CONTRIBUTION OF THE NET PLANKTON AND NANNOPLANKTON TO THE STANDING STOCKS AND PRIMARY PRODUCTIVITY IN MONTEREY BAY, CALIFORNIA DURING THE UPWELLING SEASON

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ABSTRACT

Net plankton and nannoplankton standing stocks and primary production were measured in Monterey Bay, Calif. from January through August 1972. Throughout the period of seasonal upwelling, the phytoplankton stocks were dominated by net plankton. Both fractions showed seasonal changes: the net plankton concentrations increased dramatically during upwelling, while nannoplankton concentrations were decreased. Nannoplankton growth rates exceeded net plankton rates at incubator light levels; however, at higher in situ light levels near the surface, this relationship appeared to be reversed.

Nannoplankton decreases may have been related to their selective removal from the area of upwelling by horizontal advection or selective grazing on the nannoplankton fraction. Net plankton dominance during upwelling has been related to their higher growth rates when populations are retained in shallow nutrient-rich nearshore waters.

Frequently, phytoplankton are divided into two size classes, depending on whether they are retained by fine mesh nets (net plankton) or pass through the mesh (nannoplankton). The inadequacy of net collections for estimating standing stocks or production is clear. The standing stocks of the two fractions and their relative contributions to primary productivity, however, are less well-known. The size distribution, which may be environmentally controlled (Semina 1972; Parsons and Takahashi 1973), is an important feature of the phytoplankton populations because the size of the primary producers may affect the length and efficiency of pelagic food chains (Ryther 1969; Parsons and LeBrasseur 1970). The purpose of this study was to determine the relative importance of the two fractions during the upwelling season in Monterey Bay, a neritic environment of the California Current system.

Most previous studies reported that the nannoplankton fraction usually exceeds the net plankton fraction, often accounting for 80 to 100% of the standing stocks and primary production (e.g., Steeman Nielsen and Jensen 1957; Holmes 1958; Yentsch and Ryther 1959; Kawamura 1961; Holmes and Anderson 1963; Teixeira 1963; Gilmartin 1964; Saijo 1964; Anderson 1965;

Saijo and Takesue 1965; Malone 1971a, c; Parsons 1972; McCarthy et al. 1974). Only a few authors reported net plankton dominated communities (Digby 1953; Subrahmanyan and Sarma 1965). It is difficult to compare these studies, however, because mesh sizes of 22 to 110 μm have been variously used to separate the net plankton and nannoplankton fractions.

The nannoplankton fraction may show little seasonal fluctuation, while the net plankton shows pronounced seasonal trends with periods of abundance corresponding to increased water temperatures (Yentsch and Ryther 1959), peak periods of primary production (Subrahmanyan and Sarma 1965), or seasonal upwelling (Malone 1971c). Malone (1971a) reported higher net: nanno ratios for standing stocks and production in neritic environments as compared with oceanic areas and pronounced onshore to offshore lowering of the ratio in the California Current region during upwelling (Malone 1971c). The growth rate (as indicated by the assimilation ratio = mg C mg Chl a^{-1} h^{-1}) of the nannoplankton fraction is greater than that of the net plankton fraction (Yentsch and Ryther 1959; Saijo and Takesue 1965; Malone 1971a, c).

Arguments presented for the predominance of net plankton or nannoplankton in a given environment relate cell area to volume ratios (Malone 1971a, c; Eppley 1972; Parsons and Takahashi 1973). There is a general relationship between

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cell size and the ability to take up nutrients (Dugdale 1967; Eppley et al. 1969; Eppley and Thomas 1969). Large species generally have higher half saturation constants (K_s) and may have higher maximum uptake rates (V_{max}), whereas small species have lower K_s and V_{max} (Dugdale 1967). Maximum net plankton growth rates are favored at higher ambient nutrient concentrations while nannoplankton reach their maximum growth rates at lower ambient nutrient levels. There is also a direct relationship of increasing cell size (or chain length) with increasing sinking rates (Smayda 1970), and larger cells and chain formers tend to be aggregated in areas of upward advection, while motile or positively buoyant cells tend to be concentrated in areas of downward advection (Stommel 1949). Net plankton will have a longer residence time in the euphotic zone and concentrate in areas of upwelling, while the nannoplankton (if the population is primarily motile flagellates) will be concentrated in areas of downwelling.

Parsons and Takahashi (1973) related the growth rate (μ) to physiological characteristics of the cell (maximum growth rate, half saturation constants for nutrients and light, and sinking rates) and environmental conditions (incident radiation, extinction coefficients, mixed layer depth, and upwelling rates) and used the relationship to explain characteristic phytoplankton cell size in a number of environments. Recently, Laws (1975) expanded the Parsons and Takahashi model and showed that under certain light conditions the decreasing respiration rate with increasing cell size may regulate the growth rate of large versus small cells.

