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by
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(Con resumen en Español)

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III. CONDICIONES GENERALES ECOLOGICAS, Y LA DINAMICA DEL FITOPLANCTON A LOS 8°45'N, 79°23' O, DESDE NOVIEMBRE 1954 HASTA MAYO 1957

by
THEODORE J. SMAYDA[2]

ABSTRACT

Bi-weekly phytoplankton samples were collected at 0, 10, and 20 m and enumerated by the Utermöhl sedimentation technique; ^{14}C productivity measurements at 10 m, oblique zooplankton tows, and routine hydrographic observations were also made. Northerly winds induce upwelling during December—April, followed by a rainy season; a slight resurgence in upwelling may occur during July and/or August. Annual variations in upwelling intensity and rainfall occur. During upwelling, the upper 50 m, about 30 per cent of the total volume of the Gulf of Panama, is replaced with water 5 to 10 C colder than the more stratified, turbid and nutrient impoverished watermass present during the rainy season. The mean annual runoff accompanying an average annual precipitation of 2731 mm is estimated to equal a layer of fresh water 3.2 m thick. About 10 per cent of the phytoplankton phosphate and inorganic nitrogen requirements during the rainy season are accreted.

About 330 phytoplankton taxa were distinguished. The average upwelling season phytoplankton standing crop as cell numbers and biomass exceeded rainy season levels by about 6- and 9-fold, respectively. Diatoms overwhelmingly dominated the communities in comprising 86 and 71 per cent of the average cell numbers, and 97 and 99 per cent of the average biomass during the upwelling and rainy seasons, respectively. Unlike other groups, diatoms exhibited a species succession during upwelling. A daily natural mortality rate of about 10 to 15 per cent of the phytoplankton community is suggested by the data. Phytoplankton abundance during

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[1] Contribution from the Narragansett Marine Laboratory, University of Rhode Island, Kingston, Rhode Island, and the Institute for Marine Biology, Sect. B, University of Oslo, Oslo, Norway.

[2] Narragansett Marine Laboratory, University of Rhode Island, Kingston, Rhode Island.

the upwelling seasons expressed as cell numbers, biomass and cell surface area was statistically significantly and directly related to winds at Balboa when expressed in various ways for 1 and, especially, 3 days, and occasionally for 7 days prior to the sampling date. Mean monthly phytoplankton biomass, and annual differences in mean biomass during the upwelling season were also directly related ($r = \geq 0.90$) to Balboa winds. Mean phytoplankton biomass in the upper 20 m during the upwelling seasons estimated from Balboa winds expressed in various ways and the surface temperature (t_o) using equations of the form: $\sqrt{\text{winds}/t_o}$, agreed within ± 15 per cent of observed levels at two-thirds of the stations used, and within 2 to 5 per cent for the mean 1955 and 1957 upwelling season standing crops, respectively. In general, phytoplankton growth during the rainy season, as during upwelling, appeared to be primarily dependent on the occurrence of northerly winds, although the exact relationship with environmental conditions remains obscure.

An annual gross production rate of 255 to 280 g C m^{-2} is estimated, based in part on Forsbergh's (1963) net production estimate of 180 g C m^{-2}, of which 90 g is fixed during the upwelling season. The productive zone appears to be restricted primarily to the upper 15 m.

The mean upwelling season zooplankton biomass exceeded rainy season levels about 1.7-fold. The average phytoplankton biomass exceeded zooplankton biomass 83-fold at the individual stations. Direct and inverse correlations were found between phytoplankton and zooplankton standing crops when compared in various ways. Zooplankton respiration, grazing and production rates were estimated. Less than 10 per cent of the phytoplankton standing crop, as carbon, was grazed daily by zooplankton. Two independent estimates of daily zooplankton production rate gave 29 and 98 per cent for the combined upwelling seasons, and -12 and -18 per cent for the rainy season.

Strong, positive correlations occurred between 1) mean anchoveta (*Cetengraulis mysticetus*) length during February, April and May and mean phytoplankton biomass during January and February, and 2) mean monthly anchoveta growth increment and phytoplankton biomass during January—May, 1955—1957. The mean daily anchoveta standing crop, respiration and grazing rates during the upwelling seasons were calculated. The mean daily grazing rate for all years was about 18 per cent of the phytoplankton standing crop carbon, and ranged from about 9 to 27 per cent for the individual upwelling seasons. The average daily anchoveta carbon production rate for all years was about 1.5 per cent of the standing crop.

A mechanism permitting the maintenance and succession of autochthonous phytoplankton communities in upwelling areas is proposed. A classification and description of five types of phytoplankton cycles and communities found in tropical inshore areas are presented. It is suggested that the occurrence of wind-induced enrichment of the euphotic zone is a cardinal prerequisite for increased phytoplankton growth in tropical inshore areas.

INTRODUCTION

The Inter-American Tropical Tuna Commission has maintained a hydro-biological station located at 8°45′N, 79°23′W in the Gulf of Panama in connection with their ecological investigation of the anchoveta, *Cetengraulis mysticetus*, a tuna baitfish (see Peterson 1961 for references). Routine hydrographic and biological observations at this station, where the mean depth is approximately 42 m at mean low water, have been made (Schaefer, Bishop and Howard 1958, Schaefer and Bishop 1958, Forsbergh 1963).

The relationship between ^{14}C assimilation and the diatom standing crop at this station (Smayda 1965a) and the regional and seasonal variations in phytoplankton growth in the Gulf of Panama (Smayda 1963) have also been described. This paper presents the results of the phytoplankton investigation at the hydro-biological station from November 1954 to May 1957, along with an evaluation of the environmental and biological factors influencing phytoplankton dynamics, and some of the consequences of this growth to other trophic levels. A comparison of the ecological principles and organic production characterizing phytoplankton growth in the Gulf of Panama with that in other regions, and the floristic and biogeographical aspects of this community will be presented in subsequent publications.

There have been few *quantitative* investigations of the *annual* phytoplankton cycle in tropical inshore waters; the investigations of Marshall (1933) and Bainbridge (1960) are especially notable. Thus, there is a great need for a quantitative evaluation and description of such cycles, independent of any food-chain consequences of such investigations. An effort has been made herein to describe and to evaluate quantitatively the conditions of existence and response in a tropical inshore upwelling area. To a certain extent this attempt has been frustrated by gaps in the data, as will become apparent, lack of observations on critical parameters and the impossibility of conducting nutrient enrichment or grazing experiments. An attempt has been made to overcome the limitation of numerical phytoplankton censuses by converting cell numbers to equivalent cell volume (biomass).

ACKNOWLEDGEMENTS

The author did not personally participate in the Gulf of Panama sampling program. Therefore, he is especially indebted to Dr. Milner Schaefer, Mr. Izadore Barrett, Dr. William Bayliff, Mr. Eric Forsbergh, Mr. Gerald Howard, Mr. Antonio Landa and Mr. Clifford Peterson, all formerly or presently affiliated with the Inter-American Tropical Tuna Commission, for their assistance in the collection and forwarding of the samples, in providing data and for rendering various other services. The author is also indebted to Professor Trygve Braarud for providing facilities at the Institute for Marine Biology, Sect. B, Oslo, Norway, and to Mrs. Karen Ringdal Gaarder, Mrs. Grethe Rytter Hasle and Mr. Einar Ramsfjell for assistance in the identification of certain species.

Dr. Richard Cooper and Professor Robert Myers kindly made available their linear regression and correlation coefficient programs, respectively, written for an IBM 1410 computer. Miss Brenda Boleyn, Miss Joan Nash and Mrs. Linda Brodin provided valuable drafting and clerical assistance.

This study was conducted in part during the tenure of a Fulbright Fellowship and a Woods Hole Oceanographic Associates' Fellowship.

METHODS

The hydro-biological station at 8°45′N, 79°23′W (Fig. 1) was sampled 112 times (stations) at approximately 2-week intervals from 29 November 1954 to 3 June 1959 (Forsbergh 1963). Each sampling date will be referred to as a station in this paper, which will deal principally with the hydrographic and biological observations made at the first 63 stations sampled through 20 May 1957 (Appendix Table 1).

The sampling program consisted of a Nansen bottle cast at the surface, 5, 10, 20 and approximately 40 (bottom) m for the determination of salinity (Knudsen Method), oxygen (Winkler procedure) and, beginning in July 1955 (station 16), inorganic phosphate (Déniges-Atkins procedure). Particulate iron determinations were made on surface and 30 m samples collected from December 1954 (station 2) to December 1955 (station 28) (Schaefer and Bishop 1958). Temperature was measured with a bathythermograph, which was corrected with readings taken at the surface with a bucket thermometer and at 20 m with a reversing thermometer (Forsbergh 1963). Oxygen saturation values were determined using the nomogram of Richards and Corwin (1956).

Secchi disc measurements of water transparency were made beginning at station 39 (19 June 1956). The extinction coefficient (k) was calculated by the Poole and Atkins (1929) formula:

$$k = 1.7/D$$

where D equals the Secchi disc disappearance depth in m. Pyrheliometric measurements of the total daily radiation were initially made at the Albrook Air Force Base and then at Curundu, near Balboa (Fig. 1), located about 45 km from the hydro-biological station. The radiation measurements were made from 0700 to 1800 hours, and are expressed as langleys per day (ly/day), where 1 langley equals 1 g cal per cm^2 (Strickland 1958). These data were obtained by the Inter-American Tropical Tuna Commission from the *U. S. Weather Bureau.*

Observations on sea-level and surface temperature at Balboa (Fig. 1) and wind data collected at Balboa Heights were provided by the Panama Canal Company (*vide* Schaefer, Bishop and Howard 1958). This company also provided their monthly and annual "Climatological Data" reports for the Panama Canal Zone and Panama, an important source of information. River runoff data were provided by the Servicio Cooperativo Interamericano de Fomento Economico (S. C. I. F. E.) for the *Rio Santa Maria* (monitoring station located at San Francisco, about 60 km inland from Parita Bay), *Rio Grande* (monitoring station located at Rio Grande, about 20 km from Parita Bay), and the *Rio Mamoni*, monitored at its confluence with the Rio Chepo about 20 km inland from its entrance into the Gulf of Panama to the east of the Panama Canal (Figs. 1, 19).

Water bottle samples for phytoplankton enumeration were collected from the surface, 10 and 20 m, dispensed into 400 ml citrate bottles, preserved with neutralized formalin and shipped to the Institute for Marine Biology, Sect. B, Oslo, Norway. Enumeration was then carried out on 2 ml and 50 ml sub-samples employing Utermöhl's (1931) inverted microscope (sedimentation) method. The manufacturer's specified volume of the 2 ml and 50 ml settling chambers used in the enumeration was not checked. It has since been discovered, however, that such chambers should be re-calibrated; chambers purported to have a capacity of 50 ml have been found with an actual capacity of only 47 ml!

Enumeration was hampered by the frequent occurrence of large quantities of aragonite[3] and macroscopic flakes of a thin, transparent, cellophane-like substance in the samples. These substances appeared to be a consequence of preservation. They did not occur together in a given sample. (Nordli [1950] also found a flaky precipitate in preserved phytoplankton samples [chemical analyses suggested that it was calcium silicate] which he postulated as possibly being associated with the quality of the glass used in the bottles.)

Of the 189 phytoplankton samples collected at the 63 stations, 23 contained the cellophane-like contaminant and could not be enumerated. Agitation of these samples prior to dispensing the 2 and 50 ml sub-samples for enumeration broke up the flakes into many fine particles which settled onto the chamber bottom and obscured the phytoplankton cells.

The 2 ml sub-samples from those containing aragonite, however, could be enumerated with effort, whereas the 50 ml sub-samples could not. Therefore samples containing aragonite were treated as follows to dissolve

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[3] Determined by Dr. Hans Holtedahl of the Geology Department, University of Oslo.

this substance but still permit an enumeration of the coccolithophores. The 2 ml sub-sample was poured from a 100 ml sub-sample taken from the well-shaken parent sample. The aragonite in the remaining 300 ml of parent sample was dissolved by adding dilute HCl, and neutralizing with N_aOH. (It was necessary to neutralize the acid-treated sample prior to enumeration to prevent dissolution of the adhesive attaching the thin cover slip to the bottom of the settling chamber.) The 50 ml sub-sample was then dispensed from the treated parent sample, and enumerated with relative ease.

Thirty samples collected during the rainy season from 25 July to 1 December 1955 (stations 17 to 26) were lost in transit. The present report is therefore based on the enumeration of 136 samples covering the 1955, 1956 and 1957 upwelling seasons (December—April) and the 1956 rainy season (Appendix Table 2).

In addition to cell numbers, phytoplankton abundance will be expressed as biomass and, occasionally, as plasma volume and cell surface area (Appendix Table 1). The methods of deriving the latter three standing crop indices from the cell counts are given by Smayda (1965a). The expression biomass is used synonymously with tissue volume or wet weight in the text, and is derived from estimates of cell volume assuming a specific weight of 1.0 — the units $mm^3\ L^{-1}$ and $mg\ L^{-1}$ being used interchangeably. While there are many shortcomings in the derivation and use of biomass (Lund 1964), this measure of phytoplankton standing crop abundance has been used to evaluate those quantitative aspects of phytoplankton—environmental relationships and food chain dynamics, the adequate evaluation of which is not possible with cell numbers alone.

Estimates of the mean standing crop size ($\overline{N}$) in the upper 20 m have been derived using the method given by Riley (1957):

$$\overline{N} = \frac{1}{20}\left[\frac{10(N_0 + N_{10})}{2} + \frac{10(N_{10} + N_{20})}{2}\right]$$

where N_0 is the number of cells (or biomass, etc.) at the surface, N_{10} at 10 m, and N_{20} at 20 m.

^{14}C productivity experiments were conducted at 10 m at 30 of the 63 stations (Smayda 1965a). Forsbergh (1963) has described in detail the methodology of the productivity experiments, as well as the results of experiments conducted after station 63 was sampled. The samples were collected at the hydro-biological station, but were incubated *in situ* for 24 hours at a location near Taboga Island approximately 16 km northwest of the collection site (Fig. 1).

Vertical phytoplankton net hauls with a No. 20 net were made from the bottom. The sample volumes, expressed as mm^3 or mg per m^3, were measured after settling 24 hours in a graduate cylinder. Zooplankton were sampled by a 25-minute oblique tow from near the bottom to the surface with a half meter net. The net, fitted with an Atlas Current meter, was made of 40 XXX grit gauze (0.500 mm aperture) in the primary funnel and 56 XXX grit gauze (0.318 mm aperture) in the cod-end. Wet volumes, expressed as ml/1000 m^3 or g/1000 m^3 (assuming a specific weight of 1.0), were found by displacement and do not include any organisms over 5 cm in length. The Inter-American Tropical Tuna Commission chose to present the zooplankton settling volumes per 1000 m^3. These data have also been used in the text as zooplankton biomass per m^3 or per m^2 based on a water column depth of 40 m.

The evaluation of the results was facilitated considerably by computer programs which calculated linear regressions by the least squares method (kindly made available by Dr. Richard Cooper) and sample correlation coefficients (kindly made available by Professor Robert Myers). The latter program was especially valuable and permitted the calculation of more than 300 correlation coefficient estimates that otherwise would not have been feasible.

Additional procedures employed during the investigation will be described within the main body of the text.

THE GULF OF PANAMA AS AN ENVIRONMENT

Physiography

The *Gulf of Panama* will refer herein to the region north of latitude 7°26′46″N bounded by the Isthmus of Panama (Fig. 1). The area south of this parallel extending to 2°S and eastwards from longitude 81°W (Wooster 1959) to the arcuate coastline formed by the Colombian-Ecuadorian coast will comprise the Panama Bight.

The Gulf of Panama, which approximates a circular embayment, occupies 28,850 km^2 and extends 175 km inland from its entrance to the south where the distance from Cape Mala to the opposite (eastern) shore is 205 km. *San Miguel Bay* and *Parita Bay*, two important drainage loci, are prominent features of the central region of the Gulf where the maximum distance along its east-west axis is 245 km. The Gulf progressively constricts towards its inner reaches, where *Chame Bay* is the most conspicuous coastal indentation. The hydro-biological station is located near *Taboga Island* situated northeast of Chame Bay (Fig. 1).

Numerous volcanic islands (Terry 1956) comprising about 1,150 km^2 cluster in the central region of the Gulf to form the *Pearl Islands* (Archipielago de las Perlas). This island complex extends about 50 km along the north-south axis to divide the central Gulf region into two major "passages". The sea floor of the smaller passage between the Pearl Islands and San Miguel Bay to the east is characterized by a prominent extension of

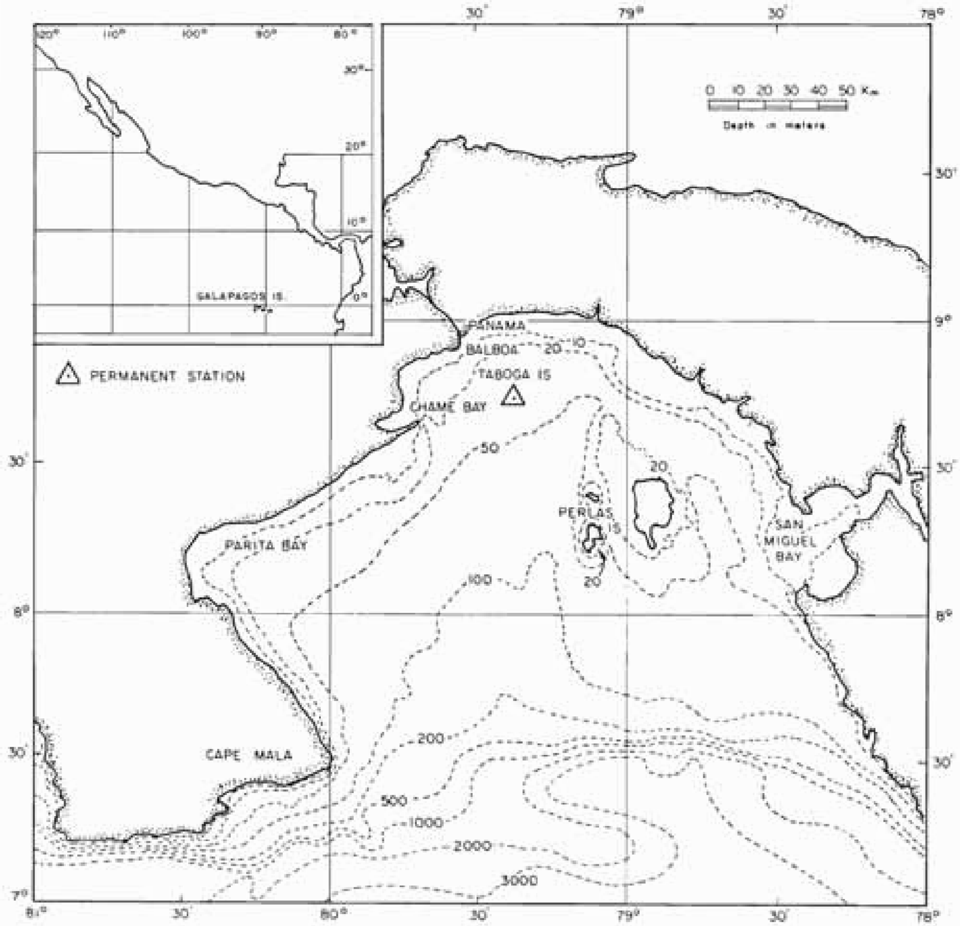

FIGURE 1. Principal features of the Gulf of Panama, and location of the hydrobiological station maintained by the Inter-American Tropical Tuna Commission.

the 50 m isobath into an otherwise relatively shallow area. This channel will be shown to influence the movement of upwelled waters.

The Gulf of Panama is relatively shallow throughout most of its expanse. The bottom gradually slopes southwards to the edge of the continental shelf where it deepens precipitously, as along the 79°W meridian where the depth increases from 200 to 3,000 m in 10 km (Fig. 1). The mean depth of approximately 135 m reflects these great depths at the entrance to the Gulf.[4] This datum is somewhat misleading, however. Table 1 indicates that 91.4 per cent of the total area of the Gulf of Panama is shallower than 200 m, yet this area comprises only 53 per cent of the total

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[4] Panama Map AMS 1301 (GSGS 4646) Edition 1-AMS 1954 was used in the preparation of Figure 1 and the section on morphometry.

TABLE 1. Morphometric data for the Gulf of Panama

Isobath (m)	Area (km²)	Per cent of surface	Water between isobaths (m)	Volume ($m^3 \times 10^9$)
0	28,500	100	0 - 10	274.0
10	25,984	90.1	10 - 20	245.6
20	23,170	80.3	20 - 50	595.7
50	16,720	58.0	50 - 100	553.5
100	6,260	21.7	100 - 200	419.7
200	2,430	8.4	200 - 500	525.2
500	1,150	4.0	500 - 1000	471.5
1000	750	2.6	1000 - 2000	577.1
2000	420	1.5	2000 - 3000	276.7
3000	155	0.5		
			Total Volume	$3{,}939.0 \times 10^9$

volume; 83 per cent of the Gulf is less than 100 m deep. The mean depth within the 200 m isobath is approximately 60 m.

A submarine valley is a conspicuous topographical feature of the Gulf of Panama floor. Beginning north of the Pearl Islands, as indicated by the northeast protrusion of the 50 m isobath, this arcuate valley continues southwards to the west of the Pearl Islands archipelago and remains detectable at the Gulf entrance near the 200 m isobath (Fig. 1). Terry (1941) states that this valley begins at the head of the Gulf south of the Chepo (Bayano) River near the 40 m contour (Fig. 19) and remains perceptible almost to the 725 m isobath where its radiating channels suggest an earlier delta. His original interpretation that this valley represents the ancient bed of the Chepo (Bayano) River has since been discarded in favor of a faulting origin (Terry 1956). This submarine valley will be demonstrated to be important in controlling the incursion of offshore water masses during the upwelling season.

In response to intense precipitation during the rainy season (*vide* page 390), an extensive drainage system (Fig. 19) consisting of approximately 325 streams and rivers (Anonymous 1929) has evolved; eastern Panama exhibits the most advanced drainage system (Terry 1956). Large quantities of terrigenous material accompany runoff into the Gulf of Panama (Jerlov 1953), the sedimentation of which is probably modifying the submarine topography, especially near important drainage loci such as Parita Bay and San Miguel Bay (Fig. 1). In the southern half of the Gulf, a reduced sedimentation influence appears to be a consequence of the less extensive drainage system and, possibly, the scouring action of currents.

Littoral diatoms, empty silicoflagellate tests and an abundance of terrigenous material in the surface water samples indicate that a roiling of the bottom accompanies upwelling in the "shallow flats" region outlined by the 20 m isobath (Smayda 1963). This stirring can also be expected to augment nutrient supplies, such as phosphate, through their release from the sediments (Seshappa and Jayaraman 1956).

Climatology

The Isthmus of Panama is located within the path of the north-south seasonal movement of the Tradewind-Calm Belt (Doldrums) system (Fig. 2). The Gulf of Panama, consequently, is successively influenced by the Northeast Trade Winds of the Atlantic, the Equatorial Calm Belt (Doldrums), and the Southeast Trade Winds of the Pacific during a calendar year (Chapel 1927, Wooster 1959). The Doldrums are light, variable winds which develop where the Northeast and Southeast Trade Winds approach one another (Wooster 1959). The actual convergence of these trade wind systems within the Doldrums is called the Intertropical Convergence, and is accompanied by heavy rains. The Tradewind-Calm Belt (Doldrums) system lies at its farthest southward position during the northern winter and migrates to its most northerly position during the northern summer (Fig. 2).

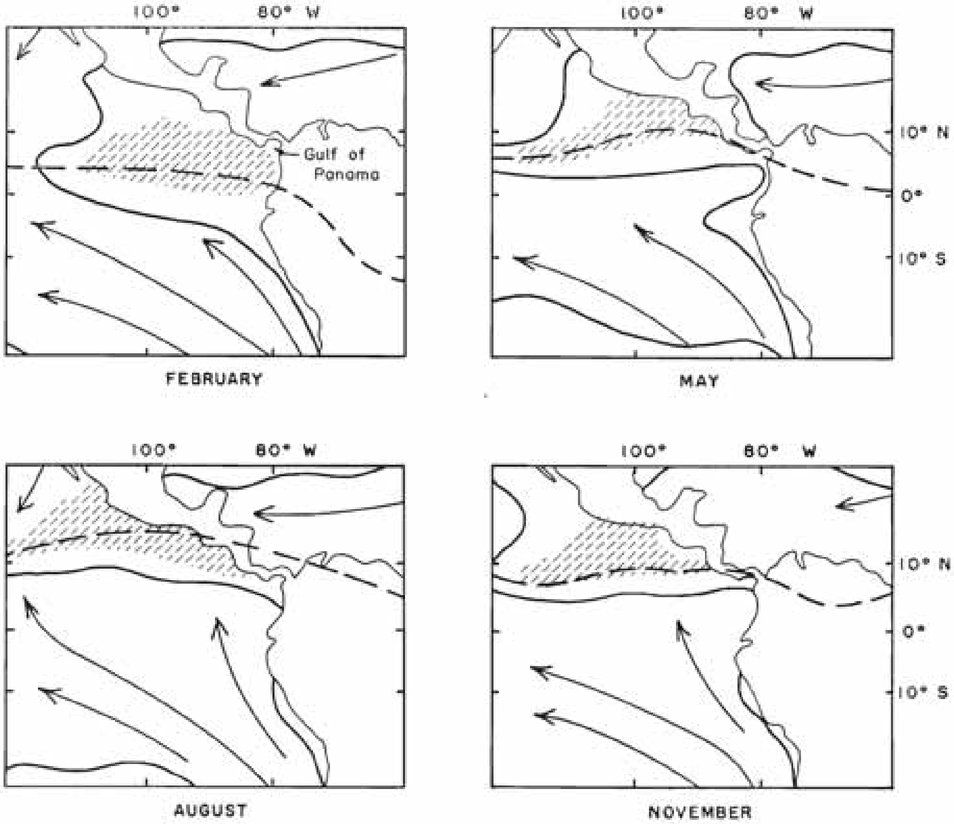

FIGURE 2. Average positions of the limits of trade-wind circulation (heavy solid lines), doldrums (shaded), and the Intertropical Convergence (heavy dashed lines); arrows indicate average direction of air flow (taken from Wooster 1959).

From January through April, but occasionally including December and May, the Doldrums are displaced to the south and the dry, upwelling inducing Northeast Trade Winds then prevail over the Gulf of Panama (Fig. 2). Although true north and northeast wind components predominate on the Caribbean side of the isthmus, the winds shift to the northwest quadrant on the Pacific side (Fig. 3), as observed at Balboa (Schaefer *et al.* 1958) and at Cape Mala (Fig. 1), because of inland topographical features (Chapel 1927).

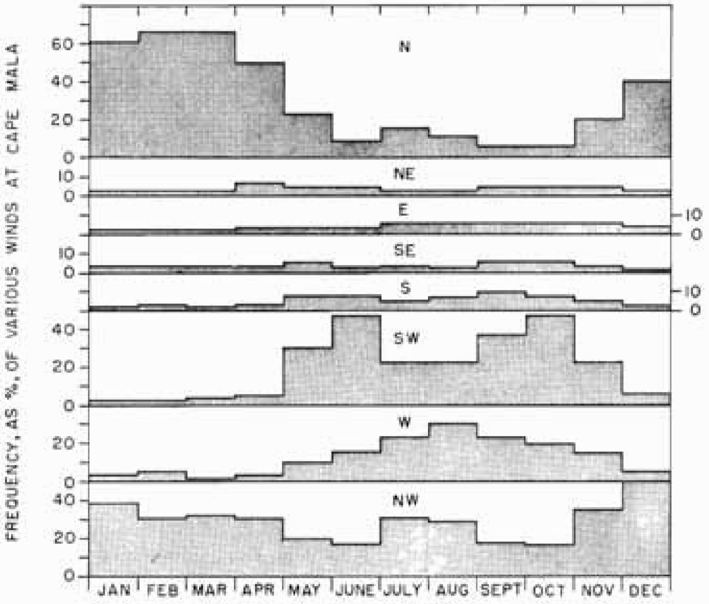

FIGURE 3. Relative predominance of winds from various directions throughout the year at Cape Mala (after Chapel 1927).

The Northeast Trade Winds usually weaken and disappear in late April or May when the wind system moves northward (Figs. 2, 3, 4). The Gulf of Panama then becomes increasingly influenced by the Doldrums and the rain-bearing southwest winds of the onshore Southeast Trade Winds which usually persist until mid-December. There is usually a slight resurgence of northerly winds, especially from the northwest (Figs. 3, 4), during July and/or August. These relatively light and shallow winds during the middle of the rainy season are believed to represent mild monsoon influences associated with the tradewind system located over the eastern Caribbean at that time (Chapel 1927). A progressive southerly migration of the Tradewind-Calm Belt (Doldrums) system occurs during the rainy season re-establishing the Northeast Trade Winds in the Panama region by December (Figs. 2, 3, 4).

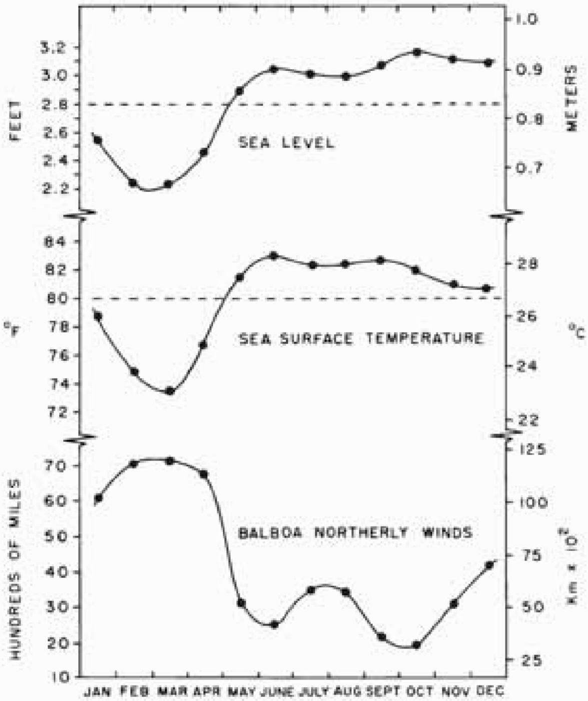

FIGURE 4. Long-term monthly averages of sea-level, sea-surface temperature (1908-1953) and northerly winds (1915-1956) at Balboa (modified from Schaefer, Bishop and Howard 1958). The number of miles of northerly winds per month (weighted to a 31-day basis) was calculated by weighting the mean velocity of the north, northwest and northeast winds during a given month by the mean number of hours blowing. Measurements of the wind direction, velocity and duration of blowing were obtained for the years 1915-1956 from continuously recording anemometers located at Balboa.

General hydrographic conditions at 8°45′N, 79°23′W

The dry, northerly, offshore winds associated with the Northeast Trade Winds displace the watermass in the upper 40 to 78 m offshore (Fleming 1939, Schaefer *et al.* 1958, Forsbergh 1963) lowering the sea-level and causing an upwelling of 1) *colder*, 2) more *saline* and 3) *nutrient-rich* water to the surface during January through April (Figs. 4, 5, 6). The rain-bearing, southerly, onshore winds associated with the Southeast Trade Winds and Intertropical Convergence within the Doldrums prevail during the remainder of the year. The sea-level rises, the watermass becomes 1) *warm*, 2) *diluted* and 3) *nutrient-impoverished*, and flushing and admixture with more fertile waters are hindered. A slight resurgence of northerly winds during July and/or August may induce mixing or even cause a slight upwelling.

Schaefer *et al.* (1958) and Forsbergh (1963) have demonstrated statistically that northerly winds induce upwelling in the Gulf of Panama.

In addition to finding highly significant correlations between average monthly sea-level, sea-surface temperature and northerly wind intensity at Balboa (Fig. 4), Schaefer and co-workers demonstrated that the sum of all northerly winds was a better index of effective upwelling winds than due north or due northwest winds alone. Forsbergh, in turn, found that the bottom (about 40 m) temperature at the hydro-biological station from November 1954 to June 1959 was well correlated (r = −0.68) with the "three-day mean net northerly wind" monitored at Balboa (Fig. 1). Although statistical analyses have not been made, increased precipitation during the rainy season is undoubtedly attributable to the prevalence of southerly winds (Figs. 5, 6).

Hydrographic conditions accompanying the upwelling and rainy seasons at the hydro-biological station from November 1954 to May 1957 are

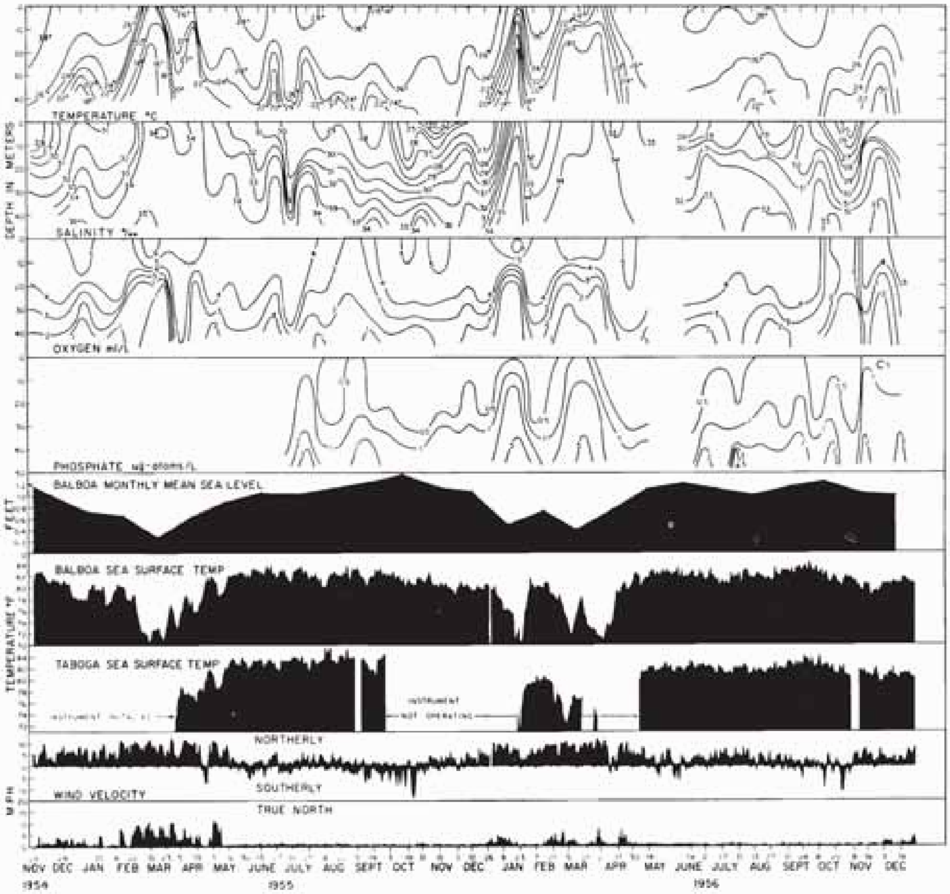

FIGURE 5. Meteorological (at Balboa) and oceanographic conditions from November 1954 to December 1956 at the hydro-biological station located at 8°45′N, 79°23′W in the Gulf of Panama (prepared by the Inter-American Tropical Tuna Commission).

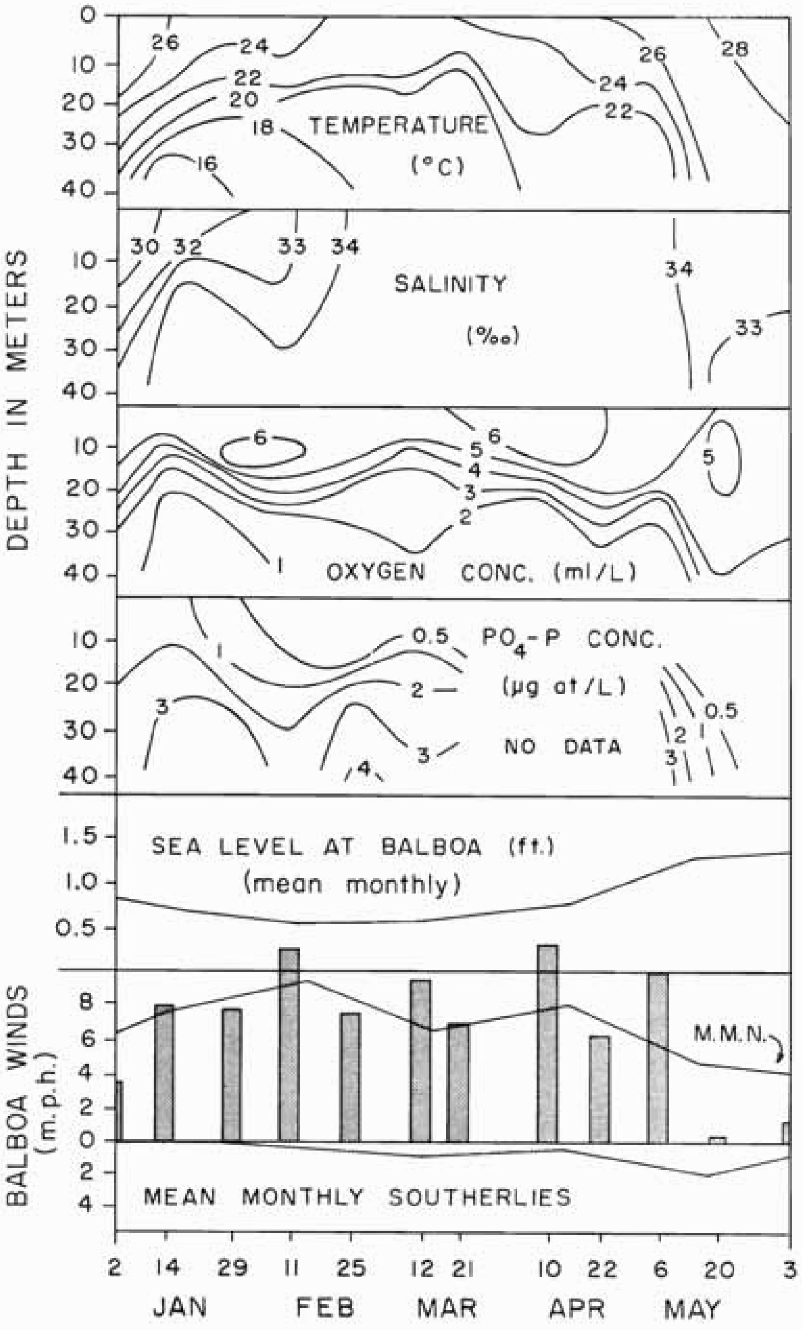

FIGURE 6. Meteorological (at Balboa) and oceanographic conditions from January to 3 June 1957 at the hydro-biological station located at 8°45'N, 79°23'W in the Gulf of Panama (modified from Forsbergh 1963). (The histograms in the second panel from the bottom represent the mean intensity of northerly wind for 3 days prior to the sampling date; M. M. N. refers to the mean monthly northerly winds.)

presented in Figures 5 and 6. The relative upwelling intensity or degree of stratification during the rainy season at a given station has been inferred from the station-to-station differences in hydrographic conditions, particularly from the vertical oscillations of the temperature and salinity isopleths. A clear relationship between wind behavior and hydrographic conditions at any given station is not to be expected. The hydrographic characteristics are also influenced by past wind conditions as well, as in the usual 2-week interim between sampling dates. Therefore only the general hydrographic features will be outlined here.

1954-1955

During November and December 1954 the watermass in the upper 20 m ranged from 26 to 29 C and from 27.00 to 30.00 ‰ in salinity (Fig. 5). The watermass became generally cooler and more saline during January and February 1955 when upwelling was occurring, as indicated by the pronounced incursion of a cold (18 to 20 C), saline (34.00 to 35.00 ‰) and oxygen-poor (1 ml L^{-1}) watermass below 20 m and the lower mean sea-level at Balboa. Upwelling intensified during March along with northerly winds; the 20 C and 34.00 ‰ isopleths, observed at approximately 30 m during February, were now at the surface. On 10 March (station 7), for example, the surface water was 19.4 C and 34.67 ‰, corresponding to a decrease of 9.56 C and an increase of 7.37 ‰ since 29 November 1954 (station 1). An even more pronounced decline in temperature occurred at 38 m (bottom) during this period:

	Station 1 (29 Nov. 1954)	**Station 7 (10 March 1955)**	△
Surface C	29.00	19.44	− 9.56
38 m C	26.33	15.33	−11.00
Surface ‰	27.30	34.67	+ 7.37
38 m ‰	32.50	35.00	+ 2.50

It is obvious that the entire water column is replaced during upwelling.

A pronounced reduction in upwelling intensity accompanied the partial subsidence of northerly winds during early and late-April, interspersed by a period of slightly more intense upwelling (Fig. 5). During mid-May the northerly winds suddenly diminished and southerly winds increased (and progressively intensified through October), signaling the end of the upwelling period and the beginning of the rainy season. An immediate temperature increase to pre-upwelling levels occurred and persisted through the rainy season. The surface temperature fluctuated between 27.3 and 28.6 C, while at 20 m it remained at approximately 26 C. Salinity, however, progressively decreased as the rain-bearing southerly winds intensified (Fig. 5). By mid-November (station 25) the surface salinity was 21.68 ‰, a decrease of 13.00 ‰ from that observed during mid-march (station 7) at the height of the upwelling season:

Station 25:	**C**	‰	σ_t
Surface	27.50	21.68	12.61
38 m	25.11	31.76	20.90

The watermass is usually well stratified during the rainy season, a condition which has important biological consequences, as will be discussed below.

A sequence of four upwelling "pulses" is detectable *below* 20 m, as indicated by the vertical movements of the 26 C isopleth, from mid-June to September; the pulses appear to accompany resurgent northerly winds at those times (Fig. 5). However, these winds were too weak to overcome the pronounced stratification of the watermass and the influence of the opposing southerly (onshore) winds and cause upwelling to extend to the surface, as during the upwelling season.

1956

Three upwelling pulses occurred in 1956 (Fig. 5). Intense northerly winds and upwelling occurred in late December and early January, slackened until mid-February, intensified from late February to mid-March, and subsided again until early April. The north wind component has four distinct peaks during this period (Fig. 5); the first three are accompanied by a sharp drop in sea surface temperature at Balboa. This upwelling sequence is also clearly reflected in the temporal and vertical distribution of temperature, salinity, phosphate and oxygen. The magnitude of the change in these environmental factors from pre-upwelling levels (station 25) was considerable:

	Station 25 (15 Nov. 1955)	**Station 30 (23 Jan. 1956)**	△
Surface C	27.50	23.00	− 4.50
38 m C	25.06	13.28	−11.78
Surface ‰	21.68	33.17	+11.49
38 m ‰	31.76	35.11	+ 3.35
Surface PO_4-P	0.08 (μg-at L^{-1})	0.42	+ 0.34
38 m PO_4-P	1.34	2.71	+ 1.37
Surface O_2	5.28 (ml L^{-1})	5.71	+ 0.43
38 m O_2	2.58	0.55	− 2.03

Upwelling ceased in mid-April; the temperature in the upper 20 m increased to above 26 C and remained at that level until December. Northerly winds were more intense and persistent during the 1956 rainy season than in 1955, the converse of the southerly wind behavior (Fig. 5; Table 2). The hydrographic consequences included a slight, persistent upwelling below 20 m during July and August 1956, in contrast to the multiple 1955 pulses, and a more saline, though still quite dilute, watermass during the height of the 1956 rainy season in early November:

Station 29:	C	‰	σ_t
Surface	27.67	24.88	14.95
40 m	26.83	32.89	22.18

TABLE 2. Mean monthly wind velocities at Balboa for northerly and southerly quadrants, as miles per hour (modified from Forsbergh 1963)

	1954		1955		1956		1957	
	N	S	N	S	N	S	N	S
Jan.			6.0	0.2	6.6	0.2	7.8	0.0
Feb.			7.8	0.2	7.6	0.1	9.5	0.3
Mar.			8.7	0.1	9.2	0.1	6.5	0.7
Apr.			6.8	0.9	7.1	0.5	8.0	0.3
May			5.2	0.6	4.2	0.9	4.5	1.8
June			2.2	2.0	3.1	1.3		
July			2.6	1.4	4.7	0.4		
Aug.			2.6	1.3	4.1	0.4		
Sept.			1.2	3.4	2.8	1.3		
Oct.			0.9	4.9	1.8	3.0		
Nov.	2.6	0.7	2.7	1.0	4.0	0.7		
Dec.	5.3	0.2	3.9	0.4	4.4	0.1		

During mid-November the northerly winds intensified and southerly winds weakened as the seasonal migration of the Tradewind-Calm Belt (Doldrums) system re-established the upwelling-inducing Northeast Trade Winds over the Gulf of Panama.

1957

Strong upwelling began during December and gradually increased in intensity through February, corresponding to an increase in northerly wind intensity (Figs. 5, 6). The following hydrographic characteristics on 25 February 1957 (station 57) and their change (△) from pre-upwelling levels on 8 November 1956 (station 49) were observed:

	C	‰	PO_4-P (μg-at L^{-1})	O_2 (ml L^{-1})
Surface	22.7	34.07	0.08	4.56
△	− 5.0	+ 9.19	− 0.29	− 0.06
36 m	18.0	34.20	3.99	1.56
△	− 5.6	+ 1.31	+ 2.80	− 0.12

Northerly winds and upwelling intensity gradually subsided thereafter, and ceased completely at the termination of the investigation on 20 May (station 63) when the surface and bottom (37 m) temperatures were 28.3 and 26.9 C, respectively.

Upwelling rates, and annual variations in upwelling intensity

The rate of upwelling varies with the duration and intensity of the northerly winds rather than remaining constant within a given season or from year-to-year (Figs. 5, 6). Forsbergh (1963) estimated that the maximum daily upwelling rates, averaged over 2-week periods, ranged from 2.1 to 2.8 m per day based on the observed upward movement of the salinity isopleths. He cites Roden (SIO Ref. 61-26) as stating that in the Gulf of Panama "the maximum rate of upwelling, estimated from the curl of the wind stress, is about 10 m per day."

TABLE 3. Rise in meters of isotherms and isohalines, and estimated mean upwelling rates during the 1955, 1956 and 1957 upwelling seasons at 8°45'N, 79°23'W (modified from Forsbergh 1963)

Upwelling Period	Total Rise in Meters			Days	Daily Mean Upwelling Rate (m day^{-1})
	Isotherms	Isohalines	Mean		
24 Dec. 1954—3 May 1955	73	68	70	131	0.53
26 Dec. 1955—30 April 1956	74	103	88	127	0.70
17 Dec. 1956—6 May 1957	49	62	55	141	0.40

Forsbergh (*vide* page 11 in 1963) calculated the *total* vertical displacement of water during the various upwelling seasons from the rise of isotherms and isohalines between successive measurements (stations). From these data, the mean rates of upwelling during 1955, 1956 and 1957 ranged from 0.4 to 0.7 m per day (Table 3).

Although upwelling is an annual phenomenon in the Gulf of Panama (Schaefer *et al.* 1958, Wooster 1959), annual variations in relative upwelling intensity occur (Figs. 5, 6). From the total rise in isotherms and isohalines (Table 3), upwelling appears to have been most intense during 1956 and least intense during 1957. Another estimate of the relative upwelling intensity is provided by the northerly wind-stress index (Wooster 1959), computed by adding the total miles of wind from the true north during a given period to the true north component of the northwesterly and northeasterly winds during the same period. This sum, divided by the number of hours in the period used, gives the average northerly wind component of the wind velocity in miles per hour, the square of which is the wind-stress index. Presumably, the greater the wind stress the greater the expected upwelling rate. Wooster used the February-March period to calculate this index, since the mean sea-level and sea-surface temperature at Balboa are usually lowest at this time indicating upwelling to be especially intense (Figs. 5, 6). The northerly wind-stress index has been calculated for this period and for the entire upwelling period from December to April:

	February—March	December—April
1955	53	34
1956	40	27
1957	36	34

The February-March index suggests that the relative upwelling intensity progressively declined from 1955 to 1957, whereas the index computed for the entire upwelling season (December-April) suggests that upwelling was equally intense during 1955 and 1957 and exceeded that in 1956. Based on the mean upwelling rate per day calculated from the rise in isotherms and isohalines (Table 3), the annual rank order of relative upwelling intensity is 1956 > 1955 > 1957. Thus, these three independent estimates do not provide any conclusive or consistent information as to the relative annual differences in upwelling intensity occurring during 1955 and 1957. They do confirm, however, that annual differences occur, as is apparent from Figures 5 and 6.

There is evidence that the relative upwelling intensity during February-March was below average during the 1955, 1956 and 1957 upwelling seasons. The 42-year (1915 to 1956) mean February-March northerly wind-stress index is 66 (Wooster 1959) which is considerably higher than that calculated for 1955 (53), 1956 (40), and 1957 (36).

The influence of the rate of upwelling on the development and maintenance of plankton communities will be discussed below.

Regional and seasonal hydrographic conditions throughout the Gulf of Panama

Upwelling appears to be limited to the Gulf of Panama. The seasonal decline in sea surface temperature characteristic of upwelling does not occur in the Panama Bight where the mean monthly temperature ranges from 26.1 to 27.8 C (Schaefer *et al.* 1958). It is therefore desirable to establish to what extent upwelling and rainy season conditions vary regionally within the Gulf of Panama: 1) to determine how representative of the Gulf conditions at the hydro-biological station are, and 2) to gain further insight into the general ecological conditions characterizing this body of water. The regional phytoplankton surveys (Smayda 1963) suggest that the phytoplankton composition and seasonal cycle at the hydrobiological station are generally representative of the entire Gulf, even though this station was located within the most productive region.

Considerable regional temperature data have been collected within the Gulf of Panama during various bathythermograph surveys conducted by the Inter-American Tropical Tuna Commission. Salinity data, however, are sparse. But since there is a general inverse relationship between temperature and salinity during upwelling (Figs. 5, 6), the general level of the latter can frequently be inferred from the temperature conditions. The general regional hydrographic conditions have been reconstructed from observations made over several years, since monthly surveys were not made throughout a given year.

The average surface temperature during 18-21 March 1958 bathythermograph survey (Fig. 7) was 26.71 C (62 observations), approximately 3 C warmer than during the March surveys in 1955 and 1957. This suggests that upwelling was least intense during 1958 of the March surveys. The temperature distribution at 10 m during March 1958 exhibits well-defined regional variations which undoubtedly reflect differences in upwelling intensity (Fig. 7). The surface salinity distribution (no observations from 10 m) generally corroborates the upwelling pattern suggested by the thermal conditions (Fig. 8). Upwelling was most pronounced in the innermost regions of the Gulf, especially in areas shallower than 50 m, where a relatively *cold* (< 24 C) *saline*, (> 33.7‰) watermass was generally present (Figs. 7, 8). Indeed, notwithstanding the surface salinity distribution, the temperature data suggest that relatively intense upwelling occurred throughout the inner region north of 8°30′N. To the south, a slightly warmer, more dilute watermass occurred in the region overlying the submarine valley described previously (Fig. 1), and within the Pearl Island straits. This watermass was wedged between the appreciably warmer, more dilute waters of Parita Bay and San Miguel Bay. The extensive occurrence of the stagnant, dilute watermass in the Parita Bay region west of the 26 C isotherm is especially notable (Figs. 7, 8). An upwelling of cold water, less than 24 C, is detectable south of the Pearl Islands (Fig. 7).

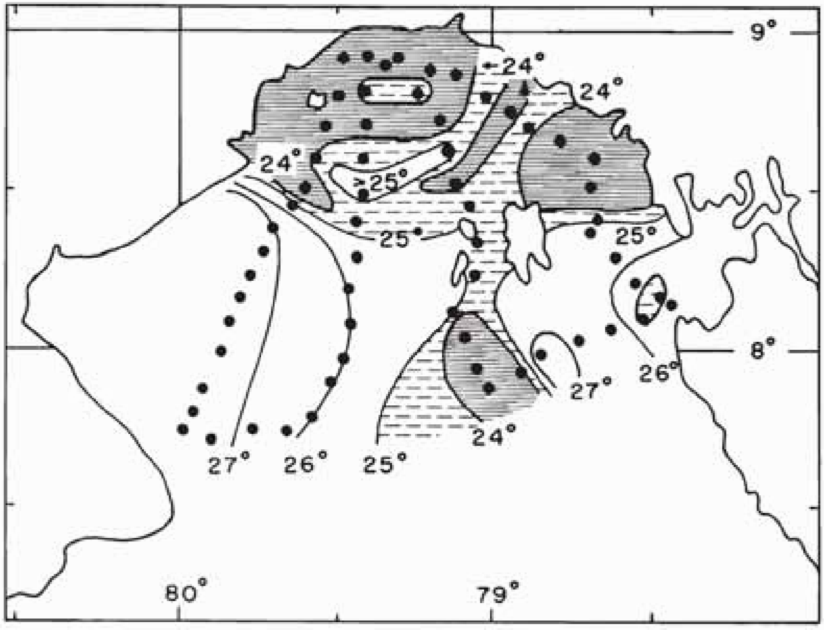

FIGURE 7. Temperature distribution at 10 m during the survey of 18-21 March 1958.

During the less extensive bathythermograph survey of 5-6 April 1956 the mean surface temperature was 24.6 C and the mean salinity 34.17‰ (Fig. 9). The regional temperature and salinity distribution is similar to the upwelling pattern during the March 1958 survey. The coldest and most saline waters again occurred near the head of the Gulf and over the submarine canyon, while some dilution and considerable warming characterized the waters in the San Miguel Bay region.

The surface salinity during the rainy season survey of 4-6 September

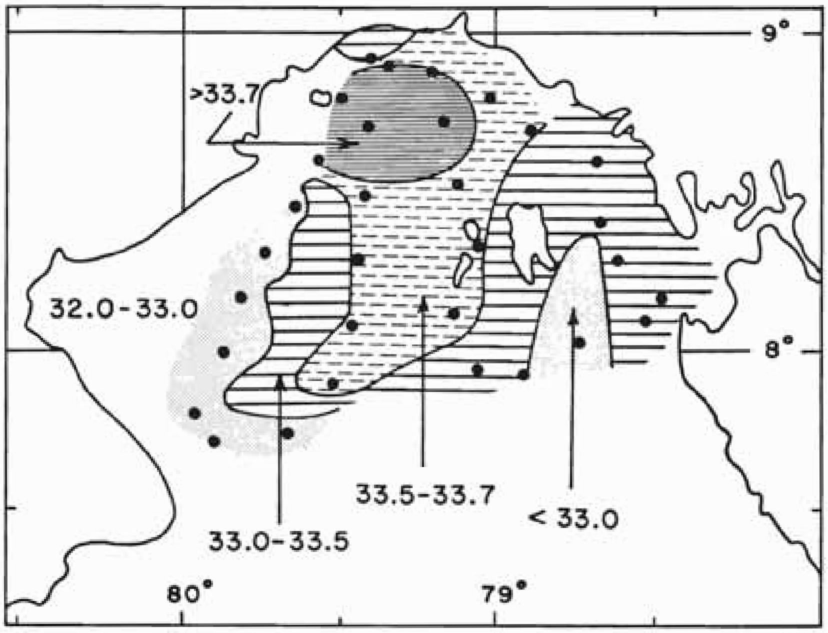

FIGURE 8. Surface salinity distribution during the survey of 18-21 March 1958.

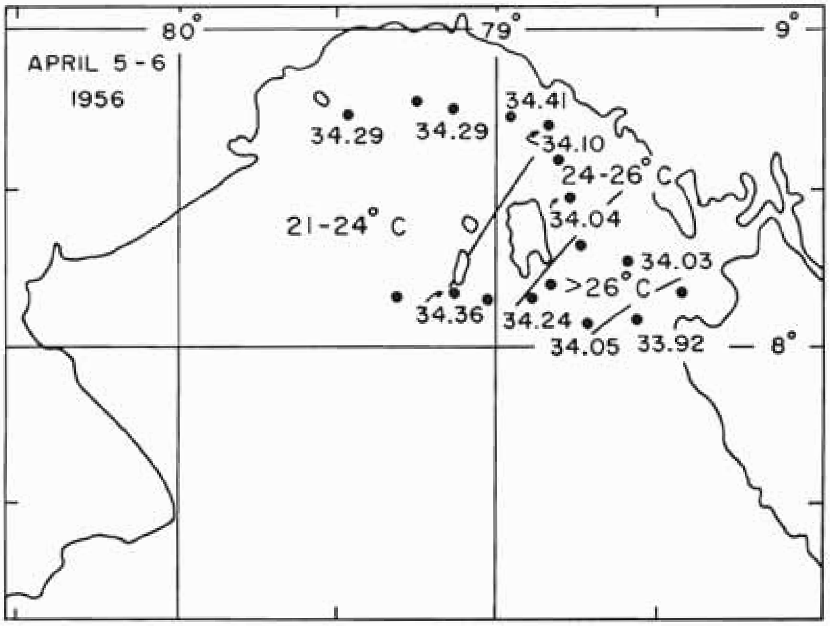

FIGURE 9. Surface temperature and salinity distribution during the survey of 5-6 April 1956.

1956 (Fig. 10) was 5.0 to 7.0 ‰ lower than during the March and April surveys (Figs. 8, 9). The few salinity observations (15) available suggest that the lowest salinities are now encountered in the innermost region of the Gulf, i.e., the converse of that found during upwelling, and in the region extending southwestwards from San Miguel Bay (Fig. 10). These two "dilute" areas are separated by a watermass of higher salinity (30.0 to 30.8 ‰) located in the central region of the Gulf overlying the submarine canyon and extending towards Parita Bay. The highest surface temperatures measured during this survey were frequently found within the more saline watermass; they were consistently lower (< 28 C) off Parita Bay and San Miguel Bay. The temperature-depth profile in the upper 25 m during this survey mirrored those of the July 1955 and 1957 surveys (Fig. 11). Below this depth, the thermal conditions were intermediate between those of the July surveys and those of the November 1955 and 1957 bathythermograph surveys (Fig. 11).

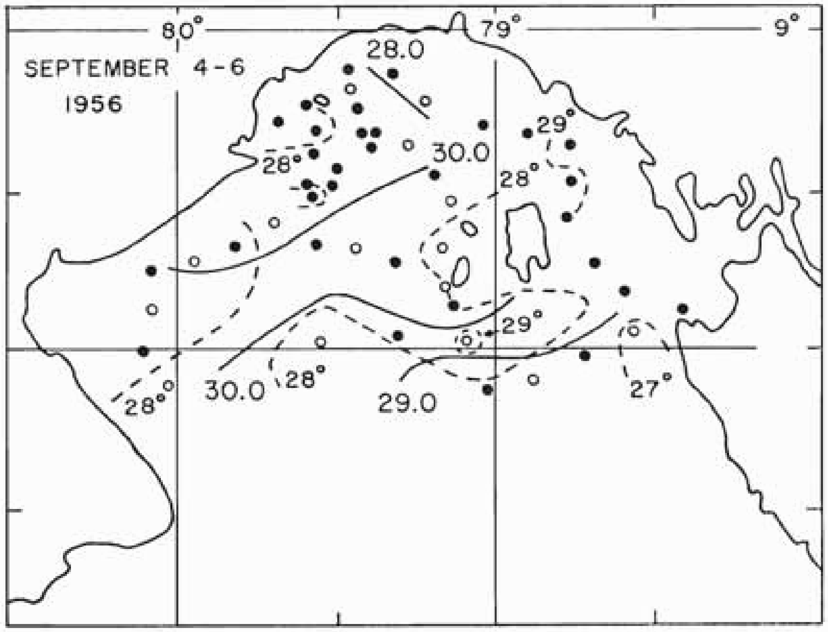

FIGURE 10. Surface temperature and salinity distribution during the survey of 4-6 September 1956. (Open circles [o] represent stations for which salinity determinations were made.)

Observations of surface salinity during the 7-8 November 1957 survey provide little indication that the height of the rainy season then prevailed —the salinity values were only slightly lower than those during the September 1956 survey (Fig. 12). It is recalled that the surface salinity decreased to 21.68 ‰ at the hydro-biological station during November 1955 (Fig. 5). Nonetheless, dilute and warm surface waters characteristic of

TABLE 4. Mean surface salinity in the Gulf of Panama during various bathythermograph surveys

Month	Mean ‰	Observations (n)
March, 1958	33.31	31
April, 1956	34.17	10
September, 1956	29.69	15
November, 1957	29.36	16

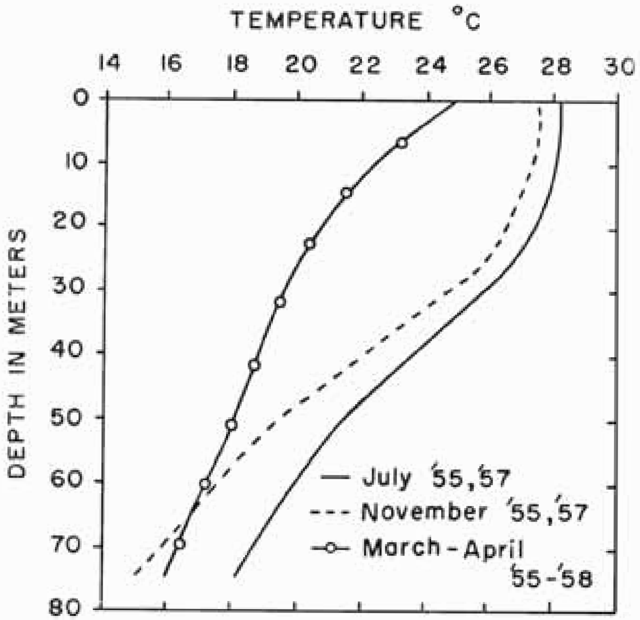

FIGURE 11. Mean thermal conditions in the upper 75 m of the Gulf of Panama during certain months, based on bathythermograph observations.

the rainy season occurred throughout the Gulf during the November 1957 survey, as during September 1956. The seasonal change in mean surface salinity based on the bathythermograph surveys is demonstrated in Table 4.

The characteristic hydrographic conditions observed at the hydrobiological station during the upwelling and rainy seasons (Figs. 5, 6) also occur throughout the Gulf of Panama. Regional differences are found, however.

The magnitude of the hydrographic changes occurring between seasons, suggested by the vertical temperature profiles (Fig. 11), is especially apparent from a comparison of the thermal fields observed during the March 1957 and July 1955 surveys (Figs. 13, 14; Table 5). The temperatures are considerably lower during March, notwithstanding the wide range in temperature encountered during both surveys: 14.1 to 26.3 C (March), 17.3 to 29.4 C (July). A mean temperature increase of from 3.9 to 10.4 C

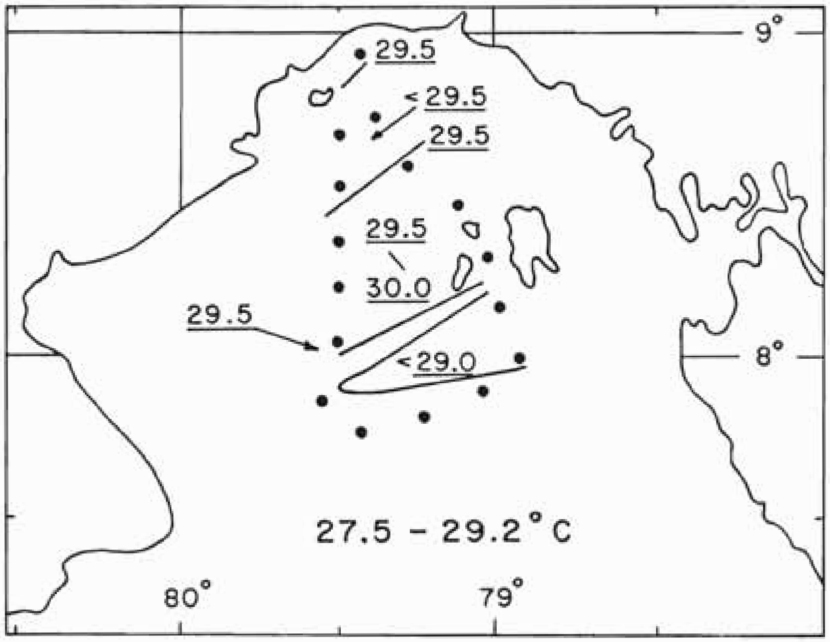

FIGURE 12. Surface salinity distribution during the survey of 7-8 November 1957; the surface temperatures ranged from 27.5 to 29.2 C.

above March levels occurred at various depths during July (Table 5), demonstrating the pronounced temperature increase occurring throughout the water column following the termination of upwelling (Figs. 11, 13, 14). The *lowest* July temperature was 17.3 C at 85 m at station 25 located in the *outer* reaches of the Gulf and within the submarine valley (Fig. 14). In contrast, 16 C water occurred at 35 m at March survey station 2 located near the *head* of the Gulf (Fig. 13). The most pronounced seasonal changes occurred in the southernmost transect across the submarine valley. Here, July temperatures increased about 10 C over March levels in the layer between 20 and 50 m, while at 80 m a modest increase from 14.5 to 16 C occurred (Figs. 13, 14). The 16 C isotherm during March exhibits a conspicuous ascent inwards and a "spilling" over onto the shallow Parita Bay "flats" (< 50 m) and off San Miguel Bay, and demonstrates the influence of the bottom profile on upwelling. In general, this isotherm lies deeper in the watermass overlying the submarine canyon.

During both surveys, superficial waters were slightly warmer in the inner reaches of the Gulf than farther offshore. The mean surface temperature during the March 1957 survey was 23.45 C, a mean temperature found at about 50 m during the July 1955 survey (Table 5). Thus, at a minimum, the upper 50 m, or about 30 per cent of the total volume of the Gulf (Table 1), is replaced during the upwelling season with water 5 to 10 C colder than that present during the rainy season.

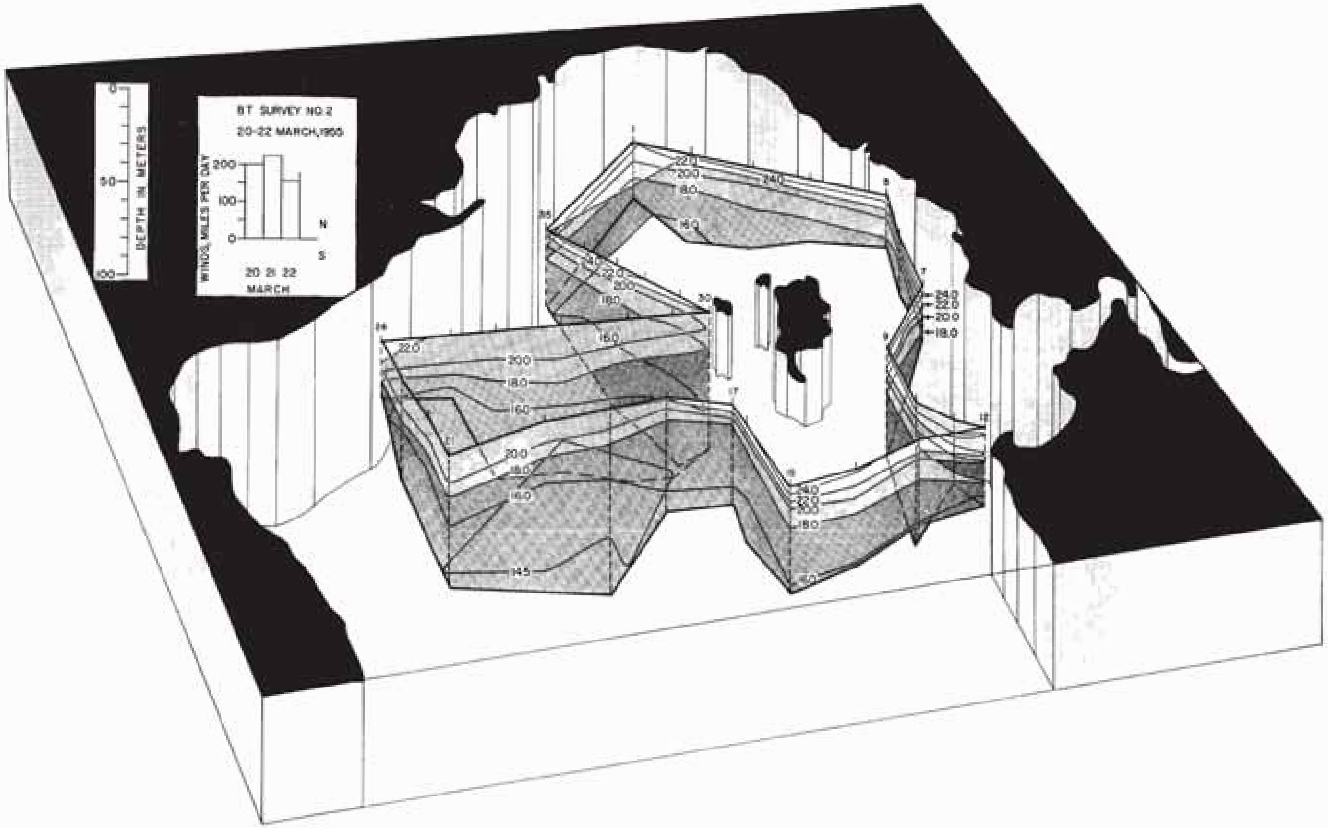

FIGURE 13. Isometric presentation of the thermal conditions in the Gulf of Panama during the upwelling season, as observed during the bathythermograph survey of 20-22 March 1955.

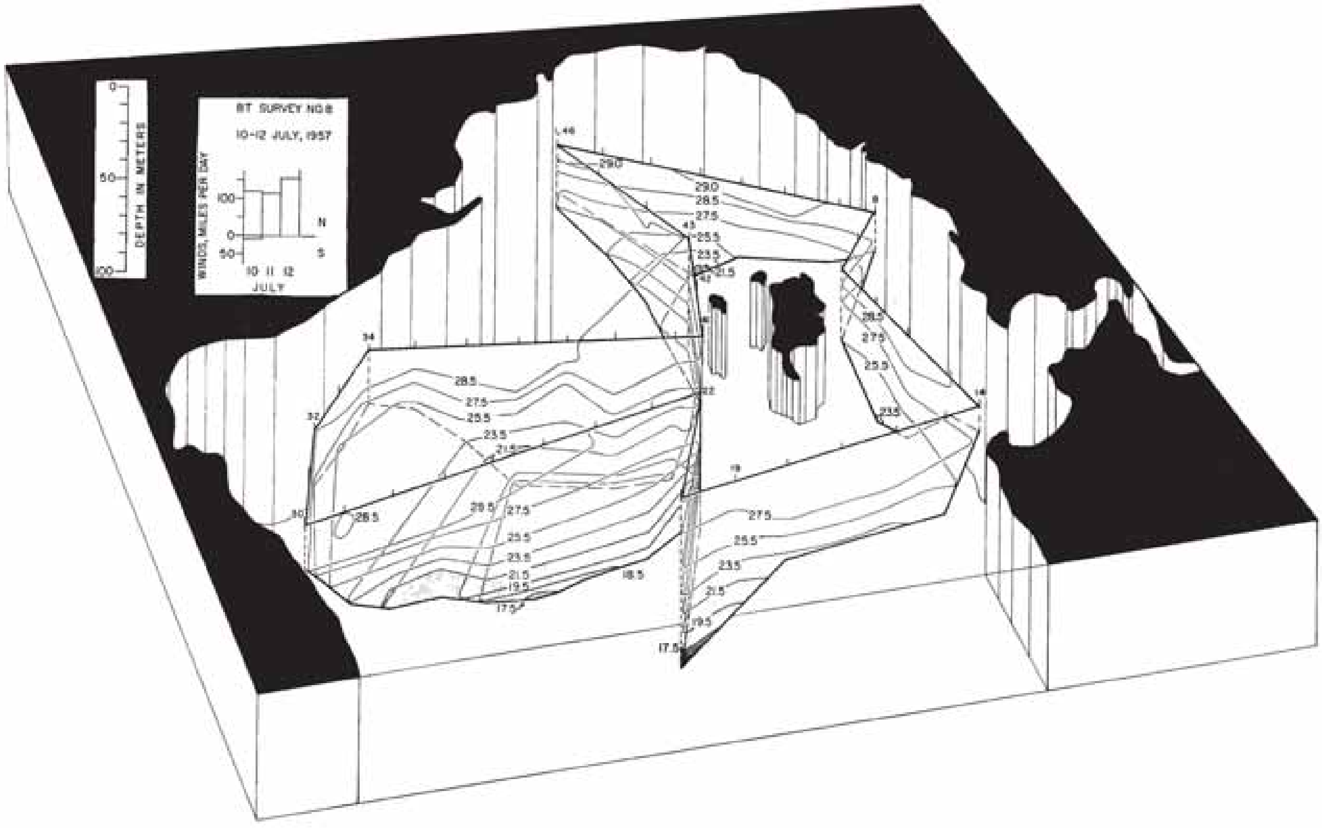

FIGURE 14. Isometric presentation of the thermal conditions in the Gulf of Panama after the upwelling season, as observed during the bathythermograph survey of 10-12 July 1957.

TABLE 5. Average temperature (C) at various depths during the March 1955 and July 1957 bathythermograph surveys (n = number of observations)

Depth (m)	March	n	July	n	Temp. Change
0	23.45	35	28.59	46	+ 5.14
5	22.05	35	28.56	46	+ 6.51
10	20.39	35	28.54	46	+ 8.15
25	17.22	35	27.63	42	+10.41
50	15.55	21	22.86	25	+ 7.31
75	14.84	10	18.74	10	+ 3.90

These diverse bathythermograph survey results indicate, therefore, that 1) upwelling of unequal intensity occurs concurrently throughout the Gulf of Panama in the upper 75 m (there are few observations below this depth) (Figs. 8, 9, 11, 13; Table 5) and 2) regional hydrographic differences also occur during the rainy season when the upper 80 m are uniformly well-heated, with no indication of an influx of deep water similar to that described for the upwelling season, and when conspicuous surface dilution also occurs (Figs. 10, 11, 12, 14; Tables 4, 5).

Proposed upwelling circulation pattern

During upwelling, the upper 40 (Schaefer *et al.* 1958) to 78 m (Fleming 1939, Forsbergh 1963) is driven offshore and replaced by a colder, more saline and nutrient-rich watermass (Figs. 5, 6). The source of the Gulf of Panama upwelled water is not completely resolved. Fleming (1939) suggested that it originates south of the equator off Peru, but this is an unlikely source since the Peru Current probably continues westward south of the equator (Wooster 1959). Schaefer *et al.* (1958) report that the watermass at the hydro-biological station during upwelling is hydrographically similar to that encountered at 35 to 50 m during November 1955 (rainy season) near the entrance to the Gulf.

The upwelling circulation system within the Gulf of Panama is also unknown, other than evidence from the bathythermograph (Figs. 7, 8, 9, 13) and phytoplankton (Smayda 1963) surveys that regional differences in upwelling intensity occur. The phytoplankton surveys further indicated that growth during the upwelling season is influenced in an undetermined way by the depth of the water column. This latter observation suggests that the upwelling intensity is also related, in part, to the depth of the water column (Smayda 1963). This, coupled with Fleming's (1938) observations on Gulf of Panama tidal currents, suggests that the regional upwelling circulation pattern might be approximated from a consideration of the bottom topography. Accordingly, the principal upwelling current movements and the relative upwelling intensity throughout the Gulf of Panama have been predicted (Fig. 15) and compared with hydrographic observations, including those made by the U.S.S. *Hannibal*[5] (Fig. 16). The

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[5] The cruise of the U.S.S. *Hannibal* was made during 9-24 March 1933 (Anonymous 1934), a period of intense upwelling (Wooster 1959).

predicted circulation pattern was arrived at as follows:

Assume that upwelling circulation in the Gulf of Panama approximates a two-layered system where the surface waters are driven offshore and are replaced by an onshore compensatory bottom current which upwells. This is not an unreasonable simplification since the nearly circular outline of the Gulf restricts the northerly wind-driven watermass exchanges to the Panama Bight located to the south (Fig. 1). Since the volume of the entering watermass is related in part to the depth, the submarine valley at the Gulf entrance is probably the sight of a considerable influx, although a significant inflow possibly occurs east of this valley as well (Fig. 1). The final assumption is that the relative upwelling intensity throughout the Gulf under similar wind conditions can be inferred from the slope and other topographical features of the bottom. Fleming (1938), for example, held that Gulf of Panama tidal currents had a vertical component near the bottom with a velocity determined by their horizontal velocity and the slope of the bottom, while the amplitude of the vertical displacement was determined by the mean slope of the bottom times the distance traveled. Since upwelling currents flow along the bottom prior to their ascent (Fig. 13), extension of Fleming's observations to these non-tidal currents seems appropriate. During upwelling, of course, the magnitude of the vertical velocity (i.e., the rate of upwelling) and the vertical range are also related to the wind stress.

Application of these assumptions predicts the following upwelling circulation pattern in the Gulf of Panama (Fig. 15). Significant vertical turbulence (upwelling) of the incurring watermass is expected near the entrance to the Gulf, although it is uncertain whether it would extend to the surface, because of the considerable inward slope characterizing this region. For example, east of the submarine valley the depth decreases inwards from 2000 to 200 m over a distance of from 8 to 20 km (Figs. 1, 15). Fleming (1938) demonstrated that along a profile at 79°23′W tidal currents passing over the continental slope will have a vertical amplitude of approximately 85 m at the 2000 m contour which decreases to about 25 m near the 200 m contour.

The sea floor in the eastern half of the Gulf gradually slopes upwards and inwards between the 200 and 50 m isobaths, with an abrupt rise at the Pearl Islands (Fig. 1). These islands are separated from San Miguel Bay to the east by a relatively deep channel outlined by the 50 m isobath. Thus, bottom currents would be expected to upwell significantly upon flowing against the Pearl Islands, as well as during flow over the rapidly shoaling bottom between the 50 and 20 m isobaths near the entrance to San Miguel Bay (Fig. 15). A progressive increase in upwelling intensity of the watermass flowing northwards in the deep (greater than 50 m) channel between the Pearl Islands and San Miguel Bay is also expected as it is funneled onto the rapidly shoaling area to the northeast of the Pearl Island archipelago. Upwelling in these three areas is expected to be more intense than

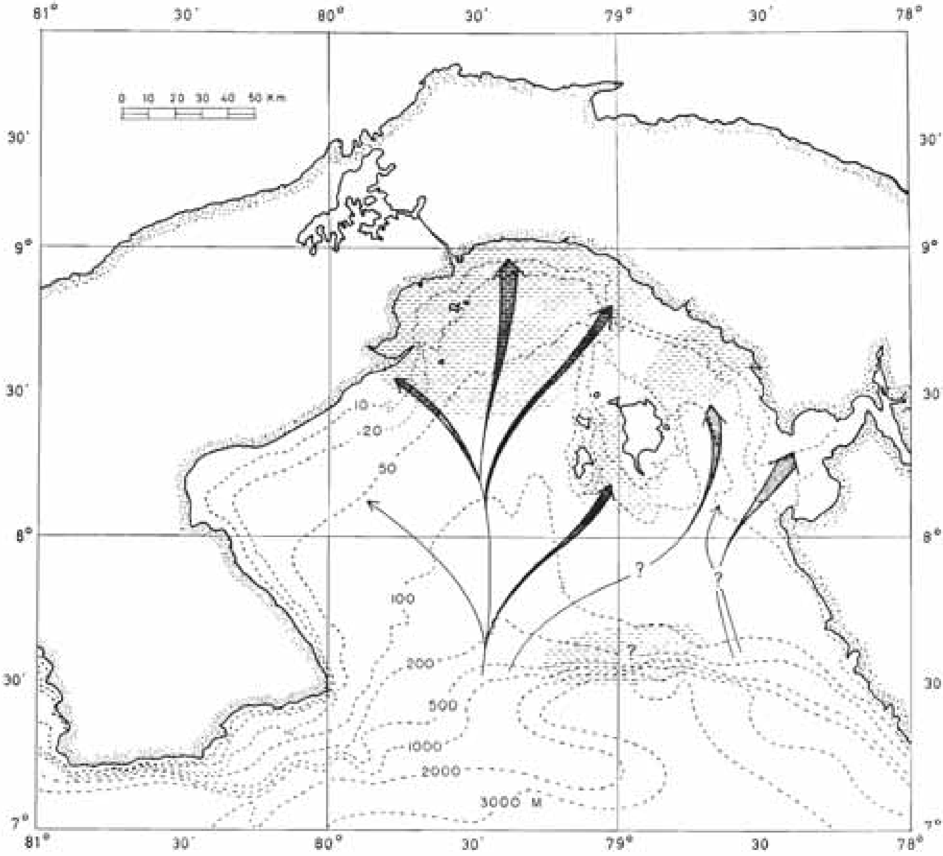

FIGURE 15. Major upwelling current movements along the bottom, and regions of intense upwelling (shaded) hypothesized for the Gulf of Panama.

elsewhere in this general region between the 200 and 50 m isobaths (Fig. 15).

