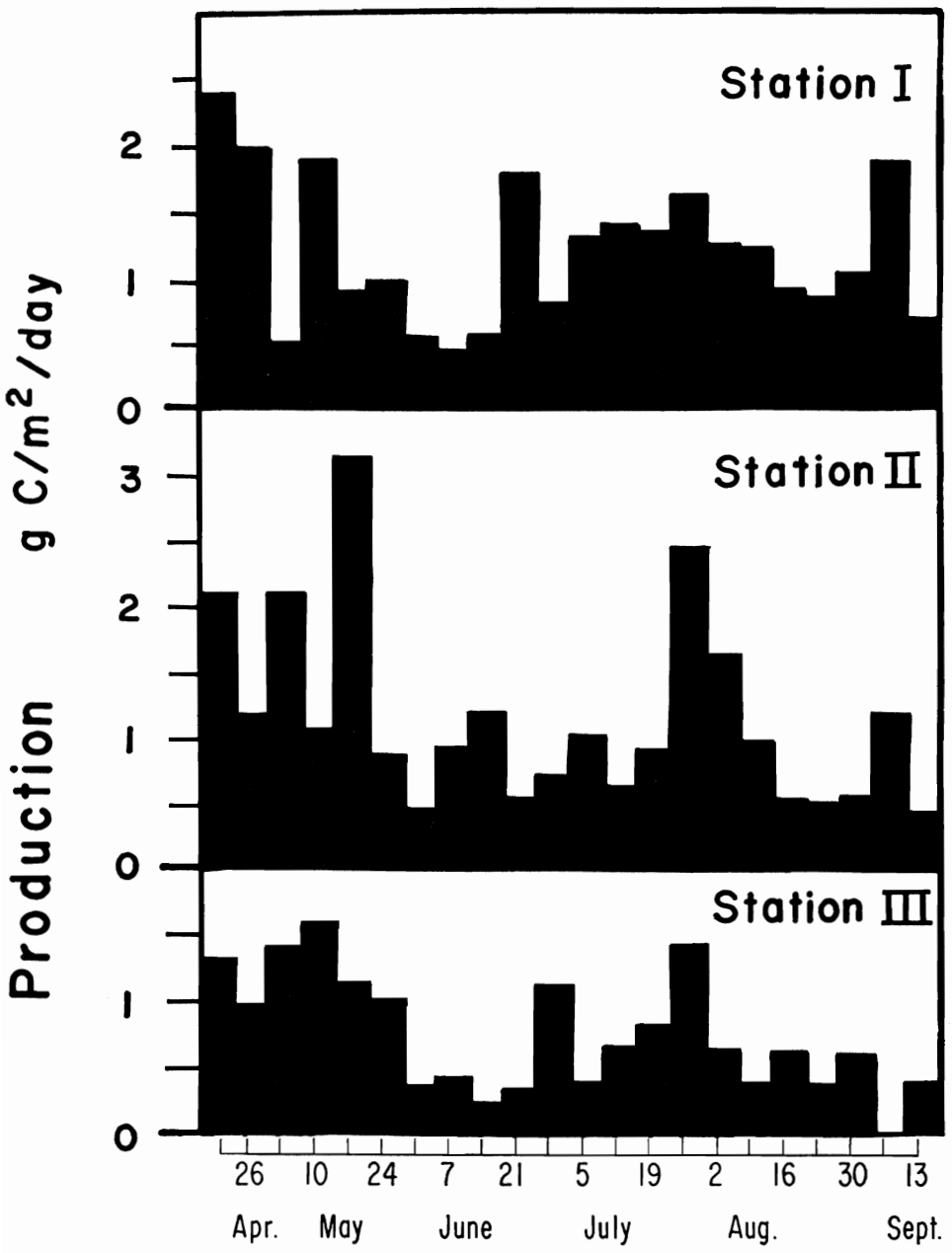

Fig. III-4. Primary production at stations 1, 2, and 3.

TABLE III-2

COMPARISON OF AVERAGE VALUES OF SEVERAL CHARACTERISTICS OF THE PHYTOPLANKTON BY STATION

Parameter	Units	Average value at station		
		1	2	3
Phytoplankton crop (from cell volume)	gC/m^2	2.51	2.50	1.15
Phytoplankton crop (from fluorometer)	gC/m^2	2.11	2.14	1.21
Heterotrophic phytoplankton crop	gC/m^2	0.28	0.19	0.06
Cell carbon/chlorophyll *a*				
Crop (from cell volume)/chl.[a]	g/g	118	91	55
Crop (from fluorometer)/chl.[a]	g/g	99	78	58
Cell chlorophyll *a* concentration	mg/cm^3	1.47	1.57	1.90
Specific growth rate	doublings/day	0.63	0.70	0.78

[a] Chlorophyll determined after extraction of an integrated sample of phytoplankton collected during lowering of the profiling pump.

TABLE III-3

SOME COMPARISONS OF PHYTOPLANKTON PRODUCTION CALCULATED FROM THE STANDING STOCK AS CARBON ("CROP FROM FLUOROMETER") AND (*a*) AVERAGE RATE OF PHOTOSYNTHESIS FROM TABLE 1 AND (*b*) SPECIFIC GROWTH RATE FROM EQUATION (2)

Date	Station	Production $gC/m^2 \cdot day$	
		(*a*) From photosynthesis	(*b*) From growth-rate equation
17 May 1967	2	1.7	2.0
21 June 1967	1	1.2	1.1
2 Aug. 1967	1	1.3	0.72
9 Aug. 1967	1	0.88	0.62
"	2	0.38	0.41
"	3	1.6	1.6
23 Aug. 1967	1	0.58	0.50
"	2	0.40	0.17
"	3	0.50	0.30
13 Sept. 1967	1	0.94	0.73
"	3	0.35	0.25

PHYTOPLANKTON SPECIFIC GROWTH RATE

Specific growth rates were calculated for each date and station using equation (1) and averaged by station (table III-2). The values suggest actively growing crops with doubling times of the order 1–3 days. Such rates are somewhat lower than rates for laboratory cultures growing with near optimal irradiance and temperature (0.3–2 days for doubling) but are consistent with rates observed in cultures when irradiance is somewhat less than saturating for growth, as was the case at sea judged from comparisons of crop distribution with depth and profiles of submarine light.

REFERENCES

CASTENHOLZ, R. W.

1964. The effect of daylength and light intensity on the growth of littoral marine diatoms in culture. Physiol. Plantarum, 17:951–963.

EPPLEY, R. W.

1968. An incubation method for estimating the carbon content of phytoplankton in natural samples. Limnol. Oceanogr., 13:574–582.

EPPLEY, R. W., and J. L. COATSWORTH

1966. Culture of the marine phytoplankter, *Dunaliella tertiolecta*, with light-dark cycles. Arch. Mikrobiol., 55:66–80.

EPPLEY, R. W., and P. R. SLOAN

1966. Growth rates of marine phytoplankton: Correlation with light absorption by cell chlorophyll *a*. Physiol. Plantarum, 19:47–59.

HOLM-HANSEN, O., C. J. LORENZEN, R. W. HOLMES, and J. D. H. STRICKLAND

1965. Fluorometric determination of chlorophyll. J. Conseil Int. Explor. Mer, 30:3–15.

LORENZEN, C. J.

1966. A method for the continuous measurement of *in vivo* chlorophyll concentration. Deep-Sea Res., 13:223–227.

MULLIN, M. M., P. R. SLOAN, and R. W. EPPLEY

1966. Relationship between carbon content, cell volume, and area in phytoplankton. Limnol. Oceanogr., 11:307–311.

MYERS, J.

1946. Influence of light intensity on the photosynthetic characteristics of Chlorella. J. Gen. Physiol., 29:429–440.

PAASCHE, E.

1968. Marine algae grown with light-dark cycles. II. *Ditylum brightwellii* and *Nitzschia turgidula*. Physiol. Plantarum, 21:66–77.

STRATHMANN, R. R.

1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. Limnol. Oceanogr., 12:411–418.

UNIVERSITY OF CALIFORNIA, INSTITUTE OF MARINE RESOURCES

1968. Research on the marine food chain; progress report, Jan. 1967–June 1968. Part IV. Data record, coastal plankton survey, 1967. Section II. The plankton. Unpubl. MS (SIO Ref. 68-38, IMR Ref. 69-3).

YENTSCH, C. S., and D. W. MENZEL

1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Res., 10:221–231.

THE ECOLOGY OF THE PLANKTON OFF LA JOLLA, CALIFORNIA, IN THE PERIOD APRIL THROUGH SEPTEMBER, 1967

EDITED BY

J. D. H. STRICKLAND

PART IV

RELATIONSHIPS OF PHYTOPLANKTON SPECIES DISTRIBUTION TO THE DEPTH DISTRIBUTION OF NITRATE

BY

R. W. EPPLEY

INTRODUCTION

As EARLY AS 1928 Moberg stated "a causal relation between the abundance of diatoms and the quantity of nitrate is . . . strongly indicated" in regard to diatoms and upwelling in the sea off southern California. Sverdrup and Allen (1939) and Sargent and Walker (1948) studied further the relationship of diatoms to upwelling. Diatoms were abundant in recently upwelled water characterized by a shallow thermocline but were sparse in "offshore" water with a deeper thermocline. A similar situation is found in parts of the Atlantic Ocean as well (Hulburt, 1966). A possible explanation of these observations is provided in the present account. It is recognized that other factors, such as turbulence, grazing, and species differences in growth rate with temperature, play an important role in phytoplankton species distribution. The reader is to consider this account a speculative exercise, done primarily to stimulate thinking on physiological approaches to phytoplankton species distribution.

Several species encountered during the study are now in culture, largely through the efforts of Mr. J. B. Jordan. Kinetics of uptake of nitrate and ammonium by these cultures and others were studied as a means of understanding the relationship between species distribution and the form and concentration of available nitrogen in the water. In particular we expected to find a relationship between the half-saturation constant for uptake (K_s), that is, the nitrate concentration supporting an uptake rate one-half the maximum rate, and species distribution (Dugdale, 1967). Present evidence suggests that the half-saturation constant determined for uptake is the same as that for growth (Eppley and Thomas, 1969). Ideally, in addition to the K_s values and nitrate vs. depth profiles, we should have species lists for several depths at each week and station. Because we had only the species composition from samples integrated over the entire euphotic zone (pigment layer) a detailed analysis by depth could not be undertaken. Some simple relationships are apparent, however, even at this preliminary level of analysis.

ACKNOWLEDGMENT

This research was supported in full by the United States Atomic Energy Commission, Contract No. AT(11-1)GEN 10, P.A. 20.

RESULTS AND DISCUSSION

By way of illustration, the variation of specific growth rate with nitrate concentration for *Coccolithus huxleyi* and *Skeletonema costatum* at 20°C and with 12 hours light/day is shown in figure IV-1. Because of its low half-saturation "con-

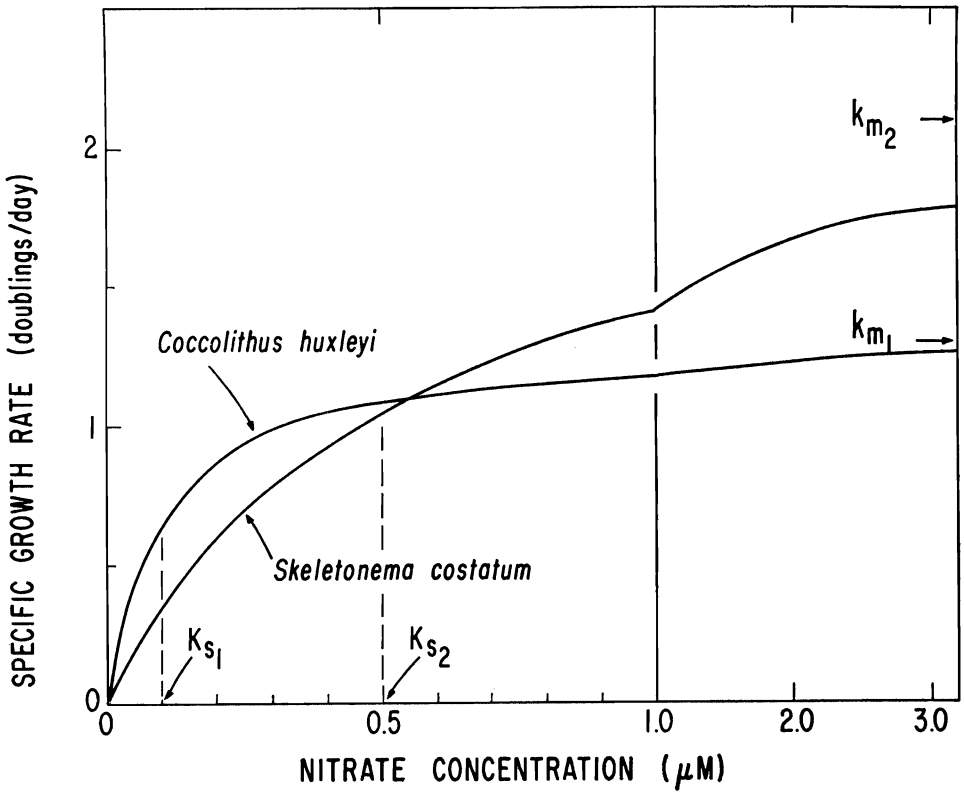

Fig. IV-1. Variation in specific growth rate with nitrate concentration of *Coccolithus huxleyi* and *Skeletonema costatum*. Maximum specific growth rates were taken as 1.3 (km_1) and 2.1 (km_2) doublings/day for *C. huxleyi* (Paasche, 1967) and *S. costatum* (Jitts *et al.*, 1964), respectively, assuming 12 hours of light per day with an irradiance saturating for growth and 20°C. Half-saturation constants for *C. huxleyi* (Ks_1) and *S. costatum* (Ks_2) are indicated on the abscissa. Note scale change at 1 μM nitrate concentration.

stant" for nitrate uptake *C. huxleyi* appears to be the more successful competitor when nitrate concentration is less than about 0.5 μM. At higher nitrate levels *S. costatum* appears to be the better because of its higher maximum specific growth rate. Neither species should have an advantage at the crossover point of the curves, about 0.5 μM nitrate. These considerations are discussed more fully by Dugdale (1967), Eppley and Coatsworth (1968), and MacIsaac and Dugdale (1969).

From a knowledge of the half-saturation constants for nitrate and ammonium uptake (table IV-1) and measurements of growth rates (table IV-2) of these species came the following hypotheses: (1) The distribution of ubiquitous species, as represented here by *C. huxleyi*, should be independent of the availability of nitrate in the euphotic zone because of its ability to use very low levels of ammonium ion.

TABLE IV-1

HALF-SATURATION "CONSTANTS" FOR UPTAKE OF NITRATE AND AMMONIUM BY CERTAIN MARINE PHYTOPLANKTON
(Culture data from Eppley, Rogers, and McCarthy, 1969)

Organism	Nitrate μM	Ammonium μM	Temperature °C
Oceanic species			
Coccolithus huxleyi F	0.1	0.1	18
C. huxleyi BT-6	0.1	0.1	18
Neritic diatoms			
Skeletonema costatum	<0.1		8
	0.5	0.6	18
	1.0		27
Leptocylindrus danicus	1.3	0.7	18
Rhizosolenia stolterfothi	1.7	0.5	18
Rhizosolenia robusta[a]	3.0	8.6	18
Neritic dinoflagellate			
Gonyaulax polyedra	10.3	5.3	18
Natural communities			
Oceanic	≦0.2	0.1–0.6	(MacIsaac and
Neritic	≧1.0	0.6–1.3	Dugdale, 1969)

[a] An oceanic species according to Cupp (1943).

TABLE IV-2

SCATTERED OBSERVATIONS ON THE SPECIFIC GROWTH RATE (μ), IN DOUBLINGS/DAY, OF SOME MARINE PHYTOPLANKTON
(All values for temperature approximately 20°)C

Organism	μ	Comment or reference
Oceanic species		
Coccolithus huxleyi F	1.85	Paasche, 1967; continuous light
C. huxleyi BT-6	1.85	Eppley and Sloan, 1966; continuous light
Neritic diatoms[a]		
Skeletonema costatum	>2	Curl and McLeod, 1961; Jitts *et al.*, 1964; Eppley and Sloan 1966
Leptocylindrus danicus	1 to <2	Institute of Marine Resources, unpublished
Rhizosolenia stolterfothi	1 to <2	" " " " "
Rhizosolenia robusta[b]	~0.8	" " " " "
Neritic dinoflagellates		
Gonyaulax polyedra	~0.5	" " " " "

[a] Specific growth rates cited for diatoms, except *S. costatum* by Jitts *et al.*, 1964, were measured in continuous light and may be less than rates when light is provided only 12–16 hours each day (Castenholz, 1964; Paasche, 1968).
[b] An oceanic species according to Cupp (1943).

(2) The distribution diatoms, represented by *S. costatum, Rhizosolenia stolterfothi, R. robusta,* and *Leptocylindrus danicus,* should be essentially dependent upon the presence of nitrate in the euphotic zone at depths shallow enough to allow the relatively high light intensities required for them to realize their potential for rapid growth. Their growth on ammonium should be limited because of its assumed low concentration and the fairly high half-saturation constants for ammonium uptake. (3) The distribution of coastal photosynthetic dinoflagellates,

TABLE IV-3

OCCURRENCE OF SPECIES COMPARED WITH DEPTH RANGE WHERE NITRATE WAS ENCOUNTERED AT 1 μM CONCENTRATION

(Scores are number of occurrences of a species/number of occurrences of NO_3^- at 1 μM in the depth range indicated.)

1 μM NO_3^- depth	Station 1		Station 2		Station 3		All stations		All stations as percentile	
	≦15 m	>15 m	≦15 m	>15 m	≦15 m	>15 m	≦15 m	>15 m	≦15 m	>15 m
Coccolithus huxleyi	8/9	11/12	7/7	14/14	10/10	9/11	25/26	34/37	96	92
Gonyaulax polyedra	7/9	10/12	2/7	6/14	5/10	5/11	14/26	21/37	54	57
Skeletonema costatum	11/11[a]	0/10[a]	8/9[a]	5/12[a]	8/11[b]	0/10[b]	27/31	5/32	87	16
Leptocylindrus danicus	7/11	2/12	7/8[b]	3/13[a]	6/12[a]	2/9[a]	20/31	7/34	65	21
Rhizosolenia stolterfothi	3/10[b]	1/11[b]	7/9[a]	3/12[a]	4/10	0/11	14/29	4/34	48	12
Rhizosolenia robusta	1/9	0/12	3/8[b]	0/13[b]	3/11[b]	3/10[b]	7/28	3/35	25	9

NOTE: Scores of diatoms are corrected for a "spillover" effect, judged as the continued occurrence of a diatom species in the week just following a shallow (<15 m) nitrate level.

[a] Includes two samples considered "spillover" from previous week although the depth to 1 μM nitrate had fallen below 15 m.

[b] Includes one "spillover."

represented by *Gonyaulax polyedra,* was expected to be less dependent upon the depth distribution of nitrate because they can migrate vertically from day to night in the water column over 10–15 m, allowing this particular species to alternate in any 24-hour period from a level of low light and high nitrate to a shallower depth with high light and low nitrate (Eppley, Holm-Hansen, and Strickland, 1968).

Two assumptions were recognized for these hypotheses. (1) It was assumed that ammonium was uniformly present at a concentration about 0.5 μM as a result of a balance between consumption by phytoplankton and excretion by zooplankton. That this is a typical value is supported by measurements in a variety of locations (e.g., Thomas, 1969). (2) Nitrogen was the principal rate-limiting dissolved nutrient during the study (Eppley, 1968).

Graphs of nitrate concentration vs. light intensity (irradiance) in the water column indicated that nitrate was always present in the lower part of the euphotic zone (irradiance 1 to 20 percent of surface values). The average irradiance was higher at the 1 μM nitrate depth at the more offshore stations 3 and 2 than the nearshore station 1. Since the higher average nitrate concentrations were not reflected by higher phytoplankton crops at stations 3 and 2 it is likely that another factor limits the size of the crop. This factor is probably grazing, although it is not the only one possible. Since grazing might be species selective it was decided to compare phytoplankton species distribution with nitrate concentration on the basis of presence or absence of a species instead of comparing some measure of dominance.

Table IV-3 shows a comparison of occurrence in local water of species studied in the laboratory with the depth at which nitrate concentration was 1 μM. Phytoplankton data was from University of California, Institute of Marine Resources, 1968. If a higher NO_3^- concentration had been selected results would have been similar because of the sharp increase in nitrate concentration with depth. The occurrence of *C. huxleyi* and *G. polyedra* was not related to the depth of the 1 μM nitrate isoline. The diatoms were found most frequently, however, when 1 μM nitrate was encountered at depths as shallow as 10–15 m. The relationship is stronger if (as in table IV-3) occurrence the week following a shallow nitrate level is also considered. On several occasions two or more of the diatoms of table IV-1 were noted in the samples. Of these co-occurrences, thirty-eight out of forty-three took place when the 1 μM nitrate depth was 15 m or less.

These simple comparisons of species occurrence with the depth of nitrate are consistent with the hypothesis of a close relationship of species distribution to nitrogenous nutrients. We noted earlier a direct relationship between a shallow nitrate and the size of the phytoplankton crop at station 1 (Eppley, Reid, and Strickland, Part III, above). The present analysis extends the importance of the depth distribution of nitrate to include its action as a selective factor for groups of species.

REFERENCES

CASTENHOLZ, R. W.

1964. The effect of daylength and light intensity on the growth of littoral marine diatoms in culture. Physiol. Plantarum, 17:951–963.

CUPP, EASTER E.

1943. Marine plankton diatoms of the west coast of North America. Univ. of California Press. Berkeley and Los Angeles. 237 pp.

CURL, H., and G. C. MCLEOD

1961. The physiological ecology of a marine diatom, *Skeletonema costatum* (Gren.) Cleve., J. Mar. Res., 17:70–88.

DUGDALE, R. C.