The effect of grazing on the net:nanno ratios and, conversely, the size of the primary producers on food chains have not been well documented. Grazing may ultimately control net plankton stocks (Malone 1971c; Ryther et al. 1971) and determine the lower net:nanno standing stock ratios in oceanic as opposed to neritic areas (Malone 1971a). Grazing has been suggested as the primary cause for failure of phytoplankton stocks to develop in otherwise favorable waters (Mc Allister et al. 1960; Strickland et al. 1969). Shorter food chains have been shown for some clupeid fishes which feed directly on the large phytoplankton species (e.g., Bayliff 1963; Rojas de Mendiola 1969; Dhulkhed 1972) and for herbivorous euphausids in the diatom-rich antarctic region (Marr 1962). The general argument for larger phytoplankton cells resulting in shorter, more efficient food chains may not always apply to the smaller grazers, as Parsons and LeBrasseur (1970) have reported on selective feeding related to cell shape.

Previous studies have been made on the hydrographic seasons in Monterey Bay and their relationship to the seasonal phytoplankton blooms (Bolin and Abbott 1963; Abbott and Albee 1967). Malone (1971c) reported the seasonal variability of the net plankton and nannoplankton in the California Current, which included one deep station on the edge of Monterey Bay. The present study was part of a monthly sampling program conducted by Moss Landing Marine Laboratories to provide information on the hydrographic conditions and plankton populations in Monterey Bay, particularly from the extensive shallow areas of the bay. Although it was not possible to carry this study through a complete seasonal cycle, information is presented for the upwelling period, when seasonal blooms of phytoplankton appear in Monterey Bay.

MATERIALS AND METHODS

Measurements of primary productivity and phytoplankton standing stocks were made at stations 3 and 8 for the period January through August 1972 and at station 15 for the period June through August 1972 (Figure 1). The stations were located over the Monterey Submarine Canyon at depths of 110, 240, and 718 m, respectively. Samples were taken monthly during hydrographic and plankton cruises conducted by Moss Landing Marine Laboratories and, occasionally, between these periods on instructional cruises. Sampling times varied between cruises but fell between 0700 and 1100 h.

Samples were collected with 5-liter Niskin water sampling bottles from depths corresponding to 100, 50, 25, 10, and 1% light penetration levels as measured with a submarine photometer or calculated using the relationship: depth of 1% light = 3.5 × Secchi disk (Silver and Hansen 1971a). Hydrographic parameters (salinity, ‰; temperature, °C; O_2) and nutrients (PO_4, NO_3, NO_2, NH_3, SiO_2) were samples at standard depths (Broenkow and Benz 1973).

Primary productivity was measured using the carbon-14 method (Steeman Nielsen 1952). For each depth two light and one dark bottles were innoculated with 5 or 10 μCi of $Na_2^{14}CO_3$. The
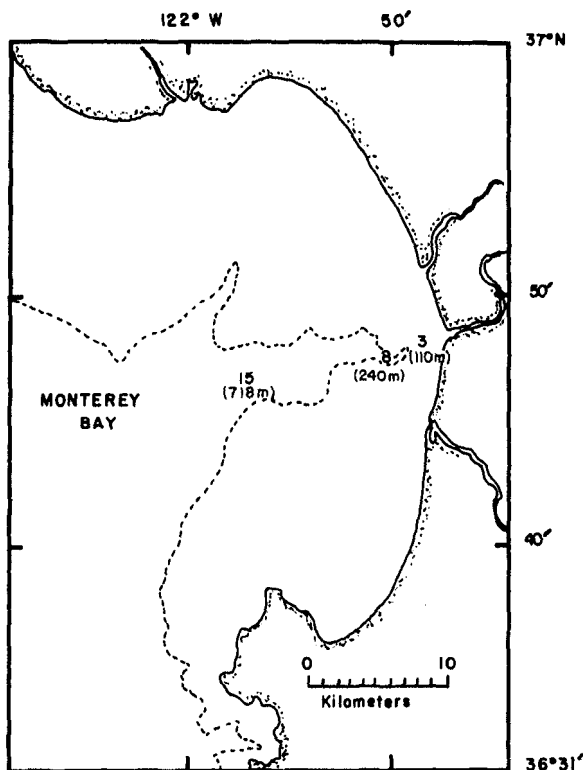
FIGURE 1.—Location of stations in Monterey Bay. Broken lines indicate the position of the 100-fathom (183-m) contour line.

samples were incubated immediately after collection for 3 to 4 h in a shipboard incubator (Doty and Oguri 1958) using Luxor Magnalux fluorescent lamps[2] (approx. 0.06 langley min^{-1}). Neutral density filters of 50, 25, 10, and 1% transmittance were used on subsurface samples.

The net plankton and nannoplankton fractions were separated by passing the samples through a 22-μm Nitex-net filter (net plankton) and then a Gelman, type A glass-fiber filter having 0.3-μm pore size (nannoplankton). Both filters were washed with approximately 20 ml of freshly filtered seawater and placed directly in scintillation fluor for counting at a later time.

All samples were counted for at least 10 min with a Nuclear Chicago (Unilux II) scintillation counter. Carbon uptake was calculated as outlined in Strickland and Parsons (1968). Since Malone (1971b) reported no diurnal periodicity in assimilation ratios in the California Current regions, daily production was estimated by using

the sunrise to sunset interval as the day length and multiplying by the hourly production rates that were determined during the first part of the day.

