THE RELATIVE IMPORTANCE OF NANNOPLANKTON AND NETPLANKTON AS PRIMARY PRODUCERS IN THE CALIFORNIA CURRENT SYSTEM

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ABSTRACT

Nannoplankton and netplankton primary productivity and standing crop were measured on a seasonal basis in Monterey Bay (October 1969 to February 1971) and along four transects of the California Current between lat 35° and 50° N. Nannoplankters accounted for 60 to 99% (mean = 86%) of the observed productivity and standing crop both inshore and offshore under oceanic conditions. Seasonal and geographical variations in the nannoplankton fraction were remarkably stable, and variations in phytoplankton productivity and standing crop were due primarily to the netplankton. The assimilations ratios of both fractions were relatively constant.

Increases in the netplankton fraction were closely coupled with the occurrence of coastal upwelling, and netplankton productivity and standing crop exceeded that of the nannoplankton only during the strongest upwelling pulses. These increases were probably due to the suspension effect of positive vertical advection and to increases in ambient NO_3-N concentrations above 1 to 3 μM. Decreases were in response to increases in grazing pressure and downward water movements. A model is suggested to account for the following observations: (1) the nannoplankton fraction varied within narrow limits compared with the netplankton; (2) nannoplankton assimilation ratios (and presumably growth rates) were consistently high and twice those of the netplankton; and (3) netplankton productivity and standing crop increased relative to the nannoplankton during periods of upwelling. The model is based on the response of particles of varying sinking rates to vertical and horizontal advection, and on the degree of coupling between the production of organic matter by primary producers and grazing by primary consumers.

The phytoplankton can be divided into two size classes based on their retention by fine mesh nets (aperture size 20 to 90 μ). Those retained are commonly called "netplankton" while those which escape are referred to as "nannoplankton." Seasonal and geographic variations in netplankton and nannoplankton primary productivity and standing crop are neither well documented nor understood. Previous investigations in both temperate (Yentsch and Ryther, 1959; McAllister et al., 1959; Gilmartin, 1964; Anderson, 1965) and tropical marine environments (Steeman Nielsen and Jensen, 1957; Holmes, 1958a; Teixeira, 1963; Saijo and Takesue, 1965; Malone, in press a) have demonstrated that the nannoplankton are usually responsible for 80 to 100% of the observed phytoplankton productivity and standing crop. Netplankton productivity is often higher in neritic than in oceanic waters (e.g., Steeman Nielsen and Jensen, 1957; Malone, in press a) but rarely exceeds that of the nannoplankton. However, neritic phytoplankton communities dominated by the netplankton in terms of cell number (Digby, 1953) and chlorophyll concentration (Subrahmanyan and Sarma, 1965) have been reported.

The ecological significance of these two size classes lies in the role of cell size and surface area-to-volume (A/V) ratios in the dynamics of phytoplankton productivity and energy flow through pelagic food chains. Small cells generally have shorter generation times and higher growth rates in a given environment than do larger cells (Findenegg, 1965; Williams, 1965; Eppley and Sloan, 1966; Eppley and Thomas, 1969; Eppley et al., 1969). Recent observations on the kinetics of nutrient uptake by phytoplankton (Eppley et al., 1969) indicate that the half-saturation constants (K_s) for nitrate and ammo-

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nium uptake vary in proportion to cell size, presumably a consequence of the high A/V ratios of smaller cells (Munk and Riley, 1952). Some evidence is also available that maximum uptake rates (V_m), while not species specific, do increase with increasing cell size (Dugdale, 1967; Eppley et al., 1969) so that netplankters with high K_s and V_m values would be favored when nitrate concentrations are high while nannoplankters with low K_s and V_m values would be favored when nitrate concentrations are low.

High A/V ratios facilitate suspension (Munk and Riley, 1952; Smayda and Boleyn, 1966a, b; Eppley et al., 1967) increasing the potential residence times of cells in the photic zone under stratified conditions. Also, since sinking rates generally increase as cell size increases, larger cells will tend to be concentrated in regions of upward water flow while smaller cells will be distributed along a gradient toward regions of downward water flow (Stommel, 1949; Semina, 1968). In this way, small cells will tend to be spread over a greater volume than larger cells, and motile cells seeking to maintain their position in the water column will be concentrated in regions of downward flow (Hutchinson, 1967).

In addition, the distribution of productivity and biomass among different size classes of phytoplankton should be reflected in the distributions and abundances of herbivores which selectively graze on the basis of particle size. Nannoplankters appear to be the preferred food of many planktotrophic larvae (Bruce et al., 1940; Thorson, 1950) and microzooplankton (Beers and Stewart, 1969; Parsons and Le Brasseur, 1970), while herbivorous copepods actively select netplankton species (Harvey, 1937; Mullin, 1963; Conover, 1966; Mullin and Brooks, 1967; Richman and Rogers, 1969). Phytoplankton cell size may also affect the efficiency of energy transfer to large predators, since nannoplankton-based food chains appear to require one or two additional energy transfers to reach a given sized consumer than do netplankton-based food chains (Ryther, 1969; Parsons and Le Brasseur, 1970).

The California Current system and Monterey Bay provide ideal environments in which to study variations in netplankton and nannoplankton productivity and standing crop, since nutrient concentrations and vertical water movements vary markedly both seasonally and geographically. The California Current system is discussed by Reid et al. (1958), and the monthly mean charts of geostrophic flow have been prepared by Wyllie (1966). The southerly flow of the California Current is typically strongest during the spring and summer when northerly winds are best developed. At this time the coastal boundary of the Current is marked by upwelling. During the fall and winter northerly winds are weak or reversed, and a coastal countercurrent (the Davidson Current) often develops between the California Current proper and the coast. Thus, the hydrography of the coastal region off California is generally characterized by upward water movements and high nutrient concentrations during the spring and summer, and downward water movements and low nutrient concentrations during the fall and winter.

The annual cycle of hydrographic conditions in Monterey Bay has been described by Bolin and Abbott (1961) and Bolin (1964). Skogsberg (1936) divided the annual cycle in the upper 100 m into three hydrographic periods:

1. An Upwelling Period (March to September) characterized by low surface temperatures (9.5° to 11.5° C), high salinities (33.2 to 33.9‰), and high nutrient concentrations (>2.0 μM PO_4-P, >5.0 μM NO_3-N, and >10.0 μM SiO_3-Si).
2. An Oceanic Period (September to November) characterized by high surface temperatures (12.0° to 15.0° C), decreasing salinities (33.0 to 33.6‰) and low nutrient concentrations (0.2 to 2.0 μM PO_4-P, 0.0 to 0.5 μM NO_3-N, and 1.0 to 10.0 μM SiO_3-Si).
3. The Davidson Current Period (November to March) characterized by decreasing temperatures (11.0° to 13.5° C), low salinities (32.4 to 33.2‰), and low nutrient conditions.

Water of oceanic origin is brought into the Bay during both Oceanic and Davidson Current Periods, at first passively as the high density upwelled water begins to subside and then actively when southerly winds prevail. Since both periods are characterized by a downward flux of water (subsidence and downwelling) and low nutrient concentrations in the upper half of the photic zone, they will be consolidated and referred to as the "Oceanic Period."

The purpose of this study is to document temporal and spatial variations in nannoplankton and netplankton productivity and standing crop and to evaluate these variations with respect to dissolved inorganic nitrogen concentrations, vertical water movements, and grazing pressure.

METHODS AND MATERIALS

Measurements of netplankton and nannoplankton primary productivity and standing crop were made at 17 stations in the California Current system between lat 35° and 50° N during July, August, and November 1970, and at California Cooperative Oceanic Fisheries Investigations (CalCOFI) station 3 in Monterey Bay from October 1969 to February 1971 (Figure 1). The latter station is located over the Monterey Submarine Canyon in about 1000 m of water (lat 36°46.8′ N, long 122°01′ W). All data were collected during cruises of the RV *Proteus* (Stanford University).

Netplankton and nannoplankton photosynthetic capacities (rate of carbon fixation as measured by the carbon-14 technique at light saturation), chlorophyll-a concentrations, and cell numbers were estimated from duplicate water samples collected from 2 m below the surface with two Van Dorn bottles. The duplicate Van Dorn bottle samples were taken 3 hr before local apparent noon and again 3 hr after local noon. Four light and two dark bottles (a total of 12 125-ml Pyrex bottles) were drawn from each sample, inoculated with $5\,\mu c$ of $Na_2{}^{14}CO_3$, and incubated under fluorescent light (about 0.06 langley/min) for 2 to 3 hr at sea-surface temperatures (Doty and Oguri, 1958). Following incubation, half of the light and dark bottles from each Van Dorn sample were fractionated by passing the water first through Nytex-net discs with $22\text{-}\mu$ apertures (netplankton) and then through HA Millipore[2] filters (nannoplankton). The remaining four light and two dark bottles were HA Millipore filtered directly as controls. The filter discs were washed with about 30 ml of filtered seawater, dried in a CO_2 free atmosphere, and their activity measured with a Nuclear Chicago scalar (model 161A) equipped with a model D47 gas flow chamber with a micromil window. Each filter was counted for at least 5 min, and rates of carbon fixation were calculated as described by Doty and Oguri (1958) after averaging duplicate light bottle values. Mean coefficients of variation between duplicate light bottles were 6 ± 1% for the nannoplankton and 26 ± 5% (95% confidence limits) for the netplankton. The mean coefficient of variation between phytoplankton productivity values calculated from the sum of the nannoplankton and netplankton fractions and the unfractioned controls was 10 ± 2%.