1967. Nutrient limitation in the sea: Dynamics, identification, and significance. Limnol. Oceanogr., 12:685–695.

EPPLEY, R. W.

1968. An incubation method for estimating the carbon content of phytoplankton in natural samples. Limnol. Oceanogr., 13:574–582.

EPPLEY R. W., and J. L. COATSWORTH

1968. Uptake of nitrate and nitrite by *Ditylum brightwellii*—kinetics and mechanisms. J. Phycology, 4:151–156.

EPPLEY, R. W., O. HOLM-HANSEN, and J. D. H. STRICKLAND

1968. Some observations on the vertical migration of dinoflagellates. J. Phycology, 4:333–340.

EPPLEY, R. W., JANE N. ROGERS, and J. MCCARTHY

1969. Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. Limnol Oceanogr., 14:912–920.

EPPLEY, R. W., and P. R. SLOAN

1966. Growth rates of marine phytoplankton: Correlation with light absorption by chlorophyll *a*. Physiol. Plantarum, 19:47–59.

EPPLEY, R. W., and W. H. THOMAS

1969. Comparison of half-saturation constants for growth and nitrate uptake of marine phytoplankton. J. Phycology, 5:375–379.

HULBURT, E. M.

1966. The distribution of phytoplankton, and its relationship to hydrography, between southern New England and Venezuela. J. Mar. Res., 24:67–81.

JITTS, H. R., C. D. MCALLISTER, K. STEPHENS, and J. D. H. STRICKLAND

1964. The cell division rates of some phytoplankters as a function of light and temperature. J. Fish. Res. Board Can., 21:139–157.

MACISAAC, J. J., and R. C. DUGDALE

1969. The kinetics of nitrate and ammonia uptake by natural populations of marine phytoplankton. Deep-Sea Res., 16:415–422.

MOBERG, E. G.

1928. The interrelationship between diatoms, their chemical environment, and upwelling water in the sea, off the coast of southern California. Proc. U. S. Nat. Acad. Sci., 14:511–517.

PAASCHE, E.

1967. Marine plankton algae growth with light-dark cycles. I. *Coccolithus huxleyi*. Physiol. Plantarum, 20:946–956.

1968. Marine plankton algae growth with light-dark cycles. II. *Ditylum brightwellii* and *Nitzschia turgidula*. Physiol. Plantarum, 21:66–77.

SARGENT, M. C., and T. J. WALKER

1948. Diatom populations associated with eddies off southern California in 1941. J. Mar. Res., 7:490–505.

SVERDRUP, H. U., and W. E. ALLEN

1939. Distribution of diatoms in relation to the character of water masses and currents off southern California in 1938. J. Mar. Res., 2:131–144.

THOMAS, W. H.
1970. On nitrogen deficiency in tropical Pacific oceanic phytoplankton: photosynthetic parameters in poor and rich water. Limnol. Oceanogr. In press.
UNIVERSITY OF CALIFORNIA, INSTITUTE OF MARINE RESOURCES
1968. Research on the marine food chain; progress report, Jan. 1967–June 1968. Part IV. Data record, coastal plankton survey, 1967. Section II. The plankton. Unpubl. MS (SIO Ref. 68–38; IMR Ref. 69–3).

THE ECOLOGY OF THE PLANKTON OFF LA JOLLA, CALIFORNIA, IN THE PERIOD APRIL THROUGH SEPTEMBER, 1967

EDITED BY

J. D. H. STRICKLAND

PART V

PHYTOPLANKTON TAXONOMY AND STANDING CROP

BY

F. M. H. REID, E. FUGLISTER, AND J. B. JORDAN

ABSTRACT

Phytoplankton samples collected with a profiling hose system have been counted from three stations normal to the coast during a 21-week period. Results are expressed as total plant organic carbon per liter held by each taxon, by certain groupings, and by the sample as a whole. The succession of organisms has been indicated for the 21 weeks and the relationship between the three stations discussed. The total crop decreased offshore. The two inner stations showed increases in total crop size corresponding with periods of upwelling and the floristic composition of these two stations was often similar. Overall, dinoflagellates and "monads" contributed most to the total biomass, the former showing three major peaks during the period studied and the latter being fairly evenly distributed. After a bloom in April–May, diatoms were of minor importance. Coccolithophorids were most abundant at the innermost station but their relative importance in the total phytoplankton population increased offshore. They showed little seasonal variation.

A study of the size distribution of the phytoplankton cells showed that the plant biomass was made up mostly of cells with equivalent diameters from 15 μ to 70 μ.

INTRODUCTION

THE COMPREHENSIVE study of coastal plankton ecology undertaken by the Food Chain Research Group of the Institute of Marine Resources, University of California, has made it possible to investigate the phytoplankton in conjunction with other aspects of the plankton ecology of the region (Strickland *et al.*, Part I, above).

The phytoplankton of the coastal waters of southern California has been studied previously but not as part of a wider ecological program. Allen did extensive work in this area from 1921 to 1946 (Allen, e.g., 1928, 1941). He made quantitative studies of diatoms and dinoflagellates and collaborated in Sverdrup and Allen (1939) in a discussion of the distribution of diatoms in relation to the character of the water masses and currents. Sargent and Walker (1948) considered the diatom populations associated with eddies off southern California. Cupp (1943) made a detailed study of diatoms and Kofoid and Swezy (e.g., 1921) were particularly concerned with dinoflagellate taxonomy. Balech (1960) compared the phytoplankton composition in years with above-average and below-average water temperatures. Holmes *et al.* (1967) have summarized work by others on red-water conditions and have added some recent findings.

In the present study the weekly sampling program at three stations normal to the coast has given a detailed picture of the phytoplankton population during 21 weeks from April to September, 1967. The material covered in this paper is primarily of a taxonomic nature, other aspects of the phytoplankton ecology being treated in Eppley *et al.* (Part III, above). The results are given in terms of phytoplankton organic carbon as this is more useful than direct counts in the consideration of food chain ecology.

ACKNOWLEDGMENT

This research was supported in full by the United States Atomic Energy Commission, Contract No. AT(11-1)GEN 10, P.A. 20.

The advice of Dr. John Beers was of considerable assistance in this work.

METHODS

The use of a profiling pump system, described in University of California, Institute of Marine Resources (1968*a*, *b*), provided integrated samples through the pigment layer, that is, from the surface to a depth where a continuous *in vivo* fluorometric chlorophyll measurement indicated that little phytoplankton remained in the water (Strickland *et al.*, Part I, above). From an unconcentrated sample preserved in 0.5 percent neutral formalin, the average density, but not the vertical distribution, of phytoplankters over the column of water could be determined. In addition to this, a concentrated sample, collected on a 35-μ mesh cloth, was used for enumeration of larger phytoplankton cells in the same water column. It was obtained from the deck-mounted plankton collector used primarily for microzooplankton analyses by Beers and Stewart (Part VI, below). At station 1 where the profile depth was 21 m we have assumed that the pigment-layer depth was 25 m (Strickland *et al.*, Part I, above); at stations 2 and 3 it varied but was never greater than 60 m. Results are expressed as the quantity per liter of unfiltered composite sample.

COUNTING

Three size categories of phytoplankton organisms were counted in each sample in an attempt to obtain accurate estimates of all sizes of phytoplankton. The technique of Utermöhl was used employing an inverted phase microscope. Small cells with diameters in the range of approximately 1–20 μ were counted by settling 0.5 ml of the unconcentrated sample in a small-diameter settling chamber of 1.5 ml capacity. They were counted with 400× magnification and either the whole base of the chamber or alternate rows were examined. Cells with diameters of approximately 20–50 μ were counted by settling 10 to 100 ml of unconcentrated sample in Zeiss settling chambers and were examined at 160×. Large cells with diameters of about 50 μ or more, which had not been seen or had been found only in low numbers in the above sample, were counted in the material collected on the 35-μ mesh cloth. Five ml of this sample were taken with a straight-bore pipette and diluted to a known volume of 10 ml or more. One ml of this diluted suspension was added to a 10-ml Zeiss settling chamber and the whole base examined at 100×. Cells with diameters much greater than 250 μ would not be recorded by this method as the sample had been passed through a 202-μ exclusion net before the 35-μ net.

Since one of the main purposes of the study was to estimate biomass, identification to species was carried out only where it was relatively easy and convenient to do so. In many cases we have been content with a taxon described only to genus or division with some estimate of size. Empty diatom frustules were omitted from the counts. A recount was sometimes undertaken if a taxon had poor counting statistics and if the data for that station had indicated that it might be contributing a significant fraction of plant carbon.

Cell Volumes and Carbon Estimates

The shapes devised by Kovala and Larrance (1966) for measuring phytoplankton volumes have been used in a computer program. If possible, twenty cells of each taxon were measured and these sets of measurements were used to calculate the average cell volumes used throughout. In some instances certain dimensions had to be estimated from sources in the literature. A few diatoms were nearly always present as fragments (e.g., *Rhizosolenia, Thalassiothrix*). In these cases the number counted was halved to give cell counts.

The organic carbon content of the cells was calculated from the equations given by Eppley, Reid, and Strickland (Part III, above). Cell number, cell volume, and total carbon per liter were calculated for each taxon, for certain groupings, and for the sample as a whole. Confidence limits have been calculated for the carbon estimates.

RESULTS AND DISCUSSION

An example of one of the data sheets presented in the data record (University of California, Institute of Marine Resources, 1968*b*) is included as table V-1. In discussing the distributions the total carbon content of the cells or taxa has been expressed throughout in μg C per liter or gC/m^2 as we are particularly concerned with questions of biomass.

Cell Numbers

The highest numbers of cells recorded were always in the "monad" group: up to 3×10^6 cells per liter at station 1 on 26 July. The highest counts in the diatom group were 0.8×10^6 cells per liter for a *Chaetoceros* species at station 2 on 3 May and 0.5×10^6 cells per liter for *Leptocylindrus danicus* at station 1 on 17 May. *Coccolithus huxleyi* reached 0.4×10^6 cells per liter at station 1 on 2 August. The small, naked dinoflagellates were always more numerous than the thecate forms, though the identification of the former is less reliable. Their maximum number was 0.3×10^6 cells per liter at station 1 on 17 May. The highest count for the thecate forms was 0.2×10^6 cells per liter for *Exuviaella* cf. *ovum* on 10 May at station 3. Of the larger dinoflagellates *Gonyaulax polyedra* reached 0.04×10^6 cells per liter on 6 September at station 1 when there was a weak red-tide bloom. (The station was near, but not actually in, a red-tide patch.) Since the concentration was measured over the entire pigment depth, the concentration of *Gonyaulax* at the surface may have been much higher.

Total Crop Carbon

At stations 1 and 2 there were four periods of increasing phytoplankton crop size which corresponded with periods of upwelling: in mid-May, late June, late July

TABLE V-1

SAMPLE DATA SHEET FOR MAY 10, STATION 2, FROM DATA RECORD

		EQUIVALENT DIAMETER (MICRONS)	CELL VOLUME (CUBIC MICRONS)	NO./LITER X E-05	VOL/LITER X E-06 (CUBIC MICRONS)	CARBON (MICROGRAMS/ LITER)	CONFIDENCE LIMITS (MICROGRAMS/ LITER)	
24	CERATIUM CF. KOFOIDII	25	8278	.000327	.27	.04	.01-	.09
68	CERATIUM TRIPOS *	57	99374	.000327	3.25	.41	.13-	.96
26	DINOPHYSIS ACUMINATA	30	13647	.001178	1.61	.23	.14-	.36
27	EXUVIAELLA CF. OVUM	7	212	.168421	3.57	.65	.28-	1.28
28	EXUVIAELLA VAGINULA	10	587	.021053	1.24	.21	.01-	1.18
30	GONYAULAX SPINIFERA	30	14137	.000262	.37	.05	.01-	.13
32	PERIDINIUM CONICUM	71	185820	.001636	30.40	3.69	2.39-	5.43
34	PERIDINIUM DEPRESSUM (MEDIUM)	64	134269	.001898	25.48	3.15	2.11-	4.52
25	PERIDINIUM DEPRESSUM (LARGE)	125	1027165	.001636	168.06	18.40	11.92-	27.08
35	PERIDINIUM CF. GLOBULUS	26	8809	.001832	1.61	.24	.16-	.34
81	PERIDINIUM MINISCULUM	19	3780	.005263	1.99	.30	.10-	.71
36	PERIDINIUM OCEANICUM	50	66306	.000589	3.91	.50	.23-	.96
33	PERIDINIUM CF. TROCHOIDEUM	18	3014	.036842	11.11	1.73	1.20-	2.40
38	PHALACROMA OVUM	37	26958	.000720	1.94	.26	.13-	.46
39	PROROCENTRUM GRACILE	16	2055	.001053	.22	.03	.00-	.19
48	THECATE DINOFLAGELLATES (MICRO)	8	288	.042105	1.21	.22	.03-	.78
	SUB-TOTALS =			.2868	261.29	30.79		
	NON-THECATE DINOFLAGELLATES							
41	NAKED DINOFLAGELLATES (MICRO)	10	498	.400000	19.91	3.45	2.09-	5.37
43	NAKED DINOFLAGELLATES(MEDIUM)	42	37518	.007368	27.64	3.69	1.48-	7.60
51	NAKED DINOFLAGELLATES (LARGE)	60	113097	.001053	11.90	1.49	.04-	8.29
	SUB-TOTALS =			.4084	59.46	8.62		
	COCCOLITHOPHORIDS							
44	ACANTHOICA QUATTROSPINA	11	655	.010526	.69	.12	.06-	.22
86	COCCOLITHUS CF. CARTERI	17	2474	.005263	1.30	.20	.07-	.48
45	COCCOLITHUS HUXLEYI	7	146	.252632	3.70	.69	.36-	1.20
	SUB-TOTALS =			.2684	5.69	1.01		
	OTHERS							
46	CHILOMONAS MARINA	10	532	.021053	1.12	.19	.00-	1.08
80	DISTEPHANUS SPECULUM	21	4980	.001053	.52	.08	.00-	.44
83	EUTREPTIA	16	2136	.042105	8.99	1.43	.17-	5.15
47	MONADS (A)	2	4	9.305263	3.90	.90	.81-	.98
92	MONADS (B)	5	65	.589474	3.86	.75	.50-	1.09
93	MONADS (C)	12	905	.189474	17.14	2.86	1.31-	5.43
	SUB-TOTALS =			10.1484	35.54	6.21		
	TOTALS =			13.1598	1461.99	111.06	101.21-	120.90

*THE LARGEST DIMENSION IS GREATER THAN THE EQUIVALENT DIAMETER BY AT LEAST A FACTOR OF 3

TABLE V-1 (*continued*)

STATION NO. II DATE 10MAY 67 DEPTH 0-40 METERS

			EQUIVALENT DIAMETER (MICRONS)	CELL VOLUME (CUBIC MICRONS)	NO./LITER X E-05	VOL/LITER X E-06 (CUBIC MICRONS)	CARBON (MICROGRAMS/ LITER)	CONFIDENCE LIMITS (MICROGRAMS/ LITER)	
PENNATE DIATOMS									
1	GYROSIGMA SP.	*	38	27835	.000262	.73	.03	.01-	.08
2	NITZSCHIA CF. CLOSTERIUM	*	6	90	.063158	.57	.10	.02-	.29
3	NITZSCHIA SPP. (MEDIUM)	*	11	664	.117895	7.83	.84	.69-	1.00
4	NITZSCHIA SPP. (LARGE)	*	16	2103	.016842	3.54	.29	.17-	.47
5	PENNATES (MICRO)		10	466	.042105	1.96	.23	.03-	.83
59	PENNATE (MEDIUM)		25	7917	.005263	4.17	.25	.08-	.58
6	THALASSIOTHRIX MEDITERRANEA	*	30	13568	.011579	15.71	.82	.40-	1.43
	SUB-TOTALS =				.2571	34.51	2.56		
CENTRIC DIATOMS									
7	CENTRIC (MICRO)		10	492	.063158	3.11	.36	.07-	1.05
8	CENTRIC (SMALL)		27	10522	.121053	127.37	7.08	5.78-	8.37
9	CENTRIC (MEDIUM)		41	36274	.000524	1.90	.08	.03-	.15
50	CENTRIC (LARGE)		151	1800207	.000065	11.78	.19	.00-	1.06
65	CHAETOCEROS CONCAVICORNIS		24	7548	.000262	.20	.01	.00-	.03
84	CHAETOCEROS CONVOLUTUS		21	4570	.000196	.09	.01	.00-	.02
11	CHAETOCEROS COSTATUS		14	1410	.314737	44.38	3.99	3.54-	4.45
13	CHAETOCEROS CF. DEBILIS		18	3003	.198947	59.74	4.48	3.84-	5.12
12	CHAETOCEROS DIDYMUS		18	2938	.013684	4.02	.30	.16-	.52
57	CHAETOCEROS SPP.		13	1155	.027368	3.16	.30	.20-	.44
87	COSCINOSIRA POLYCHORDA		40	33251	.000720	2.39	.10	.05-	.18
60	EUCAMPIA ZOODIACUS		13	1141	.001053	.12	.01	.00-	.06
14	HEMIAULUS SINENSIS		29	12333	.096842	119.43	6.39	5.08-	7.69
15	LEPTOCYLINDRUS DANICUS		17	2446	.450526	110.21	8.69	7.87-	9.51
49	LITHODESMIUM UNDULATUM		45	48755	.000262	1.28	.05	.01-	.13
61	RHIZOSOLENIA ALATA	*	35	21670	.001053	2.28	.11	.00-	.59
16	RHIZOSOLENIA DELICATULA		27	10043	.255789	256.89	14.43	12.62-	16.25
66	RHIZOSOLENIA ROBUSTA		181	3081224	.000065	20.17	.29	.01-	1.60
17	RHIZOSOLENIA STOLTERFOTHII	*	33	19301	.135789	262.09	12.59	10.41-	14.76
55	SCHRODERELLA DELICATULA		30	14259	.000785	1.12	.06	.03-	.10
18	SKELETONEMA COSTATUM		17	2425	.102105	24.76	1.96	1.57-	2.35
19	STEPHANOPYXIS TURRIS		84	306508	.000131	4.01	.10	.01-	.36
20	THALASSIOSIRA ROTULA		26	9121	.005497	5.01	.29	.23-	.35
	SUB-TOTALS =				1.7906	1065.50	61.85		
THECATE DINOFLAGELLATES									
54	CERATIUM CF. BUCEPHALUM		44	44977	.000065	.29	.04	.00-	.22
21	CERATIUM DENS		51	67442	.000262	1.77	.23	.06-	.58
22	CERATIUM FURCA		35	21820	.001374	3.00	.41	.26-	.63

TABLE V-1 (*continued*)

STATION NO. II DATE 10MAY 67 DEPTH 0-40 METERS

ALPHA = 4.329
1.0 - SIMPSONS INDEX = .494
(1.0-SIMPSONS)/(1.0-MIN.SIMPSONS) = .502
INFORMATION = 1.908E 06
INFORMATION/MAX.INFORMATION = .353
AVERAGE PERCENT CARBON DOMINANCE = .296
WHERE DOMINANCE IS THE COMBINED CARBON CONCENTRATIONS OF THE TWO TAXA CONTAINING THE MOST CARBON DIVIDED BY THE TOTAL CARBON CONCENTRATION IN THE SAMPLE. THE TAXA ARE PERIDINIUM DEPRESSUM (LARGE) AND RHIZOSOLENIA DELICATULA

EQUIVALENT DIAMETER RANGE	CARBON DISTRIBUTION			
	DIATOMS	DINOFLAGELLATES	COCCOLITHOPHORIDS	OTHERS
1- 5	0	0	0	1.65
6- 10	.69	4.52	.69	.19
11- 15	5.15	0	.12	2.86
16- 20	15.72	2.06	.20	1.43
21- 25	.27	.04	0	.08
26- 30	29.06	.52	0	0
31- 35	12.69	.41	0	0
36- 40	.13	.26	0	0
41- 45	.13	3.73	0	0
46- 50	0	.50	0	0
51- 55	0	.23	0	0
56- 60	0	1.90	0	0
61- 65	0	3.15	0	0
66- 70	0	0	0	0
71- 75	0	3.69	0	0
76- 80	0	0	0	0
81- 85	.10	0	0	0
86- 90	0	0	0	0
91- 95	0	0	0	0
96-100	0	0	0	0
101-105	0	0	0	0
106-110	0	0	0	0
111-115	0	0	0	0
116-120	0	0	0	0
121-125	0	18.40	0	0
126-130	0	0	0	0
131-135	0	0	0	0
136-140	0	0	0	0
141-145	0	0	0	0
146-150	0	0	0	0
151-155	.19	0	0	0
156-160	0	0	0	0
161-165	0	0	0	0
166-170	0	0	0	0
171-175	0	0	0	0
176-180	0	0	0	0
181-185	.29	0	0	0
186-190	0	0	0	0
191-195	0	0	0	0
196-200	0	0	0	0
TOTALS	64.42	39.42	1.01	6.21

SOURCE: University of California, Institute of Marine Resources, 1968*b*.

and late August–early September in a minor red-water condition. The crop size at station 3 showed less marked oscillations, the major peak being in early July. In most weeks the total crop decreased offshore from station 1 to station 3 (Eppley *et al.*, Part III, above).

Except for a diatom bloom in mid-May, dinoflagellates and "monads" were the most important groups contributing to the total plant biomass.