Phytoplankton standing stocks were measured as chlorophyll a by using the fluorometric method of Holm-Hansen et al. (1965). The Turner fluorometer (model 111) was calibrated using the spectrophotometric method for chlorophyll a as outlined by Strickland and Parsons (1968). The two size fractions were separated by taking two replicate samples from each depth and passing one through a Gelman glass-fiber filter (total chlorophyll) while the other sample was filtered through 22 μm Nitex-net filter and then a glass-fiber filter (nannoplankton). Both filters were immediately frozen, stored in the dark, and analyzed within a month after collection. Net plankton was calculated as the difference between total chlorophyll and nannoplankton chlorophyll.

Productivity and chlorophyll a values determined for the discrete samples were integrated to the depth of the 1% light level by trapezoidal approximation. Carbon:chlorophyll a ratios vary widely and depend on light and nutrient conditions. For most of the study, nutrient levels were high and a C:Chl a ratio of 40 was used to convert chlorophyll a to carbon biomass (Lorenzen 1968; Eppley et al. 1970; Eppley et al. 1971). Phytoplankton growth rate and standing stock doubling time were calculated using exponential growth expression.

RESULTS

In January, the weak thermal gradient in the upper 50 m (Figure 2) is indicative of the Davidson Current period, when the subsurface countercurrent extends to the surface and flows northwestward on the inshore side of the California Current (Reid et al. 1958; Bolin and Abbott 1963; Smethie 1973). Rising isotherms and nitrate isopleths from February through May indicate upwelling over the Monterey Submarine Canyon. After May there was a slacking or an end to upwelling, and the isotherms and isopleths are found progressively deeper as denser upwelling waters subside. In July and August, conditions of the oceanic period were evident with low nutrient levels, higher surface temperatures, and lower salinities; however, upward movement of the isotherms and isopleths in August may indicate a developing upwelling pulse.
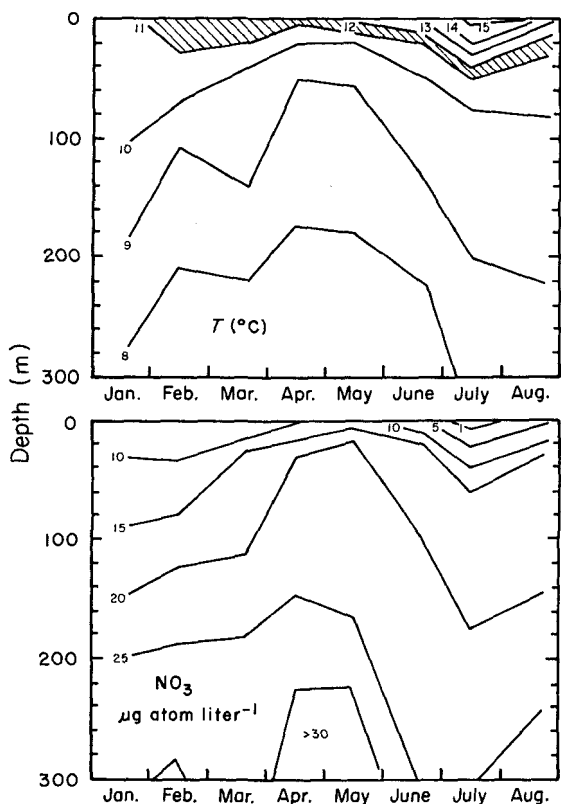
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FIGURE 2.—Average depth of isotherms and nitrate isopleths for hydrographic stations samples over Monterey Submarine Canyon, January through August 1972 (data from Broenkow and Benz 1973).
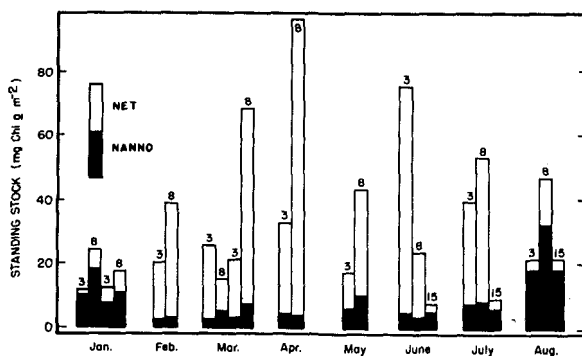

FIGURE 3.—Phytoplankton standing stocks in the euphotic zone, January through August 1972. Numbers over histogram bars refer to stations.
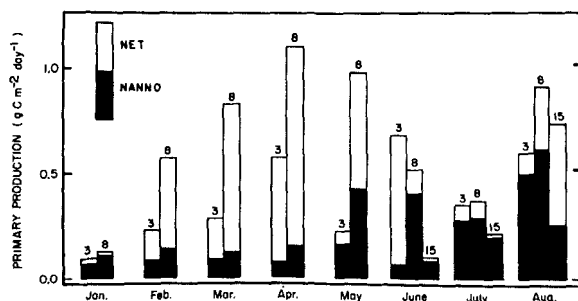

FIGURE 4.—Estimated primary production in the euphotic zone, January through August 1972. Numbers over histogram bars refer to stations.