The incursion of a cold, saline watermass into the submarine valley at the entrance which then flows towards the head of the Gulf is expected (Figs. 1, 13, 15, 16). As this water flows inwards, a progressive increase in relative upwelling intensity resulting from the shoaling depths and narrowing of the submarine valley is anticipated. Therefore, intense upwelling is expected throughout the region located *within* the 50 m isobath and extending from south of Chame Bay, but east of 80°W (Fig. 1), to the coastal area at approximately 79°W north of the Pearl Islands (Fig. 15). Significant upwelling of the bottom water south of the Chame Bay peninsula (Figs. 1, 15) is also expected because of the steep slope accompanying a depth decrease from 50 to 10 m over a distance of 20 km. Fleming (1938), for example, determined that near the 50 m contour along the 79°23′W profile, tidal current bottom water ascends approximately 7 m, whereas in the inner shallower regions this vertical movement is halved, although it is still slightly greater than that occurring between the 60 and 100 m isobaths. Intense upwelling is nonetheless to be expected within the 50 m isobath because of the large volume of water flowing northwards within the submarine valley. The northeast curvature of this valley can also be expected to contribute to intense upwelling along the northeast coastal regions of the isthmus north of the Pearl Island archipelago (Fig. 15). Upwelling in this region may merge with or be distinguishable from the nearby upwelled waters resulting from the previously described influx of water *via* the channel *east* of the Pearl Islands within the San Miguel Bay area (Fig. 15).

The location of Parita Bay probably prohibits an influx of water directly from the south during the upwelling season. Any flow into this general area must occur laterally from the southwest, i.e., across the western slope of the submarine valley. This requirement, coupled with the prevalence of northerly winds at Cape Mala (Fig. 3), undoubtedly restricts both the volume and upwelling intensity of the incurring watermass, especially if all flow is due north-south as stipulated in the working hypothesis. An additional factor may be a stowing of warmer and more dilute water in the Parita Bay region expected to accompany the southerly (offshore) surface currents set up during upwelling. Therefore higher salinities and lower temperatures would be expected to occur in San Miguel Bay than in Parita Bay during upwelling.

This model suggests that upwelling in the Gulf of Panama is most pronounced within the inner regions lying within the 50 m isobath; south of and to the northeast of the Pearl Islands; in the offing of San Miguel Bay and possibly near the Gulf entrance. Upwelling is expected to be least intense near Parita Bay and in the region overlying the submarine valley between the 50 and 200 meter isobaths (Fig. 15).

The predicted (Fig. 15) and observed regional upwelling pattern, as inferred from the temperature and salinity distribution, agree well (Figs. 7, 16). The expected incursion of a cold, saline watermass into the submarine valley and its subsequent transport towards the head of the Gulf are discernible during the March 1955 bathythermograph survey (Fig. 13), as well as from a comparison of the temperature-salinity profiles at *Hannibal* stations 102, 85, 80 and 71 with those (stations 32, 37, 48) located at the Gulf entrance (Fig. 16). Further, the temperature distribution at 10 m during the March 1958 survey (Fig. 7) indicates that upwelling, as predicted, was pronounced in the inner Gulf region at depths less than 50 m. The predicted intense upwelling south of the Chame Bay peninsula is strikingly confirmed by temperature data (Fig. 7), by the March 1958 surface salinity distribution (Fig. 8) and conditions at *Hannibal* stations 88 and 89 (Fig. 16) as well. Similarly, the anticipated upwelling of *two* watermasses in the region north of the Pearl Islands resulting from an influx of 1) water flowing northeastwards within the submarine valley *west* of this archipelago, and 2) water flowing northwards *east* of the Pearl Islands in the smaller valley found in that region is generally confirmed by the thermal distribution (Fig. 16). Also, two distinct phytoplankton communities found in this general region during March 1958 (Smayda 1963) provide biological evidence for the anticipated incursion of two watermasses there.

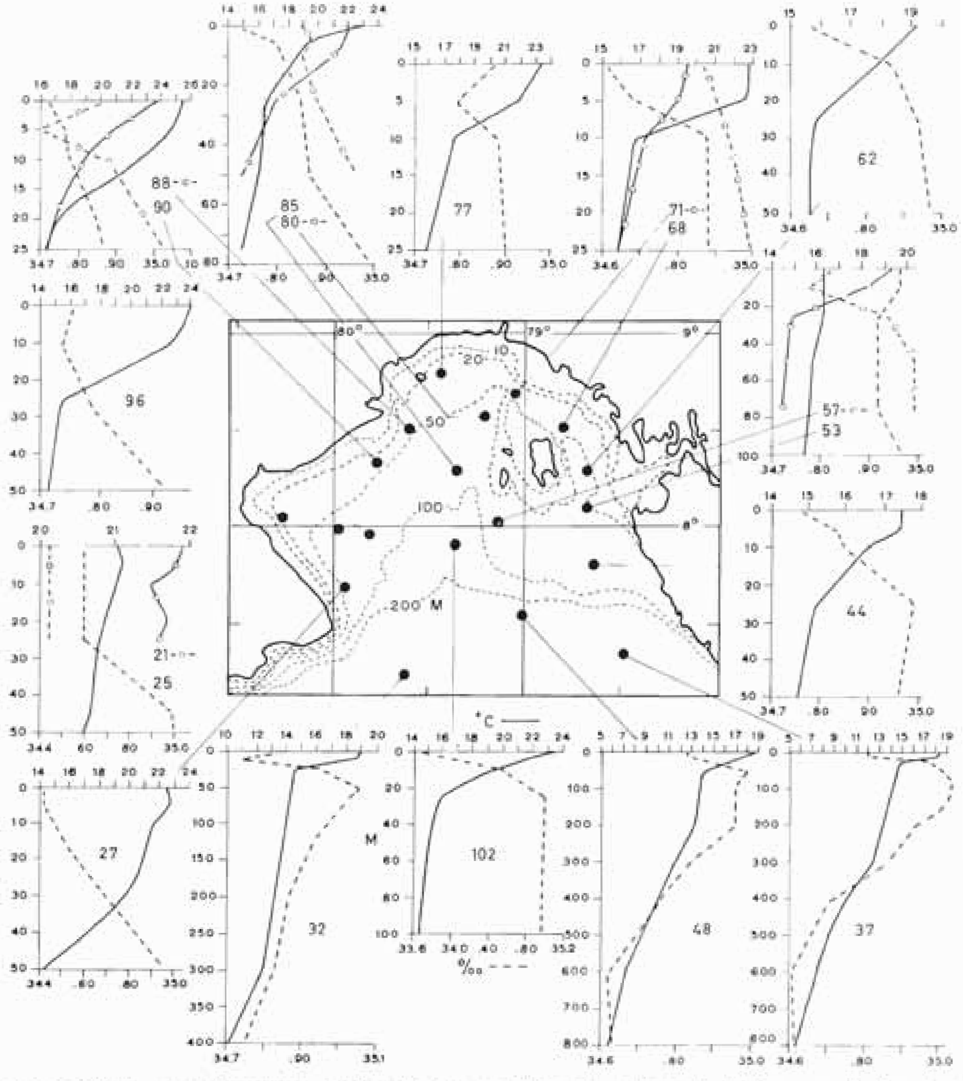

FIGURE 16. Temperature and salinity profiles at selected stations made by the U.S.S. *Hannibal* during 9-24 March 1933 (based on data presented in Anonymous 1934).

Intense upwelling at the southern tip of the Pearl Island archipelago is also confirmed (Fig. 7), whereas that predicted to occur in the offing of San Miguel Bay is not (Fig. 15). However, the expected occurrence of lower temperatures and higher salinities indicative of more intense upwelling in San Miguel Bay compared to Parita Bay is observed (Figs. 7, 8, 13, 16). The reduced upwelling in the central region between the 50 and 200 m isobaths overlying the submarine valley, and the progressively increasing stagnation westwards to Parita Bay also agree with expectations (Figs. 7, 8, 16).

Hannibal stations 32, 48 and 37 located near the Gulf entrance (Fig. 16) indicate the presence of a cold, saline watermass which may be symptomatic of the expected intense upwelling occurring there. The surface temperature decreased from 18-19 C to 14 C in the 25 to 50 m stratum, to approximately 10 C at 400 m and 5-6 C at 800 m. The salinity in the upper 25 to 50 m ranged from 34.75 to 34.90 ‰, increased to approximately 35.00 ‰ down to 200 m, and then decreased below that depth. The temperature-salinity conditions at station 44 approximated those found at the entrance to the Gulf, which could be further related to station 53 located near San Miguel Bay where intense upwelling was occurring. This suggests that the incursion of upwelling water into the Gulf of Panama is not restricted to the submarine valley, but occurs to the east of this structure flowing into the San Miguel Bay region.

It can be concluded, then, that 1) upwelling is not of equal intensity throughout the Gulf of Panama, 2) the hydro-biological station lies in an area of intense upwelling, and 3) the bottom topography influences upwelling intensity and its circulation.

Surface circulation in the Gulf of Panama

The hydrography of the eastern Tropical Pacific region adjoining the Gulf of Panama and Panama Bight is dominated by the Equatorial Current system. Herein is the eastern terminus of the Equatorial Counter Current and place of origin of the westward flowing North and South Equatorial Currents (Fig. 17). These currents exhibit considerable meridional displacement and related seasonal changes in width, definition and velocity in response to the atmospheric movements of the Tradewind-Calm Belt (Doldrums) system (*vide* page 364) responsible for the upwelling and rainy seasons in the Gulf of Panama (Fleming 1939, Cromwell and Bennett 1959, Wooster 1959). However, this current system does not appear to influence directly circulation within the Gulf of Panama except, perhaps, during June when the Equatorial Counter Current flows into the Panama Bight (Figs. 17, 18).

The surface circulation of the Gulf of Panama and Panama Bight is distinguishable as a counterclockwise eddy except during February and March in the Panama Bight (Figs. 17, 18). During these months of the upwelling season, the southernmost loop of this eddy in the Panama Bight continues directly into the South Equatorial Current (Cromwell and Bennett 1959) rather than flowing eastward toward the coast of South America

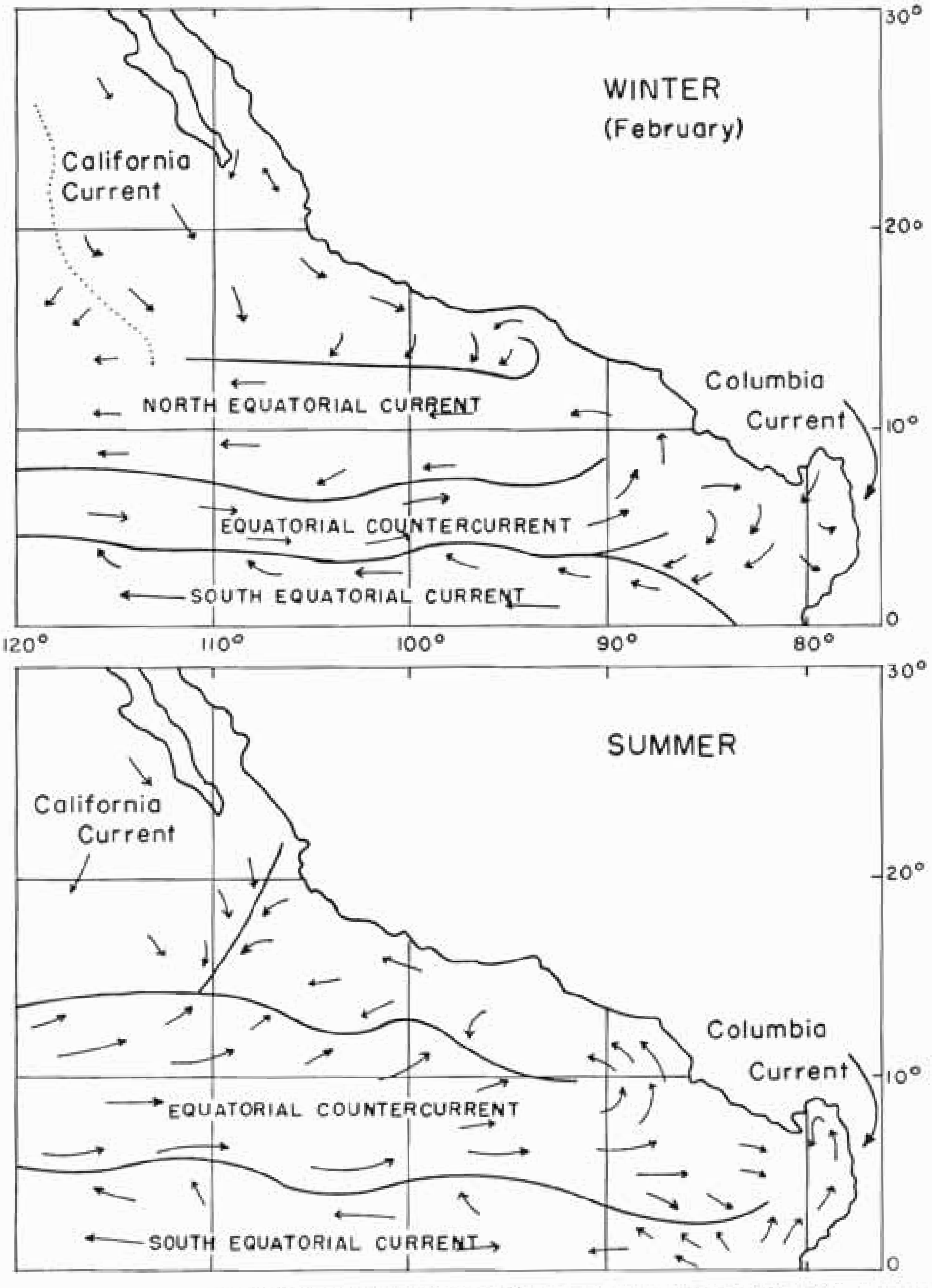

FIGURE 17. Schematized surface circulation in the eastern tropical Pacific (taken from Cromwell and Bennett 1959).

(Fig. 18) and then northward into the Gulf of Panama again as the Colombia Current (Wooster 1959). Generated by southerly winds blowing parallel to the coast and supplied from the western limb of the general counterclockwise circulation, the approximately 160 km wide Colombia Current begins at about 1°N and flows northward *throughout* the year with an average velocity of 25 cm sec^{-1} (Wooster 1959). Despite its origin near the equator, Wooster states that it is unlikely that the Colombia Current is a continuation of the Peru Current.

The Colombia Current flows into the Gulf of Panama from the southeast with an average velocity of 30-40 cm sec^{-1} during the upwelling season, and decreases thereafter to 20-30 cm sec^{-1} (Fig. 18). The ensuing counterclockwise drift is maintained within the Gulf throughout the year. The southerly outflowing current lies west of the Pearl Island archipelago and is strongest within the innermost regions of the Gulf where it maintains a velocity of 30 to 40 cm sec^{-1} throughout the year. In the Cape Mala region, however, the velocity decreases to 10 to 20 cm sec^{-1} during April-June and October-December (Fig. 18). This excurrent then continues into the southernmost regions of the Panama Bight where it supplies the Colombia Current from the west (Figs. 17, 18).

The monthly current charts prepared by Cromwell and Bennett (1959), apparently from the same source material (United States Navy Hydrographic Office Publication 570) utilized by Wooster (1959), indicate periodic changes in surface drift direction and velocity near San Miguel Bay that are obscured in Wooster's quarterly current charts (Fig. 18). These observations have been inserted onto Wooster's current maps (Fig. 18) and appropriately identified. The eastern limb of the Gulf counterclockwise circulation is especially pronounced between San Miguel Bay and the Pearl Islands during February and August. During March, April, July and October, however, a weak current also flows southwest from San Miguel Bay.

There is little directly applicable information available on the subsurface circulation.

Precipitation and runoff

The 8-month rainy season in the Gulf of Panama from May through December was briefly discussed earlier. The mean annual rainfall (based on measurements at 55 localities on the Isthmus of Panama) is 2731 mm (Anonymous 1956), approximately 2.5-fold greater than the 1175 mm recorded for the temperate Long Island Sound area (Riley 1956), for example. A zone of especially intense rainfall (2540 to 5080 mm per year) extends inland from the Caribbean coast, whereas the Pacific side is significantly dryer (Fig. 19).[6] The vegetation changes accordingly from a

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[6] Data (Anonymous 1956) which became available after Figure 19 was prepared indicate that the most intense zones of mean annual precipitation extend closer to the Gulf of Panama than depicted. Although the general features of Figure 19 appear to be representative, calculations of the mean annual rainfall over the entire Gulf of Panama drainage basin based on planimetered measurements of isohyet areas were increased by 38 per cent to accord with the more recent data.

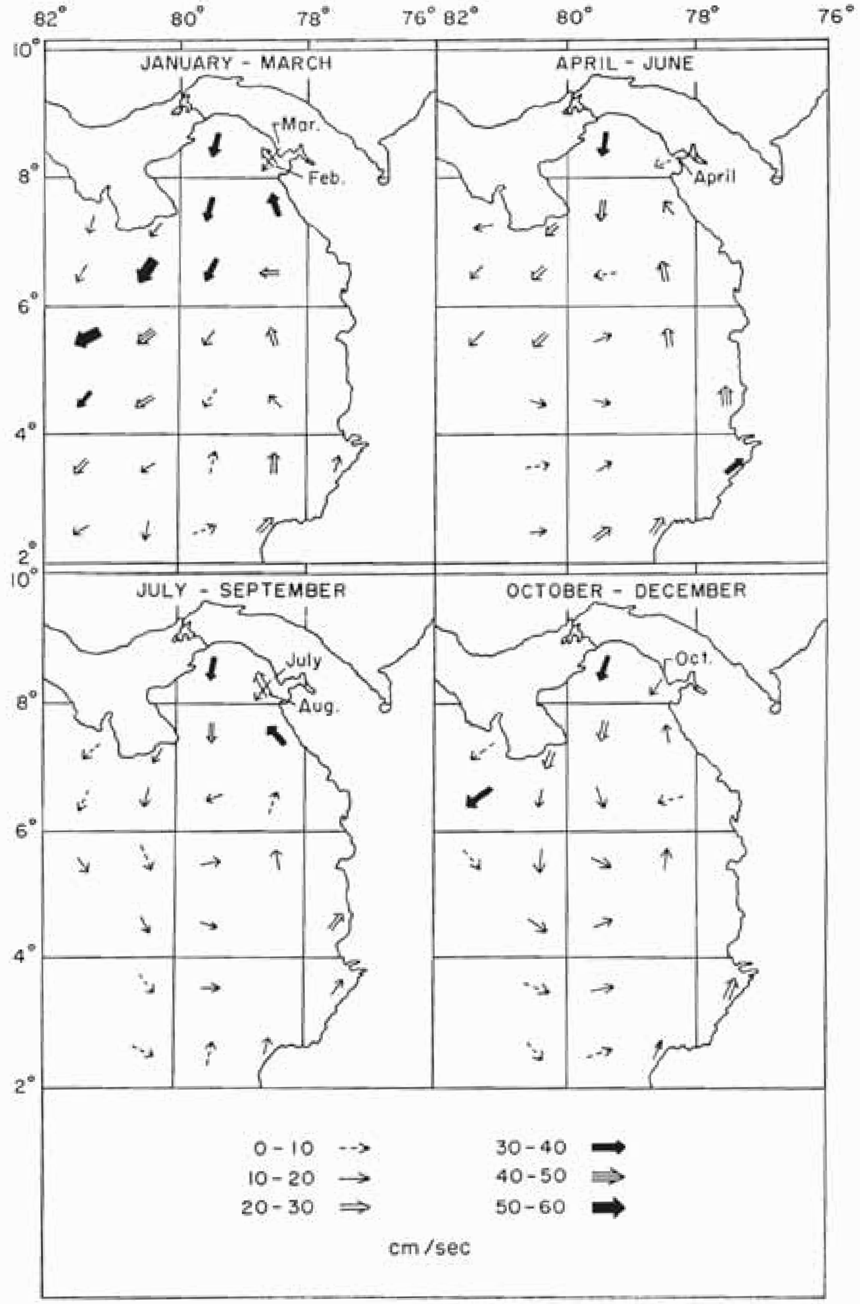

FIGURE 18. Surface circulation in the Panama Bight and Gulf of Panama (modified from Wooster 1959). Current vectors identified by month taken from Cromwell and Bennett 1959, as described in the text.

tropical rain forest to a semi-deciduous forest (James 1950), although portions of the Pacific coastal region can be classified as tropical savannahs (Anonymous 1956).

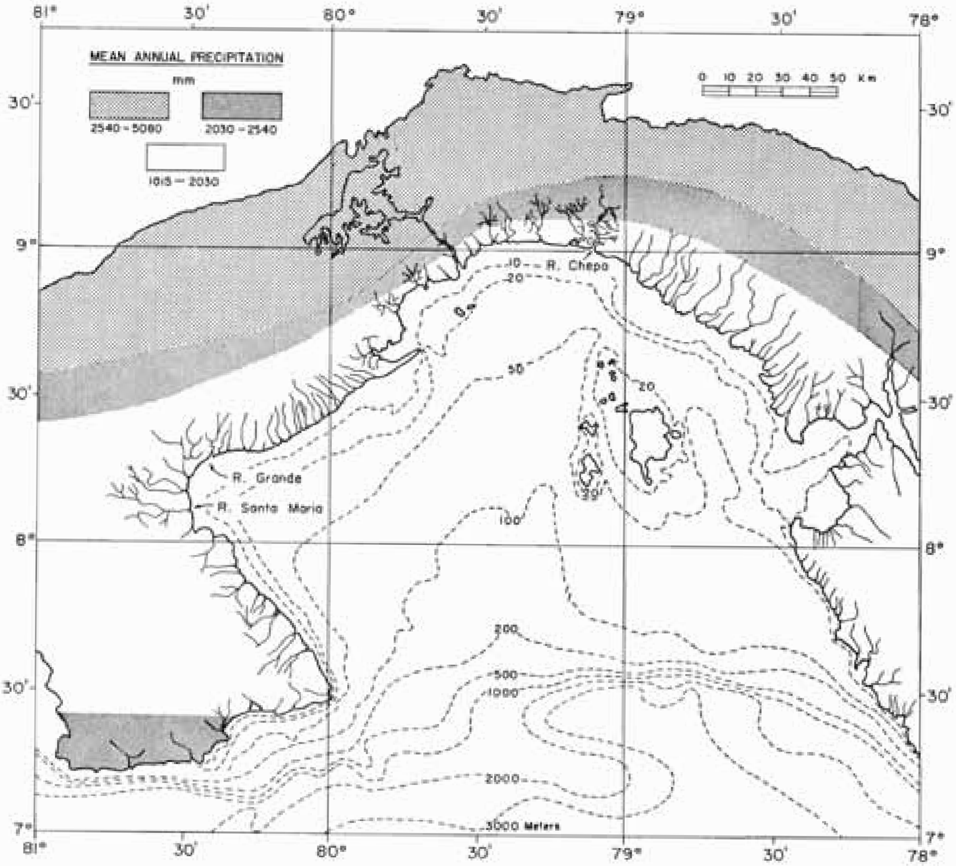

FIGURE 19. Precipitation zones (after Jones 1950) and drainage characteristics of the Isthmus and Gulf of Panama.

A pronounced increase in precipitation (Table 6) and runoff (Tables 7, 8) occurs during May following the termination of the upwelling season. The sudden transition to intense rainfall, in fact, is startling. The total rainfall at Balboa (Fig. 1) increased from 3.8 mm during April to 168.4 mm during May 1955, from 63.5 to 264.2 mm during 1956 and from 28.4 to 224.3 mm during 1957 (Table 6). An October or November maximum usually occurs (Figs. 20, 21; Table 6), followed by a progressive decline in and considerably lower precipitation during the upwelling season. These seasonal changes in precipitation are reflected in pronounced seasonal changes in surface salinity throughout the Gulf of Panama (Figs. 8, 10, 21; Table 4).

TABLE 6. Monthly precipitation (mm) at Balboa during 1955 to 1957, and deviation (△ x) from mean (T = trace)

	Precipitation (mm)					
	1955	△ x	1956	△ x	1957	△ x
Jan.	89.9	+ 62.0	62.2	+ 33.8	7.9	— 20.6
Feb.	65.8	+ 51.3	14.7	+ 0.3	T	— 14.5
Mar.	14.5	— 3.8	6.6	— 11.7	0.0	— 18.3
Apr.	3.8	— 71.4	63.5	— 11.4	28.4	— 46.5
May	168.4	— 29.2	264.2	+ 65.5	224.3	+ 25.7
June	189.5	— 13.2	238.8	+ 35.6	154.9	— 48.3
July	236.5	+ 53.6	307.1	+121.9	302.3	+117.1
Aug.	268.7	+ 77.7	285.8	+ 93.2	278.9	+ 85.4
Sept.	191.5	— 1.8	116.6	— 75.4	158.0	— 36.6
Oct.	145.5	—107.7	323.6	+ 69.1	227.1	— 27.4
Nov.	339.3	+ 88.9	258.6	+ 7.9	213.9	— 36.8
Dec.	241.3	+100.1	90.2	— 50.0	14.2	—126.0
Total	1954.7	+201.3	2031.9	+278.5	1609.9	—143.5

Monitored river flow of the Rio Santa Maria (1956 to 1958) and the Rio Grande (1956 to 1957) (Figs. 19, 20) indicates that three distinct run-off periods can be distinguished (Table 7). More than 50 per cent of the total annual drainage occurs from September through December (Period III), whereas Period II represents a transition after the upwelling season (Period I) when runoff is about 3-fold lower than during the height of the rainy season. This seasonal variation in runoff is probably representative of the entire Gulf region, as suggested by the partial data available for the Rio Mamoni which drains into the Chepo (Bayano) river (Fig. 19; Table 8). Runoff during the upwelling season (January to April) was $51.3 \times 10^6 m^3$, while that for Period III is $176.4 \times 10^6 m^3$, or approximately 3-fold greater, as also found for the Rio Santa Maria and Rio Grande (Table 7).

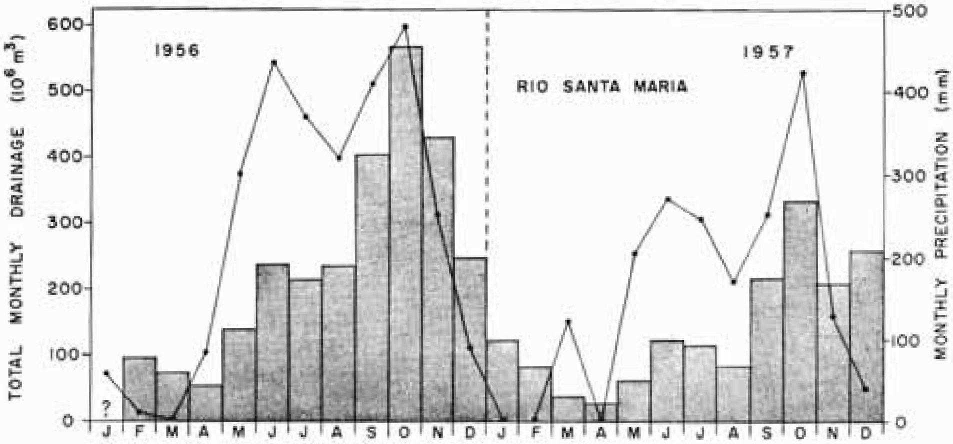

FIGURE 20. Monthly precipitation at San Francisco and run-off volume of the Rio Santa Maria (monitored at San Francisco) during 1956 and 1957.

TABLE 7. Seasonal drainage of Rio Santa Maria and Rio Grande in per cent of total annual runoff

Period:	**Jan.—April (I)**	**May—Aug. (II)**	**Sept.—Dec. (III)**
Per cent of total runoff occurring	18.5	28.0	53.5

TABLE 8. Monthly flow of Rio Mamoni at Chepo (as $10^6 m^3$)

Month	Flow	Month	Flow
Jan. '58	24.5	July '57	16.0
Feb. '58	11.1	Aug. '57	17.3
Mar. '58	8.9	Sept. '57	27.6
Apr. '58	6.8	Oct. '57	51.0
May	no data	Nov. '57	63.2
June	no data	Dec. '57	34.6

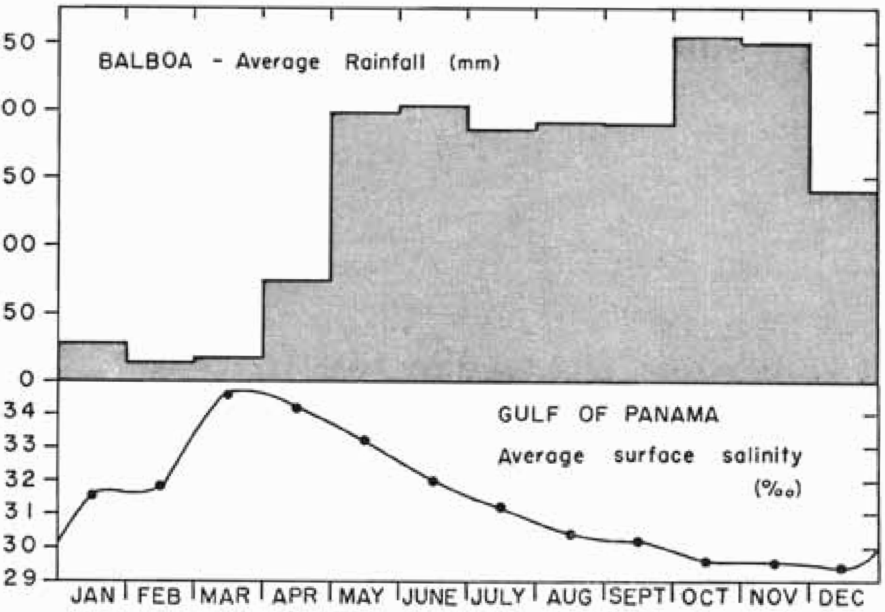

FIGURE 21. Average monthly precipitation at Balboa (from Anonymous 1956) and mean monthly surface salinity throughout the Gulf of Panama (modified from Fleming 1939).

A well-developed drainage system (Fig. 19) of approximately 325 streams and rivers (Anonymous 1929) has evolved in response to the intense precipitation; eastern Panama has the most mature erosional system (Terry 1956). The Gulf of Panama drainage basin incompasses 33,828 km², slightly greater than the actual Gulf area of 28,850 km². The Gulf drainage basin can be sub-divided into seven regions which differ markedly in their contribution to the total runoff into the Gulf of Panama (Fig. 22). San Miguel Bay (Fig. 22) drains 44 per cent of the entire Gulf drainage basin over which 45 per cent of the total annual precipitation occurs. The Chepo (Bayano) River basin receives 17 per cent of the total precipitation, as does the Parita Bay drainage basin. A comparison of these seven regions (Fig. 22) reveals that: 1) 69.5 per cent of the total mean annual precipitation occurs over the eastern half of the Gulf drainage basin (region from Chepo River basin to Coast B); 2) 67.6 per cent of the total precipitation occurs over the area draining into the northeast quadrant of the Gulf along the approximately 100 km coastline extending from San Miguel Bay to the Chepo (Bayano) River; and 3) 95 per cent of the total rainfall occurs north of 8°N. Runoff occurs principally in the innermost reaches of the Gulf of Panama, especially in the 100 km sector extending from San Miguel Bay to the Chepo (Bayano) River. Furthermore, more than 50 per cent of the total annual runoff occurs during the four month period from September through December (Tables 7, 8).

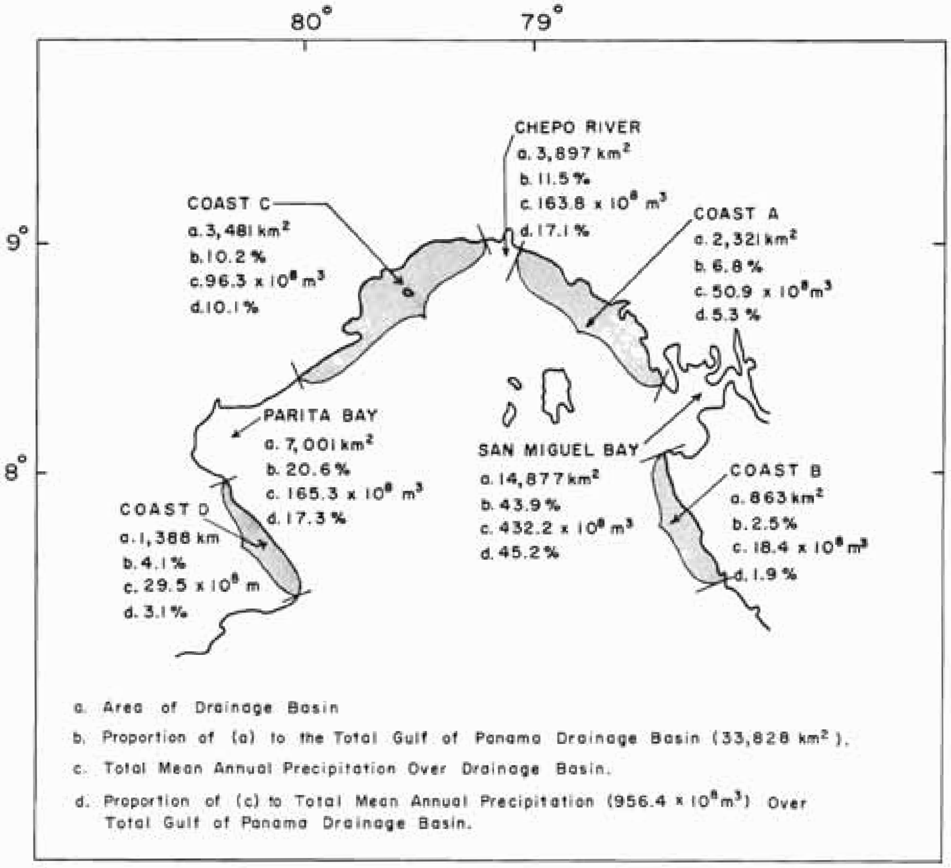

FIGURE 22. Gulf of Panama drainage basin characteristics.

Actual runoff constitutes only a fraction of the total precipitation over a drainage basin. For example, Hutchinson (1957 p. 230) states that 80 per cent of the total rainfall over a large catchment area such as the Mississippi River Basin is evaporated. Since river flow data are too sparse for a direct estimate of the average annual runoff into the Gulf of Panama, an indirect estimate which considers evaporation must be made. Evaporation at three localities in Panama during 1956 was approximately 50 per cent of the total annual rainfall there (Anonymous 1956). The monthly flow data of the Rio Santa Maria and Rio Grande (Figs. 19, 20) during 1956 and 1957 permit an independent estimation of evaporation. These two rivers drain approximately 25 per cent of the total (7,000 km^2) Parita Bay catchment area (Fig. 22). The average annual precipitation over this basin is $165 \times 10^8 m^3$ (Fig. 22), or $236 \times 10^4 m^3$ per km^2. The combined annual flow of these two rivers amounted to:

$207 \times 10^4 m^3$ per km^2	1956
$121 \times 10^4 m^3$ per km^2	1957

corresponding to 51 to 87 per cent of the total precipitation during 1957 and 1956, respectively. The high 1956 value may reflect the above average rainfall that year which increased the Madden-Gatun Lakes of the Panama Canal system (Fig. 1) to 20 per cent above normal (Anonymous 1956). All things considered, runoff into the Gulf of Panama will be considered to be 50 per cent of the total precipitation over the entire drainage basin in subsequent calculations.

The mean annual precipitation over the drainage basin is $95.6 \times 10^9 m^3$ (Fig. 22), while that falling directly into the Gulf (1015 to 2030 mm zone) is $44.5 \times 10^9 m^3$. Assuming 50 per cent evaporation from the terrestrial basin, the total average annual influx of fresh water into the Gulf of Panama is estimated to be $92.5 \times 10^9 m^3$, or about 2.5 per cent of the total Gulf volume (Table 1). This runoff is equivalent to a layer 3.2 m thick throughout the Gulf of Panama (28,500 km^2). Ecologically significant environmental changes must be associated with the observed rainfall level and subsequent drainage into the Gulf of Panama. The ecological parameters most likely to be affected are: 1) salinity and stability of the watermass, 2) transparency, and 3) nutrient content either through accretion or dilution. These conditions will now be examined.

Watermass stability

The importance of vertical stability to the dynamics of natural phytoplankton populations has been summarized by Braarud (Braarud, Gaarder and Grøntved 1953). The greater the density difference between strata the more stratified the water column is and, hence, more resistant to vertical mixing. The degree of mixing will influence, of course, the nutrient supply and the phytoplankton residence time within the euphotic zone.

The stability diagrams for the hydro-biological station (Figs. 23, 24) indicate stratification persists throughout the year, notwithstanding the occurrence of upwelling. This differs from the classical condition in Temperate, Boreal and Arctic inshore regions where the water column is well-mixed during winter and becomes gradually stratified through vernal warming, followed by increasing stability during summer (Braarud and Klem 1931, Gran and Braarud 1935, Riley 1942, Braarud, Gaarder and Nordli 1958).

The hydrographic conditions responsible for the presumed stratification during the upwelling season differ from those during the rainy season. In fact, the stability diagrams indicating more or less stagnant conditions during the upwelling season are misleading. During upwelling, the dense watermass entering at the bottom, as described earlier, is gradually warmed and diluted as it ascends to the surface (Figs. 5, 6). This leads to the observed vertical density differences and, hence, an apparent stratified condition analogous to that found during the summer in other regions, or during the rainy season in the Gulf of Panama (Figs. 23, 24). However, the apparent static conditions suggested by the vertical density distribution obscure a dynamic upwelling condition being generated by northerly winds. The surface waters are actually being continuously renewed and displaced offshore at variable rates, notwithstanding the apparent stratification. This permits a continuous influx, though at a variable rate, of nutrient-rich water (Figs. 5, 6). Since the net transport is towards the surface, two prime requirements for the development of a phytoplankton bloom are satisfied—an adequate, continuous nutrient supply, and confinement of the developing population to the euphotic zone. Thus, the apparent paradox of a period of active phytoplankton growth in the Gulf of Panama (Smayda 1963) despite a seemingly persistent stratification (Figs. 23, 24) can be readily explained. The water column tends to become more homogeneous, approaching a well-mixed condition, during especially intense upwelling. If the rate of upwelling were excessive, then the phytoplankton residence time within the euphotic zone would be inadequate to establish a growing population. The paucity of phytoplankton accompanying such a "well-mixed" watermass would be similar to that found during the winter in more northerly waters, although the responsible mechanisms would be considerably different. The influence of the upwelling rate on phytoplankton density and behavior will be returned to later.

The temperature and salinity levels during the rainy season (Figs. 5, 6, 21) especially favor the marked stratification occurring then (Figs. 23, 24; Table 9). The prevalence of high temperatures (26.0 to 28.0 C) throughout the rainy season, and the progressive warming of the deeper layers until November are noteworthy (Table 9). These high temperatures are an important characteristic of the tropical milieu. For example, the high and constant temperatures ranging from 25.0 to 28.7 C found at 20 m during the rainy season contrast sharply with the thermal conditions at this depth in the temperate Long Island Sound where the June to October range is 13.0 to 20.0 C (Riley 1956, p. 31), and in the arctic Balsfjord,

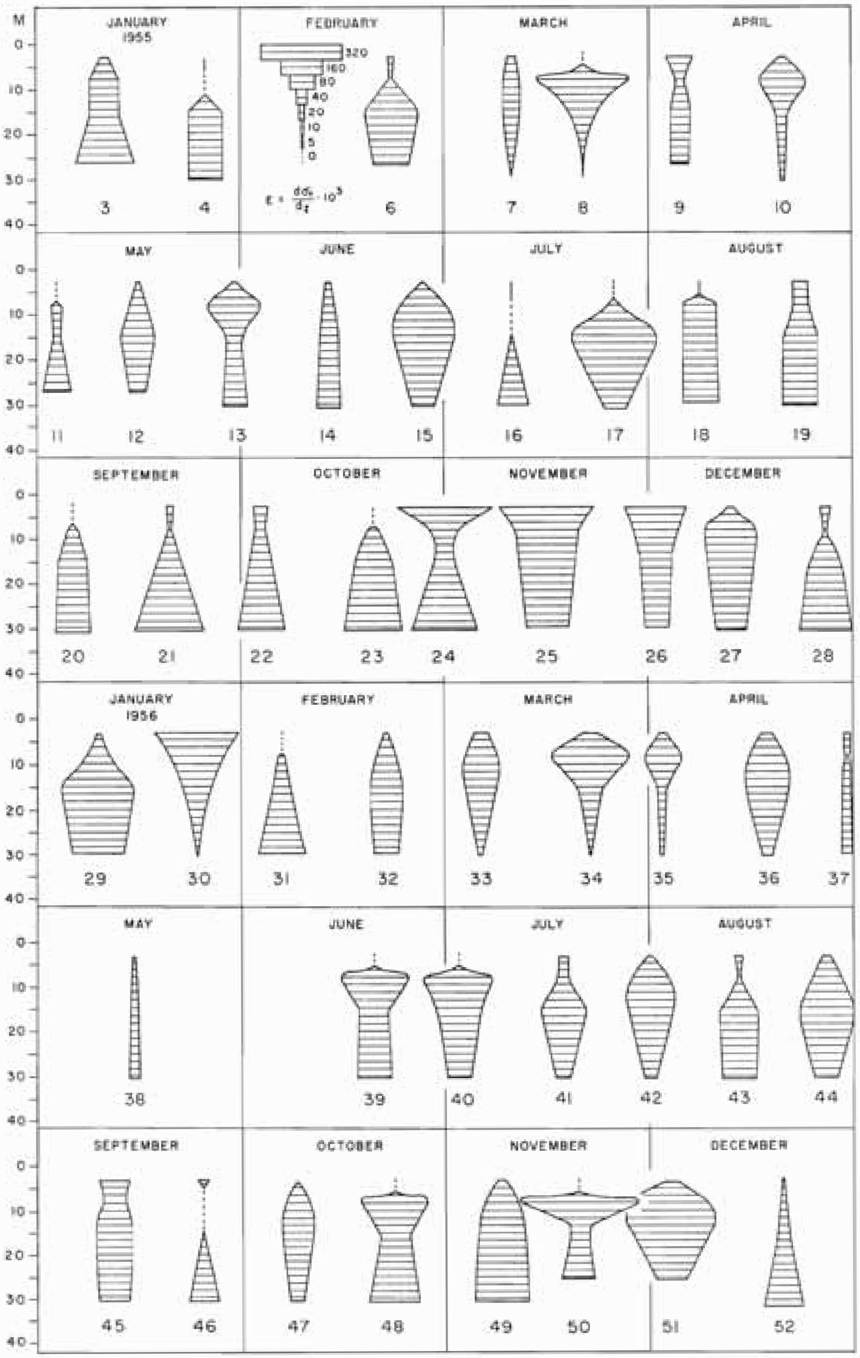

FIGURE 23. Stability characteristics of the watermass at the hydro-biological station during 1955 and 1956.

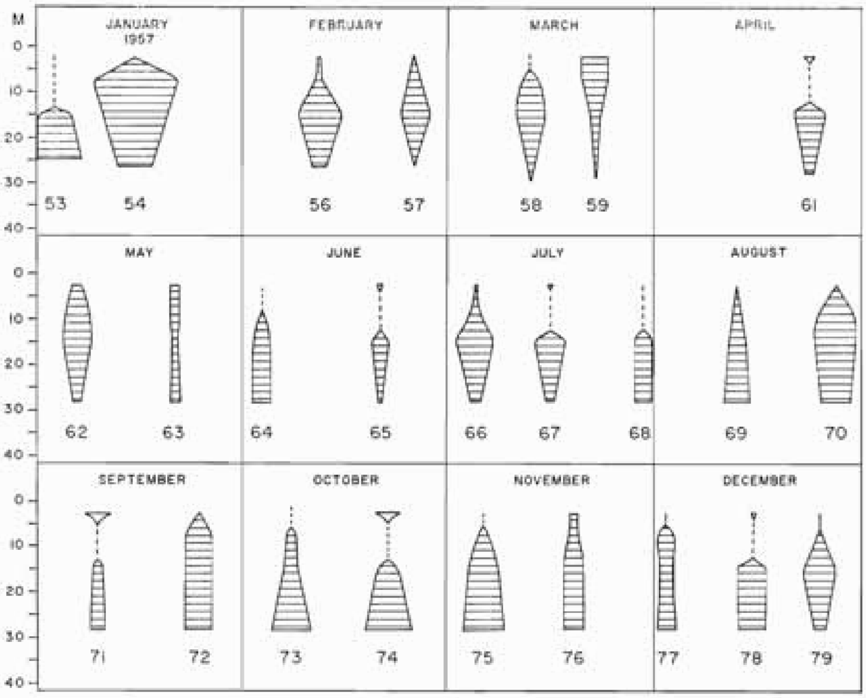

FIGURE 24. Stability characteristics of the watermass at the hydro-biological station during 1957.

Norway (69°30′N) where this 6-month range is 7.0 to 10.0 C (Gaarder 1938). These thermal differences can be expected to contribute to regional differences in both the relative degree of watermass stability and the rates at which temperature-dependent responses of the phytoplankton communities proceed (Riley, Stommel and Bumpus 1949).

While temperature alone appears sufficient to cause stratification during the rainy season, the progressively increasing dilution accompanying rainfall is more important and results in maximum stability usually during October to November (Figs. 21, 23, 24; Tables 7, 9). The general inverse relation between the surface and 20 m density difference and surface salinity demonstrates that stability increases with rainfall (Fig. 25). The annual rainfall at Balboa during 1957 was below average; the rainy season level was 190.5 and 229.0 mm less than during 1955 and 1956, years of above average precipitation (Tables 6, 10). The effect of this reduced rainfall was the considerably less stable watermass which characterized most of the rainy season during 1957 in comparison with 1955 and 1956 (Figs. 23, 24; Table 10).

Stratification during the rainy season represents a considerably more

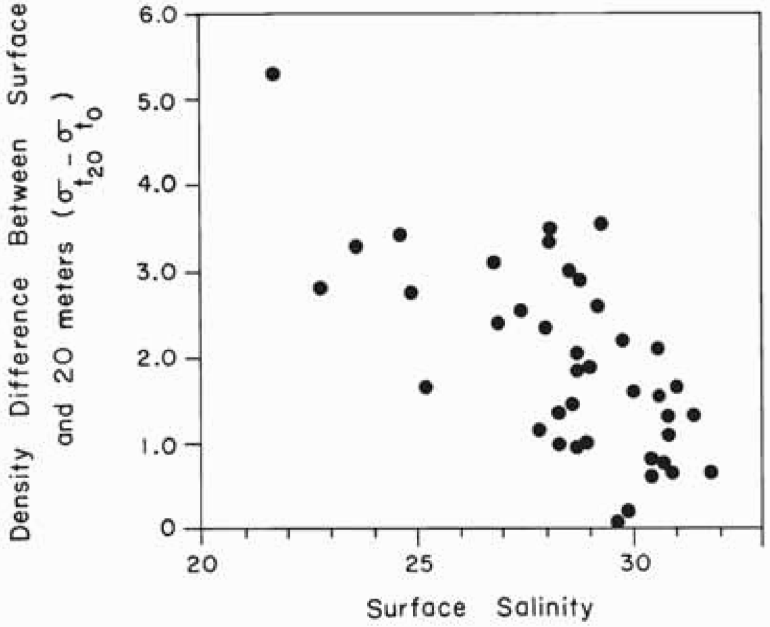

FIGURE 25. The relationship between the density difference between 20 m $(\sigma_{t_{20}})$ and the surface (σ_{t_0}) and the surface salinity at the hydro-biological station during July-December, 1955 to 1957.

stagnant situation than that occurring during upwelling. That watermass stability is related to precipitation volume has significant ecological implications. It raises the question whether the reduced stability accompanying decreased precipitation, as during 1957, or periods of excessive rainfall are more advantageous in enhancing phytoplankton growth during the rainy season. To answer this requires an analysis of the other consequences of drainage, namely transparency of the watermass and nutrient accretion. Also, annual and regional differences in stability attributable to variations in dilution accompanying rainfall can be expected during the rainy season.

Radiation and transparency

Pyrheliometric measurements of the total daily radiation were made at the Albrook Air Force Base from January, 1955 through August, 1956, and thereafter through December, 1957 at Curundu as described under **METHODS** (Fig. 1).

The incident radiation is most intense during the upwelling season (Fig. 26; Table 11). A precipitous drop in intensity occurs during late May for approximately 2 weeks, marking the transition from the high intensity during the upwelling season to the generally reduced radiation

TABLE 9. Representative vertical temperature (C) salinity (‰) and density (σ_t) distribution at selected stations sampled during July to December, 1955 to 1957, at 8°45′N, 79°23′W (38/44 = sample collected between 38 and 44 m)

	1955			1956			1957		
	C	‰	σ_t	C	‰	σ_t	C	‰	σ_t
	25 July			**31 July**			**29 July**		
0 (m)	27.72	29.29	18.22	28.17	29.24	18.05	28.5	30.66	19.00
20	25.00	32.88	21.77	26.67	32.09	20.65	28.4	31.64	19.76
38/44	21.44	34.19	23.78	24.33	32.55	21.71	27.4	32.74	20.91
	22 August			**27 August**			**26 August**		
0	28.00	28.98	17.90	28.11	28.58	17.57	28.4	30.55	18.95
20	27.22	31.17	19.79	26.11	31.76	20.59	26.6	32.57	21.04
38/44	22.44	33.11	22.68	23.78	33.19	22.36	23.8	33.96	22.94
	19 September			**24 September**			**23 September**		
0	27.67	27.84	17.15	28.33	29.85	18.45	28.8	30.99	19.14
20	27.17	29.01	18.19	27.67	29.85	18.66	28.3	32.97	20.79
38/44	21.33	33.75	23.47	25.89	31.89	20.75	25.3	33.91	22.45
	19 October			**22 October**			**21 October**		
0	27.33	25.20	15.30	27.61	26.85	16.44	28.6	30.44	18.81
20	27.44	27.45	16.94	27.11	29.85	18.84	28.7	31.58	19.62
38/44	25.17	31.98	21.03	22.94	33.25	22.65	24.6	33.80	22.58
	15 November			**19 November**			**18 November**		
0	27.50	21.68	12.62	27.39	27.36	16.89	27.8	28.93	17.93
20	26.33	28.27	17.90	26.33	30.37	19.43	27.6	30.14	18.90
38/44	25.06	31.76	20.91	23.56	32.23	21.70	26.1	31.42	20.33
	12 December			**3 December**			**28 December**		
0	26.78	26.82	16.67	26.67	28.09	17.66	27.5	30.84	19.46
20	25.22	30.31	19.76	24.89	31.98	21.12	26.0	31.94	20.75
38/44	22.67	32.50	22.16	19.83	33.23	23.49	25.4	32.86	21.62

TABLE 10. Total monthly precipitation and deviation from mean (△x), and vertical density differences between the surface (σ_{t0}) and 20 m (σ_{t20}), and the bottom (σ_{tbot}) during the 1955 to 1957 rainy seasons (density data from stations in Table 9)

Month	Year	σ_{t20}-σ_{t0}	σ_{tbot}-σ_{t0}	Rain (mm)	△x (mm)
July	1955	3.55	5.56	236.5	+ 53.6
	1956	2.60	3.66	307.1	+121.9
	1957	0.76	1.91	302.3	+117.1
August	1955	1.89	4.78	268.7	+ 77.7
	1956	3.02	4.76	285.8	+ 93.2
	1957	2.09	3.99	278.9	+ 86.4
September	1955	1.17	6.32	191.5	— 1.8
	1956	0.21	2.30	116.6	— 75.4
	1957	1.65	3.31	158.0	— 36.6
October	1955	1.64	5.73	145.5	—107.7
	1956	2.40	6.21	323.1	+ 69.1
	1957	0.81	3.77	227.1	— 27.4
November	1955	5.28	8.29	339.3	+ 88.9
	1956	2.54	4.81	258.6	+ 7.9
	1957	0.97	2.40	213.9	— 36.8
December	1955	3.10	5.49	241.3	+100.1
	1956	3.46	5.83	90.2	— 50.0
	1957	1.29	2.16	14.2	—126.0

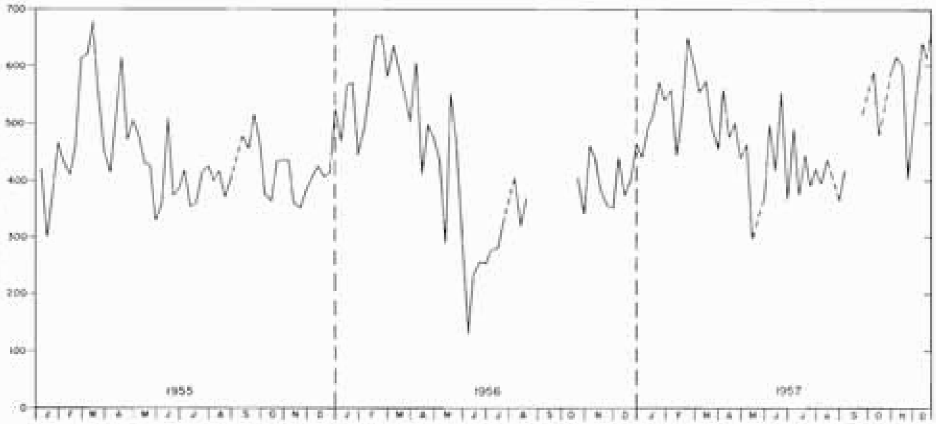

FIGURE 26. Mean weekly incident radiation, as gm cal cm^{-2} day^{-1}, measured at the Albrook Air Force Base from January 1955 through August 1956, and thereafter at Curundu.

characterizing the rainy season. This decrease in radiation level can be attributed to the overcast conditions accompanying the southerly rain-bearing winds then prevalent. Considerably higher incident intensities occurred during the 1957 rainy season than during 1955 and 1956. Furthermore, the average extinction coefficients (k) per meter (based on Secchi disc measurements) indicate a significantly more transparent watermass during the 1957 rainy season than in 1956 (Fig. 27). (Secchi disc measurements were begun at station 39 in mid-June, 1956 [Appendix Table 1].) It is recalled that below average rainfall occurred during 1957 (Tables 6, 10). These annual differences in watermass transparency are

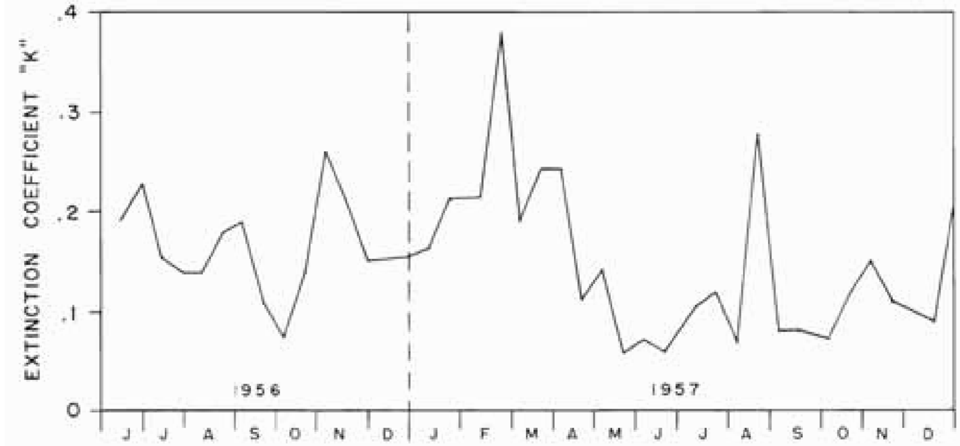

FIGURE 27. Extinction coefficients (k) per meter derived from Secchi disc measurements at the hydro-biological station from June 1956 to December 1957. (Secchi disc observations were begun during June 1956.)

TABLE 11. Mean monthly radiation, g cal cm^{-2} day^{-1}

Month	1955	1956	1957
Jan.	392	513	512
Feb.	480	588	548
Mar.	542	571	555
Apr.	526	497	496
May	417	498	429
June	409	290	459
July	388	294	425
Aug.	399	365	399
Sept.	479	?	466
Oct.	402	?	552
Nov.	380	398	526
Dec.	436	420	613

related to differences in runoff volume, as is clearly demonstrated by the *inverse* relationship existing between density at 5 m and the average extinction coefficient (k) for the entire column during the June to December rainy season (Fig. 28). (A similar relation exists using density at 10 m.) Thus, increased precipitation during the rainy season not only increases watermass stability, but 1) reduces the incident radiation (Fig. 26), and 2) decreases the transparency through silt-laden runoff (Fig. 29) as well. As with stability, then, annual, seasonal and regional variations in light available for photosynthesis might be expected during the rainy season.

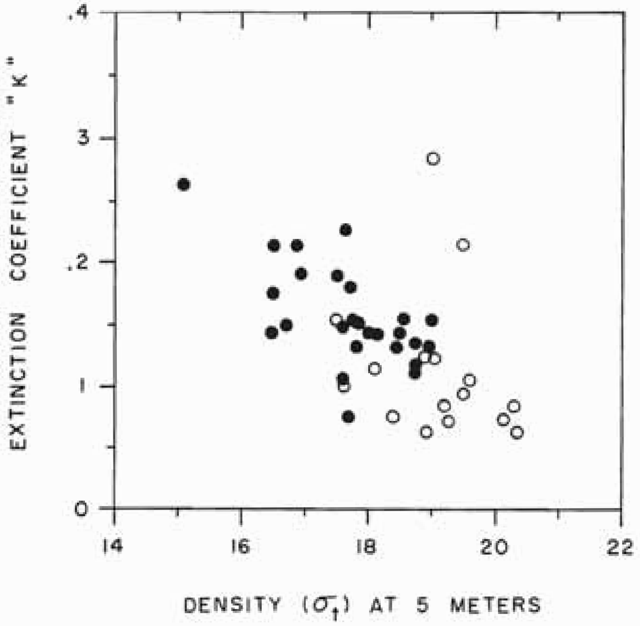

FIGURE 28. The relationship between watermass turbidity using the extinction coefficient (k) based on Secchi disc measurements and the density at 5 m at the hydro-biological station during July-December 1956-1958; open circles represent 1957 observations.

TABLE 12. Range and mean depths (m) of the 50%, 10% and 1% isolumes

ISOLUME:	**50%**		**10%**		**1%**	
Period	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**
June—Dec. 1956	2.6— 9.0	3.8	8.8—30.4	15.2	17.6—60.8	30.4
Jan. —Apr. 1957	1.8— 4.4	3.5	6.1—20.2	12.0	12.2—40.5	24.0
June—Dec. 1957	3.2—11.2	7.4	10.8—37.8	24.8	21.6—75.6	49.6

With the incident radiation and extinction coefficient data, the 50%, 10% and 1% isolumes (Fig. 29) have been prepared as follows:

$$\frac{I}{I_0} = e^{-kL}$$

where I_0 represents the incident intensity and I the intensity at depth L in m. Accordingly, the depth of

$50\%\ I_0 \quad L = (1/k)(0.69)$
$10\%\ I_0 \quad L = (1/k)(2.30)$
$1\%\ I_0 \quad L = (1/k)(1.35)$

or, with the extinction coefficient from the Secchi disc measurements calculated from the Poole and Atkins equation: $k = 1.7/D$ (see **METHODS**), the above equations become:

$50\%\ I_0 \quad L = 0.41\ D$
$10\%\ I_0 \quad L = 1.35\ D$
$1\%\ I_0 \quad L = 2.70\ D$

where D is the Secchi disc depth in m.

Notwithstanding the several errors introduced in preparing and utilizing these isolumes, their general features (Fig. 29; Table 12) are probably representative of actual conditions. The mean depth of the 50% isolume was 7.4 m during the 1957 rainy season, or approximately 2-fold deeper than during the wetter 1956 rainy season (Tables 6, 12). Similarly, the mean rainy season depth of the 1% isolume descended from 30 m during 1956 to approximately 50 m during 1957. Since the 1% isolume depth is generally believed to circumscribe the euphotic zone (Strickland 1958), and since the average depth at the hydro-biological station is approximately 40 m, the euphotic zone extended to the bottom during the 1957 rainy season, unlike during 1956 and during the upwelling period (Fig. 29; Table 12). The isolume characteristics during the 1957 upwelling season and 1956 rainy season are similar. The increased upwelling season turbidity, however, is probably attributable to the increased plankton density (Smayda 1963) rather than to terrigenous particles as found during the rainy season (Jerlov 1953).

The mean radiation levels at the 50% isolume depth, and a regional comparison are presented in Tables 13 and 14. The 1956 rainy season mean of 184 g cal cm^{-2} day^{-1} at 3.8 m (50% isolume depth) *exceeds the mean*

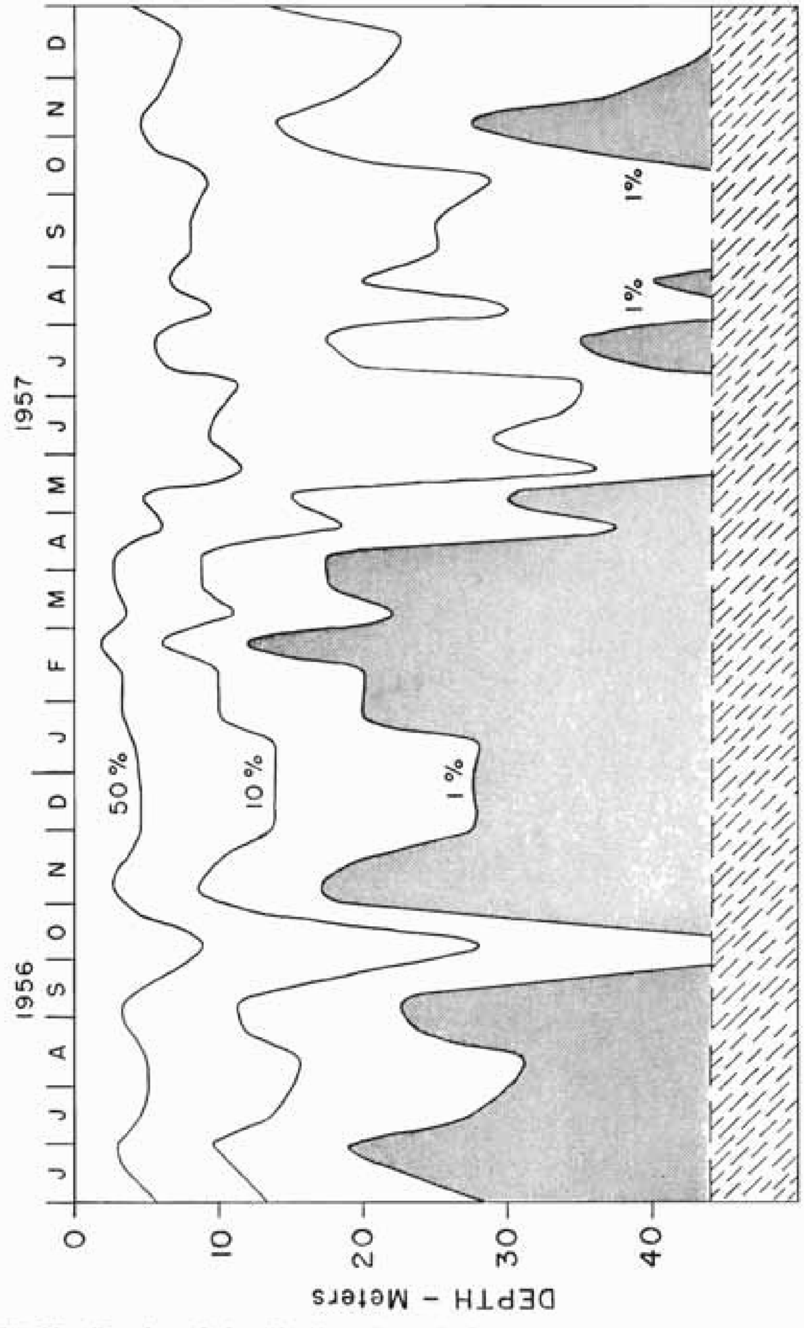

FIGURE 29. Depths of the 50, 10 and 1% isolumes from June 1956 to December 1957 at the hydro-biological station, based on extinction coefficients derived from Secchi disc measurements presented in Figure 27.

TABLE 13. Range and mean radiation intensity, g cal cm^{-2} day^{-1}, at the mean 50% isolume depth

Period	Mean Depth (m)	Radiation Intensity Range	Radiation Intensity Mean
June—Dec. 1956	(I) 3.8	138—219	184
Jan.—Apr. 1957	(II) 3.5	220—298	266
June—Dec. 1957	(III) 7.4	197—328	259

TABLE 14. Mean radiation (g cal cm^{-2} day^{-1}) at the 50% isolume ($I_{50\%}$) depth in the Gulf of Panama during various periods, and the period when the incident radiation (I_o) in other regions is lower than this intensity ($I_{50\%}$). (The Gulf of Panama periods used are identified in Table 13.)

Gulf of Panama Period	Gulf of Panama Mean Depth (m) of 50% Isolume	$I_{50\%}$	Months in Other Regions When I_o < Panama $I_{50\%}$: Long Island Sound (41°N)	Oslofjord (60°N)	Tromsø (70°N)
I	3.8	184	November to mid-February	mid-September to mid-March	September to March
II	3.5	266	November to March	September to March	August to mid-April
III	7.4	259			
Number of months when Gulf of Panama $I_{50\%}$ exceeds the I_o in the regions chosen for comparison:			3½ to 5	6 to 7	7 to 8½

daily surface intensity from November through mid-February in the temperate Long Island Sound (Riley 1956, S. Conover 1956); from mid-September through mid-March in the boreal Oslofjord and from September through March in the arctic Tromsø (Balsfjord) district (Smayda 1959). That is, the mean daily radiation at 3 to 4 m during the most turbid period in the Gulf of Panama *exceeds* the incident radiation during approximately 4, 6 and 8 months of the year in the Temperate, Boreal and Arctic regions, respectively, chosen for comparison. S. Conover (1956) demonstrated that at 5 m in Long Island Sound the mean monthly radiation never exceeded 60 g cal cm^{-2} day^{-1}. These data demonstrate an additional major ecological distinction between tropical and other biogeographic regions in the intense radiation available throughout the year for photosynthesis in the tropics. Indeed, Atkins (1925) concluded that radiation is always adequate for phytoplankton growth in the tropics, unlike that in other regions (*vide* Ryther 1963; Steemann Nielsen 1963).

Nutrients

Phosphate-rich water during the upwelling season which becomes progressively depleted during the rainy season (Figs. 5, 6, 30; Tables 15, 16) characterizes the mean annual phosphate cycle at the hydro-biological station. The mean phosphate concentration in the entire water column was 55.18 mg-at m^{-2} during the upwelling season (January to April), and

34.14 mg-at m^{-2} during the remainder of the year. Slight phosphate enrichment below 20 m during July and August accompanies upwelling induced by the brief resurgence of weak northerly winds (Figs. 4, 5, 6).

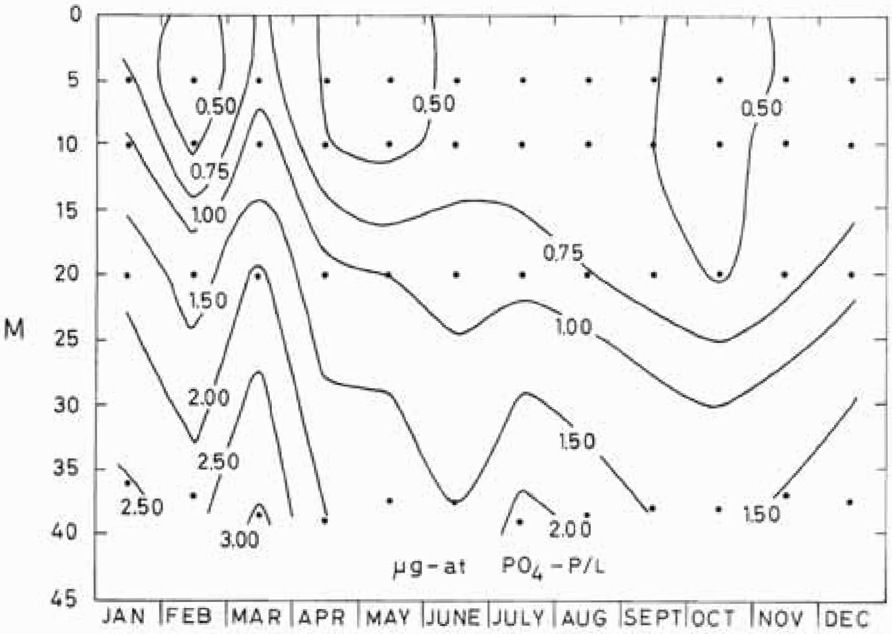

FIGURE 30. Mean monthly phosphate concentration in the upper 40 m at the hydro-biological station, based on observations made from 25 July 1955 to 2 December 1958.

The dissolved oxygen and inorganic phosphate concentrations in the inflowing watermass during the upwelling season are inversely related (Fig. 31). This oxygen-poor, phosphate-rich water becomes oxygenated and phosphate-poorer due to phytoplankton activity as it ascends to the surface (Figs. 5, 6, 30; Table 15). Forsbergh (1963) has determined that an average increase of 1.9 ml of oxygen accompanies a phytoplankton assimilation of 1.0 μg-at of phosphate-phosphorus in the water column.

An especially low dissolved oxygen concentration is frequently accompanied by high phosphate levels in the bottom water (Fig. 31). For example, of the 24 observations plotted in Figure 31, 50 per cent of the phosphate values exceed 2.5 μg-at L^{-1}, and 28 per cent of the oxygen values are below 1 ml L^{-1}. As discussed earlier, the exact source of the upwelled water entering the Gulf of Panama is unknown, although water of a similar character has been found in the Panama Bight (Schaefer *et al.* 1958). The phosphate and oxygen conditions at stations[7] sampled in the Panama Bight

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[7] The Dana (D) data have been taken from Thomsen (1937), the Carnegie data from Fleming *et al.* (1945), the Swedish Deep-Sea Expedition (SW) data from Bruneau, Jerlov and Koczy (1953), the Scot data from Holmes and Blackburn (1960), and the Scope data from Holmes (1958).

during various expeditions (Table 17) have been compared to the bottom water conditions at the hydro-biological station (Fig. 31) in an attempt to resolve this question. However, the oxygen and phosphate concentrations in the bottom water at the hydro-biological station can not be related unequivocally to any of the Panama Bight stations used in the comparison. Bottom water oxygen concentrations below 1 ml L^{-1} suggest an origin of this watermass from within the oxygen minimum layer found below approximately 100 m in the Panama Bight (Table 17; p. 179 in Wooster and Cromwell 1958). Water derived from this depth is not unreasonable because about 70 m of water are possibly displaced offshore during upwelling (Forsbergh 1963). However, except for Carnegie station 35 (Fig. 32; Table 17), the commonly observed bottom water phosphate concentrations of 2.5 μg-at L^{-1} (Fig. 31) occur *below* 200 m in the Panama Bight, and those exceeding 3.0 μg-at L^{-1} below 300 m. It is unlikely that water derived from such great depths in the Panama Bight enters into and is upwelled within the Gulf of Panama (Fleming 1939, Schaefer *et al.* 1958, Wooster 1959). Phosphate concentrations of 2.5 to 3.0 μg-at L^{-1} are found at 50 to 85 m near the Peruvian coast below the equator (Wooster and Cromwell 1958). However, Wooster (1959) contends that the current systems prevent this from being the source of the Gulf of Panama upwelled water.

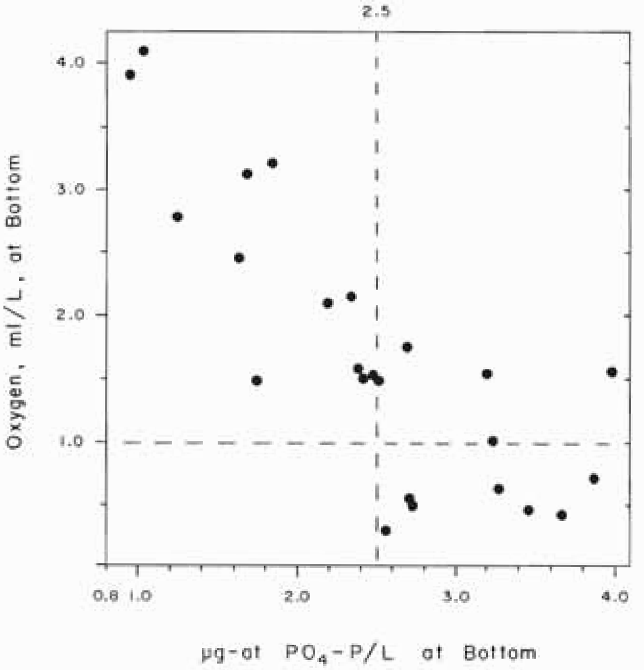

FIGURE 31. Relationship between dissolved oxygen concentration and phosphate present in the bottom water (about 40 m) at the hydro-biological station during the 1956-1958 upwelling seasons.

TABLE 15. Mean monthly phosphate concentrations at given depths (μg-at L^{-1}) and for the entire water column (mg-at m^{-2}) at the hydro-biological station (stations 17 to 102 are included; 25 July 1955 to 2 December 1958)

Month	Depth (m) 0	5	10	20	(Bottom) 36 to 40	mg-at m^{-2}	Number of Observations
Jan.	0.74	0.75	1.05	1.88	2.52	58.50	7
Feb.	0.35	0.22	0.43	1.27	2.26	41.58	6
Mar.	0.79	0.86	1.19	2.07	3.06	77.07	6
Apr.	0.48	0.49	0.52	1.07	2.06	43.56	5
May	0.26	0.34	0.32	1.01	1.94	36.00	4
June	0.65	0.61	0.68	0.84	1.49	34.69	4
July	0.55	0.61	0.65	0.86	2.18	43.10	8
Aug.	0.58	0.54	0.64	0.75	1.87	37.00	7
Sept.	0.53	0.53	0.50	0.64	1.46	29.45	6
Oct.	0.36	0.31	0.41	0.47	1.46	25.04	7
Nov.	0.55	0.54	0.61	0.66	1.51	30.27	7
Dec.	0.57	0.53	0.56	0.87	1.94	37.61	8

TABLE 16. Mean phosphate content of the water column (mg-at m^{-2}) during various periods of the year

Jan.—Apr.	May—Dec.	May—Aug.	Sept.—Nov.	Sept.—Dec.
55.18	34.14	37.70	28.25	30.59

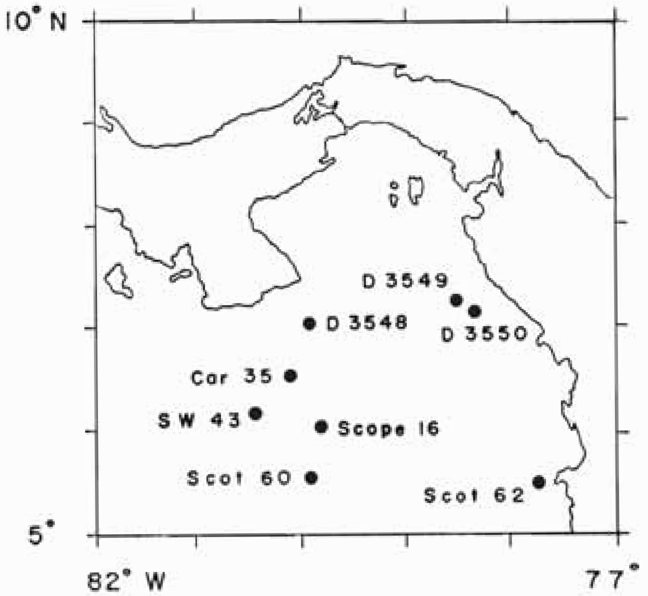

FIGURE 32. Location of stations sampled in the Panama Bight during various expeditions where oxygen and phosphate observations were made, and which have been compared to the concentrations of these substances found in the bottom water at the hydro-biological station during the upwelling season.

Thus, phosphate concentrations ranging from 2.5 to about 4.0 μg-at L^{-1} and accompanied by oxygen concentrations of less than 1 ml L^{-1} are frequently encountered in the bottom water at the hydro-biological station prior to actual upwelling (i.e., prior to photosynthesis). These concentrations *exceed* the phosphate levels of the prospective watermass sources located in the Panama Bight. The occurrence of high phosphate concentrations, particularly those above 3.0 μg-at L^{-1} (Fig. 31), suggests, then that *phosphate may be released into the water column from the interstitial water of the bottom sediments through scouring and roiling during the incursion of the upwelled watermass* (*vide* Miller 1952, Seshappa and Jayaraman 1956). Further evidence for the probable agitation of the bottom sediments during upwelling has been presented on page 363.

The gradual reduction in phosphate concentration during the rainy season is indicated by the progressive descent of the 0.75 and 1.0 μg-at L^{-1} isolines (Fig. 30), and decline in total water column concentration (Tables 15, 16). During the height of the rainy season, the mean phosphate concentration in the upper 20 m is less than 0.50 μg-at L^{-1} (Fig. 30; Table 15). Since this phosphate reduction accompanies intense rainfall and runoff, a relationship between phosphate concentration and salinity was sought. An unequivocally strong, direct relationship between these variables was found, however, only at 10 m during November (Fig. 33). Earlier, the extinction coefficient (k) of the water column was demonstrated to be inversely related to the density (σ_t) at 5 m (Fig. 28) and 10 m.