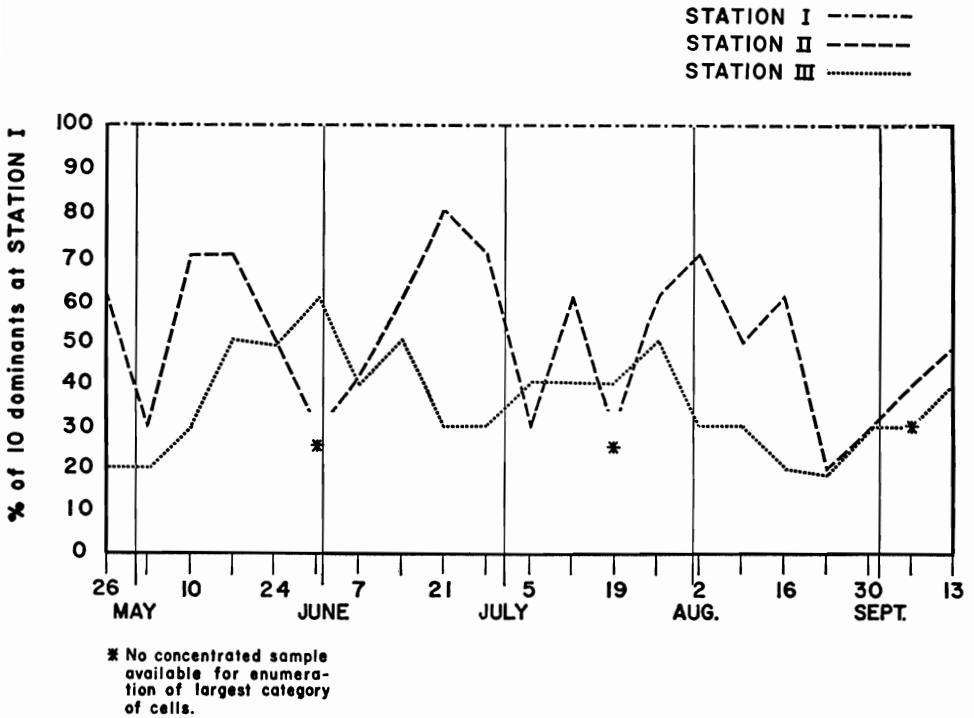

Fig. V-1. Percentage of ten dominant species at station 1 also present at stations 2 and 3 from 26 April to 13 September (based on cell volumes).

Floristic Relationships

The floristic relationship among the three stations was considered on the basis of the ten species contributing most carbon to the total plant biomass on each date. For this purpose "monads" and nonthecate dinoflagellates, common to all stations, were excluded, and certain taxa, which had been separated with respect to size for volume determinations, were combined: for example, various species of *Nitzschia,* some other pennate diatom species, and the two size classes of *Peridinium depressum.*

Of the ten dominant species at station 1 on each date, figure V-1 shows the percentage dominant also at stations 2 and 3. Thus, station 1 is assigned the percentage of 100, and a high percentage at the other two stations indicates a similar association of organisms. In 10 out of 21 weeks the dominants at station 2 were 60 percent or more of those at station 1. In only one out of 21 weeks was there 60 percent or more at station 3. This figure indicates that stations 1 and 2 were more nearly alike than stations 1 and 3 from a floristic standpoint.

Table V-2 shows the numbers of times certain taxa occurred as one of the dominant ten throughout the period of sampling. *Coccolithus huxleyi* and *Peridinium depressum* seemed to be permanent components of the plankton at all three stations. The taxa showing a decrease offshore were *Gonyaulax polyedra, Ceratium furca, Ceratium dens, Skeletonema costatum* and, to a lesser extent, *Chaetoceros* species. *Prorocentrum micans,* which was found to be one of the major local species by Allen (1941), was of relatively minor importance during this period. The *Chaetoceros* species present at the beginning of the study were mainly *Chaetoceros*

TABLE V-2

NUMBER OF TIMES CERTAIN TAXA APPEARED IN THE TEN DOMINANT SPECIES LIST DURING THE 21-WEEK STUDY

Organism	Station 1	Station 2	Station 3
Skeletonema costatum	5	6	1
Chaetoceros spp.	9	11	3
Rhizosolenia spp.	9	10	13
Gonyaulax polyedra	10	5	3
Peridinium depressum	17	19	19
Prorocentrum micans	2	1	1
Peridinium conicum	6	5	5
Ceratium furca	9	6	2
Ceratium dens	9	4	4
Coccolithus huxleyi	15	17	18
Coccolithus cf. *leptoporus*	4	4	4
Cricosphaera sp.	6	5	7

costatus, Ch. cf. *curvisetus,* and *Ch.* cf. *debilis,* but after mid-July some warm-water species such as *Chaetoceros atlanticus* var. *neapolitana, Chaetoceros messanensis,* and *Chaetoceros decipiens* appeared though never in large numbers and only at stations 2 and 3. Although all the species of *Rhizosolenia* encountered occurred at all stations the relative importance of the species varied. At station 1 the main contributors to the biomass were the neritic species, *Rhizosolenia delicatula, Rh. stolterfothii,* and *Rh. fragilissima.* At station 3, and to a lesser degree at station 2, the oceanic forms, *Rh. robusta, Rh. styliformis,* and *Rh. alata* were more important, especially from late-July onward. Other oceanic species occurred mostly toward the latter part of the period as the water temperature rose but at no time did they reach large numbers. At stations 2 and 3 these species included *Ceratium azoricum, C. candelabrum, C. concilians, C. gravidum, Triposolenia* sp., *Hemiaulus hauckii, Planktoniella sol,* and *Oxytoxum elegans. Eucampia cornuta, Amphisolenia* sp., *Ceratium massiliense, C. platycorne, C. schroteri,* and *C. trichoceros* were found exclusively at station 3.

DIATOMS

Diatoms were more important at stations 1 and 2 than at station 3 (figs. V-2, V-3, and V-4). There was a heavy bloom of *Leptocylindrus danicus* at all stations on 17 May. Occurring with this were *Rhizosolenia delicatula, Rh. stolterfothii, Chaetoceros costatus, Ch.* cf. *curvisetus, Ch.* cf. *debilis,* and some small centric

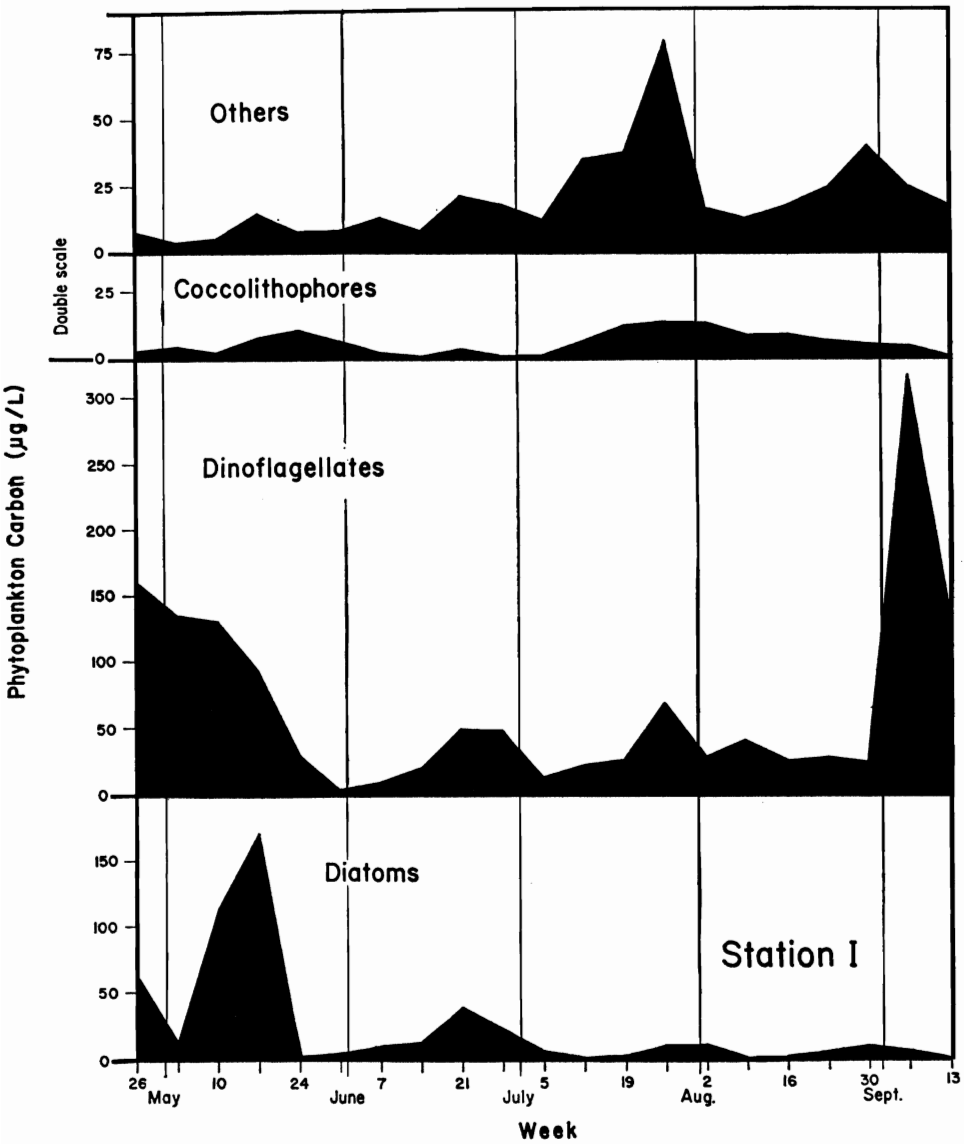

Fig. V-2. Distribution of phytoplankton carbon in four main groups from 26 April to 13 September at station 1. Carbon expressed in µg C/l.

diatoms. At station 3 the quantity of these species, except for *Ch. costatus,* was much reduced. There was an abrupt change in the temperature-nitrate and temperature-silicate curves at stations 1 and 2 on this date (Strickland *et al.,* Part I, above). The chlorophyll *a* concentration was one of the highest encountered during this study: 10 to 20 µg per liter during the week of 17 May at these two stations.

Prior to this period, on 3 May, there had been a large diatom bloom at station 2 attributable to *Chaetoceros* cf. *debilis, Ch.* cf. *curvisetus,* and other *Chaetoceros* species, *Rhizosolenia stolterfothii, Rh. delicatula,* and *Skeletonema costatum,* to-

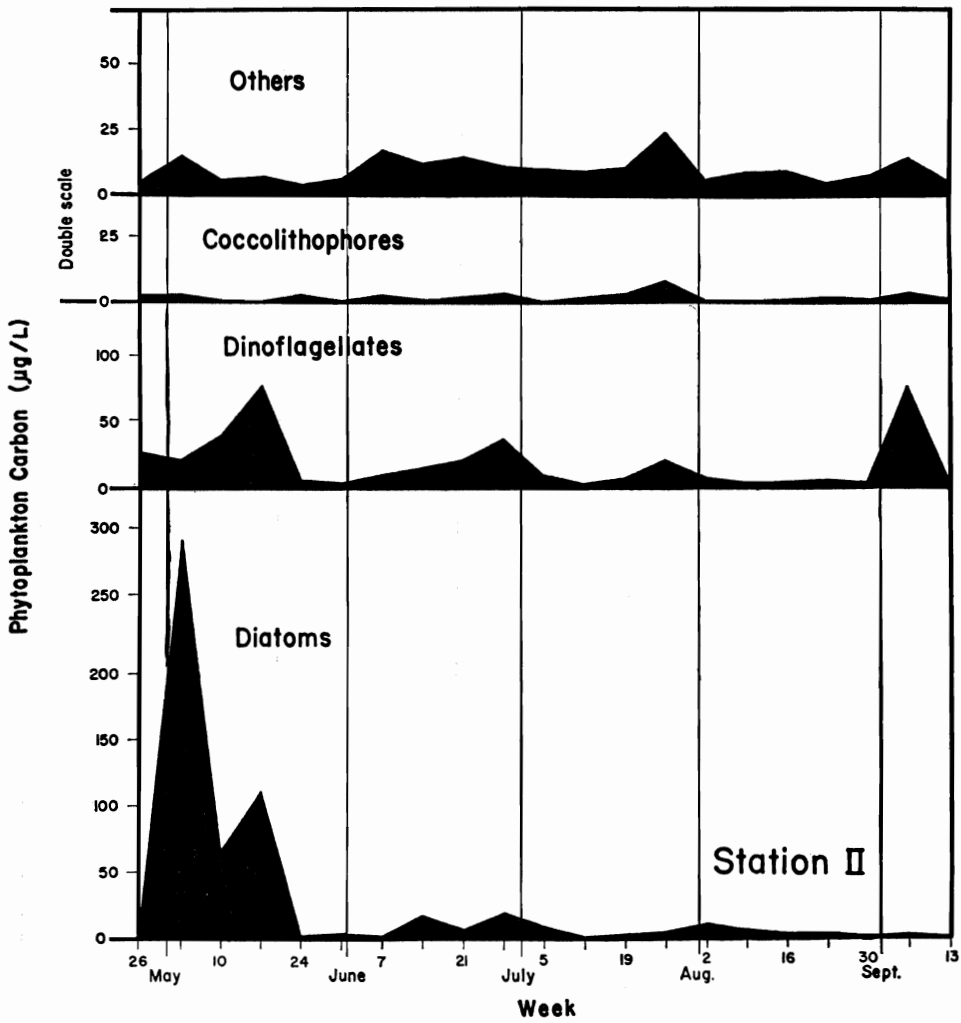

Fig.V-3. Distribution of phytoplankton carbon in four main groups from 26 April to 13 September at station 2. Carbon expressed in μg C/1.

gether with small centric diatoms and *Nitzschia* species. These diatom species are mostly neritic forms and it has been theorized by Eppley (Part IV, above) that their distribution should be essentially dependent on the presence of nitrate in the euphotic zone at depths where the relatively high light intensity required for them to grow rapidly is available.

As reported by Strickland *et al.* (Part I, above) the total amount of nitrate and silicate in the top 100 m of the water column increased to a maximum by mid-May at both stations 2 and 3; after this there was a linear decrease until early September. The samples showed diatoms to be an insignificant part of the plankton at these stations after the end of May. There was a minor peak at station 1 in late June consisting of *Chaetoceros costatus, Ch.* cf. *curvisetus, Ch.* cf. *debilis* associated with *Rhizosolenia fragilissima* and *Skeletonema costatum.* This peak coincided

with a marked drop in water temperature at both NEL Tower and Scripps pier and a period of upwelling. After 2 August, when the temperature of the water rose, several warm-water species occurred, though never in large numbers.

The majority of the diatoms found throughout the study were chain forms such as *Chaetoceros* species, *Skeletonema costatum,* and *Leptocylindrus danicus.* Other centric diatoms and pennates, apart from *Nitzschia* species, appeared to contribute little to the total plant biomass.

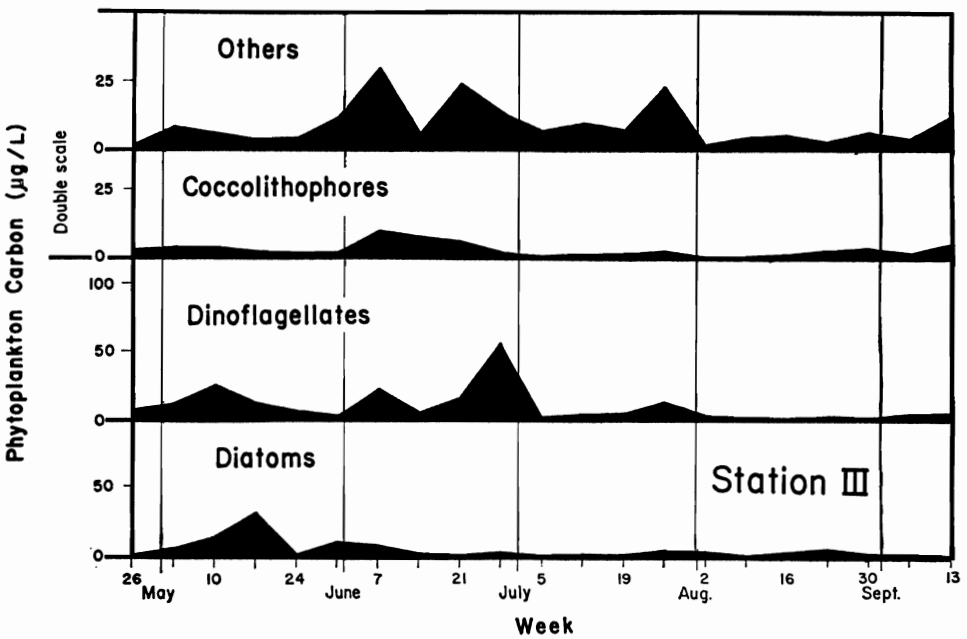

Fig. V-4. Distribution of phytoplankton carbon in four main groups from 26 April to 13 September at station 3. Carbon expressed in µg C/l.

Dinoflagellates

There were three major dinoflagellate peaks during the period of the study: early May, late June, and early September (figs. V-2, V-3, and V-4). These peaks appeared in varying degrees at all stations and were ascribable to increases in both thecate and nonthecate forms. There was an additional peak of nonthecate forms in late July, when ciliates also showed a rise (Beers and Stewart, Part VI, below). The September peak was the largest, especially at station 1, and reflected the minor red-water condition in the area caused mainly by *Gonyaulax polyedra.* This organism had also been a major contributor to the plankton during early May but was insignificant throughout the summer. From laboratory studies it was expected that the distribution of coastal photosynthetic dinoflagellates such as this might be independent of a vertical distribution of nitrate because of an ability to migrate (Eppley, Part IV, above). The occurrence of *G. polyedra* was not related to the depth of the µM nitrate isoline.

In the late June peak *Ceratium* species became important, especially *C. furca, C. fusus,* and *C. dens.* These species were also present during the peak in May,

but were not associated with *G. polyedra* in September. The *Peridinium* species did not show much variation with time, their contribution to the biomass at the three stations decreasing offshore.

Some of the dinoflagellates enumerated are undoubtedly heterotrophic or phagotrophic. From the literature the following species are considered to be in this category: *Peridinium depressum, P. conicum, P. divergens, P. excentricum, P. globulus, P. oceanicum, P. pellucidum, P. steinii, Phalacroma cuneus,* and *Phalacroma ovum* (Schiller, 1933, 1937). It was not possible to determine which of the naked dinoflagellates were autotrophs and this was especially so in the case of the smallest forms, recognized only on the basis of the apparent presence of a girdle.

The time variation of dinoflagellate abundance during the period under study was essentially the same whether the total dinoflagellates or only the thecate dinoflagellates were considered. An exception was the peak on 26 July to which the thecate forms did not contribute.

Coccolithophorids

Except for one peak in early June at station 3 the largest quantity of coccolithophorids occurred at station 1 though the relative importance of this group increased offshore (figs. V-2, V-3, and V-4). *Coccolithus huxleyi* was found throughout and was responsible for a peak on 24 May at station 1 and for the June peak at station 3. The distribution of *C. huxleyi,* according to Eppley (Part IV, above), should be independent of the availability of nitrate in the euphotic zone because of the ability to use very low levels of ammonium ion as a nitrogen source.

By early August, as the water temperature rose, there was an increase in a large-celled species of *Cricosphaera,* and *Coccolithus* cf. *leptoporus* and *Rhabdosphaera* sp. appeared. The only other species identified were *Acanthoica quattrospina* and *Coccolithus carteri.*

"Others"

This group is a catchall for organisms of doubtful taxonomic position, some more positively identified than others. The numbers present were very large so that the biomass represented was of significance despite the predominantly small size of the organisms (mostly $< 20\ \mu$). Of the flagellates included here, *Chilomonas marina* and *Eutreptia* sp. were easily identified as were the silicoflagellate species. For the rest, we have assigned cells that appear to contribute to the biomass to one of three size ranges. The estimate in this group may be conservative as only objects readily recognizable as cells have been counted, and many damaged, lysed, or ill-preserved cells will not have been enumerated. It is also possible, of course, that some of these "cells" may be cysts, badly preserved naked dinoflagellates, rounded off cytoplasm from thecate dinoflagellates, and ciliates or fungal spores. There is a probability that some of the smallest members of this group did not settle in the chamber at all. With these considerations in mind, this artificial group showed a fairly even distribution throughout the period sampled, station 1 having generally higher volumes (figs. V-2, V-3, and V-4). There was a peak at station 3 in early June and a larger one in late August at

station 1, both attributable to "Monad C." The peak at station 1 on 26 July also resulted from "Monad C" and this station is the same one at which, as noted, there was a large increase in the naked dinoflagellate and ciliate populations. Stations 2 and 3 showed this to a lesser degree. No chloroplast structure could be

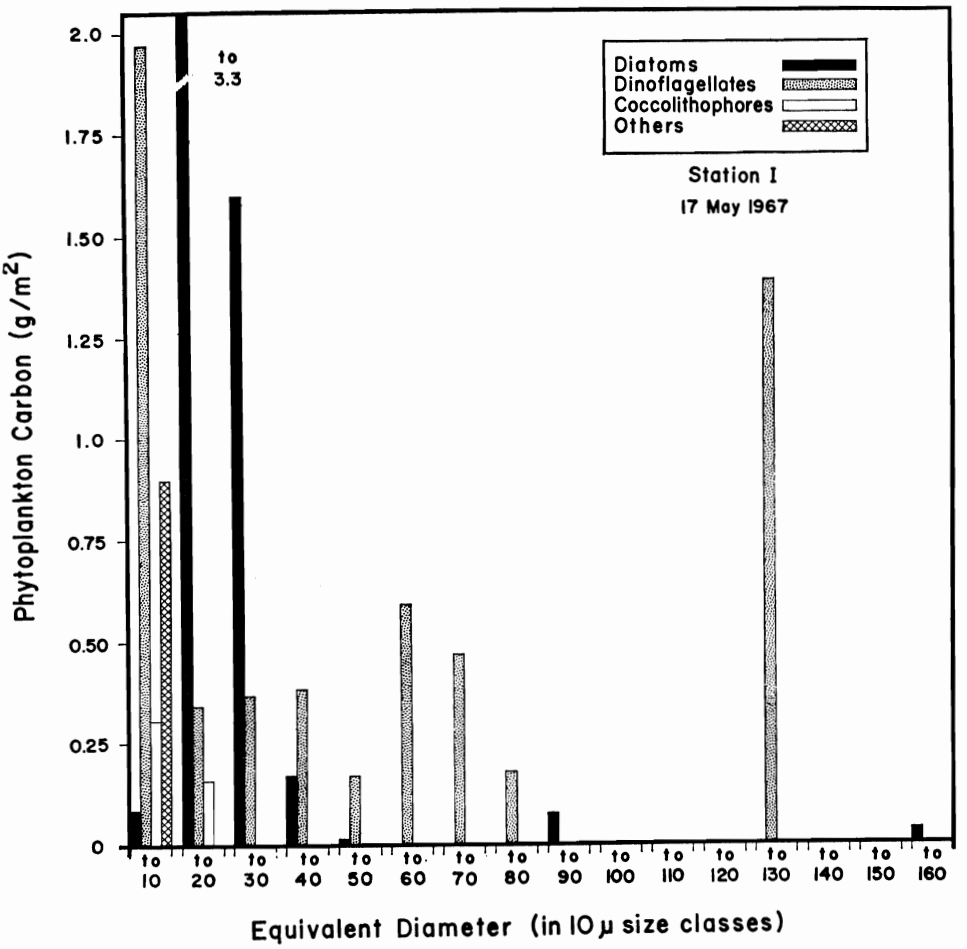

Fig. V-5. Fraction of total carbon held in cells of various sizes in the four main groups. Sizes given as equivalent diameters. Selected dates at station 1. Carbon expressed in grams C/m³.

readily identified in many of the smaller organisms, and it is likely, therefore, that this group must contain many heterotrophic cells that add to the biomass but do not contribute to the chlorophyll measurement (Eppley *et al.*, Part III. above).