Standing Stocks and Primary Production

In January, at the end of the Davidson Current period, standing stocks were near their lowest levels and nannoplankton dominated (Table 1, Figure 3). Throughout the period from February through July, however, the net plankton fraction exceeded the nannoplankton. In August, the standing stocks were again predominantly nannoplankton. Estimated primary production followed the general trend shown by the standing stocks (Figure 4), but lower production per unit chlorophyll for the net plankton fraction in January and July is apparent. The highest standing stock was measured in April at the time the isotherms and nutrient isopleths reached their highest positions (see Figure 2). At this peak, the stocks were 97% net plankton, and net plankton concentrations in the euphotic zone ranged from 4.63 to 6.88 mg Chl a m^{-3}. Concentrations of net

plankton as high as 9.26 mg Chl a m^{-3} were recorded in June. During the April peak, the corresponding total productivity was approximately 1.1 g C m^{-2} day^{-1}. It is difficult to equate incubator productivity to in situ productivity; however, these values are similar to productivity estimates calculated from nutrient uptake and oxygen production in the water column (Smethie 1973).

The changes in the ratios of the two fractions were largely a result of changes in the biomass of the net plankton fraction. The net plankton fraction experienced large seasonal changes in concentrations, and occasionally there was significant vertical stratification within the water column; however, nannoplankton fluctuations fell within a much narrower range (Figure 5). There were significant differences in the average concentrations in the euphotic zone of the two fractions in all three hydrographic seasons, and both fractions showed significant differences between seasons (Mann Whitney U test; $P = 0.01$). The

TABLE 1. — Standing stock, primary production, and growth rate (μ) of the net plankton and nannoplankton in Monterey Bay for the period January through August 1972.

Date	Station	Euphotic zone depth (m)	Phytoplankton standing stock (mg Chl a m^{-2})		Primary production (g C m^{-2} day^{-1})		Growth rate, (doubling day^{-1})	
			Net	Nanno	Net	Nanno	Net	Nanno
20 Jan.	3	20	2.2	10.2				
	8	28	5.8	18.5				
27 Jan.	3	15	4.6	7.8	0.017	0.076	0.1	0.3
	8	35	6.0	12.0	0.012	0.113	0.1	0.3
15 Feb.	3	15	18.2	2.4	0.142	0.084	0.3	0.9
	8	15	36.4	3.0	0.437	0.137	0.4	1.1
1 Mar.	3	12	23.2	2.8				
	8	35	10.0	4.4				
8 Mar.	3	10	17.6	3.2				
	8	40	61.0	7.6				
23 Mar.	3	11			0.262	0.116		
	8	15			0.706	0.126		
18 Apr.	3	23	29.8	3.0	0.491	0.075	0.5	0.7
	8	16	95.4	2.6	0.955	0.153	0.5	1.3
16 May	3	30	11.6	5.8	0.058	0.160	0.2	0.8
	8	30	34.0	9.6	0.558	0.418	0.5	1.1
20 June	3	10	73.0	3.4	0.612	0.067	0.3	0.6
	8	20	20.8	3.4	0.401	0.115	0.6	0.9
	15	30	2.0	5.0	0.011	0.093	0.2	0.5
20 July	3	20	31.6	8.2	0.172	0.276	0.2	0.9
	8	50	45.0	8.6	0.085	0.286	0.1	0.9
	15	65	7.6	9.6	0.010	0.207	>0.1	0.6
29 Aug.	3	30	[1]1.4	20.2	0.094	0.507	1.4	0.7
	8	30	[1]4.6	32.4	0.309	0.612	0.6	0.6
	15	29	[1]3.2	18.7	0.488	0.252	2.3	0.4

[1]Value appears low, corresponding growth rate (μ) may be too high.

seasonal effect during upwelling seems to be a reduction of the average concentration of nannoplankton and an increase in the average concentration of net plankton.
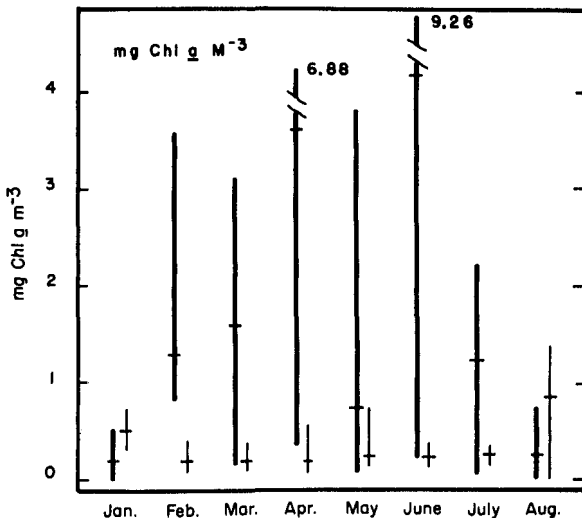

FIGURE 5.—Seasonal changes in the concentration of net plankton chlorophyll (heavy line) and nannoplankton chlorophyll (thin line). (Davidson Current period—January; upwelling period—February through June; oceanic period—July, August.) Average and range of concentrations in the euphotic zone are shown. The number of samples for each month is given in Table 1.