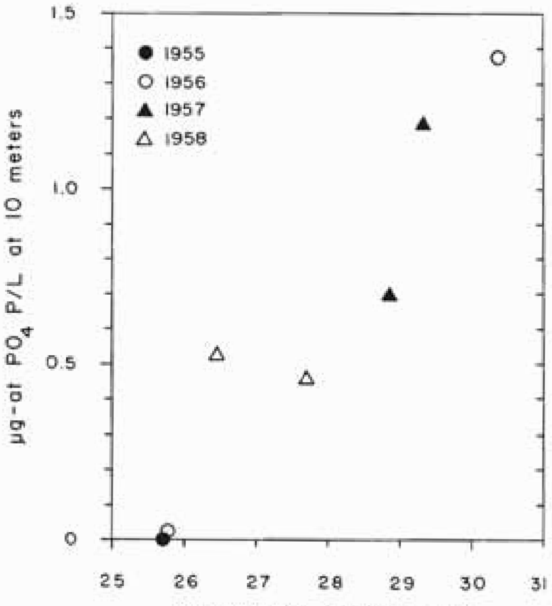

FIGURE 33. Relationship between inorganic phosphate concentration and salinity at 10 m at the hydro-biological station during November 1955-1958.

TABLE 17. Summary of phosphate and oxygen conditions in the Panama Bight as observed during various expeditions (depths in m)

			Phosphate				
Expedition	Station	Date	Maximum Conc. Observed (μg-at L^{-1})	Depth of Max. Conc.	Depth of 2.0 μg-at L^{-1}	Depth of 2.5 μg-at L^{-1}	Depth of 1 ml O_2 L^{-1}
DANA	3548	3 IX '28	2.66	500	285	425	75
DANA	3549	4 IX '28	n	—	—	—	155
DANA	3550	4 IX '28	n	—	—	—	160
CARNEGIE	35	26 X '28	3.91	421	58	86	x
SWEDISH DEEP-SEA	43	29 VIII '47	3.29	731	92	243	138
SCOPE	16	1 XII '56	2.18	720	359	z	89
SCOT	60	18 V '58	3.13	759	167	268	127
SCOT	62	19 V '58	3.20	645	139	227	147

n = phosphate determinations not made; x = oxygen not determined;
z = level not observed

Using density[8] at 10 m as an index of dilution, therefore, and all stations sampled during June[9] through December, a fairly good direct relationship existed between phosphate concentration and runoff (i.e., density) during 1955 and, to a lesser extent, during 1956 (Fig. 34). However, there is no conclusive relationship during the "dry" 1957 rainy season or during 1958 when the amount of rainfall approximated that in 1955 (Table 6). The actual phosphate concentration—rainfall relationship (Fig. 34) is possibly somewhat obscured by long-term trends and/or station-to-station variations in the hydrographic and biological conditions influencing this relationship. Therefore, the mean monthly phosphate concentration in the entire water column was then related to the mean monthly density at 10 m, and grouped into months irrespective of sampling year (Figs. 35, 36). A *direct*, general relationship occurs during June through August which strengthens during September through October, notwithstanding the deviant 1957 data (Fig. 35), and becomes even stronger during November through December (Fig. 36) confirming that found previously using November phosphate and salinity levels at 10 m (Fig. 33). That is, *the amount of phosphate at the hydro-biological station during the rainy season is inversely related to rainfall and runoff, a relationship which strengthens as the rainy season progresses.*

Since salinity and density are indirect indices of relative precipitation intensity, it is desirable to seek confirmation of the apparent inverse relationship existing during the rainy season between phosphate and rainfall by using the latter data directly. Relating the mean monthly surface phosphate concentration (or that at 10 m, or for the entire water column) during June—December to the total monthly rainfall at Balboa (Fig. 1) confirms the general inverse trend between these variables, although

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[8] Since the temperature in the upper 20 m is relatively constant around 28 C during the rainy season (Figs. 5, 6), changes in density at 10 m are primarily attributable to salinity changes.

[9] Phosphate determinations were not made during June 1955.

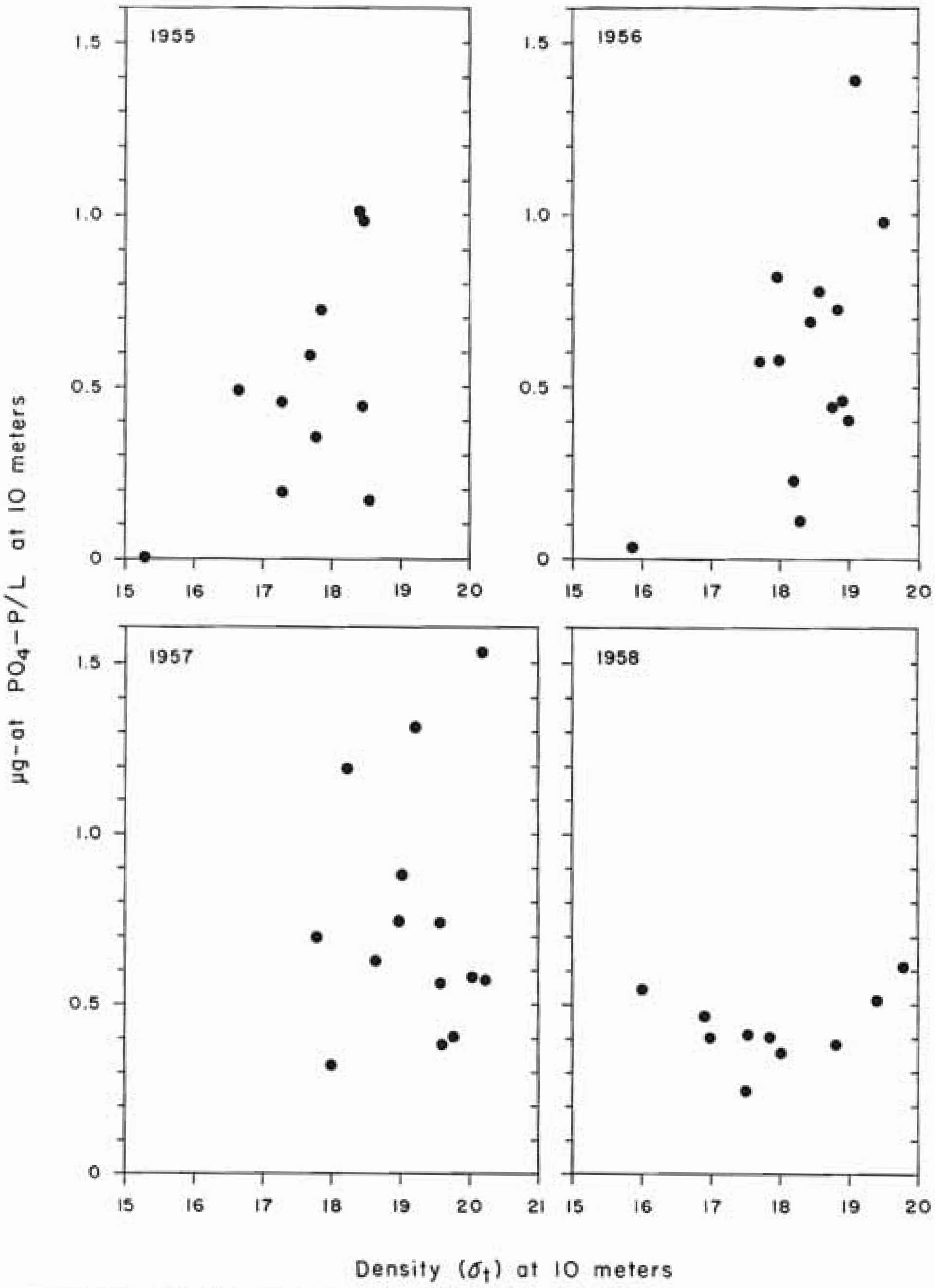

FIGURE 34. Relationship between inorganic phosphate concentration and density at 10 m at the hydro-biological station during June-December, 1955-1958.

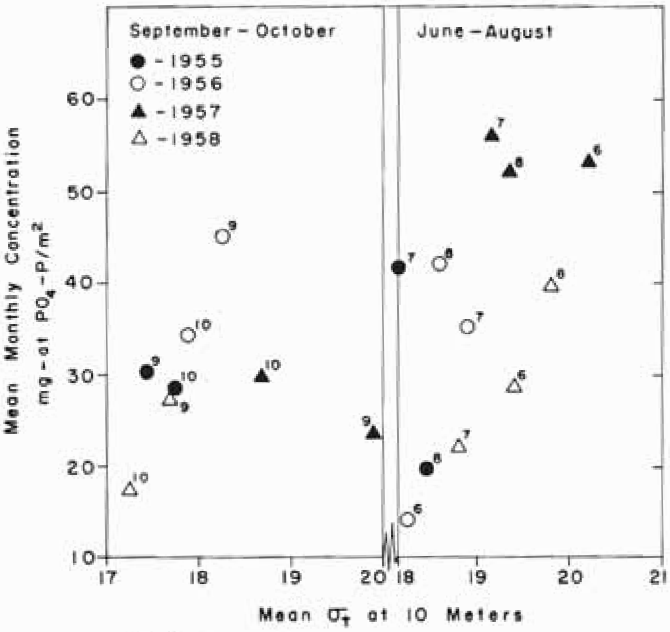

FIGURE 35. Relationship between the mean monthly phosphate concentration and mean monthly density at 10 m during June-August, and from September-October at the hydro-biological station. (Numerals beside the plotted points indicate months, i.e., 6 = June, 7 = July, etc.)

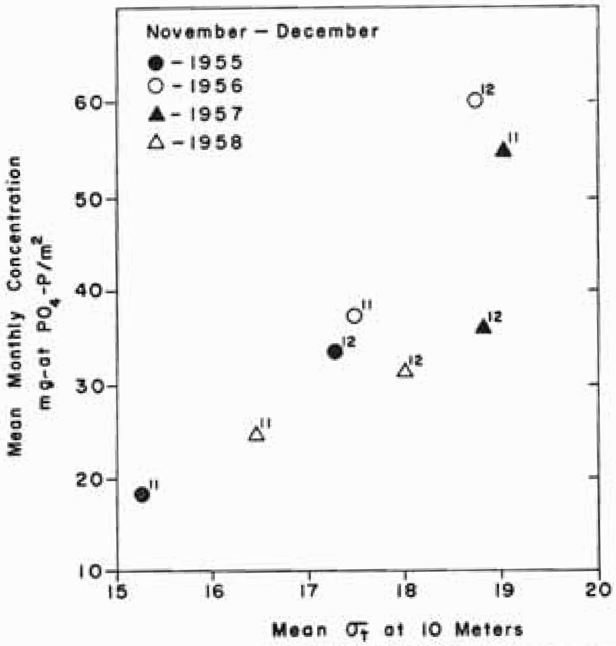

FIGURE 36. Relationship between the mean monthly phosphate concentration and mean monthly density at 10 m during November to December at the hydro-biological station (11 = November; 12 = December).

annual differences in correlation occur (Fig. 37). A fairly good inverse relationship exists during 1955 and 1956, while there is no apparent relationship during 1957 and, especially, 1958, confirming that obtained using 10 m density and phosphate levels (Fig. 34). The inverse relationship between surface phosphate and precipitation is most pronounced during September—November (Fig. 38).

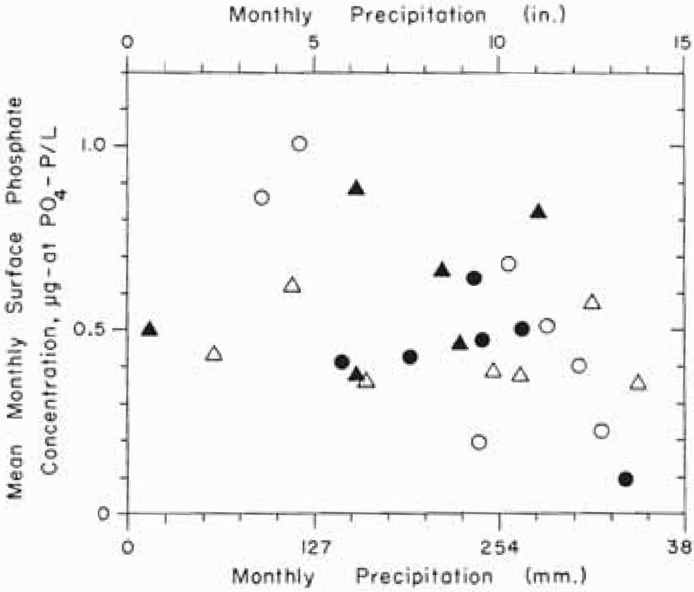

FIGURE 37. Relationship between mean monthly surface phosphate concentration at the hydro-biological station and the total monthly precipitation recorded at Balboa from June to December, 1955-1958. (Symbols used to designate years are as identified in legend to Figure 36.)

Since there are annual differences in rainfall during the rainy season (Table 6), the above observations suggest that this would cause *annual* variations in mean phosphate concentration. Relating the mean phosphate content of the entire water column to the mean 10 m density during July through December[10] shows that a strong, direct relation, in fact, does occur (Fig. 39). That is, the average phosphate content during the rainy season of the dryer 1957 considerably exceeds that during the "wet" years of 1955 and 1958. The strong inverse correlation between mean phosphate content and rainfall is confirmatory (Fig. 40). In fact, *the mean rainy season phosphate content can be satisfactorily related to the total rainfall occurring from September through December*; there is no correlation with July and August precipitation (Fig. 40B).

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[10] Since phosphate observations were not made during June 1955, the rainy season is considered here to extend from July through December for the purposes of this analysis.

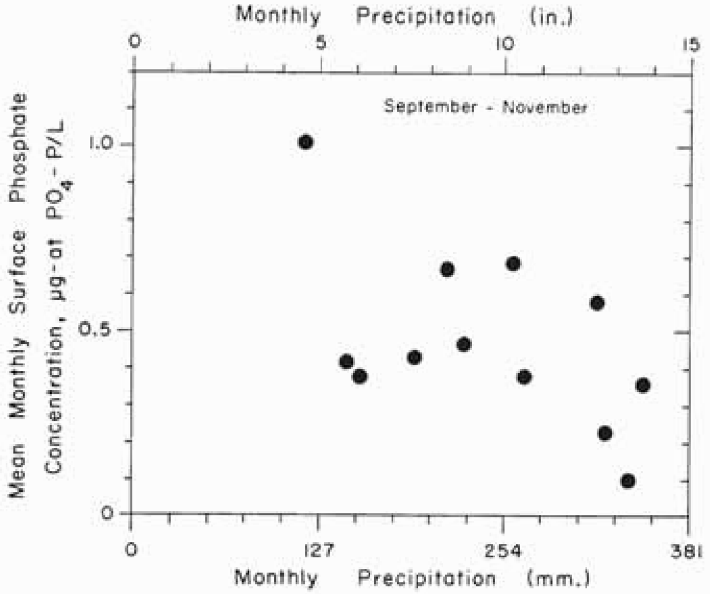

FIGURE 38. Relationship during September-November, 1955-1958 between the mean monthly surface phosphate concentration at the hydro-biological station and the total monthly precipitation recorded at Balboa.

The reduction in phosphate concentration during the rainy season, including annual variations, is clearly related somehow to rainfall. However, it is unknown to what extent dilution, sorption of phosphate onto terrigenous material associated with runoff and/or the reduced mixing accompanying increased stability (Figs. 23, 24) are responsible for this effect. If dilution were solely responsible, then one should be able to calculate the expected phosphate content at a given station from a knowledge of the salinity change occurring between two stations and the phosphate content of the diluent. Assuming runoff and rainfall to be devoid of phosphate, such calculations give phosphate concentrations far in excess of that usually encountered (Table 18).

Forsbergh (1963) found that the assimilation of 1.0 μg-at PO_4-P L^{-1} was accompanied by the evolution of 1.9 ml L^{-1} of oxygen. With this relationship, a comparison of the phosphate and oxygen changes between stations indicated that on some occasions the observed phosphate decline accompanying a reduction in salinity could be satisfactorily accounted for by biological activity (Table 18). However, such activity also does not provide an adequate general explanation for the observed rainfall—phosphate relationship occurring during the rainy season.

Phosphate may not be detectable in the upper 10 m during the height of the rainy season when pronounced dilution occurs, as at the November stations 25 and 49 (Table 18). This suggests that the accretion of phos-

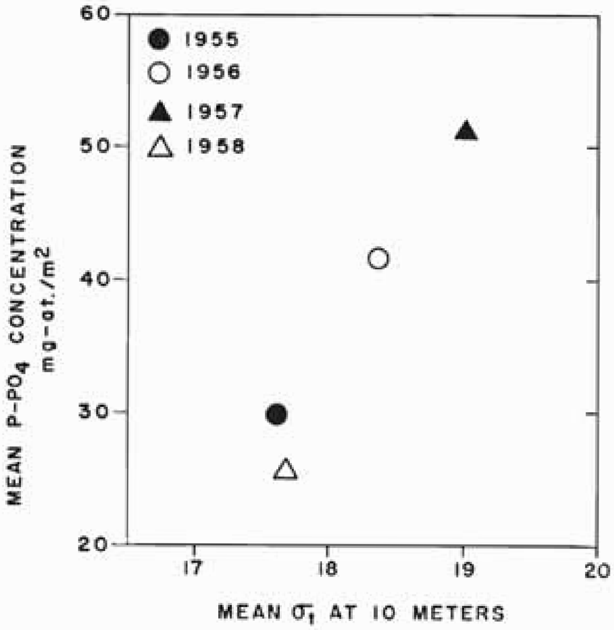

FIGURE 39. Relationship between the mean phosphate concentration in the entire water column at the hydro-biological station during July-December, 1955-1958 and the mean density at 10 m.

phate through runoff, or directly from rain, is minimal. Attempts to have phosphate determinations made on river runoff were unsuccessful. Esslinger (1962, personal communication) wrote, however, "that all rivers in this area (Panama Canal) are low in phosphate level." In contrast, Carter's (1934) phosphate analyses of several rivers in British Guiana which is climatologically and geologically (Harrison 1934, Ijzerman 1931, Woodring 1957) similar to Panama, indicate a mean concentration ranging from 0.63 to 1.47 μg-at L^{-1} during the rainy season. Ingham (1950) found a surprisingly high average phosphate concentration of 0.47 μg-at L^{-1} in rain water at Natal, Africa (*vide*, however, p. 549 in Hutchinson 1957). An influx of such phosphate-rich water into the Gulf of Panama during the rainy season would be expected to *increase* rather than decrease the phosphate content of the surface layers. Increased turbidity of the water column accompanies dilution (Fig. 28), which appears to be primarily attributable to terrigenous particles (Jerlov 1953), rather than to biological activity (Smayda 1963, 1965a). The extent to which sorption of phosphate onto these particles (Carritt and Goodgal 1954) contributes to the lowered phosphate concentration during the rainy season is unknown. All things considered, it appears that the observed decline in phosphate during the rainy season is primarily due to biological utilization *without* an

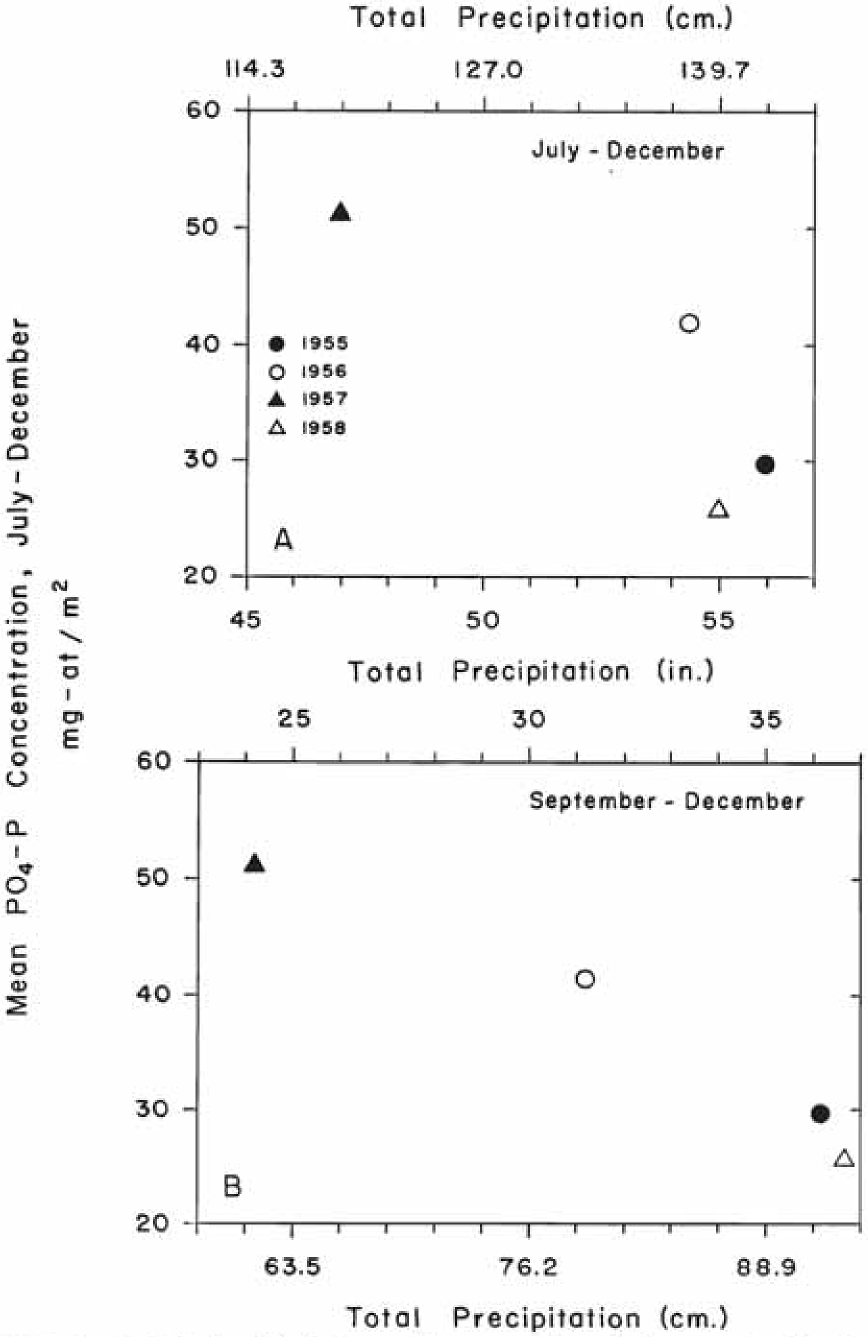

FIGURE 40. A. Relationship between the mean phosphate concentration in the entire water column at the hydro-biological station during July-December, 1955-1958 and the total precipitation occurring at Balboa during this period.
B. Relationship between the mean phosphate concentration in the entire water column at the hydro-biological station during July-December, 1955-1958 and the total precipitation during September-December at Balboa.

TABLE 18. Salinity, oxygen and phosphate concentrations at selected November stations, and calculations of the mean salinity dilution and expected phosphate and oxygen concentrations in the upper 10 m accompanying sea water dilution and phytoplankton activity (assumptions and nature of calculations given in the text)

	Salinity			Phosphate (μg-at L^{-1})			Oxygen (ml L^{-1})		
Station:	**22**	**25**	△	**22**	**25**	△	**22**	**25**	△
Depth (m)									
0	28.33	21.68	—6.65	0.41	0.08	—0.33	?	5.28	?
5	28.44	24.04	—4.40	0.15	0.00	—0.15	4.78	5.17	+0.39
10	28.61	26.07	—2.91	0.35	0.00	—0.35	4.74	5.08	+0.34
15	29.20	28.27	—0.93	0.52	0.15	—0.37	4.31	4.72	+0.41
38/40	32.58	31.76	—0.81	1.84	1.34	—0.50	2.10	2.58	+0.48
Mean in upper 10 m	28.46	23.81	—4.65	0.30	0.03	—0.27	4.77*	5.18	+0.41

% Fresh Water: (i.e., dilution) $\dfrac{28.46 - 23.81}{28.46} \times 100 = 16.3\%$

Expected phosphate concentration resulting from dilution:
$(0.84)(0.30) + (0.16)(0) = 0.25$ μg-at L^{-1}

Observed phosphate concentration at station 25: ....0.03 μg-at L^{-1}

Expected O_2 evolution accompanying an assimilation of 0.27 μg-at PO_4-P L^{-1}:
$(1.9)(0.27) = 0.41$ ml L^{-1}
Expected O_2 concentration at station 25: ....$4.77 + 0.41 = 5.18$ ml L^{-1}
Observed O_2 concentration at station 25: ....5.18 ml L^{-1}

	Salinity			Phosphate			Oxygen		
Station:	**48**	**49**	△	**48**	**49**	△	**48**	**49**	△
Depth (m)									
0	26.85	28.44	—1.97	0.21	0.37	+0.16	4.56	4.62	+0.06
5	26.82	24.86	—1.96	0.21	0.00	—0.21	4.86	4.20	—0.66
10	28.48	25.76	—2.72	0.57	0.03	—0.54	4.86	4.23	—0.63
20	29.85	28.23	—1.62	0.71	0.15	—0.56	4.38	3.51	—0.87
40	33.25	32.89	+0.36	2.88	1.19	—1.69	3.20	1.68	—1.52
Mean in upper 10 m	27.38	25.17	—2.21	0.33	0.13	—0.20	4.76	4.35	—0.41

% Fresh Water: $\dfrac{27.38 - 25.17}{27.38} \times 100 = 8\%$

Expected phosphate concentration resulting from dilution:
$(0.92)(0.33) + (0.08)(0) = 0.30$ μg-at L^{-1}

Observed phosphate concentration at station 49: ....0.13 μg-at L^{-1}

Expected O_2 evolution accompanying an assimilation of 0.20 μg-at PO_4-P L^{-1}:
$(1.9)(0.20) = 0.38$ ml L^{-1}
Expected oxygen concentration at station 49: ....$4.76 + 0.38 = 5.14$ ml L^{-1}
Observed oxygen concentration at station 49: ....4.35 ml L^{-1}

* Calculated assuming a surface O_2 concentration equalling that at 5 m

appreciable phosphate gain through accretion either because of a low phosphate content of the runoff and/or significant sorption of phosphate onto terrigenous particles accompanying runoff. Under certain conditions there might also be a further apparent phosphate decline due to dilution of the residual concentration and/or sorption. Furthermore, enrichment of the surface waters with regenerated phosphate through mixing is hindered, usually, by the highly stable watermass present during the rainy season (Figs. 23, 24).

The particulate iron cycle during 1955 at the hydro-biological station has been described by Schaefer and Bishop (1958). The average surface concentration was 94 μg L^{-1}; maximum concentrations were found during the upwelling season. Their Figure 9 suggests that, as with inorganic phosphate (Fig. 30), the particulate iron content decreases with increasing runoff during the height of the rainy season. However, the iron content of two samples collected from Rio Escota, which empties into Parita Bay (Fig. 1), was 692 and 863 μg L^{-1}, respectively. This suggested to them that iron is being accreted into the Gulf of Panama during runoff, and that particulate iron is not limiting to phytoplankton growth.

Although other nutrient analyses were not undertaken, the general importance of nutrient accretion in the various nutrient cycles of the Gulf of Panama merits further analysis. The occurrence of a tropical rain forest in much of the Gulf of Panama drainage basin, coupled with an intense precipitation, suggests terrestrial nutrient supplies might be important. Jenny (1950) has shown that the luxuriant plant growth characterizing tropical rain forests yields large amounts of organic matter subject to rapid decomposition. For example, the leaf-fall in the Colombian rain forests ranges from 800 to 1000 g m^{-2}, dry weight, or 10 to 15 g of organic nitrogen m^{-2}. Goldman (1961) has demonstrated that drainage through stands of the nitrogen-fixing alder tree (*Alnus tenuifolia*) provided a significant nitrogen supply to a California lake and promoted primary production. It is of considerable interest, therefore, that 50 per cent of the trees in the Colombian tropical rain forest have been reported to be leguminous (Jenny 1950).

The nitrogen content of tropical rain is quite high, although pronounced regional variations occur. The mean ammonia concentration in Bermuda rain water is 4.97 μg-at NH$_4$-N L^{-1} (Menzel and Spaeth 1962), 13.0 μg-at L^{-1} in Rhodesia (Weinmann 1955), and 47.4 μg-at L^{-1} at Natal, Africa (Ingham 1950). Menzel and Spaeth (1962) present evidence that a large fraction of the ammonia occurring in the surface waters of the Sargasso Sea is contributed by rain. The average nitrate content of tropical rain has been reported to range from 1.61 μg-at NO$_3$-N L^{-1} (Ingham 1950) to 1.77 μg-at L^{-1} (Weinmann 1955). Ingham's phosphate analysis of rain water was mentioned earlier. In addition, a significant enrichment of plant nutrients in rain water can occur from tree leaves, as shown by Ingham (1950):

	RAIN	**TREE DRIPS**
NH$_4$-N	47.40 μg-at L^{-1}	144.4
NO$_3$-N	1.61	1.6
PO$_4$-P	0.47	28.0

Thus, the rapid decomposition of a probably high leaf-fall in the surrounding rain forest, coupled with a presumedly relatively nutrient-rich rain

TABLE 19. Silicate, nitrate (both as μg-at L^{-1}) and iron (μg L^{-1}) concentrations in Gatun Lake and in two hot springs on Coiba Island

	SiO_3-Si	NO_3-N	Fe
Gatun Lake	346.6	0.64	190.0
Hot Spring 1	1583.3	11.3	110.0
Hot Spring 2	1350.0	6.45	10.0

water, might materially influence the nutrient cycles in the Gulf of Panama during the rainy season, especially considering the extensive rainfall and runoff occurring then (Figs. 19, 20, 22; Tables 6, 7, 8). A general approximation of the importance of nutrient accretion to the nutrient cycles and primary production in the Gulf of Panama is, therefore, necessary.

Aside from Schaefer and Bishop's (1958) two analyses of particulate iron in the Rio Escota, mentioned previously, published nutrient analyses of river and rain water in Panama appear to be lacking. Galtsoff (1950), however, has determined the silicate, iron and nitrate concentrations in two hot springs on Coiba Island, and Esslinger (1962, personal communication) has provided the results of an analysis made during mid-October in Gatun Lake[11] (Table 19). Phosphate concentration was not determined. The hot springs exhibit a considerably greater concentration of silicate and nitrate than Gatun Lake; the iron content is lower than the mean of 778 μg L^{-1} (two samples) found in Rio Escota (Schaefer and Bishop 1958). A mean NO_3-N concentration of 6.0 μg-at NO_3-N L^{-1}, based on Table 19, will be assumed for runoff in subsequent calculations. Esslinger's communication that rivers in the vicinity of the Panama Canal are low in phosphate is consistent with observations in tropical Sierra Leone (Bainbridge 1960) and along the Great Barrier Reef in Australia (Orr 1933). Because of this and the previous analysis of the phosphate cycle, a mean phosphate content of 0.65 μg-at L^{-1} will be assumed for runoff water. This is the lowest mean phosphate content (maximum was 1.47 μg-at L^{-1}) reported for river water during the rainy season in British Guiana (Carter 1934) where "moderately high" phosphate levels are reported to occur.

The average annual runoff into the Gulf of Panama (excluding precipitation directly into the Gulf) was found earlier to be 48×10^{12} liters (*vide* page 394). Since 80 per cent of the runoff occurs during May through December (Table 7), and the Gulf of Panama is 28,500 km^2, about 1700 liters of runoff water per m^2 of sea surface enter the Gulf during the rainy season. The average total rainfall during the rainy season is about 162 cm (Anonymous 1958). A mean phosphate content of 0.47 μg-at PO_4-P L^{-1} (Ingham 1950); 5.0 μg-at NH_4-N L^{-1} (Menzel and Spaeth 1962), and 1.70

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[11] Coiba Island is located off the Panama coast at approximately 7°30′N, 81°45′W. Gatun Lake is part of the Panama Canal System (Fig. 1); the water was collected and analyzed at the "Miraflores Filter Plant", and is stated to be chemically similar to that discharged into the Gulf of Panama by lockages at the Panama Canal.

TABLE 20. Comparison of the accretion of PO_4-P and NO_3-N during May through December, and the requirements for these nutrients assuming a total carbon production of 90 g m^{-2} (values as g m^{-2})

	PO_4-P	**NO_3-N**	**NH_4-N**
Runoff	0.13	0.96	0.07
Rain	0.07	0.17	0.14
Σ Runoff + Rain	0.20	1.13	0.21
Required	2.25	14.00	
% of Requirement Supplied by Accretion	8.9	8.1	1.5

μg-at NO_3-N L^{-1} (Ingham 1950, Weinmann 1955) will be assumed for rain water.

Forsbergh (1963) reported that 90 g of carbon are produced m^{-2} during May through December. If one assumes the following ratio (Strickland 1960):

$$C:N:P = 40:6.5:1$$

then the production of 90 g C m^{-2} requires the assimilation of 2.25 g of PO_4-P and about 14.0 g of NO_3-N. The quantities of these nutrients entering the Gulf during this period in runoff and rain water, using the above assumptions, are given in Table 20. About 9 per cent of the phosphate requirement and about 10 per cent of the inorganic nitrogen requirement are provided through accretion. Even if this nutrient supply is considerably underestimated, regeneration within the water column must provide the bulk of the phosphate and nitrate requirements during the rainy season.

The high concentration of particulate iron in river water reported by Schaefer and Bishop (1958) is consistent with the widespread occurrence of iron in tropical lateritic soils (Mohr and Van Baren 1954). For example, the island name, Barro Colorado (located in Gatun Lake), means red clay in Spanish, and ". . . well describes the character of the soil . . ." which contains large amounts of reducible ferric oxide (Kenoyer 1929). In addition, lateritic soils contain large quantities of erodable Al_2O_3 and SiO_2 (Mohr and Van Baren 1954). This is reflected in the high silicate concentrations observed in Gatun Lake and, especially, the Coiba Island hot springs (Table 19). The mean silicate concentration is about 1100 μg-at L^{-1}. If this is assumed to be the average silicate content of river water, and the silicate introduced in the approximately 1700 liters of runoff m^{-2} of sea surface during the rainy season is distributed homogenously throughout the 40 m water column at the hydro-biological station, the average silicate concentration is 47 μg-at L^{-1}. Even if the Gatun Lake concentration of about 346 μg-at L^{-1} were used, copious quantities of silicate are still introduced during the rainy season. In contrast, Wooster and Cromwell (1958) report that dissolved silicate is not detectable in the surface waters of most of the eastern tropical Pacific. Thus, it might be that silicate is not a limiting plant nutrient in the Gulf of Panama, as suggested for particulate iron (Schaefer and Bishop 1958). These nutrients have been reported as limiting phytoplankton growth in tropical, oceanic waters (Menzel and Ryther 1961a, Menzel, Hulburt and Ryther 1963, Smayda 1964).

Burkholder and Burkholder (1958) found a considerable synthesis of B vitamins in the watershed of and within the mangrove lined tropical Bahia Fosforescente in Puerto Rico, which would appear to be in excess of phytoplankton demands there. Sufficient edaphic similarities between this small embayment and the Gulf of Panama suggest that adequate vitamin supplies might also be present in this latter region.

THE SEASONAL PHYTOPLANKTON CYCLE AT 8°45′N, 79°23′W

The sampling period has been arbitrarily divided into periods of variable length to facilitate description of the phytoplankton dynamics. Since diatoms were principally responsible for the major quantitative differences in phytoplankton abundance observed between stations and seasons, as will become apparent, general statements as to changes in phytoplankton abundance will usually refer to diatom behavior, unless stated otherwise. Similarly, diatom abundance will be frequently expressed as a percentage of the "total population", where population will represent the diatom community only. The abundance of a dominant species, when given, will be its maximum abundance observed at that station. Finally, population densities enclosed in parenthesis following a species name will represent the number of cells per liter (c/L) when used in the text proper.

Attempts to derive a quantitative index of upwelling intensity were unsuccessful. Since some index of relative upwelling intensity from station-to-station is desirable, the terms *positive* and *negative* hydrographic changes will be used. A *positive* hydrographic change will refer to an increase in upwelling intensity occurring since the previous station was sampled. A temperature decrease and/or salinity increase between stations will be considered to indicate increased upwelling. A decrease in upwelling intensity occurring between stations, i.e., a temperature increase and/or salinity decrease, will be termed a *negative* hydrographic change. Changes in wind direction and intensity will also be used as a guide for evaluating relative upwelling intensity. Hence, all statements about relative upwelling intensity are qualitative.

Since the stations were sampled at approximately 2-week intervals, the intervening upwelling pattern can also be expected to influence community abundance and thus obscure somewhat the exact relationship between hydrographic conditions and phytoplankton structure on a given sampling date. The temperature and salinity conditions in the upper 20 m at each station, as well as the total wind force at Balboa (Fig. 1) from the true north (upwelling winds) and true south for 7 and 3 days prior to sampling date are given as a guide to relating phytoplankton dynamics to environmental conditions.

Stations 1-6: 29 November 1954—22 February 1955

The temperature and salinity profiles in the upper 20 m during this period (Fig. 41) indicate a conspicuous, progressive cooling and heightened salinity accompanied the northerly, upwelling-inducing winds (Fig. 42). Only station 1 exhibited pre-upwelling conditions: a distinct halocline (mean of 27.40 ‰ in the upper 10 m, and 30.74 ‰ at 20 m) and high temperatures (28.5 to 29.0 C). Upwelling became intense at station 3 during mid-January, lessened temporarily at stations 4 and 5, and then intensified at station 6 (Fig. 41). The surface salinity by then increased 4.50 ‰ over that at station 1. Unlike salinity, temperatures in the upper 20 m were not significantly lower than pre-upwelling levels.

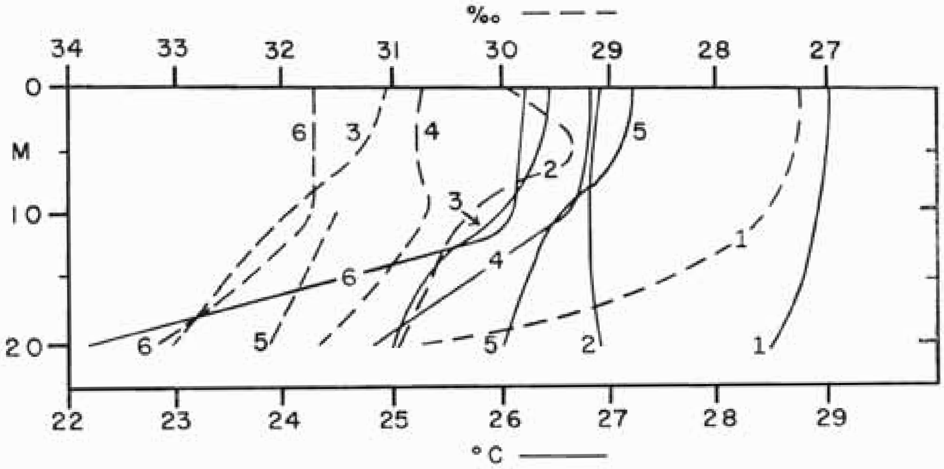

FIGURE 41. Temperature and salinity distribution in the upper 20 m at stations 1-6 (29 November 1954—22 February 1955). (—— represents the temperature isopleth; ----- represents the salinity isopleth, and values within the figure, i.e., 1, 2, etc. identify the stations.)

The temperature—salinity conditions at these stations are clearly related to the true north wind intensity for 7 days prior to the sampling dates (Fig. 42). Lower temperatures and higher salinities accompanied increasing northerly winds, as at stations 2 and 6, whereas ebbing northerly winds depressed upwelling, as at station 4 (Figs. 41, 42).

A sparse phytoplankton population characterized the pre-upwelling environment at station 1 (Table 21). A *Fragilaria* sp. dominated the surface community; it closely resembled *Fragilaria nana*, important in the Norwegian Sea (Ramsfjell 1960). This meager population persisted at station 2, sampled during late December, despite a 3-fold increase in abundance at

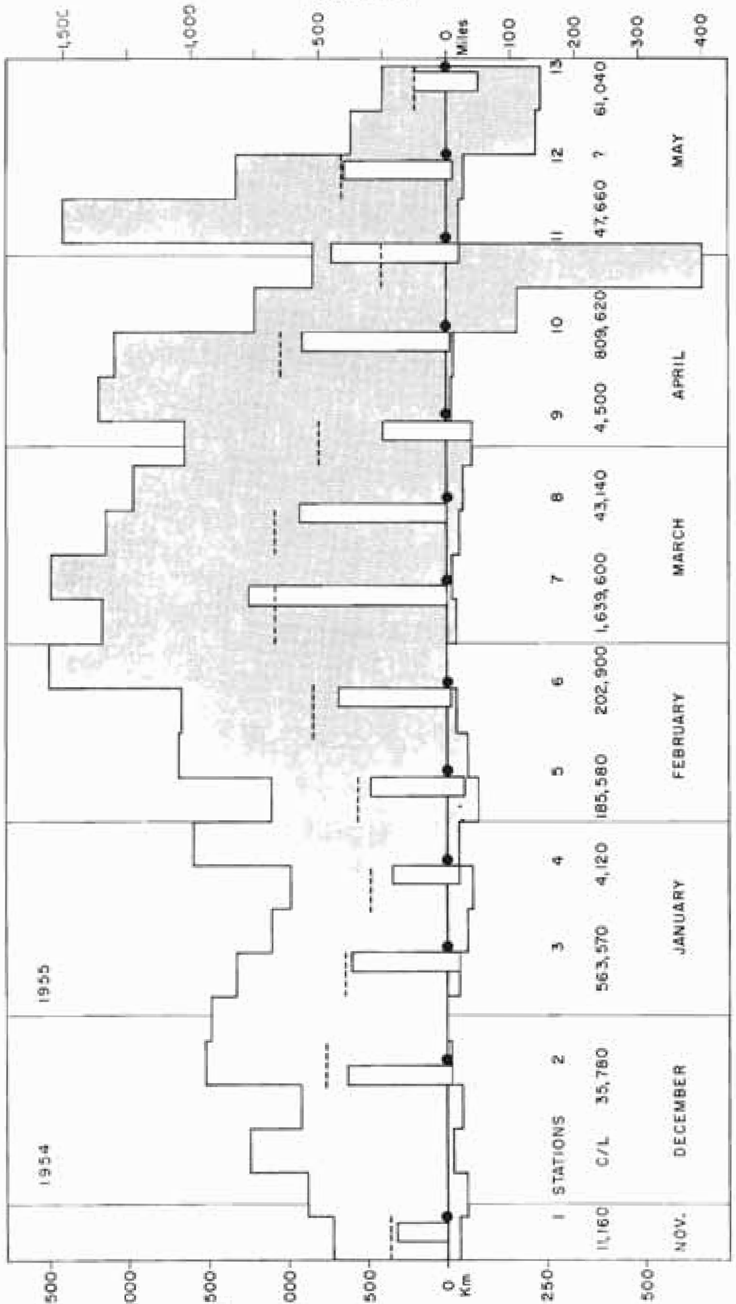

FIGURE 42. Total intensity of upwelling (offshore) winds from the true north and non-upwelling (onshore) winds from the true south recorded at Balboa for 7 days (shaded histograms) and 3 days (open histograms) prior to the sampling date (●) at stations 1 to 13 (29 November 1954 to 30 May 1955), as well as for the 7-day periods between sampling dates. The broken line, - - - -, represents the 50% level of the total upwelling winds recorded during the 7 days preceding station sampling date. The population densities given at c/L represent the maximum diatom abundance observed at that station.

TABLE 21.

Station	**1**			**2**		
Date	**29 November 1954**			**24 December 1955**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	29.00	28.89	28.50	26.89	26.78	26.89
S ‰	27.30	27.59	30.74	30.01	30.36	30.92
σ_t	16.33	16.58	19.06	19.03	19.33	19.71
O_2 % Sat.	101.5	100.0	84.4	102.6	103.7	100.0
DIATOMS (cells/liter)*	11,160	4,640	11,180	35,780	nd	10,700
DINOFLAGELLATES	6,160	1,080	1,660	1,000		840
COCCOLITHOPHORES	4,000	5,000	3,040	3,500		2,500
MONADS	6,500	6,500	36,500	4,500		8,000
TOTAL	27,820	17,220	52,380	44,780		22,040
DIATOMS:						
Ch. appendiculatus	—	—	+	3,500		—
brevis	—	—	—	7,000		+
compressus	1,000	1,500	+	5,000		—
Fragilaria sp.	6,500	—	—	1,000		—
Hemiaulus hauckii	—	—	—	4,500		—
Nitz. delicatissima	+	—	4,500	1,000		—
pacifica	—	—	—	5,000		—
Rhiz. delicatula	—	—	—	3,500		—
stolterfothii	—	1,500	+	+		2,500
Skel. costatum f. *tropicum*	—	—	+	+		2,680

* The complete phytoplankton census for each station is given in Appendix Table 2; the text tables will present the general phytoplankton community characteristics at those stations; + = less than 1,000 cells/liter; — = absent; nd = no data.

the surface (Table 21). The composition and abundance of the surface and 20 m communities differ somewhat.

An intense diatom efflorescence (Table 22; Fig. 42) accompanied heightened upwelling at station 3 (Fig. 41). The surface and 20 m populations increased approximately 10- and 55-fold, respectively, since station 2 (Table 21). *Chaetoceros compressus* (167,000) and *Ch. costatus* (235,000), comprised 42 to 50 per cent of their respective communities. As at station 2, the bottom community, where *Ch. costatus* predominated, was constituted somewhat differently. This diatom was absent at the surface and comprised only 4 per cent of the population at 10 m. A secondary chaetocerid element comprising from 4 to 10 per cent of the diatom population was also present: *Ch. brevis, constrictus, curvisetus, decipiens, didymus, laciniosus,* and *lorenzianus*. Additionally, *Nitzschia delicatissima, Rhizosolenia stolterfothii* and *Skeletonema costatum* f. *tropicum* were present, each contributing approximately 10 per cent of the total diatom standing stock.

The vertical distribution in abundance at station 3 contrasts with conditions in inshore temperate and boreal waters during the late winter or vernal augmentation. The presence of maximum populations at similar depths (20 m) in those areas usually indicates a sinking, senescent population. Yet the scarcity of resting spores, the presence of well-pigmented cells and recognizable states of cell division attest to an active community at 20 m at station 3. Furthermore, because of the intensive upwelling oc-

TABLE 22.

Station	**3**				**4**		
Date	**11 January 1955**				**25 January 1955**		
Depth (m)	**0**	**10**	**20**		**0**	**10**	**20**
°C	26.39	26.11	25.00		26.78	26.61	24.83
S ‰	31.16	31.99	33.02		30.77	30.67	31.65
σ_t	20.05	20.76	21.87		19.63	19.61	20.89
O_2 % Sat.	114.0	123.3	78.0		103.0	102.6	84.2
DIATOMS (cells/liter)	336,140	264,130	563,570		4,120	3,200	nd
DINOFLAGELLATES	2,020	3,220	1,100		200	1,620	
COCCOLITHOPHORES	2,000	1,500	1,500		3,000	1,500	
MONADS	9,000	14,500	4,000		9,000	1,000	
TOTAL	349,160	283,350	570,170		16,320	7,320	
DIATOMS:							
Ch. brevis	8,500	13,500	18,500		—	—	
compressus	167,000	101,000	54,000		—	—	
constrictus	—	+	30,000		—	—	
costatus	—	11,000	235,000		—	—	
curvisetus	4,000	1,000	26,000		—	—	
didymus	3,000	6,000	29,000		—	—	
laciniosus	34,000	—	22,500		—	—	
lorenzianus	11,000	15,000	4,500		—	—	
Nitz. delicatissima	6,500	23,000	7,500		+	1,500	
pacifica + pungens	4,660	4,900	19,500		—	—	
Rhiz. stolterfothii	10,500	27,000	24,500		—	—	
Skel. costatum f. *tropicum*	12,000	27,000	24,500		+	—	

curring, it is difficult to attribute the observed vertical distribution to sinking. The species diversity at this station is remarkable: 72 diatoms, 21 dinoflagellates and 8 coccolithophores.

An abrupt disappearance of the *Ch. compressus + costatus* dominated community, and a precipitous decline in diatom abundance to approximately 4,000 c/L characterized station 4 (Table 22; Fig. 42). Although a population decline is predictable from the reduced upwelling resulting from slackened northerly winds (Figs. 41, 42), the magnitude of this subsidence is unexpected.

A phytoplankton increase occurred during early February at station 5; the community observed at station 3 reappeared in part (Tables 22, 23). This increase since station 4 probably accompanied the intensification of northerly winds (upwelling) during late January (Fig. 42). Growth was most intense at the surface. The composition of the community in the upper 10 m differed from that at 20 m where *Rh. stolterfothii* (47,000) dominated a species-poor, monotonous population. *Ch. compressus* (23,500) and *Ch. laciniosus* (19,000) also dominated the community which differed from that at station 3 principally in its reduced abundance, the unimportance of *Ch. costatus*, and absence of many previously important secondary species (Appendix Table 2A).

Intense growth occurred in the upper 10 m at station 6 (Table 23) where heightened upwelling accompanied increasing northerly winds (Figs. 41, 42). The secondary chaetocerid element attained a density similar to

TABLE 23.

Station	**5**			**6**		
Date	**8 February 1955**			**22 February 1955**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	27.22	26.56	26.00	26.22	26.11	22.22
S ‰	—	31.52	32.07	31.76	31.76	33.17
σ_t	—	20.26	20.85	20.55	20.58	22.79
O_2 % Sat.	—	106.1	97.8	103.2	102.6	53.7
DIATOMS (cells/liter)	185,580	46,660	59,180	186,660	202,900	15,960
DINOFLAGELLATES	1,860	580	6,080	1,160	220	2,060
COCCOLITHOPHORES	3,000	500	500	1,500	1,000	500
MONADS	19,500	10,500	26,500	22,500	42,000	36,520
TOTAL	209,940	58,240	92,260	211,850	246,120	55,040
DIATOMS:						
Bact. hyalinum	+	+	—	11,000	8,000	—
Ch. brevis	2,000	6,000	—	1,500	12,000	+
compressus	23,500	9,000	—	25,000	45,000	—
decipiens	16,000	—	—	3,500	2,000	—
laciniosus	19,000	7,500	3,500	19,500	29,000	—
lorenzianus	14,500	1,500	—	1,500	3,500	+
Nitz. delicatissima	10,000	—	—	11,500	11,500	—
Rhiz. stolterfothii	22,000	12,500	47,000	48,500	17,500	5,500
Skel. costatum f. *tropicum*	1,500	+	—	31,000	24,000	—

that at station 3 (Table 22), while *Rh. stolterfothii* (48,000) and *Ch. compressus* (45,000) persisted as impoverished co-dominants. *Skeletonema costatum* f. *tropicum* and *Ch. laciniosus* were also important.

In summary, the salient feature of this sampling period is the general relationship existing between relative upwelling intensity, as inferred from the temperature-salinity conditions in the upper 20 m, and phytoplankton abundance: changes in abundance tended to parallel directly changes in upwelling intensity.

Stations 7—12; 10 March—16 May 1955

Upwelling increased considerably when station 7 was sampled; the surface salinity increased by 2.91 ‰ since station 6 while the temperature decreased from 6.5 to 7.8 C at the various depths (Fig. 43). Thereafter, upwelling slackened significantly through station 9, intensified at station 10, and then subsided through station 12 when the salinity in the upper 20 m approximated that at station 6 during late February (Fig. 41). Well-developed thermoclines were observed at stations 8 and 10 (Fig. 43). The observed station-to-station temperature and salinity fluctuations are again correlated with wind conditions (Fig. 42). The pronounced negative hydrographic change at station 11 (3 May) signaling the end of the upwelling season, reflects the reduced true north component and marked increase in winds from the true south (Fig. 42).

In summary, upwelling was more intense throughout this period than at stations 1 to 6 (Fig. 41). But following a maximum intensity on 10

TABLE 24.

Station	**7**			**8**		
Date	**10 March 1955**			**23 March 1955**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	19.44	18.28	15.72	23.39	17.83	16.78
S ‰	34.67	34.85	34.96	34.41	34.58	34.78
σ_t	24.68	25.11	26.21	23.40	25.01	25.42
O_2 % Sat.	130.7	107.5	31.1	123.7	83.6	14.5
DIATOMS (cells/liter)	1,228,840	1,639,600	153,420	43,140	nd	nd
DINOFLAGELLATES	100	1,240	160	260		
COCCOLITHOPHORES	—	1,000	—	500		
MONADS	30,500	58,500	47,500	26,000		
TOTAL	1,259,440	1,700,340	201,080	69,600		
DIATOMS:						
Bact. delicatulum	—	—	—	9,500		
Ch. densus	4,260	20,500	1,500	—		
holsaticus + pelagicus	—	—	—	26,500		
Guinardia flaccida	11,200	16,275	+	—		
Lauderia annulata	1,124,000	1,523,000	144,000	—		
Rhiz. stolterfothii	70,500	47,750	5,500	3,000		

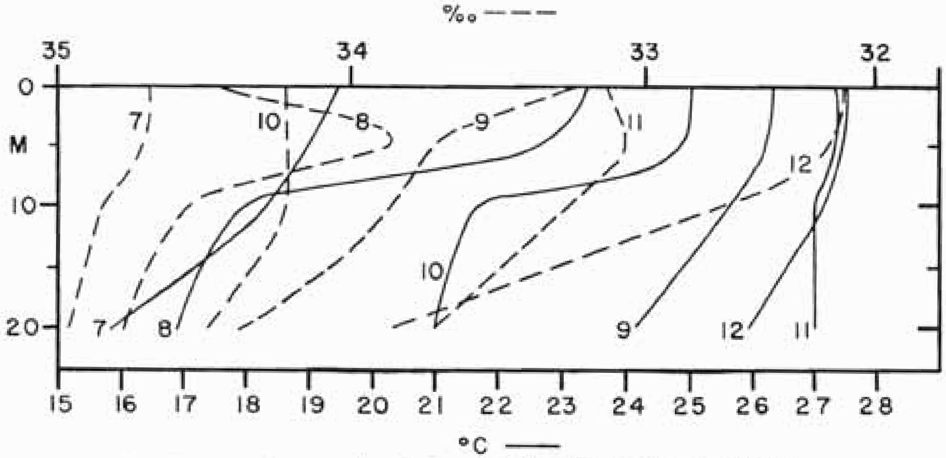

FIGURE 43. Temperature and salinity distribution in the upper 20 m at stations 7-12 (10 March—16 May 1955).

March (station 7), upwelling subsequently subsided to a level similar to the maximum intensity observed during the previous period.

The intense upwelling noted at station 7 during early March was accompanied by an enormous development of *Lauderia annulata* (1,523,000) in the upper 10 m which comprised 93 per cent of the diatom population (Table 24). Of the species previously encountered, only *Rh. stolterfothii* (70,500) attained significant growth; *Ch. compressus* disappeared as a dominant species for the remainder of the upwelling season. The observed efflorescence of *Lauderia annulata* is *not* expected from its earlier recorded performance; at station 3 it attained only 3,500 c/L. This fact, coupled with the disappearance of many other species accompanying the incursion of the dense water mass at station 7 (Fig. 43), suggests that *Lauderia annulata* may be allochthonous.

TABLE 25.

Station		**9**			**10**	
Date		**5 April 1955**			**19 April 1955**	
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	26.33	25.61	24.17	25.00	21.61	21.00
S ‰	33.21	33.86	34.34	34.20	34.22	34.51
σ_t	21.61	22.32	23.11	22.76	23.76	24.14
O_2 % Sat.	110.3	107.8	99.8	117.0	102.2	52.5
DIATOMS (cells/liter)	4,500	20	—	809,620	389,040	nd
DINOFLAGELLATES	760	220	—	680	6,540	
COCCOLITHOPHORES	—	—	—	9,500	1,500	
MONADS	12,520	14,500	25,020	59,500	53,500	
TOTAL	17,780	14,740	25,020	879,300	450,580	
DIATOMS:						
Ch. brevis	—	—	—	10,500	—	
compressus	—	—	—	18,500	14,500	
curvisetus	—	—	—	1,680	35,500	
debilis	—	—	—	10,000	10,000	
decipiens	—	—	—	13,500	2,000	
socialis	—	—	—	43,500	44,500	
Eucampia cornuta	—	—	—	57,500	29,000	
Nitz. delicatissima	—	—	—	29,000	15,500	
pacifica	—	—	—	44,000	8,000	
pungens	3,000	—	—	—	5,000	
Rhiz. delicatula	+	—	—	43,000	5,500	
fragilissima	—	—	—	48,000	3,000	
stolterfothii	1,000	—	—	427,000	182,000	
DINOFLAGELLATES:						
Peridinium granii	—	—	—	—	1,940	
minutum	—	—	—	—	940	

Pronounced warming, indicative of a subsidence in upwelling, occurred in the upper 5 m at station 8 and throughout the water column at station 9; the temperature increased approximately 4 C and from 7 to 9 C, respectively, above that at station 7 (Fig. 43). As at station 4, the phytoplankton decline to a singularly sparse population was greater than might be expected (Tables 22, 24, 25). *Lauderia annulata* disappeared, and *Rh. stolterfothii* was decimated. (Although an excessive detrital content in the 10 and 20 m samples from station 8 prevented their enumeration, a semiquantitative analysis confirmed the paucity of phytoplankton at those depths as well.)

A slight positive hydrographic change occurred at station 10 during mid-April (Fig. 43), accompanied by a substantial diatom increase (Table 25). *Rhizosolenia stolterfothii* (427,000) comprised 53 per cent of the diatom community in which an impressive number of species attained their maximum for the 1955 upwelling season:

Eucampia cornuta	57,500 c/L	*Nitzschia pacifica*	44,000
Rhizosolenia fragilissima	48,000	*Rhizosolenia delicatula*	43,500
Chaetoceros socialis	44,500	*Chaetoceros curvisetus*	35,500
	Nitzschia delicatissima 29,000		

Relative to stations 8 and 9, where marked negative hydrographic changes occurred, the community suddenly appearing at station 10 would appear

TABLE 26.

Station	**11**			**12**		
Date	**3 May 1955**			**16 May 1955**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	27.28	27.06	27.00	27.44	27.11	25.83
S ‰	33.16	33.26	33.71	32.10	32.50	33.85
σ_t	21.27	21.41	21.70	20.42	20.83	22.24
O_2 % Sat.	102.7	102.0	105.1	102.7	104.0	87.0
DIATOMS (cells/liter)	nd	47,660	680	nd	nd	nd
DINOFLAGELLATES		660	240			
COCCOLITHOPHORES		4.500	1,500			
MONADS		11,500	3,500			
TOTAL		64,320	5,920			
DIATOMS:						
Rhiz. fragilissima		22,500	—			
stolterfothii		14,000	—			

to be allochthonous. However, the *Rh. stolterfothii* maximum at station 10 (Table 25) is consistent with its continuous and increasingly abundant growth detectable during the early stages of upwelling (Tables 22, 23, 24). Its abundance therefore, is no surprise, as was the development of *Lauderia annulata* at station 7 (Table 24). The partial reappearance of the waning, heterogeneous chaetocerid element (*vide* page 423), and the presence of secondary species which can be related to previous communities, where their behavior portends subsequent increased growth, are notable. The community at station 10 appears to represent a natural successional stage evolved from that present at station 7 and during earlier phases of upwelling, rather than being foremost a community molded by a sequence of erratic hydrographic changes. The problem of species succession and sequence (Gran and Braarud 1935), and autochthonous *versus* allochthonous populations during upwelling will be considered later.

A pronounced negative hydrographic change in early May at station 11 followed a precipitous increase in southerly winds (Fig. 42). The thermal structure approximated that at station 2 in December (Figs. 41, 43), and indicated that the upwelling season had terminated. A marked decline in phytoplankton abundance occurred (Table 26).

Stations 13—16: 30 May—11 July 1955

The movement of the Tradewind—Calm Belt (Doldrums) system northward (Fig. 2) terminating the upwelling season and initiating the rainy season, first detectable at station 11 (Fig. 42), firmly established the southerly, rain-bearing winds over the Gulf of Panama now (Fig. 45). The ecological conditions accompanying the prevalence of southerly winds, coupled with a decrease in northerly winds, contrast sharply with upwelling season conditions (Figs. 42, 45). A progressive dilution and persistence of high temperatures, detectable at stations 11 and 12 (no plankton data), continued through mid-July (Fig. 44). The paucity of phytoplankton noted at station 11 persisted at stations 13 through 16, although the abundance fluctuated somewhat between stations (Tables 27, 28). The communities at these stations were characterized by rather sparse "dominant" species and a change in secondary species:

Station 13 (late May)	—	*Rhizosolenia stolterfothii*	(17,500; 29%)
Station 15 (late June)	—	*Chaetoceros compressus*	(13,500; 23%)
Station 16 (mid-July)	—	*Skeletonema costatum* f. *tropicum*	(14,500; 52%)

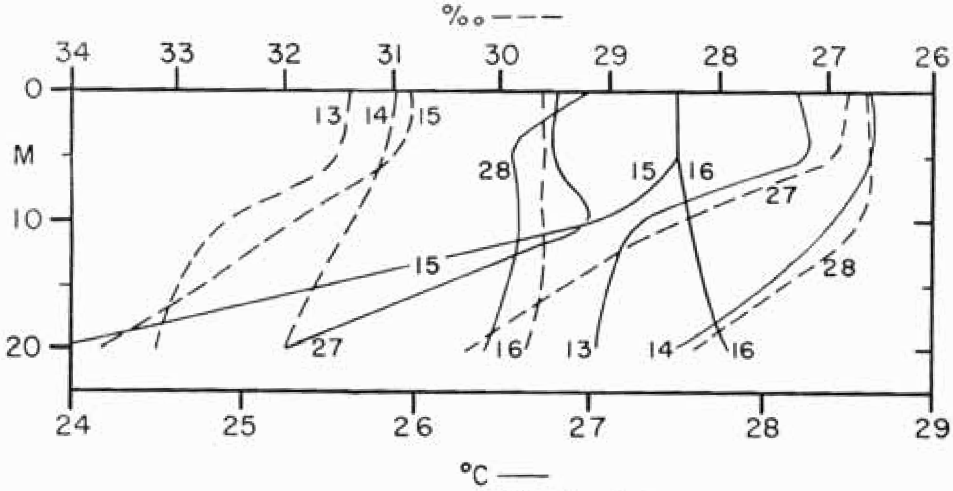

FIGURE 44. Temperature and salinity distribution in the upper 20 m at stations 13-16 (30 May—11 July 1955) and at stations 27-28 (12-26 December 1955).

Incursion of a cold, dense watermass below 10 m at station 15 accompanied a brief resurgence of northerly winds (Figs. 44, 45). At 10 m, 13,000 c/L of the coccolithophore, *Gephyrocapsa oceanica*, were found, the maximum coccolithophore abundance observed hitherto; diatoms reached only 1,500 c/L (Table 28). Plankton data are not available for 20 m; the oxygen saturation level (Table 28) suggests limited phytoplankton growth. The coccolithophores, commonly believed to be of major importance in tropical waters, have thus far been conspicuous by their numerical scarcity in the Gulf of Panama. The well-mixed water at station 16 is reflected in the vertical diatom distribution; the monads (micro-flagellates) attained their maximum concentration encountered thus far at this station (Table 28).

Synopsis of the 1955 upwelling season

The data for this period indicate that 1) the observed temperature and salinity fluctuations are generally correlated with the magnitude of northerly winds, and 2) major changes in phytoplankton abundance and composition are effected by hydrographic changes, although a natural succession occurs (Table 29).

TABLE 27.

Station		**13**			**14**	
Date		**30 May 1955**			**13 June 1955**	
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	28.17	27.28	27.06	28.56	28.39	27.50
S ‰	31.42	32.61	33.21	30.99	31.38	31.98
σ_t	19.68	20.86	21.38	19.23	19.58	20.31
O_2 % Sat.	108.5	109.6	102.8	104.0	106.2	96.3
DIATOMS (cells/liter)	nd	61,040	10,060	16,080	23,620	nd
DINOFLAGELLATES		520	20	940	—	
COCCOLITHOPHORES		—	500	1,000	1,000	
MONADS		6,500	17,000	6,500	10,000	
TOTAL		68,060	27,580	24,520	34,620	
DIATOMS:						
Bact. delicatulum		3,000	—	—	—	
hyalinum		2,500	+	4,500	+	
Ch. affinis		4,000	—	—	—	
brevis		8,500	2,000	4,500	—	
curvisetus		7,000	—	+	—	
didymus		—	—	4,500	1,500	
Rhiz. stolterfothii		17,500	6,500	+	5,000	
Skel. costatum f. *tropicum*		7,000	—	—	—	
Thal. nitzschioides		+	+	+	8,000	

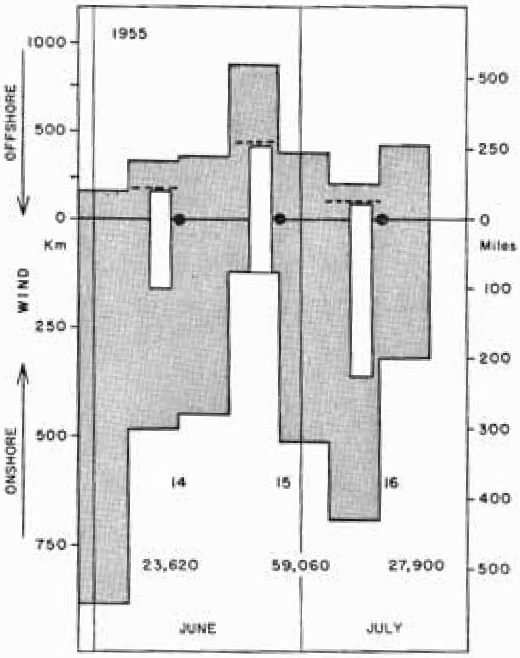

FIGURE 45. Total intensity of upwelling (offshore) winds from the true north and non-upwelling (onshore) winds from the true south recorded at Balboa for 7 days (shaded histograms) and 3 days (open histograms) prior to the sampling date (●) at stations 14-16 (13 June—11 July 1955). Otherwise, as given in the legend to Figure 42.

TABLE 28.

Station	**15**			**16**		
Date	**27 June 1955**			**11 July 1955**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	27.50	27.06	24.00	27.50	27.56	27.78
S ‰	30.86	31.95	33.72	29.59	29.58	29.75
σ_t	19.47	20.43	22.70	18.52	18.49	18.55
O_2 % Sat.	102.4	96.7	73.4	103.3	105.2	103.3
PO_4 µg at/L	nd	nd	nd	0.65	0.98	0.92
DIATOMS (cells/liter)	59,060	1,520	nd	12,200	27,900	19,840
DINOFLAGELLATES	2,540	1,020		500	2,780	5,060
COCCOLITHOPHORES	—	13,000		500	—	1,000
MONADS	36,500	16,000		4,000	60,500	64,500
TOTAL	98,100	28,540		17,200	91,180	90,400
DIATOMS:						
Ch. atlanticus	7,000	—		—	1,000	—
compressus	13,500	—		3,000	+	6,000
laevis	6,000	—		—	6,000	2,000
Fragilaria sp.	7,500	—		—	—	—
Nitz. delicatissima	4,500	—		—	—	—
Rhiz. stolterfothii	4,000	—		6,000	1,500	1,500
Skel. costatum f. *tropicum*	+	—		1,000	14,500	6,000
COCCOLITHOPHORES:						
Gephyrocapsa oceanica	—	13,000		+	—	1,000

TABLE 29. Diatom succession during the 1955 upwelling season

Stage	Period	Dominant Species	Secondary Species
I	mid-January (3)*	*Ch. compressus* *Ch. costatus*	chaetocerid element *Rh. stolterfothii* *Skel. costatum* f. *tropicum*
II	February (5-6)	*Ch. compressus* *Rh. stolterfothii*	Stage I secondary species
III	mid-March (7)	*Lauderia annulata*	*Rh. stolterfothii*
IV	mid-April (10)	*Rh. stolterfothii*	*Rh. delicatula, fragilissima* *Nitz. pacifica, delicatissima* *Eucampia cornuta* *Ch. socialis, curvisetus*

* Numerals in parentheses refer to station number

The transition between the various *phytoplankton stages* (Table 29) was abrupt. Although this partly reflects the sampling schedule, such changes can be easily related to wind conditions, especially to those during the 3-day period prior to the sampling date (Fig. 42). A significant decline in northerly winds at station 4 terminated the stage I community; the stage III community appeared after the intense upwelling following station 6 and disappeared when northerly winds ebbed significantly at stations 8 and 9; the stage IV community appeared at station 10 following a resurgence in northerly winds (Fig. 42). Thus, wind-induced hydrographic changes, especially negative ones, influence community succession during the upwelling season.

The station-to-station changes in *maximum diatom abundance* exhibit a general direct relationship with changes in northerly wind intensity. The very sparse diatom populations present at stations 4 and 9 following a period of subsiding northerly winds, and the abundant populations at stations 7 and 10 after a period of increasing northerly winds clearly demonstrate this (Fig. 42). However, although diatom populations progressively increase with northerly winds (compare stations 4 to 7), even a modest ebbing of these winds may cause a considerable decimation in abundance (stations 4, 8, 9) (Fig. 42). Also, intense upwelling, as inferred from temperature and salinity, does not necessarily sustain greater phytoplankton populations than periods of less intense upwelling. For example, the low temperatures and high salinities at station 8, indicative of intense upwelling, were accompanied by a modest diatom population, whereas the populations at stations 1 through 6 were similar to or exceeded that at station 8 despite indications of less intense upwelling (Figs. 41, 43; Tables 21 to 24).

The upwelling season had terminated when station 11 was sampled. The increased southerly wind component was accompanied by a marked decline in phytoplankton abundance terminating stage IV (Fig. 42; Table 26). A reduced phytoplankton abundance accompanied the persistent southerly winds thereafter through mid-July at station 16 (Figs. 42, 45). Phytoplankton abundance suddenly increased at station 15 during late June with a resurgence of northerly winds; further demonstration of the importance of northerly (upwelling) winds in fostering phytoplankton growth, while southerly winds retard growth.

Stations 27—34: 26 December 1955—21 March 1956

The phytoplankton samples from stations 17 through 26 (mid-July to mid-December) were lost in transit. The hydrographic conditions during this rainy period included a marked freshening of the watermass until mid-November (station 25) when the surface salinity was 21.68 ‰, or 7.91 ‰ lower than that at station 16 (Fig. 5). The surface salinity at station 27, sampled about 5 months after station 16, was only 2.77 ‰ lower.

Three hydrographically distinct conditions are distinguishable between 26 December 1955 and 21 March 1956 (Figs. 44, 46): 1) a dilute, warm watermass typical of early upwelling conditions at stations 27—29; 2) intense upwelling at stations 30, 33 and 34 when similar temperature and salinity levels occurred; and 3) a subsidence in upwelling with considerable warming of the watermass at stations 31—32. Except for station 30, the changing temperature and salinity conditions are related to the northerly (upwelling) wind behavior, as during the 1955 upwelling season (Figs. 44, 46, 47).

The 20 m diatom community at station 27 differs from that in the upper 10 m in being about 3-fold more abundant and dominated by *Skel.*

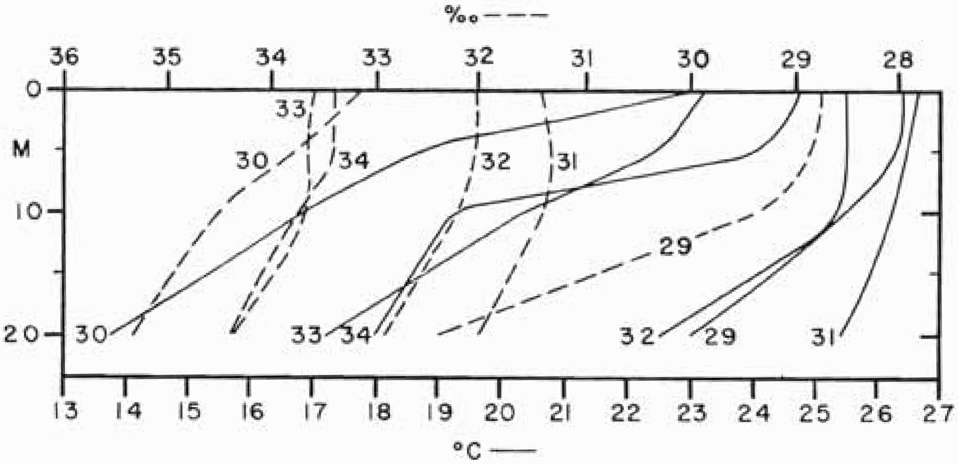

FIGURE 46. Temperature and salinity distribution in the upper 20 m at stations 29-34 (9 January—21 March 1956).

costatum f. *tropicum* (161,500; 62%) (Table 30). This suggests only gradual upwelling at this station, and that the *Skeletonema* population may be allochthonous. Otherwise, a greater abundance of this species than observed (1,500 c/L) in the upper 10 m might be expected. *Rhizosolenia stolterfothii* and a secondary chaetocerid element were present throughout the water column, as during the 1955 upwelling season (Table 22).

An abundant population persisted at station 28 despite the slight negative hydrographic change (Fig. 44) which decimated the *Skeletonema* stock and elevated *Ch. compressus* to dominancy throughout the water column (Table 30). This species, together with *Ch. laevis, Bact. elegans* and *Nitz. delicatissima*, abundant in the upper 10 m, comprised 46 per cent of the total abundance at 20 m, where *Ch. affinis* and *Rh. stolterfothii* were also important. The heterogeneous and relatively abundant coccolithophore component at station 28 is noteworthy:

Braarudosphaera sp.	1,500 c/L	*Discosphaera tubifera*	500
Coccolithus huxleyi	10,500	*Gephyrocapsa oceanica*	12,000
Coccolithus cf. *pelagicus*	500	*Halopappus adriaticus*	500
Pontosphaera maxima	500		

Gephyrocapsa oceanica was the only coccolithophore found at the surface, and co-dominated with *Coccolithus huxleyi* at the other depths.

A pronounced hydrographic change during early January at station 29 accompanying increased northerly winds (Fig. 47) stimulated intense growth of the diatom community present during December. The population increased 15- and 5-fold at the surface and 10 m, respectively; little change occurred at 20 m (Fig. 47; Table 31). The community was now characterized by *Ch. compressus* (229,000; 20%) and a resurgence of *Skel.*

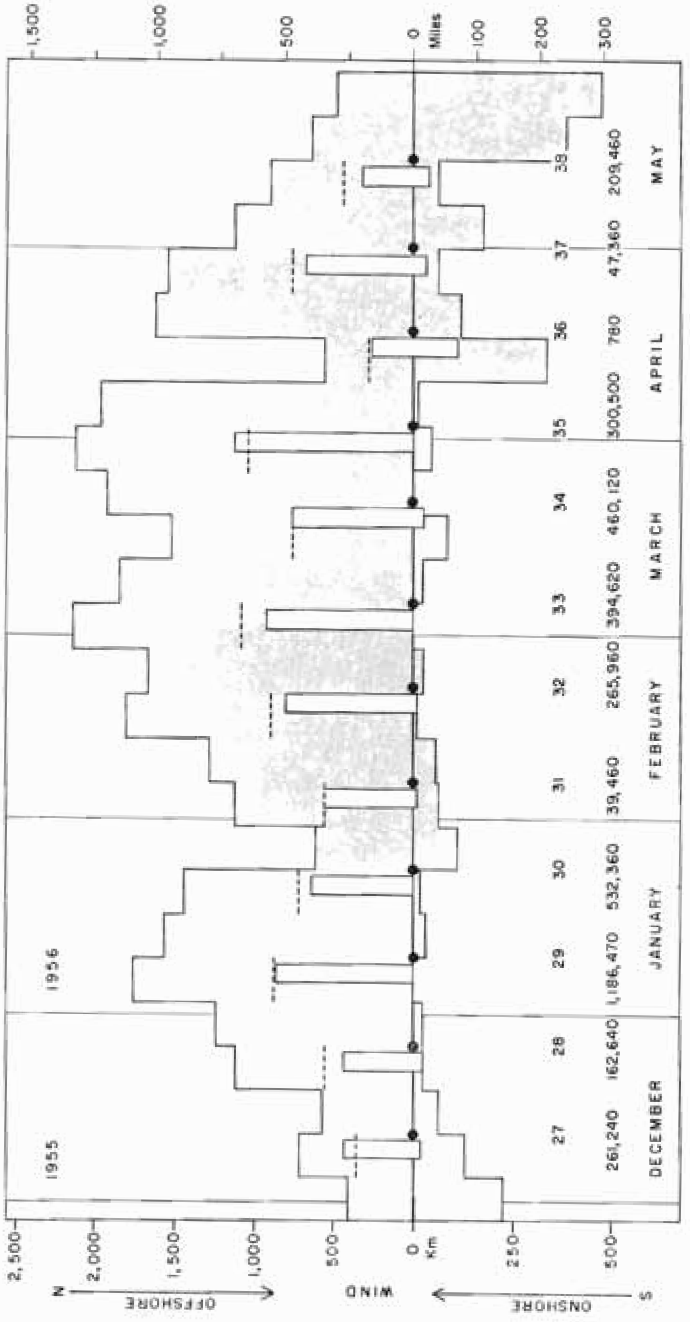

FIGURE 47. Total intensity of upwelling (offshore) winds from the true north and non-upwelling (onshore) winds from the true south recorded at Balboa for 7 days (shaded histograms) and 3 days (open histograms) prior to the sampling date (●) at stations 27-38 (12 December 1955—14 May 1956). Otherwise, as given in the legend to Figure 42.

TABLE 30.

Station	**27**			**28**		
Date	**12 December 1955**			**26 December 1955**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	26.78	27.00	25.22	27.00	26.61	26.39
S ‰	26.82	28.41	30.31	26.60	26.68	28.25
σ_t	16.67	17.80	19.77	16.44	16.62	17.87
O_2 % Sat.	102.1	103.4	86.1	104.0	104.4	105.1
PO_4 μg at/L	0.65	0.72	0.99	0.45	0.49	0.37
DIATOMS (cells/liter)	80,540	105,880	261,240	81,420	162,640	132,720
DINOFLAGELLATES	1,440	1,040	5,240	1,840	3,760	1,100
COCCOLITHOPHORES	—	—	20	12,000	9,000	18,020
MONADS	12,500	34,000	49,500	12,500	45,520	13,000
TOTAL	94,480	140,920	316,000	107,760	220,920	164,840
DIATOMS:						
Bact. elegans	+	1,600	—	8,000	17,000	6,500
hyalinum	2,880	—	—	+	4,000	—
varians	2,240	6,500	+	—	—	+
Ch. affinis	2,640	5,500	6,500	1,080	6,000	16,000
atlantidae	—	9,000	4,500	+	—	—
brevis	—	+	7,500	+	+	3,500
compressus	8,500	15,000	9,000	18,000	38,000	41,000
curvisetus	+	10,500	3,580	+	—	+
laciniosus	2,580	+	2,000	7,500	+	+
laevis	4,000	10,500	1,000	13,500	11,500	8,500
lorenzianus	2,540	2,440	+	2,460	8,000	9,000
Nitz. delicatissima	11,000	7,000	—	6,000	29,000	5,000
pacifica	—	—	—	7,000	3,500	—
pungens	—	8,000	1,500	+	—	—
Rhiz. stolterfothii	20,500	7,000	38,500	2,500	11,000	13,500
Skel. costatum f. *tropicum*	1,460	+	161,500	—	8,000	1,440
Thal. nitzschioides	1,640	1,480	2,560	1,980	12,000	2,400
DINOFLAGELLATES:						
Exuviaella baltica	—	—	2,500	+	1,500	+
COCCOLITHOPHORES:						
Coccolithus huxleyi	—	—	—	—	3,000	10,500
Gephyrocapsa oceanica	—	—	—	12,000	4,000	5,000

costatum f. *tropicum*. A *Bacteriastrum* element consisting of *delicatulum*, *elegans*, *hyalinum*, *hyalinum* var. *princeps*, and *varians* became important (2 to 7 per cent of the diatom population). These species, which appeared in December (Table 30), were also present during the early stages of upwelling during 1955. The active and important chaetocerid element characteristic of upwelling in 1955 also prevailed. The relatively sparse 1956 maximum of 36,000 c/L of *Lauderia annulata* observed at this station contrasts with its prodigious flowering during March 1955 (Table 24).