Cell Size

Figures V-5, V-6, and V-7 show three samples of graphs indicating the fraction of the total carbon held in cells of various sizes in the four main groups. The sizes are given as the equivalent diameters of spheres of the same volume as the cells. Chain diatoms and a few taxa such as *Rhizosolenia* and *Thalassiothrix* which are

much longer in one dimension should perhaps be considered separately in grazing studies.

There were very few organisms with an equivalent diameter above 70 μ. The most obvious were *Peridinium depressum* and a few centric diatoms including *Rhizosolenia* species, which were mostly well over 100 μ. The majority of the

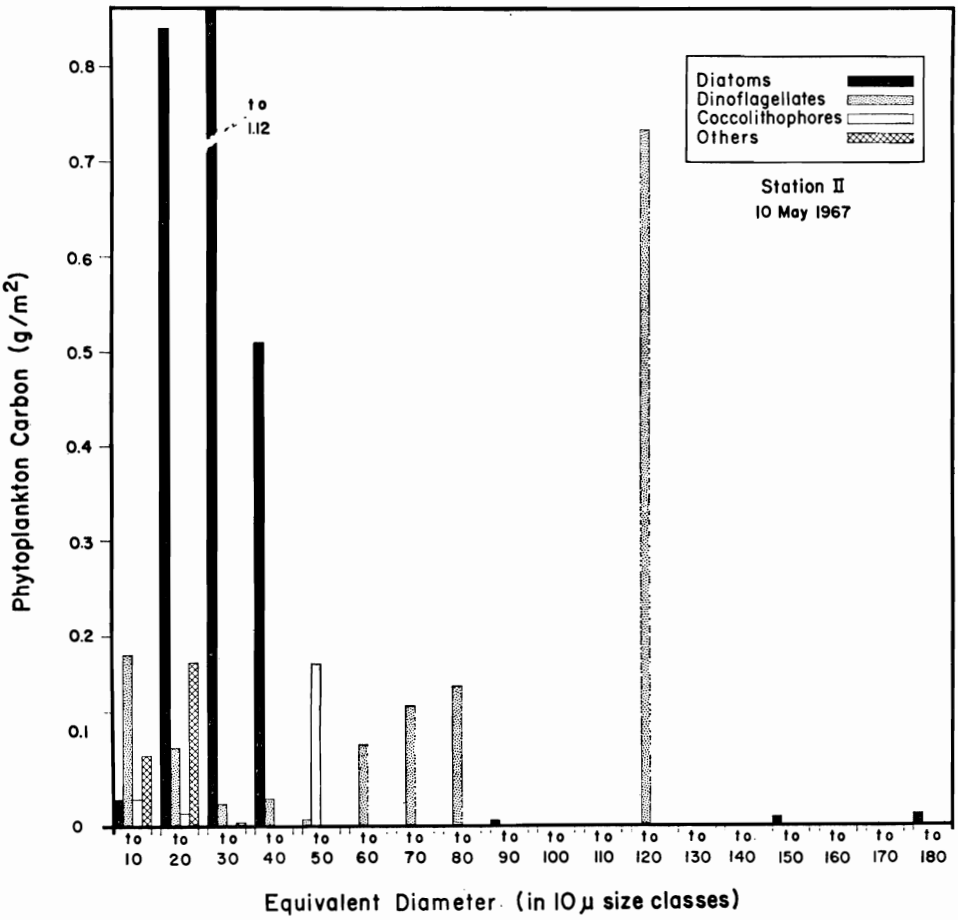

Fig. V-6. Fraction of total carbon held in cells of various sizes in the four main groups. Sizes given as equivalent diameters. Selected dates at station 2. Carbon expressed in grams C/m².

< 20-μ plankton consisted of naked dinoflagellates, "monads," or coccolithophorids, although *Exuviaella cf. ovum, E. vaginula,* and a small *Peridinium* were frequently found.

The major part of the plant biomass therefore fell within the range from about 15 μ to 70 μ, although in some cases where the smallest organisms were present in large numbers they assumed greater importance. The diatoms, when present, seemed to be more important in the ranges below 45 μ while the dinoflagellates were found to be generally larger.

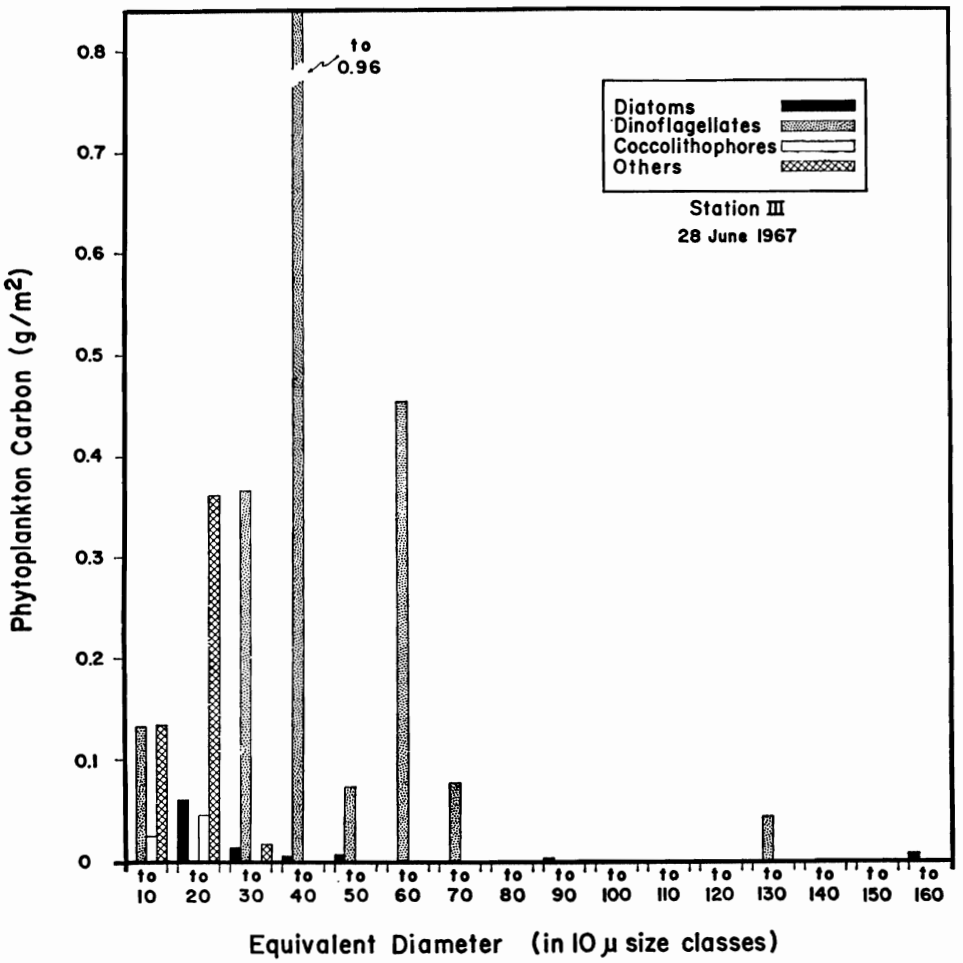

Fig. V-7. Fraction of total carbon held in cells of various sizes in the four main groups. Sizes given as equivalent diameters. Selected dates at station 3. Carbon expressed in grams C/m².

Phytoplanton below the Pigment Layer

The data obtained represent an integrated sample through the pigment layer. Two samples were counted from below this layer on 10 May and 6 September, both at station 2. On the former date the total carbon in the column between 40–81 m was 6 percent of that in the upper layer. Fifty-six percent of this 6 percent was contributed by the "monad" group. At the latter station the total carbon in the column between 59–100 m was 13 percent of the total pigment-layer carbon, 36 percent of which resulted from "monads." It appears from this that the dinoflagellate, diatom, and coccolithophorid groups are minor contributors to the plant biomass at lower levels.

REFERENCES

ALLEN, W. E.

1928. Review of five years of studies on phytoplankton at southern California piers, 1920–1924, inclusive. Bull. Scripps Inst. Oceanogr. Tech. Ser., 1(16):357–401.

1941. Twenty years' statistical studies of marine plankton dinoflagellates of southern California. Amer. Mid. Nat., 26:603–635.

BALECH, E.

1960. The changes in the phytoplankton population off the California coast. Calif. Coop. Oceanic Fish. Invest., 7:127–132.

CUPP, E. E.

1943. Marine plankton diatoms of the west coast of North America. Bull. Scripps Inst. Oceanogr., 5(1):1–238.

HOLMES, R. W., P. M. WILLIAMS, and R. W. EPPLEY

1967. Red water in La Jolla Bay, 1964–1966. Limnol. Oceanogr., 12:503–512.

KOFOID, C. A., and O. SWEZY

1921. The free-living unarmored dinoflagellata. Mem. Univ. Calif., 5:1–562.

KOVALA, T. E., and J. D. LARRANCE

1966. Computation of phytoplankton cell numbers, cell volume, cell surface and plasma volume per liter from microscopical counts. Spec. rep. no. 38. Univ. of Washington, Dept. of Oceanogr. Ref. M66-41.

SARGENT, M. C., and T. J. WALKER

1948. Diatom populations associated with eddies off southern California in 1941. J. Mar. Res., 7(3):490–505.

SCHILLER, J.

1933. In Rabenhorst's *Kryptogamen-Flora.* Peridineae. Bd. X, Abt. III, Teil I. Leipzig. Pp. 1–616.

1937. In Rabenhorst's *Kryptogamen-Flora.* Peridineae. Bd. X, Abt. III, Teil II. Leipzig. Pp. 1–589.

SVERDRUP, H. U., and W. E. ALLEN

1939. Distribution of diatoms in relation to the character of water masses and currents off southern California in 1938. J. Mar. Res., 2:131–144.

UNIVERSITY OF CALIFORNIA, INSTITUTE OF MARINE RESOURCES

1968*a*. Research on the marine food chain; progress report, Jan. 1967–June 1968. Part III. Data record, coastal plankton survey 1967. Section I. Chemistry and productivity. Unpubl. MS (SIO Ref. 68-20; IMR Ref. 68-8).

1968*b*. Research on the marine food chain; progress report, Jan. 1967–June 1968. Part IV. Data record, coastal plankton survey, 1967. Section II. The plankton. Unpubl. MS (SIO Ref. 68-38; IMR Ref. 69-3).

THE ECOLOGY OF THE PLANKTON OFF LA JOLLA, CALIFORNIA, IN THE PERIOD APRIL THROUGH SEPTEMBER, 1967

EDITED BY

J. D. H. STRICKLAND

PART VI

NUMERICAL ABUNDANCE AND ESTIMATED BIOMASS OF MICROZOOPLANKTON

BY

J. R. BEERS AND G. L. STEWART

ABSTRACT

The numerical abundance and estimated biomass of the microzooplankton populations in the "pigment layer" of three nearshore sites off La Jolla and from the bottom of this layer to 100 m (only stations 2 and 3) were determined at weekly intervals over a 5-month period. The average biomass, as organic carbon, of the total microzooplankton over the pigment layer was 5.9, 3.0, and 2.4 mg C/m^3 or 148, 131, and 112 mg C/m^2 at stations 1, 2, and 3, respectively. In the pigment layer protozoan forms accounted for 96–97 percent of the total microzooplankton numbers/m^3 at each site but only 32 percent, 23 percent, and 24 percent of the microzooplankton biomass. Ciliates dominated the protozoan fraction of the microzooplankton populations. Naupliar and postnaupliar copepod Crustacea were the most important metazoans.

The standing stock of microzooplankton carbon was small relative to that of other seston components. At stations 2 and 3 where the larger zooplankton were also sampled, the microzooplankton organic carbon over the upper 100 m was estimated to be approximately 17–21 percent of that of the total zooplankton populations. Approximate estimates were made of the percentage of the daily phytoplankton production that might be consumed by the total microzooplankton and by the ciliates.

INTRODUCTION

SINCE THE pioneering works of Lohmann (e.g., 1908) few opportunities have been taken to examine quantitatively *changes* in the populations of the smaller zooplankton in marine waters coupled with those of all other plankton trophic levels. Studies such as those of Gran (1933), Braarud (1934), and Bigelow, Lillick, and Sears (1940) in the Gulf of Maine, however, related the abundance of the protozoan elements of the zooplankton populations to the phytoplankton assemblages.

The abundance of microzooplankton[1] and its role in marine food webs has interested us in several studies made since the development of a large-volume pumping system for its collection (Beers, Stewart, and Strickland, 1967). The purposes of these earlier studies, however, have been mainly to examine the microzooplankton, in terms of numbers and biomass, at *specific instances of time* in relation to various types of marine environments (Beers and Stewart, 1967), their vertical distribution (Beers and Stewart, 1969*a*), and relationship to other seston components (Beers and Stewart, 1969*b*). As a part of the comprehensive

[1] Microzooplankton, as we use the term here, includes all animal plankters, other than phagotrophic flagellates which will pass a 202-μ mesh filtering cloth.

5-month study of nearshore plankton ecology by the Food Chain Research Group of the Institute of Marine Resources (University of California, Institute of Marine Resources, 1968*a*, *b*) the fluctations in microzooplankton populations have been monitored at weekly intervals at locations approximately 1.4, 4.6, and 12.1 km off La Jolla. Strickland, Solórzano, and Eppley (Part I, above) described the complete program, station positions, and discussed the broad objectives of the study.

Acknowledgments

The comprehensive study of nearshore plankton ecology was supported mainly through the United States Atomic Energy Commission, Contract AT(11-1)GEN 10, P.A. 20. The microzooplankton work received support also from the National Science Foundation, Grant GB-6357.

We thank Freda M. H. Reid and James B. Jordan for their enumeration of the ciliate protozoans in some of the unconcentrated samples.

MATERIALS AND METHODS

Sampling

Microzooplankton was collected with a submersible pump/profiling hose system (University of California, Institute of Marine Resources, 1968*a*) and a deck-mounted plankton-concentrating unit (fig. VI-1). Integrated samples were obtained through the pigment layer (see Strickland *et al.*, Part I, above) at each station and from the bottom of the pigment layer to 100 m at stations 2 and 3. Large volumes of water were filtered providing material for determining the average density of microplankton over the depth intervals described but not giving information of spatial relationships within the intervals sampled. Generally, 10 liters or more of metered water were filtered from each meter of the water column during the descent of the pump at a uniform rate. The microzooplankton were collected on 35-μ mesh netting after passing a 202-μ mesh filter cloth that excluded the larger organisms. To clear the 35-μ mesh net, the "plastic hats" (figure VI-1) were removed and the nets washed down from the inside with filtered seawater under pressure. Samples were preserved with approximately 5 percent formalin having the pH adjusted to 8.0–8.2 with sodium borate.

A comparison of microzooplankton numbers in the pigment layer obtained by this means with that from unconcentrated samples integrated over the same depth interval for phytoplankton analyses (Reid, Fuglister, and Jordan, Part V, above) indicated that the 35-μ mesh net was not allowing passage of significant numbers of any of the various microzooplankton groups except the ciliates. Most nonloricate ciliates ("Ciliata other than Tintinnida" in our results) are of a size that readily pass a 35-μ mesh net. For the tintinnid ciliates, on the basis of the numbers counted, the lower limit of expectation from the unconcentrated sample was greater than the upper limit of expectation on the net sample in more than one-third of the instances. Although the numbers of ciliates enumerated in the unconcentrated samples were often small and, therefore, have relatively wide limits of confidence, these have been used here since they undoubtedly give a truer picture of the total microzooplankton as defined above.

Although unconcentrated integrated samples from the bottom of the pigment

layer to 100 m were taken, only a few have been examined to date. Five of these, selected at various times when there was a relatively high ciliate level in the pigment layer, were counted for ciliated organisms and the numbers found indicated that large amounts should be added to the protozoan biomass of this depth interval (average, +178 percent; range, 82–288 percent) as estimated from the 35-μ net

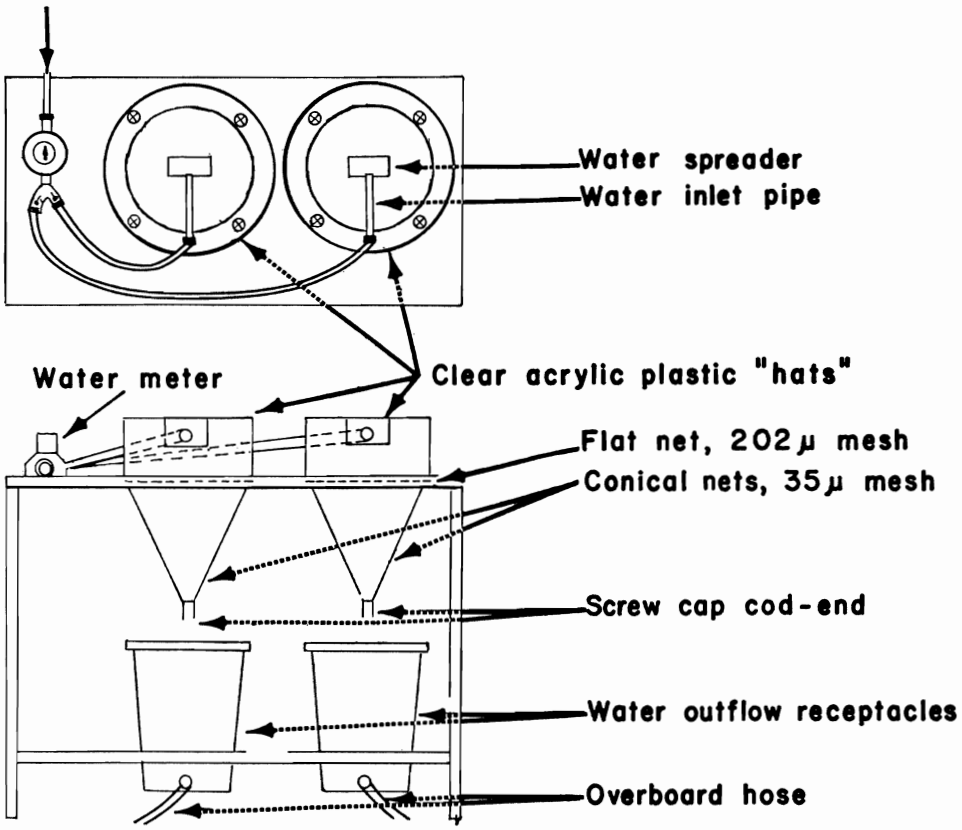

Fig. VI-1. The deck-mounted microplankton collector.

samples. The total microzooplankton (i.e., Protozoa + Metazoa) organic carbon would be increased by an average of only 15 percent, however (range, 9–21 percent), 9 percent of which was due to "Ciliata other than Tintinnida" and 6 percent to the tintinnids.

Counting

Enumeration of the microzooplankton in the 35-μ mesh net samples was by an inverted microscope procedure at 100× magnification based on Utermöhl (1931). At least a hundred organisms were counted from each sample. In general, a single

aliquot of 1–10 ml removed with a widemouthed pipette from the randomly mixed sample was used. The ciliates were also counted by the sedimentation method but at a magnification of 200×.

Complete data on the volumes of seawater filtered, the numbers of organisms counted in the subsamples, and confidence limits for all counts are included in University of California, Institute of Marine Resources (1968*b*).

Animal Volume and Organic Carbon Estimation

Volume estimates of the microzooplankton "soft body" material, that is, the protoplasm, were made from size measurements of twenty representatives of each taxonomic group collected in the five concentrated net samples on dates selected from the early, middle, and late parts of the survey (see University of California, Institute of Marine Resources, 1968*b*). Variations in the calculated average volumes of the organisms at the three stations on any given day of sampling and between the different dates were usually of the same general order as variations found within the groups of animals from any given date and station. Hence, an average determined for all these dates has been used to estimate microzooplankton volumes throughout the 5-month period. Ciliate volumes were calculated for each week and station using the measurements of the total numbers of these organisms counted in the unconcentrated water samples.

An approximate biomass, in terms of organic carbon content, was calculated for the various microzooplankton groups from the volume estimates assuming a specific gravity of one, a water content of 80 percent of the "wet weight," and organic carbon as 40 percent of the "dry weight" (i.e., carbon = 0.08 volume).

RESULTS

Total Microzooplankton

The weekly numerical abundance and estimated biomass of the various groups of microzooplankters from all samples are included in University of California, Institute of Marine Resources (1968*b*). These data are summarized in tables VI-1–VI-3 for the pigment-layer depths at stations 1, 2, and 3, respectively, and in table VI-4 for the portion of the water column sampled below the pigment layer at stations 2 and 3.