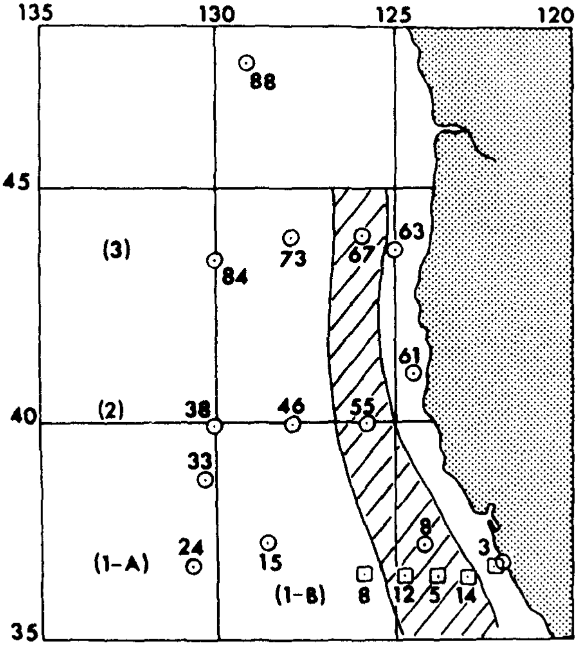

FIGURE 1.—Stations occupied along transects (1-A, B, 2, and 3) of the California Current during July and August (○) and during November (□), 1970; the shaded area represents the transition zone between offshore and inshore regions.

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[2] The use of trade names is merely to facilitate descriptions; no endorsement is implied.

Samples for pigment analysis were also collected 2 to 3 hr before local apparent noon from 13 depths between the surface and 100 to 200 m. The upper 6 to 10 depths sampled were within the photic zone, depending on its depth, and were chosen on the basis of the thermal structure of the water column. Sample depths were evenly spaced through the mixed layer and evenly but more closely spaced across the thermocline. Samples were always taken at the base of the photic zone and at two depths below to at least twice the photic zone depth. Chlorophyll-a and phaeopigment concentrations were determined by a fluorometric technique (Strickland and Parsons, 1968). Water samples were fractionated by the same procedure described for the carbon-uptake experiments except Whatman GF/C glass fibre filters coated with 2 ml of 1% $MgCO_3$ suspension were used in place of membrane filters, and the netplankton chlorophyll fraction was calculated from the difference between fractionated and unfractionated values. Duplicate values for each fraction were averaged (mean coefficients of variation were 10 ± 2% for the nannoplankton and 22 ± 8% for the netplankton fraction). The use of glass filters may have led to no more than a 10% underestimation of nannoplankton chlorophyll-a (Malone, in press a).

Samples for phytoplankton enumeration and identification were preserved with Lugol's solution made basic with sodium acetate in place of acetic acid. Aliquots of 100 ml were placed in Nessler tubes and the cells allowed to settle for 72 hr. Depending on the concentration of cells, from 50 to 90 ml of the supernatant was then siphoned off and 2 ml aliquots were added to settling chambers. After 48 hr the samples were counted by the inverted microscope technique of Utermöhl (Lund et al., 1958). All organisms longer than about 30 μ were counted at 100× while smaller cells were counted in 100 random fields at a magnification of 400×. For lack of better criteria, phytoplankton having dimensions of 30 × 22 μ or less were classified as nannoplankton and those with larger dimensions as netplankton. This did not present much of a problem, however, because the nannoplankton fraction was dominated by cells whose longest dimension was in the range of 2 to 15 μ, while the netplankton fraction was dominated by chain-forming diatoms with cell lengths of 40 μ or more, e.g., *Nitzschia pacifica*. Dominant netplankton forms were identified to species, and less numerous forms to genus. The remaining phytoplankters were classified as pennate or centric diatoms, thecate or nonthecate dinoflagellates, coccolithophores, silicoflagellates, or "others." Mean coefficients of variation between duplicate samples were 14 ± 4% for the nannoplankton fraction and 27 ± 11% for the netplankton fraction.

Standard hydrographic and bathythermograph casts were made 2 to 4 hr before local apparent noon in conjunction with productivity and standing crop measurements to estimate the vertical distributions of dissolved inorganic nitrogen compounds, temperature, and density in the water column. Additional hydrographic casts made for the CalCOFI Program in Monterey Bay are utilized in this paper. Nitrate concentrations were determined by the manual procedure described by Strickland and Parsons (1968) and ammonium by the phenolhypochlorite method (Solorzano, 1969). A Secchi disc was used to estimate photic zone depths (3.5 × Secchi disc reading).

The ratio of phaeopigments-to-chlorophyll in the water column (to 100 m for inshore stations and to 200 m for offshore stations) was used as a rough index of relative grazing pressure on the phytoplankton standing crop (Lorenzen, 1967; Beers and Stewart, 1969). In the present study, a highly significant ($P = 0.01$) regression of phaeopigment concentration on $\log_{10}$ transformed zooplankton wet weights was found, and it was concluded that the phaeopigment-chlorophyll ratio could be used as a first order index of grazing pressure.

TEMPORAL VARIATIONS IN MONTEREY BAY

ENVIRONMENTAL FACTORS

The hydrographic conditions observed at CalCOFI 3 from October 1969 to February 1971 are summarized in Figure 2 and Table 1. Sur-

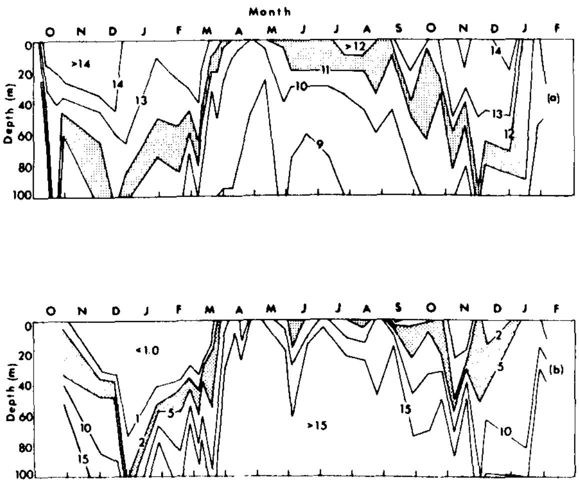


FIGURE 2.—a. Vertical distribution of temperature (°C) at CalCOFI 3 from October 1969 to February 1971. b. Vertical distribution of NO_3-N (μM).

TABLE 1.—Environmental factors monitored at the surface, concurrently with measurements of productivity and standing crop at CalCOFI station 3 in Monterey Bay.

Date	Temperature	Salinity	NO_3-N	NH_4-N	Mixed layer	Photic zone
	°C	‰	μM	μM	m	m
28 Oct. 69	14.20	33.51	1.7	--	30	60
2 Dec.	14.68	33.39	0.3	--	30	55
26 Feb. 70	13.10	32.68	0.3	0.3	50	60
5 Mar.	13.20	32.99	0.4	0.6	30	50
10 Mar.	13.17	32.98	0.1	0.2	25	65
18 Mar.	12.06	33.11	0.4	0.4	15	30
31 Mar.	11.17	33.49	7.8	0.3	0	25
8 Apr.	10.45	33.65	14.5	0.1	30	45
18 June	12.44	33.81	6.5	0.5	10	15
2 July	11.02	33.71	13.9	1.5	0	40
26 July	12.95	33.82	6.5	3.3	0	40
12 Oct.	13.56	33.53	1.1	0.6	0	70
26 Oct.	13.03	33.41	3.1	0.8	30	65
6 Nov.	13.59	32.99	0.7	0.2	40	65
18 Nov.	14.29	33.26	0.2	--	15	60
30 Nov.	13.40	33.28	2.4	--	45	55
7 Dec .	13.24	33.02	1.3	--	50	55
17 Jan. 71	11.50	33.43	6.6	0.4	50	60
27 Jan.	10.84	33.52	8.7	0.8	20	30
3 Feb.	11.79	33.33	3.8	0.4	15	50

face water of oceanic origin was found in the Bay from October 1969 to mid-March 1970. The intrusion of oceanic water and the general subsidence of the water mass are evidenced by the descending isotherms and nitrate isopleths, high surface temperatures, and low salinities. Mixed layer and photic zone depths were about 30 and 60 m respectively, and NO_3-N concentrations were less than 0.5 μM throughout most of the photic zone.

Upwelling was initiated in March as indicated by the ascending isotherms and nitrate isopleths, NO_3-N concentrations in excess of 5.0 μM over the entire photic zone, low surface temperatures, and high surface salinities. With the exception of a minor intrusion of oceanic water late in July and early August, upwelling continued uninterrupted into September with peaks in early April and early September. "Mixed layer" depths varied between 0 and 30 m, and at no time exceeded the depth of the photic zone, which ranged from 15 to 45 m.

From September through December the hydrography of the Bay was confused and neither oceanic nor upwelling conditions ever predominated. Weak upwelling surges bracketed by influxes of oceanic water occurred during late October and late November (Figure 2). Surface NO_3-N concentrations were variable (0.2 to 3.1 μM) reflecting the indecisiveness of the system. Then, following a period of oceanic water during December and early January, a strong upwelling pulse occurred which was about as intense as the upwelling during late March and early April of the previous year.

Hydrographically, three periods can be distinguished in the Bay during the period of this study:

1. A stable Oceanic Period from October 1969, into March 1970,
2. A stable Upwelling Period from March into September,
3. A "Mixed" Period from September through December punctuated by a strong upwelling pulse in January.

The grazing pressure index declined during the transition from oceanic to upwelling conditions to a low of 0.03 in early April (Figure 3). Grazing pressure then increased rapidly during the steady upwelling of June and July to an annual maximum of 2.03 which was followed by a gradual decline during the Mixed Period ending with a sharp rise in late January to a peak in early February.