The hydrographic change at station 29 is unique in not introducing a new dominant species or otherwise significantly altering the community structure, although the following species destined to play an important role were introduced:

Chaetoceros socialis	67,500 c/L	*Leptocylindrus minimus*	5,500
Chaetoceros costatus	14,500	*Thalassiosira aestivalis*	42,500

TABLE 31.

Station		**29**			**30**	
Date		**9 January 1956**			**23 January 1956**	
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	25.44	25.33	23.06	23.06	16.83	13.72
S ‰	28.76	29.38	32.37	33.17	34.53	35.09
σ_t	18.54	19.01	21.95	22.57	25.21	26.33
O_2 % Sat.	104.4	102.7	44.7	118.2	88.2	13.1
PO_4 µg at/L	0.66	0.68	1.74	0.42	1.23	2.46
DIATOMS (cells/liter)	1,186,470	795,400	113,860	532,360	445,900	315,440
DINOFLAGELLATES	2,420	2,280	80	2,220	—	40
COCCOLITHOPHORES	8,500	5,000	1,000	8,500	—	500
MONADS	92,000	85,500	9,000	24,500	47,500	42,000
TOTAL	1,289,390	888,180	123,940	567,580	493,400	357,980
DIATOMS:						
Bact. delicatulum	23,000	16,000	—	1,000	—	—
elegans	58,000	1,000	—	—	—	—
hyalinum	84,500	35,500	—	+	+	+
varians	11,500	5,000	3,000	—	—	—
Ch. affinis	43,500	33,000	+	—	+	—
brevis	29,500	51,000	+	+	+	—
compressus	229,500	185,500	10,500	24,500	19,000	1,500
curvisetus	52,500	42,000	17,500	10,500	52,000	45,000
curvisetus rest. sp.*	—	—	—	—	150,000	79,000
decipiens	45,000	26,000	4,000	25,000	+	+
didymus	32,000	20,060	5,500	—	+	+
laciniosus	28,500	2,000	—	—	—	—
lorenzianus	32,500	28,000	—	+	+	+
socialis	67,500	5,000	—	286,500	253,000	181,000
socialis rest. sp.	—	—	—	—	2,000	2,500
Lauderia annulata	36,000	19,000	3,040	12,500	24,000	15,000
Nitz. delicatissima	67,000	14,000	3,000	6,500	—	+
pungens	—	—	—	15,000	—	+
Rhiz. delicatula	23,400	—	—	21,500	—	—
stolterfothii	29,500	44,000	12,500	58,000	9,000	10,500
Skel. costatum f. tropicum	89,500	148,000	34,000	13,500	40,500	5,500
Thal. aestivalis	42,500	8,500	—	—	17,000	18,000
Thal. frauenfeldii	24,240	6,480	1,680	2,220	4,400	7,200

* rest. sp. = resting spores

Despite intense upwelling at station 30 (the surface and 20 m salinities increased by 4.41 ‰ and 2.72 ‰, respectively, and a temperature difference of 9.3 C existed between these depths), the diatom population in the upper 10 m was halved while a 3-fold increase occurred at 20 m (Table 31). ***Skeletonema*** and ***Ch. compressus*** declined precipitously, and relinquished their dominance to ***Ch. socialis*** (286,500), introduced at station 29, which comprised 53 to 57 per cent of the diatom population at all depths. This species attained a 1955 maximum of only 44,500 c/L during mid-April (Table 25). The ***Bacteriastrum*** and chaetocerid elements declined, the major secondary species being ***Rh. stolterfothii*** and ***Ch. curvisetus.***

The dominant species at station 30 were present at station 29 (Table 31). This fact, together with the behavior of ***Rh. stolterfothii*** and ***Rh. delicatula*** between sampling dates and the persistence of species such as ***Ch. socialis*** (which appeared initially at station 29), suggests that the dominant

TABLE 32.

Station	**31**			**32**		
Date	**6 February 1956**			**21 February 1956**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	26.67	26.22	25.39	26.33	25.50	22.56
S ‰	31.39	31.39	32.01	32.02	32.24	32.91
σ_t	20.10	20.27	20.99	20.71	21.13	22.50
O_2 % Sat.	107.6	106.5	100.6	102.6	103.0	79.9
PO_4 µg at/L	0.04	0.10	0.16	0.30	0.48	0.83
DIATOMS (cells/liter)	39,460	13,140	13,300	242,060	265,960	44,380
DINOFLAGELLATES	820	1,620	2,180	4,400	11,080	4,760
COCCOLITHOPHORES	—	16,500	12,500	79,500	89,000	47,500
MONADS	40,500	29,000	31,000	61,500	54,520	28,000
TOTAL	80,780	60,260	58,980	387,460	420,560	124,640
DIATOMS:						
Ch. anastomosans	—	—	—	15,500	20,500	+
compressus	—	+	—	32,500	18,000	14,500
socialis	—	—	—	1,500	37,000	—
Fragilaria sp.	15,500	5,000	3,500	4,000	—	—
Nitz. closterium	2,000	—	—	6,500	4,000	1,000
delicatissima	2,500	2,500	4,000	9,500	7,000	1,500
Rhiz. delicatula	2,000	+	—	104,000	26,500	3,000
stolterfothii	+	+	+	28,000	59,500	10,500
Skel. costatum f. *tropicum*	6,500	1,500	5,000	11,000	54,000	3,520
COCCOLITHOPHORES:						
Coccolithus huxleyi	—	10,500	1,000	34,000	52,000	14,500
Gephyrocapsa oceanica	—	6,000	10,500	41,500	35,000	28,000

species at this latter station underwent a natural decline in abundance, notwithstanding the hydrographic disturbance. Interestingly, *Ch. compressus*, following a January maximum, also became unimportant during the 1955 upwelling season (Tables 22, 23). The large number of resting spores and increased abundance of *Ch. curvisetus* with depth suggest a declining population. *Ch. socialis* also produced resting spores.

The marked subsidence in northerly winds and upwelling at station 31 during early February (Figs. 46, 47) was accompanied by a remarkable change in community structure (Table 32). The intense development observed at station 30 ceased; the important diatoms disappeared; and below the surface coccolithophores rivaled diatoms for dominance. At 10 m *Gephyrocapsa oceanica* was subordinate to *Coccolithus huxleyi*, a situation reversed at 20 m.

Upwelling intensified with northerly winds at station 32 (Figs. 46, 47); the surface, 10 and 20 m populations increased approximately 6-, 20- and 3-fold, respectively, above the previous station levels (Table 32). The community is related to that at station 30, characterized by the importance of *Rh. delicatula, stolterfothii, Ch. compressus, socialis* and *Skel. costatum* f. *tropicum*. The restriction of *Rh. delicatula's* (104,000) dominance to the surface layers is noteworthy; at 10 m *Rh. stolterfothii* (59,500) and *Skeletonema* (54,000) co-dominated, while *Ch. compressus* (14,500) highlighted a relatively sparse population at 20 m. The coccolithophores were more abundant then at station 31, and distributed throughout the water column.

TABLE 33.

Station	**33**			**34**		
Date	**5 March 1956**			**21 March 1956**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	23.17	20.06	17.22	24.78	19.33	18.00
S ‰	33.62	33.72	34.42	33.44	33.76	34.43
σ_t	22.86	23.79	25.04	22.25	24.01	24.86
O_2 % Sat.	118.3	92.7	36.0	115.4	88.5	52.3
PO_4 µg at/L	1.18	1.66	2.69	1.39	2.08	2.81
DIATOMS (cells/liter)	394,620	176,800	109,560	460,120	253,380	7,260
DINOFLAGELLATES	11,000	18,440	120	4,640	5,960	16,060
COCCOLITHOPHORES	22,000	12,500	2,060	45,500	44,000	4,500
MONADS	16,100	54,660	5,060	8,100	26,860	16,060
TOTAL	443,720	262,400	116,800	515,360	330,200	43,880
DIATOMS:						
Ch. compressus	—	11,000	25,000	16,000	—	—
costatus	187,000	30,500	6,000	—	—	—
costatus rest. sp.	—	5,500	8,500	—	—	—
decipiens	19,000	9,500	+	+	+	—
laciniosus	6,000	10,000	2,500	—	+	—
laciniosus rest. sp.	—	—	6,000	—	—	—
socialis	—	40,500	12,000	14,000	A	—
socialis rest. sp.	—	22,500	25,000	42,000	—	—
Nitz. closterium	4,500	6,000	+	4,500	7,500	+
delicatissima	12,000	2,500	+	133,000	82,500	+
pacifica	—	+	+	9,000	—	2,000
pungens	5,000	5,000	+	8,000	10,500	+
Rhiz. delicatula	—	5,000	1,020	30,500	25,500	+
fragilissima	2,400	+	—	—	12,000	+
stolterfothii	25,000	27,000	6,000	182,500	75,000	1,000
Skel. costatum f. *tropicum*	—	+	+	5,800	9,380	—
DINOFLAGELLATES:						
Exuviaella baltica	5,500	5,000	—	1,500	2,000	2,000
Peridinium minusculum	—	+	+	—	+	2,500
COCCOLITHOPHORES:						
Coccolithus huxleyi	—	7,500	+	26,000	31,000	4,500
Gephyrocapsa oceanica	22,000	1,000	1,500	19,000	13,000	—

Upwelling further intensified with northerly winds at station 33 during early March (Figs. 46, 47). ***Rh. delicatula*** (5,000) declined, ***Skeletonema*** (740) ended its important role in the upwelling season, and coccolithophores became less abundant (Table 33). ***Chaetoceros costatus*** (187,000; 47%), which attained about 400 c/L in the upper 10 m at station 32, now dominated at the surface. (This species attained a January maximum of 235,000 c/L in 1955 [Table 22].) ***Chaetoceros costatus*** co-dominated with ***Ch. socialis*** (40,500) at 10 m, and was considerably subordinate to ***Ch. compressus*** (25,000) at 20 m. A similar change in dominant species with increasing depth was observed at station 32 (Table 32).

Upwelling slightly intensified at station 34 (Fig. 46), notwithstanding a decline in northerly winds (Fig. 47), resulting in a somewhat heightened diatom response in the upper 10 m, whereas a 16-fold decrease occurred at 20 m (Table 33). ***Chaetoceros costatus*** disappeared and ***Rh. stolterfothii*** (182,500; 40%) and ***Nitz. delicatissima*** (133,000; 30%) co-dominated; both attained their maximum abundance for the 1956 upwelling season. ***Chae-***

toceros socialis (A) persisted, and *Rh. delicatula* commenced renewed growth. Otherwise, a waning chaetocerid element persisted.

Stations 35—40: 2 April—2 July 1956

Upwelling further intensified at station 35, and then progressively declined (temperature increased and salinity decreased in the upper 20 m [Fig. 48]), with ebbing northerly and increasing southerly winds (Figs. 47, 49). The imminent termination of upwelling is apparent during mid-April at station 36 when southerly winds intensified (Fig. 47) and less than 1,000 c/L of diatoms occurred (Table 34). Surface temperatures exceeded 27 C from station 36 on, considerably above the 1956 upwelling season surface minimum of 21.56 C observed at station 35 (Table 34). The upwelling season terminated by mid-June (station 39) when the surface and 20 m salinity was 5.47 and 2.39 ‰, respectively, lower than that observed 4 weeks earlier at station 38 (Fig. 48; Tables 35, 36). A slightly denser, enriched watermass occurred at station 40 (Fig. 48; Table 36) during early July when a resurgence in northerly winds induced very slight upwelling (Fig. 49).

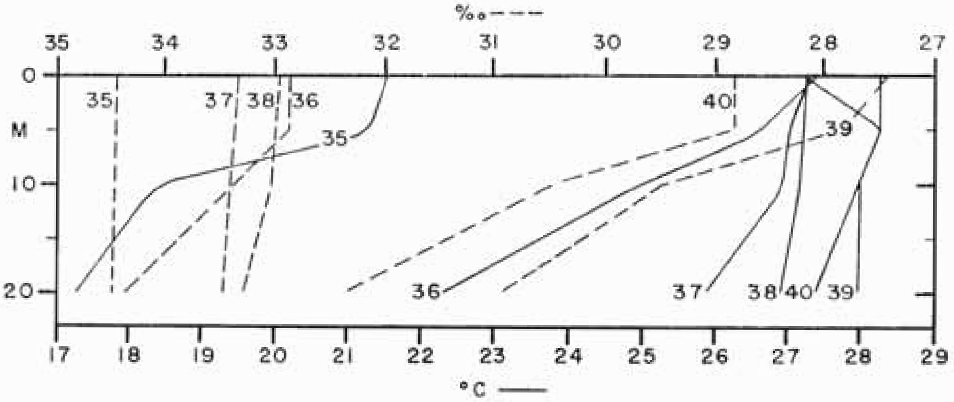

FIGURE 48. Temperature and salinity distribution in the upper 20 m at stations 35-40 (2 April—2 July 1956).

Rhizosolenia stolterfothii (174,000) was the diatom dominant at station 35, as at station 34, while *Nitz. delicatissima* declined 10-fold (Table 34). The mass occurrence of an unidentified, pigmented flagellate (1,713,000) in the upper 10 m was the most conspicuous floristic feature at this station (Table 34).

A pronounced diatom decrease to less than 800 c/L accompanied the considerable warming at station 36 (Table 34). The flagellate present at station 35 disappeared.

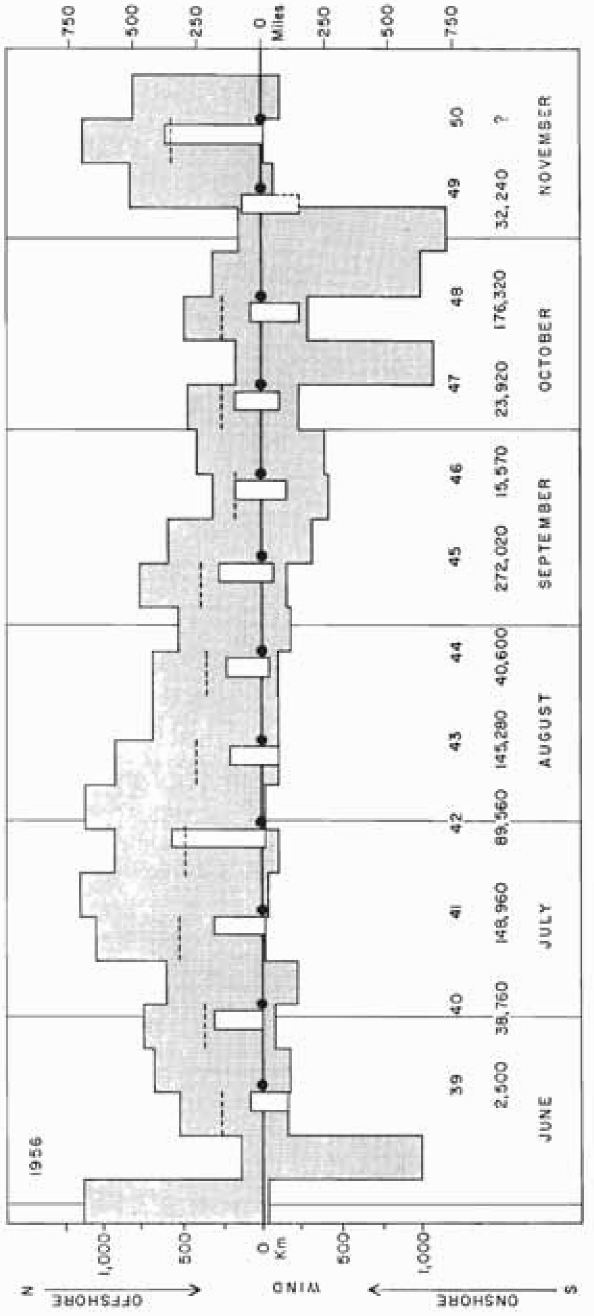

FIGURE 49. Total intensity of upwelling (offshore) winds from the true north and non-upwelling (onshore) winds from the true south recorded at Balboa for 7 days (shaded histograms) and 3 days (open histograms) prior to the sampling date (●) at stations 39-50 (19 June—19 November 1956). Otherwise, as given in the legend to Figure 42.

TABLE 34.

Station	**35**			**36**		
Date	**2 April 1956**			**17 April 1956**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	21.56	18.44	17.33	27.39	25.28	22.33
S ‰	34.43	34.43	34.51	32.83	33.29	34.37
σ_t	23.92	24.75	25.08	20.98	21.99	23.69
O_2 % Sat.	111.2	93.8	37.2	109.1	106.5	101.7
PO_4 µg at/L	0.38	0.59	2.01	0.50	0.38	0.42
DIATOMS (cells/liter)	163,240	300,500	9,980	—	240	780
DINOFLAGELLATES	280	1,200	700	40	20	—
COCCOLITHOPHORES	7,000	7,000	—	500	500	500
MONADS	911,000	1,713,000	229,500	6,000	8,000	4,500
TOTAL	1,081,520	2,021,700	240.180	6,540	8,760	5,780
DIATOMS:						
Ch. decipiens	11,500	7,000	—	—	—	—
Eucampia cornuta	+	10,000	+	—	+	—
Nitz. delicatissima	13,500	10,000	+	—	—	—
Rhiz. delicatula	2,000	35,000	+	—	—	—
fragilissima	—	6,500	—	—	—	—
stolterfothii	113,000	174,500	—	—	—	—
COCCOLITHOPHORES:						
Coccolithus huxleyi	—	1,000	—	—	—	+
Gephyrocapsa oceanica	7,000	6,000	—	+	+	—

TABLE 35.

Station	**37**			**38**		
Date	**30 April 1956**			**14 May 1956**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	27.33	26.94	25.89	27.28	27.17	26.89
S ‰	33.33	33.40	33.46	32.90	33.04	33.27
σ_t	21.38	21.56	21.93	21.07	21.21	21.47
O_2 % Sat.	111.1	111.7	109.8	105.8	106.6	106.2
PO_4 µg at/L	0.12	0.13	0.24	0.21	0.24	0.27
DIATOMS (cells/liter)	47,360	35,160	33,760	209,460	nd	nd
DINOFLAGELLATES	34,940	4,580	1,840	760		
COCCOLITHOPHORES	—	620	120	4,060		
MONADS	17,500	18,500	15,500	11,020		
TOTAL	99,800	58,860	51,220	225,300		
DIATOMS:						
Bact. hyalinum	—	—	—	11,360		
Ch. anastomosans	—	—	—	13,500		
compressus	—	—	—	10,940		
socialis	—	—	—	7,500		
Nitz. closterium	—	+	—	5,000		
delicatissima	30,000	20,500	—	15,000		
pacifica	+	—	27,000	8,500		
pungens	—	9,500	55,000	1,000		
Rhiz. alata f. genuina	11,500	3,900	+	+		
delicatula	—	—	—	69,000		
stolterfothii	—	—	—	24,500		
DINOFLAGELLATES:						
Peridinium heterospinum + *pellucidum*	15,500	—	—	—		
Prorocentrum # 33	15,500	—	—	—		

A moderate diatom population and noteworthy qualitative differences in vertical distribution characterized the well-mixed watermass at station 37 (Table 35). *Nitz. delicatissima* (30,000) dominated in the upper 10 m and

TABLE 36.

Station	**39**			**40**		
Date	**19 June 1956**			**2 July 1956**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	27.17	28.06	27.94	28.28	28.06	27.39
S ‰	27.43	29.51	30.88	28.82	30.44	32.34
σ_t	17.35	18.28	19.35	17.70	18.98	20.62
O_2 % Sat.	102.8	104.8	103.1	104.4	104.4	106.4
PO_4 µg at/L	0.19	0.10	0.22	0.39	0.42	0.57
DIATOMS (cells/liter)	nd	2,500	1,780	22,720	38,760	nd
DINOFLAGELLATES		9,640	1,020	5,740	4,100	
COCCOLITHOPHORES		—	3,500	7,500	16,020	
MONADS		12,000	7,000	16,000	26,000	
TOTAL		24,140	13,300	51,960	84,880	
DIATOMS:						
Ch. affinis		+	—	2,000	1,740	
compressus		+	—	6,500	6,500	
laevis		+	1,500	5,000	1,000	
Nitz. delicatissima		+	—	+	3,000	
Rhiz. stolterfothii		—	—	2,000	6,500	
COCCOLITHOPHORES:						
Gephyrocapsa oceanica		—	3,500	6,000	14,000	

Nitz. pacifica (27,000) at 20 m. Important subordinate species included *Rh. alata* f. *genuina* at the surface and *Nitz. pungens* var. *atlanticus* at 10 and 20 m.

Rhizosolenia delicatula (69,000) dominated at well-mixed station 38 sampled during mid-May; there were many subordinate species (Table 35). The community was similar to that at March stations 34 and 35 (Tables 33, 34). The 5-fold increase in surface diatom population (no sub-surface plankton data) may reflect the phosphate enrichment of the upper 10 m (Table 35) accompanying the reduced southerly winds (Fig. 47).

A marked dilution of the entire water column occurred at station 39 during mid-June; the upwelling season had definitely terminated. The water column was almost barren of phytoplankton (Table 36). A modest diatom response accompanied the slightly more saline and enriched water-mass at station 40 during early July when *Ch. compressus, laevis,* and *Rh. stolterfothii* reappeared (Table 36).

Synopsis of the 1956 upwelling season

Upwelling winds, except in January, were less intense in 1956 than in 1955 (Figs. 42, 47). Nonetheless, the wind—phytoplankton relationships observed during the 1955 upwelling season were also evident in 1956, although minor differences occurred.

Although an abrupt transition between the various phytoplankton stages frequently occurred, the new communities generally represented logical successive stages from their antecedents (Table 37). A marked reduction in northerly winds, coupled with increased southerly winds (Fig.

TABLE 37. Diatom succession during the 1956 upwelling season

Stage	Period	Dominant Species	Secondary Species
I	December-January (27-29)	*Skel. costatum* f. *tropicum* *Ch. compressus*	*Bacteriastrum* spp. Chaetocerid element *Rh. stolterfothii* *Nitz. delicatissima*
II	late January (30)	*Ch. socialis*	Stage I dominants *Ch. curvisetus* *Rh. stolterfothii*
III	late February (32)	*Rh. delicatula*	Stage I, II dominants *Rh. stolterfothii* Coccolithophores
IV	early March (33)	*Ch. costatus*	Stage II dominant *Rh. stolterfothii*
V	late March-early April (34-35)	*Rh. stolterfothii* *Nitz. delicatissima*	none
VI	mid-May (38)	*Rh. delicatula*	Stage V dominants

47), accompanied the abrupt withdrawal of the Stage II and Stage V communities at stations 31 and 36 respectively (Table 37). Succession of the Stage III community to Stage V was accompanied by slight periodic reductions in northerly wind intensity and associated changes in southerly winds. However, these wind fluctuations did not appear to have grossly influenced the observed phytoplankton succession. The appearance of the Stage VI community at station 38 coincided with a reduced southerly component, but without a corresponding increase in northerly winds. (Since only surface plankton data are available for station 38, however, this response cannot be properly assessed.)

The direct correlation frequently observed between changes in phytoplankton abundance and direction of change in northerly winds was not evident at stations 34, 35 and 38 (Fig. 47).

Stations 41—46: 17 July—24 September 1956

A progressive decline in the northerly winds, and a concomitant increase in the southerly, rain-bearing winds characterized this period (Fig. 49). The stations during this period of the rainy season were hydrographically similar (Fig. 50). Surface temperatures ranged from 28.1 to 28.6 C and, at 20 m, from 26.1 to 27.7 C. A halocline persisted through mid-September (station 45) accompanying the progressive dilution of the upper 10 m. A denser, homogeneous watermass at station 46 possibly resulted from mixing induced by intense southerly winds (Fig. 49).

The upper 10 m at station 41 was slightly cooler and more saline than at the previous station, reflecting the intensified northerly winds (Figs. 49, 50). Diatoms increased 4- to 5-fold with this hydrograhic change; the population at 20 m was considerably poorer (Tables 36, 38). *Skeletonema*

TABLE 38.

Station		**41**			**42**	
Date		**17 July 1956**			**31 July 1956**	
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	28.33	27.56	27.17	28.17	27.72	26.67
S ‰	29.76	29.94	32.17	29.24	30.17	32.09
σ_t	18.36	18.76	20.56	18.05	18.89	20.66
O_2 % Sat.	104.2	105.7	96.9	90.1	90.6	82.9
PO_4 µg at/L	0.37	0.43	0.57	0.44	0.45	0.48
DIATOMS (cells/liter)	129,280	148,960	49,500	89,560	67,800	25,280
DINOFLAGELLATES	3,800	9,620	5,780	5,260	7,180	2,520
COCCOLITHOPHORES	14,500	18,500	6,500	1,520	9,600	8,000
MONADS	20,500	16,000	19,500	22,000	51,000	14,500
TOTAL	168,080	193,080	81,280	118,340	135,580	50,300
DIATOMS:						
Bact. hyalinum	9,000	5,500	2,500	1,400	—	+
Ch. compressus	26,000	48,500	13,000	4,140	18,500	2,500
diversus	10,000	—	—	—	—	—
holsaticus	16,000	5,500	2,500	—	—	—
laciniosus	—	4,000	5,000	5,860	2,500	+
laevis	4,000	7,500	1,000	15,500	+	+
Nitz. delicatissima	3,000	3,000	—	7,000	2,500	+
Rhiz. delicatula	3,500	+	—	1,120	—	6,500
stolterfothii	—	+	—	+	6,000	3,500
Skel. costatum f. *tropicum*	36,500	54,000	22,500	31,500	18,000	4,000
COCCOLITHOPHORES:						
Coccolithus huxleyi	—	—	+	—	4,500	—
Gephyrocapsa oceanica	12,500	14,000	5,500	1,500	3,500	5,000

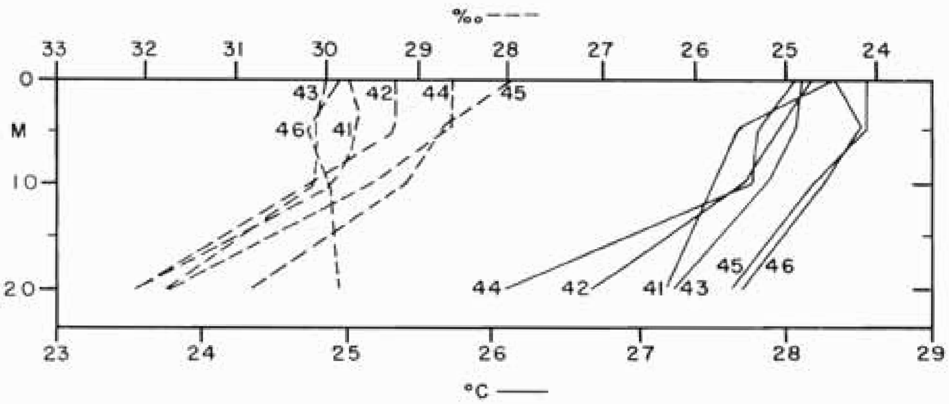

FIGURE 50. Temperature and salinity distribution in the upper 20 m at stations 41-46 (17 July—24 September 1956).

(54,000) and *Ch. compressus* (48,500) dominated, accompanied by a rudimentary chaetocerid and *Bacteriastrum* spp. component (Table 38). The occurrence of the *Skeletonema* + *Ch. compressus* association and the secondary *Chaetoceros* + *Bacteriastrum* component parallels a similar response noted during the early stages of upwelling (Tables 29, 37). A modest coccolithophore population was present.

TABLE 39.

Station		**43**			**44**	
Date		**13 August 1956**			**27 August 1956**	
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	28.11	27.89	27.22	28.11	27.78	26.11
S ‰	30.01	30.13	31.81	28.58	29.49	31.76
σ_t	18.64	18.80	20.27	17.57	18.36	20.58
O_2 % Sat.	105.9	104.0	96.7	100.9	101.3	88.4
PO_4 μg at/L	0.35	0.71	0.81	0.67	0.68	0.97
DIATOMS (cells/liter)	17,280	145,280	nd	40,600	32,780	10,300
DINOFLAGELLATES	1,000	3,120		3,620	3,500	620
COCCOLITHOPHORES	1,000	2,500		2,500	500	2,500
MONADS	42,000	48,500		14,000	11,500	19,000
TOTAL	61,280	19,940		60,720	48,280	32,420
DIATOMS:						
Bact. elegans	—	—		3,080	+	—
hyalinum	2,500	44,500		+	—	—
Ch. compressus	2,000	32,000		4,860	1,200	—
decipiens	+	+		1,500	1,740	—
diversus	—	7,500		+	—	—
laevis	1,000	5,000		2,160	—	—
lorenzianus	+	+		1,760	3,520	—
Hemiaulus sinensis	—	8,000		+	+	—
Nitz. delicatissima	4,000	7,500		1,760	—	3,500
pungens	2,000	—		+	1,500	+
Rhiz. stolterfothii	1,000	7,500		2,300	7,500	+
Skel. costatum f. *tropicum*	—	7,000		3,500	3,500	+

The population decreased approximately 30 to 50 per cent at station 42 coincident with superficial dilution (Table 38). *Skeletonema* and *Ch. compressus* persisted as dominants, although the latter was subordinate to *Ch. laevis* at the surface. Coccolithophores declined.

By mid-August (station 43) *Bact. hyalinum* var. *princeps* (44,500; 31%) supplanted *Skeletonema* as co-dominant with *Ch. compressus* (32,500) of an otherwise unmodified community (Table 39). All components declined at station 44 during late August with further superficial dilution and warming (Table 39).

Skeletonema (81,000; 30%) and *Ch. compressus* (68,000) dominated anew during the mid-September augmentation observed at station 45; numerous subordinate species occurred (Table 40). The chaetocerid element, excepting *Ch. lorenzianus*, differed from that active during upwelling, whereas *Bact. elegans* was also important then. The hydrographic and nutrient conditions provide no clue for the observed increased growth at station 45, notwithstanding the increased northerly winds (Fig. 49). Equally perplexing, the well-mixed, enriched watermass at station 46 (Fig. 50) supported little plankton at the surface and, inferentially, throughout the water column (Table 40). The augmentation at station 45, therefore, would appear to be 2 weeks premature.

TABLE 40.

Station	45			46		
Date	11 September 1956			24 September 1956		
Depth (m)	0	10	20	0	10	20
°C	28.56	28.17	27.61	28.33	28.28	27.67
S ‰	27.98	29.13	30.83	29.85	29.97	29.85
σ_t	16.98	17.96	19.41	18.45	18.56	18.66
O_2 % Sat.	104.6	101.1	100.7	104.1	102.9	103.9
PO_4 µg at/L	nd	0.57	0.59	1.01	0.77	1.27
DIATOMS (cells/liter)	127,140	272,020	nd	15,570	nd	nd
DINOFLAGELLATES	2,040	160		160		
COCCOLITHOPHORES	—	6,000		1,500		
MONADS	11,500	14,500		9,500		
TOTAL	140,680	292,680		26,730		
DIATOMS:						
Bact. elegans	12,120	8,000		2,000		
Ch. affinis	1,920	24,000		1,000		
compressus	8,000	68,000		1,500		
didymus	2,140	16,500		1,040		
laevis	10,500	19,500		5,000		
lorenzianus	9,000	17,000		1,470		
socialis	10,500	3,500		—		
Nitz. delicatissima	15,000	5,000		—		
Skel. costatum f. *tropicum*	18,520	81,000		+		

Stations 47—52: 8 October—17 December 1956

Progressive dilution occurred at stations 47 through 49 during a period of intense, rain-bearing southerly winds (Figs. 20, 49, 51; Table 6). Salinity then increased markedly at station 50 with increased northerly winds, which persisted at stations 51 and well-mixed 52 (Figs. 49, 51, 52). The temperature at 20 m at station 47 was 27.89 C (Table 41). Progressive cooling occurred through station 51 where the incursion of colder water reduced the temperature further to 23.62 C at 20 m (Fig. 51). Station 52 became considerably warmer.

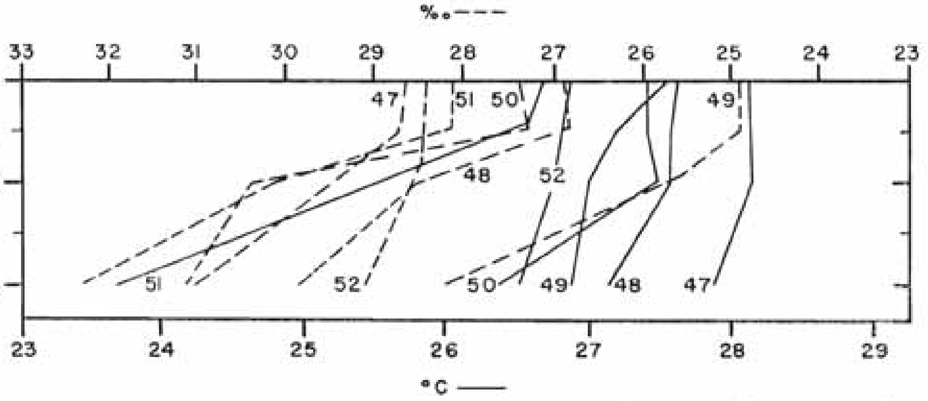

FIGURE 51. Temperature and salinity distribution in the upper 20 m at stations 47-52 (8 October—17 December 1956).

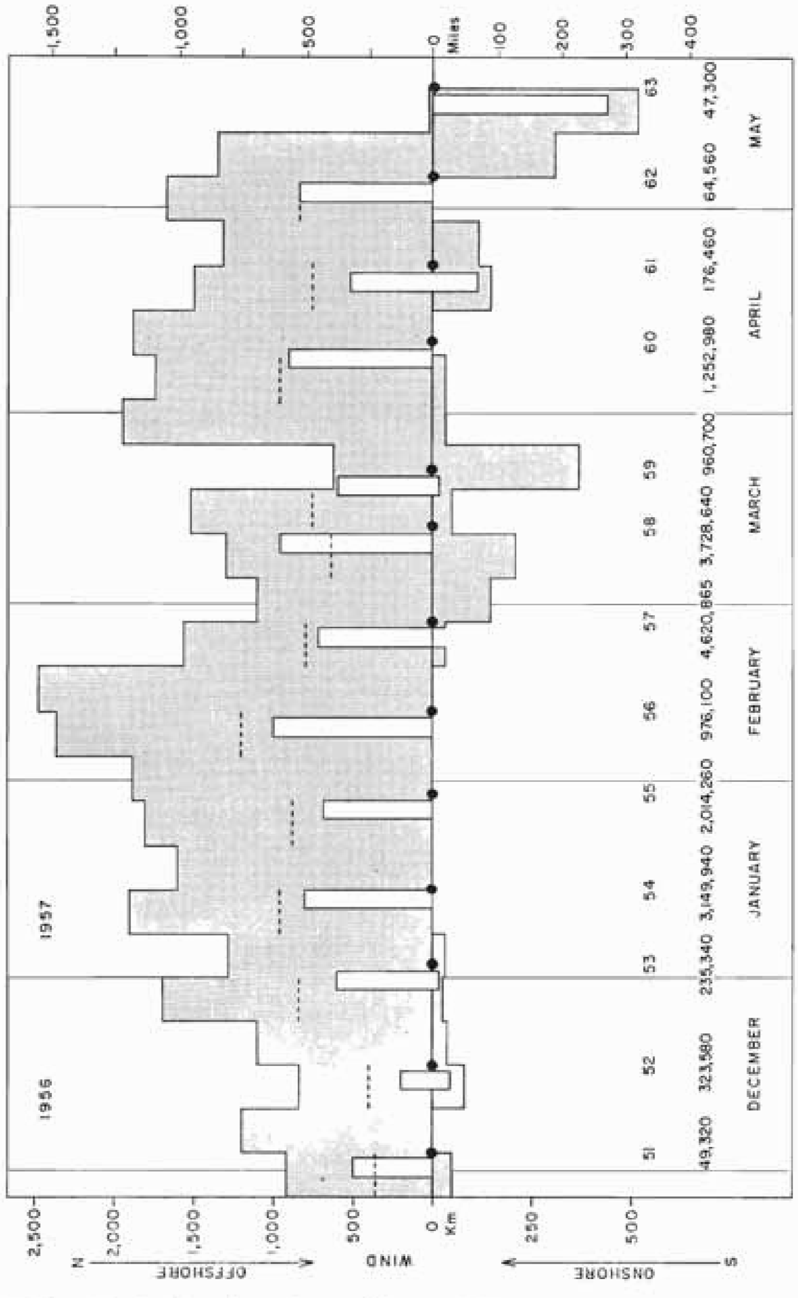

FIGURE 52. Total intensity of upwelling (offshore) winds from the true north and non-upwelling (onshore) winds from the true south recorded at Balboa for 7 days (shaded histograms) and 3 days (open histograms) prior to the sampling date (●) at stations 51-63 (3 December 1956—20 May 1957). Otherwise, as given in the legend to Figure 42.

TABLE 41.

Station	**47**			**48**		
Date	**8 October 1956**			**22 October 1956**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	28.11	28.17	27.89	27.61	27.56	27.11
S ‰	28.66	29.36	31.02	26.85	28.48	29.85
σ_t	17.63	18.13	19.47	16.44	17.67	18.84
O_2 % Sat.	100.4	100.7	104.0	97.6	103.4	94.8
PO_4 μg at/L	0.23	0.22	0.32	0.21	0.57	0.71
DIATOMS (cells/liter)	23,920	11,260	780	49,440	176,320	14,300
DINOFLAGELLATES	1,640	3,100	2,120	2,820	1,740	1,620
COCCOLITHOPHORES	6,000	4,500	3,540	—	—	—
MONADS	21,500	19,000	18,500	17,000	21,000	7,000
TOTAL	53,060	37,860	24,940	69,260	199,060	22,920
DIATOMS:						
Bact. elegans	+	+	—	8,500	8,000	—
hyalinum	—	—	—	+	11,000	+
Ch. affinis	2,480	4,500	—	1,800	+	+
compressus	1,500	+	—	+	25,500	+
laciniosus	+	—	—	2,300	1,420	+
laevis	3,500	+	—	4,000	1,000	+
lorenzianus	+	+	—	6,500	14,000	+
socialis	2,300	—	—	—	2,000	—
Nitz. closterium	2,000	+	—	1,000	1,000	1,000
delicatissima	3,000	—	—	2,500	3,000	+
pacifica	1,000	1,000	—	7,500	21,000	+
Rhiz. delicatula	+	—	—	2,500	+	—
stolterfothii	+	+	—	2,500	14,500	5,000
Skel. costatum f. *tropicum*	—	+	+	3,460	58,000	1,000

The importance of increased northerly winds to phytoplankton growth during the rainy season is clearly demonstrated by events at stations 48 to 50. Sub-surface phosphate reserves increased approximately 2.5-fold at station 48 after a considerable ebbing of the southerly winds and a concomitant increase in northerly winds (Fig. 49; Table 41). Then, significantly reduced phosphate concentrations accompanied (Tables 41, 42) the return to typical rainy season wind conditions at station 49, i.e., intensification of southerly winds (Fig. 49). A pronounced resurgence of northerly winds at station 50 then greatly increased the phosphate concentrations (Fig. 49; Table 42). The extensive dilution at station 48 completely obscured the northerly wind-induced hydrographic changes responsible for the increased phosphate levels. The observed inverse relationship between salinity and phosphate at this station might have been (erroneously?) explained as an instance of nutrient accretion with runoff, were the wind data ignored in the analysis.

The hydrographic data during this period also demonstrate the transition from intense rainy season to early upwelling conditions.

A heterogeneous, sparse phytoplankton community occurred at station 47 during early October (Table 41). ***Skeletonema*** (58,000; 33%) dominated the community at station 48, where phosphate increased at 10 m (Table 41). ***Chaetoceros compressus*** (25,500) and ***Nitz. pacifica*** (21,000) domi-

TABLE 42.

Station	**49**			**50**		
Date	**8 November 1956**			**19 November 1956**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**15**
°C	27.67	27.00	26.83	27.39	27.44	26.33
S ‰	24.88	25.76	28.23	27.36	30.33	30.37
σ_t	14.95	15.81	17.71	16.89	19.10	19.47
O_2 % Sat.	97.7	89.1	74.8	100.0	93.9	91.4
PO_4 µg at/L	0.37	0.03	0.15	0.98	1.38	1.33
DIATOMS (cells/liter)	32,240	14,720	22,280	nd	nd	nd
DINOFLAGELLATES	3,940	1,660	1,600			
COCCOLITHOPHORES	—	4,000	—			
MONADS	5,000	—	1,000			
TOTAL	41,180	20,380	24,880			
DIATOMS:						
Ch. affinis	5,300	1,400	+			
compressus	2,200	+	11,500			
decipiens	3,000	1,400	+			
Rhiz. stolterfothii	3,500	+	+			
Skel. costatum f. *tropicum*	2,640	2,360	4,300			
Thal. nitzschioides	1,480	2,360	1,400			

nated the secondary component which comprised many species which persisted during the rainy season: *Rh. stolterfothii, Ch. lorenzianus, Bact. elegans, Bact. hyalinum* var. *princeps.*

The population declined at station 49 (most pronounced at 10 m [Table 42]) with extensive dilution and phosphate reduction associated with increased southerly winds (Figs. 49, 51). (Plankton data are not available for station 50 where a cooler, phosphate-enriched watermass accompanied increased northerly winds [Figs. 49, 51; Table 42].) A modest diatom response, dominated by *Ch. compressus* (22,500), occurred at station 51 during early December (Table 43) where the hydrographic conditions would appear to have been even more favorable for phytoplankton growth (Fig. 51).

Favorable environmental conditions persisted at station 52 (mid-December) where extensive phytoplankton growth was in progress (Table 43). The 1957 upwelling season appears to have commenced at this station. *Chaetoceros compressus* (122,000; 37%), recognizable as the pioneer dominant of the 1955 and 1956 upwelling seasons (Tables 29, 37), dominated in the upper 10 m. *Skeletonema* (30,500), usually co-dominant during this stage, characterized a less abundant 20 m community. Interestingly, a similar predominance of *Skeletonema* at this depth during the early stages of upwelling was observed during December 1955 (Table 30). Numerous subordinate species were present: *Ch. lorenzianus, laciniosus, laevis, Bact. elegans,* and *Rh. delicatula.* Of these species, present during the rainy season in varying densities, only *Ch. laevis* failed to achieve greater abundance now. *Rhizosolenia delicatula* and *Ch. laciniosus*, important during the 1956 upwelling season, were especially inactive during the rainy season.

TABLE 43.

Station	**51**			**52**		
Date	**3 December 1956**			**17 December 1956**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**25**
°C	26.67	25.72	23.62	26.83	26.72	26.00
S ‰	28.09	30.12	32.29	28.38	28.45	29.49
σ_t	17.66	19.47	22.51	17.83	17.91	18.91
O_2 % Sat.	103.2	89.2	54.8	115.1	109.4	96.6
PO_4 μg at/L	0.82	0.97	1.72	0.90	0.81	1.37
DIATOMS (cells/liter)	49,320	35,020	29,340	323,580	181,480	88,880
DINOFLAGELLATES	600	4,060	1,080	4,620	5,640	1,980
COCCOLITHOPHORES	5,500	1,500	2,500	7,040	10,000	1,600
MONADS	20,500	15,500	7,500	27,500	15,000	22,000
TOTAL	75,920	56,080	40,420	362,740	212,120	114,460
DIATOMS:						
Bact. elegans	+	+	—	22,000	19,500	—
Ch. compressus	22,500	6,500	3,500	122,000	71,000	22,500
laciniosus	+	+	+	21,500	3,500	+
laevis	1,400	1,620	+	14,500	9,000	1,000
lorenzianus	1,420	+	+	33,000	21,000	+
sp.	4,000	2,000	2,000	32,000	7,000	—
Nitz. closterium	+	+	7,500	1,000	1,000	4,000
delicatissima	3,500	4,000	2,500	10,500	8,500	4,000
pacifica	+	—	+	13,000	3,000	7,500
Rhiz. delicatula	—	—	—	14,000	5,500	1,000
stolterfothii	4,500	+	+	11,500	14,500	5,000
Skel. costatum f. *tropicum*	+	12,500	2,720	3,780	2,360	30,500
Pennate sp.	5,000	2,500	2,000	11,500	9,000	2,500
DINOFLAGELLATES:						
Exuviaella baltica	—	1,000	—	1,000	3,500	1,000
COCCOLITHOPHORES:						
Coccolithus huxleyi	1,000	+	—	2,000	3,500	1,000
Gephyrocapsa oceanica	3,500	1,000	1,500	3,500	3,000	—

Synopsis of the 1956 rainy season

A significant decline in northerly wind intensity and a concomitant increase in southerly winds during May and June (Figs. 42, 45, 47, 48) signaled the termination of the upwelling season. (An inverse relationship exists between northerly and southerly wind intensity throughout the year.) A progressive increase in rain-bearing southerly winds to their maximum intensity during October and November, coupled with increased dilution of the watermass, characterizes the rainy season (Figs. 5, 21, 49). An important ecological consequence is that the retardation and eventual cessation of upwelling is accompanied by an increased southerly component which holds in place the turbid, warm, diluted and nutrient-impoverished surface waters (Figs. 5, 6, 23, 24, 28, 29). These conditions progressively extend deeper into the water column, and hinder flushing and admixture with more fertile waters.

The general decline in phytoplankton abundance during May and June was followed by an augmented diatom community induced by the temporary, but characteristic, resurgence of northerly winds during July (Figs. 3, 42, 49). Accordingly, at station 15 during 1955 (Fig. 42; Table 28) and station 41 during 1956 (Fig. 49; Table 38) *Skel. costatum* f. *tropicum* and *Ch. compressus* reappeared to dominate a community similar in composition to that of Stage I of the upwelling season. However, there was no detectable succession of this community during the 1956 rainy season. Rather, Stage I persisted throughout this season exhibiting a series of minor pulses, as at stations 45, 48, and 51 (Tables 40, 41, 43), usually in response to resurging northerly winds (Fig. 49). The chaetocerid element (*Ch. affinis, diversus* and *laevis*) which persisted was somewhat more abundant than during upwelling, while *Bact. elegans* and *Bact. hyalinum* var. *princeps* approximated abundance during upwelling.

Phytoplankton abundance decreases during the rainy season. The direct relationship between northerly winds and phytoplankton density generally observed during the 1955 and 1956 upwelling periods occurs during the rainy season, i.e., increasing northerly winds lead to higher maximum populations, whereas a population decline accompanies wind subsidence (Fig. 49). Station 43 appears to be at variance with this relationship, yet a response consistent with the general trend is obtained if the mean population density in the upper 10 m, rather than maximum diatom density, is used.

Termination of the 1956 rainy season and a gradual transition to upwelling conditions accompany the increased northerly winds at stations 50 to 52 (Figs. 49, 52). The upwelling season commenced at this latter station where *Ch. compressus* dominated the upwelling pioneer Stage I community (Tables 29, 37).

These general events suggest that nutrient limitation prevents significant phytoplankton growth during most of the rainy season. Population augmentation appears to be dependent on increased phosphate supplies accompanying slight upwelling or wind-induced mixing with nutrient-rich bottom water. Similarly, increased phytoplankton growth during the initial upwelling phase appears to be primarily a response to increased nutrient concentrations, since the thermal conditions are as yet not significantly different from those during the rainy season. Finally, the Stage I community initiating the upwelling season appears to be an autochthonous one responding to improved growth conditions after having persisted through the rainy season, rather than being introduced in the upwelled waters.

Stations 53—58: 2 January—12 March 1957

The progressive cooling and increase in salinity accompanying increased northerly winds during mid-November and December (Fig. 51) continued during this period (Figs. 52, 53). A homogeneous salinity distribution occurred in the upper 20 m at stations 56 to 58, despite a pronounced thermocline. The hydrographic data suggest that upwelling was most pronounced at station 57 during late February, following a period of very intense northerly winds (Fig. 52).

TABLE 44.

Station	**53**			**54**		
Date	**2 January 1957**			**14 January 1957**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	26.8	26.7	25.9	26.1	25.6	22.1
S ‰	29.00	28.90	30.50	30.24	32.23	34.07
σ_t	18.30	18.26	19.70	19.45	21.09	23.51
O_2 % Sat.	117.4	112.6	80.0	107.5	62.4	18.3
PO_4 µg at/L	1.19	1.65	1.93	1.15	2.24	2.93
DIATOMS (cells/liter)	235,340	177,560	nd	542,280	3,149,940	133,440
DINOFLAGELLATES	1,000	40		1,060	80	—
COCCOLITHOPHORES	—	—		—	500	—
MONADS	5,500	5,000		6,000	5,000	9,500
TOTAL	241,840	182,600		549,340	3,155,520	142,940
DIATOMS:						
Ast. japonica	—	—		+	74,000	+
Bact. elegans	12,500	7,000		65,000	23,000	+
hyalinum	20,000	11,500		6,000	4,500	—
varians	26,000	14,500		—	3,500	—
elegans + varians	4,000	28,000		—	—	—
Ch. affinis	+	1,000		12,000	6,500	+
compressus	43,000	29,000		78,000	44,000	11,000
compressus rest. sp.	—	—		—	6,500	1,000
costatus	—	—		—	142,500	+
costatus rest. sp.	—	—		—	2,500	+
curvisetus	+	+		9,000	233,000	3,020
curvisetus rest. sp.	—	—		—	13,500	+
decipiens	—	+		18,000	23,000	+
laevis	9,000	8,000		12,500	2,000	+
lorenzianus	+	+		28,000	12,000	+
socialis	3,000	8,000		—	21,500	—
sp.	—	—		32,500	9,500	—
Eucampia cornuta	+	—		+	42,000	+
Lauderia annulata	—	—		+	30,000	+
Nitz. closterium	1,000	1,000		4,500	44,000	—
delicatissima	1,000	8,000		14,500	51,000	—
pacifica	12,500	7,500		—	—	—
pungens	9,000	5,500		—	—	—
pacifica + pungens	—	—		39,500	139,000	—
Rhiz. delicatula	32,500	—		42,000	20,500	+
fragilissima	13,500	6,000		6,000	7,000	—
stolterfothii	31,000	25,500		40,000	77,000	+
Skel. costatum f. *tropicum*	2,500	4,000		73,000	1,930,000	101,000

The community at station 53 evolved from that at station 52, the surface population having declined (Table 44). The reduced *Ch. compressus* (43,000; 18%) stock vied with *Rh. stolterfothii* and *Rh. delicatula* for dominance. *Bact. elegans, hyalinum* var. *princeps* and *varians* were important.

A precipitous diatom increase occurred during mid-January at station 54 (Table 44) where *Skel. costatum* f. *tropicum* (1,930,000) comprised 61 per cent of the population at 10 m; only 4,000 c/L were found at the previous station. Conspicuous, less intense increases were achieved by *Ch. costatus* and *Ch. curvisetus*; only *Bact. elegans* of that genus remained important. A considerably lower population density occurred at the surface where *Skeletonema* (73,000) co-dominated with *Ch. compressus* (78,000); a monotonous *Skeletonema* stand dominated at 20 m.

TABLE 45.

Station	**55**			**56**		
Date	**29 January 1957**			**11 February 1957**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	25.2	23.1	19.1	24.5	23.7	19.0
S ‰	nd	nd	34.04	32.88	32.75	33.33
σ_t	nd	nd	24.28	21.91	22.05	23.77
O_2 % Sat.	nd	nd	37.3	116.9	127.8	68.7
PO_4 µg at/L	0.80	0.60	2.18	0.22	0.26	1.42
DIATOMS (cells/liter)	319,960	2,014,260	1,526,400	976,100	882,080	224,480
DINOFLAGELLATES	2,180	180	20	840	10,220	120
COCCOLITHOPHORES	—	—	—	—	—	—
MONADS	5,000	55,000	2,000	12,100	24,580	8,020
TOTAL	327,140	2,069,440	1,528,420	989,040	916,880	232,620
DIATOMS:						
Ch. affinis	+	+	—	35,000	+	+
brevis	10,500	12,000	—	56,000	32,500	19,000
compressus	104,500	142,000	—	55,000	46,500	—
costatus	48,000	100,000	36,500	20,500	1,680	—
curvisetus	12,000	21,000	38,500	9,000	23,000	+
curvisetus rest. sp.	—	—	3,000	—	—	—
lorenzianus	44,000	+	—	46,500	14,000	7,000
socialis	—	95,000	17,500	89,000	67,500	38,500
socialis rest. sp.	—	—	8,500	—	—	—
sp.	—	96,000	9,500	29,000	15,000	6,000
Eucampia cornuta	+	239,000	25,000	16,000	40,000	15,000
Leptocylindrus minimus	3,500	157,000	93,000	40,500	131,500	9,500
Nitz. closterium	2,500	84,000	16,000	13,000	13,000	10,000
delicatissima	9,500	79,000	7,000	15,000	4,500	2,500
pacifica + *pungens*	12,500	94,000	+	40,000	19,500	22,000
Rhiz. delicatula	11,000	91,000	18,500	225,000	196,000	22,500
fragilissima	14,000	7,000	—	30,500	19,500	7,000
stolterfothii	33,500	92,000	21,000	164,000	198,500	25,500
Skel. costatum f. *tropicum*	—	532,000	1,068,000	48,500	31,000	29,000
Thal. aestivalis	—	134,000	122,000	8,500	5,000	5,000

The population declined in the upper 10 m at station 55, but increased 12-fold at 20 m (Table 45). *Skeletonema* disappeared from the surface community, dominated by *Ch. compressus* (104,500; 33%), but dominated (532,-

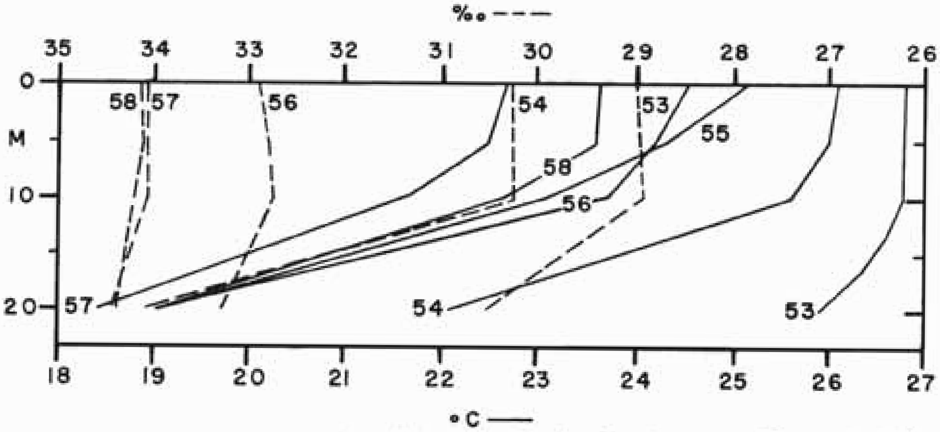

FIGURE 53. Temperature and salinity distribution in the upper 20 m at stations 53-58 (2 January—12 March 1957).

000; 26%) a heterogeneous community at 10 m which included *Ch. socialis* and *Thalassiosira aestivalis*. *Skeletonema* (1,068,000) also dominated at 20 m where only *Thal. aestivalis*, of the secondary species, approached its abundance at 10 m; *Ch. compressus* was absent.

Upwelling further intensified during mid-February at station 56 (Figs. 52, 53). Diatoms increased 3-fold at the surface; a significant decrease occurred at the greater depths. *Rh. delicatula* and *Rh. stolterfothii* dominated in the upper 10 m; *Leptocylindrus minimus* remained significant (Table 45).

A pronounced efflorescence of *Eucampia cornuta* (4,213,670) accompanied the incursion of phosphate-rich water at station 57 during late February (Table 46). This was the greatest observed density of any species during the investigation. The community was otherwise characterized by the *Rhizosolenia* dominants observed at the previous stations, an increased *Nitz. delicatissima*, *pacifica* + *pungens* association, and the virtual disappearance of the previously important dominant and secondary species (Tables 45, 46).

The hydrographic conditions at stations 57 and 58 during mid-March were similar (Fig. 53), suggesting only a slight, if any, hydrographic change. Yet, *Eucampia cornuta* disappeared completely, replaced by *Nitz. pacifica* + *pungens* (1,987,000) and *Nitz. delicatissima* (1,339,000). An abundant *Rhizosolenia* association persisted. The factors responsible for this floristic change remain obscure. However, the wind data indicate a significant increase in southerly winds in the sampling interval between stations 57 and 58 (Fig. 52). Furthermore, a significant phosphate increase occurred in the upper 10 m at the latter station. The wind and phosphate data suggest, then, an environmental change not revealed by the temperature and salinity data, which might have contributed to the observed events.

Stations 59—63: 21 March—20 May 1957

Upwelling waned and terminated during this period. The watermass progressively warmed, whereas the salinity through station 62 approximated that at station 58 (Fig. 54). The upwelling season terminated at station 63 when a decrease in salinity of about 2.0 ‰ and a further rise in temperature accompanied a pronounced increase in southerly winds (Fig. 52).

An abundant but moribund *Nitzschia* community continued at the surface at station 59 (Table 47). Otherwise, this station was barren, probably because of the pronounced wind change at that time (Fig. 52).

A prodigious *Rh. stolterfothii* (953,000; 85%) development characterized the upper 10 m at station 60 during mid-April (Table 47). Its frequent associate, *Rh. delicatula*, was considerably less abundant at 10 m and absent from the surface. *Ch. curvisetus* and *socialis*, last observed at station 56 (Table 45), and *Eucampia cornuta* at station 57 (Table 46), reappeared as

TABLE 46.

Station		**57**			**58**	
Date		**25 February 1957**			**12 March 1957**	
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	22.7	21.6	18.4	23.6	22.7	19.2
S ‰	34.07	34.04	34.38	34.11	34.20	34.41
σ_t	23.34	23.62	24.81	23.11	23.36	24.54
O_2 % Sat.	94.6	112.4	49.1	114.1	78.9	48.9
PO_4 μg at/L	0.08	0.10	2.71	0.33	1.06	2.15
DIATOMS (cells/liter)	4,620,865	2,331,700	441,820	3,728,640	1,097,240	20,940
DINOFLAGELLATES	4,920	41,500	1,880	13,720	11,700	6,600
COCCOLITHOPHORES	11,500	2,000	—	—	—	—
MONADS	5,500	77,000	13,500	1,000	8,500	4,500
TOTAL	4,642,785	2,452,200	457,200	3,743,360	1,117,440	32,040
DIATOMS:						
Cerataulina bergonii	19,500	40,000	17,500	+	—	—
Eucampia cornuta	4,213,670	2,058,000	369,500	—	—	—
Nitz. delicatissima	30,195	10,000	3,500	1,339,000	660,000	3,500
pacifica + pungens	92,465	9,000	8,500	1,987,000	321,000	15,000
Rhiz. delicatula	122,655	89,000	1,500	171,000	33,000	+
stolterfothii	107,560	116,000	24,500	122,000	43,000	1,500
Thal. aestivalis	2,500	—	7,500	100,000	38,000	—
DINOFLAGELLATES:						
Exuviaella baltica	1,000	22,000	1,000	+	—	—
vaginula	—	—	—	4,000	3,000	—
Oxytoxum variabile	+	1,500	—	—	5,000	+
Peridinium globulus var. *ovatum*	+	3,420	+	—	—	—
COCCOLITHOPHORES:						
Coccolithus huxleyi	6,500	—	—	—	—	—
Gephyrocapsa oceanica	5,000	1,500	—	—	—	—

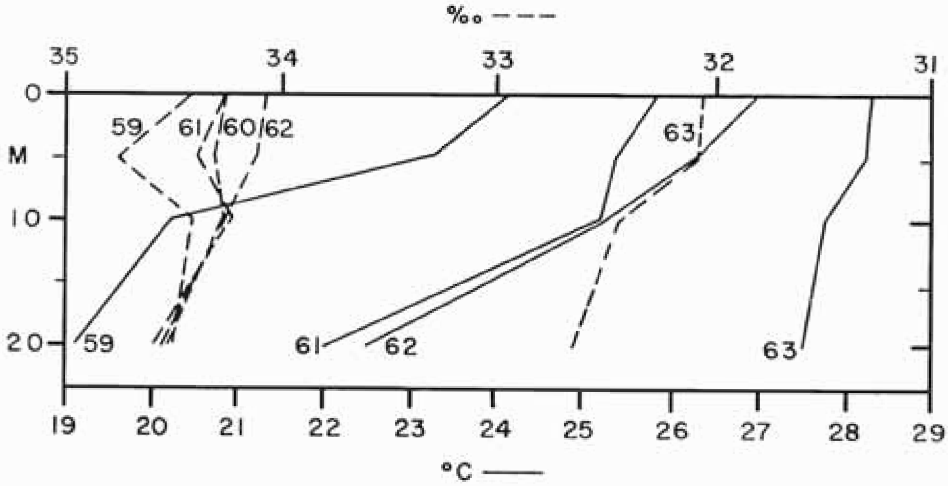

FIGURE 54. Temperature and salinity distribution in the upper 20 m at stations 59-63 (21 March—20 May 1957).

TABLE 47.

Station		**59**			**60**	
Date		**21 March 1957**			**10 April 1957**	
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	24.1	20.3	19.1	24.4	nd	22.6
S ‰	34.40	34.40	34.49	34.23	34.27	34.52
σ_t	23.18	24.25	24.63	22.96	nd	23.70
O_2 % Sat.	128.9	99.0	50.5	138.4	136.7	42.4
PO_4 µg at/L	0.14	0.41	2.25	nd	nd	nd
DIATOMS (cells/liter)	960,700	1,020	3,160	1,252,980	1,124,600	7,000
DINOFLAGELLATES	—	2,000	340	5,140	1,720	100
COCCOLITHOPHORES	500	500	—	—	—	—
MONADS	1.500	1,000	500	33,020	11,000	3,500
TOTAL	962,700	4,520	4,000	1,291,148	1,137,320	10,600
DIATOMS:						
Ch. curvisetus	—	—	—	29,500	20,500	+
socialis	—	—	—	129,000	15,500	—
sp.	—	—	—	26,500	8,500	—
Eucampia cornuta	—	—	—	92,000	53,360	+
Nitz. delicatissima	223,890	—	1,000	8,000	—	—
pacifica + pungens	724,350	—	—	23,000	8,000	1,500
Rhiz. delicatula	6,500	—	—	—	59,000	+
stolterfothii	3,000	—	—	916,000	953,000	2,000
DINOFLAGELLATES:						
Peridinium trochoideum	—	1,840	+	—	—	—

important secondary species. Neither the efflorescence of *Rh. stolterfothii*, nor its restriction to the upper 10 m, can be related to the seemingly unchanged hydrographic conditions However, northerly winds decreased considerably during the 3-week interval between sampling dates (Fig. 52).

Despite similar hydrographic conditions at stations 60 and 61 (Fig. 54), a considerably reduced *Rh. stolterfothii* population occurred at the latter station (Table 48). *Nitz. pacifica + pungens* (61,000) and *Rh. delicatula* (121,500) dominated at the surface and 10 m, respectively.

Notwithstanding increased northerly winds, the population was sparse at station 62 during early May; *Thal. aestivalis* (29,500) and *Rh. stolterfothii* (18,500) dominated (Table 48).

A meager population dominated by a *Rhizosolenia + Nitzschia* association (Table 49) accompanied the dilution and warming induced by southerly winds at the well-mixed station 63 when the 1957 upwelling season had terminated.

Synopsis of the 1957 upwelling season

Intense upwelling winds (Fig. 52) characterized the first half of the 1957 upwelling season. The northerly wind intensity during December approximated 1955 levels, and increased through mid-February to exceed considerably the 1955 and 1956 intensities observed during this same period (Figs. 42, 47, 52). During March a low barometric pressure area de-

TABLE 48.

Station	**61**			**62**		
Date	**22 April 1957**			**6 May 1957**		
Depth (m)	**0**	**10**	**20**	**0**	**10**	**20**
°C	25.8	25.2	22.0	26.9	25.2	22.5
S ‰	34.25	34.23	34.60	34.07	34.25	34.52
σ_t	22.36	22.72	23.94	22.06	22.81	23.73
O_2 % Sat.	132.8	134.1	98.4	116.9	120.3	63.6
PO_4 µg at/L	nd	nd	nd	0.36	0.55	2.63
DIATOMS (cells/liter)	107,120	176,460	1,880	19,160	64,560	1,120
DINOFLAGELLATES	4,800	16,580	680	580	7,760	40
COCCOLITHOPHORES	500	—	—	—	500	—
MONADS	8,000	26,500	26,500	5,500	28,500	8,500
TOTAL	120,420	219,540	29,060	25,240	101,320	9,660
DIATOMS:						
Nitz. pacifica + pungens	61,000	5,500	+	—	4,500	1,000
Rhiz. delicatula	26,500	121,500	+	3,000	1,500	—
fragilissima	—	+	—	4,000	1,240	—
stolterfothii	16,500	22,500	+	4,500	18,000	—
DINOFLAGELLATES:						
Exuviaella baltica	4,000	12,500	—	+	+	—

TABLE 49.

Station	**63**		
Date	**20 May 1957**		
Depth (m)	**0**	**10**	**20**
°C	28.3	27.7	27.5
S ‰	32.05	32.43	32.63
σ_t	20.11	20.58	20.81
O_2 % Sat.	109.6	116.9	111.5
PO_4 µg at/L	0.05	0.02	0.14
DIATOMS (cells/liter)	47,300	25,340	2,700
DINOFLAGELLATES	1,040	1,220	80
COCCOLITHOPHORES	—	—	—
MONADS	19,120	1,020	11,020
TOTAL	67,460	27,580	13,800
DIATOMS:			
Nitz. delicatissima	11,000	10,500	1,000
Rhiz. delicatula	3,500	2,120	—
fragilissima	4,000	1,240	+
stolterfothii	16,500	2,560	+

veloped north of the Isthmus of Panama (Anonymous 1957) which resulted in increased southerly winds and a concomitant collapse in northerly wind intensity (Fig. 52). These relatively weak northerly upwelling winds contrast with March 1955 and 1956 conditions when they attained their maximum upwelling season intensity (Figs. 42, 47). A resurgence in upwelling winds occurred during April (Fig. 52), a month when northerly winds subsided during 1955 and 1956 (Figs. 42, 47).

A conspicuous diatom succession (Table 50) accompanied the progressive increase in northerly winds from December through mid-February (stations 52 to 56): *Ch. compressus* → *Skeletonema costatum* f. *tropicum* → *Rh.*

TABLE 50. Maximum populations of the most important diatoms from 17 December 1956 through 20 May 1957, stations 52—63 (cells/10 ml) (+ = less than 1)

Date	**17-XII**	**2-I**	**14-I**	**29-I**	**11-II**	**25-II**	**12-III**	**19-III**	**10-IV**	**22-IV**	**6-V**	**20-V**
Station	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**
Ch. compressus	1,220	430	780	1,420	550	—	—	—	—	—	3	2
Skel. costatum f. *tropicum*	305	40	19,300	10,680	485	60	35	35	—	2	1	3
Ch. costatus	—	—	1,425	1,000	205	—	—	—	265	—	3	2
curvisetus	—	32	2,330	385	230	—	—	—	295	3	2	3
Bact. hyalinum var. *princeps*	—	200	60	54	26	—	—	—	—	—	—	8
varians	—	260	35	—	20	—	—	—	—	—	—	—
elegans	220	125	650	—	—	—	—	—	—	—	—	4
Thal. aestivalis	—	—	910	1,340	85	75	1,000	10	—	—	295	—
Lept. minimus	—	—	—	1,570	1,315	15	—	—	—	—	—	—
Ch. socialis	40	80	215	950	890	—	—	—	—	—	—	—
Rhiz. delicatula	140	325	420	910	2,225	1,226	1,710	65	590	1,215	30	35
stolterfothii	145	310	770	920	1,980	1,160	1,220	30	9,530	225	180	165
Eucampia cornuta	+	+	420	2,390	400	42,136	—	—	920	1	3	5
Nitz. delicatissima	105	80	510	790	150	302	13,390	224	40	165	15	110
pacifica+pungens	130	215	1,390	940	400	925	19,870	724	230	610	45	18

stolterfothii + *delicatula*. The first two species are recognized as dominants of the Stage I community of previous upwelling seasons, while *Rh. stolterfothii* and *Rh. delicatula* characterized the February Stage II community in 1955 and 1956, respectively (Tables 29, 37). A remarkably heterogeneous secondary component accompanied *Skeletonema's* dominance (Table 50).

Following station 56, the weekly northerly wind-product increased further and then subsided significantly during late February at station 57 (Fig. 52). The net hydrographic consequence was the incursion of a denser, enriched watermass (Fig. 53) which undoubtedly influenced community organization at station 57. Nonetheless, the mass occurrence of *Eucampia cornuta*, the virtual disappearance of the previously declining *Chaetoceros*, *Skeletonema* and *Bacteriastrum* species, and the persistence of an active *Rhizosolenia* + *Nitzschia* association at this station, are consistent with the observed trend of succession (Table 50).

The mid-March dominance of the *Nitzschia* component and persistence of the *Rhizosolenia* species during a resurgence of northerly winds likewise appear to be a natural succession, although the precipitous disappearance of *Eucampia cornuta* is unexpected. A significant subsidence in upwelling winds at station 59 (Fig. 52) and a marked attenuation in diatom abundance coincided. Hitherto in 1957, negative hydrographic changes were not observed to influence community organization and abundance, an effect frequently observed during the 1955 and 1956 upwelling seasons. Resurgence of northerly winds during mid-April elevated *Rh. stolterfothii* to dominance; it was succeeded by *Rh. delicatula*. The upwelling season ended by mid-May (station 63).

Unlike the previous upwelling and rainy seasons, the maximum diatom populations (or the mean in the upper 10 m) during the 1957 upwelling

TABLE 51. Maximum monthly diatom abundance as c/L (nd = no data)

Month	1955	1956	1957
Jan.	563,570	1,186,470	3,149,940
Feb.	202,900	265,960	4,620,865
Mar.	1,639,600	460,120	1,097,240
Apr.	809,620	300,500	1,124,600
May	61,040	209,460	64,560
June	59,060	2,500	
July	27,900	148,960	
Aug.	nd	145,280	
Sept.	nd	272,020	
Oct.	nd	176,320	
Nov.	nd	32,440	
Dec.	261,240	323,580	

season appeared to be related to neither the weekly nor the 3-day northerly wind-product (Figs. 42, 45, 47, 49, 52). Perhaps the seemingly natural succession associated with the virtual absence of disruptive negative hydrographic influences accounts for this discrepancy.

SUMMARY AND QUALITATIVE ASPECTS OF PHYTOPLANKTON GROWTH AT 8°45′N, 79°23′W

The annual diatom cycle

Maximum diatom abundance occurred during the upwelling season, although annual variations occurred, with especially dense populations characterizing 1957 (Table 51). Considerable annual variations in the maximum diatom abundance occurred during various months. A pronounced decline in diatom abundance accompanied the cessation of upwelling during May 1955 and 1957, and June 1956. Data for a complete rainy season, available only for 1956, indicate, however, that sizeable populations occurred during each month except during June, as noted previously, and during the height of the rainy season in November.

Of the approximately 175 diatom species identified (Appendix Table 3), the dynamics of only 25 species were primarily responsible for the main features of the annual diatom cycle (Table 52). Of these, *Ch. compressus, Nitz. delicatissima, Rh. delicatula, Rh. stolterfothii* and *Skel. costatum* f. *tropicum* usually dominated a distinct succession of communities occurring during the upwelling season (Table 53). Observations during the rainy season (made only in 1956) suggest that diatom succession ceases upon termination of upwelling in May. A diatom community similar to that during the early phases of upwelling then appears and persists throughout the rainy season (Tables 36, 38 to 43).

A remarkable similarity in diatom community succession occurred despite annual and weekly differences in the rate and periods of upwelling.

TABLE 52. Maximum monthly abundance of major diatoms observed from January, 1955 to May, 1957 (cells/liter; + = less than 500 c/L; nd = no data)

DIATOMS	YEAR	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
Chaetoceros compressus													
	1955	167,000	23,500	—	18,500	1,000	13,500	6,000	nd	nd	nd	nd	41,000
	1956	229,500	32,500	25,000	—	10,940	+	48,500	32,000	68,000	25,500	11,500	122,000
	1957	142,000	55,000	—	—	+							
Skeletonema costatum f. *tropicum*													
	1955	27,000	31,000	—	—	3,500	—	14,500	nd	nd	nd	nd	161,500
	1956	148,000	54,000	880	1,500	660	560	54,000	7,000	81,000	58,000	4,300	30,500
	1957	1,930,000	48,500	3,500	+	+							
Bacteriastrum delicatulum													
	1955	6,500	6,000	9,500	3,000	3,000	—	—	nd	nd	nd	nd	8,000
	1956	23,000	5,500	+	—	2,000	—	4,000	2,500	—	—	—	—
	1957	—	1,500	—	—	640							
Bacteriastrum elegans													
	1955	—	—	—	—	500	620	+	nd	nd	nd	nd	17,000
	1956	58,000	1,220	+	—	—	—	—	3,080	12,120	8,500	+	22,000
	1957	65,000	—	—	560	+							
Bacteriastrum hyalinum													
	1955	5,000	11,000	2,000	—	5,460	6,000	—	nd	nd	nd	nd	4,000
	1956	84,500	1,080	+	—	11,360	—	9,000	44,500	3,000	11,000	780	+
	1957	20,000	+	—	1,260	+							
Bacteriastrum varians													
	1955	1,000	—	—	—	—	—	—	nd	nd	nd	nd	6,500
	1956	11,500	—	—	—	—	—	—	—	4,500	+	—	—
	1957	26,000	+	—	—	—							
Chaetoceros costatus													
	1955	235,000	3,500	—	—	—	—	—	nd	nd	nd	nd	—
	1956	14,500	+	187,000	—	1,600	—	1,100	860	—	+	—	—
	1957	142,000	20,500	—	26,500	+							
Chaetoceros curvisetus													
	1955	26,000	+	+	35,500	7,000	+	+	nd	nd	nd	nd	10,500
	1956	52,500	3,880	11,000	—	+	—	1,500	600	1,320	1,420	1,340	+
	1957	233,000	23,000	—	29,500	+							

TABLE 52 (continued)

DIATOMS	YEAR	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
Chaetoceros affinis													
	1955	800	7,000	+	720	4,000	1,560	500	nd	nd	nd	nd	16,000
	1956	43,500	1,180	+	+	4,240	—	3,780	1,480	24,000	4,500	5,300	2,260
	1957	12,000	35,000	+	4,800	+							
Chaetoceros brevis													
	1955	13,500	12,000	+	10,500	8,500	4,500	—	nd	nd	nd	nd	7,500
	1956	51,000	1,000	840	8,000	+	—	2,000	+	640	+	+	540
	1957	12,000	56,000	—	1,120	580							
Chaetoceros socialis													
	1955	—	—	5,000	44,500	1,500	—	—	nd	nd	nd	nd	—
	1956	286,500	37,000	40,500	—	7,500	—	1,000	1,500	10,500	2,300	—	4,000
	1957	95,000	89,000	—	129,000	—							
Chaetoceros laevis													
	1955	2,500	7,500	2,000	—	5,000	6,000	6,000	nd	nd	nd	nd	13,500
	1956	8,000	3,000	—	—	+	1,500	15,500	7,500	19,500	4,000	—	14,500
	1957	12,500	—	—	—	1,500							
Chaetoceros laciniosus													
	1955	34,000	29,000	—	6,000	1,500	1,500	—	nd	nd	nd	nd	7,500
	1956	28,500	+	10,000	4,000	1,240	—	5,860	940	720	2,300	+	21,500
	1957	4,000	3,500	—	—	—							
Chaetoceros decipiens													
	1955	6,000	16,000	+	13,500	+	—	—	nd	nd	nd	nd	1,520
	1956	45,000	1,780	19,000	11,500	1,480	+	740	1,740	2,500	580	3,000	+
	1957	23,000	+	—	960	+							
Chaetoceros lorenzianus													
	1955	15,000	14,500	+	1,000	500	2,860	1,500	nd	nd	nd	nd	9,000
	1956	32,500	1,700	+	+	+	+	2,280	3,520	17,000	14,000	1,520	33,000
	1957	44,000	46,500	—	+	900							
Lauderia annulata													
	1955	6,500	+	1,523,000	5,500	+	—	—	nd	nd	nd	nd	+
	1956	36,000	+	+	+	+	—	+	—	+	—	+	+
	1957	30,000	1,220	+	1,100	—							

TABLE 52 (continued)

DIATOMS	YEAR	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
Eucampia cornuta													
	1955	3,500	3,000	9,000	69,000	500	+	—	nd	nd	nd	nd	6,500
	1956	19,000	1,880	4,000	10,000	540	—	+	+	+	+	+	+
	1957	239,000	4,213,670	—	92,000	520							
Rhizosolenia delicatula													
	1955	2,000	9,500	1,500	43,000	1,500	1,500	1,500	nd	nd	nd	nd	7,000
	1956	23,400	104,000	30,500	35,000	69,000	—	6,500	1,720	1,500	2,500	+	14,000
	1957	91,000	222,500	171,000	121,500	3,500							
Leptocylindrus minimus													
	1955	10,500	6,500	—	14,500	—	—	—	nd	nd	nd	nd	—
	1956	5,500	5,500	+	—	—	—	—	—	—	—	—	—
	1957	157,000	131,500	—	—	—							
Thalassiosira aestivalis													
	1955	—	—	—	—	—	—	—	nd	nd	nd	nd	—
	1956	42,000	—	4,000	—	—	—	+	—	—	—	—	—
	1957	134,000	131,500	—	—	—							
Nitzschia closterium													
	1955	500	2,000	—	—	—	—	—	nd	nd	nd	nd	2,000
	1956	7,000	6,500	7,500	3,500	5,000	—	3,000	1,500	500	2,000	500	7,500
	1957	84,000	13,000	1,000	2,500	1,000							
Nitzschia delicatissima													
	1955	23,000	11,500	3,500	29,000	—	4,500	—	nd	nd	nd	nd	29,000
	1956	67,000	9,500	133,000	30,000	15,000	—	6,500	7,500	15,000	3,000	+	10,500
	1957	79,000	30,195	1,339,000	16,500	11,000							
Nitzschia pacifica + *pungens*													
	1955	20,000	6,000	4,500	49,000	—	4,500	—	nd	nd	nd	nd	15,000
	1956	17,000	3,500	12,500	36,500	9,500	—	6,000	3,620	5,000	22,000	1,240	15,000
	1957	139,000	92,465	1,987,000	61,000	4,500							
Rhizosolenia stolterfothii													
	1955	27,000	48,500	70,500	427,000	17,500	5,000	6,000	nd	nd	nd	nd	38,500
	1956	58,000	59,500	182,500	174,500	24,500	—	6,500	7,500	6,500	14,500	3,500	14,500
	1957	92,000	198,000	122,000	953,000	18,000							

TABLE 53. Composite successional pattern of the major diatom species during the 1955-1957 upwelling seasons. (Values enclosed in parenthesis indicate year in which species was important, i.e., ('57) = 1957; otherwise, response was observed during all years.)