During the 21 weeks we observed the three sites several major changes were detected in the water mass under examination. The study could therefore be divided into sections: (period A) beginning of survey through 17 May; (period B) 24 May–28 June; (period C) 5 July–19 July + 26 July; and (period D) 2 August through 30 August. The last weeks of the study were marked by a small bloom of the dinoflagellate, *Gonyaulax polyedra,* at the nearshore site. Evidence that the marked changes were principally the result of upwelling is given by Strickland *et al.* (Part I, above). The periods so delineated are approximately a month in length. Each period can be characterized in terms of its microzooplankton abundance although the most striking differences were found between the initial period and the remainder of the study. At station 1 microzooplankton over the pigment layer was high during the initial period averaging 343 mg organic carbon/m^2 compared with 91 mg/m^2 through the rest of the program. At

station 2 the microzooplankton abundance was 50 percent greater during this initial period than it was over the remainder of the study, while at station 3 the reverse was found, the average, exclusive of the first period, being about 50 percent greater than that for the first period.

Generally decreasing numbers of microzooplankton were found from station 1 in the most shallow water sampled to the site furthest offshore. Over the 21 weekly observations the average numbers of total microzooplankton in the pigment layer were 2,700, 1,100, and $850 \times 10^3/m^3$ at stations 1, 2, and 3, respectively. Median values for the three stations were 1,600, 600, and $490 \times 10^3/m^3$, respectively. Both sets of data suggest an average threefold difference in the standing stock between the inshore site less than one mile off the coast with a total water column of approximately 25 m and station 3 five miles offshore in water of 350 m. Of the average numbers of microzooplankton organisms, protozoans accounted for all but 3–4 percent at each of the sites. Totaled over the pigment layer, that is, the number/m^2, the average numbers at the three sites were more similar, differing by a factor of slightly less than two between stations 1 and 3 ($67.5 \times 10^6/m^2$, sta. 1; $47.3 \times 10^6/m^2$, sta. 2; and $35.7 \times 10^6/m^2$, sta. 3).

The estimated organic carbon of the average total microzooplankton population in the pigment layer was 5.9, 3.0, and 2.4 mg C/m^3 at stations 1, 2, and 3, respectively. Median levels at these same sites were 4.8, 2.6, and 2.1 mg C/m^3. Protozoan forms accounted for 32 percent of the average at station 1 and 23–24 percent at stations 2 and 3. Microzooplankton organic carbon over the pigment layer averaged throughout the study was 148 mg C/m^2 at station 1; 131 mg C/m^2 at station 2, and 112 mg C/m^2 at station 3.

Taxonomic differentiation of the microzooplankton has been limited to the major groups of protozoans and metazoans found in the samples. More specific identification of many of these groups is not possible owing to the presence of young individuals that are indistinguishable as to genus and/or species until later stages of development. In terms of their trophodynamic interrelationships it is probably justifiable to consider the forms within each major group, except the "Other Metazoa," as being similar feeding types and having similar predators. The weekly numerical abundance of the various taxonomic groups is shown in figures VI-2–VI-5. Estimated organic carbon content of the total protozoan and metazoan groups in the microzooplankton populations at the different stations through the study is given in figure VI-6.

Ciliata Other than Tintinnida

Included in this category are the Oligotricha such as *Strombidium* spp. and *Lohmanniella* spp. Many of the nonloricate ciliates are small forms (diameter, 10–20 μ; average volume, 1800 μ^3) often spheroidal in the formalin-preserved samples and are difficult to identify to genus or species. Relatively large forms such as the holotrich, *Tiarina* cf. *fusus* with a calculated volume of 15,000 μ^3, were found occasionally.

At stations 1 and 2 these ciliates were in greatest abundance during the early part of the study when upwelling provided nutrients and the phytoplankton crops were the highest that we observed. Average numbers during the initial period

TABLE VI-1

RANGE, AVERAGE, AND MEDIAN NUMERICAL ABUNDANCE (No/m³) AND ORGANIC CARBON (mg/m³) CONTENT OF THE MICROZOOPLANKTON IN THE PIGMENT LAYER OF STATION 1 AT WEEKLY INTERVALS
(26 April–13 September, 1967)

	Numerical abundance				Organic carbon content			
	Range (No/m³)	Average (No/m³)	Median (No/m³)	Average as a percentage of tota lmicro-zooplankton	Range (mg/m³)	Average (mg/m³)	Median (mg/m³)	Average as a percentage of total micro-zooplankton
Protozoa								
Foraminifera	0– 17,000	5,000	3,400	0.2	0 – 0.08	0.02	0.02	0.4
Radiolaria	660– 94,000	18,000	8,000	0.7	<0.01– 0.29	0.06	0.03	0.9
Tintinnida	0–5,000,000	1,200,000	480,000	43.0	0 – 5.26	1.35	0.58	23.0
Ciliata other than Tintinnida	84,000–5,600,000	1,400,000	810,000	52.0	0.04– 1.69	0.47	0.32	8.0
Total Protozoa	390,000–9,300,000	2,600,000	1,600,000	96.0	0.29– 6.49	1.90	1.04	32.0
Metazoa								
Copepoda, naupliar	22,000– 180,000	63,000	51,000	2.3	0.88– 7.46	2.60	2.08	44.0
Copepoda, postnaupliar	0– 43,000	7,200	3,900	0.3	0 – 6.31	1.06	0.57	18.0
Other Metazoa	0– 24,000	7,500	6,400	0.3	0 – 1.17	0.38	0.29	6.3
Total Metazoa	28,000– 240,000	78,000	67,000	3.0	1.34–14.40	4.02	3.25	68.0
Total microzooplankton	430,000–9,600,000	2,700,000	1,600,000		1.93–20.89	5.92	4.81	

TABLE VI-2

RANGE, AVERAGE, AND MEDIAN NUMERICAL ABUNDANCE (No/m³) AND ORGANIC CARBON (mg/m³) CONTENT OF THE MICROZOOPLANKTON IN THE PIGMENT LAYER OF STATION 2 AT WEEKLY INTERVALS

(26 April–13 September, 1967)

	Numerical abundance				Organic carbon content			
	Range (No/m³)	Average (No/m³)	Median (No/m³)	Average as a percentage of total microzooplankton	Range (mg/m³)	Average (mg/m³)	Median (mg/m³)	Average as a percentage of total microzooplankton
Protozoa								
Foraminifera	680– 31,000	9,600	6,800	0.9	<0.01–0.14	0.05	0.03	1.5
Radiolaria	1,100– 33,000	11,000	7,500	0.9	<0.01–0.10	0.03	0.02	1.1
Tintinnida	0–3,100,000	390,000	71,000	35.0	0 –2.88	0.35	0.06	12.0
Ciliata other than Tintinnida	32,000–3,100,000	650,000	390,000	59.0	0.01–1.39	0.30	0.16	10.0
Total Protozoa	69,000–4,800,000	1,100,000	560,000	96.0	0.05–3.18	0.72	0.50	24.0
Metazoa								
Copepoda, naupliar	13,000– 81,000	33,000	30,000	3.0	0.53–3.32	1.36	1.20	45.0
Copepoda, postnaupliar	0– 12,000	4,900	4,800	0.4	0 –1.74	0.72	0.71	24.0
Other Metazoa	0– 22,000	2,500	1,200	0.2	0 –0.98	0.13	0.07	6.1
Total Metazoa	16,000– 109,000	41,000	35,000	4.0	0.97–5.07	2.26	2.04	76.0
Total microzooplankton	98,000–4,800,000	1,100,000	600,000		1.28–6.97	2.98	2.55	

TABLE VI-3

RANGE, AVERAGE, AND MEDIAN NUMERICAL ABUNDANCE (No/m^3) AND ORGANIC CARBON (mg/m^3) CONTENT OF THE MICROZOOPLANKTON IN THE PIGMENT LAYER OF STATION 3 AT WEEKLY INTERVALS
(26 April–13 September, 1967)

	Numerical abundance				Organic carbon content			
	Range (No/m^3)	Average (No/m^3)	Median (No/m^3)	Average as a percentage of total microzooplankton	Range (mg/m^3)	Average (mg/m^3)	Median (mg/m^3)	Average as a percentage of total microzooplankton
Protozoa								
Foraminifera	1,200– 26,000	9,800	7,200	1.1	0.01–0.12	0.05	0.03	1.9
Radiolaria	1,300– 18,000	6,900	6,600	0.8	<0.01–0.04	0.02	0.02	0.9
Tintinnida	0–2,300,000	260,000	74,000	30.0	0 –1.85	0.27	0.14	12.0
Ciliata other than Tintinnida	0–3,000,000	550,000	330,000	63.0	0 –1.12	0.22	0.15	9.0
Total Protozoa	11,000–3,100,000	820,000	470,000	96.0	0.04–1.99	0.55	0.38	23.0
Metazoa								
Copepoda, naupliar	9,800– 52,000	26,000	22,000	3.1	0.40–2.12	1.07	0.89	45.0
Copepoda, postnaupliar	980– 16,000	4,800	3,800	0.6	0.14–2.29	0.71	0.56	30.0
Other Metazoa	0– 2,600	400	220	0.1	0 –0.21	0.04	0.02	1.7
Total Metazoa	11,000– 70,000	32,000	28,000	4.0	0.55–4.61	1.82	1.53	77.0
Total microzooplankton	32,000–3,150,000	850,000	490,000		0.83–4.83	2.37	2.13	

were 3.7 and $1.9 \times 10^6/m^3$ at these two sites, respectively. The same magnitude of difference was seen throughout the study. Station 3 average and median levels were slightly, but perhaps not significantly, lower than station 2 over the entire study, but they were only half as much during the first period. The high phytoplankton levels of stations 1 and 2 did not extend to station 3.

TABLE VI-4

RANGE, AVERAGE, AND MEDIAN NUMERICAL ABUNDANCE (No/m^3) AND ORGANIC CARBON (mg/m^3) CONTENT OF SOME MICROZOOPLANKTON GROUPS FROM THE BOTTOM OF THE PIGMENT LAYER TO 100 m AT STATIONS 2 AND 3
(26 April–13 September, 1967)

	Numerical abundance			Organic carbon content		
	Range (No/m^3)	Average (No/m^3)	Median (No/m^3)	Range (mg/m^3)	Average (mg/m^3)	Median (mg/m^3)
Station 2						
Protozoa						
Foraminifera	1,500–14,000	4,800	4,400	0.01–0.07	0.02	0.02
Radiolaria	1,300–27,000	11,000	7,800	<0.01–0.08	0.03	0.02
Tintinnida (35-μ net)	2,900–68,000	16,000	13,000	<0.01–0.09	0.02	0.02
Metazoa						
Copepoda, naupliar	1,000–15,000	7,700	6,800	0.04–0.62	0.31	0.28
Copepoda, postnaupliar	330– 5,600	2,400	2,200	0.05–0.82	0.34	0.32
Other Metazoa	0– 930	280	170	0 –0.06	0.02	0.01
Station 3						
Protozoa						
Foraminifera	1,200– 7,200	3,100	2,600	0.01–0.03	0.01	0.01
Radiolaria	3,800–23,000	10,000	8,900	0.01–0.07	0.03	0.03
Tintinnida (35-μ net)	2,100–16,000	6,400	5,300	<0.01–0.02	0.01	0.01
Metazoa						
Copepoda, naupliar	1,900–11,000	6,100	5,600	0.08–0.45	0.25	0.23
Copepoda, postnaupliar	180– 2,800	1,300	1,200	0.03–0.41	0.20	0.18
Other Metazoa	0– 300	53	0	0 –0.03	0.01	0

Within the pigment layer, the highest contributions of the "Ciliata other than Tintinnida" to the total microzooplankton standing stock biomass were from 26–30 percent at each of the three sites. On the average, their estimated biomass was 8–10 percent of that of the total microzooplankton.

In the small number of samples (five) analyzed from below the pigment layer, the numbers and organic carbon per unit volume of the "Ciliata other than Tintinnida" was quite variable relative to that of the pigment layer. Ratios of numbers varied between 0.5:1 (pigment layer : below pigment layer) and 16.8:1, averaging 5.7:1. Organic carbon varied from 1.1:1 to 35.0:1. On three of the dates these ratios indicated a significantly larger size for the ciliates in the upper waters compared with those below the pigment layer whereas the other two dates showed the reverse situation.

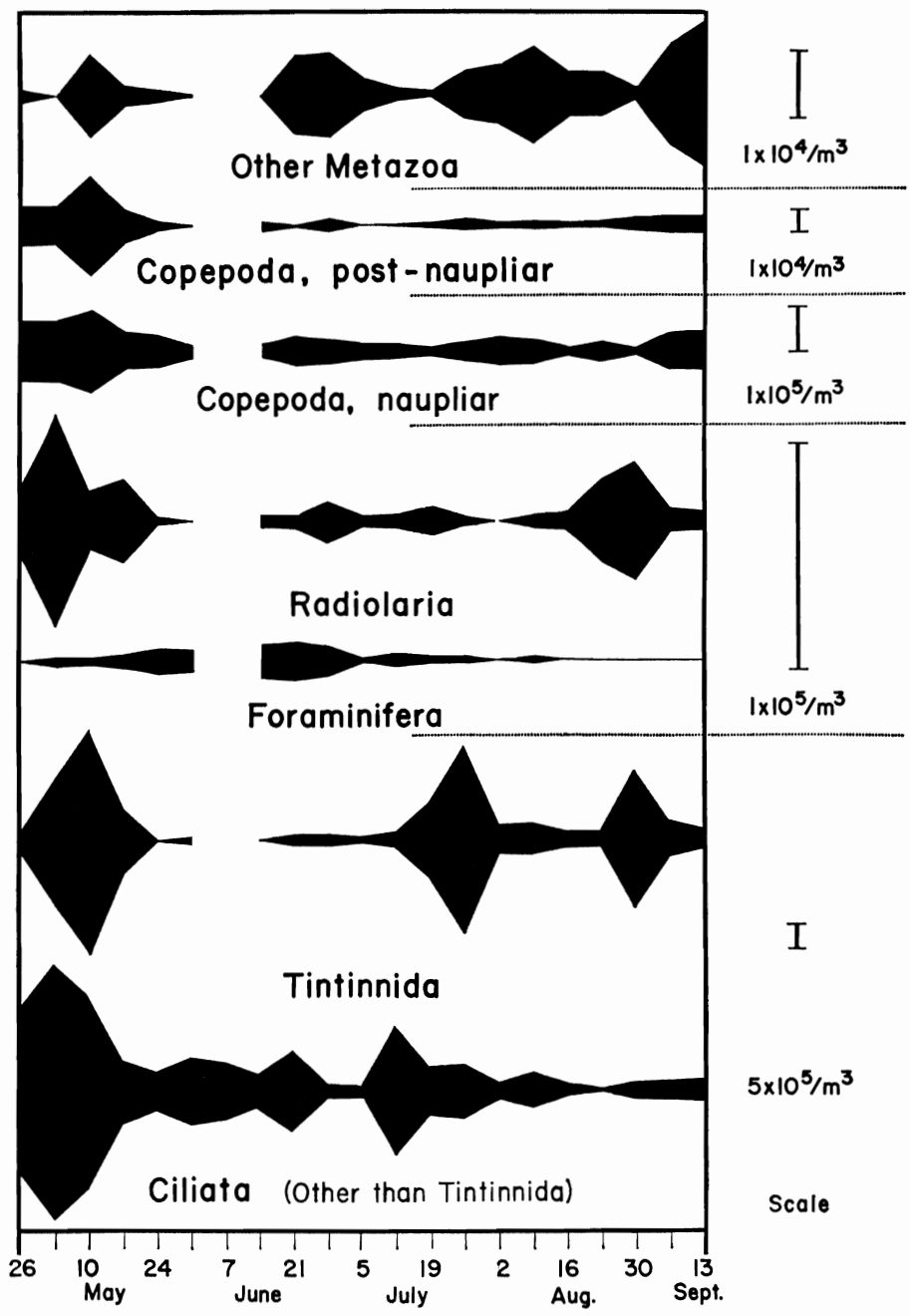

Fig. VI-2. The weekly abundance (numbers/m³) of the various taxonomic groups of the microzooplankton populations in the pigment layer at station 1. (Data on Tintinnida and Ciliata other than Tintinnida from sample for phytoplankton enumeration; all other from 35-μ cloth samples.)

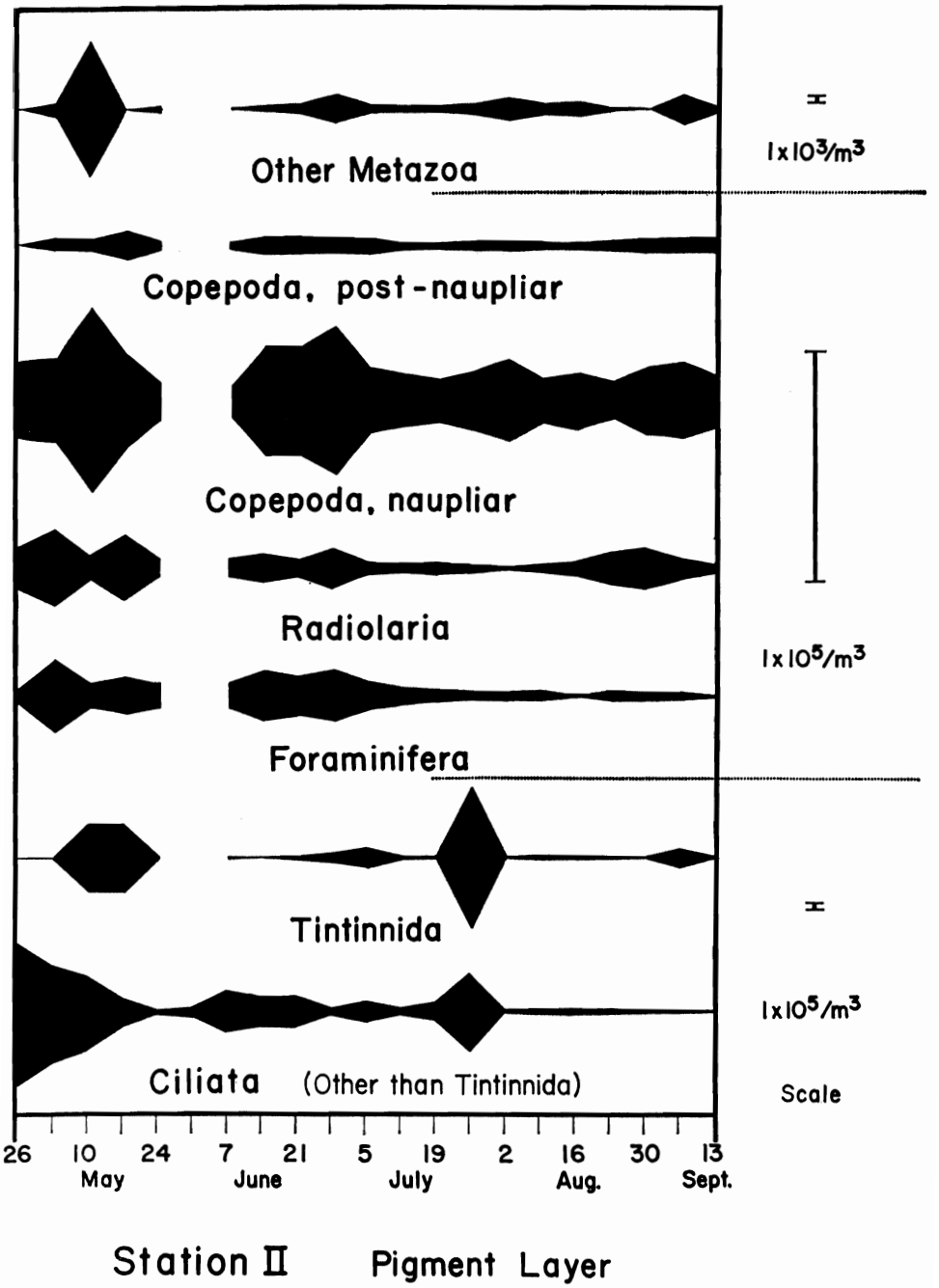

Fig. VI-3. The weekly abundance (numbers/m³) of the various taxonomic groups of the microzooplankton populations in the pigment layer at station 2. (Data on Tintinnida and Ciliata other than Tintinnida from sample for phytoplankton enumeration; all other from 35-μ cloth samples.)