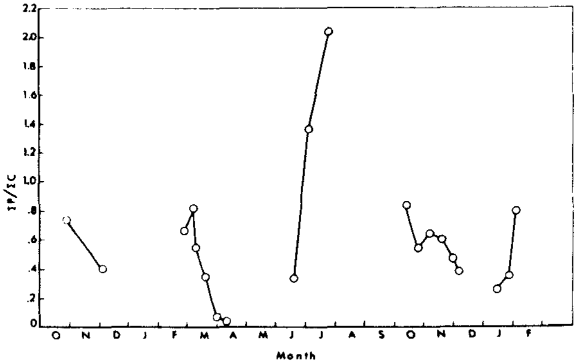
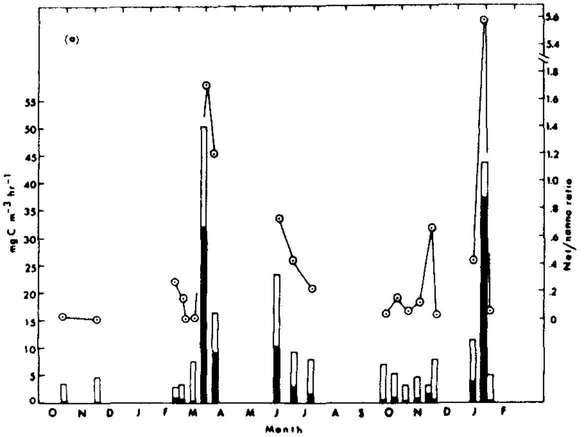
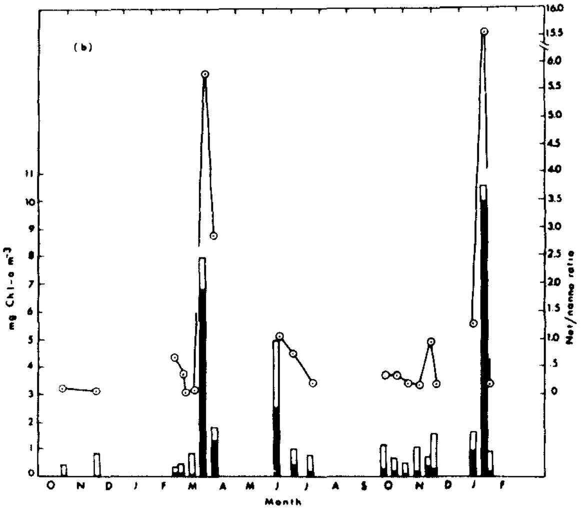


FIGURE 3.—Temporal variations in the ratio of phaeopigments-to-chlorophyll-a (P/C) integrated over the upper 100 m at CalCOFI 3.



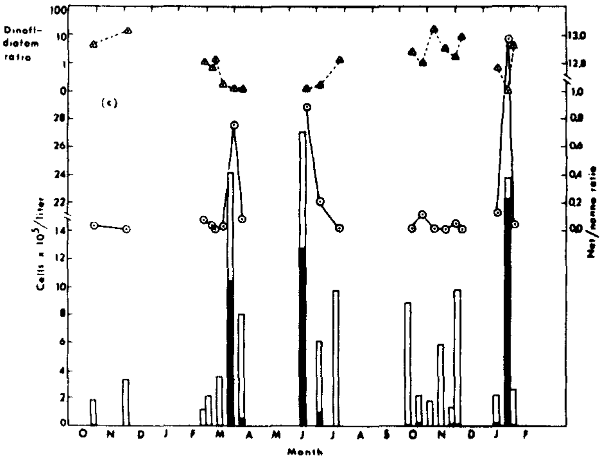


SURFACE PRIMARY PRODUCTIVITY AND STANDING CROP

Seasonal variations in surface productivity and standing crop are shown in Figure 4. Since a significant difference (F-test, $P<0.01$) was not observed between morning and afternoon values (see Malone, in press b), only data collected during the morning sampling will be considered.

Phytoplankton productivity and standing crop remained below 5.0 mgC m^{-3} hr^{-1}, 1.00 mgChl-a m^{-3}, and 3.5 $\times$ 10^5 cells/liter during the Oceanic Period. Values above 10.0, 1.50, and 10.0 $\times$ 10^5 were observed only during the Upwelling Period and the January Upwelling pulse. The Mixed Period was characterized by intermediate levels of productivity and standing crop. Three peaks were observed, of which the two greatest coincided with the two most intense upwelling pulses: (1) 50.4 mgC m^{-3} hr^{-1}, 7.92 mgChl-a m^{-3}, and 24.2 $\times$ 10^5 cells/liter on the last day of March, and (2) 43.4, 10.46, and 23.9 $\times$ 10^5 during the last week of January. The third, less pronounced peak, was in mid-June during steady upwelling.

FIGURE 4.—a. Temporal variations in surface netplankton (■) and nannoplankton (□) productivity (mgC m^{-3} hr^{-1}) and the net/nanno ratio (⊙) at CalCOFI 3. b. Temporal variations in surface chlorophyll-a (mg m^{-3}) and the net/nanno ratio. c. Temporal variations in surface cell numbers, the net/nanno ratio, and the ratio of dinoflagellates-to-diatoms (△).



Phytoplankton assimilation ratios (mgC hr^{-1} mgChl-a^{-1}) were relatively constant, with most values falling between 5 and 10 (mean = 7.4 ± 1.0, 95% confidence limits). Fluctuations in the amount of chlorophyll-a per cell (10^{-6} μg) were also within comparatively narrow limits. Values varied from 0.85 to 6.97 with a mean of 2.62 ± 0.66.

Surface levels of nannoplankton productivity and standing crop were remarkably stable through the year. Productivity and standing crop values were less than 8.0 mgC m^{-3} hr^{-1}, 0.80 mgChl-a m^{-3}, and 3.3×10^5 cells/liter during the Oceanic Period. During the Upwelling Period productivity ranged from 6.6 to 18.6, chlorophyll-a from 0.46 to 2.44, and cell numbers from 5.1 to 14.4×10^5. Thus, while nannoplankton productivity and standing crop were lower under oceanic than upwelling conditions, the differences were not marked.

In contrast, netplankton productivity and standing crop varied tremendously during the year, from less than 0.6 mgC m^{-3} hr^{-1}, 0.14 mgChl-a m^{-3}, and 0.1×10^5 cells/liter during the Oceanic Period to greater than 2.8, 0.40, and 0.6×10^5 during the Upwelling Period. Two prominent peaks were observed (31.8 mgC m^{-3} hr^{-1}, 6.76 mgChl-a m^{-3} and 36.8 and 9.83), both in association with the two most intense upwelling pulses. A secondary peak occurred in mid-June. Netplankton cell numbers reached successive peaks of 24.2, 27.1, and 23.8×10^5 cells/liter which coincided with peaks in productivity and chlorophyll-a. During the fall and early winter Mixed Period, intermediate values were observed with small peaks associated with each short burst of upwelling. Thus, netplankton productivity and standing crop varied from an order of magnitude less than that of the nannoplankton during the Oceanic Period to an order of magnitude greater during the Upwelling Period. Comparison of mean squares and ranges of variation (Table 2) clearly demonstrates that temporal variations in phytoplankton productivity and standing crop were primarily due to the netplanktón fraction with the nannoplankton maintaining a relatively stable background level.

Variations in the ratio of netplankton-to-nannoplankton (net/nanno) are also shown in Figure 4. The net/nanno productivity ratio never exceeded 0.3 during intrusions of oceanic water (either during the Oceanic Period or the Mixed Period), and was greater than 1.0 on only two occasions: during the strong upwelling pulses of late March and late January. The same pattern was found for the net/nanno chlorophyll and cell number ratios except the chlorophyll ratios were consistently higher and the cell number ratios lower than the productivity ratios. This is reflected in the assimilation ratios and cell chlorophyll-a content of the two fractions, both of which were relatively constant during the study. The mean nannoplankton assimilation ratio of 9.4 ± 1.5 was significantly higher than the netplankton mean of 4.7 ± 1.3. Similarly, the nannoplankton had more cells per unit chlorophyll-a than did the netplankton. The mean chlorophyll-a content per netplankton cell was $23.6 \pm 13.1 \times 10^{-6}$ μg which is significantly higher than the nannoplankton mean of $1.9 \pm 0.5 \times 10^{-6}$ μg.

Peaks in the ratio of netplankton-to-nannoplankton cell numbers coincided with peaks in netplankton cell number, but the ratio exceeded 1.0 only during the January bloom. This probably reflects the dominance of the small-celled (<20 μ in length), chain-forming diatoms *Chaetoceros socialis* and *Skeletonema costatum* in the netplankton fraction. In contrast, the netplankton blooms of late March and mid-June were dominated by large-celled (>40 μ in length) chain-forming diatoms *Nitzschia pacifica* and *Rhizosolenia fragilissima,* respectively. *Nitzschia* spp., *Skeletonema costatum, Leptocylindricus* sp., and *Chaetoceros* spp. accounted for

TABLE 2.—Mean squares and range factors (maximum/minimum) for nannoplankton and netplankton productivity (PP = mgC m^{-3} hr^{-1}), chlorophyll-a concentration (mg m^{-3}, m^{-2}), and cell numbers (no./liter) at CalCOFI station 3.

Fraction	Mean squares			
	PP	*mg* m^{-3}	*no./liter*	*mg* m^{-2}
nannoplankton	16	0.2	17	86
netplankton	109	6.5	32	1,680
	Range factors			
nannoplankton	9	12	13	4
netplankton	1,800	4,200	4,400	120

70% of the netplankton in the March bloom. In mid-June *Rhizosolenia* spp. and *Nitzschia* spp. made up 80% of the netplankton. The nannoplankton fraction was dominated by small monads 2 to 15 μ in length in all but one of the samples examined. The one exception occurred at the peak of the March-April netplankton bloom when small diatoms dominated the nannoplankton fraction. When the net/nanno ratio was high (during upwelling), diatoms were more numerous than dinoflagellates; but when the ratio was low (during oceanic conditions), dinoflagellates were more numerous (Figure 4c).

VERTICAL DISTRIBUTION OF PIGMENTS

The chlorophyll-a content of the water column (0 to 100 m) varied between 14 and 30 mg m^{-2} during the Oceanic Period and between 24 and 152 mg m^{-2} during the Upwelling Period (Figure 5). The seasonal pattern of variation was much the same as that observed for surface chlorophyll concentrations, but the range of variations was less.

Variations in netplankton and nannoplankton chlorophyll content of the water column were also similar to the surface pattern. Nannoplankton chlorophyll-a values fluctuated between the low of 9.6 mg m^{-2} observed during the Oceanic Period and the high of 44.2 observed during the Mixed Period. Water column levels of netplankton chlorophyll-a, however, were less than 8.0 during the Oceanic Period and surpassed 110 during both strong upwelling pulses. Again, changes in the phytoplankton chlorophyll content of the water column and in the net/nanno ratio were due primarily to variations in the netplankton fraction with the nannoplankton fraction remaining comparatively constant (Table 2).