December—January	February	March	April
A. Dominant Species			
Ch. compressus *Ch. costatus* *Skel. costatum* f. *tropicum*	*Rh. delicatula*	*Nitz. delicatissima*	*Rh. stolterfothii*
B. Occasional Dominant Species			
Ch. socialis ('56)	*Eucampia cornuta* ('57)	*Lauderia annulata* ('55) *Ch. costatus* ('56) *Nitz. pacifica* + *pungens* ('57)	*Ch. socialis* ('57)
C. Secondary Species			
Bact. delicatulum			*Eucampia cornuta*
Bact. elegans			*Nitz. delicatissima*
Bact. hyalinum			*Nitz. pacifica* + *pungens*
Bact. varians			
Ch. decipiens			
Ch. laciniosus			
Ch. affinis..........	....		
Ch. brevis..........	....		
Ch. lorenzianus..........	....		
Lept. minimus..........	....		
Rh. stolterfothii..........	....	....	
Rh. delicatula		....	....
Ch. curvisetus			....
	Ch. compressus	..........('56)..........	
	Ch. socialis	..........('56)..........	
	Skel. costatum f. *tropicum*		

Four communities, or stages, are recognizable (Table 53). In every year a *Chaetoceros compressus* + *Skeletonema costatum* f. *tropicum* association initiated the upwelling cycle during December and January (Table 53). February was characterized by the dominance of *Rh. delicatula*, although during 1956 there was also a mass occurrence of *Eucampia cornuta*. A new successional stage accompanying the intense upwelling generally characteristic of March exhibited marked annual variations in the co-dominant species. Although *Nitz. delicatissima* usually achieved a modest abundance during this stage, it was accompanied by an unpredictable co-dominant: *Lauderia annulata* (1955); *Ch. costatus* (1956) and *Nitz. pacifica* + *Nitz. atlanticus* var. *pungens* (1957). During all years, the upwelling season terminated in April with the dominance of *Rh. stolterfothii* (Tables 52, 53).

Numerous species of secondary importance were present during January, notably representatives of *Bacteriastrum* and *Chaetoceros*, most of which became unimportant as upwelling progressed (Tables 52, 53). The dominant species of the later successional stages, however, were among the January secondary species. This contrasts with observations from other regions where the dominant species of the different successional stages generally appear shortly before their efflorescence (Braarud and Bursa 1939, Bursa 1961a, S. Conover 1956).

TABLE 54. Minor diatom species attaining a maximum abundance > 10,000 c/L, and their maximum observed abundance

Asterionella japonica	74,000	*Chaetoceros subsecundus*	14,000
Cerataulina bergonii	40,000	*Corethron hystrix*	11,000
Chaetoceros anastomosans	20,500	*Fragilaria* sp.	15,500
Chaetoceros atlantidae	29,000	*Hemiaulus sinensis*	19,000
Chaetoceros debilis	10,000	*Rhizosolenia alata* f. *genuina*	11,500
Chaetoceros densus	20,500	*Rhizosolenia fragilissima*	48,000
Chaetoceros didymus	32,000	*Thalassionema nitzschioides*	12,000
Chaetoceros holsaticus	16,000	*Thalassiothrix frauenfeldii* var. *panama*	24,240
Chaetoceros lauderii	11,000		

Of the remaining diatoms, only 17 species attained densities greater than 10,000 c/L (Table 54). Of these, 14 species reached this level only once; *Asterionella japonica, Ch. didymus* and *Ch. subsecundus* twice, and *Rh. fragilissima* four times.

The influence of upwelling intensity on diatom abundance and succession, as well as the quantitative aspects of the influence of upwelling on phytoplankton dynamics, will be returned to later. A regional comparison of the Gulf of Panama diatom cycle, as well as that of the entire phytoplankton community, will also be deferred until later.

The annual dinoflagellate cycle

It is convenient to distinguish between the brown, thecate dinoflagellates and the Gymnodiniaceae, which comprise primarily indeterminable, naked, colorless forms, otherwise characterized by the presence of a girdle. Both groups were remarkably sparse during the investigation, considering that dinoflagellates, along with coccolithophores, are presumed to be a predominant component in tropical waters. Maximum abundance occurred during the upwelling season; the thecate dinoflagellates (maximum of 38,000 c/L) were numerically superior to the Gymnodiniaceae (maximum of 11,500 c/L) except during June and July (Table 55).

Of the approximately 105 dinoflagellate species, forms and varieties identified (Appendix Table 3), only 15 achieved densities greater than 1,000 c/L:

Exuviaella baltica	22,000	*Exuviaella* cf. *vaginule*	3,000
Prorocentrum # 33	15,500	*Peridinium minusculum*	2,500
Peridinium heterospinum		*Ceratium furca* var. *eugrammum*	2,200
+ *pellucidum*	15,500	*Peridinium granii* f. *mite*	1,940
Peridinium # 57	11,000	*Gymnodinium* # 1	1,500
Oxytoxum variabile	5,000	*Dinophysis fortii*	1,160
Peridinium globulus var. *ovatum*	3,420	*Prorocentrum micans*	1,010
Amphidinium minutissima	3,000	*Peridinium minutum*	940

The thecate dinoflagellates did not exhibit a succession. Their frequent pulses (Table 55) primarily reflected the growth of *Exuviaella baltica.*

TABLE 55. Maximum monthly abundance (c/L) of the thecate and gymnodinioid (naked) dinoflagellates (nd = no data)

	Thecate Forms			Gymnodiniaceae		
	1955	1956	1957	1955	1956	1957
Jan.	3,220	2,220	1,680	500	2,000	1,000
Feb.	1,080	3,080	38,000	5,000	8,000	4,500
Mar.	740	6,940	8,200	500	11,500	9,000
Apr.	6,520	33,940	13,080	500	1,000	3,500
May	660	760	3,260	500	—	4,500
June	440	2,140		2,500	7,500	
July	560	3,760		4,500	7,000	
Aug.	nd	2,600		nd	1,500	
Sept.	nd	2,040		nd	—	
Oct.	nd	2,820		nd	1,500	
Nov.	nd	2,440		nd	1,500	
Dec.	2,740	4,640		2,500	3,000	

Prorocentrum micans and *Glenodinium lenticula* f. *minor* were also perennial species, whereas the annual occurrence and abundance of the other species were unpredictable.

The *absence* of a succession from a diatom to a dinoflagellate community accompanying the increased temperature and stability of the watermass during the rainy season is a notable feature of the phytoplankton cycle. The July and November phytoplankton surveys indicate this to be characteristic of the entire Gulf of Panama (Smayda 1963), in contrast to other regions. A succession from a diatom to a dinoflagellate community during the warmest time of the year is a characteristic occurrence in many Temperate, Boreal, and, in some instances, Mediterranean inshore areas (S. Conover 1956, Gran and Braarud 1935, Margalef, Muñoz and Herrera 1957, Braarud and Bursa 1939, Braarud, Gaarder and Nordli 1958, Gaarder 1938). A general dinoflagellate paucity and the absence of a post-diatom abundance, similar to that in the Gulf of Panama, also characterized the dinoflagellate cycle in the tropical inshore environs of the Great Barrier Reef near Low Isles, Australia (Marshall 1933), a Sierra Leone estuary (Bainbridge 1960) and, apparently, near Monaco in the Mediterranean Sea (Bernard 1939). Dinoflagellates were likewise insignificant in the Sargasso Sea near Bermuda where their maxima were less than 1,000 c/L (Riley 1957, Hulburt, Ryther and Guillard 1960). However, fragmentary quantitative observations from Mozambique, the upwelling area off the west coast of India and, especially, from some Puerto Rican embayments indicate that not all tropical inshore areas are characterized by a dearth of dinoflagellates (Table 56). Indeed, Margalef (1961a) implies that the characteristic succession to a dinoflagellate community in other biogeographical areas also occurs in certain Puerto Rican embayments.

The significantly greater species diversity in the Gulf of Panama and other tropical regions compared to other biogeographical regions is indicated in Table 56. That dinoflagellates are favored by high temperatures, even at 28 to 29 C prevalent during the rainy season is a common observa-

TABLE 56. Regional comparison of dinoflagellate species number and maximum abundance (c/L)

Area	Interval	Author	Species No.	Maximum Abundance
Gulf of Panama	XI '54—V '57	Present Report	105	38,000
Low Isles, Australia	VII '28—VII '29	Marshall 1933	32+	2,570
Mozambique, Africa	IX—X '57	Silva 1960	81	27,000
Puerto Rico	VII—VIII '58	Margalef 1961a	117*	$>4 \times 10^6$
Sargasso Sea	XI '57—XI '58	Hulburt, *et al.* 1960	20	925
Pacific, 0°N, 145°W	III '57	Hasle 1959	53	1.5×10^4
India, West Coast	VII—X '54	Subrahmanyan 1959a	?	35,000†
Long Island Sound	III '52—III '54	Conover 1956	32+	$>10^6$
Igloolik, 69°N, 82°W	IX '55—IX '56	Bursa 1961a	32	45,000
Oslofjord, polluted	1935—1939	Braarud 1945	47+	$>5 \times 10^6$
Oslofjord, non-polluted	1935—1951	Braarud, *et al.* 1939, 1958	47+	$>5 \times 10^5$
Balsfjord, 69°N, 18°W	V '30—IV '31	Gaarder 1938	54	28,820

* net samples; † monthly mean

tion (Braarud 1961). Thus it seems improbable that either an inadequate species "pool" or inhibitory temperatures limit dinoflagellate growth in the Gulf of Panama. Indeed, the presence of a highly stable watermass (Figs. 23, 24) held within the Gulf by the prevailing southerly winds suggests that physical conditions capable of sustaining a red tide bloom occur during the rainy season (Kierstead and Slobodkin 1953). This points to the conspicuous nutrient impoverishment occurring during the rainy season (Figs. 30, 39, 40) as a possible cause of the dinoflagellate paucity relative to that in other biogeographical regions, including "richer" tropical environments (Table 56). This possibility is strengthened by the paucity of the predominantly heterotrophic Gymnodiniaceae (Table 56) compared to northern waters (Braarud 1945, Braarud, Gaarder and Nordli 1958, among other publications). However, although inorganic nutrient accretion *via* runoff appears inadequate to sustain sizeable autotrophic plant populations (Smayda 1963), a considerable influx of dissolved organic substances, including vitamins, might be expected with runoff, as discussed previously.

Therefore, the cause of the unimportance of dinoflagellates in the Gulf of Panama is obscure. These observations suggest, however, that while higher temperatures may select dinoflagellates over diatoms in tropical waters, the former will remain sparse unless nutrients are supplied by upwelling, or unless the community is isolated in an area where enrichment from terrestrial sources or *in situ* processes occurs. The considerably greater dinoflagellate maxima and role generally observed in more northerly inshore waters (Table 56), where heightened eutrophication probably has accompanied human progress, may reflect this view.

TABLE 57. Maximum monthly coccolithophore abundance, as c/L (nd = no data)

Month	1955	1956	1957
Jan.	3,000	8,500	500
Feb.	3,000	89,000	11,500
Mar.	1,000	45,500	500
Apr.	9,500	7,000	500
May	4,500	4,060	500
June	13,000	3,500	
July	1,000	18,050	
Aug.	nd	2,500	
Sept.	nd	6,600	
Oct.	nd	6,000	
Nov.	nd	4,000	
Dec.	18,020	1,000	

The annual coccolithophore cycle

During the investigation 22 coccolithophores were identified to genus or better, while several forms defied identification:

Acanthoica sp.
Acanthoica lithostratos
Acanthoica cf. *quadricornu*
Anthosphaera sp.
Anoplosolenia brasiliensis
cf. *Braarudosphaera* sp.
Calciosolenia sinuosa
Calciosolenia cf. *murrayi*
Coccolithus huxleyi
Coccolithus leptoporus
Coccolithus pelagicus
Cyclococcolithus sibogae
Discosphaera tubifera
Gephyrocapsa oceanica
Halopappus adriaticus
cf. *Helicosphaera carterae*
Michaelsarsia elegans
Pontosphaera maxima
Pontosphaera sp.
Syracosphaera mediterranea
Syracosphaera nodosa
Tergestiella adriatica

The coccolithophores were most abundant during the upwelling season, with a maximum observed abundance of 89,000 c/L (Table 57). Thereafter, a secondary pulse accompanied the resurgence of northerly winds during June and July (Figs. 45, 49), followed by a decline during the rainy season.

Considerable annual variations occurred in the magnitude of the coccolithophore upwelling season maximum; unusually intense growth occurred during 1956 (Table 57). The annual cycle reflects primarily the growth of *Gephyrocapsa oceanica* and *Coccolithus huxleyi*, as indicated by the data for 1956 (Table 58). *Coccolithus huxleyi* occurs only during the upwelling season, whereas *Discosphaera tubifera* is a rainy season form (Table 58). Otherwise, no conspicuous species succession was observed; *Calciosolenia sinuosa*, the third most important coccolithophore, was perennial.

Coccolithophores were more abundant than the dinoflagellates during the upwelling season and approximately equal to them during the rainy season, but were considerably less abundant than the diatoms (Tables 51, 55, 57).

TABLE 58. Maximum monthly abundance (as c/L) of the major coccolithophore species during 1956

Month	*Gephyrocapsa oceanica*	*Coccolithus huxleyi*	*Calciosolenia sinuosa*	*Discosphaera tubifera*
Jan.	6,500	2,000	1,500	500
Feb.	51,500	52,000	4,000	—
Mar.	22,000	31,000	4,000	—
Apr.	7,000	1,000	—	—
May	3,500	—	—	—
June	3,500	—	—	—
July	14,000	—	1,500	3,500
Aug.	2,500	—	500	500
Sept.	5,000	—	500	—
Oct.	3,000	500	500	500
Nov.	—	—	—	—
Dec.	12,000	60	1,000	500

TABLE 59. Regional comparison of coccolithophore species number and maximum abundance (c/L)

Area	Author	Species No.	Maximum Abundance
Gulf of Panama	Present investigation	23+	89,000
Low Isles, Australia	Marshall 1933	5	250
*Mozambique, Africa	Silva 1960	?	63,000
*Pacific, 0°N, 145°W	Hasle 1959	33	ca. 40,000
Sargasso Sea, Bermuda	Hulburt *et al.* 1960	23	13,680
Gulf of Maine	Gran and Braarud 1935	8	64,800
*Gulf of Maine: 42°50′N, 67°W	Braarud 1934	1	308,000
Labrador Sea: 56°31′N, 51°W	Holmes 1956	2	300
Igloolik, 69°N, 82°W	Bursa 1961a	8	60,000
Hudson Bay	Bursa 1961b	2	$>10^6$
Weathership M, 66°N, 2°E	Halldal 1953	16	275,000
Norwegian Coastal Waters:			
59—61°N	Braarud 1945	1	35×10^6
(Utsira) 59°N	Braarud *et al.* 1958	12	$>10^6$
(Lofoten) 68°N	Braarud *et al.* 1958	12	325,000
(Balsfjord) 69°30′N	Gaarder 1938	5	300,000

* not an annual cycle

Although few quantitative investigations of the coccolithophores have been made, sufficient data exist to permit an initial assessment of their role in the Gulf of Panama relative to other regions (Table 59).

This regional comparison indicates that the maximum coccolithophore abundance (89,000 c/L) observed in the Gulf of Panama exceeds that reported for other tropical inshore and offshore areas. This observation may be somewhat misleading, however, if the mean annual coccolithophore abundance in these other areas is greater and/or they are more important as a group than the diatoms and dinoflagellates in the annual cycle. For example, coccolithophores, principally *Coccolithus fragilis*, comprise from 50 to 88 per cent of the total nannoplankton biomass in the waters off Monaco and Algiers in the Mediterranean Sea (Bernard 1948). Also, despite a lower maximum abundance than that observed in the Gulf of Panama, the coccolithophores, principally *Coccolithus huxleyi*, in the Sargasso Sea near Bermuda predominate throughout the year except during the brief diatom bloom (Hulburt, Ryther and Guillard 1960). Riley (1957), however, observed that they were numerically subordinate to both diatoms and dinoflagellates in the north central Sargasso Sea (35°N, 48°W).

As with dinoflagellates (Table 56), tropical coccolithophore communities are characterized by a greater number of species, but attain a lower maximum than observed in other biogeographical regions (Table 59). Whether the absence or relative scarcity of coccolithophores reported from waters along the eastern North American coast south of the Gulf of Maine (Table 59) represents actual conditions or reflects the methods of enumeration used is not known (S. Conover 1956, Hulburt 1956, Lillick 1937, Pratt 1959, Smayda 1957). However, *Coccolithus huxleyi* is important in the annual phytoplankton cycle of more northerly coastal waters (Table 59), including the Gulf of Maine, especially in Norwegian waters where it represents a distinct stage in phytoplankton succession (Braarud and Bursa 1939, Braarud 1945, Braarud, Gaarder and Grøntved 1953, Braarud, Gaarder and Nordli 1958, Braarud, Føyn and Hasle 1958, Gaarder 1938, Hasle and Smayda 1960). Birkenes and Braarud (1952) and Berge (1962) have described the extraordinary efflorescence of *Coccolithus huxleyi* of up to 115 × 10^6 c/L causing water discoloration during certain summers in Norwegian coastal waters. This phenomenon suggests the salient ecological requirements of the coccolithophores include high light intensities and high temperatures. The light requirement would appear to be satisfied in the Gulf of Panama. Berge's (1962) suggestion that coccolithophores might be able to withstand light intensities inhibitory to other groups because of the attenuation and reflectance of light by the coccoliths is not supported by recent observations (Paasche 1964). Nonetheless, light might select coccolithophores over diatoms on occasion in tropical waters. Also the phototactic coccolithophores (Mjaaland 1956) and dinoflagellates (Hasle 1950, Halldal 1958) are theoretically better endowed to withstand, or avoid, high light intensities.

Although the nutrient requirements of this group are poorly known, recent experiments by Ryther and Kramer (1961) on the iron requirements of *Coccolithus huxleyi* suggest that this nutrient does not limit coccolithophore growth in the Gulf of Panama (Schaefer and Bishop 1958). Nonetheless, the increased growth during upwelling and the relative paucity of coccolithophores during the rainy season suggest that certain nutrients may be limiting their growth.

TABLE 60. Maximum monthly micro-flagellate abundance (c/L) (nd = no data)

	1955	1956	1957
Jan.	14,500	92,000	55,000
Feb.	42,000	61,500	77,000
Mar.	58,500	54,660	8,500
Apr.	59,500	1,713,000	33,020
May	17,000	11,020	28,500
June	36,500	12,000	
July	64,500	51,000	
Aug.	nd	19,000	
Sept.	nd	14,500	
Oct.	nd	21,500	
Nov.	nd	5,000	
Dec.	49,500	27,500	

Although coccolithophores are generally considered to be thermophilic, Mjaaland's (1956) experiments on *Coccolithus huxleyi* indicate that northern clones of this species exhibited little or no growth above 25 C. The absence of this species during the rainy season (Table 58) when temperatures greater than 27 C characterize the upper 20 m (Figs. 5, 6) has been pointed out. However, it seems likely from Braarud's (1961) experiments with dinoflagellates that tropical clones of this species would show better growth at higher temperatures than that observed by Mjaaland (1956). Tentatively, the relative paucity of coccolithophores during the rainy season is probably a consequence of suboptimal nutrient concentrations and, possibly, inadequate (high) temperature levels.

The annual micro-flagellate cycle

Although micro-flagellates (also designated as naked flagellates, μ-flagellates or monades in the literature) are destroyed upon preservation, a significant number remain enumerable with the Utermöhl inverted microscope counting technique, permitting a semi-quantitative glimpse of their general dynamics (*vide* Hasle and Smayda 1960, Smayda 1965a).

This group attained maximum abundance in the Gulf of Panama during the upwelling season, with an indication of a secondary pulse during July (Table 60).

The micro-flagellates were considerably more abundant than the dinoflagellates and coccolithophores (Tables 55, 57, 60; Appendix Table 1). Since both autotrophic and heterotrophic modes of nutrition are undoubtedly represented in the micro-flagellate communities, their relative contribution to the annual production is difficult to assess. However, they appear to be less important than the diatoms as primary producers in the Gulf of Panama (Smayda 1965a). Grøntved (1958), has demonstrated that "naked flagellates" may account for more than 50 per cent of the total production in Limfjord, Denmark during certain summer months.

Although comparable observations on this group are lacking from other tropical areas, micro-flagellates may be important in the Sargasso

Sea (Riley 1957, Hulburt, Ryther and Guillard 1960). In more northerly waters, examination of unpreserved samples from Narragansett Bay (41° 30′N, 71°20′W) has demonstrated that micro-flagellates are a persistent dominant element, undergoing a cyclic periodicity (Smayda 1957, Pratt 1959). Average abundance over a 3-year cycle was approximately 800,000 c/L (Pratt 1959). These organisms are also abundant in shallow Danish fjords, where a maximum density of 4×10^6 c/L and average populations of from 200,000 to 500,000 c/L have been found in preserved samples (Grøntved and Steemann Nielsen 1957, Grøntved 1958).

Although a discussion of the micro-flagellate community is usually not included in reports of phytoplankton observations conducted in Boreal and Arctic waters, these investigations frequently do include an enumeration of this group, the results of which are often listed as *monads* in the tables. (Braarud and Bursa 1939, Braarud, Gaarder and Grøntved 1953, Braarud, Føyn and Hasle 1958, Halldal 1953, Holmes 1956, Paasche 1960a, Ramsfjell 1960, among others). Populations in excess of 200,000 c/L are commonplace. Hasle and Smayda (1960) calculated a mean population of 245,000 c/L at Drøbak, Oslofjord, where a cyclic periodicity similar to that observed in Narragansett Bay (Smayda 1957) was observed.

Therefore, the occurrence of a micro-flagellate population in the Gulf of Panama is consistent with observations in northerly inshore areas, although the population may not be as abundant.

The colorless flagellate *Chilomonas marina* was always present, and attained a modest upwelling maximum of 7,000 to 16,000 c/L (Appendix Table 2). Its occurrence in the Gulf of Panama and the open Pacific (Hasle 1960) indicates its ubiquity, although it appears to attain greater densities in Boreal and Arctic waters (*vide* references cited for micro-flagellates).

The Euglenaceae attained a maximum abundance of 8,500 c/L (Appendix Table 2), and were not as important as in Norwegian coastal waters (Braarud, Gaarder and Nordli 1958).

The annual silicoflagellate cycle

Twelve species and varieties of silicoflagellates were observed during the investigation:

Dictyocha fibula
Dictyocha fibula var. *aspera*
Dictyocha fibula var. *messanensis*
Distephanus crux
Distephanus speculum
Distephanus speculum var. *octagonum*
Distephanus speculum var. *polyactis*
Ebria tripartita
Mesocena polymorpha
Mesocena polymorpha var. *binonaria*
Mesocena polymorpha var. *bioctonaria*
Mesocena polymorpha var. *octonaria*

Gemeinhardt's (1930) classification was used. However, Proschkina-Lavrenko (1959) places the varieties of *Mesocena polymorpha* under *Dictyocha* (*Distephanus*) *speculum*, as Marshall (1934) did with var. *bioctonaria*.

The silicoflagellates attained a maximum of 180 to 240 c/L during the upwelling season (December to January), but were usually rare except during August 1956 when 380 c/L were observed (Appendix Table 2). The *bioctonaria* and *octonaria* varieties of *Mesocena polymorpha* were primarily responsible for the observed silicoflagellate dynamics. *Dictyocha fibula* var. *messanensis* was also significant. The upwelling stock was conspicuously devoid of cell contents which, coupled with their maximum in December and January, suggests that they might have been roiled up from the bottom during the initial phases of upwelling.

Although Gemeinhardt (1930) suggests that *Dictyocha* and *Mesocena* have tropical tendencies, the sparsity of silicoflagellates observed in the Gulf of Panama is consistent with other quantitative tropical investigations (Marshall 1934, Silva 1960). This group appears to be considerably more important in northern inshore waters (Gran and Braarud 1935, Gaarder 1938, S. Conover 1956), especially in Long Island Sound where S. Conover found *Distephanus speculum* to exceed 10^5 c/L, and *Ebria tripartita* 40×10^3 c/L. S. Conover concluded that *Distephanus speculum* has moderate requirements for light, nutrients and temperature. Should the *Mesocena polymorpha* varieties belong to this taxon, as discussed above, then the excessive temperatures and/or marked oligotrophy of the Gulf of Panama might inhibit this character species.

Annual cyanophycean cycle

The presence of a pelagic cyanophycean community, principally *Trichodesmium* (*Skujaella*), is a hallmark of tropical phytoplankton communities (Aikawa 1936). Nine representatives were identified during the present investigation:

Anabaena sp.
Katagnymene spiralis
Lyngbya cf. *aestuarii*
Oscillatoria cf. *bonnemaisonii*
Oscillatoria cf. *niger*
Oscillatoria cf. *nigro-viridis*
Richelia intercellularis
Trichodesmium cf. *contortum*
Trichodesmium cf. *thiebautii*

In addition, an unidentified large, branched form possessing heterocysts was abundant during the rainy season (Appendix Table 2).

The sampling and enumeration techniques used are quite inadequate to describe the cyanophycean cycle. *Trichodesmium* threads, for example, collect in bundles which aggregate in windrows. Since only the relative frequency of these forms was recorded, comments on their abundance and seasonal changes in the Gulf of Panama are strictly qualitative.

There is some indication that a succession occurred. *Trichodesmium* was common (c) to abundant (A) during the upwelling season, but disappeared during the rainy season. At this time, the unidentified branching form, which was rare during the upwelling period, became common and attained a considerable abundance during October and November at the height of the rainy season. This form appeared to be equally abundant throughout the water column. The other taxa occurred sporadically and were never abundant.

Trichodesmium is the most commonly reported cyanophycean from tropical waters, tending to predominate when the abundance of the other phytoplanktonic groups is minimal (Aikawa 1936, Takano 1960, Dugdale, Menzel and Ryther 1961, among others). Marshall (1933) found *Trichodesmium* to occur irregularly, being most important during "the calmer months." She reported a maximum density of 1,000 threads per liter. Dugdale, Menzel and Ryther (1961) observed that this form occurred only during the summer and fall in the Sargasso Sea after the watermass became thermally stratified and the surface temperature reached 25 C.

The abundance of the unidentified cyanophycean during the nutrient impoverished rainy season may be related to an ability to fix nitrogen, as established for *Trichodesmium* (Dugdale, Menzel and Ryther 1961).

Few quantitative data exist on the importance of cyanophyceans in more northerly waters, although this group might be important in dilute embayments (*vide* Valikängas 1926).

Although the intriguing *Richelia intercellularis* has been most frequently reported in *Rhizosolenia imbricata* var. *shrubsolei*, it was commonly associated with *Rhiz. styliformis* in the Gulf of Panama, the host from which it was originally described (Ostenfeld and Schmidt 1901). Margalef (1957) has reported that *Richelia* also occurs in *Rhiz. hebetata* f. *semispina* in Puerto Rican waters.

The annual tintinnid and ciliate cycles

Efforts to identify these grazers were cursory at best. The 27 tintinnids identified to genus or better is a minimal estimate of the species present:

Canthariella cf. *septinaria*
Codellonopsis cf. *turgescens*
Codellonopsis sp.
Dictyocysta mexicana
Epiorella curta
Metacylis annulifera
Metacylis jorgensii
Parafavella sp.
Parundella aculeata
Parundella sp.
Ptychocylis sp.
Rhabdonella amor
Rhabdonella brandtii
Rhabdonella cf. *cuspidata*
Rhabdonella cf. *lohmanni*
Rhabdonella poculum
Rhabdonella sp.
Salpingacantha ampla
Salpingacantha sp.
Salpingella subconica
Salpingella sp.
Steenstrupiella sp.
Tintinnus apertus
Tintinnus inquilinus
Tintinnus stramentus
Tintinnus tenue
Tintinnus sp.

Although specimens containing recognizable diatom or flagellate remains were observed, the relative sparsity of the tintinnids suggests that they were not important grazers during the investigation. *Metacylis annulifera* attained 7,020 c/L during March 1956, the maximum abundance of tintinnids observed. Otherwise, an upwelling maximum of approximately 400 c/L usually resulted, followed by less than 80 c/L during the remainder of the year. *Tintinnus inquilinus* was found only in association with *Chaetoceros dadayi* (Cupp, 1943: Fig. 64).

The remarkable heterogeneity of tintinnids reported from tropical inshore waters, especially by Silva (1954, among other papers) who has found 100 or more species, suggests their potential importance as grazers.

Marshall (1934) observed 56 species in Australian waters. In more northerly waters, *Tintinnopsis* spp. appear to be significant grazers at times (Gaarder 1938, Grøntved and Steemann Nielsen 1957).

The ubiquitous ciliate community (Braarud, Gaarder and Nordli 1958, Gran and Braarud 1935, Hasle 1960) comprising *Strombidium* (*Laboea*) *conicum*, *crassulum*, cf. *emergens*, *strobilum*, cf. *vestitum* and *Lobmaniella oviformis*, were unimportant grazers in the Gulf of Panama. The upwelling maximum was 150 c/L, except during February 1957 when 7,000 c/L occurred. Less than 50 c/L were present at other times.

Marshall (1934) observed "naked ciliates" to be present throughout the year, with a maximum of 200 c/L. Silva (1960) reports a sizeable persistent ciliate population, 4,000 c/L maximum, from Mozambique.

The *Strombidium*[12] (*Laboea*) community is considerably more abundant in more northerly waters where it tends to succeed a diatom bloom (Braarud and Bursa 1939, Braarud 1945, Braarud, Gaarder and Nordli 1958, Bursa 1961a, Gaarder 1938, Grøntved and Steemann Nielsen 1957, among others).

Observations on cell vitality

The communities always included a variable fraction of chlorotic or empty cells representing many taxa. Although such diagnoses are necessarily subjective, these specimens were clearly different from the more vigorous cells present in the same preserved samples. The contrast in cell condition was especially striking during the upwelling season when the cells were usually well-pigmented and robust. This suggests that the sickly appearance of such representatives was not primarily an artifact of preservation.

The relative frequency of moribund individuals varied from a trace to 100 per cent of the community as at station 59 (Table 47) where approximately 10^6 c/L were observed, a remnant population of a previous *Nitzschia* efflorescence. The dinoflagellates exhibited a similar condition at this station, especially *Dinophysis forti* (1,160), as they did at station 30 (Table

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[12] Classification according to Kahl (1932).

31) where the normally pigmented *Prorocentrum* and *Peridinium* species were important. Moribund communities also predominated at 20 m at station 28 (Table 30), at mid-depth at stations 41 and 43 (Tables 38, 39) and at the surface at station 55 (Table 45), except for *Rh. stolterfothii*. At other stations, senile individuals were subordinate to "healthy" ones, though frequently numerically important, as during the 1955 *Lauderia annulata* maximum (Table 27) when approximately 185,000 c/L were present.

The moribund cells were invariably intact, suggesting that their physiological condition did not result from zooplankton grazing, during which the voided non-digestible frustules would probably be broken. There was also no gross indication that the moribund cells were parasitized, although pennate diatoms, especially *Nitzschia* cf. *sigma*, were frequently covered with hyaline, hyphae-like "organisms," and the diatoms *Dactyliosolen mediterraneus* and *Ch. coarctatus* were heavily infested by their normal ciliate epibionts (*vide* Cupp 1943). Accordingly, it is suggested that the mean observed incidence of moribund individuals of 10 to 15 per cent of the diatom community represents the minimal natural daily mortality rate.

Moribund specimens in tropical waters have been reported previously. The moribund fraction comprised approximately 33 per cent of the net plankton communities present during March 1933 in the Gulf of Panama (Allen 1939). In the Gulf of California, Cupp and Allen (1938) observed that sickly cells comprised more than 10 per cent of the total population in half the net hauls where the population exceeded 10^4 c/L, whereas Osorio Tafall (1943) observed a maximum of 6 per cent. Recently, Occhipinti, Magliocca and Teixeira (1961) reported a mean incidence of 10 per cent (range, 5 to 23 per cent) of the total population, from a brief quantitative study off Brazil. The general correspondence in incidence of moribund individuals during these tropical investigations is striking, though probably fortuitous. However, their widespread occurrence in tropical waters is further indicated by Bainbridge's (1960) observations in a Sierra Leone estuary where he found large numbers of empty diatom frustules after each diatom peak, a phenomenon which he suggested to be due to "natural mortality."

QUANTITATIVE ASPECTS OF PHYTOPLANKTON GROWTH AT 8°45′N, 79°23′W

The preceding sections have demonstrated that phytoplankton growth in the Gulf of Panama is strongly influenced by climatologically induced variations in environmental conditions. The more quantitative aspects of this relationship and other aspects of the phytoplankton cycle will now be evaluated.

A phytoplankton census provides an important and, frequently, indispensable measure of the success, growth and stage of succession, *inter alia*, of a species or community. However, it is generally accepted that there is no constant quantitative relationship between the number of phytoplankton cells present in a community and the magnitude, food value or physiological attributes of their tissue (biomass) (Smayda 1965a) and, thus, a numerical census alone has limited value as a measure of the standing crop when considered from the standpoint of production or food-chain dynamics. An especially striking example of the lack of correspondence between cell numbers and biomass contribution is presented in Figure 55. Although diatoms comprised only 27.5 per cent of the total phytoplankton community as cell numbers at station 1, they represented 95.6 per cent of the community biomass. Monads (micro-flagellates), however, which dominated the community as cell numbers in comprising 48.8 per cent of the total community, contributed only 1.2 per cent of the biomass. Therefore, depending on the estimate of standing crop used, diatoms were either overwhelmingly dominant (as biomass) or of secondary importance (as cell numbers) at this station. If considered in terms of food-chain dynamics, for example, then diatoms, despite their numerical inferiority, provided the major momentary food source at station 1. Since the ensuing analyses will attempt to relate quantitatively the magnitude of the phytoplankton standing crop to the accompanying environmental conditions, as well as to estimate the magnitude of zooplankton and anchoveta grazing on phytoplankton, some index of standing crop other than cell numbers is needed. Consequently, the cell counts have been converted to equivalent biomass (tissue or cell volume), as done in the analysis of primary productivity (Smayda 1965a). The species' cell size characteristics and the method of converting cell counts into biomass estimates are presented in that paper.

Mean phytoplankton cycle, and annual variations in abundance

Three major characteristics of the Gulf of Panama phytoplankton cycle are:

1. A seasonal cycle in abundance occurs (Figs. 56, 57; Table 61).
2. The diatoms overwhelmingly dominate the phytoplankton community, both numerically and as biomass (Tables 62, 63).
3. Annual variations in abundance occur during the upwelling season (Table 63).

Within the average seasonal phytoplankton cycle three growth phases can be distinguished (Figs. 56, 57; Tables 61, 62):

1. Intense growth occurs during the upwelling season (December through April) followed by a precipitous numerical decline during May and June.
2. A slight resurgence in abundance occurs during July accompanying the reappearance of mild upwelling winds.
3. An annual minimum occurs during the rainy season (during the northern summer and autumn). The mean population cell density during

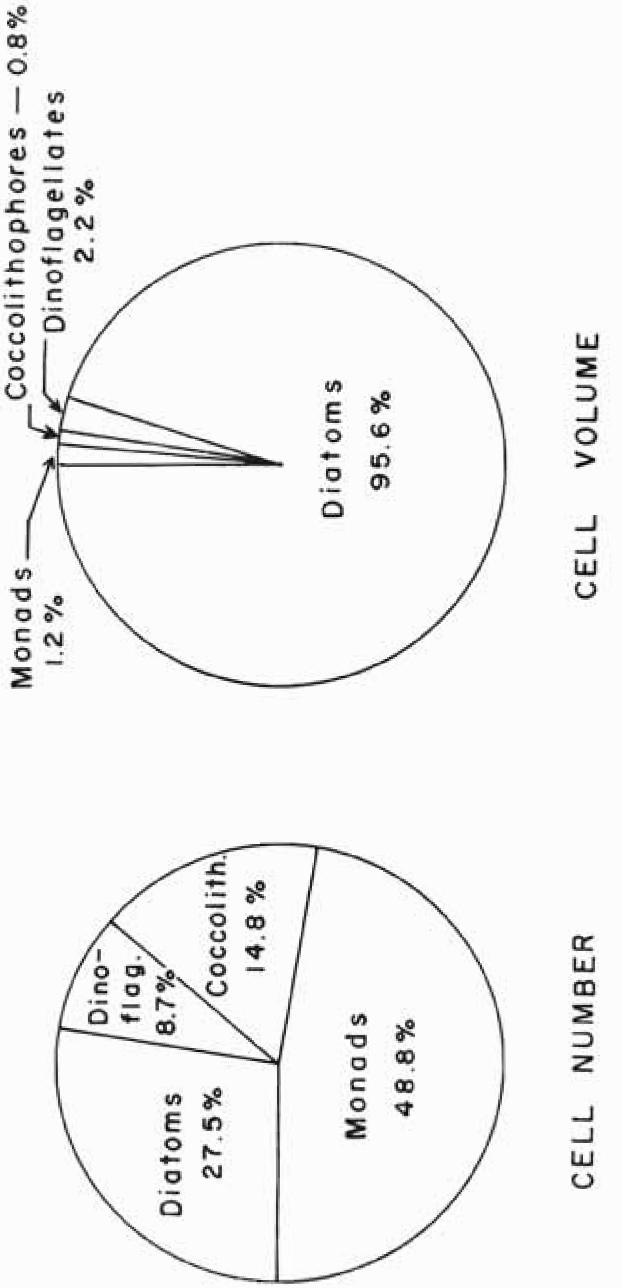

FIGURE 55. Relative proportions of the major floristic groups comprising the mean standing crop of phytoplankton in the upper 20 m at station 1 (29 November 1954) when expressed as cell numbers and total cell volume.

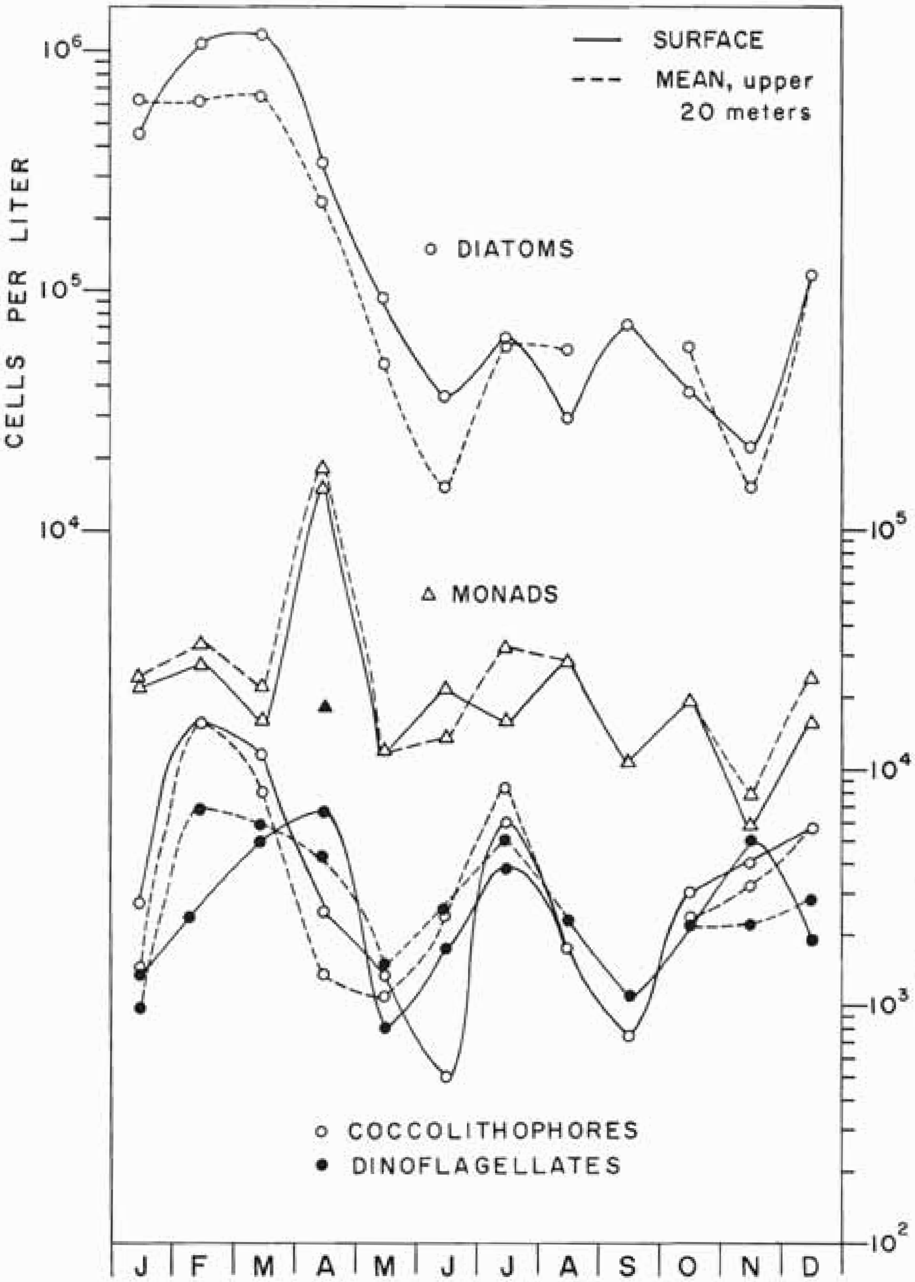

FIGURE 56. Mean monthly diatom, coccolithophore, dinoflagellate and monad abundance at the surface and in the upper 20 m at the hydro-biological station from 29 November 1954 to 20 May 1957. The monad datum (▲) represents the mean standing crop in April excluding the solitary, mass occurrence of an unidentified green flagellate, as discussed in the text.

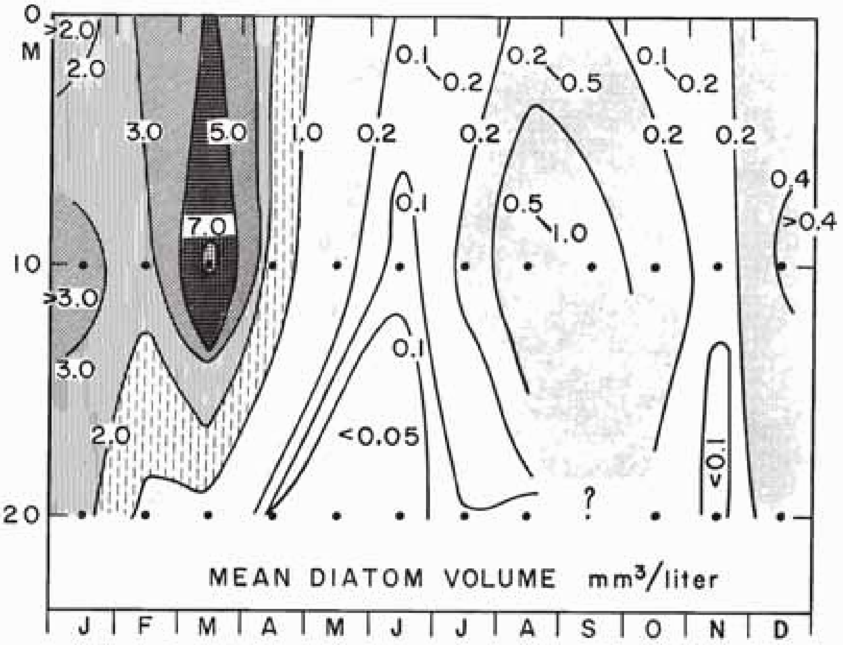

FIGURE 57. Mean monthly diatom biomass (cell volume) in the upper 20 m at the hydro-biological station during the investigation.

the upwelling season is approximately 6-fold greater than that during the rainy season (Table 62). The average abundance and response during the rainy season are unknown since observations are available for August through October only during 1956. It is uncertain, then, whether the diatom pulse observed during September represents average conditions.

The average annual diatom biomass cycle generally parallels that for cell numbers (Figs. 56, 57; Tables 61, 62, 63). A 5-fold decline in diatom biomass from April levels accompanied the termination of upwelling. A slight increase in biomass accompanied the resurgence of mild upwelling winds during July, but a more significant increase, centered around 10 m, occurred during August and September in contrast to the otherwise relatively low and uniform biomass characteristic of the rainy season. (Remember that the August through October response is based on observations in 1956 only, whereas the mean of 2 or 3 years' observations were used for the other months [Table 61].) The vertical distribution in diatom biomass demonstrates that the productive zone at the hydro-biological station is relatively shallow. The most productive stratum lay between 5 and 15 m, while relatively sparse standing crops were frequently encountered at 20 m. There is a general direct correspondence between the average phosphate distribution in the upper 20 m (Fig. 30) and diatom biomass (Fig. 57).

The principal features of this seasonal phytoplankton cycle (specifically the diatoms) at the hydro-biological station are also observed through-

TABLE 61. Mean monthly cell density (cells (L^{-1}) and biomass (as mm^3 m^{-3}) in the upper 20 m at the hydro-biological station from November 1954 to May 1957 (nd = no data; id = incomplete data)*

	DIATOMS		DINOFLAGELLATES		COCCOLITHOPHORES		MONADS	
	Cells L^{-1}	mm^{3}m^{-3}	Cells L^{-1}	mm^{3}m^{-3}	Cells L^{-1}	mm^{3}m^{-3}	Cells L^{-1}	mm^{3}m^{-3}
Jan.								
'55	250,260	710	1,762	1.10	1,750	.23	7,125	.47
'56	578,840	3993	1,735	.73	3,750	.47	54,190	3.53
'57	1,189,240	3009	405	.25	85	.01	13,650	.89
$\overline{X}$	613,645	2675	965	.62	1,436	.20	23,968	1.56
Feb.								
'55	118,315	591	1,595	1.00	1,065	.14	26,350	1.63
'56	112,715	291	4,695	2.94	42,560	5.70	41,005	2.75
'57	1,586,380	5719	13,900	8.69	1,940	.25	25,825	1.97
$\overline{X}$	605,613	2201	6,738	4.21	15,458	2.03	32,515	2.12
Mar.								
'55	608,135	12360	405	.25	320	.05	38,565	2.42
'56	228,980	629	10,080	6.30	25,200	3.05	26,045	1.67
'57	863,745	667	6,008	3.48	190	.03	3,315	.22
$\overline{X}$	642,990	4450	5,682	3.46	8,015	1.05	21,838	1.35
Apr.								
'55	199,030	1385	1,870	1.18	1,560	.21	23,760	2.10
'56	77,245	295	4,225	2.57	2,045	.27	388,675	726.83
'57	496,390	2366	5,915	3.77	65	.01	18,255	1.19
$\overline{X}$	232,113	1199	4,150	2.51	1,338	.12	181,886	321.80
May								
'55	id	id	id	id	id	id	id	id
'56	id	id	id	id	id	id	id	id
'57	31,255	161	2,465	1.55	125	.015	12,900	.84
$\overline{X}$	48,728	259	1,492	1.87	1,088	.140	11,411	.77
June								
'55	id	id	id	id	id	id	id	id
'56	id	id	id	id	id	id	id	id
$\overline{X}$	14,430	64	2,468	1.55	2,833	.45	13,458	.89
July								
'55	21,960	74	2,780	1.74	375	.05	47,375	3.08
'56	72,065	201	5,755	3.60	11,130	1.45	24,675	1.61
$\overline{X}$	59,173	168	5,030	3.14	8,380	1.09	31,334	2.04
Aug.								
'56	54,325	563	2,390	1.50	1,815	.24	26,750	1.74
Sept.								
'56	id	id	id	id	id	id	id	id
Oct.								
'56	57,950	232	2,235	1.40	2,320	.31	18,000	1.17
Nov.								
'54	7,905	67	2,495	1.56	4,260	.55	14,000	.91
'55	nd	nd	nd	nd	nd	nd	nd	nd
'56	22,280	167	2,215	1.39	2,000	.26	1,500	.10
$\overline{X}$	14,473	117	2,168	1.48	3,235	.41	7,750	.51
Dec.								
'54	id	id	id	id	id	id	id	id
'55	136,620	641	2,405	1.51	6,000	.91	30,820	1.51
'56	115,515	338	3,590	2.17	4,955	.61	17,315	1.13
$\overline{X}$	115,304	452	2,880	1.75	5,198	.73	22,628	1.22

* The biomass levels have been reported as mm^3 m^{-3} because of the low concentrations of the flagellate groups, whereas the cell numbers are given as cells L^{-1}. Incomplete data (id) refers to the absence of samples from a given depth which prevents the estimation of the mean population in the upper 20 m for a given year. However, sufficient data from all depths (0, 10 and 20 m) were usually available after lumping all the annual data to permit the estimation of a grand monthly mean ($\overline{X}$) for the period of investigation. No data (nd) indicates that samples were not available for that period.

TABLE 62. Mean population density and biomass in the upper 20 m during the upwelling and rainy seasons at 8°45'N, 79°23'W from November, 1954 to May, 1957

POPULATION DENSITY (cells per liter):

	Upwelling (A)	% of Total	Rainy (B)	% of Total	A:B
DIATOMS	407,506	85.8	57,900	71.0	7:1
DINOFLAGELLATES	4,067	.9	2,361	2.8	1.7:1
COCCOLITHOPHORES	6,289	1.3	3,348	4.1	1.9:1
MONADS	56,567	11.9	17,965	21.9	3.1:1
TOTAL	474,429		81,664		5.8:1

BIOMASS (mm^3 per liter):

	Upwelling (A)	% of Total	Rainy (B)	% of Total	A:B
DIATOMS	2.1950	96.9	.2570	98.8	8.5:1
DINOFLAGELLATES	.0025	.1	.0015	.6	1.7:1
COCCOLITHOPHORES	.0008	+	.0005	.2	1.8:1
MONADS	.0656	2.8	.0010	.4	65.6:1
TOTAL	2.2639		.2600		8.8:1

out the Gulf of Panama (Smayda 1963) and generally confirm the cycle tentatively proposed for "tropical neritic" regions by Heinrich (1962). The annual occurrence of a minor July and/or August pulse, and possibly one in September, is the principal deviation from Heinrich's proposed cycle. There are insufficient data to determine whether Heinrich's scheme, or the Gulf of Panama seasonal cycle, if either, is generally representative of tropical inshore *upwelling* situations. However, neither cycle is representative of non-upwelling tropical inshore environments such as the Great Barrier Reef region (Marshall 1933) where the sparse population does not exhibit a real seasonal cycle, or in a Sierra Leone estuary (Bainbridge 1960) where only a modest change in phytoplankton abundance is associated with alternating wet and dry seasons.

The overwhelming dominance of the diatoms both numerically and as biomass is shown in Tables 62 and 63. The average diatom cell density varied from 64 to 97 per cent of the total standing crop during the various upwelling seasons (Table 63), and comprised a grand average of approximately 86 and 71 per cent of the total population during the upwelling and rainy seasons, respectively (Table 62). As biomass, the diatoms comprised from about 89 to nearly 100 per cent of the mean total community biomass during the various upwelling seasons (Table 63), and between 97 to 99 per cent of the total biomass during the upwelling and rainy seasons, respectively (Table 62).

Of the flagellate groups, the monads (micro-flagellates) outranked the coccolithophores and dinoflagellates in average cell abundance, with the coccolithophores slightly more important than the latter (Tables 61, 62, 63). The coccolithophores were considerably less important than the other groups as biomass, however. The considerably high average monad standing crop

TABLE 63. Mean population density and biomass in the upper 20 m during the 1955, 1956 and 1957 upwelling seasons at 8°45′N, 79°23′W

POPULATION DENSITY (cells per liter):

	1955	% of Total	1956	% of Total	1957	% of Total
DIATOMS	269,334	90.9	226,774	63.8	850,254	97.4
DINOFLAGELLATES	1,390	.5	4,628	1.3	5,964	.7
COCCOLITHOPHORES	1,325	.4	15,911	4.5	1,447	.2
MONADS	24,146	8.2	108,147	30.4	15,672	1.8
TOTAL	296,195		355,460		873,337	

BIOMASS (mm^3 per liter):

	1955	% of Total	1956	% of Total	1957	% of Total
DIATOMS	3.500	99.8	1.170	88.5	2.420	99.7
DINOFLAGELLATES	.001	+	.003	.2	.004	.2
COCCOLITHOPHORES	.0002	+	.002	.1	.0001	+
MONADS	.002	.1	.147	11.1	.001	+
TOTAL	3.5032		1.322		2.4251	

during the 1956 upwelling season (Table 63) reflects the extraordinary abundance of a large green flagellate (1,713,000 c/L at 10 m) at station 35 (Table 34). Omitting this station, the average monad standing crop becomes about 35,000 c/L, or 12.4 per cent of the total population. The cell volume of this flagellate was 1,950 μ^3, or 30-fold greater than that estimated for the monads in general. Excluding the green flagellate population from the calculations, the average monad standing crop in the 1956 upwelling season becomes 0.002 mm^3 per liter, as contrasted to 0.147 mm^3 per liter; that is, a level similar to that encountered in 1955 and 1957 (Table 63).

The average upwelling standing crop for all groups exceeds their rainy season levels. The diatoms increase 7- and about 9-fold as cell numbers and biomass, respectively, during upwelling, while the dinoflagellates and coccolithophores increase less than 2-fold. The considerable difference in biomass levels of the monads during both seasons reflects, again, the influence of the solitary occurrence of the green flagellate at station 35 (Table 63). However, the relative importance of the flagellate groups increased during the rainy season due to a relatively greater decline in diatom abundance from upwelling levels.

Although the flagellate groups are characterized by a greater seasonal stability in average abundance than the diatoms (Table 62), they, especially the monads, exhibit a considerably more erratic seasonal cycle than the diatoms; the dinoflagellates and coccolithophores exhibit three growth pulses (Fig. 56). Besides the significant seasonal differences in abundance of the diatoms, all groups exhibited considerable station-to-station fluctuations in abundance (Appendix Table 1), as demonstrated by the following observed ranges in cell density:

Diatoms	0 to 4,620,865 c/L
Monads	1,000 to 1,713,000
Coccolithophores	0 to 89,000
Dinoflagellates	0 to 34,940

Thus, phytoplankton communities in the Gulf of Panama are also characterized by a considerably less stable level of abundance than that observed or hypothesized for tropical oceanic and certain non-upwelling inshore areas (Marshall 1933, Steemann Nielsen 1958, Cushing 1959a, Bainbridge 1960, Heinrich 1962). According to Cushing, fluctuations in phytoplankton abundance such as observed in the Gulf of Panama will favor an "unbalanced" predator—prey system in which the algal reproductive rate will initially exceed the herbivore grazing rate. If this is so, one would expect the upwelling phytoplankton biomass maximum to precede the zooplankton maximum, as in inshore temperate and boreal waters (Heinrich 1962), rather than to occur simultaneously, as proposed for tropical oceanic regions (Heinrich 1962). This will be reconsidered in the section on zooplankton.

Annual variations in phytoplankton abundance during the upwelling season and during the period of maximum growth within an upwelling season (Tables 61, 63) are consistent with that expected to accompany a wind-regulated biological cycle, as previously demonstrated in the station-to-station fluctuations in phytoplankton abundance (Figs. 42, 45, 47, 49, 52). Thus, the average total phytoplankton standing crop (as cell numbers) during the 1957 upwelling season was approximately 2.5- to 3-fold greater than during the two previous upwelling periods (1957 > 1956 > 1955), while maximum abundance occurred during March in 1955, January in 1956 and February in 1957 (Tables 61, 63). Although the average diatom cell density in 1957 was approximately 3-fold greater than that in 1955, the mean biomass during the latter year was about 1.5-fold greater (1955 > 1957 > 1956) (Table 63). This "discrepancy" primarily reflects the solitary mass occurrence (1,523,000 c/L) of *Lauderia annulata* at station 7 during 1955 (Table 24). This voluminous diatom has a mean cell volume of 23,107 μ^3 (Smayda 1965a). The following demonstrates the magnitude of *Lauderia's* influence on the 1955 average results:

	c/L	mm³/L
With *Lauderia*	269,334	3.500
Omitting *Lauderia*	138,847	0.912

Thus, as with the green flagellate population, inclusion of the solitary mass occurrence of *Lauderia annulata* tends to mask the average annual variation in diatom importance. Notwithstanding the great importance of *Lauderia* during 1955, a ranking of the upwelling seasons as to biomass is probably 1957 > 1956 > 1955. Quantitative relationships between wind direction and intensity and phytoplankton growth will be treated later.

Comparison of No. 20 net plankton settling volumes with phytoplankton biomass estimates derived from cell enumeration

The No. 20 net (and No. 25) is still used in phytoplankton investigations as a quantitative sampler despite frequent reminders (*vide* Braarud 1958) that, at best, it is only semi-quantitative. Lohmann (1908, p. 195) long ago provided the definitive criticism of the inadequacies of net collections as a quantitative tool in phytoplankton research: "Es handelt sich nicht darum, dass ½ oder ¾ des Vollplanktons beim Netzplankton fehlt, sondern darum, dass dieser Verlust die einzelnen Arten des Planktons in der aller verschiedensten Weise trifft und daher der im Wasser verbleibende Teil eine andere artliche und physiologische Zusammensetzung hat als der im Netz gefangene Teil". Notwithstanding the phytoplankton loss and selectivity associated with the use of nets, additional information is needed for determining whether the capture of voluminous species can compensate for the biomass loss of the smaller species which pass through the net and thereby still provide a reasonable quantitative estimate of the standing crop magnitude for use in food-chain studies. Such a comparison can be made for 26 stations where both biomass estimations of the standing crop in the upper 20 m (*vide* METHODS, and Smayda 1965a) and settling volume determinations of the No. 20 net tows, not hindered by the occurrence of excessive gelatinous material, are available (Fig. 58; Table 64). A strict comparison between these estimates is not possible, however. The calculated biomass represents the mean standing crop in the upper 20 m, whereas estimates of the No. 20 net biomass are based on unmetered vertical tows from the bottom to the surface (40 m), with the volume filtered calculated from the diameter of the net and the distance hauled (Schaefer, Bishop and Howard 1958).

The net plankton, in general, reflects the main trends in phytoplankton abundance based on biomass estimates derived from cell counts (Fig. 58; Table 64). In fact, a fairly good relationship exists between these two estimates. The sample correlation coefficient (r) is 0.47 (P .02). (There is some indication that the stations sampled during 1954 and 1955 can be distinguished from those sampled during 1956 and 1957.) However, there is not a constant relationship between settled and calculated biomass estimates, sustaining the view that a single net tow, as might be taken during a synoptic survey, or tows in general do not provide a reliable index of the phytoplankton standing crop. For example, despite a similar settling volume at several stations there was considerable variation in the calculated biomass present:

Station	**Settling Volume** ($g\ m^{-3}$)	**Calculated Volume** ($g\ m^{-3}$)
6	2.19	0.657
9	2.19	0.005
52	2.23	0.565
57	2.14	7.180

Furthermore, in 85 per cent of the cases the *settled volumes exceeded* those

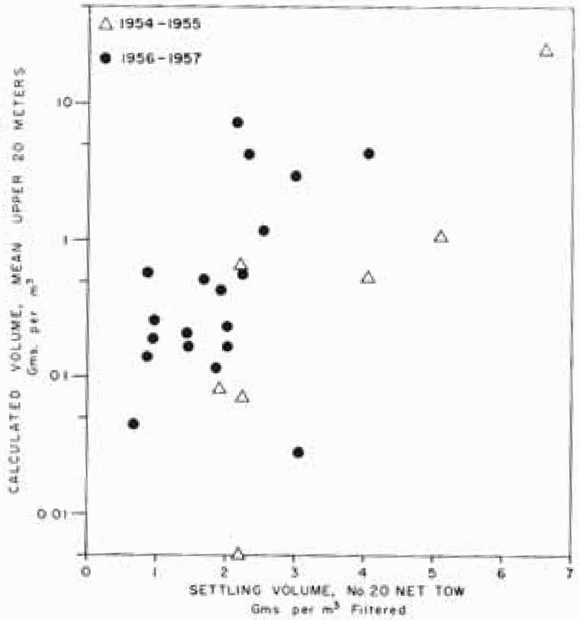

FIGURE 58. Comparison between the calculated mean total phytoplankton (diatoms and flagellate groups) biomass in the upper 20 m and the settling volume of No. 20 net plankton tows, from data presented in Table 64. The sample correlation coefficient (r) is 0.47 (P 0.02).

calculated by 1.2- to 480-fold, whereas the reverse situation occurred at only four stations (stations 7, 56, 57, 60) where *Lauderia annulata* and *Rh. delicatula* and *Rh. stolterfothii* were especially abundant (Table 64).

The persistent and, frequently, considerable excess of settled over calculated biomass is the converse of Lohmann's (1908, p. 203) observations in Kiel Bay where the mean monthly calculated biomass *exceeded* the settled biomass by 7- to 210-fold. He, too, found considerable variability between simultaneous net and calculated volumes, however.

The considerable, and unexpected (Lohmann 1908), excess of settled over calculated volume undoubtedly is partly, if not entirely, attributable to errors associated with net sampling and the determination of settling volume. An important source of error is the unmetered net—only a rough estimate of the water filtered can be calculated from the net diameter and the distance towed (Schaefer, Bishop and Howard 1958). Furthermore, measurements of settling volume give excessively high values for the plankton biomass, being 4-fold greater, on the average, than the more accurate displacement volume technique (Sverdrup, Johnson and Fleming 1942, p. 929). This latter error reflects the inherent bias of net sampling for the capture of setose forms (*Chaetoceros, Bacteriastrum*) which settle inadequately. Indeed, Lohmann (1908) concluded that seasonal variations in net settling volumes primarily reflected the behavior of *Chaetoceros*

TABLE 64. A comparison between the plankton biomass estimated from No. 20 net plankton settling volumes (40 m vertical tow) and the mean phytoplankton biomass* in the upper 20 m calculated from the cell count data (as g m^{-3})

Station	No. 20 Net Settled Volume (A)	Mean Calculated Volume (B)	$\frac{A}{B}$
1	2.23	0.070	31.9
3	5.09	1.056	4.8
5	4.04	0.529	7.6
6	2.19	0.657	3.3
7	6.59	23.899	0.3
9	2.19	0.005	438.0
16	1.92	0.079	24.3
31	3.04	0.028	108.6
32	0.86	0.577	1.5
41	2.02	0.232	8.7
42	1.44	0.208	6.9
44	0.96	0.257	3.7
47	0.67	0.045	14.9
48	1.92	0.426	4.5
49	1.44	0.168	8.6
51	1.87	0.117	16.0
52	2.23	0.565	3.9
55	2.99	2.950	1.0
56	4.06	4.280	0.95
57	2.14	7.180	0.3
58	2.53	1.177	2.1
59	2.02	0.164	1.2
60	2.29	4.223	0.5
61	1.67	0.519	3.2
62	0.96	0.188	5.1
63	0.86	0.138	6.3

* Diatom and flagellate groups included

species. The discrepancy between settled and calculated biomass may possibly result from the net collections being primarily voluminous species which are usually sparse and, thus, inadequately sampled by water bottles or during subsequent enumeration (Hasle 1959). Unfortunately, the net tow samples were not available for microscopic examination. However, this possible cause of the discrepancy between settled and calculated volumes was cursorily checked by examining a net tow collected in the upper 100 m at 6°58′N, 80°39′W in the offing of the Gulf of Panama. The sparse net community was dominated by setose *Chaetoceros* and *Bacteriastrum* species, with only an insignificant giant diatom community, (*Planktoniella sol, Rhizosolenia acuminata*). In addition, a significant juvenile copepod community was present which exceeded the phytoplankton in biomass. This latter observation suggests an additional cause of the discrepancy between the settled and calculated biomass estimations. Thus, the rapid determination of phytoplankton biomass by net sampling techniques provides inadequate standing crop estimates and can not be applied to quantitative analyses of production or food-chain dynamics.

Primary production

The annual primary production at the hydro-biological station has been estimated by Forsbergh (1963) to be approximately 180 g of carbon per m^2, of which about 90 g are produced during the upwelling season (considered to extend from January through April by him). The relationship between ^{14}C assimilation and the diatom standing crop at this station has been examined in detail (Smayda 1965a). A strong direct relationship, irrespective of the species composition, environmental conditions, or dynamic state of the communities, was found between carbon uptake and the magnitude of the diatom standing crop when the latter was expressed as either surface area or plasma volume. Further, the diatom community cell surface area:cell volume ratio (μ^2:μ^3) appeared to influence the rate of ^{14}C assimilation, within certain limits, and the rate of carbon uptake per unit of standing crop was inversely related to the magnitude of the standing crop.

The mean monthly rates of ^{14}C assimilation (as mg C m^{-3} day^{-1}) of the 10 m community based on 24 hour *in situ* experiments are presented in Figure 59. In general, seasonal and monthly variations in ^{14}C uptake parallel that expected from the standing crop cycle (Figs. 56, 57), with well-defined maximum rates of carbon fixation occurring during the upwelling season. Forsbergh (1963: Table 2), with data collected from December 1955 to April 1958, calculated the mean rate of carbon fixation at

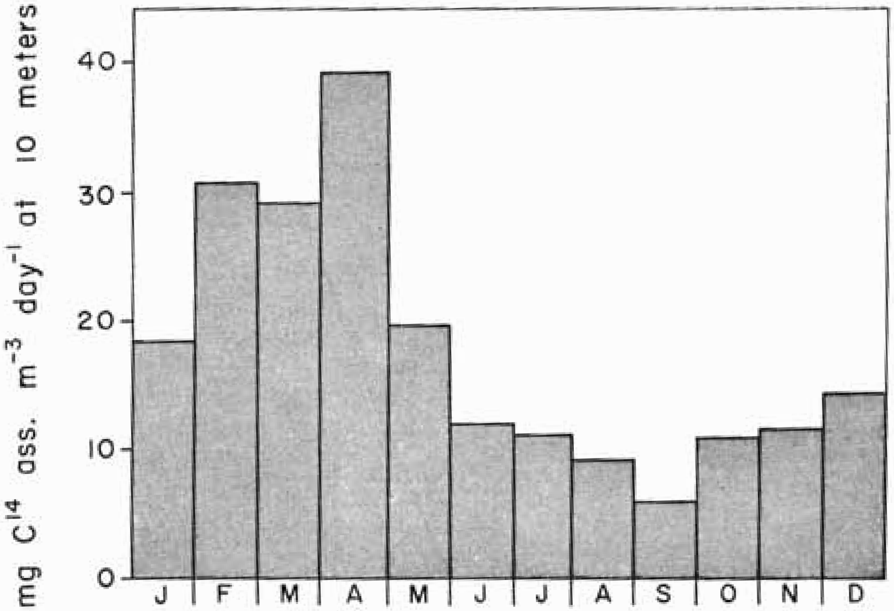

FIGURE 59. Mean monthly ^{14}C assimilation at 10 m at the hydro-biological station from November 1954 to June 1959, based on 79 experiments (modified from Forsbergh 1963).

10 m to be 30 mg C m^{-3} day^{-1} during the upwelling season and 12 mg C m^{-3} day^{-1} during the rainy season. The daily rate of ^{14}C uptake ranged from 1.2 to 57.0 mg C m^{-3} at the stations where phytoplankton counts were made (Appendix Table 1); Forsbergh reported assimilation rates of 180 mg C m^{-3} during the 1959 upwelling season.

Beginning in April 1958 (Station 87) production experiments were made at the surface, 5, 10 and 15 m at 23 stations (Forsbergh 1963: Appendix Table B). Representative vertical profiles of these *in situ* experiments are presented in Figure 60. That considerably greater carbon fixation rates in the upper 15 m usually occurred during the upwelling season rather than during the rainy season is apparent. The frequent occurrence of maximum photosynthetic rates at the surface and a relatively shallow productive zone are also notable.

Of the 23 stations, maximum production occurred at the surface at 16 (about 70 per cent); a similar rate was also found concurrently at greater depths on five occasions. Forsbergh (1963) suggests that the saturation intensity of the Gulf of Panama population is about 70 ly day^{-1} total radiation. The incident total radiation during the productivity experiments ranged from 103 to 692 ly day^{-1} (Forsbergh 1963: Appendix Table B), i.e., usually considerably in excess of this suggested saturation intensity and, therefore, presumably at inhibitory levels. Thus, one might expect that maximum photosynthetic rates would usually not occur at the surface, as appears to be characteristic of the Gulf of Panama (Fig. 60), but at a depth where the light intensity is reduced to about 2- or 3-fold below surface levels (Steemann Nielsen 1963)—at or below the depth of the 50 per cent isolume (Fig. 61). This would usually correspond to a depth of about 5 m at the hydro-biological station (Tables 12, 13). The phytoplankton community was usually more abundant at the surface than at greater depths (Appendix Table 1). It is unknown whether these vertical differences in population density are sufficient to mask any actual inhibition of photosynthesis that might be occurring at the surface; this inhibition is frequently encountered in tropical waters (Steemann Nielsen 1963).

Relatively low rates of carbon fixation at 15 m during both the upwelling and rainy seasons (Fig. 60) suggest a fairly shallow production zone at the hydro-biological station, where the total depth is about 40 m, in agreement with the distribution of standing crop (Fig. 57). (Maximum rates of photosynthesis were observed at 15 m at only 3 of the 26 stations [13 per cent], but a similar rate occurred concurrently at upper depths at 2 of these stations.) To examine this further, the average carbon uptake profiles in the upper 15 m and average light penetration have been prepared for the 1958 rainy season and 1959 upwelling season using data presented in Forsbergh's Appendix Table B (Fig. 61). Incident radiation observations are incomplete during the 1958 rainy season. Since the mean Secchi disc characteristics during the 1956 and 1958 rainy seasons are

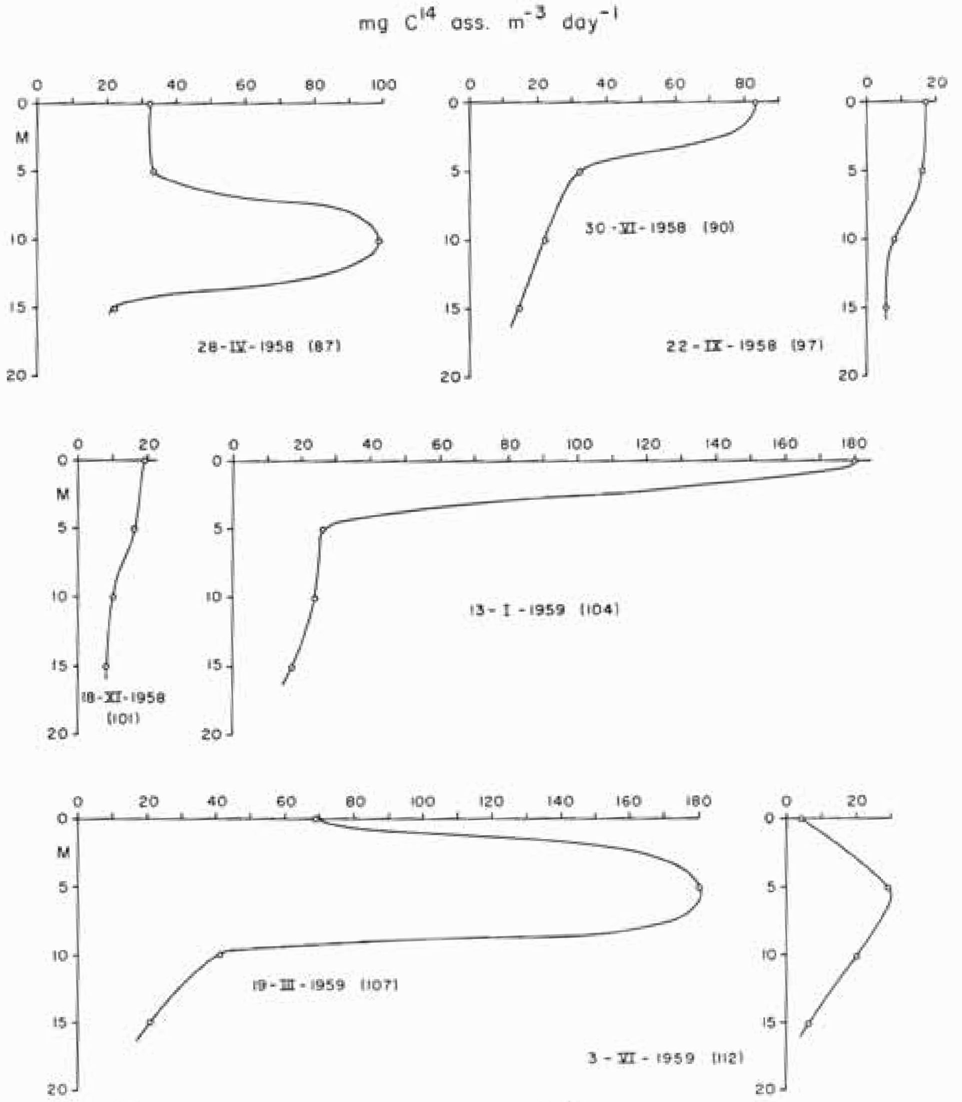

FIGURE 60. Representative vertical profiles of 24-hour *in situ* ^{14}C experiments in the upper 15 m at the hydro-biological station from data presented in Forsbergh (1963). The numerals enclosed in parenthesis, i.e., (87), identify the station.

similar (Tables 12, 13), the mean radiant energy flux at the various isolume depths during the 1958 rainy season (Fig. 61) was derived from the 1956 mean radiation levels.

The mean 50, 10 and 1 per cent isolume depths are similar during the upwelling and rainy seasons, and are found at about 5, 15 and 30 m (Fig. 61). The greater energy flux at these depths during the upwelling season

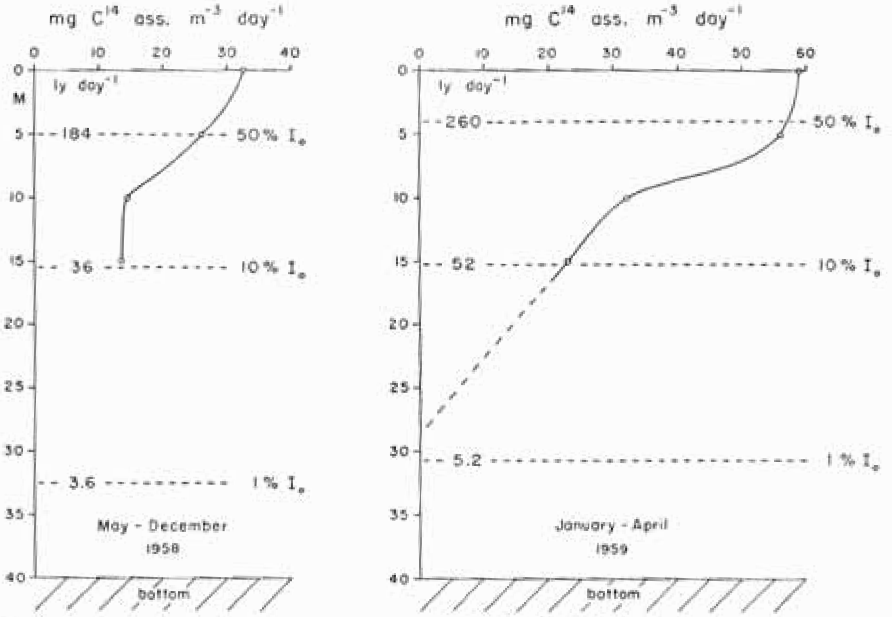

FIGURE 61. A comparison of the average rates of ^{14}C assimilation in the upper 15 m and mean light intensity (langleys per day) at the 50, 10 and 1% isolume depths at the hydro-biological station during the 1958 rainy season and 1959 upwelling season, from data in Forsbergh (1963) and in Tables 12 and 13. See text for further explanation.

is primarily attributable to the greater incident intensities then than during the rainy season (Fig. 26; Table 11). Extrapolation of the mean production curve for the 1959 upwelling season indicates zero production at about 30 m, the approximate mean depth of the photic zone. Extrapolation of the mean rainy season profile suggests carbon fixation continues to the bottom. However, zero production during this season more likely occurs between 15 and 25 m (Fig. 60; Tables 12, 13).

Thus, inadequate light intensities appear to prevent the mean productive zone from extending to the bottom (40 m) during the upwelling and rainy seasons. This is especially likely during the rainy season when reduced incident radiation and increased turbidity of the water column associated with runoff occur (Figs. 26 to 29). However, the associated decrease in plant nutrients during this period (Figs. 30, 37, 39; Tables 15, 16) may be an important secondary factor. During the upwelling season, however, light intensity may be less important in restricting the depth of the production zone. The ascent of the watermass towards the surface during this period may minimize the extension of the production zone much below 20 m, as the results of the phytoplankton enumeration suggest (Appendix Table 1). Nutrient limitation would not appear to be important.

Estimates of production obtained by Steemann Nielsen's (1952) ^{14}C method appear to lie somewhere between "net and gross production"

(Strickland 1960). The 24 hour *in situ* incubation under natural radiation used for the Gulf of Panama experiments differs from the 4- to 6-hour experiments normally conducted using constant, artificial illumination. Thus, the opportunity for re-assimilation of ^{14}C during respiration (Ryther 1956) and the secretion of ^{14}C-labeled organic substances (Fogg 1958), processes favoring a net production estimate, are especially great in the Gulf of Panama experiments. Forsbergh's (1963) estimation of an annual primary production in the Gulf of Panama of about 180 g of carbon per square meter of sea surface, 90 g of which are fixed during the upwelling season might, thus, be considered to represent net particulate production. However, there is also evidence that the ^{14}C experiments in the Gulf of Panama permit an estimate of the standing crop (Smayda 1965a). Nonetheless, it will be assumed that the estimates of production in the Gulf of Panama (Forsbergh 1963) are net production estimates; it is therefore desirable to estimate the annual gross production rate.