Standing Stock Growth Rate

The growth rate, μ (doublings day^{-1}), and assimilation ratio (mg C mg Chl a^{-1} h^{-1}), of the nannoplankton fraction was greater than the corresponding value for the net plankton during all three seasons, and both fractions showed their highest growth rate during the upwelling period; however, assimilation ratios of the surface samples for both fractions were higher in the oceanic period than during upwelling (Table 2). There is no correlation ($P > 0.10$) between the growth rates of either phytoplankton fraction and average nutrients (NO_3, SiO_2) in the upper 10 m on individual sampling days for the three hydrographic periods.

Net plankton growth rates exceeded nannoplankton growth rates in only two of the samples;

TABLE 2. — Growth rates of the standing stocks in the euphotic zone and assimilation ratios of surface samples.[1]

Hydrographic period	Growth rate, μ (doublings day^{-1})		Assimilation ratio (mg C mg Chl a^{-1} h^{-1})	
	Net	Nanno	Net	Nanno
Davidson Current	0.1 ± 0.0(2)	0.3 ± 0.1(2)	0.4 ± 0.2(2)	2.2 ± 0.5(2)
Upwelling	0.4 ± 0.1(9)	0.9 ± 0.2(9)	2.7 ± 1.5(9)	5.2 ± 2.2(9)
Oceanic	0.2 ± 0.3(4)	0.7 ± 0.2(6)	3.0 ± 1.6(3)	10.3 ± 1.2(4)

[1]Growth rates were calculated from daily productivity and standing stock estimates integrated to the depth of 1% light penetration, while assimilation ratios are for surface samples incubated at 0.06 langley min^{-1}. $\bar{X}$ ± SD(N); questionable data indicated in Table 1 have been excluded.

however, the growth rates were determined at incubator light levels which were not representative of in situ conditions. The regression of light level on the ratio of the growth rates (μ net:μ nanno) is significant ($P < 0.01$) during the upwelling months (Figure 6). Light levels approximately equivalent to full incubator light are found at depths of 8 to 15 m during the upwelling period, and the upper one-fourth to one-third of the euphotic zone receives light which is in excess of incubator light levels.
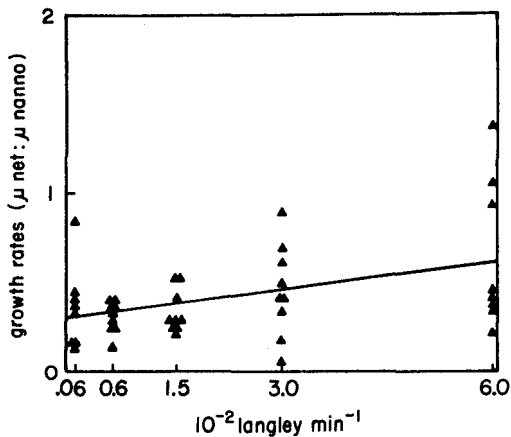

FIGURE 6.—Regression of incubator light levels on the net:nanno growth rates.

Distribution in the Water Column

Since nannoplankton concentrations were relatively homogeneous in the water column, maxima were often not well defined. Net plankton maxima, however, were usually apparent and corresponded to the depth of the seasonal pycnocline. There was no regularly observed depth relationship between nannoplankton and net plankton maxima, and they often were at the same depth. Phaeophytin peaks appeared at the surface and in conjunction with, or just below, the chlorophyll maxima. High NH_3 concentrations in the deeper phaeophytin maxima may be indicative of grazing on the phytoplankton stocks in the chlorophyll maxima (see Figures 7-10).

During the Davidson Current period there is little vertical stability in the water column, and the net plankton stocks are poorly developed (Figure 7). With the onset of upwelling net plankton stocks develop above the strong, shallow pycnocline (Figures 8, 9) and the nanno-
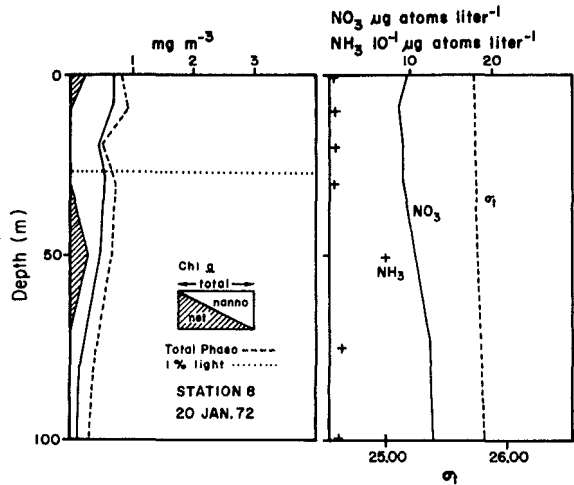