The vertical distribution of chlorophyll-a always exhibited a maximum which was in the photic zone above or in association with the phaeopigment maximum. The netplankton maximum was always located below the nannoplankton maximum except during strong upwelling when both maxima occurred in the upper 10 m of the photic zone (Figure 6). Four stations have been selected to illustrate the different types of vertical pigment distributions encountered (Figure 7). Two basic patterns were observed, a stable oceanic distribution with low chlorophyll concentrations and low net/nanno ratios (Figure 7a), and an upwelling distribution with high chlorophyll concentrations and high net/nanno ratios (Figure 7b). Under oceanic conditions, the nannoplankton maximum was found in the upper half of the photic zone, near the bottom of the mixed layer and in nitrate-poor water

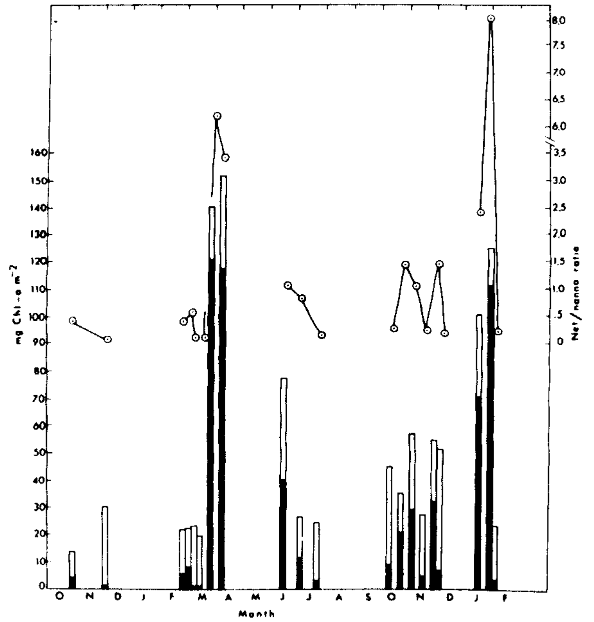


FIGURE 5.—Temporal variations in netplankton (■) and nannoplankton (□) chlorophyll-a content of the water column (mg m^{-2}, 0 to 100 m) and the net/nanno ratio (⊙) at CalCOFI 3.

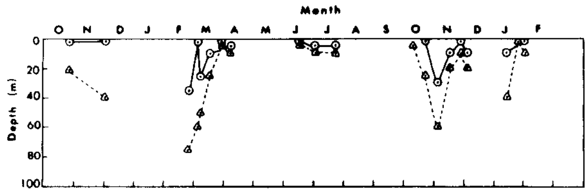


FIGURE 6.—Temporal variations in the depths of the nannoplankton (⊙) and netplankton (△) chlorophyll-a maxima at CalCOFI 3.

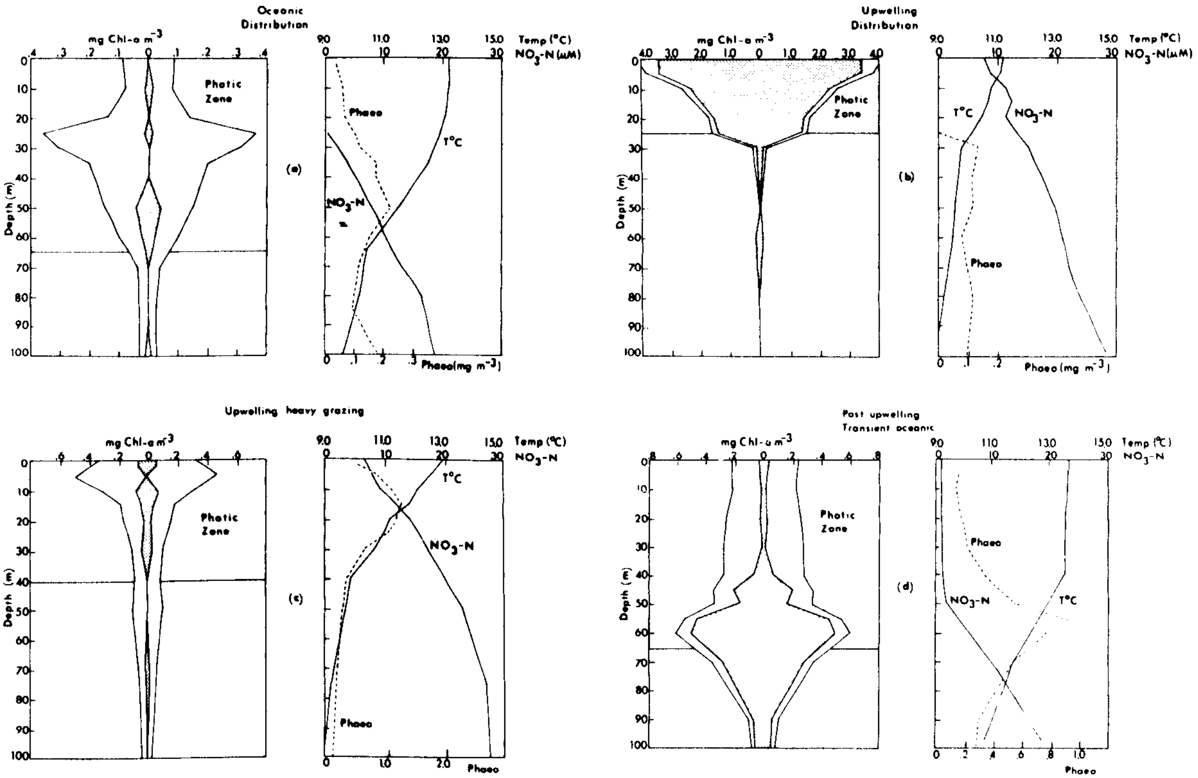


FIGURE 7.—Vertical profiles of netplankton (▨) and nannoplankton (□) chlorophyll-a (mg m^{-3}), NO_3-N (μM), and temperature (°C) at CalCOFI 3: (a) Oceanic Period (10 March), (b) Upwelling Period (31 March), (c) Upwelling Period with peak grazing pressure (26 July), and (d) Mixed Period during post-upwelling subsidence (6 November).

(<0.5 μM NO_3-N); while the netplankton maximum was located in the lower half of the photic zone, in the thermocline, and in nitrate-rich water (>5.0 μM NO_3-N). Maximum phaeopigment concentrations occurred in association with or just below the netplankton maximum. With the onset of upwelling, the netplankton maximum gradually shifted from a depth of 75 m to the surface (Figure 6). Initially, upwelling had a dilution effect which was followed by a rapid increase in the netplankton fraction and later by a slight increase in the nannoplankton fraction (Figure 5). The upwelling distribution observed on March 31 is shown in Figure 7b. Both netplankton and nannoplankton chlorophyll maxima were at the surface and nitrate concentrations were high (>5.0 μM NO_3-N) throughout the photic zone.

The remaining two examples represent special cases which evolved from an upwelling distribution such as the one just described. Figure 7c shows the distribution observed during late July that developed over the period of steady upwelling during which the grazing pressure index increased markedly (Figure 3). Note that both netplankton and nannoplankton maxima were in the upper 10 m, and NO_3-N concentrations were in excess of 5 μM throughout the photic zone; but that the concentration of netplankton chlorophyll has been greatly reduced and the net/nanno ratio was low. Phaeopigments were high with a maximum just below the netplankton chlorophyll maximum. The distribution shown in Figure 7d (November 6) developed during a period of subsidence following an upwelling pulse. At this time, the netplankton maximum was near the bottom of the photic zone 30 m below the nannoplankton maximum; the net-plankton chlorophyll concentration and net/nanno ratio were still high; and NO_3-N concentrations were greater than 2 μM throughout most of the photic zone.

GEOGRAPHIC VARIATIONS IN THE CALIFORNIA CURRENT

ENVIRONMENTAL FACTORS

Four transects across the core of the Current were made for this study (Figure 1). Transects 1-A, 2, and 3 were made during late July and August 1970, and transect 1-B was made during the first week of November 1970. CalCOFI station 3 in Monterey Bay was the inshore station for transects 1-A and B. The hydrographic conditions observed along these transects are summarized in Table 3 and Figures 8 and 9.

The July-August transects were made during a period of coastal upwelling and were characterized by shoreward rising isotherms and nitrate isopleths. Based on the upward slope of these isopleths, upwelling was least intense at the southernmost inshore station and most intense at the northernmost station, which is typical for this time of year (Reid et al., 1958). Nitrate concentrations were high in the upper half of the photic zone at the three inshore stations and low at the two outermost stations of each transect. Ammonium concentrations were relatively high (>1 μM NH_4-N) in the photic zone at the stations of transect 1-A but were low (typically 0.1 to 0.5 μM) throughout the water column at most of the remaining stations. The surface mixed layer was never observed to extend below the photic zone, inshore or offshore. An undercurrent was present below the thermocline between stations 5 and 8 of transect 1-A as indicated by the spreading isotherms (cf. Wooster and Gilmartin, 1961). Based on the temperature (Figure 8) and nitrate profiles (Figure 9), the stations along each transect were divided into three groups:

1. Stations within about 100 km of the coast were classified as inshore (stations 3, 61, and 63),
2. Stations between 100 and 250 km offshore were classified as transitional (stations 8, 55, and 67),

TABLE 3.—Environmental factors monitored concurrently with measurements of productivity and standing crop in the California Current system between lat 35° and 50° N.