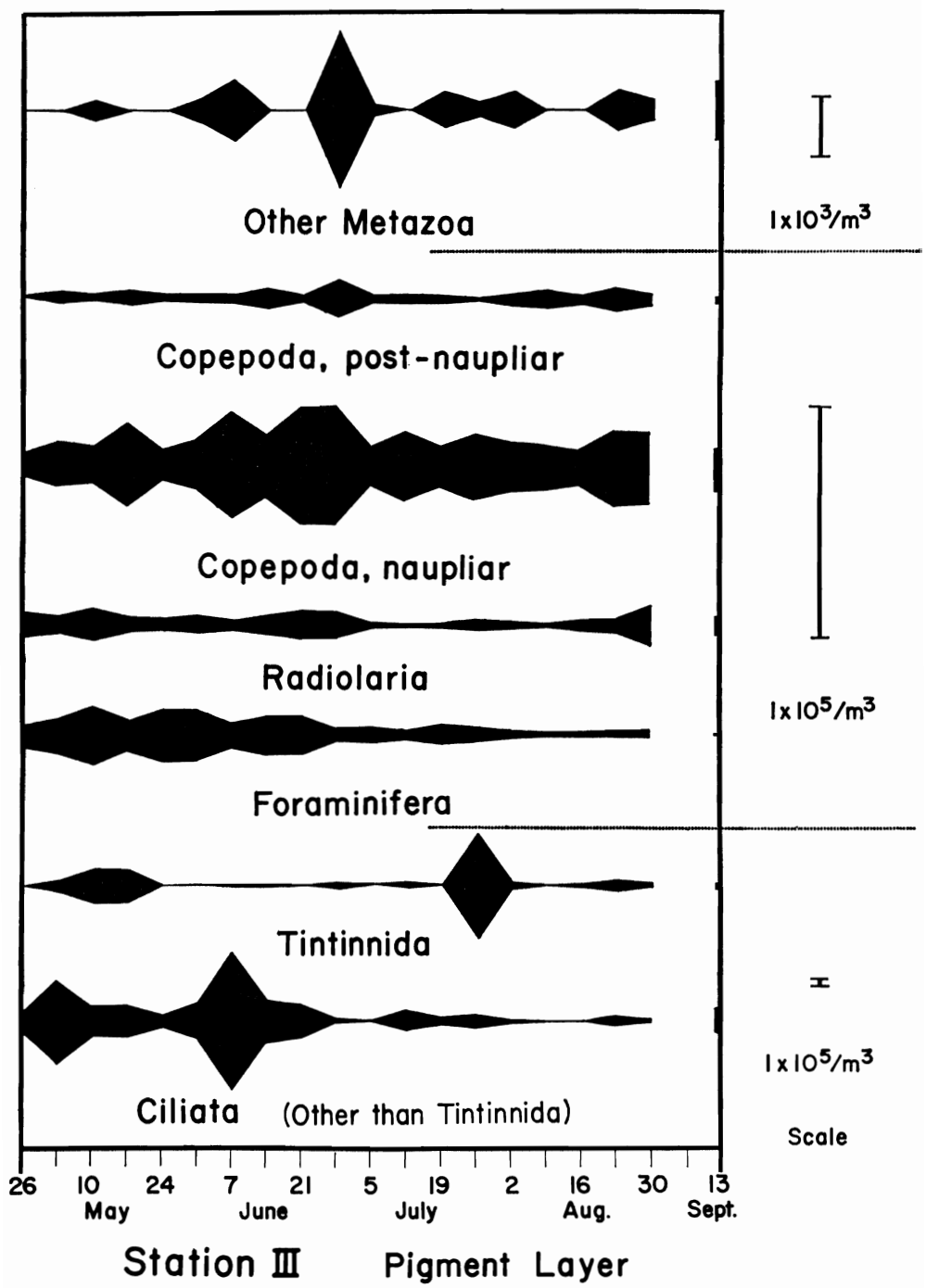

Fig. VI-4. The weekly abundance (numbers/m³) of the various taxonomic groups of the microzooplankton populations in the pigment layer at station 3. (Data on Tintinnida and Ciliata other than Tintinnida from sample for phytoplankton enumeration; all other from 35-μ cloth samples.)

Tintinnida

At least twenty-five species of tintinnid ciliates were identified at various times from each of the stations. Forms that were often dominant in the tintinnid populations included *Helicostomella* cf. *subulata* with a lorica volume of approximately 18,500 μ^3, *Tintinnopsis* spp., *Eutintinnus* spp. (e.g., *E. pectinis*, lorica volume

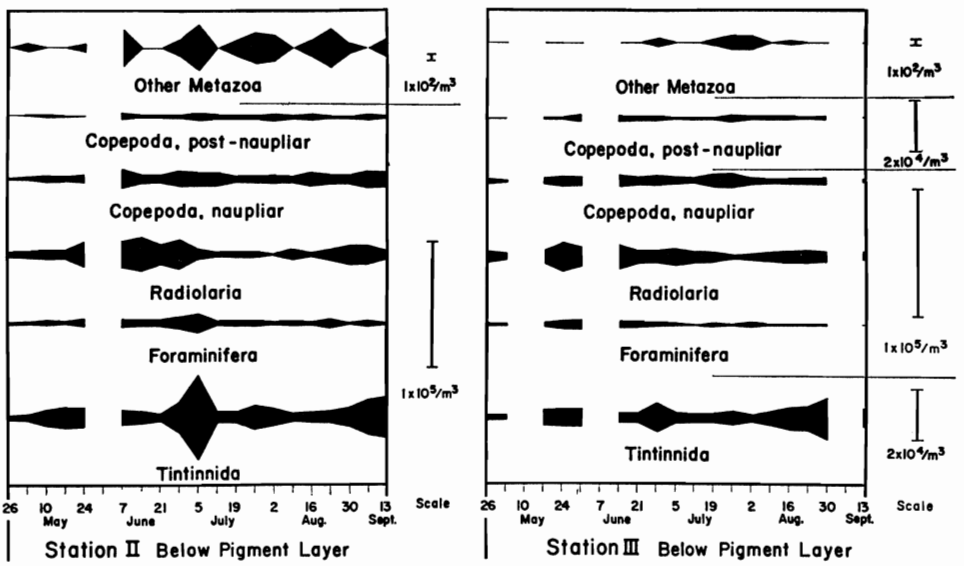

Fig. VI-5. The weekly abundance (numbers/m³) of the varios taxonomic groups of the microzooplankton populations from the bottom of the pigment layer to 100 m at stations 2 and 3. (All data from 35-μ cloth samples.)

26,000 μ^3) and *Amphorellopsis* cf. *acuta* (lorica volume, 57,000 μ^3). As with the other ciliate forms, the tintinnids were present in large numbers during the periods of high phytoplankton abundance early in the study at stations 1 and 2. They reached their maximum numbers, however, on 26 July. At both stations 2 and 3 numbers on this date were an increase of greater than an order of magnitude over the preceding week's population. Phytoplankton standing crops and production rates showed twofold or threefold increases over the same period. Tintinnida accounted for 90 percent of the protozoan carbon and more than half the total microzooplankton organic carbon through the pigment layer at each station on this date. By the following week their numbers showed a sharp drop.

Numbers of tintinnids/m³ below the pigment layer on the dates selected for comparisons of the concentrated "net" and unconcentrated "phytoplankton" samples ranged from less than 2 percent to approximately 33 percent of those in the upper-depth interval.

Foraminifera

The numbers of foraminifera as well as the other sarcodinian group in the samples, the radiolarians, were generally low relative to the ciliated Protozoa and did not contribute significantly to microzooplankton biomass. Their weekly variations were not as extreme as those of the ciliates but the different sampling and count-

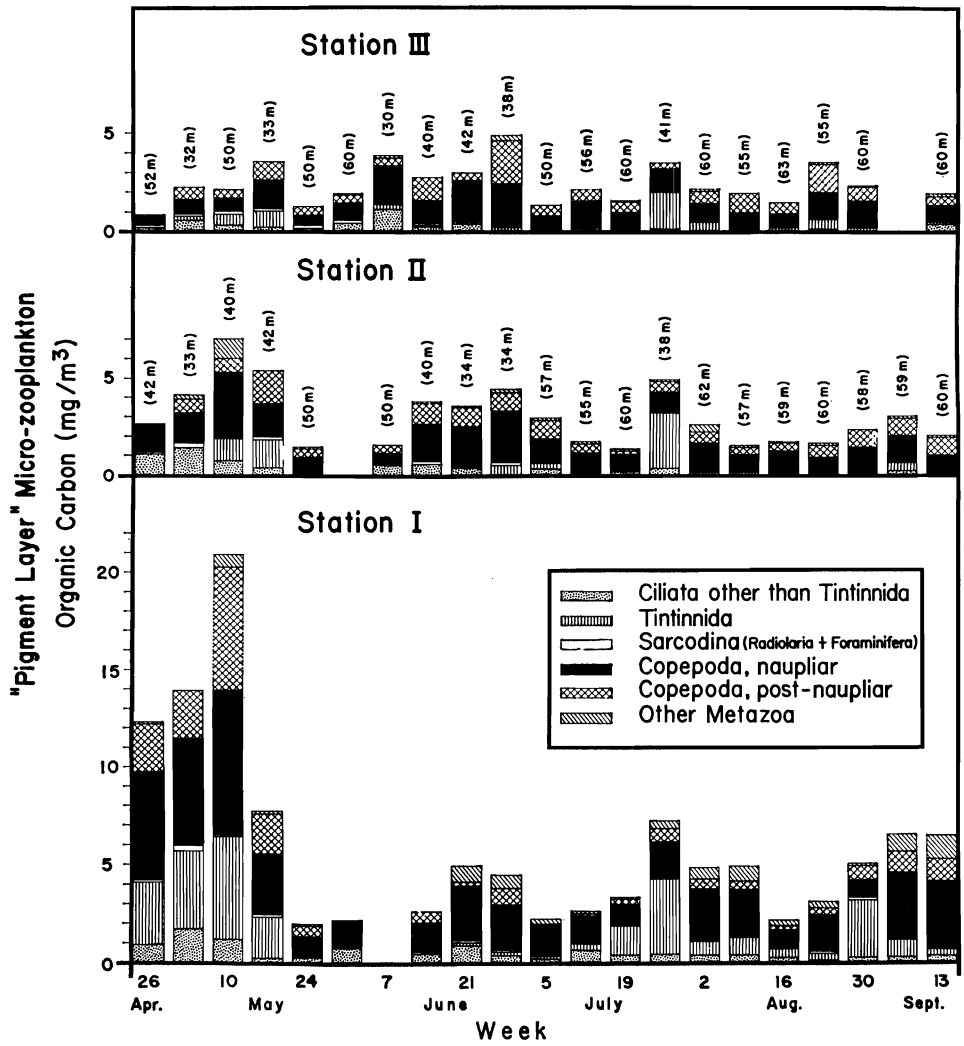

Fig. VI-6. The estimated organic carbon content (mg C/m³) of the microzooplankton in the pigment layers at stations 1, 2, and 3 at weekly intervals, 26 April–13 September, 1967. The depth of the pigment layer at stations 2 and 3 for each time of sampling is shown at the top of each bar. At station 1 the pigment layer was 25 m throughout the study.

ing methods employed for the two groups of protozoans would have an effect on this result. With few exceptions the foraminifera were planktonic species. At station 1 occasional benthic forms stirred up by the turbulence at this nearshore site were seen. Relative to station 1, the average foraminiferal population was approximately double at stations 2 and 3.

Average foraminiferal abundance below the pigment layer was approximately half that within the pigment layer at station 2 and only one-third that at station 3.

Radiolaria

Many of the radiolarians sampled were of very simple skeletal types often having a primitive triradiate skeleton with a body of small volume. These forms may be juvenile ones. Few acantharians were found in these fixed and preserved samples.[2]

The radiolarians were more abundant than the foraminifera at station 1, very similar at station 2, and somewhat less numerous offshore at station 3. In the depth interval sampled below the pigment layer the average number of radiolarians per unit volume was approximately the same as within the upper waters at station 2 and was 50 percent more at station 3.

Copepoda, Naupliar

Naupliar copepods, on the average, accounted for 59–65 percent of the total metazoan organic carbon at all stations, ranging up to more than 99 percent but never dropping below 45–46 percent. The average volume of an individual nauplius was estimated to be approximately 510,000 μ^3. Nauplii were particularly abundant during the early weeks at station 1, their average numbers during the first period of the study being more than twice that over the entire study. At station 2 the nauplii during this period were about one-third higher than the overall average while at station 3 they were below the average. The ratio of naupliar numbers/m^3 between stations during the first period was 6.8 (sta. 1):2.4 (sta. 2):1.0 (sta. 3).

The numbers of nauplii/m^3 below the pigment layer were 23 percent of that within it at both stations 2 and 3. They accounted for an estimated 47 percent and 56 percent of the metazoan carbon below the pigment layer from stations 2 and 3, respectively.

Copepoda, Postnaupliar

During many of the early weeks copepodite and adult copepod abundance was significantly higher at station 1 than further offshore. Over the remainder of the study, however, numbers were often higher at stations 2 and/or 3 than at the nearshore site. In determining biomass carbon an average postnaupliar copepod was estimated as being 1.8×10^6 μ^3.

A similar distribution to that of the nauplii was seen for postnaupliar copepod organic carbon within and below the pigment layer at station 2, but at station 3 average biomass of the postnaupliar copepods below the pigment layer was only 28 percent of that in the upper waters.

Other Metazoa

The noncopepod metazoans in the size category we were sampling included various meroplanktonic larval forms of which the pelecypods, cyphonautes, and polychaetes were the most common. Very occasionally crustacean forms, for example, barnacles, and larvae of echinoderms were found. Heteropods and chaetognaths

[2] Recent studies by us have shown a rapid dissolution of the spicular skeleton of acantharians in the fixative/preservative solution used here. It is possible that significant numbers of these organisms were not identified in the samples because of their lack of a skeleton. (Note added September, 1970.)

were the most numerous of the holoplanktonic "Other Metazoa," with infrequent occurrence of nematodes, Appendicularia, and the like.

Compared with the copepod Crustacea the "Other Metazoa" were generally a small fraction in terms of both numbers and biomass. The sparseness was particularly true in the waters sampled below the pigment layer. Within the pigment layer bivalve larvae contributed heavily to the maximum at each site. The "Other Metazoa" were an average of 8–9 percent of the metazoan biomass/m^3 at stations 1 and 2 but only 2 percent at station 3. Below the pigment layer the average number of "Other Metazoa" per cubic meter was about 11–12 percent of that of the upper sample. Average organic carbon level was 1–2 percent of the total Metazoa.

DISCUSSION

The average standing stock biomass of microzooplankton in the pigment layer relative to that of the phytoplankton (University of California, Institute of Marine Resources, 1968*b;* Reid *et al.*, Part V, above) was small throughout the study, averaging 5 percent at station 1 and 9 percent at stations 2 and 3. At station 1 this relationship was constant at 5–6 percent for each period although the absolute changes were at times large. For example, the average plant carbon dropped from 5.8 g/m^2 during period A to 1.4 g/m^2 in period B. At station 2 the average amount of microzooplankton carbon compared with the phytoplankton crop was low, approximately 3 percent, during the early part of the study. Throughout the remaining periods, the average level of microzooplankton carbon was 8–12 percent of that of the phytoplankton carbon. An even more marked difference in this relationship was found at station 3 with spring and summer (periods A and B) levels at 5–6 percent, increasing to a standing stock of small animal plankters at 22.5 percent of that of the phytoplankton crop in terms of their organic carbon content in the late summer.

Larger zooplankton were sampled with a 183-μ mesh net at stations 2 and 3 semiweekly throughout most of the program (University of California, Institute of Marine Resources, 1968*b;* Mullin and Brooks, Part VII, below). While there is some overlap in the size groups of organisms sampled by their net and our pump, it was small and probably not significant. Considering the average zooplankton carbon per cubic meter over the 325-m water column sampled by Mullin and Brooks as being evenly distributed over all depths, this can be compared with the average microzooplankton carbon/m^3 we determined over the upper 100 m (combined "pigment layer" + "below pigment layer" corrected for ciliate organic carbon). At station 2 the ratio of larger zooplankton to microzooplankton/m^3 ranged from 2.0:1 to 14.1:1 and averaged 4.9:1. Therefore the microzooplankton organic carbon would represent approximately 17 percent of that estimated for the total zooplankton population in the upper 100 m. These ratios ranged from 1.4:1 to 8.1:1, averaging 3.8:1 at station 3. The microzooplankton carbon accounted for approximately 21 percent of the total zooplankton carbon.

Using the data on the microzooplankton populations developed from the 21 weekly samples it is attractive to speculate on the magnitude of some possible dynamic relationships between the microzooplankton and the other trophic levels

observed. Strict limitations, however, must be applied to any such speculation by the nature of the sampling program we employed.

Similarly, simple feeding relationships cannot be considered as existing for the various groups of microzooplankton. Each group has its own set of interrelationships, most of which have not been demonstrated in quantitative terms. While it is too simple to consider the microzooplankton groups as herbivores, it is probable that each derives a significant portion of its nutrition directly from phytoplankton. The contributions from detritus and its associated bacterial populations, from zooxanthellae and other symbiotic autotrophs associated with the Sarcodina and possibly the tintinnids, and perhaps even from the dissolved organic carbon material cannot be quantitated although they possibly are not insignificant.

The concentration of detrital carbon is large relative to that estimated for the microzooplankton. Detritus, estimated as the total particulate carbon (University of California, Institute of Marine Resources, 1968*a*) minus the amounts calculated to be tied up in the phytoplankton and microzooplankton populations, was an average of 3.8, 4.7, and 4.1 g/m^2 over the pigment layers of stations 1, 2, and 3, respectively. The relationship between average detrital and microzooplankton carbon is thus 26:1, 36:1, and 37:1 at the three sites. Dissolved organic carbon was approximately an order of magnitude higher than detrital carbon at stations 2 and 3 and only slightly lower than this at station 1. Week-to-week changes as well as the range over the period of study were much smaller for the detrital and dissolved organic carbon fractions relative to those of the carbon tied up in any of the groups of living organisms.

For the purpose of discussion, the microzooplankton populations we have enumerated can be divided into two groups on the basis of their reproductive potential. One group includes those forms with a relatively rapid rate of reproduction, gen erally by binary fission, and measurable in terms of hours or, at the most, a few days. The "Ciliata other than Tintinnida" and the tintinnids would be included in this group. Fenchel (1968) described the growth rates of several marine benthic ciliates, reporting generation times of 2.4 to 46 hours at 20°C. Division time for a tintinnid ciliate, *Favella serrata,* grown through several generations in our laboratory at 18°C, was approximately 24 hours. Conservative estimates for the generation times of ciliates under "average" conditions found during our sampling might be 24 hours for the "Ciliata other than Tintinnida" and 48 hours for the Tintinnida.

The other types of organisms in the microzooplankton populations all have normal generation times of several weeks or longer and give rise to multiple offspring. Copepod species similar to those that often comprised the bulk of the metazoan populations in the microzooplankton samples have been shown by Mullin and Brooks (1967) to have generation lengths of approximately 8 weeks. Berger and Soutar (1967) gave evidence that four common planktonic foraminifera in the California Current have a life cycle of approximately a month. Studies with a benthic foraminiferan by Grell (1954) show an alternation of generations on a time scale of several weeks each. The Sarcodina, however, would not be of major importance to this discussion as they contributed only a very small amount to the total microzooplankton biomass.

The time between successive samplings, that is, 1-week intervals, was such that the ciliates have the probable potential for several, perhaps as many as four to ten, generations which, if predation on these forms is low, would allow for very significant changes in numbers. The resultant offspring of a ciliate dividing unchecked once per day for a week would result in an increase of numbers and biomass larger than two orders of magnitude. In reality, however, the continuously changing grazing pressure on these organisms and the movements of the water mass at our stations complicates the picture. Mullin and Brooks (1967 and personal communication) did not find good positive evidence for synchronous reproduction of *Calanus helgolandicus* (*pacificus*) and *Rhincalanus nasutus,* two important copepod species in the area studied. Therefore, it would seem probable that a variable number of new individuals could be added to the population during the week between samplings. In addition, the individuals already present are growing. Mullin and Brooks (1967) found the coefficient of exponential growth for *R. nasutus* from the first naupliar stage to the second copepodite was 0.24/day. Most of the copepods in our samples were nauplii or early copepodite forms.

Estimates of daily phytoplankton production in the pigment layer at the sites studied have been derived by Eppley, Reid, and Strickland (Part III, above). Estimates of the fraction of the daily production that might be grazed by the total microzooplankton in the same depth interval if feeding exclusively on phytoplankton can be made after making broad assumptions regarding the amounts of food intake by the various groups. The protozoans, which were primarily ciliates having division rates measurable in days or less, have been calculated as consuming three times their bodily carbon content per day. For the metazoans, daily carbon consumption by naupliar copepods was put equivalent to their body carbon content while for postnaupliar copepods and "Other Metazoa" 0.3 of the animal's carbon content was used in the calculation. The figures for copepod consumption were fixed after examining the data of Mullin and Brooks (1967 and Part VII, below) on the weights and daily rates of carbon ingestion for the various developmental stages of *Calanus helgolandicus.* Since our field samples also contained species of copepods smaller than *C. helgolandicus,* which may have had relatively higher rates of carbon ingestion per unit weight, these estimates of consumption may be conservative. In making the microzooplankton volume estimates on which organic carbon content was calculated only the "body" of the organism was considered. For example, in the tintinnids the body volume was estimated as being half that of the lorica (University of California, Institute of Marine Resources, 1968*b*). This may be low for some of the species of the smaller tintinnids which generally appear to occupy relatively more of their lorica than many of the larger forms.

On the assumptions above the estimated average percent consumption by the total microzooplankton population at station 1 over the study was 22 percent of the phytoplankton production. The range for this estimate was 5–125 percent and the median, 14 percent. During the first period of observations when the average standing stocks of microzooplankton and phytoplankton were relatively high, it was calculated that the animals if deriving all their nutrition from phytoplankton would consume 54 percent of the average plant production. Similar calculations

for the pigment layers of stations 2 and 3 indicate the small zooplankters could account for the loss of an average 16 percent (range, 8–36 percent; median, 17 percent) and 23 percent (range, 7–52 percent; median, 18 percent) of the daily plant production over the five-month period of study at the two sites, respectively.

In addition to the microzooplankton in the pigment layer, other forms that could be feeding on the phytoplankton are microzooplankton from below the pigment depth which may have a diurnal periodicity of vertical migration and the larger zooplankton, both within and, to an extent, below the pigment layer. Using the same assumptions as above, the deeper microzooplankton would account for the consumption of an additional average 7 percent of the plant production at station 2 and 8 percent at station 3.

As was shown earlier the microzooplankton may be only an average 17–21 percent of the estimated total zooplankton populations in the upper 100 m at stations 2 and 3. The larger zooplankton forms, however, are a considerably more varied group probably including a significant amount of carnivores which have not been separated in these samples, thus preventing any conjecture regarding their feeding and the standing stocks of the smaller zooplankton and phytoplankton.

A better set of organisms to examine for their predator-prey relationship might be the ciliates, both the "Ciliata other than Tintinnida" and the tintinnids, and small phytoplankters. Again, this procedure is not completely valid because of the various other sources of nutrition probably available to these organisms, for example, detritus, bacteria, zooxanthellae, and so on. Most of the abundant tintinnid species in our samples are relatively small, having lorica oral diameters of 20 μ or less. Many of the nonloricate forms are much smaller than this and a 10-μ particle would probably be the maximum with which they could cope. Comparing the ciliate organic carbon in the pigment layer with the < 20-μ (equivalent diameter) and <10-μ phytoplankton organic carbon (University of California, Institute of Marine Resources, 1968*b*) reveals a generally larger amount of ciliate carbon per unit phytoplankton carbon when the standing crop of the small phytoplankters is relatively high.