FIGURE 7.—Vertical distribution of phytoplankton standing stocks, phaeophytin, and hydrographic parameters during the Davidson Current period.
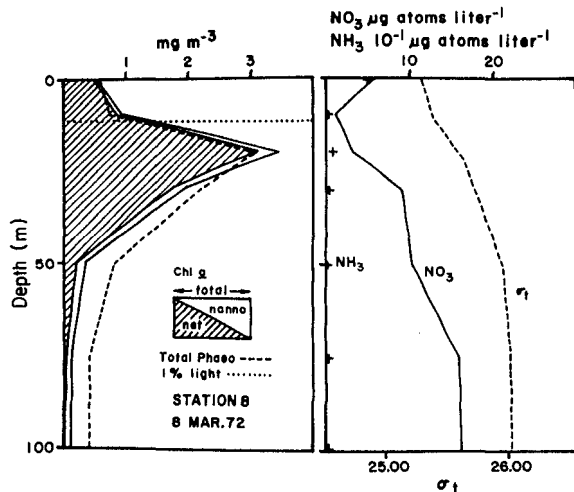

FIGURE 8.—Vertical distribution of phytoplankton standing stocks, phaeophytin, and hydrographic parameters during upwelling period. Station was sampled during a flowing tide.

plankton stocks decline. With strong or persistent upwelling, the pycnocline may intersect the surface and the phytoplankton stocks are concentrated in a relatively shallow layer (Figure 9).

After a slacking of upwelling the denser waters subside and the pycnocline depths become progressively deeper. The surface layer can be strongly stratified by the onshore movement of warmer, low salinity oceanic water, and nutrient concentrations in the near surface waters are low during the oceanic period. The net plankton
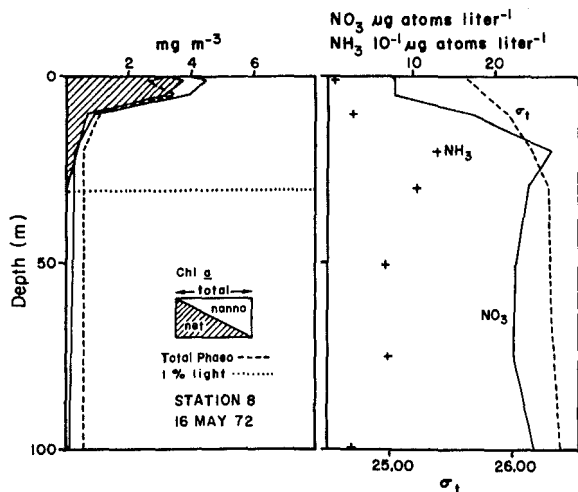
FIGURE 9.—Vertical distribution of phytoplankton standing stocks, phaeophytin, and hydrographic parameters during upwelling period. Station was sampled during an ebbing tide.
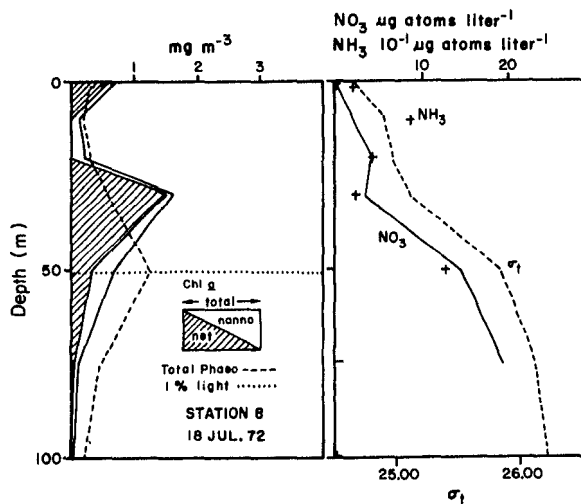

FIGURE 10.—Vertical distribution of phytoplankton standing stocks, phaeophytin, and hydrographic parameters during the oceanic period.

maximum remains associated with the sinking pycnocline and, although nutrients do not reach limiting concentrations in the pycnocline, light levels are below optimal intensity for maximum growth rates (Figure 10).

Broenkow and McKain (1972) demonstrated that tidal effects have a marked influence on the distribution of hydrographic parameters over the canyon: during a flow tide there is a down-canyon current and isotherms and isopleths over the canyon are depressed; conversely, during an ebb tide the flow is up the canyon and isotherms and isopleths are nearer the surface. The source waters for the down-canyon flow are subsurface waters from the shallow areas adjacent to the canyon. These tidal effects can be identified in the distribution of the phytoplankton stocks (Silver and Hansen 1971b), but their importance is unknown. The chlorophyll a maximum at station 8 (in Figure 8) appears to be an intrusion of stocks developed in shallower areas and carried to depth by the down canyon flow during the flow tide. Station 3 was sampled earlier during an ebb tide, and the sigma-t surface at 50 m ($\sigma t = 26.14$) was found deeper than 100 m at station 8 (see Figure 8). At a full ebb tide the pycnocline and the standing stocks may be located very near the surface (Figure 9).

DISCUSSION

The net plankton-dominated blooms that developed during this study were similar to those described by Bolin and Abbott (1963) and Abbott and Albee (1967) in their close association with seasonal upwelling and in their composition (i.e., the net plankton was dominated by colonial diatoms—M. Silver unpubl. data[3]). Malone (1971c) noted an increase in net plankton fraction during the upwelling season; however, he reported net plankton dominated stocks only during strong upwelling pulses. Malone also reported a marked decrease in net plankton chlorophyll and productivity between inshore and offshore stations near the end of the upwelling season. Although these studies cannot be directly compared, they suggest phytoplankton blooms which develop during upwelling are mostly net plankton forms, and higher standing stocks may develop inshore.