Station	Date	Distance from land	Temperature	Salinity	NO_3-N	NH_4-N	Mixed layer	Photic zone
		km	*°C*	*‰*	*μM*	*μM*	*m*	*m*
03[a]	26 July 70	15	12.95	33.82	6.5	3.3	0	40
08	27 July	155	14.88	33.11	1.3	1.4	20	65
15	29 July	470	17.69	32.95	0.2	1.8	30	105
24	31 July	675	18.49	32.88	0.1	1.7	20	100
33	2 Aug.	535	18.03	32.51	0.0	0.4	0	115
61	9 Aug.	30	11.98	33.38	8.8	0.7	10	40
55	7 Aug.	130	16.04	31.88	0.1	0.0	10	65
46	5 Aug.	310	17.25	32.08	0.1	0.4	15	105
38	3 Aug.	485	18.25	32.79	0.1	0.3	15	95
63	15 Aug.	70	11.55	33.00	0.3	0.5	10	15
67	16 Aug.	150	14.91	32.62	0.7	0.2	30	75
73	18 Aug.	315	17.24	32.04	0.1	0.5	20	55
84	20 Aug.	450	17.07	32.57	0.2	0.1	30	90
88	22 Aug.	280	15.82	32.47	0.1	0.3	20	80
03[a]	6 Nov.	15	13.59	32.99	0.7	0.2	40	60
14	5 Nov.	90	14.58	32.98	0.0	0.5	20	65
05	2 Nov.	150	14.38	32.81	0.1	0.7	20	50
12	4 Nov.	225	14.74	32.62	0.2	0.1	15	60
08	3 Nov.	290	15.31	32.46	0.1	1.0	15	60

[a] CalCOFI station 3.

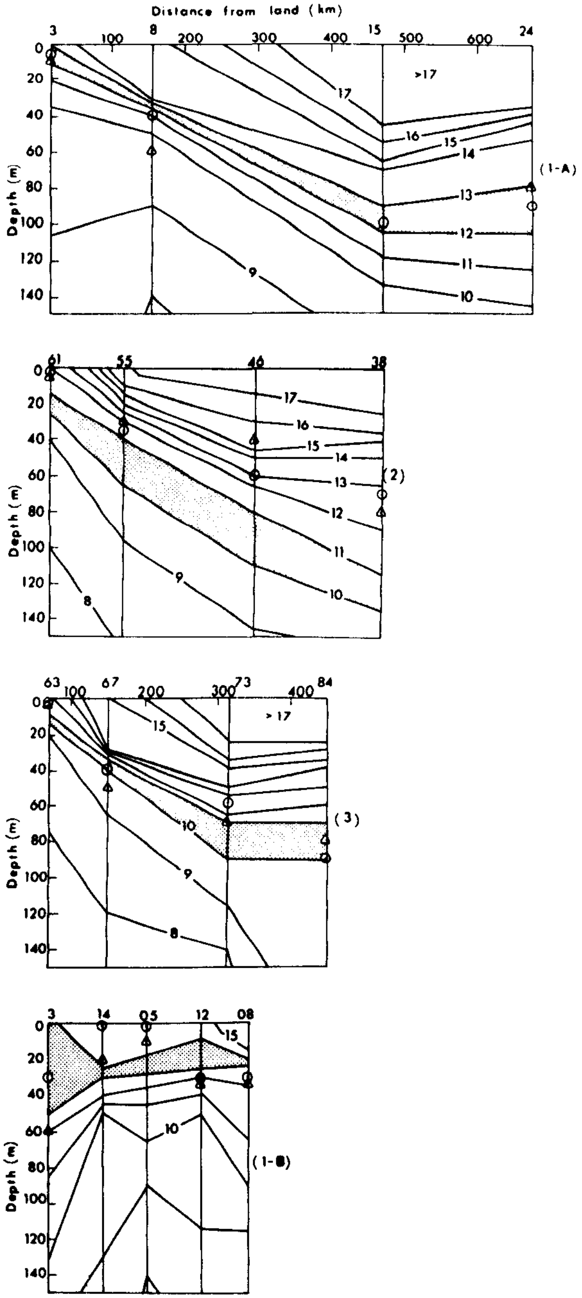


Figure 8.—Vertical distribution of temperature (°C) along four transects of the California Current system with the depths of the nannoplankton (☉) and netplankton (△) chlorophyll-a maxima: (1-A) along lat 37° N in July, (2) along lat 40° N in August, (3) along lat 44° N in August, and 1-B along lat 36°40′ in November. Vertical lines represent stations.

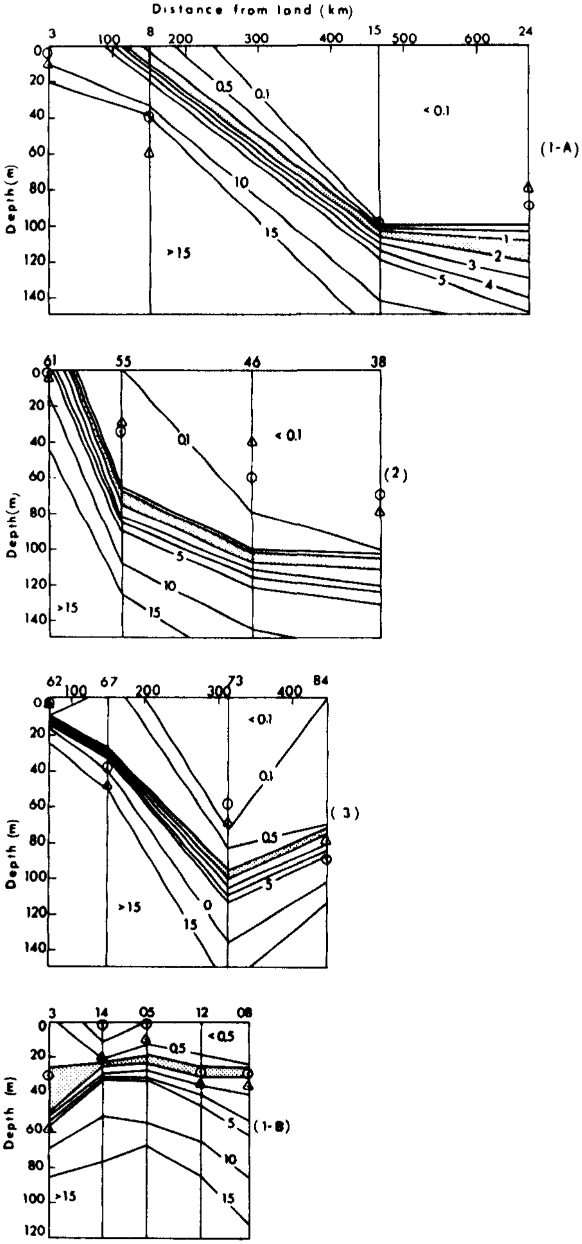


Figure 9.—Vertical distribution of NO_3-N (μM) along four transects of the California Current system with the depths of the nannoplankton (☉) and netplankton (△) chlorophyll-a maxima.

3. Stations greater than 250 km from the coast were classified as offshore (stations 15, 24, 33, 46, 38, 73, 84, and 88).

Transect 1-B was made at a time when the Davidson Current is usually developed (Bolin, 1964). The inshore station (CalCOFI 3) was occupied during an oceanic phase of the Mixed Period, and subsidence is evidenced by the downward trend of the isotherms and nitrate isopleths (Figures 2, 8, and 9). Surface temperatures were comparatively high and nitrate concentrations low. The Davidson Current was developed at stations 3 and 14, and the transition from Davidson to California Current Water occurred between stations 14 and 12 with a surface divergence probably located between stations 5 and 12. Station 8, the outermost station, was in the California Current proper.

SURFACE PRIMARY PRODUCTIVITY AND STANDING CROP

During the July-August transects, when coastal upwelling dominated the hydrographic regime of the California Current system, phytoplankton productivity and chlorophyll-a concentrations decreased markedly with distance from land (Figure 10). Inshore, productivity and chlorophyll ranged from 6.62 to 61.65 mgC m^{-3} hr^{-1} and from 0.8 to 11.5 mg m^{-3}, respectively. Pro-

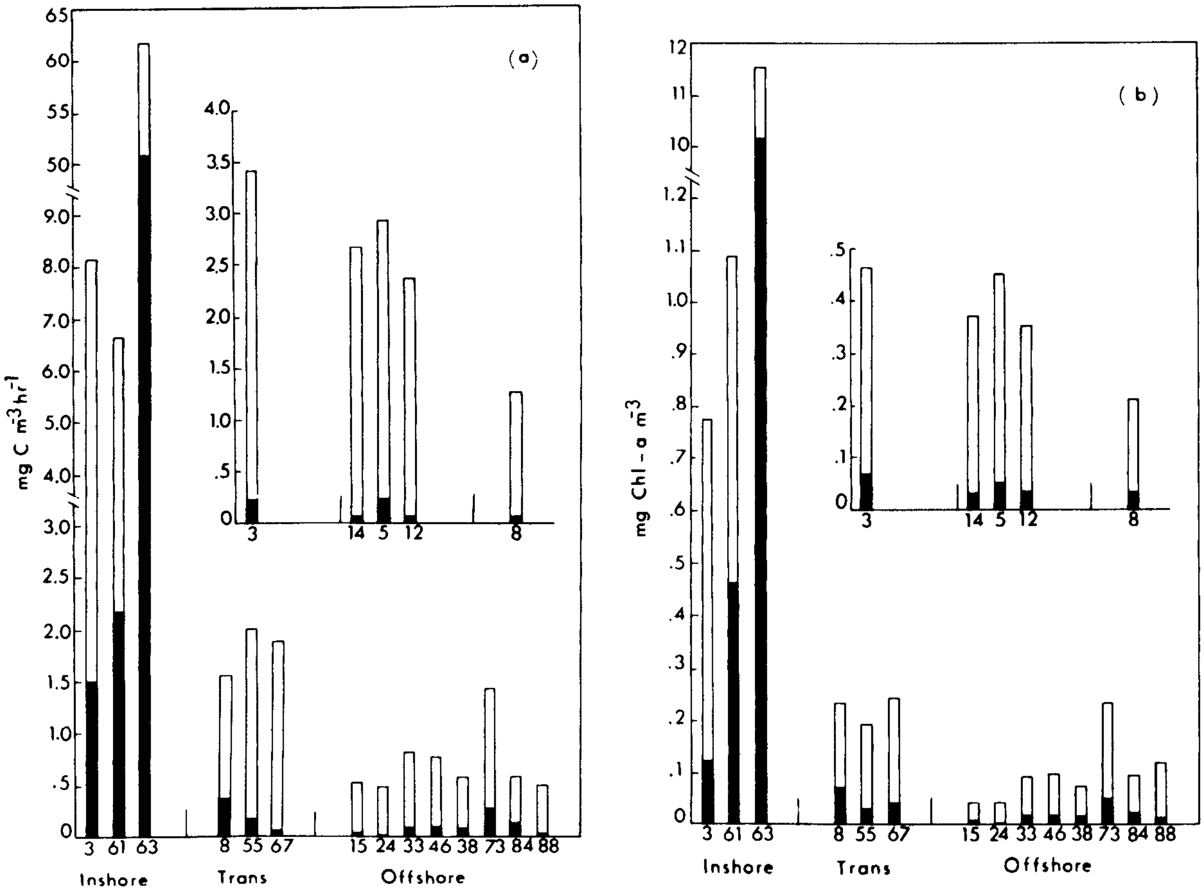


FIGURE 10.—a. Inshore-offshore variations in surface netplankton (■) and nannoplankton (□) productivity (mgC m^{-3} hr^{-1}) during the July-August transects and the November transect (inset). b. Inshore-offshore variations in surface netplankton and nannoplankton chlorophyll-a (mg m^{-3}).

ductivity and chlorophyll concentrations offshore, however, exceeded 1.0 mgC m^{-3} hr^{-1} and 0.10 mgChl-a m^{-3} only once. The highest levels of productivity and chlorophyll were found at inshore station 63 and were equivalent to the maximum values observed at CalCOFI 3 during the two most intense upwelling pulses.