Production of these small phytoplankters relative to total phytoplankton production can be estimated by assuming the same relationship as was found for the organic carbon of the < 10-μ and < 20-μ cells as a fraction of the total standing crop of phytoplankton. It is possible that this assumption gives a somewhat low estimate for the production of these small cells as Teixeira (1963) found that at six coastal and oceanic sites in the equatorial Atlantic while the numbers of nannophytoplankton (cells passing 65-μ mesh) were an average of 78 percent of the total standing crop they accounted for 90 percent of the plant production. Our use of phytoplankton organic carbon, which takes into account the disparity in size as well as number, as the basis for comparison may minimize any such possible differences. With the estimate of the productivity of these small plant cells the pigment layer ciliate organic carbon consumption of these cells can then be estimated, assuming as previously, a daily consumption by the ciliates of 3× their bodily carbon. At station 1 the estimated consumption by the total ciliates varied from 3.7 percent to 768.0 percent of the calculated <10-μ phytoplankton production, averaging 54 percent (median, 37 percent) over the entire study. A similar

calculation predicts a consumption of an average of 23 percent (median, 13 percent) of the total < 20-μ phytoplankton production. At station 3 the average consumption of the < 10-μ and < 20-μ phytoplankton production by the ciliate population was estimated to be 26 percent and 13 percent, respectively. At both sites the estimated percentage of these phytoplankton size groups was generally very low immediately following the times of most dramatic changes in the water masses as discussed above.

We have not included any flagellates in our results although holozoic forms may have been present. While most would be very small forms that would not add significantly to the microzooplankton biomass unless present in very large numbers, a few organisms fitting the description and size of the unnamed flagellate form noted by Hasle (1960) were seen. These were fusiform organisms, 40 μ in length with a maximum diameter of about 5 μ and with an estimated volume of 390 μ^3. Reasons for the decision not to include the possibly holozoic flagellates are twofold: (*a*) many of the naked flagellates are very poorly, if at all, fixed and preserved by the formalin treatment used here, making their identification very subjective; and (*b*) it is not possible to assign conclusively a feeding type to most of these organisms. While many flagellates are known to be heterotrophs their nutrition is often derived from dissolved organic matter and not from particle feeding. Eppley *et al.* (Part III, above) have estimated that the average abundance of heterotrophs during the period of our study was 5–10 percent of the total phytoplankton crop counted. This percentage is similar to that which we determined for the average standing stock abundance of microzooplankters relative to the standing crop of phytoplankton. If the heterotrophs are particle-type feeders they should properly be regarded in food-chain dynamics in a position along with that of the microzooplankton. That there may be significant numbers of animal-type feeders among these flagellates can be suggested from such demonstrations as the complete devouring by *Gyrodinium pavillardi* of a ciliate of almost equal size (B. Biecheler, in Grassé, 1952).

REFERENCES

BEERS, J. R., and G. L. STEWART

1967. Microzooplankton in the euphotic zone at five locations across the California Current. J. Fish. Res. Board Can., 24:2053–2068.

1969*a*. The vertical distribution of microzooplankton and some ecological observations. J. Conseil Int. Explor. Mer, 33(1):30–44.

1969*b*. Microzooplankton and their abundance relative to the larger zooplankton and other seston components. Marine Biol., 4:182–189.

BEERS, J. R., G. L. STEWART, and J. D. H. STRICKLAND

1967. A pumping system for sampling small plankton. J. Fish. Res. Board Can., 24:1811–1818.

BERGER, W. H., and A. SOUTAR

1967. Planktonic Foraminifera: Field experiment on production rate. Science, 156:1495–1497.

BIGELOW, H. B., L. LILLICK, and M. SEARS

1940. Phytoplankton and planktonic Protozoa of the offshore waters of the Gulf of Maine. I. Numerical distribution. Trans. Amer. Phil. Soc., 31:149–191.

BRAARUD, T.

1934. A note on the phytoplankton of the Gulf of Maine in the summer of 1933. Biol. Bull., 67:76–82.

FENCHEL, T.

1968. The ecology of marine microbenthos. III. The reproductive potential of ciliates. Ophelia, 5:123–136.

GRAN, H. H.

1933. Studies on the biology and chemistry of the Gulf of Maine. II. Distribution of phytoplankton in August, 1932. Biol. Bull., 64:159–182.

GRASSÉ, P.-P., ed.

1952. Traité de Zoologie. I. Phylogénie. Protozoaries: Généralités Flagellés. Premier fascicule. Paris: Masson et Cie. P. 317 (Biechler, B.).

GRELL, K. G.

1954. Der Generationswechel der polythalamen Foraminifere *Rotaliella heterocaryotica*. Archiv. Protistenk, 100:268–286.

HASLE, G. R.

1960. Phytoplankton and ciliate species from the tropical Pacific. Skrifter Norske Videnskaps-Akad. Oslo, I: Matematisk-Natur. Klasse, 2:1–50.

LOHMANN, H.

1908. Untersuchungen zur Feststellung des völlstandigen Gehaltes des Meeres an Plankton. Wiss. Meeresunters. Abt. Kiel, n.s., 10:131–370.

MULLIN, M. M., and E. R. BROOKS

1967. Laboratory culture, growth rate, and feeding behavior of a planktonic marine copepod. Limnol. Oceanogr., 12:657–666.

TEIXEIRA, C.

1963. Relative rates of photosynthesis and standing stock of the net phytoplankton and nannoplankton. Bol. Inst. Oceanogr., São Paulo, 13:53–60.

UNIVERSITY OF CALIFORNIA, INSTITUTE OF MARINE RESOURCES

1968*a*. Research on the marine food chain; progress report, Jan. 1967–June 1968. Part III. Data record, coastal plankton survey, 1967. Section I. Chemistry and productivity. Unpubl. MS (SIO Ref. 68-20; IMR Ref. 68-8).

1968*b*. Research on the marine food chain; progress report, Jan. 1967–June 1968. Part IV. Data record, coastal plankton survey, 1967. Section II. The plankton. Unpubl. MS (SIO Ref. 68-38; IMR Ref. 69-3).

UTERMÖHL, H.

1931. Neue Wege in der quantitativen Erfassung des Planktons. Verhandlungen Int. Vereinigung Limnol., 5:567–597.

THE ECOLOGY OF THE PLANKTON OFF LA JOLLA, CALIFORNIA, IN THE PERIOD APRIL THROUGH SEPTEMBER, 1967

EDITED BY

J. D. H. STRICKLAND

PART VII

PRODUCTION OF THE PLANKTONIC COPEPOD, *Calanus helgolandicus*

BY

M. M. MULLIN AND E. R. BROOKS

ABSTRACT

Measurements of rates of ingestion and growth of the developmental stages of *Calanus helgolandicus* (*pacificus*) as functions of temperature and concentration of food in the laboratory, plus the abundances of the developmental stages in samples taken twice a week, were used to calculate the ingestion and production by the natural populations at two stations. The rates of mortality of the natural populations were calculated from the relative abundances of successive developmental stages in the samples. Two different assumptions concerning the concentration of food in the environment led to two sets of coefficients for ingestion, growth, and mortality.

Calanus decreased in biomass from spring to summer, and was most important in late May and June, relative to primary production, as a consumer of this production and a producer of animal biomass. The observed decrease in biomass, however, could not be clearly attributed to an excess of mortality over production. The turnover of carbon by the whole population was dominated by the late copepodite stages.

INTRODUCTION

THE PREVIOUS MEASUREMENTS of natural production of marine zooplankton, the basic methods that have been employed in such studies, and the problems with each, have recently been reviewed (Mullin, 1969). The method adopted here is somewhat similar to that of Lasker (1966) in that rates of ingestion and growth measured under controlled conditions in the laboratory are applied to a natural population. The present calculation makes use of more information about the natural population, however, in that age distributions and abundances at specific times and locations are taken into account, rather than considering the "average" population as a homogeneous unit. Further, rates of production are corrected for simultaneous rates of age-specific mortality estimated from the age distributions of the natural populations.

Calanus helgolandicus (*pacificus*) is an important, particle-grazing species in the Transition Zone and California Current of the North Pacific, and closely related species are common in other temperate water masses. Phytoplankton is generally agreed to be the major source of food, although the role of particulate detritus as a nutritional source has not been fully evaluated.

ACKNOWLEDGMENTS

Sharon Davidor, Larry Klapow, Mary Sue Tilsworth, and John Pequegnat counted the copepodite stages and together with several other people, assisted

with the sampling program at sea. Drs. P. H. Wiebe and E. W. Fager gave advice on the analyses of variance, and most of the computer programs were written by Elizabeth Fuglister. We are greatly indebted to Drs. M. B. Schaefer and R. Preisendorfer for the correct derivation of equation 3. Drs. Schaefer, R. R. Hessler, and J. D. H. Strickland improved the manuscript with their criticisms. The research was supported in full by the United States Atomic Energy Commission, Contract No. AT(11-1)GEN 10, P.A. 20.

METHODS

Sampling, Counting, and Estimation of Biomass

Samples were taken between 0900 and 1600 hours twice a week (except when prevented by damage to the sampling gear) from 18 April to 18 August, 1967, at stations 2 and 3 (see fig. I-1) where the depth of the bottom was between 350 and 400 m. Tows of two types were made with paired nets, one net of each pair having a flowmeter mounted in its mouth. Each tow thus resulted in two samples, a "port" and a "starboard" catch. All nets were constructed so that the ratio of the total aperture area of the mesh to the area of the mouth of the net was 6:1.

One type of tow was made to sample copepodite stages with a bongo net (McGowan and Brown, 1966) equipped with 183-μ mesh netting. This device is a frame for towing two nets horizontally or obliquely side by side; the nets are each 0.7 m in diameter and their mouths are covered by canvas doors that are opened by a messenger. The depth of the nets was monitored on the ship during a tow by means of a depth-telemetering pinger. The nets were lowered to within 50 m of the bottom while the ship was under way at a speed of 1.5 m/sec (3 knots). The doors were then opened with a messenger and the nets were towed obliquely to the surface so that they fished approximately equal times at all depths. The volume of water filtered during such a tow was about 300 m^3 per net.

The second type of tow was made to sample naupliar stages with a pair of 0.5-m diameter nets of 102-μ mesh netting. The nets were attached to the wire side by side on a T-shaped bar, lowered backward to a depth of 100 m with the ship hove to, and then raised vertically to the surface. Horizontal tows made in April and October with the bongo net equipped with 153-μ mesh netting and rigged so as to close after filtering 100 m^3 of water indicated that naupliar stages and copepodites younger than stage V were almost entirely confined to the upper 100 m, so that sampling only this layer gave a satisfactory estimate of the abundance of nauplii. The volume of water filtered per 0.5-m net was about 25 m^3. The nets of both types were carefully washed with a saltwater spray after each tow, and catches were preserved in formalin of about 5 percent concentration by volume.

The collections from the bongo net were subsampled with a Folsom plankton splitter so that no more than ½ of any sample was examined. At least $\frac{1}{128}$ of each sample was examined and at least 50 of the most abundant copepodite stage of *Calanus* were counted. The collections from the 102-μ mesh nets were subsampled with a stempel pipette (since the nauplii are small in size and since less than 10 percent of each sample was generally counted) until at least 30 individuals of the most common naupliar stage had been counted. If, however, less than 10 individuals of all stages were encountered in the first 10 percent of the sample, the

nauplii were considered too rare to be counted. The first two naupliar stages were too difficult to distinguish from the nauplii of other species and so were not counted.

Four samples for each type of tow at each of the two stations were counted for 14 of the 33 dates on which collections were made. Only two samples of each type were counted per station for the other dates. All data were converted to numbers per m^2 surface area from the counts for each sample, knowing the volume of water from which the sample was filtered by the net and using the approximation that the bongo nets all fished from 325 m to the surface and the 0.5-m nets from 100 m to the surface.

Three-way analyses of variance were performed on log-transformed data for each developmental stage from 9 dates (26 May through 13 June and 20 through 27 June), resulting in 31 analyses for nauplii sampled with the 0.5-m nets and 57 analyses for copepodites sampled with the bongo nets. These analyses were used to compare the variance between the two successive tows at either station with that between the two nets of any single tow by an $F_{1,1}$ ratio of mean squares. The variance between the two catches of a single tow is caused by nonevenness in the distribution of animals on a very small scale, plus differences in filtering efficiencies of the two nets, plus variability introduced by subsampling and counting errors. To the extent that variability between tows exceeded variability between nets of a single tow (i.e., a significant F ratio), successive tows do not sample exactly the same population, reflecting patchiness at a single station. A nonsignificant F ratio means that values for the two tows at a station may be regarded as coming from a single population and therefore may be combined to give a single mean value for that station for the particular developmental stage being considered.

In only 2 of the 31 sets of data for nauplii was the variability between tows significantly greater ($p < 0.05$) than that between nets, and in one case the variability between nets was significantly greater than that between tows. In the 57 sets of data for copepodites there were only 2 cases in which the variability between tows significantly exceeded that between nets, and 3 cases where the reverse was true. Out of 60 F ratios 3 would appear to be significant for reasons of chance alone since the 0.05 level was used to test for significance. We conclude from this that paired tows did not give greater precision than consecutive tows and that it is appropriate to combine data from different tows at a station to give a single, mean value for each developmental stage on each date. Data in this form, which were tabulated in University of California, Institute of Marine Resources, 1968, will be provided by the authors upon request.

The variability between stations in excess of variability at a single station reflects patchiness on the scale of 5 to 6 km. This variability was not tested, since it was obvious in the data and since it was noted (see below) that the two stations differed significantly in total zooplanktonic biomass and in biomass of *Calanus*.

A fraction of each preserved sample from the bongo net was rinsed with 4 percent ammonium formate on a preweighed filter, dried at 60°C for 24 hours, and weighed. This estimate of total zooplanktonic biomass did not, of course, include

animals smaller than about 200 μ in the smallest dimension but did include some detritus and large phytoplankters. The measured dry weight was divided by three to convert to units of organic carbon (Curl, 1962; Beers, 1966). In order to judge the importance of *Calanus* relative to the total biomass of zooplankton as defined by this measurement, the numbers of the various developmental stages were converted to organic carbon biomass using the following weights (from unpublished measurements) per individual: Nauplius stage III = 0.16 μg C, N IV = 0.23 μg C, N V = 0.33 μg C, N VI = 0.68 μg C, Copepodite stage I = 1.4 μg C, C II = 2.6 μg C, C III = 4.9 μg C, C IV = 14 μg C, C V = 27 μg C, female = 68 μg C, male = 35 μg C.

Calculation of Rates of Mortality, Growth, and Ingestion

In populations that breed synchronously, and which may be sampled on successive occasions so that a discrete generation may be identified in several consecutive samples, rates of mortality may be calculated from the observed disappearance of individuals from this generation. *Calanus*, however, apparently breeds more or less continuously during the spring and summer off southern California (Mullin and Brooks, 1967), and the movement of water in the 3 to 4 days between sampling dates is unknown, so that rates of mortality must be calculated from the abundances of two successive developmental stages in the samples from each date and station. This procedure requires the assumption of constant recruitment, that is, that during the production of the two stages being compared, a constant number of eggs were laid per day by the females of the parent population. Thus, these two stages (although not necessarily all stages present on a given date) are assumed to have been associated spatially since being produced by a common group of females. For example, in using the ratio of abundances of copepodite stages III and II to calculate the rate of mortality over the duration of these stages, it is assumed that they occur together in the sample because of temporal persistence of the mass of water in which they were hatched, and that they were not produced by different concentrations of females in different areas and then brought together by mixing or migration.

If the abundances in a sample of the earlier and later of two successive developmental stages are X and Y respectively and the duration of each stage is a days, then the ratio, Y/X, equals S^a, where S is the fractional survival per day and the exponential coefficient of daily mortality, $M = -\ln(S)$. The animals generally spend a longer period of time in the later of two developmental stages, however. Thus, if a is the duration in days of the younger stage and b is the duration in days of the later stage, generally $b > a$. Assuming that mortality acts exponentially on a number of animals, N_0, just entering the earlier stage, the number of animals, N_a, surviving to reach the later stage will be $N_a = N_0 e^{-Ma}$. If X is the abundance of all individuals of the earlier stage on a specific day of sampling, then

$$X = \frac{N_0}{M}(1 - e^{-Ma}) \tag{1}$$

Similarly, the abundance of all individuals of the later stage, Y, on the same day is

$$Y = \frac{N_a}{M}(1 - e^{-Mb}) = \frac{N_0 e^{-Ma}}{M}(1 - e^{-Mb}) \tag{2}$$

Hence, the ratio of the two stages on a specific day will be

$$\frac{Y}{X} = e^{-Ma} \frac{(1 - e^{-Mb})}{(1 - e^{-Ma})} = S^a \frac{(1 - S^b)}{(1 - S^a)} \tag{3}$$

A computer-generated table of solutions for this equation for various values of a, b, and S may thus be used to find S for an observed value of the ratio, Y/X, if a and b are known for the stages being compared.

It is unlikely that the rate of mortality is constant for animals of all ages because of changes in size, morphology, mobility, and vertical distribution during development. We have therefore calculated separate values for mortality of nauplii (subscript "n"), early copepodites (stages C I, C II, and C III [subscript "ec"]), and late copepodites (stages C IV, C V, and the adult females [subscript "lc"]).

The coefficient of daily naupliar mortality, M_n, was calculated from the ratios of abundances, N IV/N III and N VI/N V, using data from rearing experiments at various temperatures and concentrations of food to estimate the duration of each naupliar stage. Mortality of early copepodites, M_{ec}, was calculated from the C III/C II ratio, with the duration of C II (a in equation 3) and that of C III (b in equation 3) also taken from laboratory data. Mortality of the late copepodites, M_{lc}, was calculated from the ratio of C Vs to C IVs in the same way.

The two stations have been treated separately and the entire period of study has been divided into four major periods—18 April to 19 May, 20 May to 30 June, 1 July to 31 July, and 1 August to 18 August (when sampling was stopped)—the separations between periods coinciding with major changes in temperature, nutrients, phytoplankton, and microzooplankton (see above, Strickland, Solórzano, and Eppley, Part I; Reid, Fuglister, and Jordan, Part V; Beers and Stewart, Part VI). The ratios of abundances of each pair of successive stages at each station were averaged over each major period to smooth out some of the variation, and the mean ratio was used to calculate the rate of mortality for the appropriate age group for each period.

We had previously (Mullin and Brooks, 1970) measured the rates of growth and ingestion by *Calanus* in the laboratory at 10°C and 15°C with the diatom, *Thalassiosira fluviatilis*, as food. These results were used to adjust measured metabolic rates to observed environmental temperatures by extrapolation. In order to examine the effects of the concentration of food, we used essentially the same experimental methods with the following changes: The diatoms used as food (*Thalassiosira* and *Cyclotella nana*) were grown in batch cultures; the seawater in which the animals were reared was filtered a second time immediately before use, and the background level of particulate matter in this water was included in the blanks in the counting of cells and measuring of particulate organic carbon; and the speed of agitation of the seawater in the 1-l beakers containing the animals was increased to 5 c.p.m. to ensure uniform suspension of the diatom cells.

The results of these (unpublished) experiments permitted us to calculate the exponential coefficients of daily growth in individual bodily carbon content (G_n, G_{ec}, and G_{lc}) of the three age groups referred to above, and the rate of

ingestion of food and the duration of each developmental stage, for the mean concentration of food observed each week at each station.

The calculation of daily ingestion, growth, and mortality of the natural population makes use of equations summarized by Ricker (1958), assuming that these three processes act uniformly throughout the day and that the day starts when the population is sampled. The observed abundance of any developmental stage at a station on a particular day (N, in animals per m^2), as determined by the mean catch of the net tows, was used to calculate the mean abundance ($\bar{N}$) of that stage for that day as:

$$\bar{N} = \frac{N}{M}(1 - e^{-M}) \tag{4}$$

where M is the appropriate exponential coefficient of daily mortality. The total daily ingestion by that stage is then $I\bar{N}$, where I is the appropriate rate of ingestion for an animal of that stage. The total ingestion by the population is therefore the sum of the rates of the various developmental stages, $\Sigma I_i\bar{N}_i$, in μg carbon per m^2 per day, where i is each stage from nauplius III through adult female.

The initial weights of bodily carbon of animals of a particular stage (W, in μg C per animal) were given above. The appropriate values of W and N were used to calculate the mean biomass ($\bar{W}\bar{N}$, in μg C per m^2) of all animals of a particular stage as

$$\bar{W}\bar{N} = \frac{WN}{M - G}(1 - e^{G-M}) \tag{5}$$

where M and G are the appropriate coefficients of mortality and growth. Production by the stage, including animals that grow but then die before the end of the day, is $G\bar{W}\bar{N}$ μg C/m^2/day, and the total production of the population is $\Sigma G_i\bar{W}_i\bar{N}_i$, where i is each developmental stage. Similarly, the total loss from the population due to mortality is $\Sigma M_i\bar{W}_i\bar{N}_i$.

This calculation ignores naupliar stages I and II, which were not counted and do not feed, and the males, which feed at very low rates and have a much higher rate of mortality. Also, adult females continue to gain weight indefinitely as reflected in G; in reality, this gain in weight goes into the production of eggs which are released into the water, and this production terminates within ten weeks.

To summarize the calculation briefly: Rates of mortality were estimated separately for nauplii, early copepodites, and late copepodites from the abundances of successive developmental stages in samples taken twice a week at two stations. Rates of daily ingestion and growth measured in the laboratory for each developmental stage were multiplied by the biomass of that stage on each sampling date, and were corrected for the animals dying before the end of the day to give the ingestion, growth, and mortality of that particular stage in units of weight of carbon per square meter per day. The values for all developmental stages were summed to give the flux of carbon through the whole population at each station on each date.