Since:

$$\text{Net production} = \text{Gross production} - \text{Respiration}$$

an estimate of respiration of the Gulf of Panama phytoplankton will permit an estimation of the gross production rate. Riley, Stommel and Bumpus (1949) suggest that the respiratory rate of phytoplankton at any given temperature can be determined by:

$$r_t = r_0 e^{sT}$$

where r_t is the respiratory coefficient in g of carbon per day per g of phytoplankton carbon at temperature T; r_0, the respiratory coefficient at 0 C, is 0.0175; and the constant s is 0.069. Mean upwelling and rainy season temperatures of 23 C and 27 C, respectively, are assumed. The calculated respiratory coefficients (r_t) are about 0.076 and 0.100 for the upwelling and rainy seasons, respectively, i.e., 7.6 and 10 per cent of the standing crop carbon. The mean phytoplankton standing crop in the upper 20 m was 2.26 and 0.26 mm^3 per liter during the upwelling and rainy seasons, respectively (Table 62). Assuming a specific weight of 1.0, and estimating the carbon content from the equation given by Strickland (1960):

$$\text{mg C} = \text{F} \times \text{mg algal weight (or mm}^3\text{ algal volume)}$$

where F is assumed to have a value of 0.12, the mean daily diatom standing crop as carbon in the upper 20 m was 5.42 and 0.62 g m^{-2} during the upwelling and rainy seasons, respectively. Applying the respiratory coefficients calculated above, the total carbon respired is:

SEASON	**Carbon Respired +**	**Net Carbon Production =**	**Gross Carbon Production**
Upwelling	60 g m^{-2}	90	150
Rainy	15	90	105
TOTAL	75	180	255

That is, gross production during the upwelling season is 150 g of carbon

m^{-2} and 105 g of carbon m^{-2} during the rainy season, or a total annual gross production of 255 g of carbon m^{-2}. These results are considerably influenced by the higher average standing crop during the upwelling season. One might, in fact, expect the converse result of higher carbon respiratory losses during the rainy season when the prevailing light and nutrient levels (*vide* Gibbs 1963) might be expected to complement the heightened respiratory rates attributable to temperature. Strickland (p. 69 in 1960) has summarized some of the literature dealing with respiration: "There is general evidence that healthy algal cells in culture and nearly all phytoplankters in nature respire at a rate somewhere between about 5% and 15% of the rate of gross photosynthesis at optimum light intensity, although the respiration may almost equal the gross rate when the latter is reduced by gross nutrient deficiencies . . ." Since optimal light and nutrient conditions are not found throughout the upwelling season, respiration is assumed to equal 10 per cent of the gross photosynthesis rate during this season, and to be one-half the gross photosynthesis rate during the nutrient-impoverished rainy season. Under these conditions:

SEASON	**Carbon Respired**	+ **Net Carbon Production**	= **Gross Carbon Production**
Upwelling	10 g m^{-2}	90	100
Rainy	90	90	180
TOTAL	100	180	280

This independent estimate of the annual gross production rate is 280 g of carbon m^{-2}, not appreciably different from that derived above. However, a considerably different picture emerges as to the carbon respired and, hence, gross production during the rainy season. While the latter approximation may be more representative than that estimated using the Riley, Stommel and Bumpus (1949) equation, this cannot be evaluated further. The total annual respiration calculated using the Riley *et al.* equation amounted to about 30 per cent of the gross production rate (75/255) and about 35 per cent (100/280) using the second procedure. For comparison, Riley (1956a) reported that about 55 per cent of the total annual primary carbon production in Long Island Sound is respired by phytoplankton.

Phytoplankton—wind relationships during the upwelling season

Station-to-station oscillations in phytoplankton abundance during the upwelling season are generally related to the total northerly wind intensity at Balboa (Fig. 1) during the 3-day period prior to the sampling date (Figs. 42, 47, 52). During the March 1958 regional survey (Smayda 1963), a well-defined inverse relationship existed between mean diatom abundance and temperature in the upper 10 m. These observations, coupled with the direct relationship between upwelling and northerly wind intensities (Fig. 4), suggest that a predictive phytoplankton abundance-wind relationship exists. This will be examined in the following section.

True north (N) and northwesterly (NW) winds predominate when winds of unequal intensity from all quadrants occur during the upwelling

TABLE 65. The sample correlation coefficient (r) between phytoplankton abundance and wind conditions at Balboa expressed in various ways for all upwelling season observations (***significance at P 0.001; **significance at P 0.01; others—significance at P 0.02)

WINDS:	**UNMODIFIED $\Sigma(N+NW)$**			**MODIFIED, $\Sigma(N+.8NW-S)$**		
DAYS:	**1**	**3**	**7**	**1**	**3**	**7**
Surface (n = 31)						
Cells	0.55**	0.56**	0.48**	0.60**	0.57**	0.49**
Biomass	0.66***	0.66***	0.57**	0.69***	0.66***	0.56**
Sfc. Area	0.67***	0.67***	0.56**	0.69***	0.65***	0.54**
Upper 20 m, Mean (n = 26)						
Cells	0.54**	0.61**	0.47	0.58**	0.62**	0.47
Biomass	0.57**	0.62***	0.51**	0.60**	0.64***	0.52**
Sfc. Area	0.60**	0.65***	0.54**	0.63***	0.67***	0.54**

season (Fig. 3). The wind data have been reduced to true north and true south vectors by calculating the true north component of the northwest winds and the true south (S) component of the southwest and southeast winds at Balboa (Appendix Table 1). That is, in the following text, northwest winds will represent the true north component of these winds, while *total* northerly and *total* southerly winds will refer to the true north and true south components, respectively, of these winds taken collectively.

Northerly winds induce upwelling while southerly winds do not. In fact the latter, when sufficiently intense and prolonged, cause a rise in sea level—the converse of upwelling (Figs. 4, 5). Therefore, an adequate estimate of the magnitude of the *effective* upwelling (i.e., northerly) winds must include the southerly wind intensity. The simplest procedure would be to subtract the latter from the northerly winds: $\Sigma (N-S)$. Statistically, true north and northwest winds appear to be equally effective in causing upwelling (Schaefer *et al.* 1958). The physiography of the Gulf (Fig. 1), however, suggests that differences might be expected. Therefore, the assumption that northwest winds are less effective by some fraction in causing upwelling (phytoplankton growth) than winds from the true north will also be examined.

The influence of unmodified, $\Sigma (N+NW)$, and modified, $\Sigma (N + .8NW - S)$, winds at Balboa on phytoplankton abundance during the upwelling seasons for 1-, 3- and 7-day periods prior to the sampling date has been assessed in 144 estimates of sample correlation coefficient (r) (Figs. 62, 63, 64; Tables 65, 66). The combined data for the upwelling season (Table 65) indicate that phytoplankton abundance expressed as cell numbers, biomass or surface area is significantly and directly related to the wind relationships used. Although the correlation coefficient (r) values are not statistically different, there is a well defined trend for phytoplankton abundance to be better correlated with 1- and 3-day winds than with 7-day winds (Table 65). The correlations on modified and unmodified winds were not appreciably different. Phytoplankton abundance during the 1955, 1956, and 1957 upwelling seasons is also significantly related to the wind

TABLE 66. The sample correlation coefficient (r) between phytoplankton abundance and wind conditions at Balboa expressed in various ways for the 1955, 1956, and 1957 upwelling seasons (** significance at P 0.01; * significance at $0.01 < P < 0.05$; others—significance at $P \leq 0.1$; values in parenthesis after years, i.e., (9), represent the number of observations)

WINDS:	**UNMODIFIED $\Sigma(N+NW)$**			**MODIFIED, $\Sigma(N+.8NW-S)$**		
DAYS:	**1**	**3**	**7**	**1**	**3**	**7**
Surface Cells						
1955 (9)	0.74*	0.73*	0.51	0.70*	0.66	0.44
1956 (11)	0.63*	0.65*	0.60	0.72*	0.68*	0.68*
1957 (11)	0.61*	0.61*	0.41	0.65*	0.67*	0.40
Surface Biomass						
1955 (9)	0.86**	0.82**	0.62	0.83**	0.76*	0.56
1956 (11)	0.62*	0.61*	0.61*	0.69*	0.69*	0.59*
1957 (11)	0.66*	0.67*	0.60	0.66*	0.69*	0.59
Surface μ^2						
1955 (9)	0.84**	0.80**	0.62*	0.80**	0.73*	0.55
1956 (11)	0.70*	0.68*	0.68*	0.76**	0.70*	0.74**
1957 (11)	0.67*	0.68*	0.54	0.70*	0.72*	0.53
Upper 20 m Cells, Mean						
1955 (5)	0.55	0.75	0.30	0.53	0.70	0.24
1956 (11)	0.64*	0.64*	0.57	0.72*	0.67*	0.65*
1957 (10)	0.67*	0.66*	0.63	0.68*	0.72*	0.66*
Upper 20 m Biomass, Mean						
1955 (5)	0.70	0.85	0.44	0.68	0.81	0.38
1956 (11)	0.55	0.51	0.52	0.61*	0.55	0.57
1957 (10)	0.63	0.61	0.72*	0.60	0.63	0.74*
Upper 20 m μ^2, Mean						
1955 (5)	0.68	0.84	0.42	0.66	0.80	0.36
1956 (11)	0.62*	0.59	0.60	0.69*	0.63*	0.65*
1957 (10)	0.71*	0.68*	0.72*	0.70*	0.71*	0.74*

relationships used (Table 66). Although significant statistical differences are not found between the individual correlation coefficient (r) values, certain trends are apparent: 1) phytoplankton abundance and winds were more strongly correlated during 1955 than during the other upwelling seasons, 2) the correlation with 7-day winds was usually lower than with 1- and 3-day winds, and 3) the correlation was usually higher with phytoplankton abundance expressed as biomass or surface area than as cell numbers.

The above phytoplankton—wind relationships also hold, though less thoroughly examined, during the various upwelling season months, as illustrated by the representative March-April conditions (Fig. 65).

The results suggest that the predictive relationship hypothesized between phytoplankton abundance and upwelling winds should be further explored. Accordingly, the relationship between the *mean monthly* biomass in the upper 20 m and some expression of wind intensity during this period was sought. During the upwelling seasons, the hydro-biological station was usually sampled twice a month at approximately 2-week intervals. (Three samples were collected during April 1956 and January 1957.) The mean monthly biomass was related, therefore, to the "3-week winds" during

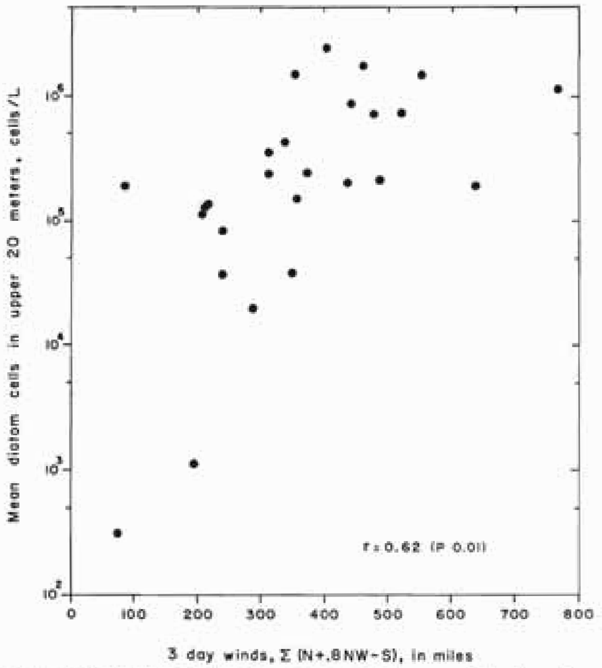

FIGURE 62. The relationship between mean diatom cell abundance in the upper 20 m and the 3-day winds, expressed as Σ (N+ 0.8NW — S), at Balboa prior to the station sampling date during the upwelling season. The sample correlation coefficient (r) is 0.62 (P 0.01).

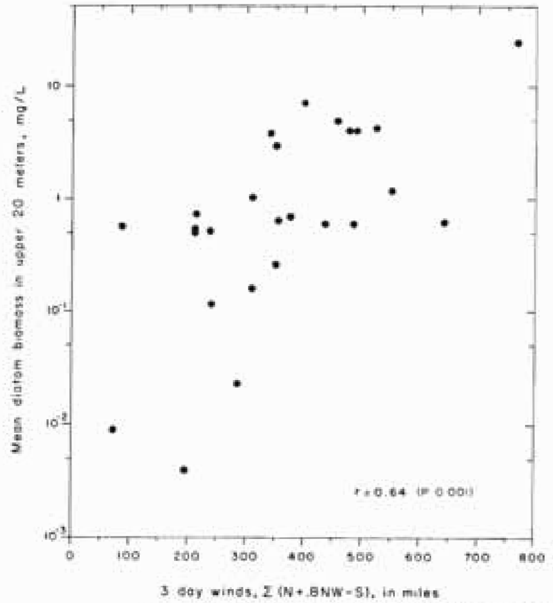

FIGURE 63. The relationship between the mean diatom biomass in the upper 20 m and the 3-day winds, expressed as Σ (N + 0.8NW — S), at Balboa prior to the station sampling date during the upwelling season. The sample correlation coefficient (r) is 0.64 (P 0.001).

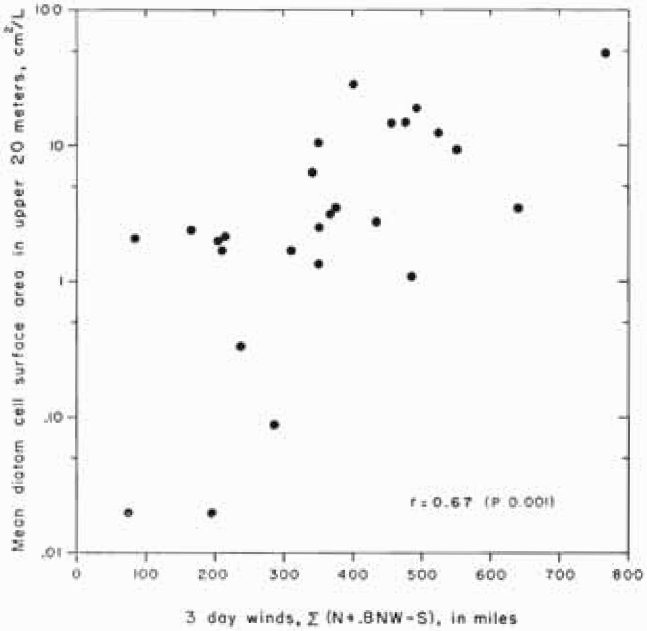

FIGURE 64. The relationship between the mean diatom cell surface area in the upper 20 m and the 3-day winds, expressed as Σ (N + 0.8NW — S), at Balboa prior to the station sampling date during the upwelling season. The sample correlation coefficient (r) is 0.67 (P 0.001).

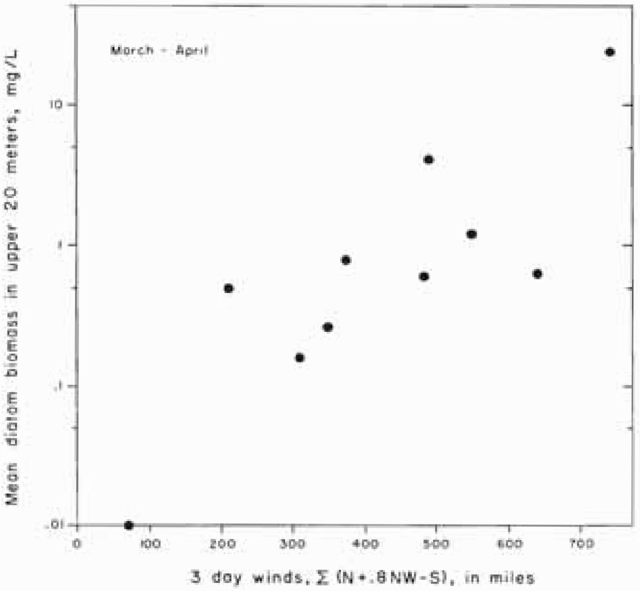

FIGURE 65. The relationship between the mean diatom biomass in the upper 20 m during March and April and the 3-day winds, expressed as Σ (N + 0.8NW — S), at Balboa prior to the station sampling date.

the months of the upwelling season (December—April) for which adequate data existed. The mean monthly biomass and the "3-week winds" were computed as shown in the following examples. During December 1955, samples were collected on the *12th* and *26th* days. The mean monthly biomass in the upper 20 m (641 mg m^{-3}) during this month is simply the mean of the standing crop found on these two sampling dates (740 and 542 mg m^{-3}, respectively). The "3-week winds" represent the total wind intensity during the period from 5 through 25 December, that is, the 3-week period (21 days) immediately preceding the last sampling date. This wind expression is considered to provide a better measure of the winds influencing the observed mean biomass concentration than the total winds during a given month. For example, use of total December 1955 winds would include winds from the *26th* through 31 December which has absolutely no influence on the mean December biomass concentration. Since the "3-week winds" proved effective in establishing a predictive phytoplankton—wind relationship (Fig. 66; Table 67), other wind periods were not tried.

Since three samples were collected during April 1956 and January 1957, the mean monthly biomass calculation for these months differed slightly, to be consistent with the use of the "3-week winds." Two "mean monthly" biomass estimates were derived for each month, as shown in the following example. Samples were collected on 2, 17 and 30 April. The two biomass means were calculated from the 2 + 17 April samples, and from the 17 + 30 April samples. Therefore, two "3-week winds" periods were also needed which extended from 27 March through 16 April, and from 9 through 29 April, respectively. If the mean monthly biomass for April 1956 were calculated using the three stations, then the "3-week winds" would cover the period extending only from 9 through 29 April. This, however, would not provide an estimate of the winds responsible for the biomass concentration found on 2 April. The only serious objection to the procedure adopted for handling the April 1956 and January 1957 data (2 of 13 upwelling season months for which adequate data exist), in contrast to that for the other months, is in the use of the designation "mean monthly biomass" (Fig. 66; Table 67; Appendix Table 4).

The relationship between mean monthly biomass and "3-week winds" was examined by computing linear regressions by the least square method (Table 67; Fig. 66; Appendix Table 4). The correlation coefficient (r) values ranged from 0.63 to 0.91, but there were no statistical differences between these values. Certain trends apparent in the initial analyses were used as a guide in incorporating the northwest and total southerly winds into the "3-week winds" expressions used. For example, the regression on true north winds, ΣN, explained 51 per cent of the observed variation, whereas the regression on $\Sigma (N+NW)$ winds explained only 40 per cent of the variation. This lent credence to the view expressed earlier that northwest winds might not be as effective as winds from the true north in causing upwelling. Therefore, the northwest winds were arbitrarily

TABLE 67. Regression equations: mean monthly phytoplankton biomass in the upper 20 m during the upwelling season on the "3-week winds" relationships (X) expressed in various ways (data presented in Appendix Table 4)

Y = Mean phytoplankton biomass in the upper 20 m, as mg/m^3

Wind Relation X =	Regression Equation	% Variation Explained by Regression	r	Probability	Standard Error of Estimate	d.f.
Σ N	$\text{Log } Y = 2.48849 + .00052(X)$	51	0.72	.01	.106	15
Σ(N+NW)	$\text{Log } Y = 1.60948 + .00049(X)$	40	0.63	.02	.118	15
Σ(N+.1NW)	$\text{Log } Y = 2.38612 + .00054(X)$	50	0.70	.01	.108	15
Σ(N+NW − S)	$\text{Log } Y = 1.58680 + .00051(X)$	48	0.69	.01	.110	15
Σ(N+.1NW − S)	$\text{Log } Y = 2.40582 + .00057(X)$	57	0.76	.001	.100	15
Σ(N+.1NW − 2S)	$\text{Log } Y = 2.45623 + .00057(X)$	64	0.80	.001	.091	15
Σ(N+.1NW − 3S)	$\text{Log } Y = 2.52282 + .00056(X)$	70	0.83	.001	.084	15
Σ(N+.1NW − 4S)	$\text{Log } Y = 2.58766 + .00054(X)$	74	0.86	.001	.078	15
Σ(N+.1NW − 6S)	$\text{Log } Y = 2.72258 + .00050(X)$	79	0.90	.001	.069	15
Σ(N+.1NW − 8S)	$\text{Log } Y = 2.84056 + .00044(X)$	81	0.90	.001	.066	15
Σ(N+.1NW − 10S)	$\text{Log } Y = 2.93885 + .00040(X)$	82	0.91	.001	.065	15
Σ(N+.1NW − 12S)	$\text{Log } Y = 3.01736 + .00035(X)$	82	0.91	.001	.065	15

assumed to be 1/10 as effective as winds from the true north leading to the relationship Σ (N+.1NW). The regression on these winds provided a fit similar to the regression on true north winds, Σ N (Table 67). Since southerly winds are unfavorable to upwelling, a term for these winds in the "3-week winds" expression is necessary. Therefore, regressions of mean monthly biomass on "3-week winds" expressed as Σ (N+NW−S) and Σ (N+.1NW−S) were computed; 57 per cent of the variation was explained by the latter wind relationship as contrasted to 48 per cent by the former (Table 67). These regressions confirmed the desirability of including only a fraction of the total northwest winds in the "3-week winds" expression, as well as including a term for the negative influence of southerly winds on upwelling. Thus, a "3-week winds" expression, Σ (N+.1NW −S), was used in subsequent regression analyses in which the southerly (S) wind term was weighted (Table 67). A progressively greater increase in the per cent of the variation explainable by the regressions accompanied increased weighting of the southerly winds. The regressions of mean monthly biomass on the "3-week winds" expressed as Σ (N+.1NW−10S) and Σ (N+.1NW−12S) explained 82 per cent of the variation ($r = 0.91$). The regression analyses were not pursued beyond these relationships, since the per cent of the variation explained by regressions of this form began to level off. However, either of the latter two regression equations can be used to predict satisfactorily the average biomass in the upper 20 m during a given upwelling season month from a knowledge of the wind conditions at Balboa (Fig. 66; Table 67).

The improved regressions accompanying an increased weighting of the negative influence of the southerly winds on size of standing crop dur-

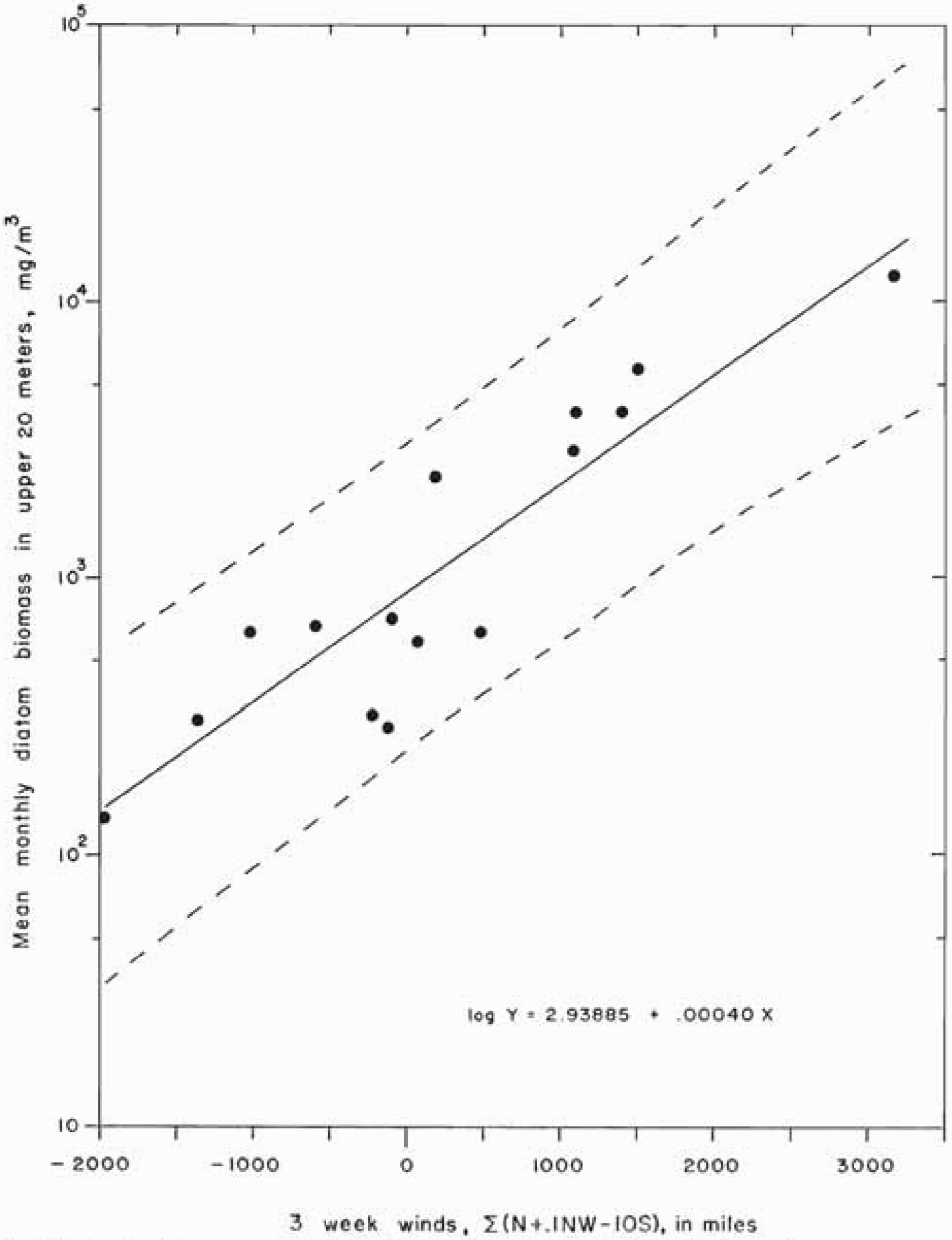

FIGURE 66. The relationship between the mean monthly diatom biomass in the upper 20 m during the upwelling season and the "3-week winds", expressed as Σ (N + .1NW — 10S), at Balboa, along with the 95% confidence limits. In the wind expression, positive (+) wind values indicate that northerly winds exceeded southerly winds during this 3-week period, and negative (—) values indicate that southerly winds exceeded northerly winds. See text for an explanation of the derivation of the regressed variables, and Table 67 for the statistical properties of the regression.

ing the upwelling season is not surprising. These winds have both a direct negative influence on upwelling and an indirect one in the form of an associated decline in northerly, upwelling winds. For example, an increase in southerly winds is usually accompanied by a decrease in northerly winds (Figs. 3, 5, 67). During the upwelling season, then, a subsidence in northerly winds not only causes a reduction in upwelling intensity, but the associated increase in southerly winds reduces the effectiveness of the prevailing northerly winds in causing upwelling. The pronounced decline in population frequently found to accompany a seemingly minor subsidence in northerly winds during the station-to-station analysis (Figs. 42, 47, 52) is undoubtedly attributable, in part, to this dual negative influence of the southerly winds.

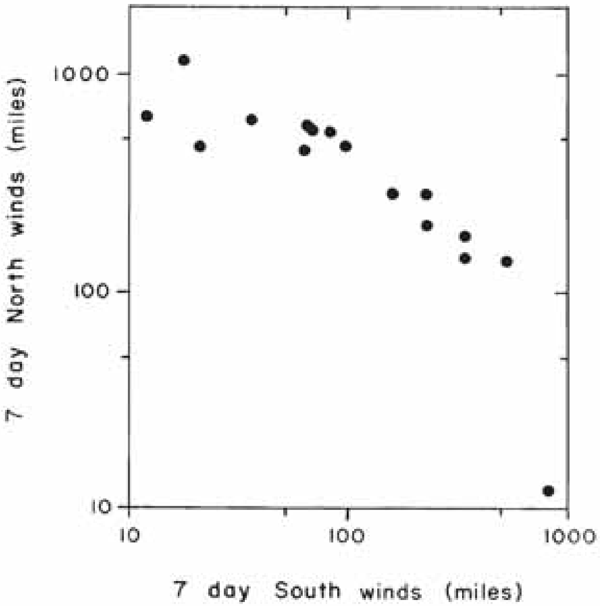

FIGURE 67. The relationship between the simultaneous total northerly winds and total southerly winds at Balboa.

The average diatom biomass in the upper 20 m during the individual upwelling seasons ranged from 1.17 mg L^{-1} in 1956 to 3.50 mg L^{-1} in 1955 (Table 63), suggesting that variations in wind intensity cause annual variations in phytoplankton abundance. The wind characteristics of these three upwelling seasons are summarized in Table 68. Significant differences in true north and northwest wind intensity occurred. The former were approximately 2-fold more intense and the northwest winds about 1.5-fold less intense than during the 1956 and 1957 upwelling seasons. Nonetheless, the *total northerly* winds, Σ (N + NW), were quite similar, being only 5 to 10 per cent less intense in 1956 than during the other years (Table

TABLE 68. Summary of wind intensity at Balboa, in miles, during the 1955, 1956 and 1957 upwelling seasons (N = north; NW = northwest; S = south; SW = southwest; SE = southeast)

Winds:	ΣN	ΣNW	Σ(N+NW)	Σ(S+SW+SE)	Σ(N+.1NW—3S)	Σ(N+.8NW—3S)
1955	12,303	8,951	21,254	860	10,618	17,945
1956	5,096	13,878	18,974	861	3,901	13,615
1957	6,073	14,088	20,161	836	4,974	14,835

TABLE 69. The sample correlation coefficient (r) between the mean phytoplankton biomass in the upper 20 m during the 1955, 1956 and 1957 upwelling seasons, and the accompanying wind intensity at Balboa, as miles, expressed in various ways (ns = not significant at P 0.1)

WIND RELATION	r	PROBABILITY
Σ (N + .1NW — 3S)	0.91	ns
Σ (N + .25NW — 3S)	0.92	ns
Σ (N + .5NW — 3S)	0.95	ns
Σ (N + .8NW — 3S)	0.96	ns
Σ (N + NW)	0.999	0.05

68). The total southerly winds were remarkably similar (about 860 miles) during the three upwelling seasons, and were only about 4 per cent as intense as the total northerly winds.

The influence of various wind relationships on the mean biomass level during the upwelling seasons is illustrated in Table 69 and Figure 68. All correlation coefficient (r) values exceed 0.90, with almost a perfect correlation between mean upwelling season biomass and total northerly winds, Σ (N+NW). This latter correlation may be somewhat misleading, however, since extrapolation of the regression line indicates that zero biomass would occur at a total northerly wind intensity of about 18,000 miles (Fig. 68). Notwithstanding the high (r) values, the other biomass—wind correlations were not statistically significant at the P 0.10 level, presumably because of the low number of observations during the upwelling season (n = 3). Nonetheless, all correlation coefficients suggest that the observed annual differences in mean phytoplankton biomass during the upwelling season are directly related to differences in total intensity of upwelling winds.

It was shown previously (page 483) that the high average biomass during the 1955 upwelling season could be attributed primarily to the solitary mass occurrence of the voluminous diatom *Lauderia annulata*. Omitting this diatom from the 1955 estimate of biomass, a mean of approximately 0.90 mg L^{-1} is obtained, i.e., 4-fold less than that with *Lauderia* included. This suggested that a more accurate ranking of the upwelling seasons based on standing crop as biomass would be 1957 > 1956 > 1955. However, the total wind intensities during the upwelling season, their correlation with mean biomass, as well as the observed mean biomass levels suggest that the ranking should be 1955 > 1957 > 1956 (Table 63).

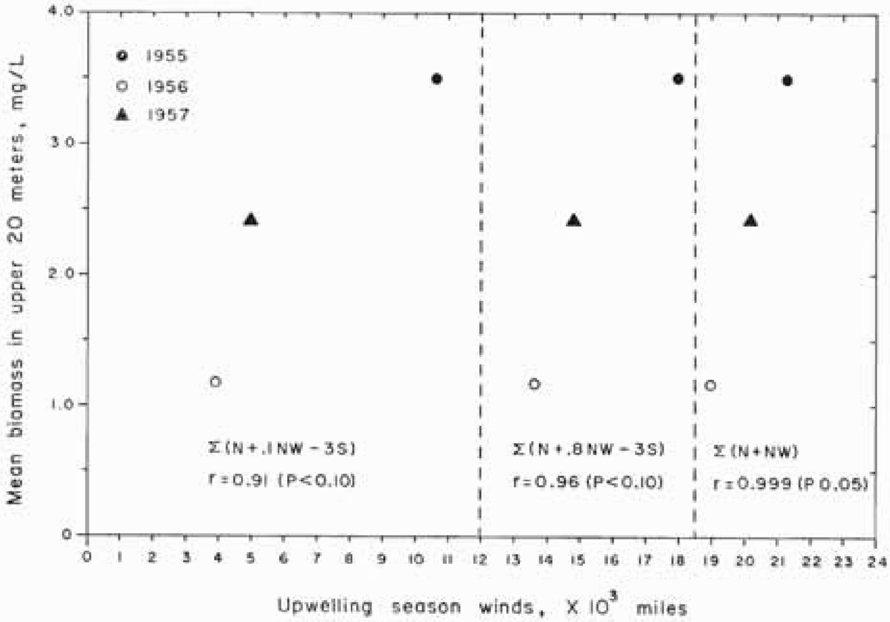

FIGURE 68. The relationship between the mean diatom biomass in the upper 20 m during the 1955, 1956 and 1957 upwelling seasons, and the total upwelling winds at Balboa during these years, expressed in various ways.

Calculation of the diatom biomass during upwelling from wind and surface temperature

Margalef, Muñoz and Herrera (1957) developed an empirical relationship in which the phytoplankton biomass in the upwelled coastal waters off Spain could be estimated from the intensity of favorable upwelling winds and the surface temperature:

$$P = c \times \frac{\sqrt{V}}{t}$$

where P is the mean upwelling season biomass expressed as Harvey Pigment Units, $\sqrt{V}$ is the mean force of the favorable upwelling winds as kg m^{-2}, and t is the mean surface temperature. The constant c has a value of 100 and is used to adjust the decimal point permitting a comparison of the observed and calculated biomass concentrations. The data presented in their Table VI indicate that for the six upwelling seasons (December—May) studied the calculated biomass varied from about −12 per cent to + 34 per cent of the observed biomass.

Similar estimates of the mean biomass (B) in the upper 20 m (mg m^{-3}) have been made at the individual upwelling season stations in the Gulf of Panama using various equations in which the biomass concentration (B) is assumed to be a direct function of the "3-day winds" (as miles) prevailing

TABLE 70. Mean diatom biomass (mg m^{-3}) in the upper 20 m observed at the upwelling season stations, and biomass calculated from the "3-day wind" intensity at Balboa prior to the sampling date and the surface temperature when expressed in various ways

Station	Observed	BIOMASS			
		$\frac{\sqrt{N}}{t_o}$	$\frac{\sqrt{NW}}{t_o}$	$\frac{\sqrt{.5NW}}{t_o}$	$\frac{\sqrt{2N} + \sqrt{.5NW}}{t_o}$
3	1,054	394	621	439	1,000
5	527	368	526	371	890
6	654	294	737	519	935
7	23,895	1,392	366	258	2,222
9	4	517	285	202	932
27	740	134	604	429	619
28	542	152	593	419	633
29	4,130	575	705	500	1,327
30	3,856	448	735	522	1,157
31	23	199	678	479	760
32	559	502	688	487	1,202
33	559	509	866	634	1,353
34	698	133	867	613	802
35	615	875	866	611	1,847
36	9	197	427	299	576
37	259	344	674	476	963
51	114	75	655	464	569
52	560	243	336	239	582
54	4,902	642	530	373	1,284
55	2,948	333	746	528	1,000
56	4,276	465	902	641	1,302
57	7,163	648	683	485	1,396
58	1,170	818	636	449	1,602
59	164	324	739	523	1,398
60	4,221	570	795	561	1,365
61	512	186	671	473	736

at Balboa prior to the station sampling date, and as an inverse function of the sea surface temperature (t_o) found on the sampling date:

$$B = \frac{\sqrt{N}}{t_o} \quad \ldots\ldots (1) \qquad B = \frac{\sqrt{NW}}{t_o} \quad \ldots\ldots (2)$$

$$B = \frac{\sqrt{.5NW}}{t_o} \quad \ldots\ldots (3) \qquad B = \frac{\sqrt{2N} + \sqrt{.5NW}}{t_o} \quad \ldots\ldots (4)$$

where $\sqrt{N}$ represents the true north winds, and $\sqrt{NW}$ represents the true north component of the northwest winds, in miles, and weighted in various ways. The estimates of biomass derived with these equations are presented in Table 70. All equations provided estimates of biomass which agreed fairly well with observed concentrations; no equation provided a consistently good estimate of biomass. A modified version of equation (4) of the form

$$B = c \times \frac{\sqrt{2N} + \sqrt{.5NW}}{t_o} \quad \ldots\ldots (5)$$

where c equals 3.25, also provided estimates of biomass in close agreement with observed values (Table 71). A comparison of the observed biomass and the biomass estimate most closely in agreement with this, and the equation used, are presented in Table 71. Of the 26 upwelling season stations used in the analysis, the observed and calculated biomass levels agreed within ± 15 per cent at 17 stations (65 per cent of the total number), within ± 30 to 40 per cent at four stations, and differed by more than ± 90 per cent at five stations. Interestingly, estimates of biomass with equation (5) agreed fairly well with observed levels at the January stations during 1956 and 1957 (Table 71). There were other trends in which a particular equation provided consistently good estimates, such as the use of equation (1) during the 1956 upwelling season. Such "historical" trends might have prevented, in part, the effective use of a single equation for all stations. Nonetheless, the remarkably good agreement between observed and calculated biomass levels at 17 of the 26 stations suggests that an adequate estimate of biomass as a direct function of favorable winds and an inverse function of temperature, as found also by Margalef *et al.* in Spanish coastal waters, may be possible for upwelling waters in general.

The average diatom biomass in the upper 20 m for the 1955, 1956 and 1957 upwelling seasons was also calculated from the total upwelling season wind intensity, expressed in various ways (including the unfavorable southerly winds), and the mean upwelling season surface temperature (Table 72). The biomass equations:

$$\mathrm{B} = \frac{\sqrt{\mathrm{N}}}{\mathrm{t}_0} \times 10 \qquad \text{and,} \qquad \mathrm{B} = \frac{\sqrt{\mathrm{N} + .1\mathrm{NW} - 3\mathrm{S}}}{\mathrm{t}_0} \times 10$$

provided remarkably good estimates for the 1955 and 1957 upwelling seasons which *agreed within 2 to 5 per cent of the observed mean biomass values;* the 1956 estimates were not in good agreement.

The above analyses of the phytoplankton abundance—wind relationships during the upwelling season in the Gulf of Panama clearly establish that phytoplankton growth during this period is directly related to effective upwelling wind intensity.

Short-term differences and annual variations in phytoplankton abundance appear to be primarily related to differences in the rate of upwelling of cold, phosphate-enriched water caused by variations in the intensity of the upwelling winds. *It would appear, therefore, that the major limiting factor of phytoplankton growth during the upwelling season is the intensity of the effective (northerly) upwelling winds: intense northerly winds promote upwelling and phytoplankton abundance, subsiding northerly winds retard upwelling and phytoplankton growth.* The collapse of the upwelling season and termination of active phytoplankton growth during late April can be attributed to inadequate northerly wind intensity.

Phytoplankton—wind relationships during the rainy season

Southerly rain-bearing winds (Figs. 3, 5), and a decline in phytoplankton abundance from upwelling season levels (Figs. 56, 57; Table 62) charac-

TABLE 71. Observed mean diatom biomass in the upper 20 m (mg m^{-3}) at the upwelling season stations, and the closest approximation calculated from the surface temperature and northerly wind intensity for 3 days prior to the sampling date

		BIOMASS		Difference (%)	
Station	**Month**	**Observed (A)**	**Calculated (B)**	$\left(\frac{B-A}{A} \times 100\right)$	**Equation Used**
3	Jan.	1,053	1,000	− 5	(4)
5	Feb.	527	526	0	(2)
6	Feb.	654	737	+ 13	(2)
7	Mar.	23,895	2,222	− 91	(4)
9	Apr.	4	202	+ 4,950	(3)
27	Dec.	740	619	− 16	(4)
28	Dec.	541	593	+ 10	(2)
29	Jan.	4,130	4,312	+ 4	(5)
30	Jan.	3,855	3,760	− 2	(5)
31	Feb.	23	199	+ 765	(1)
32	Feb.	559	502	− 10	(1)
33	Feb.	559	509	− 9	(1)
34	Mar.	698	613	− 12	(3)
35	Apr.	615	611	− 1	(3)
36	Apr.	9	197	+ 2,089	(1)
37	Apr.	259	344	+ 33	(1)
51	Dec.	114	75	− 35	(1)
52	Dec.	560	582	+ 4	(4)
54	Jan.	4,902	4,173	− 15	(5)
55	Jan.	2,948	3,250	+ 10	(5)
56	Feb.	4,275	4,232	− 1	(5)
57	Feb.	7,162	4,537	− 37	(5)
58	Mar.	1,170	817	− 30	(1)
59	Mar.	164	324	+ 98	(1)
60	Apr.	4,220	4,436	+ 5	(5)
61	Apr.	512	473	− 8	(3)

terize the rainy season. This decline in abundance is probably related to the increased watermass stability (Figs. 23, 24, 25), increased turbidity (Fig. 28) and reduced phosphate concentrations (Figs. 35 to 40) accompanying the intense precipitation (Figs. 19 to 22). Despite this general ecological condition, station-to-station differences in phytoplankton abundance during the rainy season might be related to changes in wind direction and intensity (Figs. 45, 49, 52). The strong inverse relationship between southerly and northerly wind intensity during the rainy season (Fig. 67) suggests that a temporary subsidence in southerly winds will be accompanied by a resurgence of northerly winds, a condition previously demonstrated to favor increased phytoplankton growth. Therefore, the relationship between phytoplankton abundance and various wind conditions at the rainy season stations has been examined in 48 sample correlation coefficient (r) estimates (Table 73). (As in the upwelling season analyses, northerly and southerly winds, when used collectively, will refer to the true north and true south components, respectively, and northwest winds will actually be the true north component of these winds.)

A phytoplankton census could be made at the three sampling depths (0, 10 and 20 m) at only 10 of the 17 rainy season stations. Therefore, cor-

TABLE 72. Observed mean diatom biomass in the upper 20 m (mg m^{-3}) during the 1955, 1956 and 1957 upwelling seasons, and biomass calculated from the average daily wind intensity (miles) at Balboa expressed in various ways and the average surface temperature during these upwelling seasons

UPWELLING SEASON:	1955	1956	1957
Mean Surface Temp. (C)	25.3	25.5	25.2
Mean Daily Winds:			
Σ N	81	34	40
Σ (N + NW)	141	126	134
Σ (N + .1NW − 3S)	70	26	33
Σ (N + .8NW − 3S)	119	90	98
Observed Mean Biomass	3.500	1.170	2.420
Calculated Biomass (B):			
$B = \frac{\sqrt{N}}{t_o} \times 10$	3.557	2.287	2.508
% of Observed Mean Biomass	+1.6	+ 95.5	+3.6
$B = \frac{\sqrt{N + NW}}{t_o} \times 10$	4.690	4.440	4.600
% of Observed Mean Biomass	+34.0	+279.5	+90.0
$B = \frac{\sqrt{N + .1NW - 3S}}{t_o} \times 10$	3.310	2.000	2.280
% of Observed Mean Biomass	−5.4	+70.1	−5.8
$B = \frac{\sqrt{N + .8NW - 3S}}{t_o} \times 10$	4.310	3.720	3.920
% of Observed Biomass	+23.1	+218.0	+62.0

relation analyses are based on the *surface* populations (n = 17) expressed as cell numbers and biomass. (The surface area estimate of the standing crop was not used, since it did not substantially improve the correlations above that using cell numbers or biomass during the upwelling season [Tables 65, 66].) The northwest winds were arbitrarily assumed to be only 80 per cent (.8NW) as effective as the true north winds in some of the wind expressions used. In others, the northerly wind intensity was arbitrarily increased by 2- (2N) or 4-fold (4N) for reasons analogous to those given for weighting the southerly component during the upwelling season analyses. As previously, 1-, 3- and 7-day winds will represent levels prior to the sampling dates.

Phytoplankton abundance was not correlated with the six wind expressions used (Table 73), with none of the correlation coefficients (r) being significant at the P 0.10 level. Nonetheless, two trends were apparent: 1) the strongest relationships were found using the various 7-day wind expressions (r = 0.26 to 0.27), and 2) cell number was better correlated with wind intensity than biomass.

A plot of the abundance of standing crop as a function of the intensity of the southerly winds for various days prior to the sampling dates demonstrated that they were not related.

The relationships between *mean monthly* phytoplankton abundance during the rainy season (May through November) and the mean 3- and 7-day winds prior to the sampling dates within these months were then sought (Fig. 69; Table 73). Both cell numbers ($r = 0.74$) and biomass ($r = 0.79$) were significantly related to 3-day $\Sigma(N + NW)$ winds, and biomass ($r = 0.73$) to 3-day $\Sigma(N + .8NW)$ winds. Neither the 7-day winds nor the southerly wind intensity $\Sigma(N + .8NW - S)$ expressions were significant at the P 0.10 level. Thus, the statistically significant direct correlation between *mean monthly* phytoplankton abundance and 3-day $\Sigma(N + NW)$ winds suggests that, as during upwelling, phytoplankton growth during the rainy season is primarily dependent upon northerly winds. However, the lack of a correlation between the station-to-station fluctuations in phytoplankton abundance and northerly winds during the rainy season (Table 73) differs from conditions during the upwelling season (Tables 65, 66). This suggests that either these winds are *not* primarily responsible for short-term population oscillations during the rainy season or that their influence is obscured. Consequently, other relationships between phytoplankton abundance and environmental conditions were sought.

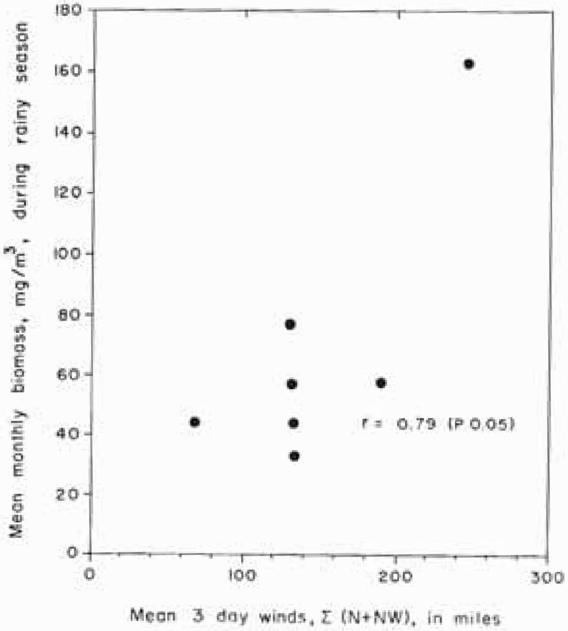

FIGURE 69. Mean monthly surface biomass during the rainy season and the mean "3-day" winds at Balboa expressed as $\Sigma(N + NW)$. See text for further explanation.

Mixing of the watermass induced by northerly winds during the rainy season is usually indicated by increased density (σ_t) of the surface waters, whereas a density decrease accompanies the southerly rain-bearing winds

TABLE 73. The sample correlation coefficient (r) between phytoplankton abundance at the surface and rainy season wind conditions at Balboa expressed in various ways

17 STATIONS:

Winds:	Σ (N + NW)			Σ (N + .8NW)			Σ (N + .8NW — S)		
Days:	1	3	7	1	3	7	1	3	7
Cells	0.19	0.15	0.27	0.19	0.14	0.26	0.02	0.18	0.26
Biomass	0.02	0.07	0.14	0.02	0.07	0.13	— 0.06	0.06	0.10
Winds:	Σ (N — S)			Σ (2N — S)			Σ (4N — S)		
Days:	1	3	7	1	3	7	1	3	7
Cells	0.04	0.18	0.26	0.19	0.17	0.27	0.20	0.16	0.27
Biomass	— 0.05	0.07	0.12	0.03	0.07	0.14	0.03	0.07	0.15

MEAN MONTHLY RELATIONSHIPS:

Winds:	Σ (N + NW)		Σ (N + .8NW)		Σ (N + .8NW — S)	
Days:	3	7	3	7	3	7
Cells	0.74*	0.59	0.64	0.55	0.40	— 0.12
Biomass	0.79**	0.61	0.73*	0.61	0.44	— 0.02

** Significant at P 0.05 level; * significant at P 0.10 level; other correlation values not significant at latter P level

(Fig. 5). This suggests that the station-to-station fluctuations in phytoplankton abundance might be better related to the density of the watermass than to the wind conditions ultimately responsible for the density changes. This might then indicate whether the oscillations in station-to-station populations, and abundance in general, during the rainy season are related to the precipitation and runoff accompanying southerly winds, or to the nutrient renewal accompanying the mixing induced by northerly winds (Fig. 5). If phytoplankton abundance and watermass density are inversely related, southerly winds might actually promote growth (probably through nutrient accretion) while northerly winds would impede growth, i.e., the converse of that observed for the upwelling season and the mean monthly responses during the rainy season (Table 73).

The density—phytoplankton abundance relationship was examined in 16 correlation coefficient analyses (Table 74; Figs. 70, 71). Using all stations (n = 17) and standing crop biomass, the correlation coefficient was 0.35 (not significant to the P 0.10 level), which exceeded those obtained with winds (Table 73); a considerably poorer correlation was obtained using cell numbers (Table 74).

Monthly variations in runoff during the rainy season (Fig. 20; Tables 7, 8) appear to influence the phosphate concentration (Figs. 33 to 40). Consequently, the stations were partitioned into those sampled during May—July (n = 9) and those during August—November (n = 8), and the density—phytoplankton abundance relationship re-examined (Table 74). The correlation coefficients were not significant at the P 0.10 level (possibly because of the low *n*). However, biomass and surface density were *directly* related at the May—July stations ($r = 0.41$), but inversely related during the August—November period ($r = -0.39$). Considerably poorer correlations were obtained with density at 10 m and, except for the August—November period, with cell numbers. *The relationships with biomass, therefore, suggest that during the height (August—November) of the rainy season increased precipitation stimulates phytoplankton growth, while growth prior to this period is dependent upon northerly winds.* Examination of the August—November data (Fig. 70) indicates that one of the eight observations is deviant which, were it not so, would have resulted in an even stronger, and perhaps statistically significant, relationship between surface biomass and density.

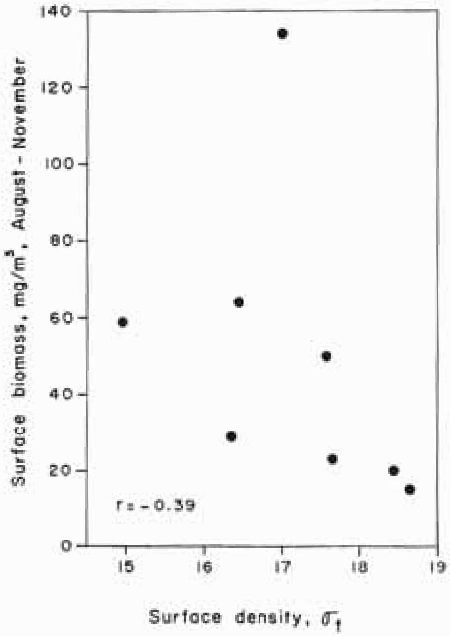

FIGURE 70. The relationship between surface biomass at the stations sampled during August-November and the density of the surface watermass. The correlation coefficient (r) is —0.39 (not significant at P 0.10).

The mean monthly abundance of phytoplankton and surface density (Fig. 71; Table 74) are strongly and significantly related directly with both cell numbers ($r = 0.72^*$) and biomass ($r = 0.79^{**}$). Both indices of standing crop are also significantly related to the 10 m density. This is consistent with the *direct*, statistically significant relationship obtained using mean monthly northerly winds expressed as Σ (N + NW) (Table 73). Partitioning the data into the May—July, and August—November sub-groups (Fig. 71) does not show the inverse relationship during the latter period found for the stations taken individually (Table 74).

Thus, the rainy season results are enigmatic. The *mean monthly* observations of both wind conditions and watermass density suggest that

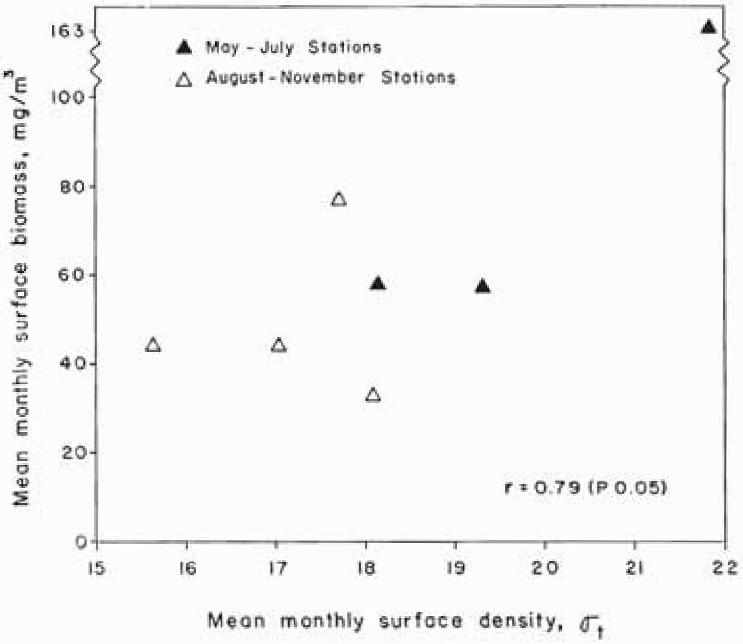

FIGURE 71. The relationship between the mean monthly surface biomass during the rainy season (May-November) and the mean density of the surface watermass.

the average month-to-month fluctuations in phytoplankton abundance can be related to the magnitude of the northerly winds, and, hence, reduction in southerly winds (Fig. 67). The causes of the station-to-station fluctuations in abundance, however, are quite uncertain. There are no clear relationships with any of the wind expressions used. The inverse correlation during August—November (Table 74) which suggests a possible beneficial action of southerly winds (runoff) on growth during this period requires confirmation. It is inconsistent with the reduction in transparency (Fig. 28) and nutrient levels (Figs. 35 to 40), increased stability (Figs. 23, 24, 25), and probable magnitude of the nutrients entering the Gulf of Panama *via* runoff (*vide* page 419) at that time. There is little doubt, however, that the reduction in phytoplankton abundance during the rainy season (Figs. 56, 57; Table 63) is influenced by the reduction in northerly (upwelling) winds (Figs. 3, 4, 5). The specific limitation to growth during the rainy season appears to be inadequate supplies of nutrients (Fig. 30).

PHYTOPLANKTON — ZOOPLANKTON RELATIONSHIPS

The mean zooplankton displacement volume at the hydro-biological station was 160 ml/1000 m^3 during the upwelling season and 92 ml/1000 m^3 during the rainy season, or 6.4 ml m^{-2} and 3.7 ml m^{-2}, respectively,

TABLE 74. The sample correlation coefficient (r) between phytoplankton abundance at the surface and density (σ_t) at the surface and 10 m for all rainy season stations, as well as for the mean monthly levels

	May—Nov.		May—July		Aug.—Nov.	
All Stations	**0 m**	**10 m**	**0 m**	**10 m**	**0 m**	**10 m**
Cells	0.12	0.19	0.07	0.06	— 0.25	0.05
Biomass	0.35	0.35	0.41	0.32	— 0.39	— 0.17
Mean Monthly						
Cells	0.72*	0.68*				
Biomass	0.79**	0.75**				

* significant at P 0.10; ** significant at P 0.05; all other r values not significant at P 0.10 level

for the 112 net tows (*vide* METHODS) made from November 1954 to June 1959 (Forsbergh 1963). Forsbergh did not find an unequivocal phytoplankton—zooplankton relationship; phytoplankton abundance expressed as chlorophyll *a* and as No. 20 net displacement volume led to somewhat different and inconsistent conclusions about this relationship. Using net phytoplankton displacement volume, the simultaneous phytoplankton—zooplankton standing crops for all stations were directly related in a general way ($r = 0.32$, significant at $P < 0.01$) (Forsbergh 1963). There was a poor relationship between the upwelling season standing crops ($r = 0.14$, not significant), and a stronger, direct relationship for the rainy season stations ($r = 0.35$, significant at $P < 0.01$). For individual years, weak, occasionally inverse, statistically non-significant (*r* ranged from −0.09 to 0.26) phytoplankton—zooplankton relationships occurred during both seasons. Lagging the zooplankton 2 weeks (i.e., the zooplankton standing crop was related to the phytoplankton standing crop at the previous station), however, usually led to higher, positive correlation coefficients for each season in the individual years, although the correlations were not statistically significant, probably because of the low number of observations.

Forsbergh's analysis of the phytoplankton—zooplankton relationship was hampered by the use of data from the inadequate No. 20 net, and chlorophyll estimates of the phytoplankton standing crop, the only measures of phytoplankton abundance available to him. It has been demonstrated on page 484 that for a No. 20 net displacement volume of about 2.2 g m^{-3}, the biomass calculations based on cell counts varied from 0.005 to 7.2 g m^{-3}. It has also been shown (Table 12 in Smayda 1965a) that the phytoplankton biomass carbon : chlorophyll *a* ratio ranged from 0.13 to 1369:1 for the Gulf of Panama community. For these reasons, and in order to estimate the magnitude of zooplankton production and grazing in the Gulf of Panama, the phytoplankton—zooplankton relationship has been re-examined using biomass derived from cell counts (Smayda 1965a) as an expression of the phytoplankton standing crop.

The analyses will be restricted to those stations where bottom-to-top oblique zooplankton tows were made (Table 75); surface tows were made at some stations (Appendix Table 1). Zooplankton abundance has been related to both the mean phytoplankton biomass in the upper 20 m (30 stations) and at the surface (39 stations) (Table 75). However, the former estimate is more representative and will be used preferentially in subsequent analyses. The zooplankton data have been presented as ml/1000 m^3 by the Inter-American Tropical Tuna Commission (Forsbergh 1963). Assuming a specific gravity of 1.0, they will also be expressed here as g/1000 m^3, mg m^{-3} and mg m^{-2}, as the need arises. Zooplankton standing crop per square meter of sea surface is based on a water column depth of 40 m.

The phytoplankton—zooplankton relationship has been examined, in part, by computing 84 sample correlation coefficients where the logarithm of the zooplankton standing crop (log [gm/1000 m^3]) is the dependent variable and the logarithm of the phytoplankton biomass (log [gm m^{-3}]) is the independent variable. The correlation existing between zooplankton and phytoplankton abundance during the upwelling and rainy seasons within any given year was not computed if less than four observations were available for that period.

The correlation between standing crops of phytoplankton and zooplankton

Considerable station-to-station variations in plankton abundance and in the ratio of the phytoplankton to zooplankton standing crops occurred (Table 75). The phytoplankton : zooplankton standing crops ratio ranged from 0.04 to 981:1 at the 30 stations used, with the average phytoplankton standing crop per m^3 83-fold *greater* than the zooplankton standing crop at these stations. The zooplankton standing crop exceeded phytoplankton abundance at only four stations (31, 36, 47, 63) (Table 75).

The mean annual phytoplankton and zooplankton cycles (Fig. 72), based on the November 1954 to May 1963 observations, indicate 1) the considerably greater phytoplankton standing crop, and 2) the tendency for a direct phytoplankton—zooplankton relationship during the upwelling season, but an inverse relationship during the rainy season. The mean monthly standing crop of zooplankton exceeded the phytoplankton standing crop only during June; otherwise the latter exceeded the zooplankton by 3- to 29-fold, with an overall average of 11-fold (Table 76). Likewise, the average standing crop of phytoplankton during the upwelling season exceeded zooplankton by about 20-fold, and by 4-fold during the rainy season. Since the zooplankton estimate is derived from sampling the entire water column (40 m), and the phytoplankton estimate from the upper 20 m, it might be thought that the considerable excess of phytoplankton over zooplankton represents a sampling artifact. This has been examined by computing the mean phytoplankton biomass per m^3 for the entire water column assuming that no phytoplankton were present below

20 m (Fig. 72). Even on this basis, the phytoplankton standing crop considerably exceeds that of the zooplankton with the exception of June, as previously, and possibly May and July.

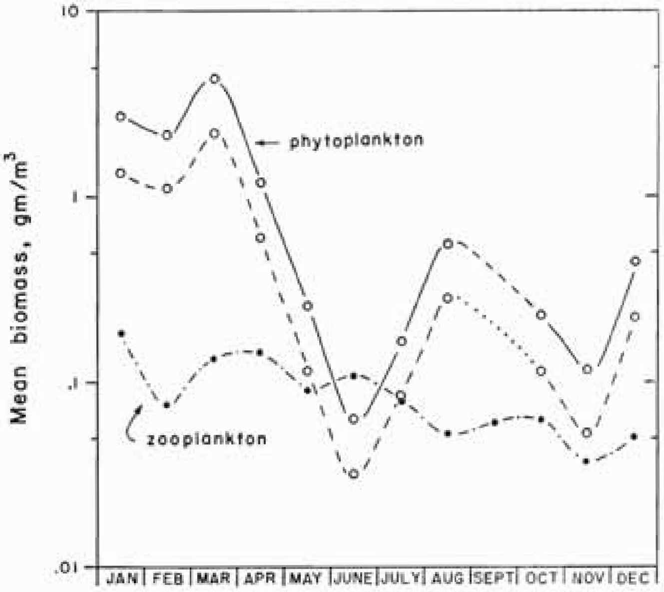

FIGURE 72. The mean annual zooplankton and phytoplankton cycles at the hydrobiological station based on observations from November 1954 to May 1957. The phytoplankton curve, —— —— ——, represents the mean biomass m^{-3} computed for the entire water column (40 m) assuming no phytoplankton exists below 20 m, whereas the phytoplankton curve, ————, represents the mean biomass in the upper 20 m. See text for further details.

The regression[14] of the mean standing crop of zooplankton on the mean standing crop of phytoplankton (Fig. 73), from data presented in Figure 72, indicates a statistically significant, *direct* relationship between these trophic levels ($r = 0.59$) with 35 per cent of the variation explained by the regression (Table 77). Partitioning these data into the upwelling and rainy seasons reveals a positive correlation ($r = 0.66$) between zooplankton and phytoplankton during upwelling, and a weak ($r = -0.15$), *inverse* relationship during the rainy season (Fig. 72). Neither correlation is significant, however, presumably because of the low number of observations.

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[14] August, September and October were not included in the regression for the following reasons: An estimate of mean phytoplankton biomass was not possible for September (Table 61). An August phytoplankton estimate is available only for 1956 when only surface zooplankton tows were made (Table 76). An October phytoplankton mean is available only for 1956, whereas those for the other months are based on 2 to 3 years' observations. Therefore October was also omitted in calculating the regression. However, this datum is indicated in Figure 73 by a filled triangle to indicate that its omission does not alter the above conclusion.

TABLE 75. Mean zooplankton displacement volume and estimated phytoplankton biomass (as mg m^{-3}) (Symbol — indicates no estimations are available)

Station	ZOOPLANKTON	PHYTOPLANKTON		
		Mean, Upper 20 m (A)	Surface (B)	Phytoplankton (A) / Zooplankton
1	6	69.5	32.7	12
2	124	—	217.4	—
3	55	1,056.0	828.7	19
4	32	—	11.3	—
5	57	529.2	643.6	9
6	44	657.3	1,062.2	15
7	50	23,899.2	25,620.4	478
8	596	—	189.0	—
9	484	5.5	18.1	87
10	71	—	6,214.6	—
14	93	—	75.3	—
15	132	—	276.5	—
16	54	79.3	84.0	1.5
27	22	742.8	696.3	34
28	17	546.9	418.1	32
30	777	3,858.8	3,239.0	5
31	206	27.7	53.4	0.13
32	50	577.4	693.9	11.5
33	16	570.3	721.4	36
34	106	709.3	1,387.4	7
35	17	2,842.9	2,472.6	167
36	276	9.8	.5	0.04
41	25	232.3	258.4	9
45	49	—	390.3	—
46	71	—	56.5	—
47	72	44.5	77.5	0.6
49	37	168.2	305.4	5
52	54	565.1	733.6	10.5
53	6	—	1,025.2	—
54	5	4,905.3	1,430.6	981
55	226	2,950.3	756.1	13
56	48	4,280.0	4,983.1	89
57	53	7,180.1	12,305.7	135
58	15	1,177.1	2,719.7	78
59	16	164.2	632.8	10
60	20	4,222.9	5,885.3	211
61	17	519.2	463.1	30
62	23	188.2	101.2	8
63	140	137.6	444.4	0.99
			MEAN	83

The mean monthly standing crop of zooplankton ranged from 37 to 183 mg m^{-3} (Table 76), about 5-fold, whereas the phytoplankton (Table 61) ranged from approximately 67 to 4,460 mg m^{-3}, about 67-fold. This greater seasonal stability of zooplankton (Fig. 72) is unexpected considering the marked fluctuations in phytoplankton abundance. In fact, the anticipated (Cushing 1959a) phytoplankton maximum during the upwelling season prior to a zooplankton maximum was not observed; both maxima occurred more or less simultaneously (Fig. 72).

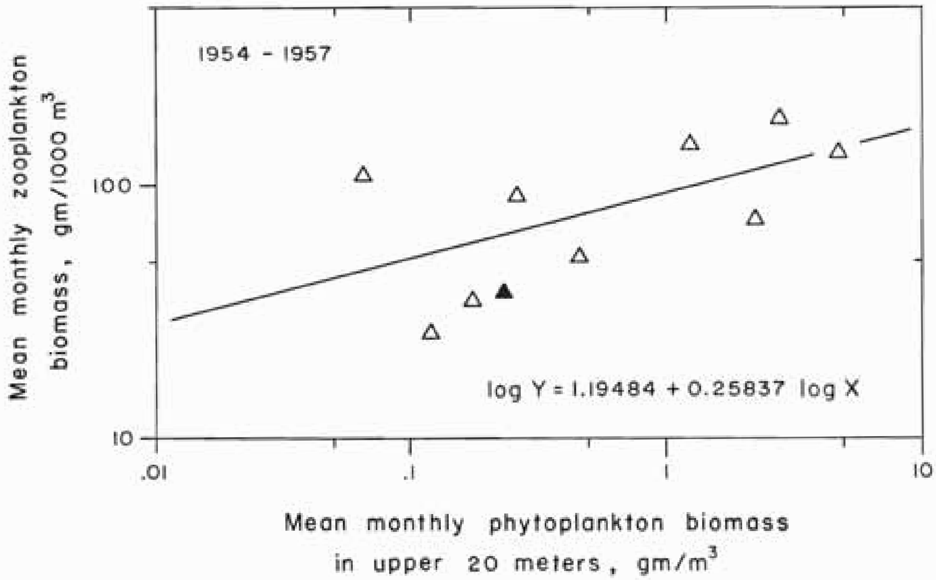

FIGURE 73. The relationship between the mean monthly zooplankton and phytoplankton biomass at the hydro-biological station based on observations from November 1954 to May 1957. The datum, ▲, represents the October standing crops and was not included in the regression calculation for reasons presented in the text. The correlation coefficient (r) = 0.59 (P 0.10).

Significant annual variations in mean zooplankton abundance occurred (Table 76). The average 1957 zooplankton standing crop was 73 mg m^{-3}—approximately 24 per cent lower than during 1955 and 1956 (1955 = 1956 > 1957) and about 75 per cent lower during the upwelling season (Table 76). Unlike these latter 2 years, the average zooplankton abundance during the rainy season in 1957 *exceeded* the upwelling season standing crop (Table 76). On the basis of the average standing crop of zooplankton during the upwelling seasons, the annual rank order is 1955 ≥ 1956 > 1957. Mean phytoplankton and zooplankton abundance during these annual upwelling periods (Table 63) are not causally related.

The correlation between the mean month-to-month variations in zooplankton and phytoplankton standing crops was then determined for the combined data as well as for the individual years (Fig. 74; Table 78). For the combined data, positive (r = 0.25) and negative correlations (r = −0.26) were again found for the upwelling and rainy seasons, respectively, neither correlation was significant. Partitioning these data into the individual years indicates that a positive, statistically significant correlation occurs between zooplankton and phytoplankton during 1955 (r = 0.77) and 1956 (r = 0.83), while an inverse, non-significant relationship (r = −0.34) occurs during 1957 (Table 78). Further partitioning of the data into the 1955, 1956 and 1957 upwelling seasons was accom-

TABLE 76. Mean monthly zooplankton abundance during 1955, 1956 and 1957, and for 1955-1957 combined (* = surface net tows only)

Year:	1955		1956		1957		1955—1957 Combined		Mean Monthly Phytoplankton / Zooplankton
Month	ml/1000 m^3	ml m^{-2}	ml/1000 m^3	ml m^{-2}	ml/1000 m^3	ml m^{-2}	ml/1000 m^3	ml m^{-2}	
Jan.	44	1.8	777	31.1	79	3.2	183	7.3	14.6
Feb.	52	2.1	128	5.1	52	2.1	76	3.0	29.0
Mar.	323	12.9	61	2.4	16	.6	133	5.3	33.5
Apr.	278	11.1	147	5.9	19	.8	147	5.9	10.4
May	122	4.9	56*	?	82	3.3	91	3.6	2.9
June	113	4.5	105	4.2	101	4.0	106	4.2	.6
July	45	1.8	25	1.0	119	4.7	71	2.8	2.5
Aug.	32	1.3	36*	?	101	4.0	53	2.1	10.7
Sept.	21	.8	60	2.4	103	4.1	61	2.4	?
Oct.	59	2.4	38	1.5	97	3.9	63	2.5	3.7
Nov.	13	.5	44	1.8	43	1.7	37	1.5	3.2
Dec.	41	1.6	36	1.4	47	1.9	41	1.6	11.1
Mean	96	3.8	95	3.8	73	2.9	88	3.5	11.1
Upwelling Season Mean:									
	168	6.7	157	6.3	43	1.7	119	4.8	19.7
Rainy Season Mean:									
	65	2.6	47	1.9	94	3.8	69	2.7	4.0

panied by a progressive decline in zooplankton—phytoplankton correlation from r = 0.80 in 1955 to r = 0.18 during 1957, of which none were significant because of the low number of observations. The correlation for the 1956 upwelling season is especially influenced by the datum located in the upper right hand corner of Figure 74. This suggests that the direct zooplankton—phytoplankton relationship during this upwelling period is not as strong as the correlation (r = 0.60) indicates. In fact, the other four observations for this period suggest the possibility of an inverse relationship. Inadequate observations prevent an analysis of the *annual* rainy season zooplankton—phytoplankton relationships.

In summary, the mean monthly standing crops of zooplankton and phytoplankton are directly related, significantly, for 1) the entire investigation (Figs. 72, 73; Table 77), and 2) during 1955 and 1956 (Fig. 74; Table 78). Although not statistically significant, direct relationships also occur during the *upwelling seasons* during these periods, along with evidence of an *inverse* relationship between zooplankton and phytoplankton during the rainy season (Tables 77, 78).

It is now desirable to assess the influence of zooplankton on the station-to-station variations in phytoplankton abundance, and *vice versa*. Either the simultaneous standing crops can be compared, or the zooplankton abundance can be related to an earlier phytoplankton level. The latter appears to evaluate better this relationship than a comparison of the simultaneous standing crops because of the slower rate of development of the zooplankton. For example, lagging the zooplankton population 2 weeks improved the correlation coefficient estimates over those based on

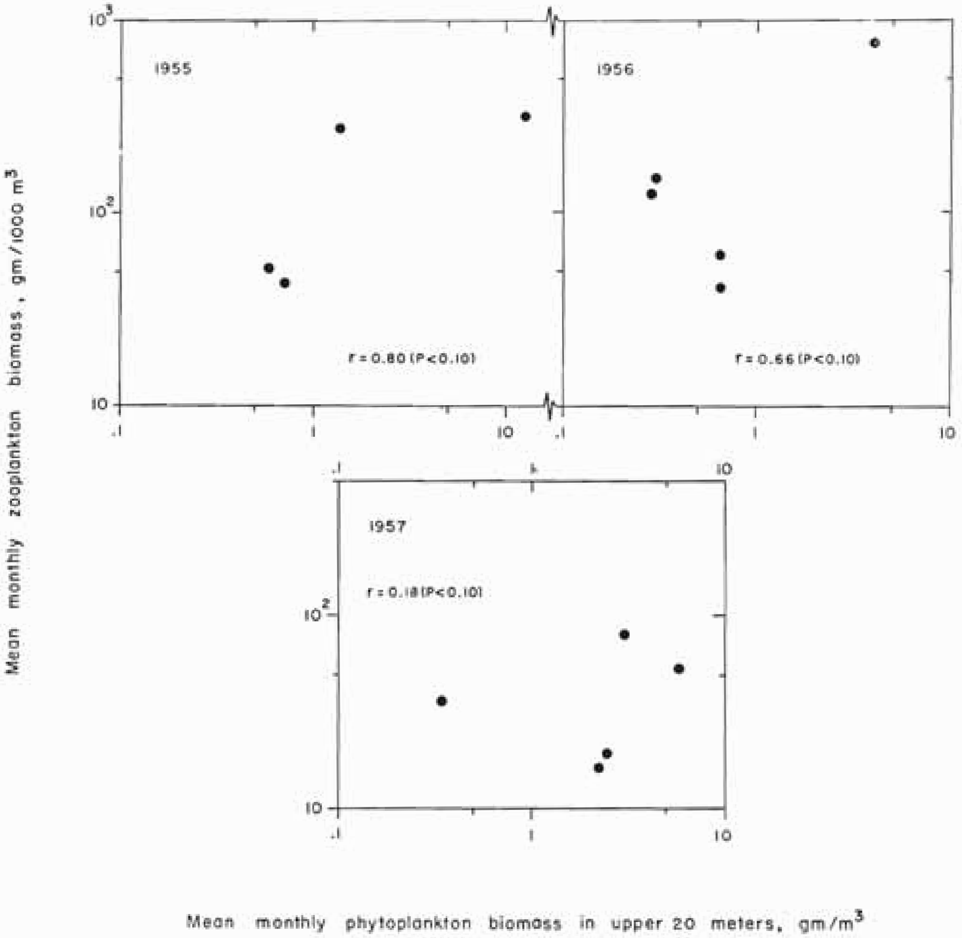

FIGURE 74. The relationship between the mean monthly zooplankton and phytoplankton standing crops during the 1955, 1956 and 1957 upwelling seasons (December-April).

simultaneous population densities (Forsbergh 1963). The 2-week lag period was chosen primarily because this was the interval between sampling dates. A constant lag period is not expected in reality since the generation and development time of the zooplankton can be expected to vary with temperature and food supply. Woodmansee (1958) concluded that *Acartia tonsa* produced 11 generations per year in the sub-tropical waters off Florida. The time interval between successive generations varied from 4 to 7 weeks depending on temperature. Delsman (1926) reported that clupeiod and scombrid fish eggs in the Java Sea hatched within 24 hours, or 3- to 6-times faster than did eggs of related species in European waters. An accelerated zooplankton growth rate at the higher temperatures of tropical waters decreases the time interval between the phytoplankton and zooplankton maxima relative to that found in colder waters.

TABLE 77. Correlation coefficients (r) and regression equation for mean monthly zooplankton (log [gm/1000 m^3]) and mean phytoplankton in the upper 20 m (log [gm/m^3]) using observations from November 1954 through May 1957 (n = number of observations; P = probability level; ns = not significant)

	n	r	P
All data	9	0.59	0.10
Upwelling Season	5	0.66	ns
Rainy Season	4	—0.15	ns

Regression Equation for All Data: $\log Y = 1.19484 + 0.25837 \log(X)$

% Variation explained by Regression	35
Correlation Coefficient	0.59
Probability	0.10
Standard Error of Estimate	0.083

TABLE 78. Correlation coefficients (r) for mean monthly zooplankton (log [gm/1000 m^3]) and mean monthly phytoplankton abundance in the upper 20 m (log [gm/m^3])

	n	r	P
All Data	19	0.35	ns
All Upwelling Data	14	0.25	ns
All Rainy Season Data	5	—0.26	ns
All 1955 Data	6	0.77	0.10
1955 Upwelling Season	4	0.80	ns
All 1956 Data	8	0.83	0.02
1956 Upwelling Season	5	0.66	ns
All 1957 Data	5	—0.34	ns
1957 Upwelling Season	5	0.18	ns

The time interval between the Gulf of Panama zooplankton and phytoplankton maxima when the latter exceeded 1.1 g biomass m^{-3} was approximately 2 weeks during 1955 and 1956 (Table 79). During 1957 a lag period of 40 days occurred between maxima in one instance, otherwise, as demonstrated previously (Table 78), there is no positive phytoplankton —zooplankton relationship during this year.

Using surface and mean (upper 20 m) phytoplankton biomass, correlation coefficient estimates of the station-to-station zooplankton relationships were made 1) using the simultaneous standing crops, 2) lagging the zooplankton 2 weeks, 3) lagging the zooplankton 4 weeks, and 4) relating zooplankton abundance to the average of the simultaneous standing crop of phytoplankton and that present at the preceding station (Table 80).