This inshore-offshore decrease in surface productivity and chlorophyll was not observed over the first 225 km of the November transect when subsidence rather than upwelling characterized. the coastal hydrographic regime. Productivity and chlorophyll concentrations were relatively constant out to station 12 (Figure 10) and corresponded with the minimum values observed at CalCOFI 3 during the Oceanic Period.

Both nannoplankton and netplankton productivity and chlorophyll decreased markedly between inshore and offshore stations along the July-August transects (Figure 10). Nannoplankton values fell by as much as an order of magnitude from above 4.0 mgC m^{-3} hr^{-1} and 0.60 mgChl-a m^{-3} to less than 1.2 and 0.18, respectively. The netplankton, however, exhibited the greatest decline. Netplankton productivity decreased by 2 to 3 orders of magnitude from 1.5 to 51.3 mgC m^{-3} hr^{-1} to offshore levels of 0.01 to 0.26. Similarly, netplankton chlorophyll values were 0.12 to 10.14 mg m^{-3} inshore and 0.002 to 0.052 offshore. This decline in the netplankton fraction relative to the nannoplankton is reflected in the net/nanno ratios (Table 4). Inshore productivity ratios ranged from 0.23 to 4.95, while offshore ratios varied from 0.02 to 0.36. Chlorophyll ratios followed the same pattern but tended to be higher.

The pattern observed in November was quite different. Levels of netplankton productivity and chlorophyll were low along the entire transect and were within the range commonly found offshore and during oceanic phases inshore (Figure 10). Nannoplankton productivity declined slightly from an inshore maximum of 3.20 to an offshore minimum of 1.21. Variations in surface chlorophyll were similar except the maximum of 0.40 was observed at station 5 which is 150 km from shore. Station 5 is particularly interesting because netplankton productivity and chlorophyll also exhibited small peaks here, and it was located near the boundary between the Davidson and California Currents which is marked by a surface divergence and associated upwelling. In this connection, it is also noteworthy that nannoplankton productivity and chlorophyll levels were about twice those observed previously for transitional and offshore regions.

Phytoplankton assimilation ratios were similar to those observed at CalCOFI 3, most values falling between 5 and 10. Excluding inshore stations, the mean assimilation ratio was 7.7 ± 1.1, which is not significantly different from the mean observed at CalCOFI 3. Nannoplankton ratios averaged 8.3 ± 1.2 which is twice the observed mean netplankton ratio of 4.1 ± 0.8. Both means are equivalent to those observed at CalCOFI 3.

VERTICAL DISTRIBUTION OF PIGMENTS

Inshore-offshore variations in the chlorophyll-a content of the water column (0 to 200 m) during the July-August transects were similar in trend but less in amplitude than that observed at the surface. Inshore, chlorophyll varied from 27.32 to 217.68 mg m^{-2} compared with the

TABLE 4.—Netplankton-nannoplankton ratios in the California Current system: primary productivity (PP = mgC m^{-3} hr^{-1}), chlorophyll-a m^{-3}, and chlorophyll-a m^{-2}.

Station	PP	m^{-3}	m^{-2}
03	0.23	0.18	0.14
08	0.30	0.48	0.36
15	0.06	0.15	0.21
24	0.02	0.05	0.14
33	0.11	0.22	0.06
61	0.49	0.75	0.75
55	0.09	0.19	0.16
46	0.12	0.22	0.31
38	0.19	0.27	0.24
63	4.95	7.31	5.82
67	0.03	0.18	0.33
73	0.22	0.28	0.22
84	0.36	0.32	0.14
88	0.07	0.09	0.09
03	0.07	0.17	1.12
14	0.02	0.10	0.18
05	0.08	0.12	0.20
12	0.03	0.11	0.10
08	0.04	0.17	0.16

offshore range of 10.72 to 25.96 mg m^{-2} (Figure 11). In November the pattern was much the same, with an inshore maximum of 66.64 and an offshore level of 23.20.

Nannoplankton chlorophyll in the water column showed little variability (Figure 11). Inshore levels of nannoplankton chlorophyll varied from 17.49 to 31.94 mg m^{-2}, while offshore levels ranged between 9.63 and 21.76. The netplankton fraction underwent much greater fluctuations (Figure 11). Inshore concentrations ranged between 3.26 and 185.74 in contrast to the offshore range of 1.00 to 4.97. The latter range is equivalent to that observed at CalCOFI 3 during the Oceanic Period and the former to that observed during the Upwelling Period. Excluding inshore stations, the mean chlorophyll-a concentration of the nannoplankton fraction was 16.55 ± 2.38 which is significantly higher ($P = 0.05$) than the netplankton mean of 3.08 ± 0.81.

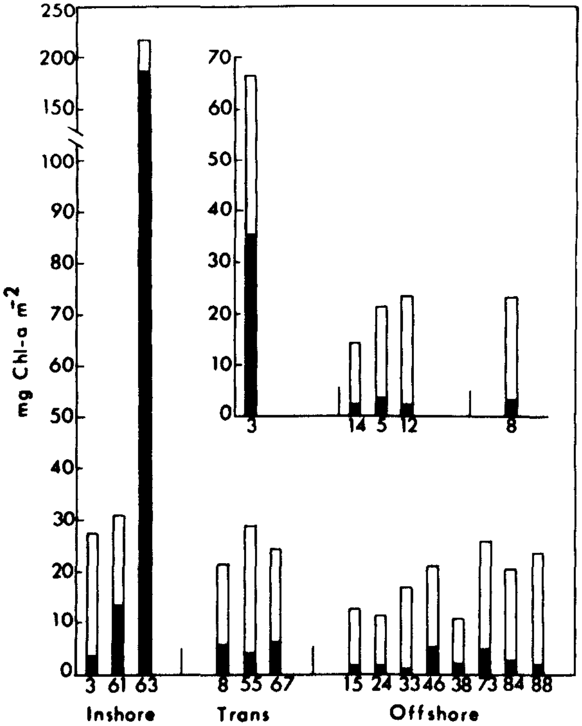


FIGURE 11.—Inshore-offshore variations in the netplankton (■) and nannoplankton (□) chlorophyll-a content of the water column (mg m^{-2}, 0 to 200 m) during the July-August transects and the November transect (inset).

The vertical distributions of chlorophyll-a and phaeopigments at the offshore stations of the July-August transects were characterized by a subsurface maximum located at the base of the photic zone, in the lower part of the thermocline, and near the upper reaches of the nitrate-rich layer (Figure 12). Netplankton and nannoplankton chlorophyll maxima were usually located near each other, but the netplankton maximum was not always deeper than the nannoplankton maximum. Netplankton chlorophyll was more evenly distributed and concentrations were much lower than in inshore waters (compare Figures 7 and 12). Both maxima gradually decreased in depth shoreward from between 80 and 100 m offshore to 10 m or less at the inshore stations paralleling the upward trend of the isotherms (Figure 8) and nitrate isopleths (Figure 9).

The pattern was much different during the November transect (1-B). The netplankton maximum was always located below the nannoplankton maximum, especially at the inshore station where the netplankton maximum was 30 m below the nannoplankton maximum (Figure 7d). Both maxima decreased in depth seaward to station 5 (Figures 8 and 9) where the vertical distribution conformed to the upwelling distribution (Figure 12), i.e., netplankton and nannoplankton maxima were in the upper 10 m and nitrate concentrations were relatively high throughout most of the photic zone. Farther offshore the depth of the chlorophyll maxima increased once again. This up and down movement of the maxima closely paralleled the depth variation of the isotherms and nitrate isopleths just as during the July-August transects.