There seems to be a fundamental contradiction in the measured growth rates of the two fractions and the observed standing stocks. The growth rates of the nannoplankton were consistently higher than those of the net plankton, whereas the standing stocks of nannoplankton decrease and the stocks of net plankton increase during the upwelling season. The observed development of the stocks could result theoretically from one or a combination of the following conditions: 1)

[3]The unpublished data supplied by M. Silver can be found in a data report filed in 1971-72 at Oceanographic Services, Inc., 135 East Ortega Street, Santa Barbara, CA 93101.

the nannoplankton fraction may be selectively removed from the area by horizontal advection because of their low sinking rates; 2) nannoplankton may be selectively grazed; 3) environmental conditions may favor higher net plankton growth rates.

Malone (1971c) discussed the argument for selective removal of nannoplankton from upwelling areas by horizontal advection. Briefly restated, nannoplankton cells tend to have slower sinking rates than net plankton cells (or they are motile) and in convection cells they will tend to be removed from the areas of upward movement and concentrated in areas of downward movement (Stommel 1949). In upwelling areas then, nannoplankton may be selectively removed by mass transport of surface waters offshore. There is little direct evidence to show that this takes place; however, the advection hypothesis is supported by the observed decrease in nannoplankton stocks between the Davidson Current period and the upwelling period. During the Davidson Current period there is a general onshore movement of surface waters with water sinking along the coast, while during the upwelling period the circulation is reversed and water moved upward along the coast, and the surface waters are transported offshore (Skogsberg 1936; Bolin and Abbott 1963). Malone (1971c) found the level of the nannoplankton stocks remained relatively constant throughout the year; however, he reported that during periods of onshore water movement there was an enhancement which could be attributed to concentrating the nannoplankton in an area of downward water movement.

The decrease in nannoplankton stocks reported in the present study may have been the result of selective grazing by microzooplankton and planktotrophic larvae (Thorsen 1950; Beers and Stewart 1969; Parsons and LeBrasseur 1970). In this area many of the benthic invertebrates have their reproductive season during the spring (M. Houk pers. commun.)[4]; increased grazing pressure by these larvae may have caused the decrease in nannoplankton stocks. However, the extent of grazing on either fraction of the phytoplankton in Monterey Bay is not known. Zooplankton samples were collected as part of the routine sampling program, but gelatinous

and colonial phytoplankton could not be separated from the zooplankton for biomass estimates.

Throughout the period of upwelling, nitrate levels in the upper 10 m remained high (> 5 μg atoms liter^{-1}) and the chlorophyll maximum was frequently located near the surface. At these shallow depths light levels were in excess of incubator light levels (0.06 langley min^{-1}). Eppley et al. (1969) have shown that the diatoms *Skeletonema costatum* and *Ditylum brightwellii* grow faster than *Coccolithus huxleyi* at high light levels (0.1 langley min^{-1}) when nitrate levels are in excess of 0.8 μg atoms liter^{-1}, while at lower light levels (0.02 langley min^{-1}), the situation is reversed and *C. huxleyi* will grow faster at any nitrate concentration. In situ nutrient and light conditions near the surface during the upwelling period should favor net plankton growth.

In the present study and in that of Malone (1971c), growth rates of the net plankton were lower than the growth rates of the nannoplankton; however, the two fractions responded differently to increasing light as shown by the ratio of the growth rates (μ net:μ nanno) increasing with higher light levels (Figure 6). The regression predicts that net plankton growth rates would exceed the nannoplankton growth rates at light levels similar to those where Eppley et al. (1969) showed a reversal of growth rate relationships. Estimated light levels in the upper part of the euphotic zone are higher than the incubator light levels which have been used in this study and that of Malone. Since the net plankton growth rates show greater enhancement with increasing light than the nannoplankton, light levels in the upper water column may favor the growth of the net plankton fraction and lead to net plankton domination of the standing stocks.

Laws (1975) suggested that, under certain environmental conditions, large cells may realize a higher net growth rate because of a decreasing respiration rate with increasing cell size. In Laws' model, when surface light levels are low or the product of the attenuation coefficient and mixed layer depth is large, integral productivity efficiency is low and respiration losses become more important. During the present study, however, under low light levels, the net growth rates of the smaller cells (nannoplankton) exceeded larger cells, and the phytoplankton populations were net plankton dominated at a time when the mixed layer was extremely shallow.

Notwithstanding the possible effects of selec-

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[4]M. Houk, Department of Natural Science, University of California, Santa Cruz, CA 95064.

tive grazing on the nannoplankton or their selective removal by horizontal advection, the development of the upwelling bloom in Monterey Bay is largely a result of the increase in the net plankton fraction and may be explained in terms of conditions which are favorable for net plankton growth. High nutrient concentrations can be maintained in the euphotic zone by downward mixing from the surface which extends below the pycnocline or by a continual input of nutrients to the surface waters by upwelling. Optimal light levels, however, are found only in the upper part of the euphotic zone. The combination of these conditions that constitute optimal growth conditions for the net plankton fraction occur when the phytoplankton stocks are restricted to a shallow mixed layer above the pycnocline which has been "pushed up" by upwelling water. Optimal growth conditions vary spatially and seasonally and may be primarily responsible for the net plankton and nannoplankton relationship observed in Monterey Bay.