With the mean phytoplankton standing crop in the upper 20 m and the *simultaneous* zooplankton abundance, the inverse relationship for the combined data ($r = -0.27$) persists when the data are partitioned into the upwelling ($r = -0.39$) and rainy ($r = -0.04$) seasons (Fig. 75; Table 80). *Inverse* relationships are also found for the combined data within

TABLE 79. Relationship between phytoplankton and zooplankton population pulses when phytoplankton peak exceeded 1.1 g per m³

Station	Mean Phytoplankton Abundance in the Upper 20 m ($g\ m^{-3}$)	Zooplankton ($g/1000\ m^3$)	Days Elapsed Between Phytoplankton and Zooplankton Peaks
7	23.899	50	—
8	.098*	596	13
9	.005	481	—
10	4.324*	71	—
11	.097	164	14
29	4.137	?	—
30	3.859	777	14
35	2.843	17	—
36	.010	276	15
54	4.905	5	—
55	2.950	226	15
56	4.280	48	Zooplankton Peak
57	7.180	53	not Observed
58	1.177	15	—
60	4.223	20	—
63	.138	140	40

* mean abundance in upper 10 m

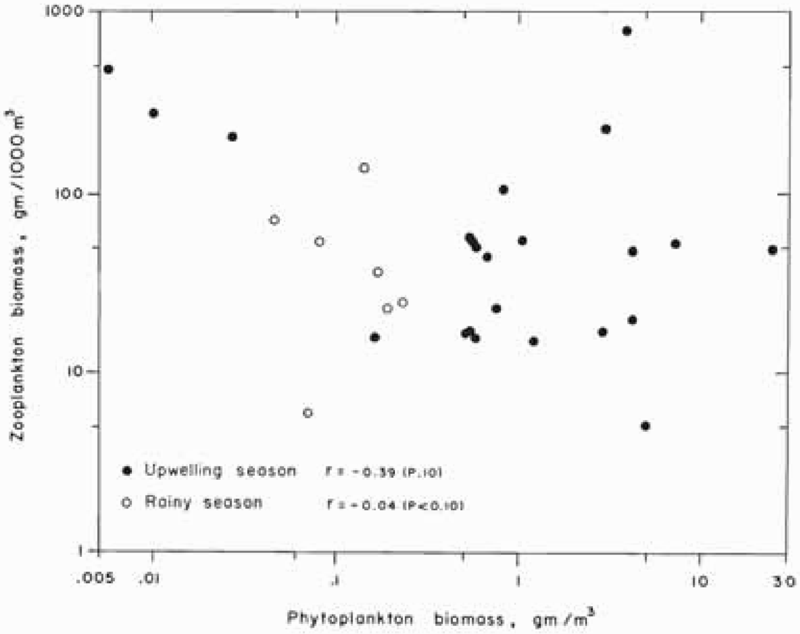

FIGURE 75. The station-to-station relationship between zooplankton abundance and the mean phytoplankton abundance in the upper 20 m at the hydro-biological station.

individual years, and during the 1955 (r = −0.64) and 1956 (r = −0.29) upwelling seasons; it was positive (r = 0.25) during the 1957 upwelling season (Table 80). The inverse correlation progressively weakened from

TABLE 80. Correlation coefficients (r) for zooplankton (log [gm/1000 m³]) and phytoplankton (log [gm/m³]) (** significant at P 0.05; * significant at P 0.1; others not significant at P 0.1)

	Simultaneous Observations		Zooplankton Lagged 2 Weeks		Zooplankton Lagged 4 Weeks	
	n	r	n	r	n	r
A. Using Mean Phytoplankton in the Upper 20 m:						
All Data	30	—0.27	29	0.23	28	0.10
All Upwelling Data	23	—0.39*	22	0.30	22	0.13
All Rainy Season Data	7	—0.04	7	—0.55	6	0.19
All 1955 Data	8	—0.64*	7	0.46	7	0.40
1955 Upwelling Season	7	—0.64*	6	0.43	6	0.35
All 1956 Data	11	—0.21	11	0.60*	11	0.45
1956 Upwelling Season	8	—0.29	8	0.59	8	0.39
All 1957 Data	10	—0.04	10	0.10	10	0.30
1957 Upwelling Season	8	0.25	8	0.45	8	0.59*
B. Using Surface Phytoplankton:						
All Data	39	—0.24	40	0.06	37	0.11
All Upwelling Data	27	—0.34*	26	0.09	23	0.13
All Rainy Season Data	12	0.46	14	0.12	13	0.10
All 1955 Data	13	—0.29	13	0.34	13	0.52*
1955 Upwelling Season	10	—0.30	8	0.29	8	0.52
1955 Rainy Season	—	—	5	0.57	5	0.69
All 1956 Data	13	—0.29	15	0.58**	13	0.44
1956 Upwelling Season	8	—0.33	9	0.55	7	0.36
1956 Rainy Season	5	—0.74	6	0.28	6	0.81
All 1957 Data	11	—0.01	11	—0.26	11	—0.03
1957 Upwelling Season	9	0.18	9	0.06	9	0.13
C. Zooplankton Related to the Average of the Simultaneous and 2 Week Previous Phytoplankton Populations in the Upper 20 m:						
All Data	21	0.15				
All Upwelling Data	18	0.21				
All 1956 Data	9	0.61*				
1956 Upwelling Season	8	0.58				
All 1957 Data	9	—0.07				
1957 Upwelling Season	7	0.49				
D. As Indicated for C, Expect that Surface Phytoplankton Used:						
All Data	35	—0.05				
All Upwelling Data	26	0.03				
All Rainy Season Data	9	0.33				
All 1955 Data	11	0.10				
1955 Upwelling Season	9	0.14				
All 1956 Data	12	0.43				
1956 Upwelling Season	8	0.56				
1956 Rainy Season	4	—0.59				
All 1957 Data	11	—0.15				
1957 Upwelling Season	9	0.17				

1955 to 1957, as for the mean monthly relationship during the upwelling season (Tables 78, 80). When the two 1957 rainy season stations were omitted so that the upwelling season coefficient could be calculated, the zooplankton—phytoplankton relationship changed from an inverse ($r = -0.04$) to a direct ($r = 0.25$) one! With surface phytoplankton biomass, weaker correlations were usually obtained, although the very weak, negative correlation ($r = -0.04$) computed for the combined rainy season data became a fairly strong, positive one (r = 0.46) which just missed significance at the P 0.10 level. Also, a negative correlation coefficient (r = −0.74) characterizes the 1956 rainy season, the only year for which an estimate could be made.

Lagging the animal standing crop *2 weeks*, gave a *direct* zooplankton—phytoplankton relationship, except for the combined rainy season data (r = −0.55), which led to a significantly improved correlation over the simultaneous standing crop comparison (r = −0.04), and for the 1957 surface phytoplankton (r = −0.26) (Table 80). Statistically significant correlations for the combined data were obtained only during 1956 (r = 0.60 and 0.58), whereas the coefficients during the individual upwelling seasons were fairly strong, but not significant (*r* ranged from 0.43 to 0.59). The lack of statistical significance which characterizes most of these relationships probably results from the low number of observations (Table 80). The correlation coefficients were usually considerably lower when based on surface phytoplankton.

The most interesting consequence of lagging the zooplankton *4 weeks* is the high, positive coefficients obtained during the 1955 (r = 0.69) and 1956 (r = 0.81) rainy seasons, with surface phytoplankton. Otherwise, except for the 1957 surface phytoplankton (r = −0.03), a *direct* zooplankton—phytoplankton relationship accompanied lagging the zooplankton by 4 weeks, although the coefficients were generally lower than those computed for the 2-week lag (Table 80).

Relating the zooplankton standing crop to the average of the simultaneous phytoplankton standing crop and that present at the previous station did not improve relations beyond those already discussed.

These diverse relationships confirm that zooplankton populations in the Gulf of Panama can be related to the phytoplankton standing crop (Figs. 72, 73). However, the nature of the relationship obtained is to a large extent governed by the method of analysis, as well as by whether short- or long-term relationships are being sought. Although the various relationships obtained can be accounted for by basic ecological considerations, whether these relationships reflect causal effects or are fortuitous remains in doubt.

Zooplankton grazing and production

Neither the species composition of the zooplankton communities in the Gulf of Panama nor their grazing and respiratory rates were determined. Yet evaluation of the influence of zooplankton predation on the station-to-station variations in phytoplankton standing crop, as well as estimation of the amount of zooplankton production are desirable. This will require the derivation of some approximate estimates of grazing and respiratory rates selected from the literature, after several simplifications of the actual system are made. It will not be possible, for example, to incorporate either the influence of phytoplankton cell size, age and population density (Mullin 1963) or inter-specific differences in zooplankton metabolism (Anraku 1964) in deriving these estimates. The following assumptions are made:

1). Copepods dominate the Gulf of Panama zooplankton communities as in other tropical inshore areas (Russell and Coleman 1934, Bainbridge 1960).

2). The zooplankton dry weight represents 10 per cent of the wet weight, half of which is carbon.

3). The mean daily zooplankton respiratory rate, as carbon, is 12.5 per cent of the dry weight, as determined for zooplankton in the Sargasso Sea (Menzel and Ryther 1961b). The mean temperature during 55 individual measurements of respiration made by these authors on mixed zooplankton tows was approximately 24 C, and ranged from 20 to 29 C; temperature dependence of respiration was not detected. They report that the mean respiratory rate of marine zooplankton found by other authors, and recalculated to 20 C, is approximately 0.10 g carbon/g dry weight of zooplankton/day. From the mean respiratory rate reported by Menzel and Ryther, coupled with the assumptions given in 2), the mean daily carbon loss through respiration is 25 per cent of the zooplankton standing crop expressed as carbon. For comparison, Conover (1956) found that the mean daily carbon requirement of zooplankton in Long Island Sound was 29 per cent of their standing crop carbon, based on the metabolic requirements of *Acartia clausii* and *Acartia tonsa*.

4). The amount of phytoplankton carbon can be derived from

$$\text{mg C} = \text{F} \times \text{mg algal weight (or mm}^3\text{ algal volume)}$$

where F has a value of 0.12 which is the mean of the range, 0.09 to 0.15, given by Strickland (1960). Procedures employed for estimating phytoplankton cell volume (biomass) have been outlined previously (Smayda 1965a). Oblique zooplankton tows were made from bottom-to-top, while phytoplankton samples were collected only in the upper 20 m of the 40 m deep water column. Since an estimation of the *mean phytoplankton standing crop* in the *entire* water column is needed, phytoplankton are assumed to be absent below 20 m in deriving this value. While both the vertical phytoplankton distribution and light transmission characteristics indicate this to be an over-simplification of actual conditions, a considerably lower standing crop is expected in the lower 20 m than in the overlying watermass (Figs. 57, 61).

The station-to-station variations in grazing rate will be estimated only at those stations (30) where estimates of phytoplankton abundance at 0, 10 and 20 m and oblique bottom-to-top zooplankton tows were made.

There are few data relating zooplankton filtration (grazing) rates to temperature. Conover (1956) has determined filtration rates as a function of temperature for summer populations of *Acartia clausii* and *Acartia* *tonsa* collected from Long Island Sound and fed *Skeletonema costatum*. These data were used for the Gulf of Panama zooplankton after deriving the average of the *Acartia clausii* and *tonsa* grazing rates (expressed as ml water filtered per mg dry weight per day) presented by Conover in his Figure 28A (1956, p. 216). The mean temperature of the entire water column at the hydro-biological station was used. The results are presented in Table 81. The principal conclusions are:

1). The daily zooplankton carbon requirements exceeded the phytoplankton standing crop, as carbon, at only 3 (9, 31 and 36) of the 30 stations.

2). Assuming 100 per cent assimilation efficiency, the zooplankton satisfied or exceeded their daily carbon requirements at only 9 stations (3, 7, 30, 35, 54, 55, 56, 58 and 60) i.e., 30 per cent of the total.

3). The maximum calculated grazing intensity was about 10 per cent of the phytoplankton standing crop at 2 stations (9 and 30), with a mean of 2 per cent.

4). The limited data for ^{14}C assimilation indicate that with the exception of stations 30 and 47 net primary production usually exceeded grazing losses.

If such grazing conditions generally existed in the Gulf of Panama, then not only would grazing be insignificant in influencing phytoplankton abundance, but zooplankton respiratory losses would not be met. If one assumes that the respiratory losses, at a minimum, are met, then the estimated rates of phytoplankton carbon assimilation are too low in most instances. However, such under-feeding is probably not due to a sparse phytoplankton standing crop, but rather to an underestimate of the grazing rate accompanying the use of Conover's *Acartia* data.

Recently, Anraku (1964) also reported grazing rates for these two *Acartia* species (collected at various times of the year) at different temperatures when fed the diatom *Thalassiosira fluviatilis*. Extrapolating the data presented by Anraku in his Figures 4 and 5, the mean grazing rate for both *Acartia clausii* and *Acartia tonsa* at 24 C is about 4,500 ml filtered per mg dry weight per day. The mean grazing rate at this temperature, using Conover's data, for both species is about 2,100 ml per mg dry weight per day, i.e., about 50 per cent of the mean value calculated from Anraku. Results based on the latter author's mean filtration value are presented in Table 82. Assuming this grazing rate, the zooplankton satisfied or exceeded their daily carbon requirements at 18 of the 30 stations, i.e., 60 per cent of the time. Further, the maximum zooplankton grazing intensity was about 35 per cent of the phytoplankton standing crop, with a mean of 4.5 per cent. If these data are representative, it again suggests that zooplankton predation is not an important determinant of the phytoplankton standing crop in the Gulf of Panama and, further, that zooplankton respiratory losses are frequently not met. But, if these data are wrong, this

TABLE 81. Phytoplankton (Phyto) and zooplankton (Zoopl) standing crops, as mg C m^{-2}, and zooplankton respiration (Resp) and grazing rates, the latter calculated from Conover's (1956) *Acartia* data. (Stations enclosed in ( ) were sampled during the rainy season)

Station	^{14}C Ass. (mg ^{14}C m^{-2} day^{-1})	STANDING CROP		ZOOPLANKTON		PHYTO GRAZED (mg C m^{-2}) (C)	% OF ZOOPL RESP REQUIREMENTS GRAZED $\left(\frac{C}{B} \times 100\right)$	% OF PHYTO POP GRAZED $\left(\frac{C}{A} \times 100\right)$	% OF PHYTO (A) NEEDED TO MEET ZOOPL RESP (B)
		Phyto (mg C m^{-2}) (A)	Zoopl (mg C m^{-2})	Resp (mg C m^{-2}) (B)	Grazing (Liters m^{-2} day^{-1})				
(1)	—	168	12	3.0	62	0.3	10	0.2	1.8
3	156	2,534	110	27.5	466	29.5	107	1.2	1.1
5	120	1,421	114	28.5	529	18.8	66	1.3	2.0
6	—	1,578	88	22.0	357	14.1	64	0.9	1.4
7	—	57,358	100	25.0	286	41.0	164	0.1	<0.1
9	—	13	968	242.0	4,279	1.3	1	10.0	186.2
(16)	—	190	108	27.0	525	2.5	9	1.3	14.2
27	63	1,783	44	11.0	200	8.9	81	0.5	0.6
28	—	1,313	34	8.5	157	5.1	60	0.4	0.6
30	221	9,261	1,554	388.5	4,351	1,007.3	259	10.9	4.2
31	—	67	412	103.0	1,821	3.1	3	4.6	153.7
32	546	1,665	100	25.0	412	17.1	68	1.0	1.5
33	—	1,369	32	8.0	110	3.7	46	0.3	0.6
34	—	1,702	212	53.0	755	32.2	61	1.9	3.1
35	403	6,823	34	8.5	111	18.9	223	0.3	<0.1
36	—	24	552	138.0	2,352	1.4	1	5.8	575.0
(41)	—	558	50	12.5	240	3.4	27	0.6	2.2
(47)	16	107	144	36.0	708	1.9	5	1.7	33.6
(49)	—	404	74	18.5	342	3.5	19	0.9	4.6
52	122	1,356	108	27.0	497	16.8	62	1.2	2.0
54	676	11,773	10	2.5	38	11.2	448	0.1	<0.1
55	416	7,081	452	113.0	1,668	295.2	261	4.2	1.6
56	312	10,272	96	24.0	365	97.9	408	1.0	0.2
57	—	17,232	106	26.5	369	159.0	600	0.9	0.1
58	338	2,825	30	7.5	111	7.8	104	0.3	0.3
59	33	394	32	8.0	114	1.1	14	0.3	2.0
60	402	10,135	40	10.0	160	40.5	405	0.4	0.1
61	338	1,246	34	8.5	137	4.3	51	0.3	0.6
(62)	90	452	46	11.5	202	2.3	20	0.5	2.5
(63)	130	330	280	70.0	1,361	11.3	16	3.4	21.2
MEAN			199	49.8		62.0	122	1.9	

is probably attributable to an underestimate of grazing, rather than to phytoplankton sparsity.

Both Russell and Coleman (1934) and Bainbridge (1960) reported the copepods *Paracalanus parvus* and *Temora* spp. to be dominant members of the zooplankton community in the Great Barrier Reef region and in a Sierra Leone estuary, respectively. Although species identifications have not been made on the Gulf of Panama samples, Wilson (1942) has presented some data on the zooplankton populations in the Panama Bight. *Paracalanus parvus*, *Pseudocalanus minutus*, and several *Oncaea* species were quite important in the solitary October sample collected by Wilson.

Anraku (1964) has also reported on grazing experiments conducted with *Pseudocalanus minutus*. However, applying the mean filtration rate of about 500 ml per mg dry weight per day at 24 C observed for this species to the Gulf of Panama data would not improve the results over those obtained with the *Acartia* data. Cushing (1959a) has presented grazing rate data for *Paracalanus parvus*. Using these grazing values, after assuming a mean dry weight of 0.06 mg per copepod and converting the Gulf of Panama zooplankton to "*Paracalanus*" units, also does not improve the grazing results over those obtained with Anraku's *Acartia* data. Similar manipulation of Cushing's *Temora* sp. data gives similar results.

Riley, Stommel and Bumpus (1949) used a grazing rate of between 34 and 52 ml per mg wet weight per day for Sargasso Sea zooplankton and 63 ml for Georges Bank zooplankton. Applying these rates to the Gulf of Panama, however, results in even lower intensities of predation than those derived with Conover's mean observations. Cushing (1959b) has presented grazing rates for adult *Calanus* with an average weight of 0.06 mg dry weight per copepod. Converting the Gulf of Panama data into "*Calanus*" units and applying a filtration rate of 2,500 ml per copepod per day results in a predation intensity approximately 20-fold greater than that obtained with the Conover data. Under these conditions, however, the surplus copepod feeding (i.e., in excess of respiratory demands) would be unreasonably high.

At this point the analysis of the station-to-station zooplankton—phytoplankton predatory relationship was discontinued because of inadequate data for grazing. Conover's and Anraku's *Acartia* data were then used for estimating the grazing intensity of the mean zooplankton population during the individual and combined upwelling seasons, and for the rainy seasons (Table 83). The mean phytoplankton standing crops presented in Tables 62 and 63 were recalculated to 40 m assuming no phytoplankton growth below 20 m. From the respiratory and grazing data presented in Table 83, the average daily rate of zooplankton carbon production was estimated from the difference between the carbon assimilated through grazing and that lost in respiration. Applying Anraku's grazing rate, the mean daily carbon production for all upwelling data is:

TABLE 82. Zooplankton grazing and respiration rates, the former calculated from Anraku's (1964) *Acartia* data. (Stations enclosed in ( ) were sampled during the rainy season)

Station	GRAZING (Liters m^{-2} day^{-1})	PHYTO GRAZED (mg C m^{-2}) (C)	% OF ZOOPL RESP REQUIREMENTS GRAZED $\left(\frac{C}{B} \times 100\right)^*$	% OF PHYTO POP GRAZED $\left(\frac{C}{A} \times 100\right)^*$
(1)	108	0.4	13	0.2
3	990	62.8	228	2.5
5	1,026	36.4	128	2.6
6	792	31.2	142	2.0
7	900	129.0	516	0.2
9	8,712	2.6	1	20.0
(16)	972	4.7	17	2.5
27	396	17.7	161	1.0
28	306	10.0	118	0.7
30	13,986	3,237.8	833	35.0
31	3,708	6.3	6	9.4
32	900	37.4	150	2.2
33	288	9.8	123	0.7
34	1,908	81.3	153	4.8
35	306	52.2	614	0.8
36	4,968	3.0	2	12.5
(41)	450	6.3	50	1.1
(47)	1,296	3.5	10	3.3
(49)	666	6.7	36	1.7
52	972	33.0	122	2.4
54	90	26.5	1,060	0.2
55	4,068	720.0	637	10.2
56	864	231.7	965	2.3
57	954	411.0	25	2.4
58	270	19.1	255	0.7
59	288	2.9	36	0.7
60	360	91.2	912	0.9
61	306	9.5	112	0.8
(62)	414	4.7	41	1.0
(63)	2,520	20.9	30	6.3
MEAN		177.0	250	4.4

* B = zooplankton respiration as mg C m^{-2}, and A = phytoplankton standing crop as mg C m^{-2}; data given in columns 5 and 3, respectively, in Table 81

294 mg C assimilated − 60 mg C respired = 234 mg C produced

The mean daily zooplankton standing crop is 240 mg C, and therefore the rate of production, assuming 100 per cent feeding efficiency, is:

$$234/240 \times 100 = 98 \text{ per cent}$$

The daily rate of zooplankton production during the individual upwelling seasons ranged from 46 to 145 per cent (Table 83). Application of Conover's grazing data gave considerably lower production rates. A mean daily production rate of 29 per cent is calculated for all upwelling data, and ranged from about 7 to 52 per cent for the individual seasons. For

TABLE 83. Mean daily phytoplankton and zooplankton standing crops, as mg C m^{-2}, during the upwelling and rainy seasons; mean respiratory and grazing rates using Anraku's (1964) and Conover's (1956) *Acartia* data; and estimates of the mean daily zooplankton production rates

SEASON	STANDING CROP		ZOOPL RESP	ANRAKU DATA			CONOVER DATA		
	Phyto (mg C m^{-2})	Zoopl (mg C m^{-2})	(mg C m^{-2}) (A)	Grazing (Liters m^{-2} day^{-1})	Phyto Grazed (mg C m^{-2}) (B)	Zoopl C Prod (mg C m^{-2} day^{-1}) (B—A)	Grazing (Liters m^{-2} day^{-1})	Phyto Grazed (mg C m^{-2}) (C)	Zoopl C Prod (mg C m^{-2} day^{-1}) (C—A)
Upwelling:									
1955	8,412	380	84	3,015	634	550	1,342	282	198
1956	3,173	315	79	2,835	225	146	1,260	100	21
1957	5,822	85	21	765	111	90	340	50	29
All Data	5,434	240	60	2,160	294	234	960	130	70
Rainy:									
All Data	624	135	34	1,215	19	—15	621	10	—24

SEASON:	UPWELLING				RAINY
	1955	1956	1957	All Data	All Data
Mean Daily Zooplankton Production Rate (%):					
Anraku Data	145	46	106	98	—12
Conover Data	52	7	34	29	—18
% of Phytoplankton Standing Crop Grazed:					
Anraku Data	7.5	7.0	2.0	5.4	3.0
Conover Data	3.4	3.2	1.0	2.4	1.6

the rainy season, however, the mean daily respiratory carbon requirement for 34 mg *exceeded* the average assimilation rates of 19 and 10 mg carbon by approximately 2- to 3.5-fold applying Anraku's and Conover's grazing data, respectively (Table 83).

The assumption of 100 per cent feeding efficiency is undoubtedly not met. Conover (1956) suggests 80 per cent assimilation is a more reasonable value. Notwithstanding the estimate of assimilation efficiency, the daily mean rate of zooplankton production during the upwelling season is about 3-fold greater using Anraku's *Acartia* data (98%) than that derived from Conover's data (29%). In comparison, Conover found a daily zooplankton production rate of 28 per cent in Long Island Sound, and summarized the results of other investigations which indicate daily zooplankton production of about 17 per cent in Block Island Sound, and 10 per cent in the English Channel.

The mean daily predation rate for the various periods was always less than 10 per cent of the daily phytoplankton carbon available (Table 83). This confirms the results of the station-to-station analysis that grazing by the No. 40 XXX net zooplankton is not an important determinant of the magnitude of the phytoplankton standing crop. Furthermore, even if grazing and respiratory rates of zooplankton were considerably underestimated, there would appear to be a large surplus of phytoplankton over that grazed. Therefore, the grazing estimates, in a general sense, are consistent with the phytoplankton—zooplankton relationships presented in Figure 72 and Table 75. Thus, *the data suggest that*, as in Long Island Sound (Riley 1956b), *there is a considerable excess of phytoplankton produced over that consumed by the zooplankton in the Gulf of Panama.*

PHYTOPLANKTON—ANCHOVETA (*Cetengraulis mysticetus*) RELATIONSHIPS

The important tuna bait fish, *Cetengraulis mysticetus*, or anchoveta, appears to be an important phytoplankton grazer during the upwelling season. Bayliff (1963) found diatoms to be the principal food of the anchoveta, and concluded that ". . . juvenile anchovetas are chiefly or entirely filter feeders of the pelagic zone." Adult anchovetas (> 100 mm), however, occur primarily over mud flats of the inner reaches of the Gulf at depths of 5 fathoms or less (Howard and Landa 1958) (Fig. 76) where they feed principally on bottom material (iliophagous) with diatoms again being a principal component of their diet (Bayliff 1963). The pelagic feeding period is of primary interest here.

The anchoveta population spawns once annually from about October to early January (Simpson 1959), i.e., just prior to the upwelling season. Simpson provides evidence that the Gulf of Panama population migrates to the principal spawning area between the Panama Canal entrance and

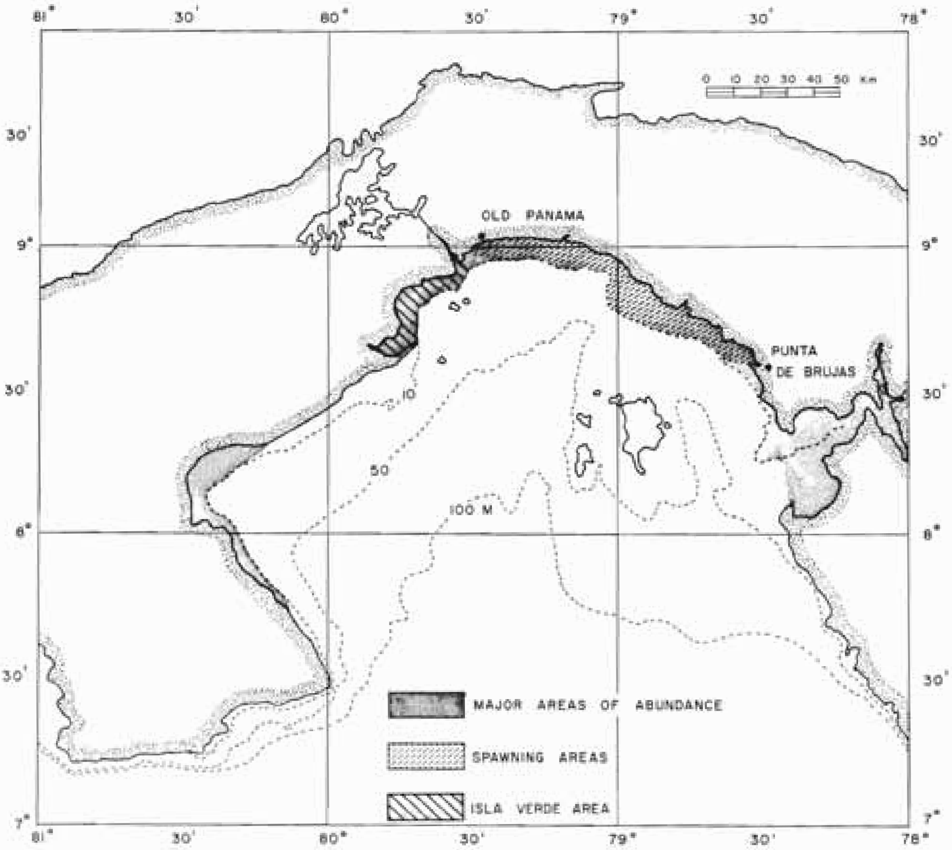

FIGURE 76. Major areas of abundance of the anchoveta, *Cetengraulis mysticetus*, longer than 100 mm standard length (after Howard and Landa 1958 and Bayliff, personal communication) and spawning areas (after Simpson 1959). The delineated area between Chame Bay and the entrance to the Panama Canal represents the area used for estimating population density of the anchoveta at Isla Verde, as discussed in the text.

Punta de Brujas, a distance of about 112 km (Fig. 76). Spawning occurs over a narrow zone in shallow water to 3 fathoms, with the eggs subsequently dispersed by currents as far as 10 km offshore. Spawning occurs between 01:30 and 04:30; the eggs are planktonic initially and then sink as embryonic development proceeds, with demersal hatching in about 20 hours at 25 to 30 C (Simpson 1959). The yolk sac is absorbed between 36 and 42 hours after hatching, and a functional mouth is present after 48 hours. The length is about 3 mm at this time. Juveniles are found in considerable schools offshore during the upwelling season where they are presumably feeding upon the phytoplankton. These schools are heavily preyed upon by larger fish, gulls (*Larus atricilla*), and by fishermen for use as tuna bait (Simpson 1959).

Average length of the juvenile anchoveta is about 25—30 mm during early January and increases to about 120 mm during April (Howard and Landa 1958, Bayliff 1964). That is, their mean length quadruples during their 4-month pelagic phytoplankton feeding stage during the upwelling season, and a 40-fold increase in length occurs in the 5- to 6-month period following the development of a functional mouth at about 3 mm length.

Upon termination of upwelling during April, or even before, the anchovetas move inshore to the shallow mud flat areas found within the 5-fathom line and assume iliophagous feeding supplemented, possibly, by some plankton feeding (Howard and Landa 1958, Bayliff 1963, 1964). There is little additional growth from May until after the following spawning season. The mean pre-spawning length of the first year fish ranged from about 120 to 140 mm during 1951 to 1962 (Bayliff 1964: Table 7). The growth rate of the second- and third-year anchovetas is most rapid during the upwelling season. Bayliff (1964, p. 5) observed that although some anchovetas ". . . survive at least to the beginning of their fourth year . . .," about 90 per cent of the population during any given year is comprised of first-year fish.

It is probable, then, that spawning and growth of the Gulf of Panama anchoveta are linked to the phytoplankton cycle. It is desirable, therefore, to attempt to 1) establish the extent of the relationship between anchoveta abundance and growth and phytoplankton abundance, and 2) to estimate the intensity of anchoveta grazing on phytoplankton during the upwelling season. Bayliff (1964: Table 8) has shown that the mean size of the first-year anchovetas may be related in some way to upwelling intensity. However, he concluded that there were other important, unknown factors also influencing anchoveta growth.

The relationship between anchoveta abundance and phytoplankton standing crop was first investigated (Fig. 77). The average catch per standard day's fishing (CSDF) expressed as scoops[15] per day for the February—April period during the 1955, 1956 and 1957 upwelling seasons (Bayliff 1964: Table 9) was used as a measure of the relative anchoveta abundance. The relative anchoveta abundance increased from 1955 to 1957: 388.5, 482.8 and 528.7 scoops per standard day's fishing, respectively. The mean upwelling season phytoplankton biomass for these years is taken from Table 63. There is no apparent relationship between anchoveta and phytoplankton abundance using these data (Fig. 77). The relationship between the mean *annual* anchoveta CSDF (Forsbergh 1963: Table 12) and phytoplankton abundance was also examined (Fig. 77). Again, there is no apparent correlation between anchoveta and mean upwelling season abundance of phytoplankton.

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[15] The tuna fishermen measure bait in "scoops," a scoop being about 8 pounds of fish lifted from the bait seine into the bait tanks by means of a small dipnet, the instrument also being called a scoop (Alverson and Shimada 1957).

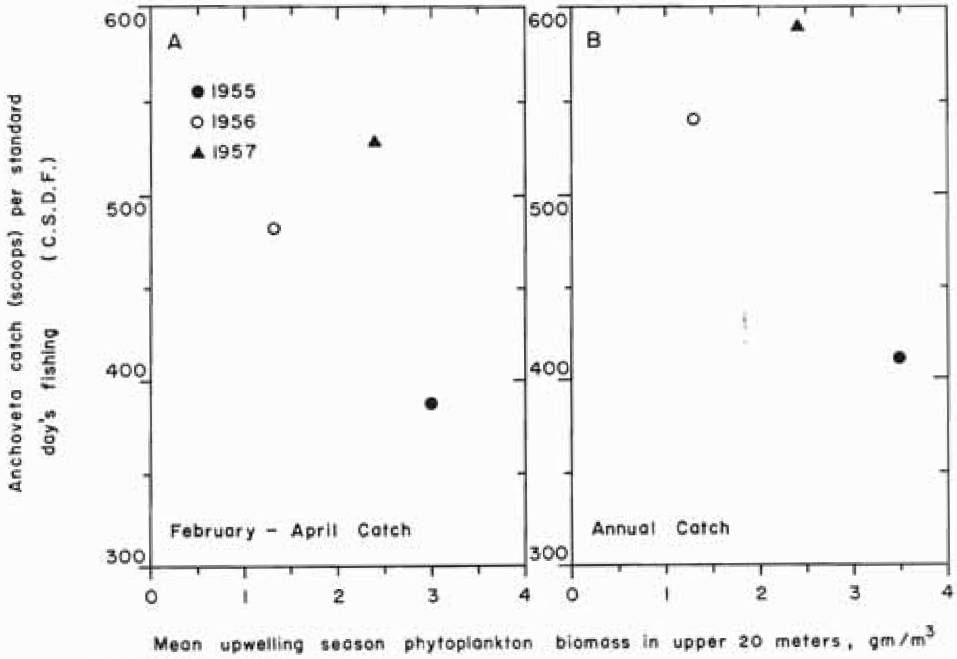

FIGURE 77. A. The relationship between relative anchoveta abundance in the Gulf of Panama based on the average catch in scoops (one scoop contains about 8 pounds) per standard day's fishing effort during February-April (from Bayliff 1964) and the mean phytoplankton standing crop during the 1955, 1956 and 1957 upwelling seasons.
B. As in A, but using the mean *annual* anchoveta catch (from Forsbergh 1963). (The catch statistics have been decreased 10-fold from those presented in Forsbergh's Table 12, since a decimal point appears to have been omitted [Bayliff, personal communication].)

The relationships between 1) mean anchoveta length during April, May and June, respectively, (from data presented in Table 3 of Howard and Landa [1958] and Table 2 of Bayliff [1964]), and 2) mean length during the pre-spawning period (Bayliff 1964: Table 7) and mean upwelling season biomass of phytoplankton during the 1955, 1956 and 1957 upwelling seasons were then examined. There are no apparent correlations (Fig. 78).

The lack of detectable positive relationships between phytoplankton abundance and the abundance and mean length of first-year anchoveta both at the termination of the upwelling season and during the pre-spawning period is not surprising. For example, the convex-shaped growth curve of the anchoveta (Howard and Landa 1958) reflects a decreasing growth rate (in length) accompanying increasing age and size. This characteristic alone, and/or should the anchoveta growth rate be influenced by its population density (*vide* page 12 in Bayliff 1964), might obscure the actual anchoveta growth—phytoplankton abundance relationship when using long-term mean values (Fig. 78). Therefore, the shorter-term phytoplankton—anchoveta relationships based on the latter's month-to-month variations in mean body length and growth rate were examined.

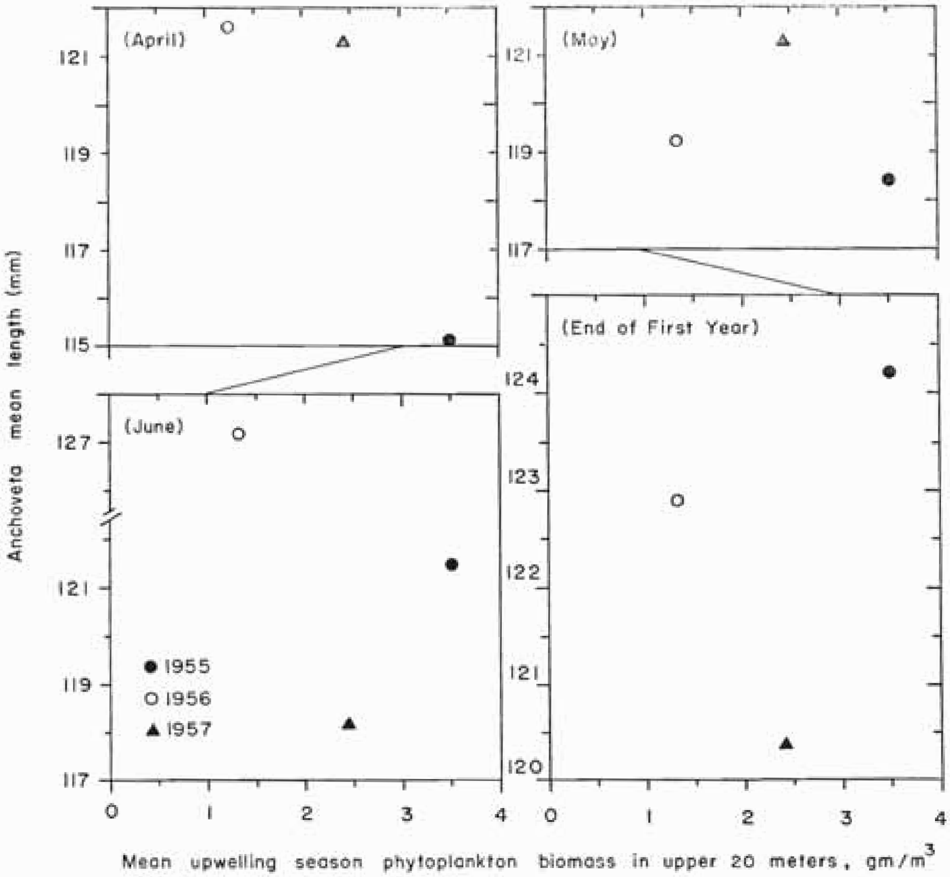

FIGURE 78. The relationships between mean anchoveta length during April, May and June (After Howard and Landa 1958, Bayliff 1964), and during the pre-spawning period (mean length during July-November, from data presented in Table 7 of Bayliff 1964) and the mean phytoplankton standing crop during the 1955, 1956 and 1957 upwelling seasons.

The mean monthly anchoveta lengths during January to May determined for the young of the year by Howard and Landa (1958) for 1955 and by Bayliff (1964) for 1956 and 1957 have been compared with the mean phytoplankton biomass during these months (Fig. 79; Table 84). (The lack of anchoveta and/or adequate phytoplankton data for several of these months prevents a rigorous analysis.) Strong positive correlations exist between mean anchoveta length during February (r = 0.99), April (r = 0.78) and May (r = 0.97) and the average phytoplankton biomass during January and February (Fig. 79C, F, L). Anchoveta length during these months is also generally well-correlated with January and/or

TABLE 84. Mean monthly anchoveta length (mm) during January—May, 1955, 1956 and 1957, and mean monthly phytoplankton biomass in the upper 20 m (g m^{-3}) (nd = no data)

	ANCHOVETA (mm)			PHYTOPLANKTON (g m^{-3})		
	1955*	1956	1957	1955	1956	1957
Jan.	nd	56.4	nd	.712	3.998	3.010
Feb.	58.5	64.9	79.8	.594	.302	5.730
Mar.	100.5	97.0	nd	12.387	.640	.671
Apr.	115.1	121.6	121.3	1.389	1.025	2.371
May	118.4	119.2	121.3	nd	nd	.163

* 1955 anchoveta data taken from Table 3 in Howard and Landa (1958); 1956 and 1957 anchoveta data taken from Table 2 in Bayliff (1964)

February phytoplankton abundance, but the greater scatter of the limited data makes these relationships less certain (Fig. 79A, B, D, E, J, K). Mean anchoveta length during April and May is less strongly and not always positively correlated with March and April phytoplankton levels (Fig. 79G, H, I, M, N, O). These observations suggest, therefore, that anchoveta size is especially influenced by phytoplankton standing crop levels present during January—February. This is not inconsistent with Bayliff's (1964) findings that anchoveta size appeared to be related to upwelling intensity only during February and March.

Notwithstanding these conclusions, it is difficult to assess to what extent the observed relationships are artifacts of the limited data, or are attributable to other causes. For example, Bayliff (personal communication of 19 May 1965) has questioned whether the relationship in Figure 79C is meaningful. He points out that anchoveta ". . . growth is rapid in February, so the average size of fish taken during that month is largely dependent upon the dates during the month the sampling is conducted. The fish tend to school by size, so the methods and locations of sampling would also influence the average size of the fish in the samples. The numbers of samples taken in February of 1955, 1956 and 1957 were 12, 10, and 3, respectively."—which he suggests may not be sufficient for an estimate of the ". . . true size . . ." of the February anchovetas. The actual number of fish measured in these samples was 3,733 in 1955 (Table 3 in Howard and Landa 1958), and 896 and 738 during February 1956 and 1957 (Table 2 in Bayliff 1964), respectively. Therefore, confirmation of the positive relationships between anchoveta size and phytoplankton abundance (Fig. 79) is desirable and was sought by comparing the deviations from *expected* anchoveta length at various ages to the amount of phytoplankton present. Bayliff (1964: p. 9) has analyzed the anchoveta growth data presented by Howard and Landa (1958) and derived approximate mean lengths expected at the *beginning* of each month: February, 48 mm; March, 82 mm; April, 104 mm; May, 115 mm (Table 85). Since the December 1 length is 0 and that on 1 February is 48 mm, the January 1 length is assumed to be 24 mm. Bayliff (1964) gives 30 mm as the mid-January length. The

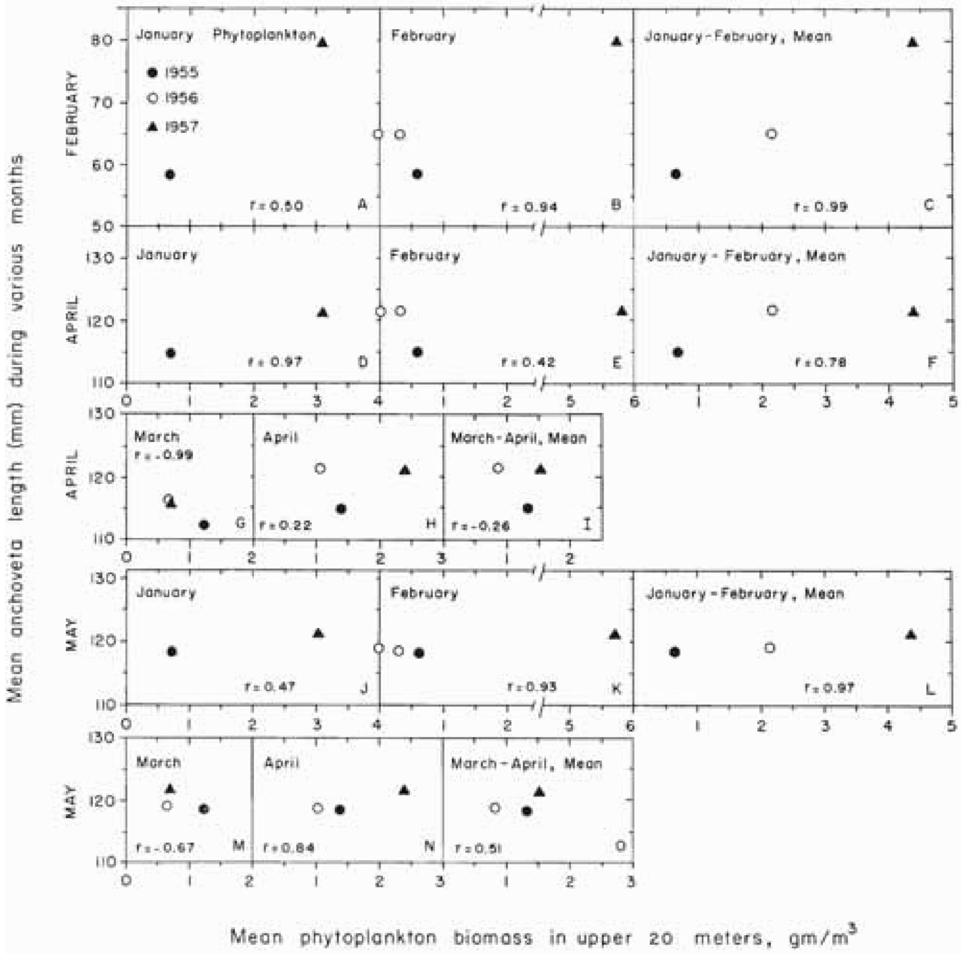

FIGURE 79. The relationships between mean monthly length of first-year anchoveta in February, April and May (after Howard and Landa 1958, Bayliff 1964) and mean phytoplankton standing crop during various months (given in upper left hand corner of each panel) in 1955, 1956 and 1957.

deviations of the observed mean anchoveta length from that expected for first-year fish have been determined for the January to May populations during 1955, 1956 and 1957 and related to phytoplankton abundance (Fig. 80; Table 85). Excluding the March 1955 datum, when an extraordinarily high average standing crop of the voluminous diatom ***Lauderia annulata*** occurred, there is a positive correlation (r = 0.77) between mean monthly anchoveta growth increment and size of the phytoplankton standing crop. (The coefficient of correlation is 0.45 when March 1955 is included.) This relationship clearly confirms the direct influence of phytoplankton abundance on anchoveta growth rate during the upwelling sea-

TABLE 85. Mean anchoveta length (mm) at the beginning of each month from January—May 1955 to 1957 as derived by Bayliff (1964), annual deviations (△) in mean anchoveta length from Bayliff values during these months, and mean phytoplankton abundance in the upper 20 m (g m^{-3})

Month:	Jan.	Feb.	Mar.	Apr.	May
Mean length at 1st of month (A)	24	48	82	104	115
Mean 1955 length*	nd	58.5	100.5	115.1	118.4
△ from A	—	+10.5	+18.5	+11.1	+3.4
Phytoplankton	—	.594	12.387	1.389	nd
Mean 1956 length*	56.4	64.9	97.0	121.6	119.2
△ from A	+32.4	+16.9	+15.0	+17.6	+4.2
Phytoplankton	3.998	.302	.640	1.025	nd
Mean 1957 length*	nd	79.8	nd	121.3	121.3
△ from A	—	+31.8	—	+17.3	+6.3
Phytoplankton	—	5.730	—	2.371	.163

* sources of 1955, 1956 and 1957 anchoveta data are as given in Table 84

son noted previously (Fig. 79). In addition, both analyses (Figs. 79, 80) suggest that the *annual* variations in anchoveta abundance and mean size (Bayliff 1964) are attributable, in part, to *annual* variations in phytoplankton abundance, notwithstanding the data shown in Figures 77 and 78.

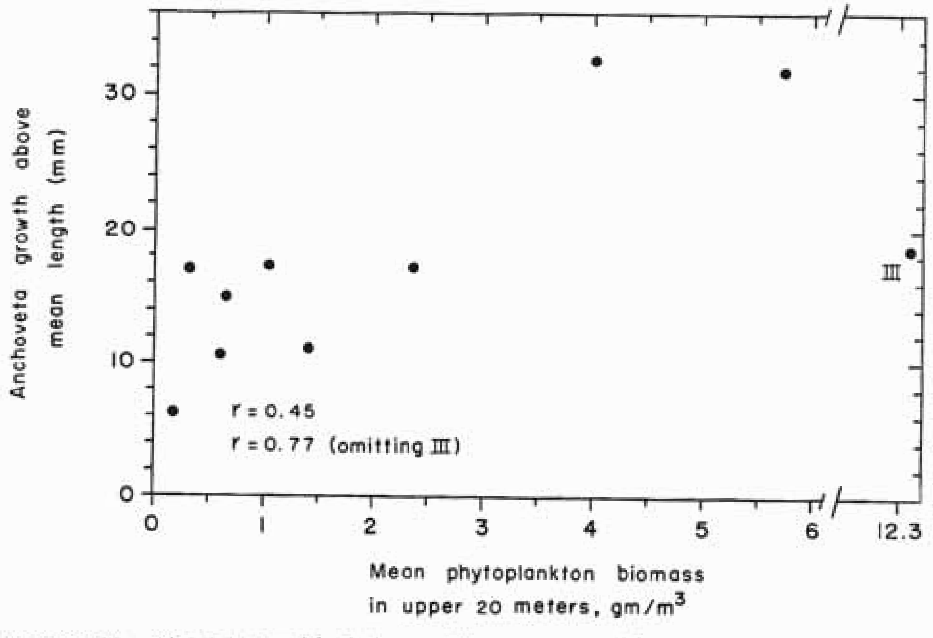

FIGURE 80. The relationship between the mean monthly anchoveta growth increment in mm above the expected mean body length at the beginning of each month from January to May, and the mean monthly phytoplankton standing crop for 1955, 1956 and 1957, from data in Table 85.

TABLE 86. Calculation of mean length (mm) of first-year anchovetas based on the data reported by Howard and Landa (1958) and Bayliff (1964) for 1951 to 1962 in the Gulf of Panama

Month	Σ (mm)	Observations (n)	Mean Length (mm)
Jan.	246.7	7	35.2
Feb.	382.2	6	63.7
Mar.	662.0	7	94.6
Apr.	936.1	8	117.0
Σ	2,227.0	28	
GRAND UPWELLING MEAN LENGTH:			79.5

Anchoveta grazing and production rates during upwelling

Since positive relationships appear to exist between anchoveta length and growth rate and phytoplankton abundance (Figs. 79, 80), it is desirable to assess the magnitude of anchoveta grazing on the phytoplankton standing crop and their daily carbon production, as estimated previously for the zooplankton (Table 83). The necessary data and assumptions for these analyses have been derived as follows:

Estimation of Wet Weight: Estimates of the average wet weight of the anchoveta during the 1955, 1956, 1957 and "all" upwelling seasons (1951-1962) are needed for a carbon estimate. This requires an estimate of the average anchoveta length during these periods. A mean length of 76 mm for 1955 is calculated from Table 3 of Howard and Landa (1958), and a mean of 85 mm for both the 1956 and 1957 populations is derived from Table 2 of Bayliff (1964)[16]. The average length for "all" upwelling seasons (79.5 mm) is considered to be the mean of the average monthly lengths of first-year fish for January, February, March and April reported by Howard and Landa (1958) and Bayliff (1964) for 1951 through 1962 (Table 86)[17]. These estimates of average length are given in line A of Table 88.

Bayliff (1965) has derived an equation permitting an estimation of anchoveta weight from length:

$$\log_{10} w = \log_{10} a + b \log_{10} l$$

where w is weight in grams, l is length in mm, and a and b are constants of variable value. Mean anchoveta lengths are available for each month of the upwelling season only during 1956 (Table 84). Therefore, the mean

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[16] The mean monthly lengths are given in Table 84. Data are lacking for January 1955, and January and March of 1957. The mean anchoveta length for 1955 was calculated assuming a January length of 30 mm (*vide* Bayliff 1964). The mean length of 85 mm calculated for 1956 was also used for 1957.

[17] Estimates of anchoveta length are lacking for some months during a given year, and especially for January. The mean January length presented in Table 86, therefore, is based on actual measurements of 56.4 mm and 40.3 mm during 1956 and 1958, respectively, and assuming an average length during five other years of 30 mm (Bayliff 1964).

anchoveta weight for each upwelling season was initially calculated using the *mean upwelling season lengths* given in line A of Table 88 and the values for constants a and b assigned to anchoveta Group number 4 (*vide* Table 2 in Bayliff 1965). Such estimates, however, are probably less representative than those based on the *mean monthly* anchoveta length-weight relationships. Therefore, the mean anchoveta weight for *each* month of the 1956, 1951—1962 ("all") and 1960[18] upwelling seasons was estimated, from which grand means were calculated (X) and compared to the mean weight estimates based on the average length for the entire upwelling season (Y):

Year	X	Y	X:Y
1956	12.361 grams	9.260	1.33:1
1960	9.258	5.837	1.59:1
1951-1962 ("all")	10.733	7.370	1.46:1
		MEAN	1.46:1

The latter procedure (Y) considerably underestimates the mean weight, and therefore the upwelling season estimates thus calculated were increased 1.5-fold. Mean wet weights of approximately 9.5, 14.0, 14.0 and 11.0 g are obtained for the 1955, 1956, 1957 and "all" upwelling seasons, respectively (entered as line B in Table 88).

Estimation of Carbon: It will be assumed that organic matter comprises 20 per cent of the anchoveta wet weight, and that 50 per cent of this is carbon, as found for fishes in general, including the anchovies (Vinogradov 1953). These estimates are presented in line C of Table 88.

Estimation of Respiration: Cushing (1964) cites Winberg (1956) as suggesting that the oxygen consumption of fish is well expressed in the equation:

$$Q = 0.3\, w^{0.8}$$

where Q is ml O_2 respired per hour at 20 C and w is the wet weight in grams. This equation will be used for estimating the anchoveta respiration rate expressed as the daily amount of carbon respired. The following assumptions are made: 1) the anchoveta has a carbohydrate metabolism with glucose being the respired substance, and 2) the organic composition of the anchoveta is 50 per cent carbon (Vinogradov 1953). Thus, mg C respired = ml O_2 consumed $\times 1.4 \times 0.375$, where 1.4 is the density of oxygen and 0.375 is the carbon : oxygen ratio of glucose. These values are given in line D of Table 88.

Estimation of Anchoveta Standing Crop: Bayliff (1966), from tag returns derived an equation which permits an estimation of the anchoveta standing crop:

$$\log N_t = 8.912822 - 0.00291918t$$

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[18] *vide* footnote to Table 87.

where t equals the number of days elapsing since 8 March 1960, and N_t represents the population density in numbers of fish of the 1959 year class in the Isla Verde area at time t. The Isla Verde area is considered to include the area between Punta Chame and the entrance of the Panama Canal (Bayliff 1966) within the 5-fathom isobath (Howard and Landa 1958) (Fig. 76). Since this equation is derived from an analysis of the 1959 year class, its application to others requires the following procedure. It is necessary to:

1) determine the mean anchoveta population (883,075,000 fish) during January—April 1960 (Table 87),

2) determine the ratio of this mean population density to the 1960 catch per standard day's fishing (CSDF) during February—April given in Table 9 of Bayliff (1964), and

3) determine the mean wet weight (9.258 g) of the 1960 upwelling season population, using the equation $\log_{10} w = \log_{10} a + b \log_{10} l$ (Table 87), since a correction must be made for differences in mean weight of the unknown anchoveta populations relative to the 1960 standard.

The mean ($\overline{X}$) upwelling season anchoveta populations during 1955, 1956, 1957, and for "all" (1951-1962) upwelling seasons have been estimated from the 1960 calculations and from the CSDF and mean wet weight data for the above upwelling periods using the following relationship (1955 taken as an example):

$$\overline{X}\text{ 1955 Anchoveta Population} = \overline{X}\text{ 1960 population} \times \frac{\text{CSDF}_{55}}{\text{CSDF}_{60}} \times \frac{\overline{X}\text{ Weight}_{60}}{\overline{X}\text{ Weight}_{55}}$$

$$\text{or,} \qquad = 883{,}075{,}000 \times \frac{389}{461} \times \frac{9.258}{9.500}$$

$$= 727{,}427{,}733$$

The results are given in Table 87.

The volume of water in the Isla Verde area is about 1.47×10^9 m^3 (derived using U. S. Navy hydrographic chart HO 5002). Therefore, the calculated anchoveta populations ranging from about 6.1 to 8.6×10^8 during the various upwelling periods represent a population density of from 0.42 to 0.59 fish m^{-3} (Table 87). If a similar population density is assumed to occur at the hydro-biological station (40 m deep) during these periods, then the mean anchoveta population ranges from 17 to 24 fish m^{-2}. The April population densities (G_2) were calculated from the mean April 1960 population density of 633,700,000 (Table 87), the mean CSDF values (Table 87), the mean April 1960 *wet* weight of 25.40 grams derived from Table 2 of Bayliff (1964) following the length-weight conversion procedure described earlier, and the mean April *wet* weights for 1955, 1956, 1957, and "all" years (Table 88). The mean April 1955 population is calculated, accordingly, as follows:

TABLE 87. Calculation of the Isla Verde area mean mid-monthly anchoveta population during 1960, and the mean population densities during the 1955, 1956, 1957 and "All" (1951-1962) upwelling seasons (January—April) following the procedure outlined in the text

Month	Anchovetas	Month	Anchovetas
Jan. 15	1,168,000,000	Mar. 15	780,600,000
Feb. 15	950,000,000	Apr. 15	633,700,000
	MEAN	883,075,000	

Year:	1960	1955	1956	1957	"ALL" (1951-1962)
Mean Weight (g)*	9.258	9.5	14.0	14.0	11.0
CSDF†	461.0	388.5	482.5	528.7	535.6
Mean Anchoveta Population:		727,427,733	611,730,779	670,102,036	864,774,154
Mean Anchoveta Population m^{-3}:		0.50	0.42	0.46	0.59
Mean Anchoveta Population m^{-2}:		20	17	19	24

* January and February 1960 lengths assumed to be 35 and 64 mm, respectively. (Table 86), the March and April 1960 lengths taken from Bayliff (1964: Table 2). In calculation of weight, values for constants *a* and *b* assigned to Group numbers 1 (January), 3 (February), 4 (March) and 5 (April) were used (Table 2 in Bayliff 1965). Other years assigned to Group number 4; the mean lengths used given in Table 88.

† CSDF = Catch per standard day's fishing; taken from Table 9 in Bayliff (1964). The value for "All" is the mean of 1951-1962 observations.

$$\overline{X} \text{ April 1955 Anchoveta population} = \overline{X} \text{ April 1960 population} \times \frac{\text{CSDF}_{55}}{\text{CSDF}_{60}} \times \frac{\overline{X} \text{ April Weight}_{60}}{\overline{X} \text{ April Weight}_{55}}$$

The procedure used to estimate the anchoveta population density per m^2 is the same as that followed to estimate the mean upwelling season populations (*vide* page 538). The mean April populations range from 16 to 20 fish m^{-2} (Table 88). These standing crop densities will be used in subsequent calculations (G_1 and G_2 in Table 88).

Estimation of Predation and Production: The 4-fold increase in anchoveta length between January and April, and the 40-fold increase occurring during the 5- to 6-month period following the formation of a functional mouth, pointed out previously, testify to a very rapid growth rate. This suggests that the daily anchoveta grazing of phytoplankton satisfies not only their respiratory losses, but permits growth. Therefore, the average daily carbon intake (grazing rate) will be assumed to be equal to that lost by respiration plus that corresponding to the increased weight. The mean daily anchoveta carbon increase was estimated from the expected weight accompanying the mean size during April, as described above, and then assuming that this represented growth during December through April (151 days). For example, the mean carbon content of a 117 mm anchoveta is 2540 mg (lines E and F in Table 88), which would correspond to an average daily carbon increase (production rate) of 2540/151, or about 17 mg carbon. It is believed that this crude procedure provides a more

TABLE 88. Mean daily anchoveta size, weight, standing crop, respiration, growth, production and grazing rates during the 1955, 1956 and 1957 upwelling seasons, and for "All" years (1951-1962)

		1955	1956	1957	"All" Years
A)	Mean Length (mm)	76	85	85	79.5
B)	Mean Wet Weight (mg)	9,500	14,000	14,000	11,000
C)	Mean Carbon Content (mg)	950	1,400	1,400	1,100
D)	Daily Carbon Respired (mg)	22.9	31.2	31.2	25.8
E)	Mean April Length (mm)	115	122	121	117
F)	Mean April Carbon Content (mg)	2,395	2,926	2,846	2,540
G_1)	Mean No. Anchovetas m^{-2}	20	17	19	24
G_2)	Mean No. Anchovetas m^{-2}, April	16	12	18	20
H)	Anchoveta Standing Crop, mg C m^{-2}, ($G_1 \times C$)	19,000	23,800	26,600	26,400
I)	Anchoveta Respiration, mg C m^{-2}, ($G_1 \times D$)	458	531	593	619
J)	April Anchoveta Standing Crop, mg C m^{-2}, ($G_2 \times F$)	38,320	46,816	51,228	50,800
K)	Daily Anchoveta Carbon Increase (mg) $\frac{J}{151}$	254	310	339	336
L)	Daily Phytoplankton Predation, mg C m^{-2}, ($I + K$)	712	841	932	955
M)	Mean Phytoplankton Standing Crop, mg C m^{-2}	8,412	3,130	5,822	5,434
N)	% of Phytoplankton Standing Crop Grazed Daily: $\frac{L}{M} \times 100$	8.7	27.0	16.0	17.6
O)	Daily Anchoveta Carbon Production as % of Standing Crop Carbon: $\frac{K}{H} \times 100$	1.3	1.3	1.3	1.3

realistic estimate of the mean daily carbon increment than that based on mean fish size for the entire upwelling season.

From the foregoing estimations and assumptions, the mean daily anchoveta standing crop, grazing and production rates calculated for the various upwelling seasons are presented in Table 88. The average daily rate of anchoveta production, as carbon, is about 1.5 per cent during the 1955, 1956, 1957 and "all" upwelling seasons. The associated daily loss of phytoplankton carbon due to anchoveta grazing is about 18 per cent for "all" upwelling seasons, and ranged from about 9 to 27 per cent per day for the individual upwelling years. Thus, even if the anchoveta population were doubled, a considerable excess of phytoplankton would remain beyond that grazed down by this fish, the various assumptions holding. Nonetheless, the anchoveta appears to be an important phytoplankton grazer during upwelling. In fact, the anchoveta standing crop and grazing intensity at the hydro-biological station considerably exceed that exhibited by the zooplankton (Table 83). The mean daily zooplankton production rate during upwelling is considerably greater, however.

The migration of the adult anchovetas to the mud flats during April and the adoption of iliophagous feeding which persists through the rainy season have been pointed out. To what extent supplemental plankton feeding (Bayliff 1963) might influence the phytoplankton standing crop level during this period cannot be determined.

SOME ECOLOGICAL PROBLEMS ACCOMPANYING PHYTOPLANKTON OCCURRENCE IN AN UPWELLING ENVIRONMENT

Although upwelling is clearly beneficial to phytoplankton growth, certain problems are associated with existence in upwelling environments, specifically those of an orderly succession of species and the related problem of community maintenance.

Phytoplankton communities may have a quantitatively definable organization and seral direction (Margalef 1958), as well as function according to measureable energetic principles (Patten 1959). Therefore, an orderly progression of phytoplankton communities rather than erratic plankton responses would be expected to have evolved in both upwelling and less dynamic areas to facilitate a more effective energy transfer among trophic levels of the food chain. Within an upwelling area this becomes a question of the relative role of autochthonous and allochthonous species. If allochthonous species were primarily responsible for the major features of upwelling phytoplankton cycles, then erratic, unpredictable community organizations and responses might be expected within a given upwelling period and between years, resulting from the vagaries of upwelling winds. The situation might be similar to the unpredictable, mass efflorescence of *Asterionella japonica* reported in European coastal waters (Gran 1929), and the unexpected late-winter flowering of *Rhizosolenia setigera* in Narragansett Bay, Rhode Island, during 1964-65 (Smayda, unpublished observations). One feels intuitively that such a phytoplankton cycle would adversely influence zooplankton dynamics whose own synchronization and succession might be linked to the cell size (Mullin 1963) and nutritive value (Moyse 1963) of the phytoplankton species present. Under such conditions, one might expect the occurrence of an herbivore population less influenced by short-term (i.e., within an upwelling period) phytoplankton fluctuations in abundance and composition. Does the extensive occurrence of small, phytoplankton feeding fish in tropical waters, such as the anchoveta, *Cetengraulis mysticetus*, in the Gulf of Panama, the pilchard, *Sardinops ocellata*, off Africa (Kollmer 1962) and the Indian oil sardine, *Sardinella longiceps*, (Nair 1953, Subrahmanyan 1959a, b), in fact, reflect this?

The phytoplankton dynamics in the Gulf of Panama strongly suggest that an *indigenous* diatom flora is primarily responsible for the observed succession. The evidence presented earlier includes:

1. The pioneering upwelling community (Stage I) is present during the preceding rainy season,

TABLE 89. Successional pattern of the major diatom species, their surface:volume ($\mu^2:\mu^3$) ratio, and the total diatom community surface:volume ratio at 10 m during the 1955—1957 upwelling seasons in the Gulf of Panama. (Species in parenthesis represent occasional dominants, as given in Table 53)

A. Dominant species and their average surface : volume characteristic:

December—January		**March**	
Chaetoceros compressus	0.53	*Nitzschia delicatissima*	2.10
Chaetoceros costatus	0.59	(*Lauderia annulata*)	0.20
Skeletonema costatum f. *tropicum*	0.56	(*Chaetoceros costatum*)	0.59
(*Chaetoceros socialis*)	0.30	(*Nitzschia pacifica* + *pungens*)	1.10
February		**April**	
Rhizosolenia delicatula	0.47	*Rhizosolenia stolterfothii*	0.32
(*Eucampia cornuta*)	0.37	(*Chaetoceros socialis*)	0.30

B. Monthly mean surface : volume ratio of the diatom community at 10 m:

	1955/56 Upwelling Season	**1956/57 Upwelling Season**
DECEMBER	0.33	0.34
JANUARY	0.34	0.35
FEBRUARY	0.46	0.38
MARCH	0.50	0.60
APRIL	0.40	0.42

2. The successional stages within each upwelling period can be related to the antecedent communities,

3. The similar pattern of succession from year-to-year (Tables 29, 37, 53) which would not be expected if allochthonous species were primarily responsible for the cycle, and

4. The succession of diatom size groups which might not be expected if allochthonous species dominated the cycle (Table 89).

Margalef (1958) has pointed out that the general pattern of phytoplankton succession proceeds from small-sized diatom cells (high area: volume ratio) to progressively larger-sized cells and, finally, terminates with motile dinoflagellates and/or coccolithophores. Notwithstanding the marked week-to-week variations in upwelling intensity in the Gulf of Panama, the dominant species exhibit a succession from small-celled diatoms belonging to *Skeletonema* and *Chaetoceros*, which initiate the upwelling season during December—January, to the large-sized dominant, *Rhizosolenia stolterfothii*, present at the termination of the upwelling season in April. This succession from smaller to larger diatoms is temporarily reversed during March when upwelling usually intensifies (Figs. 42, 47, 52). The pronounced enrichment occurring at this time undoubtedly favors those species having a higher rate of potential increase than the large-celled diatoms. If the cell surface area : cell volume ratio for the entire diatom community present at 10 m (Smayda 1965a) is considered, then the reversed size progression occurs in which a succession towards smaller-sized communities occurs until April. The great importance of *Rhizosolenia stolterfothii* during April contributes appreciably to this lower average size during this month. The significance of this latter trend is unknown, but it is additional evidence that autochthonous species are primarily responsible for the observed succession in the Gulf of Panama.

This conclusion does not exclude the occurrence and, even, importance of allochthonous species in the phytoplankton cycle. The mass efflorescence of *Lauderia annulata* during March 1955 (Tables 24, 29, 52), for example, might be accounted for in this way. Also, possibly, the major successional features described are, in part, an artifact of the sampling program (samples were collected at approximately 2-week intervals), especially during periods of intense upwelling. But although allochthonous phytoplankton species undoubtedly occur, the suggested origin of the upwelled waters (Fleming 1939, Schaefer *et al.* 1958) would appear also to restrict their number and potential influence.

Notwithstanding these considerations, the hydrographic conditions during upwelling in the Gulf of Panama would appear detrimental to the occurrence of an autochthonous population and its succession. For example, a *natural* cycle in growth variables such as light and temperature does not occur during upwelling. It has been abundantly demonstrated from other regions that the seasonal phytoplankton cycle reflects changes in stability, light, temperature and nutrients, among the non-biotic factors. This suggests, then, that a different mechanism exists in the Gulf of Panama, or in upwelling areas in general, from that in non-upwelling situations which permits the observed succession.

Theoretically, upwelling may become so intense that the indigenous as well as the allochthonous flora are continuously being translocated and sufficient cells are neither recruited nor remain within the euphotic zone long enough to initiate phytoplankton growth. This situation is analogous to that in fast flowing rivers where the excessive laminar flow frequently prevents plankton populations from maintaining themselves at a given locus (Margalef 1960). The converse situation is the condition in which a constant upwelling intensity permits growth of that species with the highest intrinsic growth rate at those conditions. The community might tend towards monospecificity or climax, but without succession. This condition is analogous to growth in continuous culture in which a constant nutrient supply permits undiminished growth. Accordingly, the *maintenance* of a phytoplankton population in an upwelling area requires either 1) an upwelling intensity which allows the rate of increase of phytoplankton to exceed that of displacement, or 2) turbulent mixing. Further, the *succession* of autochthonous communities in upwelling areas is dependent on environmental changes associated with wind-induced variations in upwelling intensity in the absence of cyclic environmental changes in temperature, light and nutrients as occur in non-upwelling areas. This condition for succession differs from sequential phytoplankton changes distinguished by Gran and Braarud (1935) in that *autochthonous* rather than allochthonous species dominate the ensuing successional stage.

A proposed mechanism permitting the *maintenance* and *succession* of autochthonous communities in upwelling areas is illustrated in Figure 81. During intense upwelling (northerly winds) the sea surface is tilted upwards offshore, while during intense non-upwelling (southerly) winds, as during the rainy season, the sea surface is tilted upwards inshore (Figs. 4, 81). During upwelling periods, fluctuations in wind intensity occur (Figs. 42, 47, 52) which can be expected to induce seiche-like movements of the watermass between these two extreme sea level states such that the superficial waters can be envisioned as "sloshing" in and out of the upwelling area (Fig. 81) according to the wind conditions. For example, during intense upwelling, cold, nutrient-rich water, in which phytoplankton growth is occurring, ascends to the surface and then flows offshore with the entrained phytoplankton community. If the growth rate exceeded the translocation losses, and if a constant upwelling rate occurred, then a continuous population without succession would occur, analogous to the continuous culture situation mentioned earlier. If upwelling intensified further (Panel A in Fig. 81), the depth of the productive zone would be expected to decrease and the *maintenance* of the community might be endangered. In the Gulf of Panama, the plankton distribution at stations 34, 35, 58, 60 and 61 (Tables 33, 34, 46-48) and the associated wind intensities (Figs. 42, 47) suggest that upwelling intensity was approaching this critical rate at those times. If upwelling intensity then subsided (Panels C and D in Fig. 81), a complete or partial reversal of the offshore displacement of the upwelled superficial waters and entrained phytoplankton would occur. The flow of this water inwards would be accompanied by a withdrawal of the upwelled water to greater depths and vertical mixing which woud distribute the phytoplankton throughout the water column and thereby lead to their retention within the embayment. The complete suppression of upwelling winds (Panel E in Fig. 81) would eventually lead to a sparse community, but under these conditions the maintenance of an *autochthonous* population, as during the rainy season, would not be an important problem. However, if a resurgence of upwelling occurred (Panels F and B in Fig. 81) then phytoplankton growth would increase with the dominant species being selected from the indigenous population retained in the embayment by the seiche-like mechanism outlined above.

Thus, the effect of this proposed mechanism is 2-fold: it generates a succession through periodic disruption and promotion of community growth, while the associated seiche-like watermass movements and turbulent mixing combine to permit the retention and maintenance of an indigenous population. However, if such oscillations in upwelling intensity influence succession, then one might expect the potential dominance of many, if not all, species depending on the particular pattern and duration of the hydrographic fluctuations. This might be reflected by the Stage III community during March when upwelling is usually very intense following variable February conditions (Figs. 42, 47, 52). Although the occurrence

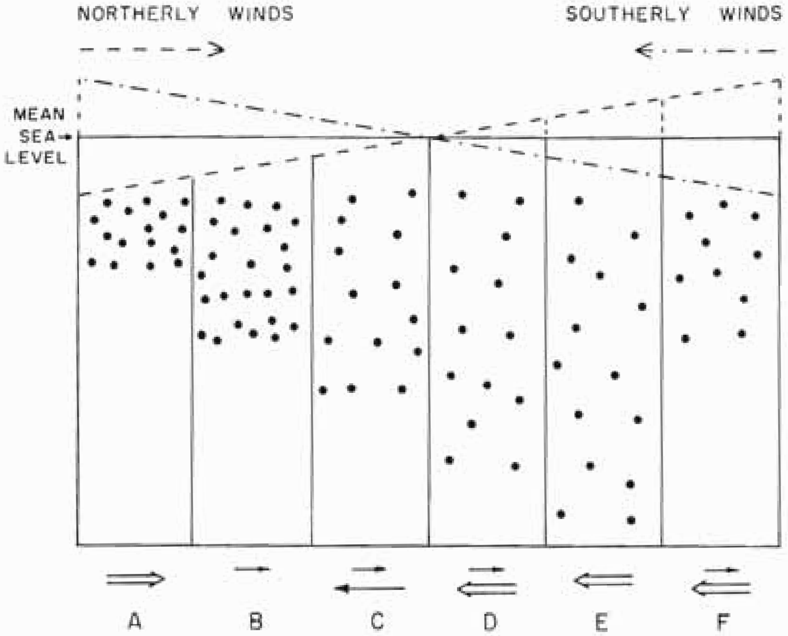

FIGURE 81. A proposed mechanism which might permit the maintenance and succession of autochthonous phytoplankton communities during periods of upwelling. See text for further explanation.

of *Nitz. delicatissima* is predictable during that time, the usually more important co-dominant species is not (Tables 52, 53, 89). Similarly, the unusually intense upwelling during February 1957 (Fig. 52) led to the mass efflorescence of *Eucampia cornuta*, a previously minor species.

While this model suggests how succession might occur in an upwelling environment, the factors determining which species will be dominant or even permitting succession to occur are completely unknown. For example, the Stage I community (Tables 29, 37, 53, 89) dominated by *Ch. compressus* and *Skel. costatum* f. *tropicum* is recognizable as that present during the rainy season. But those ecological factors responsible for their virtual disappearance following their dominance during December—January, but allowing the persistence and eventual dominance of *Rh. delicatula*, *Nitz. delicatissima* and *Rh. stolterfothii*, are completely unknown.

The problem of the maintenance of indigenous or developing phytoplankton populations is also related to their cell division rate and the upwelling intensity. As discussed previously (*vide* page 371), Forsbergh (1963) estimated that the maximum daily upwelling intensity at the hydrobiological station, averaged over 2-week periods, ranged from about 2 to 3 m per day, and cites Roden as stating that it might reach 10 m per day. Since the production zone during the upwelling season does not appear to extend much below 20 m (*vide* page 489), the retention time of the phytoplankton in the production zone at the hydro-biological station would range from 2 to 10 days at the above maximum upwelling rates. The relative abundance exhibited by a given species, then, will be related to its rate of cell division. Lanskaya (1963) has given some division rates for Black Sea phytoplankters which have been converted into the minimum and maximum number of days required for one cell division for some of the species:

Skeletonema costatum	0.12 to 2.5 days
Chaetoceros socialis	0.33 to 3.0 days
Leptocylindrus danicus	0.50 to 2.5 days
Prorocentrum micans	0.50 to 5.0 days
Peridinium triquetrum	0.50 to 2.0 days

In addition, the micro-flagellate *Carteria willei* was reported by Lanskaya to undergo four divisions per day during maximum growth. Even at an upwelling rate of 10 m per day a sizeable phytoplankton population might be expected at the maximum rates of cell division given above. Assuming that all cells produced within the productive zone at the hydro-biological station are eventually displaced offshore from this station, then a continuous supply of cells from the top of the water column must sink or be transported to depth to perpetuate phytoplankton growth. Although a mechanism of phytoplankton retention has been proposed (Fig. 81), it is uncertain, for example, if a constant upwelling intensity of 2 m per day prevailing for 10 days would remove all the cells from the water column (assuming none are transported in), or whether equally good growth would occur within a defined zone throughout this period. If the latter occurs, then additional mechanisms involving sinking and micro-turbulence are responsible for community maintenance in addition to that proposed (Fig. 81).

Many cells produced resting spores. These stages presumably sink faster than old cells (Smayda and Boleyn 1965) and settle to the bottom, notwithstanding upwelling. However, some of these spores and old cells would undoubtedly be swept up into the water column during periods of intense upwelling when conditions for their rejuvenation would appear optimal. But yet, succession, once it has begun, does not appear reversible such that following the termination of the Stage I community, as discussed above, or dominance of any given species, a subsequent efflorescence during the upwelling season does not occur. That this should occur, along with succession, remains mystifying.

Dinoflagellates (Hasle 1950) and coccolithophores (Mjaaland 1956) are phototactic. Peters (1929) has shown that the swimming speed of 12 dinoflagellates varied from about 0.008 to 0.5 mm sec^{-1}. Upwelling rates of about 3 and 10 m per day (Forsbergh 1963) correspond to about 0.04 and 0.10 mm sec^{-1}. Some of the species would encounter difficulty in swimming against the upwelling currents. If they attempted evasive movements away from high light intensities, then they would be at a distinct ecological disadvantage during the day.

The possibility that strong upwelling currents might have influenced zooplankton diurnal vertical migration, as well as have contributed to the relatively low standing crop through the loss of considerable energy expended in swimming against upwelling currents during evasive light-induced movements is not supported. Cushing (1959b) has determined the average swimming speeds of various-sized zooplankters based on their diurnal migration: zooplankters 1 mm in length exhibited an average speed of 6 m hr^{-1}, and those 6 mm in length 33 m hr^{-1}, i.e., considerably in excess of the expected maximum upwelling rates.

A REGIONAL COMPARISON OF PHYTOPLANKTON GROWTH IN TROPICAL INSHORE WATERS

There have been few *quantitative* investigations of the *annual* phytoplankton cycle in tropical waters; those of Marshall (1933) within the Great Barrier Reef in Australia and Bainbridge (1960) in a Sierra Leone estuary are especially notable. The rather impressive annual investigation of Tham (1953) in Malaysian waters and that of Subrahmanyan (1959a, b) in Indian waters over a span of 5 years suffer from the use of net-filtered samples, and can hardly qualify as quantitative studies, notwithstanding the contention of these authors to the contrary. Despite the dearth of comparative quantitative studies, a number of tropical investigations of annual or shorter duration, based on net-sampling, can be used to illustrate some of the principals and types of phytoplankton growth in tropical inshore areas. Tropical will be used here quite broadly to include the Mediterranean Sea where Bernard, and Margalef and co-workers have conducted important investigations relevant to the present discussion. No attempt has been made at a thorough appraisal of the literature.

Although tropical inshore waters are generally characterized by high incident radiation and temperatures, and wet and dry seasons associated with upwelling, monsoonal or other wind conditions, a considerable diversity in environmental conditions and associated phytoplankton growth exists. In general, tropical inshore areas are characterized either by the presence or absence of an annual phytoplankton cycle, with at least four types of the latter cycle distinguishable:

1. An annual phytoplankton cycle occurs.
2. An annual phytoplankton cycle does not occur:
    a). Great Barrier Reef Type—diatoms predominate.
    b). Monaco Type—coccolithophores predominate.
    c). Sierra Leone Type — Coscinodiscaceae and Biddulphiaceae predominate.
    d). Phosphorescent Bay Type—dinoflagellates predominate.

Areas exhibiting an annual phytoplankton cycle

An annual phytoplankton cycle in many tropical inshore areas is dependent on upwelling, as described for the Gulf of Panama. Smayda (1963) has discussed the few previous studies in this embayment. Within other regions of the eastern tropical Pacific, such as the Gulf of California (Osorio Tafall 1943) and Pisco Bay, Peru (Barreda 1958), intense diatom growth is also dependent on upwelling winds. Barreda also describes the occurrence of turbid, low salinity water accompanying river runoff reminiscent of the Gulf of Panama rainy season conditions, and dinoflagellate ("aguaje") blooms, as found also in the Gulf of California (Osorio Tafall 1943). The classical example of upwelling in this general area has been described by Gunther (1936) for the Peru Current. Upwelling has also been reported off the Venezuelan coast (*vide* Hulburt 1963), and along the western coast of Africa (Hart and Currie 1960, Kollmer 1962).

Tham (1950) and Subrahmanyan (1959a, b) have described the seasonal phytoplankton cycle in Malaysian and Indian waters, respectively, where a diatom maximum accompanies the wet, southwest monsoon winds. Here, increased phosphate and phytoplankton growth accompany a *reduction* in salinity, unlike the situation in upwelling areas; this reduction is attributable to the intense rainfall accompanying monsoon winds. Tham attributes this increase in phosphate to river runoff, while Subrahmanyan believes that it is released from bottom sediments. Banse (1959), however, contends that the increased phosphate content off the west coast of India during the southwest monsoon period is due primarily to upwelling rather than to release from sediments.

Within the Mediterranean Sea, wind is also the ". . . agent principal de fertilité . . ." (Bernard 1939). For example, Margalef, Muñoz and Herrera (1957) have demonstrated the importance of upwelling to the phytoplankton cycle (*vide* page 502). As in other upwelling areas, diatoms dominate the major pulse. Ercegovic (1936), in a quantitative study based on Utermöhl's inverted microscope technique, also demonstrated the influence of wind-induced hydrographic changes on phytoplankton growth in the Adriatic Sea where diatoms dominated a modest maximum of about 500,000 c/L. In addition to nutrient enrichment of the euphotic zone accompanying wind-induced mixing, Ercegovic also reported nutrient accretion accompanying rain to be important in promoting growth.