DISCUSSION

The constancy of the phytoplankton assimilation ratios both inshore (7.4 ± 1.0) and offshore (7.7 ± 1.1) suggests that nutrients were rarely limiting to primary productivity (Dickman, 1969). The mean assimilation ratios found are close to the value of 7.3 reported by Holmes (1958b) in the nutrient-rich waters of the Costa

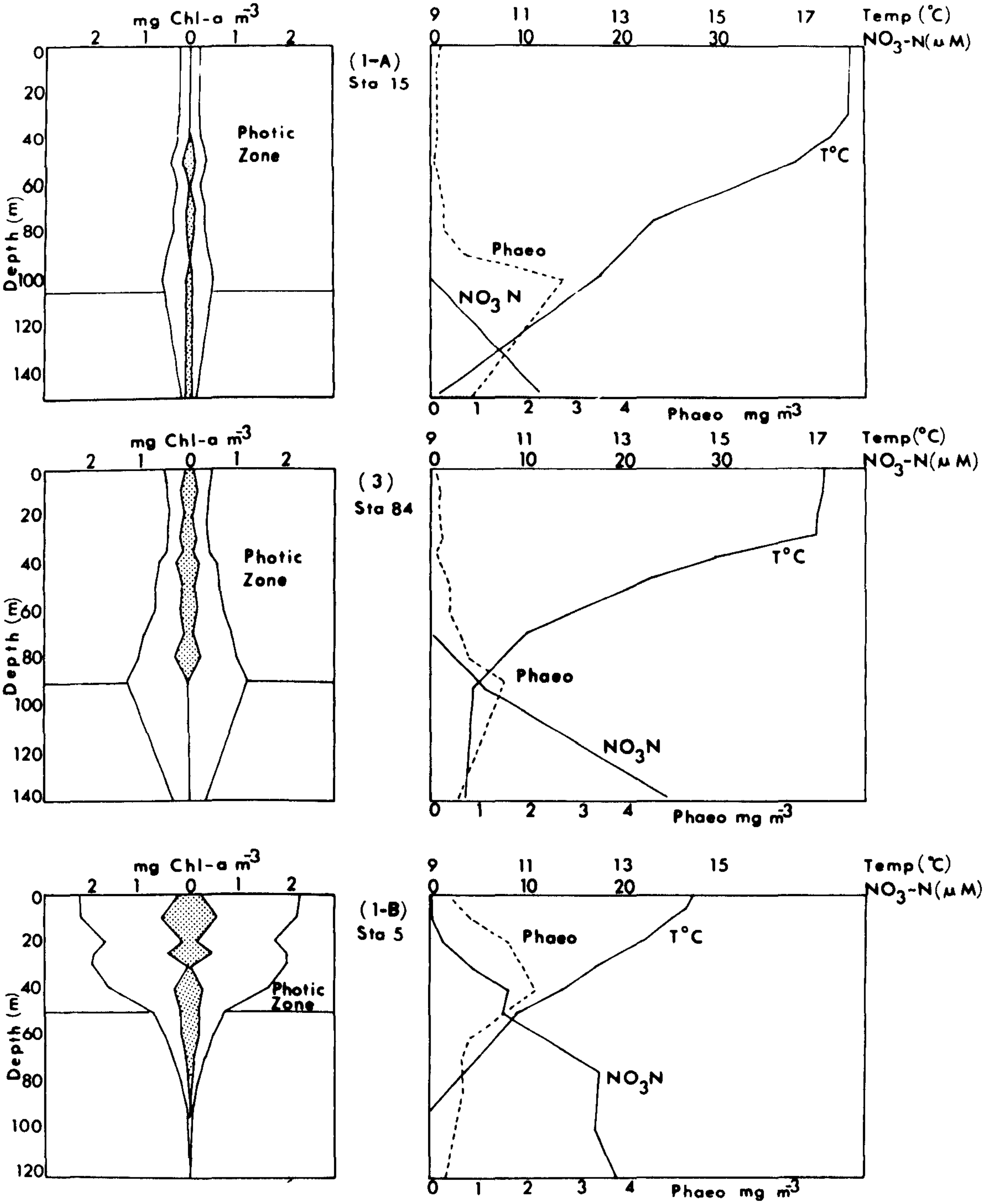


FIGURE 12.—Vertical profiles of netplankton (▨) and nannoplankton (□) chlorophyll-a (mg m^{-3}), phaeopigments (mg m^{-3}), NO_3-N (μM), and temperature (°C): transect 1-A, station 15, offshore region; transect 3, station 84, offshore; transect 1-B, station 5, transition zone.

Rica Dome (incubator light intensity about 0.06 langley/min) and are not significantly different from the mean of 8.6 ± 1.3 found by Curl and Small (1965) at light saturation based on in situ measurements. Anderson (1964), working off the Washington and Oregon coasts, obtained ratios of 1.6 to 9.8 (at about 0.02 langley/min) with low values occurring during the summer when nutrient concentrations were low and high values during the spring bloom when nutrient concentrations were high. In the eastern tropical Pacific, Thomas (1970) and Malone (in press a) found that assimilation ratios were significantly less in nitrogen-poor than in nitrogen-rich waters. These results are consistent with the observations of Curl and Small (1965), supported by McAllister et al. (1964), which suggest that ratios below 3 are indicative of a nutrient deficiency while those above 5 indicate nutrient-rich waters.

Both the nannoplankton and the netplankton exhibited relatively constant assimilation ratios, but mean nannoplankton ratios were significantly higher (9.4 ± 1.5 inshore, 8.3 ± 1.2 offshore) and twice as great as those of the netplankton (4.7 ± 1.3 inshore, 4.1 ± 0.8 offshore). The constancy of these ratios over a wide range of productivity values in spite of large variations in ambient nitrogen concentrations indicates that nutrient concentration was not an important limiting factor and that the phytoplankton were adapted to about the same light intensity over the entire year. This is conceivable since seasonal variations in day length and light intensity tend to be dampened by the seasonal pattern of cloud coverage, i.e., the summer months are usually foggy while the winter months are usually clear. The situation is similar to that found off La Jolla (Strickland et al., 1970).

Increases in the productivity and standing crop of the netplankton fraction and in the net/nanno ratio were closely coupled with the occurrence of upwelling. Each new upwelling pulse, regardless of duration (CalCOFI 3) or location (transect 1-B) was marked by an increase in net/nanno ratios and netplankton standing crop. Potentially, upwelling can affect phytoplankton productivity in at least two ways: (1) by increasing the residence time of cells in the upper reaches of the photic zone and (2) by increasing the rate at which nutrients are supplied to the photic zone. The settling velocities of phytoplankton cells range between 0 and 10 m day^{-1} (for a review see Smayda, 1970), with most values falling between 0.5 and 2 m day^{-1} (Eppley et al., 1967; Strickland et al., 1969). Average upwelling velocities are of the order of 10 m day^{-1} (Hidaka, 1954), which is quite sufficient to inhibit the sinking of negatively buoyant cells.

Since the netplankton fraction was primarily composed of nonmotile diatoms and the nannoplankton fraction of flagellates, it is probable that vertical water movements will have a greater effect on the vertical distribution of netplankton than on the nannoplankton. It is not surprising, therefore, that the depth of the netplankton maximum was more closely tied to the upward and downward trends of the isotherms, both seasonally at CalCOFI 3 (Figure 6) and along inshore-offshore transects of the California Current (Figure 8). The netplankton maximum at CalCOFI 3 was always found below that of the nannoplankton except during strong upwelling when both maxima occurred in the upper 10 m. During periods of subsidence the netplankton minimum was depressed to greater depths than the nannoplankton maximum was. This was observed during the Mixed Period even though NO_3-N concentrations in the surface layers were still high (>1.0 μM). The reverse was observed along transect 1-B in that the netplankton maximum decreased in depth as the zone of offshore upwelling was approached, moving in the process from a nitrate-rich layer (>5.0 μM NO_3-N) into a nitrate-poor layer (<0.5 μM NO_3-N). The depth distribution of nannoplankton chlorophyll (Figures 6 and 7) was more independent of vertical water movements and maximum chlorophyll concentrations were often found at the surface during influxes of oceanic water (during both Oceanic and Mixed Periods) when subsidence was most pronounced.

Most of these trends in the depth distribution of netplankton and nannoplankton chlorophyll could be explained in terms of the vertical distribution of nitrate in the photic zone. However, during the early stages of upwelling in

March, the netplankton maximum moved progressively toward the surface while the chlorophyll concentration of the maximum and in the water column steadily decreased. If this change in depth was due solely to the upward movement of the nitrate-rich layer in the photic zone, some increase in netplankton would have been observed during the time taken for the maximum to move from a depth of 75 m to 5 m. In addition, measurements made in the Peru Current, where vertical advection was not in evidence and the photic zone was well stratified (Malone, in press a), support the hypothesis that upward water movements, in addition to high nitrate concentrations, are necessary prerequisites for netplankton productivity to approach or exceed that of the nannoplankton. Netplankton productivity and the net/nanno productivity ratio were low despite high nitrate concentrations (Figure 13).

Two lines of evidence indicate that the netplankton and nannoplankton respond differently to varying nitrate concentrations. The first is based on the relationship between productivity and nitrate concentrations encountered in different environments (Figure 13). Nannoplankton productivity increased rapidly as NO_3-N increased from about 0.0 to 0.5 μM. Above 0.5 μM nannoplankton productivity increased asymptotically. In contrast, netplankton productivity increased slowly over concentrations of 0.0 to 1.5 μM and then increased rapidly with concentrations in excess of 1.5 μM (California Current system). The netplankton, therefore, tend to have higher half-saturation constants and maximum uptake rates for nitrate than the nannoplankton, so that NO_3-N concentrations above 1 to 3 μM are necessary before the netplankton can effectively compete with the nannoplankton. This agrees with the results of MacIsaac and Dugdale (1969) and Eppley et al. (1969), which indicate that small-celled oceanic species in oligotrophic waters have K_s values for nitrate uptake of less than 0.5 μM while large-celled neritic species in eutrophic waters have K_s values greater than 1.0 μM.

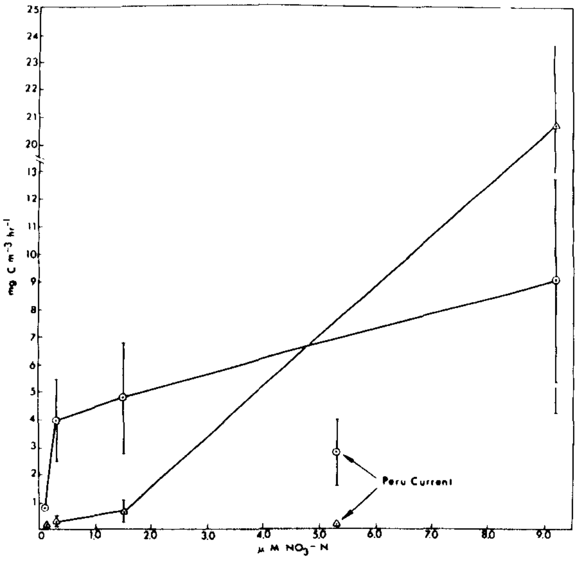


FIGURE 13.—Mean netplankton (△) and nannoplankton (⊙) productivity as a function of mean NO_3-N concentrations with 95% confidence limits: 0.1 μM, offshore oceanic region; 0.3 μM, CalCOFI 3, Oceanic Period; 1.5 μM, CalCOFI 3, Mixed Period; 9.2 μM, inshore upwelling.