Nutrients do not appear to limit the growth rates of either fraction as correlation coefficients of nutrient levels with growth rates were not significant and, although nutrient levels change seasonally, Malone (1971c) reported little seasonal variation in assimilation rates. Light levels, however, are potentially limiting a short distance from the surface and can influence the ratio of net:nanno growth rates.

An increase in the depth of the mixed layer results in a decrease in the average light exposure for phytoplankton cells in the mixed layer (Parsons and Takahashi 1973). The net plankton fraction will be more strongly influenced than the nannoplankton because their optimal growth rates occur at light levels near the surface, and their vertical distribution is strongly controlled by water movement. Upwelling water movements result in a shallow pycnocline and shallow mixed layer; with a slack in the upwelling rate, the pycnocline sinks and there is a deeper mixed layer. In the present study, net plankton maxima were concentrated above the pycnocline, whereas no particularly strong relationship between the nannoplankton maxima were observed (the nannoplankton maxima were often not well defined). Malone (1971c) showed that the net plankton maxima were located below the nannoplankton maxima during periods when upwelling was slack or that both were located at the surface during periods of upwelling, and he emphasized the

role of upward movement in controlling the vertical distribution of the net plankton fraction.

Malone (1971c) showed an onshore to offshore decrease in the ratio of net:nanno standing stocks. Yoshida (1967) showed the potential for a narrow zone of stronger upwelling associated with the edge of the continental shelf where the effects of upwelling are maximal at the edge of the shelf and decrease exponentially shoreward and seaward. A decrease in the upwelling rate away from the continental shelf would result in reduced suspension of sinking cells, a deeper mixed layer, and lower average light levels for phytoplankton cells in the mixed layer and could reduce the net:nanno growth rate ratio. Malone's data showed shallow mixed layers during periods of strong upwelling at inshore stations and a trend for an increasing mixed layer depth offshore. In Monterey Bay during the upwelling season, the mixed layer is frequently shallow or the pycnocline intersects the surface. There are considerable amounts of hydrographic data which show this characteristic distribution (Broenkow and Benz 1973) and corresponding phytoplankton standing stock data which show significant stratification of the phytoplankton standing stocks above the shallow pycnocline (Silver see footnote 3).

The depth of the pycnocline and mixed layer vary seasonally in response to the upward movement of isotherms during upwelling and the sinking of isotherms when upwelling ceases. Upwelling, however, is not a continuous process and may be particularly sporadic near the end of the upwelling season (Bolin and Abbott 1963; Smethie 1973). Malone (1971c) reported net plankton dominated stocks only during periods of strong upwelling, which suggests that in deep water continual upwelling is necessary to maintain optimal growth conditions for the net plankton fraction. During the present study the net plankton fraction dominated the phytoplankton populations in shallow water throughout the upwelling season. This evidence and previous evidence for an offshore decrease in the net:nanno ratios (Malone 1971c) suggest that physical processes in shallow water are sufficient to maintain net plankton populations and mitigate the lack of continual upwelling.

The physical processes in shallow water that could serve to maintain favorable growth conditions for the net plankton fraction or maintain the population between periods of favorable con-

ditions are poorly known. Tidal mixing and increased turbulence in shallow water could facilitate cell suspension of sinking populations or resting spores, and increase nutrient input to the surface waters. Over Monterey Canyon and, to a lesser extent, in the shallow areas of the bay, the vertical distribution of nutrients (Broenkow and McKain 1972; Smethie 1973) and phytoplankton stocks (Silver and Hansen 1971b; Silver see footnote 3) are strongly influenced by tidal effects. Turbulence and mixing in deep water results in a decrease in the average amount of light to which a phytoplankton cell is exposed; however, in shallow water the depth of mixing is limited by the bottom and mixing here may result in resuspension of sinking cells. Many of the neritic diatoms form resting spores which sink to the bottom and may be an important source of innoculum to initiate blooms if they are resuspended by turbulence during favorable growth conditions.

The decline in the net plankton populations during this study corresponded to the influx of oceanic waters in July. The end of net plankton domination of the population appears to have been the result of the low nutrient concentrations in the oceanic surface waters and subsidence of previously upwelled waters and its entrained net plankton populations. During oceanic conditions, nutrient levels in the surface waters favor the growth of nannoplankton and the light levels in the sinking net plankton maxima are not optimal for growth. Malone (1971c) suggested, however, that the net plankton are ultimately limited by grazers as the grazing index (phaeo:Chl a) increased and the netplankton concentrations decreased even before the end of the upwelling period. Direct evidence for the extent of grazing in Monterey Bay is not available; however, when upwelling becomes sporadic and periodic influxes of oceanic water occur, the stage is set for a decline in the net plankton fraction without the need for an increase in grazing pressure.

ACKNOWLEDGMENTS

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