RESULTS

The data summarized in table VII-1 show that at both stations the biomass of *Calanus* was higher in late spring than in July and August, and was also a larger

fraction of the total zooplanktonic biomass early in the season. The mean total biomass at station 2 was 2.4 g C/m² and at station 3 was 1.4 g C/m²; this difference between stations was significant ($p < 0.01$ by signed rank test). The mean biomass of *Calanus* was 0.82 g C/m² at station 2 and 0.35 g C/m² at station 3, this difference also being significant, and *Calanus* contributed a significantly greater percentage to the total biomass at station 2 than at station 3.

TABLE VII-1

MEAN STANDING CROPS, IN mg C PER m², OF PHYTOPLANKTON,[a] *Calanus*, AND TOTAL ZOOPLANKTON[b]

(For each station $\bar{x}$ is the mean and w is the range.)

Period	Station		Phytoplankton[c]	*Calanus*	Total zooplankton
18 April–19 May	2	$\bar{x}$	5,900	908	1,800
		w	2,120–10,900	323–3,025	1,206–3,021
	3	$\bar{x}$	1,400	790	1,300
		w	650–2,600	181–2,266	898–1,832
20 May–30 June	2	$\bar{x}$	1,400	1,390	3,000
		w	650–2,320	200–4,339	1,589–6,173
	3	$\bar{x}$	1,600	439	1,700
		w	600–2,820	78–1,168	890–4,019
1 July–31 July	2	$\bar{x}$	1,400	424	2,500
		w	770–2,090	196–715	739–4,853
	3	$\bar{x}$	950	160	1,500
		w	450–1,720	36–375	593–3,980
1 August–18 August	2	$\bar{x}$	1,100	86	1,900
		w	890–1,480	43–181	1,273–2,990
	3	$\bar{x}$	440	25	830
		w	340–570	17–33	390–1,955

[a] Calculated from optically measured cell volumes.
[b] Defined as the catch of 183-μ mesh net.
[c] From data summarized in figure III-1.

The mean standing crop of phytoplankton during the period in which zooplankton samples were taken at station 2 was 2.6 g C/m², while that at station 3 was 1.4 g C/m². The mean daily rates of primary production were 1.1 g C/m² and 0.8 g C/m² at stations 2 and 3, respectively. Both these differences were significant ($p < 0.005$ by signed rank test). Station 2, located in the submarine canyon and closer to shore, therefore had higher mean crops of phytoplankton, total zooplankton, and *Calanus*, and higher primary production, than station 3, and *Calanus* was a larger fraction of the total zooplanktonic biomass.

Mullin and Brooks (1970) compared laboratory-raised with wild copepods with regard to bodily carbon content, ratio of bodily carbon to nitrogen, and respiratory rate, and found that animals raised at 10°C on high concentrations

of *Thalassiosira* as food did not differ significantly from the wild individuals. Even if it is granted that the rates of ingestion and growth measured under a particular combination of controlled conditions in the laboratory would be relevant to wild *Calanus* living under the same environmental conditions, the environmental parameters that the wild population actually experiences must still be measured. For example, the daytime and nighttime vertical distributions of the various developmental stages should be related to the temperature at various depths during the study as shown in figures I-3 and I-4 in order to correct for the effects of temperature on metabolic rates. A more serious problem concerns

TABLE VII-2

COMPARISON OF BODILY SIZES, AS μg C PER ANIMAL, OF *Calanus* TAKEN IN THE FIELD WITH THOSE RAISED IN THE LABORATORY WITH VARIOUS CONCENTRATIONS OF SINGLE DIATOM SPECIES AS FOOD

(For the experimental methods, see Mullin and Brooks, 1970)

Type of food	Temperature	Mean phytoplankton concentration μg C/l	μg C per animal			
			Copepodite stage IV		Adult female	
			Mean	Range	Mean	Range
Natural.....	Natural	34[a]	13.6	10.1–21.6	67.8	47.4–81.3
Thalassiosira fluviatilis.....	10°C	226	15.5	10.7–20.3	53.5	34.3–72.7
	15°C	177	7.4	7.1–7.7	43.1	40.8–45.4
	15°C	79	7.6	6.1–9.0	26.6	25.4–27.8
Cyclotella nana.....	15°C	43[b]	no measurement		55.0	53.0–57.0
Thalassiosira fluviatilis.....	15°C	21	no measurement		14.9	14.9

[a] Mean for both stations over the whole period of study for the "plant pigment layer" (see University of California, Institute of Marine Resources, 1968).

[b] This concentration used through stage C IV. During stage C V, much higher concentrations were present,

the concentration of food for *Calanus*, which could be measured (to take the extreme cases) either as the abundance of a particular species of phytoplankton or as the total concentration of particulate organic carbon in the water. We have calculated the turnover of carbon assuming that *Calanus* is a nonselective herbivore, so that the 3-week running mean concentration of phytoplankton carbon (data reported in University of California, Institute of Marine Resources, 1968) at each station is an adequate estimate of the availability of food during a particular week.

Evidence summarized in table VII-2, however, indicates that the mean concentration of phytoplankton carbon may underestimate the effective concentration of food, since animals as large as the wild animals occur in the laboratory only when the food concentrations used during raising are higher than the mean natural concentration. We have therefore also calculated the turnover of carbon assuming that the highest rates of ingestion and growth measured in the laboratory are correct when adjusted for the warmer temperatures that prevailed in July and August and for the lower temperatures experienced by late copepodites. This latter calculation, in which we assume that rates of growth and ingestion

were not limited by the mean concentration of phytoplankton, probably gives an upper limit to the turnover of carbon by *Calanus*. Estimates of the coefficients of daily mortality are also affected, since they depend on the duration in days of the various developmental stages (a and b in equation 3). The coefficients of daily mortality of late copepodites (M_{1c} in table VII-3) were less affected by low concentrations of phytoplankton than other coefficients because low concentrations of food in laboratory experiments had much stronger effect on the durations of naupliar and early copepodite stages than on those of copepodite stages IV and V.

The mean values used for the various coefficients are tabulated in table VII-3 for each station during each major period. Note, however, that in the calculations in which the mean concentration of phytoplankton was used as an estimate of the availability of food, coefficients were assigned for each week at each station, depending on the 3-week running mean concentration of phytoplankton carbon for that week at that station. Although somewhat different coefficients of growth and mortality were used for the animals from the two different stations, these differences may not be significant, and it should not be concluded that the animals sampled at the two stations necessarily constitute distinct populations in the usual sense.

The results of the calculations are summarized in table VII-4 as mean values during each major period. The means are generally based on two observations per week except between 7 May and 19 May, during which time only one set of samples was taken. The grouping of results into periods defined by hydrographic changes is done for brevity and should not be taken to imply that the *Calanus* population within each period was distinguishable from populations sampled during other periods.

Most of the seasonal changes and differences between stations followed the same patterns as those of *Calanus* biomass (table VII-1), and in this sense the two calculations based on different sets of coefficients gave similar results. The rate of ingestion of carbon by *Calanus* greatly exceeded the rate of net primary production during the last week of May at station 2 in the calculation based on high rates of ingestion, but this never occurred in the second calculation. *Calanus* was most important as a consumer of primary production prior to 5 July in both calculations, and was very much less important in August than in the previous months. *Calanus* was somewhat more important by this same standard at station 2 than at station 3, as indicated also by its contribution to the total biomass of zooplankton.

The overall mean ratio of daily ingestion by *Calanus* to daily net primary production by phytoplankton was 0.26 at station 2 (where *Calanus* was, on the average, 32 percent of the "total zooplankton" biomass), and 0.14 at station 3 (where *Calanus* was 24 percent of the "total zooplankton" biomass) in the calculations based on the assumption that the mean concentration of phytoplankton did not limit the rates of ingestion. These ratios may be meaningless because of this assumption, however, if *Calanus* utilized other kinds of food in addition to phytoplankton (see Discussion). In the calculations in which the rates of ingestion were adjusted to the mean concentration of phytoplankton, the comparable ratios

TABLE VII-3

VALUES USED IN THE CALCULATION OF INGESTION, PRODUCTION, AND MORTALITY OF *Calanus*, ADJUSTED FOR HIGHER TEMPERATURES IN JULY AND AUGUST

(Rates of growth for late copepodites are adjusted for lower temperatures because they live in deep water during the day.)

I. Rates of ingestion and growth *not* affected by the concentration of phytoplankton carbon

Period	Station	Ingestion rate, μg C per copepod per day										Coefficients of daily growth			Coefficients of daily mortality		
		N III	N IV	N V	N VI	C I	C II	C III	C IV	C V	Female	G_n	G_{ec}	G_{lc}	M_n	M_{ec}	M_{lc}
18 April–19 May	2	0.2	0.3	0.6	0.8	1.0	1.3	3.0	6.0	10.0	16.0	0.24	0.21	0.12	0.33	0.0	0.02
	3	0.2	0.3	0.6	0.8	1.0	1.3	3.0	6.0	10.0	16.0	0.24	0.21	0.12	0.20	0.0	0.0
20 May–30 June	2	0.2	0.3	0.6	0.8	1.0	1.3	3.0	6.0	10.0	16.0	0.24	0.21	0.12	0.25	0.0	0.0
	3	0.2	0.3	0.6	0.8	1.0	1.3	3.0	6.0	10.0	16.0	0.24	0.21	0.12	0.35	0.0	0.03
1 July–31 July	2	0.3	0.4	0.7	0.9	1.1	1.5	4.0	7.0	14.0	20.0	0.30	0.27	0.15	0.45	0.0	0.0
	3	0.3	0.4	0.7	0.9	1.1	1.5	4.0	7.0	14.0	20.0	0.30	0.27	0.15	0.65	0.0	0.12
1 August–18 August	2	0.3	0.4	0.7	0.9	1.1	1.5	4.0	7.0	14.0	20.0	0.30	0.27	0.15	0.45	0.0	0.04
	3	0.3	0.4	0.7	0.9	1.1	1.5	4.0	7.0	14.0	20.0	0.30	0.27	0.15	0.65	0.0	0.08

II. Rates of ingestion and growth for each week affected by the concentration of phytoplankton carbon (estimated by 3-week running means)

Phyto-plankton μg C/l	Period	Station	Ingestion rate, μg C per copepod per day										Coefficients of daily growth			Coefficients of daily mortality		
			N III	N IV	N V	N VI	C I	C II	C III	C IV	C V	Female	G_n	G_{ec}	G_{lc}	M_n	M_{ec}	M_{lc}
190	18 April–19 May	2	0.2	0.3	0.6	0.8	1.0	1.3	3.0	6.0	10.0	16.0	0.24	0.21	0.12	0.33	0.0	0.02
28		3	0.1	0.2	0.2	0.4	0.4	0.5	1.2	2.2	2.5	3.8	0.10	0.07	0.04	0.06	0.0	0.0
42	20 May–30 June	2	0.1	0.2	0.3	0.4	0.6	0.7	1.6	2.8	3.2	4.9	0.12	0.09	0.05	0.09	0.0	0.0
40		3	0.1	0.2	0.3	0.4	0.5	0.6	1.5	2.8	3.2	4.8	0.12	0.08	0.05	0.14	0.0	0.02
30	1 July–31 July	2	0.1	0.2	0.2	0.4	0.5	0.6	1.4	2.6	3.1	4.7	0.13	0.11	0.05	0.10	0.0	0.0
22		3	0.1	0.2	0.2	0.4	0.4	0.6	1.1	2.0	2.5	3.7	0.12	0.10	0.04	0.19	0.0	0.10
22	1 August–18 August	2	0.1	0.2	0.2	0.4	0.4	0.6	1.0	2.0	2.5	3.7	0.12	0.10	0.04	0.10	0.0	0.03
12		3	0.1	0.2	0.2	0.3	0.3	0.4	0.7	1.2	1.5	2.2	0.11	0.08	0.03	0.18	0.0	0.06

TABLE VII-4

MEAN RATES OF INGESTION, PRODUCTION, AND MORTALITY OF *Calanus* DURING THE MAJOR HYDROGRAPHIC PERIODS
(The variability around each mean is of the order of that shown for biomass of *Calanus* in table VII-1.)

I. Rates of ingestion and growth *not* affected by the concentration of phytoplankton carbon

Period	Station	A. Net primary production mg C/m²/day[a]	B. Ingestion by *Calanus* mg C/m²/day	Ratio B/A	C. Production by *Calanus* mg C/m²/day	Daily production of *Calanus* per unit biomass	Ratio C/A	D. Mortality of *Calanus* mg C/m²/day
18 April–19 May.....	2	1,600	244	0.15	100	0.11	0.06	17
	3	1,310	213	0.16	89	0.11	0.07	1
20 May–30 June.....	2	770	426	0.55	172	0.12	0.22	2
	3	580	139	0.24	57	0.13	0.10	12
1 July–31 July.....	2	1,240	153	0.12	64	0.15	0.05	1
	3	820	67	0.08	26	0.16	0.03	15
1 August–18 August.....	2	1,040	24	0.02	10	0.12	0.01	3
	3	540	10	0.02	4	0.16	0.01	2

II. Rates of ingestion and growth for each week affected by the concentration of phytoplankton carbon

Period	Station	A. Net primary production mg C/m²/day[a]	B. Ingestion by *Calanus* mg C/m²/day	Ratio B/A	C. Production by *Calanus* mg C/m²/day	Daily production of *Calanus* per unit biomass	Ratio C/A	D. Mortality of *Calanus* mg C/m²/day
18 April–19 May.....	2	1,600	244	0.15	100	0.11	0.06	17
	3	1,310	54	0.04	25	0.03	0.02	0.2
20 May–30 June.....	2	770	186	0.24	81	0.06	0.11	0.8
	3	580	51	0.09	21	0.05	0.04	8
1 July–31 July.....	2	1,240	45	0.04	22	0.05	0.02	0.2
	3	820	18	0.02	8	0.05	0.01	12
1 August–18 August.....	2	1,040	6	0.006	3	0.03	0.003	1
	3	540	2	0.004	1	0.04	0.002	1

[a] From data summarized in figure III-4.

were 0.13 and 0.05 at stations 2 and 3, respectively. In contrast, Beers and Stewart (Part VI, above) estimated that the microzooplankton (a category that includes naupliar and possibly copepodite stage I *Calanus*) ingested approximately 27 percent of the net production of phytoplankton at these two stations over the same period.

In fact, *Calanus* must contribute less than 20 percent to the total grazing pressure exerted by the microzooplankton category, since the late copepodite stages of *Calanus* dominated the turnover of carbon by the whole population of this species in both calculations. This age group was responsible for about 80 percent of the total ingestion and production, and about 60 percent of the mortality, when all are expressed in units of carbon.

The overall mean ratio of production to ingestion—the gross efficiency of growth for the population—was 41 percent in the calculation in which it was assumed that the concentration of phytoplankton did not affect the rates of ingestion and growth. This value is somewhat higher than those reported in the literature (e.g., Conover, 1968; Mullin and Brooks, 1970). The mean gross efficiency of growth in the second calculation was 48 percent, which probably is unrealistically high. Since the late copepodite stages dominated the ingestion and production by the whole population, the rates of ingestion and coefficients of growth used for these stages are particularly critical in determining the gross efficiency of growth for the population.

DISCUSSION

Two of the uncertainties concerning the calculations presented above should be discussed further. Petipa (1966) presented evidence that the expenditure of energy by wild *Calanus* during diurnal vertical migration was many times greater than the expenditure estimated from the rate of utilization of oxygen in small, closed containers. The stirring of the culture vessels in our experiments stimulated swimming activity by the copepods, but it is improbable that natural levels of activity were imitated in this way. Hence, it may be incorrect to apply our measurements of ingestion or growth to the wild population.

The estimates of natural mortality may also be in error. The assumption of constant recruitment over several days and temporal persistence of the resulting animals, on which the calculation of survivorship is based, is an unlikely one. Averaging the ratios of abundances of successive developmental stages over each major period smoothed out some of the natural variation in recruitment (and in mortality) in this calculation.

If the duration of egg-laying and the fecundity of *Calanus* reported by Mullin and Brooks (1967) are taken to be correct, the coefficients of mortality given in table VII-3 determine whether the population will increase or decrease in abundance, that is, whether offspring representing a particular generation will be more or less abundant than the newborn individuals of the previous generation. Such a calculation indicates that at station 2 *Calanus* was increasing in abundance during all four major periods, while at station 3 *Calanus* was increasing in abundance during the first two periods but decreasing during the last two periods. The direction of change in population size at either station during any one period was

the same no matter which of the two sets of mortality coefficients were used, because the lower coefficients are associated with more prolonged durations of developmental stages and therefore act over longer periods. The changes in abundance indicated by these calculations do not agree very well with the seasonal changes in biomass (table VII-1), indicating that either the coefficients of mortality used in the calculations were too low or else the observed changes in biomass were due primarily to the movement of different water masses bringing different concentrations of copepods past the sampling stations.

Based on the relationship of production to mortality in units of carbon, the populations appeared to have a large net increase in biomass in almost all cases, the exceptions being the individuals at station 3 during July and August in the calculation based on phytoplankton-limited growth rates. The populations therefore appear to be much more successful in adding biomass than the observed changes in numbers of individuals or in biomass would suggest. It should be noted, however, that the naupliar stages have by far the highest rates of daily mortality. The high mortality of these individuals affects the abundance of the population very markedly, but has a much smaller effect on daily changes in biomass since each individual nauplius is so small relative to the late copepodite stages. Further, the death from physiological old age of males and spent females, which might represent a relatively large lost of biomass, is not taken into account by the coefficient of mortality, which is based on survivorship of copepodite stages IV and V.

It is probable that the two calculations give upper and lower limits to the rate of turnover of carbon by *Calanus* during the periods studied, and we feel that the "true" rates lie closer to the upper limits. Mullin (1969) summarized estimates of the rates of turnover of carbon per unit biomass by various species of zooplanktonic crustaceans and the ratio of their production to net primary production. The values for these ratios reported in table VII-4 for the calculation based on maximal coefficients of growth are similar to those reported by Petipa (1967) for *Acartia clausi* and *Calanus helgolandicus* in the open Black Sea in June. It should be recognized, however, that somewhat different methods were employed, so that the similarity may be fortuitous.

The evidence summarized in table VII-2 suggests that the mean concentration of phytoplankton in near-surface waters is an underestimate of the availability of food for *Calanus*. It has already been pointed out that there may be major differences between the metabolism of animals raised in the laboratory and those growing up naturally, and this could cause the laboratory-raised animals to mature at a small size when given a natural concentration of food.

Strickland, Solórzano, and Eppley (Part I, above) reported that, as is usually the case, detrital carbon (including associated bacteria) was present in higher concentrations than was phytoplankton, and it is possible that the wild animals feed to some degree on detritus as well as on phytoplankton. A recent study by Paffenhöfer and Strickland (1969) makes this doubtful. Organic carbon in the form of microzooplankton, while probably usable as food, was present in mean concentrations that would add only about 10 percent to the mean biomass of food available as phytoplankton (Beers and Stewart, Part VI, above).

Strickland (1968) and Eppley, Reid, and Strickland (Part III, above) showed detailed vertical profiles of chlorophyll for the studied area which indicated that concentrations of phytoplankton several times higher than the mean were often found in distinct layers or patches. If *Calanus* is able to aggregate in and feed upon these layers, as experimental work by Bainbridge (1953) would suggest, the mean concentration of phytoplankton underestimates the effective concentration of food even if phytoplankton alone is ingested.

REFERENCES

BAINBRIDGE, R.

1953. Studies on the interrelationships of zooplankton and phytoplankton. J. Mar. Biol. Ass. U.K., 32:385–447.

BEERS, J. R.

1966. Studies on the chemical composition of the major zooplankton groups in the Sargasso Sea off Bermuda. Limnol. Oceanogr., 11:520–528.

CONOVER, R. J.

1968. Zooplankton—life in a nutritionally dilute environment. Amer. Zool., 8:107–118.

CURL, H., JR.

1962. Analysis of carbon in marine plankton organisms. J. Mar. Res., 20:181–188.

LASKER, R.

1966. Feeding, growth, respiration, and carbon utilization of a euphausiid crustacean. J. Fish. Res. Board Can., 23:1291–1317.

MCGOWAN, J. A., and D. M. BROWN

1966. A new opening-closing paired zooplankton net. Scripps Inst. Oceanogr. Ref. 66-23. Unpubl. MS.

MULLIN, M. M.

1969. Production of zooplankton in the ocean: The present status and problems. Oceanogr. Mar. Biol. Ann. Rev., 7:293–314.

MULLIN, M. M., and E. R. BROOKS

1967. Laboratory culture, growth rate, and feeding behavior of a planktonic marine copepod. Limnol. Oceanogr., 12:657–666.

1970. Growth and metabolism of two planktonic, marine copepods as influenced by temperature and type of food. *In* J. H. Steele, ed., Marine food chains. Edinburgh: Oliver and Boyd. Pp. 74–95.

PAFFENHÖFER, G. A., and J. D. H. STRICKLAND

1969. A note on the feeding of *Calanus helgolandicus* on detritus. Mar. Biol., 5:97–99.

PETIPA, T. S.

1966. [On the energy balance of *Calanus helgolandicus* (Claus) in the Black Sea.] *In* Physiology of marine animals. Akad. Nauk S.S.S.R., Oceanogr. Comm. Moscow; Scientific Publ. House. Pp. 60–81. Eng. trans.

1967. [On the efficiency of the utilization of energy in the pelagic ecosystems of the Black Sea.] *In* Structure and dynamics of aquatic communities and populations. Akad. Nauk S.S.S.R., Inst. Biology Southern Seas. Kiev. Pp. 44–65. Eng. trans.

RICKER, W. E.

1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can., no. 119. 300 pp.

STICKLAND, J. D. H.

1968. A comparison of profiles of nutrient and chlorophyll concentrations taken from discrete depths and by continuous recording. Limnol. Oceanogr., 13:388–391.

UNIVERSITY OF CALIFORNIA, INSTITUTE OF MARINE RESOURCES

1968. Research on the marine food chain; progress report, Jan. 1967–June 1968. Part IV. Data record, coastal plankton survey, 1967. Section II. The plankton. Unpubl. MS (SIO Ref. 68-38; IMR Ref. 69-3).