The observed inshore vertical distributions of netplankton and nannoplankton chlorophyll were also consistent with these observations. The netplankton chlorophyll maximum was always found at depths where NO_3-N concentrations were greater than 2 μM, while during nonupwelling periods (when concentrations less than 2 μM were found in the photic zone) the nannoplankton maximum occurred at depths where the NO_3-N concentration was between 0.2 and 2.0 μM. Similar observations were made by Eppley (1970) who found that diatoms were associated with relatively high nitrate concentrations at depths where light intensities were high enough for growth to occur.

Based on these observations, netplankton productivity and standing crop will increase relative to the nannoplankton only when NO_3-N concentrations above 1 to 3 μM are found in the upper half of the photic zone and when the netplankton standing crop is supported in the photic zone by vertical advection, i.e., upwelling.

Decreases in netplankton standing crop and net/nanno ratios were related to influxes of oceanic water and increases in grazing pressure in Monterey Bay. Variations in phytoplankton productivity and grazing conformed to what Cushing (1959) has referred to as an unbalanced seasonal cycle of primary production and primary consumption. Neritic regions in temperate waters are generally characterized by about a 2-month time interval between peaks in phytoplankton and zooplankton biomass (Cushing, 1959; Heinrich, 1962), with a time lag of about 1 month between the onset of the spring bloom and the increase in zooplankton standing crop. Martin (1965) found a 2-month lag between the maximum phytoplankton standing crop and the increase in zooplankton standing stock.

In Monterey Bay, about 2 months elapsed between the March-April phytoplankton bloom and the rapid increase in grazing pressure observed during June and July (Figure 3). Although upwelling was in progress (NO_3-N concentrations were greater than 5 μM throughout the photic zone and the netplankton chlorophyll maximum was in the upper 10 m), the phytoplankton chlorophyll content of the water column declined as grazing pressure increased. The netplankton fraction fell continuously while the nannoplankton dropped at first and then increased (Figure 5). The reduction in standing crop was accompanied by a steady decline in the ratio of netplankton-to-nannoplankton chlorophyll in the water column, from 1.1 near the beginning of the increase in grazing pressure to 0.1 at its peak. Thus, it appears that (1) the phytoplankton bloom was ultimately limited by grazing; (2) the netplankton fraction, dominated by *Nitzschia* spp. and *Rhizosolenia* spp. (80% of the netplankton by number), was selectively grazed; and (3) the cycle of netplankton production and animal grazing was unbalanced.

Variations in the net/nanno chlorophyll m^{-2} ratio were significantly related to concurrent changes in the nitrate content of the photic zone (an indicator of upwelling) and to grazing pressure ($F = 5.56$, $P = 0.05$) by the multiple regression equation:

$$\text{net/nanno} = 1.76 + 0.003\ (NO_3\text{-N}) - 2.53\ (\text{Phaeo/Chl-a}).$$

This equation is based on 20 sets of data (CalCOFI 3), and the partial correlation coefficients for the interactions between the net/nanno ratio and nitrate concentration ($r = +0.51$) and between the ratio and grazing pressure ($r = -0.56$) are significant at the 0.05 level. The evidence suggests, therefore, that upwelling is a necessary precondition for netplankton productivity and standing crop to approach or exceed that of the nannoplankton in marine environments where water depth greatly exceeds the maximum depth of wind-driven turbulent mixing.

The relative constancy of the nannoplankton relative to the netplankton fraction, in spite of marked changes in the concentration of inorganic nitrogen, the intensity and direction of vertical water movements, and grazing pressure, is puzzling. The assimilation ratios of both fractions exhibited little variability, but on the average nannoplankton ratios were twice as great as those of the netplankton. Since this ratio is an index of growth rate (cf. Eppley and Strickland, 1968), the nannoplankton must have been limited primarily by "cropping" factors (Dickman, 1969), at least during those periods when netplankton productivity was increasing relative to nannoplankton productivity. This is supported by the observation that the chlorophyll content of nannoplankton and netplankton cells also exhibited little variability during the period of study. During upwelling, two processes could selectively remove nannoplankton cells from upwelling regions: (1) grazing and (2) horizontal advection.

If nannoplankton grazers were predominantly protozoans (Beers and Stewart, 1969) with short generation times and netplankton grazers were crustaceans and fishes with long generation times, the coupling between primary productivity and grazing would be much closer for nannoplankton-based food chains than for netplankton-based food chains. The cycle of nannoplankton productivity and animal grazing would be balanced (Cushing, 1959; Heinrich, 1962) in contrast to the unbalanced character of netplankton-based food chains. This would tend to dampen fluctuations in the nannoplankton fraction relative to the netplankton fraction.

Similarly, if nannoplankton cells were selectively removed from sites of upwelling by mass transport normal to the coast because of their lower sinking rates, netplankton cells would have a greater tendency to remain closer to the region of upward water movement than nannoplankton cells (Stommel, 1949). Both of these processes, selective grazing by organisms with short generation times and horizontal advection away from upwelling sites, would limit increases in nannoplankton standing crop during upwelling and could compensate for the growth rate differential between the netplankton and nannoplankton fractions. This would set the stage for netplankton productivity and standing crop to exceed that of the nannoplankton during upwelling, and also explain the discrepancy between nannoplankton growth rates and their response to photic zone enrichment. Decreases in nannoplankton standing crop due to "excessive" grazing or removal from the photic zone by downward water movements would be dampened by the short generation times (and, therefore, potentially rapid response time) and motility of the nannoplankton species.

Comparisons of the Oceanic Period in Monterey Bay with the offshore oceanic environment of the California Current reveals an interesting pattern of netplankton and nannoplankton variation which is consistent with the above model. The productivity and standing crop of the netplankton fraction did not vary significantly between the Oceanic Period inshore and the offshore oceanic zone. In contrast, the nannoplankton were significantly higher inshore than offshore (Table 5). This "inshore enhancement" effect during intrusions of oceanic water could arise in response to the overall pattern of circulation. The vertical distribution of nannoplankton chlorophyll compared with that of the netplankton indicated that nannoplankters are more independent of vertical water movements and are better able to maintain their position in the water column. This ability, probably a consequence of motility, will result in a concentration of nannoplankton in regions of downward flow (Hutchinson, 1967). In addition, the ability of nannoplankton to maintain their position in the photic zone could give rise to a situation analogous to the "island mass effect" described by Doty and Oguri (1956). The former is more likely, however, since assimilation ratios were equivalent in both inshore and offshore environments, i.e., the increase in primary productivity was a consequence of higher standing crops rather than an increase in growth rates.

TABLE 5.—Mean netplankton and nannoplankton productivity and standing crop with 95% confidence limits for the Oceanic Period at CalCOFI 3 and the offshore oceanic region of the California Current.

Oceanic region	Measurement	Nanno		Net	
Offshore	mgC m^{-3} hr^{-1}	0.69 ±	0.20	0.08 ±	0.05
Inshore		3.90	1.53	0.25	0.20
Offshore	mgChl-a m^{-3}	0.093	0.036	0.019	0.010
Inshore		0.477	0.227	0.068	0.047
Offshore	mgChl-a m^{-2}	15.60	3.22	2.58	0.92
Inshore		18.14	5.15	3.71	2.17

SUMMARY AND CONCLUSIONS

Phytoplankton productivity and standing crop were low under oceanic conditions, both inshore and offshore. During the Oceanic Period in Monterey Bay the nannoplankton accounted for 60 to 99% of the observed productivity and standing crop, while offshore this fraction was responsible for 75 to 99%. The productivity and standing crop of the netplankton fraction were exceedingly low and constant under these conditions, but the nannoplankton fraction was significantly higher inshore than offshore. Netplankton productivity and standing crop exceeded that of the nannoplankton only during periods of strong upwelling.

The netplankton fraction was composed almost exclusively of diatoms while the nannoplankton fraction was dominated by flagellates. Similar, but more detailed observations off La Jolla, Calif., (Reid et al., 1970) showed the nannoplankton to be composed primarily of naked dinoflagellates, "monads" (e.g., *Chilomonas marina* and *Eutreptia* sp.), and coccolithophores (e.g., *Coccolithus huxleyi*).

The nannoplankton fraction was surprisingly stable both seasonally in Monterey Bay and geographically in the California Current system. Variations in phytoplankton productivity and standing crop were due primarily to the netplankton with the nannoplankton maintaining a comparatively stable background level.

Increases in netplankton productivity and standing crop were closely related to upwelling, both as a consequence of the positive vertical advection and the entrainment of nitrate into the upper half of the photic zone. The requirement for positive vertical advection was probably related to both cell size and motility so that the vertical distribution of nannoplankters was more independent of vertical water movements. The relationship between cell size and A/V ratios probably accounted for the higher nitrate requirements of the netplankton. Decreases in the netplankton were primarily due to grazing and to removal from the photic zone by downward water movements.

The stability of the nannoplankton compared to the variability of the netplankton is interesting, especially in light of the marked changes observed in the concentration of inorganic nitrogen compounds and the direction and intensity of vertical water movements. Since nannoplankton assimilation ratios were consistently high and twice as great as netplankton assimilation ratios, the nannoplankton must have been limited primarily by cropping factors during upwelling periods when netplankton standing crop was increasing relative to that of the nannoplankton. Under these conditions increases in the nannoplankton fraction will be dampened by selective removal from upwelling sites by mass transport away from the coast and grazing by organisms with short generation times (e.g., protozoans). Decreases in nannoplankton standing crop due to "excessive" grazing or removal from the photic zone by downward water movements will be limited by the motility and short generation times of nannoplankton species. The motility of nannoplankters in combination with onshore mass transport and downward water movements will also favor an offshore-inshore increase in nannoplankton productivity and standing crop.

Finally, it is clear that the nannoplankton and netplankton components of phytoplankton communities respond differently to changes in their environment; that cell size, surface-to-volume ratios, and motility play important roles in mediating these responses; and that changes in netplankton and nannoplankton productivity relative to each other have definite consequences with respect to energy flow through phytoplankton-based food chains.

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