Thus, these diverse regions are characterized by a seasonal phytoplankton cycle, the major pulse of which consists of a diatom response, dependent upon *wind-induced fertilization* of the watermass through upwelling or, possibly, on nutrient *accretion* through precipitation and runoff. Such a wind-dependent cycle can be expected to exhibit annual variations in phytoplankton abundance, as demonstrated for the Gulf of Panama and off the Spanish coast (Margalef, Muñoz and Herrera 1957). The absence of favorable winds in any of these or other tropical inshore areas would also prevent the occurrence of a seasonal phytoplankton cycle, or, as demonstrated, phytoplankton abundance would decline upon subsidence or cessation of favorable winds. This type of cycle suggests, therefore, that periods of poor growth result partly from inadequate nutrient supplies (Riley 1938, Menzel, Hulburt and Ryther 1963, Smayda 1964). Riley (1938) conducted nutrient enrichment experiments on tropical inshore phytoplankton collected at the Dry Tortugas located in the eastern part of the Gulf of Mexico off Florida (24°38′N, 82°52′W). He found nitrate to be the most important limiting nutrient factor, although the addition of both phosphate and iron also stimulated growth. Menzel *et al.* (1963) found that the addition of iron produced large populations in 3-day experiments with surface phytoplankton collected near Bermuda in the Sargasso Sea, while in 7-day experiments nitrogen and phosphate alone produced large populations. These authors suggest that the response to iron enrichment may represent a catalytic effect since aluminum elicited a similar response. Smayda (1964) found that silicate limited the growth of an assay diatom in Sargasso Sea water as did (unpublished observations) the omission of copper, molybdenum and cobalt from water passed through a chelating resin. The causes of the phytoplankton decline off the west coast of India accompanying the termination of the south-west monsoon winds, however, are uncertain since Subrahmanyan (1959a, b) believes that adequate phosphate, nitrate and silicate supplies remain. He suggests that trace metal or organic substances liberated from the bottom sediments might become limiting at that time. Nonetheless, this is consistent with the view that nutrient availability is the principal factor limiting phytoplankton growth in those areas where an annual cycle occurs. One would also expect that the nutrient(s) responsible for the periods of poor phytoplankton growth in these areas would vary regionally and with the species composition.

Areas not exhibiting an annual phytoplankton cycle

a). ***Great Barrier Reef Type***—From the above discussion, one might expect the cardinal condition for an annual phytoplankton cycle in tropical inshore areas to be periodic mixing or upwelling. Marshall's (1933) quantitative investigation of the annual phytoplankton cycle (unpreserved samples enumerated) at Low Isles (16°23′S, 145°34′E), located within the Great Barrier Reef off Australia, however, indicates that such hydrographic conditions do not assure an annual cycle. Almost continual mixing associated with southeast trade winds characterized her station, 32 m deep, where sufficient light for photosynthesis penetrated to the bottom, and where high temperatures (mean of about 25.5 C) and low, constant phosphate and nitrate concentrations occurred (Orr 1933). However, neither an annual cycle in phytoplankton abundance nor in species composition was found. Maximum abundance was about 30,000 c/L, and the average abundance about 6,000 c/L. Diatoms dominated the community. The slight diatom pulses accompanying especially intense winds were attributed to the release of nutrients from sediments. Under such conditions, it is apparent that there cannot be a significant accumulation of regenerated nutrients whose periodic availability through overturn of the watermass would permit alternating periods of intense and poor phytoplankton growth, as in the classical annual cycle of temperate and boreal waters. Marshall also demonstrated that the southeast trade winds did not permit the incursion of deep, nutrient-rich offshore waters within the reef where they might upwell and lead to extensive phytoplankton growth. These observations indicate, then, that an annual phytoplankton cycle in tropical areas is dependent upon the periodic introduction of nutrient-rich water, and that mixing of the watermass *per se* will not lead to heightened phytoplankton growth unless this condition is met.

The Great Barrier Reef Type phytoplankton cycle is of considerable theoretical and practical interest. Since the products of regeneration can not accumulate under such conditions, the various "turnover" rates are especially important in determining the magnitude and seasonal variations of the standing crop, as well as in influencing other trophic levels. Russell (1934) compared the Great Barrier Reef zooplankton abundance with that off Plymouth and found a surprisingly large zooplankton population. He concluded (p. 181) that the Great Barrier Reef zooplankton standing crop (as numbers) ". . . must be of about the same abundance, on the average over the year, as that of the coastal and shallow waters of the southern North Sea and English Channel . . .". Thus, indications are that considerable production occurs in the Great Barrier Reef region, notwithstanding the sparse phytoplankton community. Whether tropical inshore upwelling areas or the Great Barrier Reef Type phytoplankton cycle are more productive is uncertain. The ecological solution to this problem will be of prime importance in influencing man's future aquacultural pursuits when artificial mixing of embayments becomes feasible.

The Great Barrier Reef Type cycle has other food chain consequences. The continuous mixing would appear to lead to the observed continuous development of a relatively small phytoplankton standing crop which is efficiently grazed down by the zooplankton. This situation suggests that little detrital material would settle to the bottom to support a rich benthic animal community. In fact, Russell (1934) did find that the benthic community "was poor" compared with northern latitudes. Although Russell reported that "small sardine-like fish" occurred in large schools, his discussion suggests that the Great Barrier Reef Type food chain is: phytoplankton → zooplankton → corals + coral reef inhabitants.

In summary, the Great Barrier Reef Type annual phytoplankton cycle is characterized by the predominance of diatoms which exhibit slight seasonal changes in abundance or composition (attributable to a constant, low supply of regenerated nutrients associated with mixing), and is seldom disrupted by the influx of a cold, nutrient-rich watermass accompanying an intensification of winds.

b). ***Monaco Type***—This phytoplankton cycle is characterized by the remarkable persistence and abundance of coccolithophores, as cell numbers and biomass, first elucidated by Bernard (1937) in Mediterranean waters off Monaco and subsequently found elsewhere in this sea (Bernard 1938, 1939, 1956, among other publications). The environmental conditions accompanying this cycle are those expected for oligotrophic tropical environments: high, and slight seasonal variations in, temperature and radiation, marked stratification, and low concentrations of nutrients. Bernard is among the few investigators to estimate phytoplankton biomass concentration from cell counts based on quantitative samples. The average annual standing crop at Monaco (Bernard 1937) was:

0.188 mm^3 L^{-1} at 10 m
0.176 at 50 m
0.196 at 350 m

The relatively low standing crop biomass compared to the Gulf of Panama (Table 62) is obvious, and provides a quantitative indication of the importance of upwelling to phytoplankton growth. The high mean annual biomass at 350 m is remarkable, and is only slightly less than the mean level of rainy season biomass in the upper 20 m of the Gulf of Panama of 0.260 mm^3 L^{-1} (Table 62) where little growth appears to occur below 20 m. Bernard (1939) calculated that the mean annual biomass during 1937 at 10 m off Monaco was 0.23 mm^3 L^{-1}, of which the coccolithophores comprised 52 per cent, naked flagellates 37 per cent, diatoms only about 9 per cent, and all other groups less than 9 per cent.

On the individual sampling dates the coccolithophores comprised from 40 to 95 per cent of the total biomass, with *Coccolithus fragilis* (Bernard 1956) the dominant species. While the coccolithophores exceeded 2×10^6 c/L, the maximum diatom concentration at Monaco was about 54,000 c/L. The seasonal and annual fluctuations in biomass were slight which Bernard (1939) attributed to the low, constant phosphate concentrations. He observed that increased winds and precipitation favored phytoplankton growth. In fact the importance of winds to phytoplankton growth in tropical areas is further illustrated by conditions at Monaco and Banyuls (located near the French-Spanish border). Bernard (1938) found that the mean 1937 biomass at 10 m off Monaco of 0.23 mm^3 L^{-1} was accompanied by a mean daily wind velocity of 1.7 m sec^{-1}. These winds shifted from onshore to offshore. At Banyuls, however, where offshore winds having a mean daily intensity of 7.2 m sec^{-1} predominated, the mean standing crop was 0.75 mm^3 L^{-1}, i.e., approximately 3.5-fold greater than the Monaco standing crop. The suggested importance of nutrient accretion to phytoplankton growth in the Singapore Straits (Tham 1950), the Adriatic Sea (Ercegovic 1936) as well as the coastal Mediterranean areas (Bernard 1937, 1938, 1939, 1956) differs from conditions in upwelling areas. In fact, the Gulf of Panama data suggest that the ecological conditions associated with the rainy season are deleterious to phytoplankton growth.

Thus, although the Monaco Type and Great Barrier Reef Type phytoplankton cycles are similar in the absence of an annual cycle, the hydrographic conditions and floristic character of the communities are considerably different. Factors responsible for the coccolithophore dominance in the Mediterranean Sea are unknown. However, the prevalence of such motile forms in this nutrient impoverished area might be interpreted as a "biological correction" for the absence of mixing or upwelling leading to nutrient replenishment. The vertical swimming movements of the coccolithophores might permit these forms to "seek out" adequate nutrient supplies, as well as permit a greater nutrient uptake rate through forced convection (Munk and Riley 1952) associated with their swimming. This does not explain, however, the relative paucity of dinoflagellates observed by Bernard.

c). ***Sierra Leone Type***—This phytoplankton cycle is found in dilute, turbid, shallow inshore tropical regions near river mouths and is dominated by members of the Coscinodiscaceae and Biddulphiaceae (Thiemann 1934, Silva and Pinto 1952, Silva 1956, Bainbridge 1960). The characteristics of this tropical phytoplankton Type are based on Bainbridge's (1960) excellent quantitative study of plankton populations in a Sierra Leone estuary (approximately 8°30′N, 13°00′W). This estuary is located in a region of wet and dry seasons, the former occurring during May—November, as in the Gulf of Panama, during which time about 90 per cent of the annual rainfall of between 254 and 320 cm occurs. The mean temperature varies from about 26 to 29.5 C and salinity from 16 to about 33 ‰. At an inner station (15 to 20 m deep) influenced by river runoff, maximum diatom abundance of about 120,000 c/L occurred, without any indication of significant annual variations in abundance. The most salient feature of the phytoplankton community was the dominance of large centric diatoms usually of minor importance in other regions. The following succession occurred:

> *Coscinodiscus concinnus* (January) → *Actinocyclus octonarius* (February—April) → *Actinocyclus octonarius* + *Coscinodiscus leptoporus* (May—June) → + *Coscinodiscus jonesianus* (June—July)

Thiemann's (1934) extensive studies of tropical estuaries influenced by large rivers showed this community to be widespread, except for the Congo and Niger River areas. In addition to *Coscinodiscus* and *Actinocyclus* species, *Biddulphia longicruris*, *mobiliensis* and *sinensis*, along with *Paralia sulcata* and *Triceratium favus* are found in Senegal and Portuguese Guiana estuaries significantly influenced by rivers (Silva and Pinto 1952, Silva 1956). The centric diatoms, *Chaetoceros, Rhizosolenia, Skeletonema,* etc., responsible for the intense diatom growth in upwelling areas, the Great Barrier Reef and (when diatom growth occurred) in the Mediterranean Sea were not as important. This large centric diatom community is not necessarily restricted to tropical waters, since Thiemann (1934) has also reported such a community where the Elbe River drains into the North Sea. Although salinity undoubtedly has an influence in selecting this community, its exact growth requirements are unknown. In fact, this community might assume a benthic existence during certain times of the year. It may be relevant that Guillard (1963) found that the large centric diatom *Coscinodiscus asteromphalus* grew equally well with nitrate, glutamic acid or glutamine as a nitrogen source, while a *Melosira* sp. also showed good growth when provided these organic substances.

Bainbridge did not detect a pronounced annual phytoplankton cycle at a station located farther offshore (20-30 m deep) and less influenced by runoff. The maximum diatom abundance was about 70,000 c/L. As at the inner station, diatoms were slightly less abundant during the rainy season with *Coscinodiscus gigas* and *Hemidiscus cuneiformis* the dominant species, although *Rhizosolenia* species were also important.

The dinoflagellates attained a maximum density of about 10,000 c/L at this station, as compared to 1,000 at the inner station.

Bainbridge attributed the sparse phytoplankton population in this Sierra Leone estuary to inadequate light, which indicates that this parameter can also be limiting in tropical waters. Phosphate and nitrate were thought to be adequate, there being a possibility of phosphate accretion through runoff. At the offshore station Bainbridge could correlate increased phytoplankton growth with the periodic increase in easterly winds during the dry season. However, the postulated influence of these winds differs from that described for other tropical areas. For Bainbridge suggests that these offshore winds might *increase* the stability of the water column through various current movements and thereby promote growth, rather than supply nutrients as in upwelling areas.

Assessment of the relative productivity of the Sierra Leone Type of tropical inshore phytoplankton cycle is difficult. The mean annual zooplankton displacement volume of 0.35 g m^{-3} is about 4-fold the Gulf of Panama 1955-1957 mean of about 0.09 g m^{-3} (Table 76). Considerable production might thus occur in the Sierra Leone Type notwithstanding the absence of pronounced seasonal variations in phytoplankton abundance.

Bainbridge observed that zooplankton were less abundant in the inner reaches of the estuary where the large centric diatoms predominated than in the seaward part of the estuary during the dry season. It is not known whether this low zooplankton standing crop resulted from inimical environmental conditions or their inability to utilize the large diatoms as food. The consequence of this relationship, however, is that a considerable fraction of the phytoplankton standing crop escapes zooplankton predation.

However, during this period an important fishery occurs in this and other west African estuaries for *Ethmalosa dorsalis*, a clupeiod fish which feeds extensively on phytoplankton, including the large centric diatoms (Bainbridge 1963). That is, this fish utilizes food poorly cropped by the zooplankton. This trophic relationship is consistent with the view expressed earlier that the wide-spread importance of small, phytoplankton feeding fishes in inshore tropical areas may reflect a more stable, effective utilization of primary production than is possible through zooplankton.

d). ***Phosphorescent Bay Type***—This tropical inshore area phytoplankton cycle Type is based on Margalef's (1961a) study of Bahia Fosforescente, Puerto Rico, famous for its luminescence associated with a continuing bloom of dinoflagellates. Margalef's net samples indicate the possibility of a slight diatom increase during July, the community otherwise being dominated by dinoflagellates such as *Pyrodinium bahamensis*. The predominance of dinoflagellates in certain tropical inshore areas has also been reported from off Dakar and the Ivory Coast, Africa by Silva (1956) and along certain areas of the Senegal and Mauritania coasts (Margalef 1961b). The abundance of dinoflagellates is usually accompanied by low populations of diatoms. A continuous dinoflagellate bloom also occurs in Falmouth Bay, Jamaica. Interestingly, Margalef (1961a) found that outside of Phosphorescent Bay centric diatoms predominated along the Puerto Rican coast, and that dinoflagellates increased inward toward the coast, attaining maximum, continuous abundance in small embayments. While hydrographic conditions contribute to the continuous dinoflagellate bloom in Phosphorescent Bay (Margalef 1961a), indications are that the warm, turbid, low-nutrient conditions of this embayment are associated with some other ecological factor which favors the observed growth of dinoflagellates. Burkholder and Burkholder (1958) detected significant vitamin B_{12} levels in Phosphorescent Bay which were potentially available to the vitamin B_{12}-requiring dinoflagellates. Whether this dinoflagellate community is ecologically similar in its requirements to the red tide blooms commonly noted in tropical environments (Osorio Tafall 1943, Barreda 1958, among others) is not known. In fact, of the various Types of tropical inshore phytoplankton cycles distinguished here, the Phosphorescent Bay Type is the most poorly known or characterized. Margalef (1961a) estimated that the annual net production of Phosphorescent Bay is around 20—40 g C m^{-2}, a production rate considerably lower than the estimated annual rate of 180 g C m^{-2} in the Gulf of Panama (Forsbergh 1963).

An additional difficulty in evaluating tropical dinoflagellate communities is: to what extent are they heterotrophic? For example, Silva (1956) found *Peridinium conicum* predominant in the west African dinoflagellate communities, a species, along with the commonly occurring *Peridinium pellucidum* and *Peridinium brevipes*, which Schiller (1937) lists as being nonpigmented ("farblos"). In addition, *Noctiluca* is also an important component of tropical dinoflagellate communities. Thus, this phytoplankton cycle Type, along with the other tropical inshore community Types, deserves further, detailed investigation.

This cursory analysis of inshore tropical phytoplankton communities indicates considerable regional diversity in dynamics and composition, rather than a common, uniform tropical phytoplankton community. The most important limitation of continued, intense growth of such communities would appear to be inadequate nutrient supplies, although even light in turbid situations might be restrictive. The degree of severity of this nutrient limitation is suggested because even modest nutrient accretion directly through precipitation or as runoff may stimulate phytoplankton growth, as observed by Bernard (l. c.) and Ercegovic (l. c.) in the Mediterranean Sea. Thus, winds which bring about nutrient enrichment of the euphotic zone either through mixing, upwelling or some other process appear to be the prime prerequisite for increased phytoplankton growth in tropical inshore areas. The analysis suggests that such nutrient enrichment will favor diatom growth over that of the flagellate or Cyanophycean groups, i.e., diatoms might be generally characterized as requiring more eutrophic conditions than these other groups. However, the ecological factors which select one group or one species over another, are completely unknown. Similarly, which of the tropical inshore phytoplankton Types distinguished here is the most productive remains unknown, as are the dynamics of the associated food-chain relationships. At best, such an investigation as presented herein can only describe some of the natural relationships in marine phytoplankton communities. Development of a quantitative theory of phytoplankton dynamics must also involve experimental synecological and autecological studies.

GULF OF PANAMA
PLANKTON — ANCHOVETA — TUNA RELATIONSHIPS

This phytoplankton investigation is essentially part of a larger study sponsored by the Inter-American Tropical Tuna Commission whose charge is ". . . to gather and interpret the factual information required to maintain the populations of tunas and tuna-bait fishes at those levels which will permit maximum sustainable harvests year after year" (Inter-American Tropical Tuna Commission, 1955: p. 24). The principal tunas involved are the skipjack, *Katsuwonus pelamis*, and the yellowfin, *Thunnus albacares*, while the anchoveta, *Cetengraulis mysticetus*, is used as a bait fish. While theoretical food-chain relations have been examined (*vide* Riley 1963), plankton investigations *per se* have contributed little to the advancement of fishery biology with respect to increased yields, and have unraveled few quantitative food chain relationships which might contribute to a better understanding of fishery dynamics. Thus it is of interest to seek relationships between trophic levels and environmental conditions which, without necessarily leading to predictive equations, will provide some insight into these relationships and which will help to document qualitatively, at least, the inadequately illustrated oceanographic axiom that phytoplankton are at the base of the food-chain and that their perturbations are detectable in other trophic levels and can be collated with environmental conditions. In this regard, the results hitherto have been especially exciting to the investigator because of the following Gulf of Panama food-chain relationships which have been established:

1. A strong, positive relationship between upwelling winds and the mean monthly phytoplankton biomass in the upper 20 m (Fig. 66).

2. A positive relationship between mean monthly zooplankton and phytoplankton biomass (Fig. 73), aside from other more complex short-term relationships.

3. Positive relationships between phytoplankton biomass and anchoveta growth increment during the upwelling season (Figs. 79, 80), notwithstanding the lack of a relationship between mean phytoplankton abundance and relative anchoveta abundance based on catch statistics (Figs. 77, 78).

Forsbergh (1963) has sought other food-chain relationships in the Gulf of Panama and found (p. 29) that ". . . attempts to correlate higher trophic levels such as anchoveta, yellowfin tuna and skipjack tuna with wind, hydrography and lower trophic levels failed, except in the case of skipjack tuna with zooplankton."

SUMMARY

1. Quantitative phytoplankton samples were collected at the surface, 10 and 20 m at 8°45′N, 79°23′W at approximately 2-week intervals between 29 November 1954 and 10 May 1957.

2. Temperature, salinity, oxygen and phosphate at the surface, 5, 10, 20 and approximately 40 (bottom) m, were measured along with Secchi disc observations. Twenty-four hour *in situ* ^{14}C productivity measurements at 10 m, No. 20 vertical net phytoplankton tows, and oblique zooplankton tows (No. 40 XXX grit gauze) from the bottom-to-surface were also made.

3. Upwelling occurs from January through April, and occasionally during December and May. A slight resurgence of northerly, upwelling winds occurs during July and/or August, followed by intense rain bearing, southerly, onshore winds during the remainder of the year.

4. During upwelling, the upper 50 m, or about 30 per cent of the total volume of the Gulf, is replaced with water 5 to 10 C colder than that present during the rainy season.

5. A hypothesized pattern of upwelling circulation based on a consideration of the bottom topography is presented; it agrees in general with that suggested by the temperature and salinity data.

6. The mean annual precipitation is 2731 mm; more than 50 per cent of the total annual run-off occurs during September to December. The average annual run-off and precipitation directly into the Gulf of Panama is 92.5×10^9 m^3—equivalent to a layer of fresh water 3.2 m thick.

7. Increased stability and turbidity, and reduced intensity of incident radiation accompany precipitation during the rainy season. The mean depth of the 50% isolume during the 1957 rainy season was 7.4 m, approximately twice that during the wetter 1956 rainy season.

8. The mean daily radiation of 184 g cal cm^{-2} day^{-1} at the 50% isolume depth found between 3 to 4 m during the most turbid period in the Gulf of Panama *exceeds the incident radiation* during approximately 4, 6 and 8 months of the year in the Temperate, Boreal and Arctic regions chosen for comparison.

9. The mean phosphate concentration was 55.18 mg-at m^{-2} during the upwelling season, and 34.14 mg-at m^{-2} during the rainy season. Phosphate may be released from interstitial water of bottom sediments as a result of roiling and scouring by the incurrent upwelling flow.

10. The gradual reduction in phosphate concentration during the rainy season appears related to the amount of rainfall. Biological utilization *without* an appreciable phosphate gain because of a low phosphate content of runoff and rain water and/or significant sorption of phosphate onto the considerable terrigenous particle load which accompanies land drainage is also important.

11. The amounts of phosphate, nitrate and ammonia accreted during the rainy season *via* runoff and rain water were estimated and compared to the photosynthetic requirements for these substances based on Forsbergh's ^{14}C productivity estimate of 90 g carbon m^{-2} during the rainy season. About 9 per cent of the phosphate and 10 per cent of the inorganic nitrogen requirements are supplied by accretion. This suggests that regeneration provides the bulk of the phosphorus and nitrogen required by phytoplankton during the rainy season.

12. A cursory analysis of iron availability and hypothesized silicate and vitamin levels suggests that these nutrients may not be important limiting substances.

13. During the 1955 and 1956 upwelling seasons, unlike 1957, major changes in phytoplankton abundance and composition were effected by hydrographic changes which, in turn, could be generally collated with the magnitude of the northerly (upwelling) winds. Phytoplankton abundance tended to increase with increasing northerly winds, but a considerable

decline in abundance accompanied even a modest ebbing of these winds. The data suggest a species succession during all upwelling periods, although allochthonous populations may occur.

14. The direct relationship between northerly winds and phytoplankton density generally observed during the 1955 and 1956 upwelling seasons also occurred during the rainy season.

15. The mean seasonal phytoplankton cycle is characterized by 1) an annual maximum during the upwelling season (December—April) and an annual minimum during the rainy season, interspersed by a brief resurgence in July accompanying the reappearance of northerly winds; 2) the average phytoplankton standing crop as cell numbers and biomass was about 6- and 9-fold greater, respectively, during the upwelling season than during the rainy season; 3) diatoms overwhelmingly dominated the average phytoplankton community, both numerically (86 and 71 per cent) and as biomass (97 and 99 per cent) during the upwelling and rainy seasons, respectively; and 4) annual variations in abundance occur during the upwelling season.

16. Of approximately 175 species of diatoms identified, the dynamics of only 25 species were primarily responsible for the main features of the annual diatom cycle.

17. A remarkable similarity in diatom community succession during the 1955-1957 upwelling seasons occurred, despite annual, monthly and weekly differences in the rate of upwelling. Four communities (stages) were recognizable. A *Chaetoceros compressus* + *Skeletonema costatum* f. *tropicum* association (Stage I) initiated the diatom bloom during December and January. February was characterized by the dominance of *Rhizosolenia delicatula* (Stage II), although during 1956 a mass occurrence of *Eucampia cornuta* also occurred. Stage III, which accompanied the intense upwelling generally characteristic of March (except for 1957), exhibited marked annual variations in the co-dominant species present. *Nitzschia delicatissima* usually attained modest abundance during this stage, accompanied by an unpredictable, more abundant co-dominant: *Lauderia annulata* (1955); *Chaetoceros costatus* (1956) and *Nitzschia pacifica* + *Nitzschia atlanticus* var. *pungens* (1957). The upwelling season terminated with the dominance of *Rhizosolenia stolterfothii* (Stage IV) during April.

18. The rainy season phytoplankton community, dominated by *Skeletonema costatum* f. *tropicum* and *Chaetoceros compressus*, was quite similar in composition to the Stage I community of the upwelling season. This suggests that the initial phytoplankton community during the upwelling season is autochthonous.

19. Thecate dinoflagellates and Gymnodiniaceae (naked dinoflagellates) were very sparse, for unknown reasons. The maximum abundance was 38,000 and 11,500 cells per liter, respectively, during the upwelling

season. Of the approximately 105 dinoflagellates taxa identified, only 15 were more abundant than 1,000 cells per liter. The dynamics of *Exuviaella baltica* (maximum of 22,000 cells per liter) was primarily responsible for the observed dinoflagellate cycle; a species succession was not observed.

20. A succession from a diatom to a dinoflagellate community did not accompany the increased temperature and stability of the watermass during the rainy season.

21. Maximum coccolithophore abundance was 89,000 cells per liter during the upwelling season; 22 taxa were recorded. The dynamics of *Coccolithus huxleyi* and *Gephyrocapsa oceanica* were primarily responsible for the observed cycle. *Gephyrocapsa oceanica* and *Calciosolenia sinuosa* (the third most important species) occurred throughout the year; *Coccolithus huxleyi* only during the upwelling season, and *Discosphaera tubifera* only during the rainy season.

22. Coccolithophores usually exceeded the dinoflagellates during the upwelling season, were approximately equally important during the rainy season, and considerably less abundant than the diatoms throughout the year.

23. The relative paucity of coccolithophores during the upwelling season might reflect sub-optimal nutrient concentrations and, possibly, high temperatures.

24. A regional comparison indicated that the tropical dinoflagellate and coccolithophore communities are characterized by a greater number of species, but attain a lower maximum abundance than observed in other biogeographical regions.

25. Micro-flagellates attained maximum abundance during the upwelling season, with a population of 1,713,000 cells per liter observed during April 1956. This group usually exceeded the dinoflagellates and coccolithophores, and were secondary to the diatoms in abundance.

26. Twelve silicoflagellate species and varieties were encountered. Maximum observed abundance was only 380 cells per liter.

27. Ten cyanophycean taxa were encountered. *Trichodesmium* was common to abundant during the upwelling season, but infrequent to absent during the rainy season when an unidentified form became important.

28. Twenty-seven tintinnids and six ciliates (*Strombidium* [*Laboea*] and *Lohmaniella*) were identified. The tintinnid *Metacylis annulifera* attained 7,020 cells per liter; otherwise, the data suggest that these groups were not important grazers.

29. The phytoplankton samples always contained chlorotic and/or empty cells representing many taxa which comprised a trace to 100 per cent of the total community. The mean incidence of moribund individuals

was 10 to 15 per cent of the community, which possibly represents the minimal natural daily mortality rate.

30. The No. 20 net plankton settling volumes collected from bottom-to-top (40 m) generally exceeded the mean phytoplankton biomass in the upper 20 m derived from cell counts by 1.2- to 480-fold.

31. For an annual net primary production of 180 g of carbon m^{-2}, of which about 90 g are produced during the upwelling season, an annual gross production rate of 255 to 280 g of carbon m^{-2} was estimated. Annual respiration losses were 30 to 35 per cent.

32. The productive zone appears to occur principally in the upper 15 m during the upwelling and rainy seasons. Maximum ^{14}C assimilation rates usually occurred at the surface, despite high light intensities which might have been expected to be inhibitory.

33. Phytoplankton abundance during the upwelling seasons, expressed as cell numbers, biomass or surface area, was statistically significantly and directly related to 1-, 3- and, to a somewhat lesser extent, 7-day wind conditions at Balboa prior to the sampling date when expressed as Σ (N + NW) or Σ (N + .8NW − S).

34. The regression of mean monthly phytoplankton biomass in the upper 20 m on the "3-week winds" intensity at Balboa, expressed as Σ (N + .1NW − 10S) and Σ (N + .1NW − 12S), accounted for 82 per cent of the variation, suggesting that the magnitude of the standing crop can be predicted from a knowledge of wind conditions.

35. Annual differences in mean phytoplankton biomass during the upwelling seasons are directly related ($r = > 0.90$) to differences in total intensity of upwelling winds.

36. The total upwelling season wind intensities, the mean upwelling season biomass levels, and the correlation between these two variables suggest the following annual ranking of upwelling intensity in the Gulf of Panama: 1955 > 1957 > 1956.

37. The mean biomass in the upper 20 m at the upwelling season stations could be estimated from 3-day winds prevailing at Balboa prior to the sampling date and the mean surface temperature (t_o) using various equations of the form: $\sqrt{\text{winds}/t_o}$. The observed and calculated estimates of biomass agreed within ± 15 per cent at 17 of the 26 stations, but no equation provided a consistently good biomass estimate. The calculated mean diatom biomass for the 1955 and 1957 upwelling seasons agreed within 2 to 5 per cent of the observed mean values, while the 1956 estimates were in poor agreement.

38. The station-to-station differences in phytoplankton abundance during the rainy season could not be statistically related to the six wind

expressions used. An analysis with density (σ_t) of the surface waters, however, suggested that phytoplankton growth during the height of the rainy season (August—November) was promoted by increased precipitation, whereas growth prior to this period was dependent upon northerly winds.

39. Mean monthly abundance of phytoplankton, expressed as cell numbers and biomass, during the rainy season, was significantly and directly related to the 3-day northerly winds at Balboa, expressed as Σ (N + NW) (for cell numbers) and Σ (N + .8NW) (for biomass), and surface and 10 m density (σ_t). These results suggest that general phytoplankton growth during the rainy season, as during the upwelling season, is *primarily* dependent on the occurrence of northerly winds, whereas short-term phytoplankton fluctuations may *not* be.

40. The average annual standing crops of zooplankton in 1955, 1956 and 1957 were 96, 95 and 73 mg m^{-3}, respectively. Unlike previous years, the average standing crop of zooplankton in 1957 during the rainy season, 94 mg m^{-3} *exceeded* that during the upwelling season. The *mean* standing crop of zooplankton during the upwelling seasons of 1955 to 1957 was 168, 157 and 119 mg m^{-3}, respectively.

41. The station-to-station phytoplankton : zooplankton standing crop ratio, as biomass, ranged from 0.04 to 981 : 1; the average phytoplankton standing crop based on 30 stations exceeded the zooplankton standing crop by 83-fold. Zooplankton biomass exceeded the phytoplankton standing crop at only four stations.

42. The mean annual phytoplankton and zooplankton cycles, based on biomass, indicated that 1) the phytoplankton standing crop was considerably greater, except during June, and 2) there was a tendency for a direct relationship during the upwelling season and an inverse relationship during the rainy season. The sample correlation coefficient was 0.59 between the mean monthly standing crop levels.

43. Both direct and inverse correlations were found between zooplankton and phytoplankton abundance when the mean monthly standing crops for any given year and station-to-station variations in abundance were compared, after lagging the zooplankton 2 weeks, 4 weeks, and when comparing the simultaneous standing crop levels.

44. Zooplankton respiration and grazing rates were estimated. The mean daily rate of predation, using several procedures, was always less than 10 per cent of the daily phytoplankton standing crop as carbon. The mean daily rate of zooplankton production for all upwelling season data was 98 per cent of the standing crop when based on Anraku's *Acartia* data, and 29 per cent when based on Conover's *Acartia* data. During the rainy season a mean daily *loss* of zooplankton carbon by respiration of 18 per cent

was derived using the former's data and a *loss* of 12 per cent using the latter's.

45. The tuna bait fish, *Cetengraulis mysticetus*, or anchoveta, is abundant in the Gulf of Panama where it is a phytoplankton feeder during the upwelling season, and a bottom feeder during the rainy season. A strong positive correlation was found between mean anchoveta length during February, April and May and the average phytoplankton biomass during January and February. A strong positive correlation was also found between the mean monthly growth increment of the anchoveta and phytoplankton abundance, as biomass, during January to May, 1955—1957.

46. For anchoveta, the mean daily standing crop, and respiration, production and grazing rates were calculated for the various upwelling seasons. The average daily rate of production as carbon for all years was about 1.5 per cent of the standing crop. The mean daily grazing intensity was about 18 per cent of the phytoplankton standing crop as carbon for all years, and ranged from about 9 to 27 per cent per day for the individual upwelling seasons.

47. Some problems of phytoplankton existence associated with their occurrence in upwelling areas were discussed. A mechanism permitting the maintenance and succession of autochthonous phytoplankton communities in upwelling areas was proposed.

48. A common, uniform tropical phytoplankton community does not occur. A classification and description of five types of phytoplankton cycles and communities found in tropical inshore areas were presented. Wind-induced nutrient-enrichment of the euphotic zone either through mixing, upwelling or some other process is probably the prime prerequisite for increased phytoplankton growth in tropical inshore areas.

49. The following elements of the Gulf of Panama environment and food-chain could be inter-correlated: upwelling winds — phytoplankton — zooplankton — anchoveta.

RESUMEN EN ESPAÑOL

1. Se recolectaron muestras cuantitativas de fitoplancton en la superficie, a 10 y 20 m, a los 8°45′N, 79°23′W, a intervalos de aproximadamente 2 semanas entre el 29 de noviembre 1954 y el 10 de mayo 1957.

2. Se tomaron las medidas de la temperatura, salinidad, oxigeno y fosfato de la superficie y de los 5, 10, 20 y aproximadamente 40 m (fondo), junto con observaciones del disco Secchi. También se tomaron medidas durante 24 horas del ^{14}C *in situ* a los 10 m, para calcular la productividad de los arrastres verticales de fitoplancton con una red No. 20, y arrastres

oblicuos de zooplancton (malla de tejido de gaza No. 40 XXX) del fondo a la superficie.

3. El afloramiento ocurrió desde enero hasta abril, y ocasionalmente durante diciembre y mayo. Aparece un ligero resurgimiento de los vientos septentrionales que impulsan el afloramiento durante julio y/o agosto, seguido por vientos intensos que traen la lluvia meridional a la costa durante el resto del año.

4. Durante el afloramiento, los 50 m superiores, o sea el 30 por ciento del volumen total del golfo, es reemplazado por agua de 5 a 10 C más fría que la que se encuentra durante la estación lluviosa.

5. Se presenta un patrón hipotético de la circulación de afloramiento, basado en la consideración de la topografía del fondo; generalmente está de acuerdo con el sugerido por los datos de temperatura y salinidad.

6. La precipitación media anual es de 2731 mm; más del 50 por ciento del drenaje total anual ocurre de septiembre a diciembre. El promedio del drenaje anual y de la precipitación directa al Golfo de Panamá es de 92.5 $\times 10^9$ m^3—equivalente a una capa de agua dulce de un espesor de 3.2 m.

7. Durante la estación de las lluvias, un aumento en la estabilidad y turbiedad, además de una intensidad reducida de la radiación incidental acompañan la precipitación. La profundidad media del isolumen del 50% durante la estación lluviosa de 1957 fue de 7.4 m, cerca del doble que la estación de lluvias de más humedad de 1956.

8. La radiación media diaria de 184 g cal cm^{-2} dia^{-1} a la profundidad del isolumen del 50% encontrada entre los 3 y 4 m durante el período más turbio en el Golfo de Panamá, *excede la radiación incidental* durante cerca de 4, 6 y 8 meses del año en la región Templada, Boreal y Artica, escogidas con fines comparativos.

9. La concentración media de fosfato fue de 55.18 mg-at m^{-2} durante la temporada de afloramiento, y 34.14 mg-at m^{-2} durante la estación de lluvias. El fosfato puede ser separado del agua intersticial de los sedimentos del fondo como resultado del enturbiamiento y frotamiento incurridos a causa de la corriente de afloramiento.

10. La reducción gradual de la concentración de fosfato durante la estación lluviosa parece estar relacionada a la cantidad de lluvia. Es también importante la utilización biológica *sin* una ganancia apreciable de fosfato, a causa del contenido bajo de fosfato del drenaje y del agua lluvia y/o adsorción significativa del fosfato sobre la carga considerable de las partículas terrígenas que acompañan el drenaje del litoral.

11. Se estimaron las cantidades de fosfato, nitrato y amoníaco adheridas durante la estación lluviosa *via* drenaje y agua lluvia, y se compararon con los requisitos fotosintéticos de estas substancias, basándose

en la estimación (hecha por Forsbergh usando el método del ^{14}C), de la productividad de 90 g de carbono m^{-2} durante la estación de lluvias. Aproximadamente el 9 por ciento de los requisitos de fosfato y el 10 por ciento del nitrógeno inorgánico son provistos por acrecencia. Esto sugiere que la reproducción provee el volumen de fósforo y nitrógeno requeridos por el fitoplancton durante la estación de lluvias.

12. Un análisis rápido de la disponibilidad del hierro y de los niveles hipotéticos del silicato y de las vitaminas sugiere que estos nutrientes pueden ser substancias limitativas sin importancia.

13. Durante las temporadas de afloramiento de 1955 y 1956, en contraste a 1957, se efectuaron cambios importantes en la abundancia y composición del fitoplancton a causa de cambios hidrográficos, los cuales, generalmente a su vez, podrían ser cotejados con la magnitud de los vientos septentrionales (de afloramiento). La abundancia del fitoplancton tendió a aumentar en proporción a los vientos del norte, pero un descenso considerable en la abundancia acompañó igualmente la disminución modesta de estos vientos. Los datos sugieren una sucesión de especies durante todos los periodos de afloramiento, aunque pueden aparecer poblaciones alógenas.

14. La relación directa entre los vientos septentrionales y la densidad de fitoplancton observada generalmente durante las temporadas de afloramiento de 1955 y 1956, se manifestó también durante la estación de lluvias.

15. El ciclo medio estacional de fitoplancton se caracteriza 1) por un máximum anual durante la temporada de afloramiento (diciembre-abril) y un mínimum anual durante la estación de lluvias, separados por un breve resurgimiento en julio que acompaña la reaparición de los vientos septentrionales; 2) las existencias de fitoplancton, expresadas como número de células y biomasa, fue de 6 y 9 veces superior, respectivamente, durante la temporada de afloramiento que durante la estación de lluvias; 3) las diatomeas dominan abrumadoramente la comunidad promedia del fitoplancton, tanto numéricamente (86 y 71 por ciento) como en biomasa (97 y 99 por ciento) durante la temporada de afloramiento y de lluvias, respectivamente, y 4) ocurren variaciones anuales en la abundancia durante la temporada de afloramiento.

16. Aproximadamente de las 175 especies de diatomeas identificadas, solamente la dinámica de 25 especies fue originalmente responsable por las características principales del ciclo anual de las diatomeas.

17. Apareció una similitud notable en la sucesión de la comunidad de las diatomeas durante las temporadas de afloramiento de 1955-1957, a pesar de las diferencias anuales, mensuales y semanales en la tasa de afloramiento. Se reconocieron cuatro comunidades (etapas); una asociación de *Chaetoceros compressus* + *Skeletonema costatum* f. *tropicum* (I Etapa) inició el desarrollo de las diatomeas durante diciembre y enero. Febrero se caracterizó por el predominio de *Rhizosolenia delicatula* (II Etapa), aunque

durante 1956 ocurrió también una aparición en masa de *Eucampia cornuta*. La III Etapa, que acompañó el afloramiento intensivo generalmente característico de marzo (con excepción de 1957), exhibió variaciones anuales marcadas en las especies codominantes presentes. *Nitzschia delicatissima* usualmente obtuvo una abundancia modesta durante esta etapa, acompañada por una codominante más abundante e imprevisible: *Lauderia annulata* (1955); *Chaetoceros costatus* (1956) y *Nitzschia pacifica* + *Nitzschia atlanticus* var. *pungens* (1957). La temporada de afloramiento terminó en abril con la dominación de *Rhizosolenia stolterfothii* (IV Etapa).

18. La comunidad de fitoplancton de la estación lluviosa dominada por *Skeletonema costatum* f. *tropicum* y *Chaetoceros compressus* fue bastante similar en composición a la comunidad de la I Etapa de la temporada de afloramiento. Esto sugiere que la comunidad de fitoplancton durante la temporada inicial de afloramiento es autóctona.

19. Los dinoflagelados Thecate y Gymnodiniaceae (dinoflagelados desnudos) eran muy escasos, por razones desconocidas. La abundancia máxima fue de 38,000 y 11,500 células por litro, respectivamente, durante la temporada de afloramiento. De las 105 taxas aproximadamente identificadas de dinoflagelados, solamente 15 alcanzaron una abundancia de más de 1,000 células por litro. La dinámina de *Exuviaella baltica* (máximo de 22,000 células por litro) fue originalmente responsable por el ciclo observado de dinoflagelados; no se observó una sucesión de especies.

20. El aumento de temperatura y la estabilidad de las masas de agua no fue acompañada durante la estación de lluvias por una sucesión de la comunidad de las diatomeas a la de los dinoflagelados.

21. La abundancia máxima de cocolitóferos fue de 89,000 células por litro durante la temporada de afloramiento; se registraron 22 taxas. La dinámica de *Coccolithus huxleyi* y *Gephyrocapsa oceanica* fue originalmente responsable por el ciclo observado. *Gephyrocapsa oceanica* y *Calciosolenia sinuosa* (la tercera especie de más importancia) apareció durante todo el año; *Coccolithus huxleyi* solamente apareció durante la temporada de afloramiento, y *Discosphaera tubifera* únicamente durante la estación de lluvias.

22. Los cocolitóferos excedieron usualmente a los dinoflagelados durante la temporada de afloramiento, pero fueron aproximadamente de igual importancia durante la estación lluviosa. Fueron considerablemente menos abundantes que las diatomeas durante todo el año.

23. La escasez relativa de los cocolitóferos durante la temporada de afloramiento puede reflejar concentraciones suboptimales de nutrientes y, posiblemente, temperaturas altas.

24. Una comparación de regiones indicó que las comunidades de los dinoflagelados y cocolitóferos tropicales se caracterizan por un número mayor de especies, pero alcanzan una abundancia máxima inferior a la observada en otras regiones biogeográficas.

25. Los microflagelados obtuvieron su abundancia máxima durante la temporada de afloramiento, con una población de 1,713,000 células por litro, observada durante abril de 1956. Este grupo excedió generalmente a los dinoflagelados y cocolitóferos, y fueron secundarios en abundancia a las diatomeas.

26. Se encontraron 12 especies y variedades de silicoflagelados; la abundancia máxima observada fue solo de 380 células por litro.

27. Se encontraron 10 taxas de cyanophyceanos. *Trichodesmium* fue de común a abundante durante la temporada de afloramiento, pero de infrecuente a ausente durante la época de lluvias cuando una forma no identificada era importante.

28. Se identificaron 27 tintinidos y 6 ciliatos (*Strombidium* [*Laboea*] y [*Lohmaniella*]). El tintinido *Metacylis annulifera* alcanzó 7,020 células por litro; de lo contrario, los datos sugieren que estos grupos no fueron fitófagos importantes.

29. Las muestras de fitoplancton siempre contenían células cloróticas o vacías representando muchas taxas que incluyeron un vestigio hasta del 100 por ciento de la comunidad total. La incidencia media de individuos moribundos fue del 10 al 15 por ciento de la comunidad, lo que posiblemente representa la tasa mínima de mortalidad natural diaria.

30. Los volúmenes de sedimentación recolectados del plancton (con la red No. 20) del fondo a la superficie (40 m) generalmente excedieron la biomasa media de fitoplancton (derivados del cálculo de células) en los 20 m superiores, de 1.2 hasta 480 veces.

31. Se estimó una tasa de producción bruta anual de 225 hasta 280 g de carbono m^{-2} para una producción neta primaria anual de 180 g de carbono m^{-2}, de la cual cerca de 90 g se producen durante la temporada de afloramiento. Las pérdidas anuales de respiración fueron de 30 al 35 por ciento.

32. La zona productiva aparece principalmente en los 15 m superiores durante la época de afloramiento y de lluvias. Las tasas máximas de asimilación de ^{14}C ocurrieron generalmente en la superficie, a pesar de las altas intensidades de luz que se podría esperar tuvieran una influencia limitante.

33. La abundancia del fitoplancton durante la temporada de afloramiento, expresada en número de células, biomasa o área de superficie, fue estadísticamente significativa y directamente relacionada a las condiciones de los vientos en Balboa de 1, 3 e inferiores a los de los 7 días, prior a la fecha del muestreo cuando se expresa como Σ (N + NO) o Σ (N + 0.8NO − S).

34. La regresión de la biomasa media mensual del fitoplancton en los 20 m superiores sobre la intensidad de los "vientos de 3 semanas" en

Balboa, expresada por Σ (N + 0.1NO − 10S) y Σ (N + 0.1NO − 12S), cuenta por el 82 por ciento de la variación, lo que sugiere que la magnitud de las existencias pueden predecirse según el conocimiento que se tenga de las condiciones del viento.

35. Las diferencias anuales de la biomasa media del fitoplancton durante la temporada de afloramiento están directamente relacionadas ($r = > 0.90$) a las diferencias en la intensidad total de los vientos de afloramiento.

36. La intensidad total del viento durante la temporada de afloramiento, los niveles medios de la biomasa durante dicha estación, y la correlación entre estas dos variables sugieren la siguiente categoría anual de la intensidad de afloramiento en el Golfo de Panamá; 1955 > 1957 > 1956.

37. Podría estimarse la biomasa media a los 20 m superiores en las estaciones del período de afloramiento basándose en los vientos de 3 días prevalecientes en Balboa prior a la fecha del muestreo y a la temperatura media de la superficie (t_0) usando varias ecuaciones de la forma: $\sqrt{\text{viento}}/t_0$. Los estimativos de la biomasa observada y calculada concordaron dentro de ± 15 por ciento en 17 de las 26 estaciones, pero ninguna de las ecuaciones proporcionó un estimativo de la biomasa uniformemente bueno. La biomasa media calculada de las diatomeas correspondiente a las temporadas de afloramiento de 1955 y 1957 estuvieron de acuerdo del 2 al 5 por ciento de los valores medios observados, mientras en 1956 los estimativos no tuvieron buen acuerdo.

38. Las diferencias de estación a estación en la abundancia del fitoplancton durante la estación de lluvias no pudieron relacionarse estadísticamente a las seis expresiones usadas del viento. Sin embargo, un análisis basado en la densidad (σ_t) de las aguas superficiales, sugiere que el crecimiento del fitoplancton durante el máximo de la estación lluviosa (agosto-noviembre) fue promovido por el aumento de la precipitación, mientras el crecimiento anterior a este período dependió de los vientos septentrionales.

39. La abundancia media mensual del fitoplancton, expresada en número de células y biomasa, durante la estación de lluvias, fue relacionada significativa y directamente a los vientos septentrionales de Balboa, de 3 días, representados por Σ (N + NO) (para el número de células) y Σ (N + 0.8NO) (para la biomasa), y las densidades de la superficie y de los 10 m (σ_t). Estos resultados sugieren que el crecimiento general del fitoplancton, durante las estaciones de lluvias como de afloramiento dependen *principalmente* de la aparición de los vientos septentrionales, mientras las fluctuaciones de fitoplancton de poco tiempo quizás *no* lo son.

40. El promedio de las existencias anuales de zooplancton en 1955, 1956 y 1957 fueron de 96, 95 y 73 mg m^{-3}, respectivamente. En contraste a los años anteriores, las existencias promedias de zooplancton en 1957 durante la estación de lluvias, 94 mg m^{-3}, *excedieron* la de la temporada de

afloramiento. Las existencias *medias* de zooplancton durante las temporadas de afloramiento desde 1955 a 1957 fueron respectivamente de 168, 157 y 119 mg m^{-3}.

41. La razón del fitoplancton de estación a estación: las existencias de zooplancton, como biomasa, varió de 0.04 a 981 : 1; el promedio de las existencias de fitoplancton, basado en 30 estaciones, excedió las existencias de zooplancton 83 veces. La biomasa del zooplancton excedió las existencias de fitoplancton solamente en cuatro estaciones.

42. Los ciclos medios anuales de fitoplancton y zooplancton, basados en la biomasa, indicaron que 1) las existencias de fitoplancton fueron considerablemente superiores excepto en junio, y 2) que habia una tendencia a una relación directa durante la temporada de afloramiento y una relación inversa durante la estación lluviosa. El coeficiente de correlación de las muestras era 0.59 entre estas existencias medias mensuales.

43. Se encontraron tanto correlaciones directas como inversas entre la abundancia del zooplancton y fitoplancton, cuando se compararon las existencias mensuales medias en cualquier año dado, con las variaciones en la abundancia de estación a estación, durante los periodos de afloramiento y de lluvia, después de rezagarse el zooplancton por 2 semanas, 4 semanas y cuando se comparaban los niveles simultáneos de las existencias.

44. Se estimaron las tasas de respiración y forraje del zooplancton. La tasa media diaria de depredación, usando varios procedimientos, fue siempre inferior al 10 por ciento de las existencias diarias del fitoplancton como carbono. La tasa media diaria de la producción de zooplancton referente a todos los datos de la temporada de afloramiento fue del 98 por ciento de las existencias, cuando se basó en los datos de *Acartia* de Anraku, y el 29 por ciento, basándose en los datos de *Acartia* de Conover. Se derivó durante la estación de lluvias, una *pérdida* media diaria de carbono del zooplancton del 18 por ciento por respiración, usando los datos de Anraku y una *pérdida* del 12 por ciento usando los de Conover.

45. El pez de carnada para capturar los atunes, *Cetengraulis mysticetus* o anchoveta, es abundante en el Golfo de Panamá, donde se alimenta de fitoplancton durante la temporada de afloramiento, y de las materias del fondo durante la estación de lluvias. Se encontró una fuerte correlación positiva entre la longitud media de la anchoveta, en febrero, abril y mayo, y la biomasa promedia del fitoplancton durante enero y febrero. También se encontró una fuerte correlación positiva entre el incremento medio mensual del crecimiento de la anchoveta y la abundancia del fitoplancton, como biomasa, de enero a mayo, 1955-1957.

46. Para la anchoveta, las existencias medias diarias, y las tasas de respiración, producción y forraje se calcularon para las diferentes temporadas de afloramiento. El promedio de la tasa diaria de producción de la anchoveta, como carbono, para todos los años, fue aproximadamente del

1.5 por ciento de las existencias. La intensidad media diaria de forraje fue cerca del 18 por ciento de las existencias del fitoplancton como carbono, para todos los años, y varió aproximadamente del 9 al 27 por ciento por día, correspondiente a las temporadas individuales de afloramiento.

47. Se discutieron algunos problemas de la existencia de fitoplancton asociada con su aparición en las áreas de afloramiento. Se propuso un mecanismo que permitiera el mantenimiento y la sucesión de las comunidades autóctonas de fitoplancton en las áreas de afloramiento.

48. No ocurre una comunidad común, uniforme de fitoplancton tropical. Se presentó una clasificación y descripción de cinco tipos de ciclos y comunidades fitoplanctónicas, encontrados en áreas tropicales cercanas a la orilla. Probablemente el requisito principal para un desarrollo en el crecimiento del fitoplancton en áreas tropicales cercanas al litoral es el enriquecimiento nutritivo producido por los vientos de la zona eufórica ya sea por mezcla, afloramiento o algún otro proceso.

49. Podrían intercorrelacionarse los siguientes elementos ambientales del Golfo de Panamá y de la cadena alimenticia: vientos de afloramiento — fitoplancton — zooplancton — anchovetas.

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APPENDIX TABLES

The results of the phytoplankton enumeration are presented in two ways (Appendix Table 2), the format used being governed by space considerations, as done previously (Smayda 1963). For those species presented in *tabular* form, the population density is given as cells per 10 ml; the less important species are presented in *text* form as cells per liter. For example, Asteromphalus flabellatus **40** 28t,31t, **60** 27s,28s,b **80** 29s, **120** 27t, in the *text* tables is read as: *Asteromphalus flabellatus* occurred with a density of 40 cells per liter at 10 meters (subscript t) at stations 28 and 31; as 60 cells per liter at the surface (subscript s) at stations 27 and 28; and also at 20 meters (subscript b) at station 28, as 80 cells per liter at the surface at station 29 (i.e., **80** 29s); and as 120 cells per liter at ten meters at station 27 (i.e., **120** 27t). This species was not observed at any other station of those covered in Appendix Table 2A. Temperature and salinity conditions accompanying the occurrence of the species are listed in Appendix Table 1.

The symbol — in the tables indicates that the species in question was not observed at that station or depth.

A phytoplankton census was not made at the following stations:

Station	Depth (m)	Station	Depth (m)	Station	Depth (m)
2	10	14	20	43	20
4	20	15	20	45	20
8	20	38	10,20	46	10,20
10	20	39	0	50	0,10,20
11	0	40	20	53	20
12	0,10,20				
13	0				

Stations 4 (0, 10 m); 8 (0, 10 m); 9 (all depths); 11 (10, 20 m); 15 (10 m); and 36 (all depths) were not included in the tables because of sparse population densities or presence of a community similar to that at the preceding station (*vide* Appendix Table 1).

The following new taxa included in Appendix Table 2 will be formally described in a subsequent paper dealing with the floristic and biogeographical aspects of the Gulf of Panama phytoplankton:

Actinoptychus undulatus var. *catenata* n. var.
Asterionella japonica f. *tropicum* n. f.
Fragilaria norma n. sp.
Leptocylindrus maximus n. sp.
Skeletonema costatum f. *tropicum* n. f.
Thalassiothrix frauenfeldii var. *panama* n. var.

APPENDIX TABLE 1. Summary of Hydrographic and Plankton Data at 8°45'N, 79°23'W from November, 1954 to July, 1955 and December, 1955 to May, 1957. (Wind data as the three day total *prior* to sampling date. Note that diatom biomass is presented as mm^3 per liter, while for other groups as mm^3 per cubic meter. Symbols: (—) absent; (nd) no data; (*) surface tow; (id) incomplete data).

STATION		1	2	3	4	5	6	7	8
DATE	meters	11/29	12/24	1/11	1/25	2/8	2/22	3/10	3/23
		1954		1955					
Temperature °C	0	29.00	26.89	26.39	26.78	27.22	26.22	19.44	23.39
	10	28.89	26.78	26.11	26.61	26.56	26.11	18.28	17.83
	20	28.50	26.89	25.00	24.83	26.00	22.22	15.72	16.78
Salinity ‰	0	27.30	20.01	31.16	30.77	nd	31.76	34.67	34.41
	10	27.59	30.36	31.99	30.67	31.52	31.76	34.85	34.58
	20	30.74	30.92	33.02	31.65	32.07	33.17	34.96	34.78
Density, σ_t	0	16.33	19.03	20.04	19.63	nd	20.55	24.67	23.39
	10	16.58	19.33	20.75	19.61	20.27	20.59	25.10	24.99
	20	19.06	19.72	21.87	20.89	20.85	22.79	25.79	25.42
Oxygen, ml/l	0	4.64	4.75	5.28	4.76	4.97	4.78	6.65	5.89
	10	4.57	4.80	5.71	4.75	4.90	4.76	5.57	4.37
	20	3.85	4.60	3.65	3.99	4.54	2.63	1.68	0.77
Oxygen, % saturation	0	101.5	102.6	114.0	103.0	nd	103.2	130.7	123.7
	10	100.0	103.7	123.0	102.6	106.1	102.6	107.5	83.6
	20	84.4	100.0	78.0	84.2	97.8	53.7	31.1	14.5
Phosphate, μg at/L	0								
	10				NO DATA				
	20								
	mg at/m^2								
Secchi Disc (meters)									
Winds (miles):									
True North		204.0	392.2	379.0	212.0	302.7	431.0	772.0	579.0
True South		—	5.0	16.1	18.7	23.8	3.5	—	—
DIATOMS									
cells/liter	0	11,160	35,780	336,140	4,120	185,580	186,660	1,228,840	43,140
	10	4,640	nd	264,130	3,200	46,660	202,900	1,639,600	3,520
	20	11,180	10,700	563,570	nd	59,180	15,960	153,420	nd
biomass (mm^3/L)	0	.028	.216	.827	.010	.641	1.060	25.618	.188
	10	.094	nd	.972	.004	.284	.678	33.448	.005
	20	.049	.159	1.444	nd	.898	.202	3.067	nd
	$\bar{x}$	.067	id	1.054	id	.527	.654	23.895	id
DINOFLAGELLATES									
cells/liter	0	6,160	1,000	2,020	200	1,860	1,160	100	260
	10	1,080	nd	3,220	1,620	580	220	1,240	40
	20	1,660	840	1,100	nd	6,080	2,060	160	nd
biomass (mm^3/m^3)	0	3.850	.625	1.263	.125	1.163	.725	.063	.163
	10	.675	nd	2.013	1.013	.363	.138	.775	.013
	20	1.038	.525	.688	nd	3.800	1.288	.100	nd
	$\bar{x}$	1.560	id	1.494	id	1.422	.572	.428	id
COCCOLITHOPHORES									
cells/liter	0	4,000	3,500	2,000	3,000	3,000	1,500	—	500
	10	5,000	nd	1,500	1,500	500	1,000	1,000	—
	20	3,040	2,500	1,500	nd	500	500	—	nd
biomass (mm^3/m^3)	0	.520	.495	.260	.390	.390	.195	—	.065
	10	.650	nd	.195	.195	.065	.130	.130	—
	20	.395	.325	.195	nd	.065	.065	—	nd
	$\bar{x}$	.554	id	.211	id	.146	.130	.063	id
MONADS & FLAGELLATES									
cells/liter	0	6,500	4,500	9,000	9,000	19,500	22,500	30,500	26,000
	10	6,500	nd	14,500	1,000	10,500	42,000	58,500	20,000
	20	36,500	8,000	4,000	nd	26,500	36,520	47,500	nd
biomass (mm^3/m^3)	0	.423	.293	.585	.585	1.268	1.463	1.983	1.040
	10	.423	nd	.943	.065	.683	2.730	3.803	1.300
	20	2.373	.520	.260	nd	1.073	2.374	3.088	nd
	$\bar{x}$	.910	id	.683	id	1.090	2.325	3.170	id
Production mg C/m^3/day at	10m				NO DATA				
Zooplankton ml/1000 m^3		6	124	55	32	57	44	50	596

APPENDIX TABLE 1. (Continued)

STATION DATE	meters	1955 9 4/5	 10 4/19	 11 5/3	 12 5/16	 13 5/30	 14 6/13	 15 6/27	 16 7/11
Temperature °C	0	26.33	25.00	27.28	27.44	28.17	28.56	27.50	27.50
	10	25.61	21.61	27.06	27.11	27.28	28.39	27.06	27.56
	20	24.17	21.00	27.00	25.83	27.06	27.50	24.00	27.78
Salinity ‰	0	33.21	34.20	33.16	32.10	31.42	30.99	30.86	29.59
	10	33.86	34.22	33.26	32.50	32.61	31.38	31.95	29.58
	20	34.34	34.51	33.71	33.85	33.21	31.98	33.72	29.75
Density, σ_t	0	21.60	22.76	21.27	20.42	19.67	19.22	19.47	18.52
	10	22.31	23.75	21.41	20.82	20.85	19.57	20.43	18.49
	20	23.12	24.14	21.70	22.24	21.37	20.31	22.70	18.55
Oxygen, ml/l	0	5.05	5.44	4.63	4.63	4.87	4.66	4.68	4.75
	10	4.97	5.01	4.63	4.72	4.91	4.77	4.44	4.84
	20	4.70	2.60	4.77	4.00	4.73	4.37	3.47	4.72
Oxygen, % saturation	0	110.3	117.0	102.7	102.7	108.5	104.0	102.4	103.3
	10	107.8	102.2	102.0	104.0	109.6	106.2	96.7	105.2
	20	99.8	52.5	105.1	87.0	102.8	96.3	73.4	103.3
Phosphate, μg at/L	0								0.65
	10								0.98
	20				NO DATA				0.92
	mg at/m^2								35.37
Secchi Disc (meters)									
Winds (miles):									
True North		240.0	559.0	457.0	391.2	123.5	100.0	261.7	45.5
True South		35.3	5.0	20.0	9.0	52.1	90.0	28.6	229.4
DIATOMS									
cells/liter	0	4,500	809,620	nd	nd	nd	16,080	59,060	12,200
	10	20	389,040	47,660	nd	61,040	23,620	1,520	27,900
	20	—	nd	680	nd	10,060	nd	nd	19,840
biomass (mm^3/L)	0	.017	6.209	nd	nd	nd	.074	.273	.083
	10	—	2.425	.352	nd	.344	.103	.001	.079
	20	—	nd	.008	nd	.097	nd	nd	.056
	$\bar{x}$	.004	id	id	nd	id	id	id	.074
DINOFLAGELLATES									
cells/liter	0	760	680	nd	nd	nd	940	2,540	500
	10	220	6,540	660	nd	520	—	1,020	2,780
	20	—	nd	240	nd	20	nd	nd	5,060
biomass (mm^3/m^3)	0	.475	.425	nd	nd	nd	.588	1.588	.313
	10	.138	4.088	.412	nd	.325	—	.639	1.738
	20	—	nd	.151	nd	.013	nd	nd	3.163
	$\bar{x}$	.188	id	id	nd	id	id	id	1.738
COCCOLITHOPHORES									
cells/liter	0	—	9,500	—	nd	nd	1,000	—	500
	10	—	1,500	4,500	nd	—	1,000	13,000	—
	20	—	nd	1,500	nd	500	nd	nd	1,000
biomass (mm^3/m^3)	0	—	1.235	nd	nd	nd	.130	—	.065
	10	—	.195	.585	nd	—	.130	1.690	—
	20	—	nd	.195	nd	.065	nd	nd	.130
	$\bar{x}$	—	id	id	nd	id	id	id	id
MONADS & FLAGELLATES									
cells/liter	0	12,520	59,500	nd	nd	nd	6,500	36,500	4,000
	10	14,500	53,500	11,500	nd	6,500	10,000	16,000	60,500
	20	25,020	nd	3,500	nd	17,000	nd	nd	64,500
biomass (mm^3/m^3)	0	.814	3.868	nd	nd	nd	.423	2.373	.260
	10	.943	3.478	.748	nd	.423	.630	1.040	3.933
	20	1.627	nd	.228	nd	1.105	nd	nd	4.193
	$\bar{x}$	1.081	id	id	nd	id	id	id	3.080
Production mg C/m^3/day at 10m					NO DATA				
Zooplankton ml/1000 m^3		484	71	164	106	96	93	132	54

APPENDIX TABLE 1. (Continued)

		1955		1956					
STATION DATE	**meters**	**27 12/12**	**28 12/26**	**29 1/9**	**30 1/23**	**31 2/6**	**32 2/21**	**33 3/5**	**34 3/21**
Temperature °C	0	26.78	27.00	25.44	23.00	26.67	26.33	23.17	24.78
	10	27.00	26.61	25.33	16.83	26.22	25.50	20.06	19.33
	20	25.22	26.39	23.06	13.72	25.39	22.56	17.22	18.00
Salinity ‰	0	26.82	26.60	28.76	33.17	31.39	32.02	33.62	33.44
	10	28.41	26.68	29.38	34.53	31.39	32.24	33.72	33.76
	20	30.31	28.25	32.37	35.09	32.01	32.91	34.42	34.43
Density, σ_t	0	16.67	16.44	18.53	22.57	20.13	20.71	22.87	22.25
	10	17.80	16.63	19.03	25.22	20.27	21.14	23.80	24.01
	20	19.76	17.87	21.95	26.33	20.99	22.49	25.03	24.86
Oxygen, ml/l	0	4.84	4.92	4.99	5.71	4.96	4.73	5.68	5.40
	10	4.84	4.97	4.90	4.70	4.94	4.80	4.69	4.53
	20	4.09	4.96	2.17	0.74	4.71	3.89	1.91	2.73
Oxygen, % saturation	0	102.1	104.0	104.4	118.2	107.6	102.6	118.3	115.4
	10	103.4	104.4	102.7	88.2	106.5	103.0	92.7	88.5
	20	86.1	105.1	44.7	13.1	100.6	79.9	36.0	52.3
Phosphate, μg at/L	0	0.65	0.45	0.66	0.42	0.04	0.30	1.18	1.39
	10	0.72	0.49	0.68	1.23	0.10	0.48	1.66	2.08
	20	0.99	0.37	1.74	2.46	0.16	0.83	2.69	2.81
	mg at/m^2	44.21	30.95	65.05	78.95	18.32	34.74	100.42	108.00
Secchi Disc (meters)				NO DATA					
Wind (miles):									
True North		276.7	273.7	541.0	394.0	354.6	502.0	573.4	474.1
True South		11.2	13.0	—	—	2.8	2.8	—	7.5
DIATOMS									
cells/liter	0	80,540	81,420	1,186,470	532,360	39,460	242,060	394,620	460,120
	10	105,880	162,640	795,400	445,900	13,140	265,960	176,800	253,380
	20	261,240	132,720	113,860	315,440	13,300	44,380	109,560	7,260
biomass (mm^3/L)	0	.695	.414	4.905	3.235	.050	.677	.711	1.378
	10	.433	.552	4.909	3.946	.013	.711	.670	.700
	20	1.401	.648	1.798	4.295	.016	.138	.186	.016
	$\bar{x}$	.740	.542	4.130	3.856	.023	.559	.559	.698
DINOFLAGELLATES									
cells/liter	0	1,440	1,840	2,420	2,220	820	4,400	11,000	4,640
	10	1,040	3,760	2,280	—	1,620	11,080	18,440	5,960
	20	5,240	1,100	80	40	2,180	4,760	120	16,060
biomass (mm^3/m^3)	0	.900	1.150	1.513	1.388	.513	2.750	6.875	2.900
	10	.650	2.350	1.425	—	1.013	6.925	11.525	3.725
	20	3.275	.688	.050	.025	1.363	2.975	.075	10.038
	$\bar{x}$	1.369	1.635	1.103	.353	.975	4.895	7.500	5.097
COCCOLITHOPHORES									
cells/liter	0	—	12,000	8,500	8,500	—	79,500	22,000	45,500
	10	—	9,000	5,000	—	16,500	89,000	12,500	44,000
	20	20	18,020	1,000	500	12,500	47,500	2,060	4,500
biomass (mm^3/m^3)	0	—	1.560	1.105	1.105	—	10.335	2.860	5.915
	10	—	1.700	.650	—	2.145	11.570	1.625	5.720
	20	.003	2.343	.130	.065	1.625	6.175	.268	.585
	$\bar{x}$	.001	1.826	.634	.293	1.479	9.913	1.595	4.486
MONADS & FLAGELLATES									
cells/liter	0	12,500	12,500	92,000	24,500	40,500	61,500	16,100	8,100
	10	34,000	45,520	85,500	47,500	29,000	54,520	54,660	26,860
	20	49,500	13,000	9,000	42,000	31,000	28,000	5,060	16,060
biomass (mm^3/m^3)	0	.813	.813	5.980	1.593	2.633	3.998	.852	.527
	10	.221	2.959	5.558	3.088	1.885	3.544	3.553	1.746
	20	3.218	.826	.585	2.730	2.015	2.470	.329	1.044
	$\bar{x}$	1.118	1.895	4.421	2.625	2.105	3.390	2.121	1.266
Production mg C/m^3/day at	10m	4.8	nd	57.0	17.0	nd	42.0	nd	1.5
Zooplankton ml/1000 m^3		22	17	nd	777	206	50	16	106

APPENDIX TABLE 1. (Continued)

		1956							
STATION **DATE**	**meters**	**35** **4/2**	**36** **4/17**	**37** **4/30**	**38** **5/14**	**39** **6/19**	**40** **7/2**	**41** **7/17**	**42** **7/31**
Temperature °C	0	21.56	27.39	27.33	27.28	27.17	28.28	28.33	28.17
	10	18.44	25.28	26.94	27.17	28.06	28.06	27.56	27.72
	20	17.33	22.33	25.89	26.89	27.94	27.39	27.17	26.67
Salinity ‰	0	34.43	32.83	33.33	32.90	27.43	28.82	29.76	29.24
	10	34.43	33.29	33.40	33.04	29.51	30.44	29.94	30.17
	20	34.51	34.37	33.46	33.27	30.88	32.34	32.17	32.09
Density, σ_t	0	23.91	20.98	21.37	21.07	17.02	17.69	18.38	18.05
	10	24.75	21.99	21.56	21.21	18.27	18.98	18.76	18.89
	20	25.08	23.67	21.92	21.47	19.35	20.61	20.56	20.65
Oxygen, ml/l	0	5.46	4.93	5.00	4.77	4.82	4.77	4.73	4.11
	10	4.86	4.94	5.06	4.82	4.79	4.74	4.85	4.14
	20	1.97	4.92	5.05	4.82	4.68	4.82	4.40	3.79
Oxygen, % saturation	0	111.2	109.1	111.1	105.8	102.8	104.4	104.2	90.1
	10	93.8	106.5	111.7	106.6	104.8	104.4	105.7	90.6
	20	37.2	101.7	109.8	106.2	103.1	106.4	96.9	82.9
Phosphate, μg at/L	0	0.38	0.50	0.12	0.21	0.19	0.39	0.37	0.44
	10	0.59	0.38	0.13	0.24	0.10	0.42	0.43	0.45
	20	2.01	0.42	0.24	0.27	0.22	0.57	0.57	0.48
	mg at/m^2	63.16	27.16	12.63	17.68	13.90	30.95	27.79	46.74
Secchi Disc (meters)						9	7.5	11	12
Wind (miles):									
True North		707.0	165.5	425.4	219.2	51.0	186.0	186.0	340.0
True South		—	65.5	10.5	25.1	89.0	2.0	11.0	13.0
DIATOMS									
cells/liter	0	163,240	—	47,360	209,460	nd	22,720	129,280	89,560
	10	300,500	240	35,160	nd	2,500	38,760	148,960	67,800
	20	9,980	780	33,760	nd	1,780	nd	49,500	25,280
biomass (mm^3/L)	0	.695	—	.546	.881	nd	.068	.253	.170
	10	.871	.010	.209	nd	.007	.261	.272	.253
	20	.024	.017	.072	nd	.008	nd	.101	.127
	$\bar{x}$	.615	.009	.259	id	id	id	.225	.201
DINOFLAGELLATES									
cells/liter	0	280	40	34,940	760	nd	5,740	3,800	5,260
	10	1,200	20	4,580	nd	9,640	4,100	9,620	7,180
	20	700	—	1,840	nd	1,020	nd	5,780	2,520
biomass (mm^3/m^3)	0	.175	.025	21.838	.476	nd	3.588	2.375	3.288
	10	.750	.013	2.863	nd	6.025	2.563	6.013	4.488
	20	.438	—	1.150	nd	.639	nd	3.613	1.575
	$\bar{x}$	.528	.013	7.179	id	id	id	4.504	3.460
COCCOLITHOPHORES									
cells/liter	0	7,000	500	—	4,060	nd	7,500	14,500	1,520
	10	7,000	500	620	nd	—	16,020	18,500	9,600
	20	—	500	120	nd	3,500	nd	6,500	8,000
biomass (mm^3/m^3)	0	.910	.065	—	.528	nd	.975	1.885	.198
	10	.910	.065	.081	nd	—	2.083	2.405	1.248
	20	—	.065	.016	nd	.495	nd	.845	1.040
	$\bar{x}$	.682	.065	.045	id	id	id	1.886	.933
MONADS & FLAGELLATES									
cells/liter	0	911,000	6,000	17,500	11,020	nd	16,000	20,500	22,000
	10	1,713,000	8,000	18,500	nd	12,000	26,000	16,000	51,000
	20	229,500	4,500	15,500	nd	7,000	nd	19,500	14,500
biomass (mm^3/m^3)	0	1776.450	.420	1.138	.716	nd	1.040	1.333	1.463
	10	3340.350	.520	1.203	nd	.840	1.690	1.040	3.315
	20	447.525	.293	1.008	nd	.455	nd	1.268	.943
	$\bar{x}$	2226.170	.431	1.139	id	id	id	1.170	2.260
Production mg C/m^3/day at	10m	31	4.7	nd	14	3.1	3.4	nd	4.5
Zooplankton ml/1000 m^3		17	276	*83	*28	105	*25	25	*52

APPENDIX TABLE 1. (Continued)

		1956						
STATION		**43**	**44**	**45**	**46**	**47**	**48**	**49**
DATE	**meters**	**8/13**	**8/27**	**9/11**	**9/24**	**10/8**	**10/22**	**11/8**
Temperature °C	0	28.11	28.11	28.56	28.33	28.11	27.61	27.67
	10	27.89	27.78	28.17	28.28	28.17	27.56	27.00
	20	27.22	26.11	27.61	27.67	27.89	27.11	26.83
Salinity ‰	0	30.01	28.58	27.98	29.85	28.66	26.85	24.88
	10	30.13	29.49	29.13	29.97	29.36	28.48	25.76
	20	31.81	31.76	30.83	29.85	31.02	29.85	28.23
Density, σ_t	0	18.64	17.57	16.98	18.45	17.63	16.44	14.95
	10	18.80	18.36	17.96	18.56	18.14	17.67	15.82
	20	20.27	20.59	19.42	18.66	19.47	18.84	17.71
Oxygen, ml/l	0	4.82	4.63	4.79	4.73	4.61	4.56	4.62
	10	4.74	4.64	4.72	4.67	4.59	4.86	4.23
	20	4.41	4.10	4.58	4.76	4.71	4.38	3.51
Oxygen, % saturation	0	105.9	100.9	104.6	104.1	100.4	97.6	97.7
	10	104.0	101.3	101.1	102.9	100.7	103.4	89.1
	20	96.7	88.4	100.7	103.9	104.0	94.8	74.8
Phosphate, μg at/L	0	0.35	0.67	—	1.01	0.23	0.21	0.37
	10	0.71	0.68	0.57	0.77	0.22	0.57	0.03
	20	0.81	0.97	0.59	1.27	0.32	0.71	0.15
	mg at/m^2	41.69	42.32	35.37	54.32	22.74	45.48	13.26
Secchi Disc (meters)		12.5	9.5	9	15.5	22.5	12	6.5
Wind (miles):								
True North		130.0	135.0	164.0	95.0	101.0	33.0	61.0
True South		68.0	33.0	47.0	96.0	72.0	146.0	125.0
DIATOMS								
cells/liter	0	17,280	40,600	127,140	15,570	23,920	49,440	32,440
	10	145,280	32,780	272,020	nd	11,260	176,320	14,720
	20	nd	10,300	nd	nd	780	14,300	22,280
biomass (mm^3/L)	0	.280	.149	.388	.056	.074	.167	.303
	10	1.587	.419	.645	nd	.042	.604	.131
	20	nd	.030	nd	nd	.006	.318	.101
	$\bar{x}$	id	.254	id	id	.041	.423	.167
DINOFLAGELLATES								
cells/liter	0	1,000	3,620	2,040	160	1,640	2,820	3,940
	10	3,120	3,500	160	nd	3,100	1,740	1,660
	20	nd	620	nd	nd	2,120	1,620	1,600
biomass (mm^3/m^3)	0	.625	2.263	1.275	.100	1.025	1.763	2.463
	10	1.950	2.188	.100	nd	1.938	1.088	1.038
	20	nd	.388	nd	nd	1.325	1.013	1.000
	$\bar{x}$	id	1.757	id	id	1.557	1.238	1.385
COCCOLITHOPHORES								
cells/liter	0	1,000	2,500	—	1,500	6,000	—	—
	10	2,000	500	6,000	nd	4,500	—	4,000
	20	nd	2,500	nd	nd	3,540	—	—
biomass (mm^3/m^3)	0	.130	.325	—	.195	.780	—	—
	10	.325	.065	.780	nd	.585	—	.520
	20	nd	.325	nd	nd	.460	—	—
	$\bar{x}$	id	.196	id	id	.603	—	.260
MONADS & FLAGELLATES								
cells/liter	0	42,000	14,000	11,500	9,500	21,500	17,000	5,000
	10	48,500	11,500	14,500	nd	19,000	21,000	—
	20	nd	19,000	nd	nd	18,500	7,000	1,000
biomass (mm^3/m^3)	0	2.730	.910	.748	.618	1.398	1.105	.325
	10	3.153	.748	.943	nd	1.235	1.365	—
	20	nd	1.235	nd	nd	1.203	.455	.065
	$\bar{x}$	id	.910	id	id	1.268	1.073	.098
Production mg C/m^3/day at	10m	3.8	3.0	nd	1.3	1.2	7.7	nd
Zooplankton ml/1000 m^3		*44	*13	49	71	72	*4	37

APPENDIX TABLE 1. (Continued)

		1956			1957			
STATION **DATE**	**meters**	**50** **11/19**	**51** **12/3**	**52** **12/17**	**53** **1/2**	**54** **1/14**	**55** **1/29**	**56** **2/11**
Temperature °C	0	27.39	26.67	26.83	26.8	26.1	25.2	24.5
	10	27.44	25.72	26.72	26.7	25.6	23.1	23.7
	20	25.64	23.62	26.24	25.9	22.1	19.1	19.0
Salinity ‰	0	27.36	28.09	28.38	29.00	30.24	nd	32.88
	10	30.33	30.12	28.45	28.90	32.23	nd	32.75
	20	30.83	32.29	29.15	30.50	34.07	34.04	33.33
Density, σ_t	0	16.89	17.66	17.83	18.30	19.44	nd	21.91
	10	19.10	19.47	17.92	18.26	21.10	nd	22.06
	20	20.06	21.12	18.54	19.70	23.51	24.28	23.77
Oxygen, ml/l	0	4.68	4.86	5.40	5.47	5.04	5.95	5.53
	10	4.31	4.19	5.23	5.26	2.90	6.33	6.12
	20	3.92	2.64	5.00	3.75	0.89	1.92	3.55
Oxygen, % saturation	0	100.0	103.2	115.1	117.4	107.5	nd	116.9
	10	93.9	89.2	109.4	112.6	62.4	nd	127.8
	20	91.4	54.8	96.6	80.0	18.3	37.3	68.7
Phosphate, μg at/L	0	0.98	0.82	0.90	1.19	1.15	0.80	0.22
	10	1.38	0.97	0.81	1.65	2.24	0.60	0.26
	20	1.44	1.72	1.37	1.93	2.93	2.18	1.42
mg at/m^2		61.27	65.69	54.95	73.27	103.58	79.58	51.16
Secchi Disc (meters)		8	11.1	11.2	11	10.3	8	8
Winds (miles):								
True North		370.0	310.2	123.3	372.0	497.8	422.2	621.0
True South		3.0	3.5	24.2	4.2	—	2.8	—
DIATOMS								
cells/liter	0	nd	49,320	323,580	235,340	542,280	319,960	976,100
	10	nd	35,020	181,480	177,560	3,149,940	2,014,260	882,080
	20	nd	29,340	88,880	nd	133,440	1,526,400	224,480
biomass (mm^3/L)	0	nd	.149	.728	1.024	1.429	.754	4.982
	10	nd	.080	.603	.860	8.672	3.981	5.561
	20	nd	.148	.307	nd	.834	3.075	.999
	$\bar{x}$	nd	.114	.560	id	4.902	2.948	4.276
DINOFLAGELLATES								
cells/liter	0	nd	600	4,620	1,000	1,060	2,180	840
	10	nd	4,060	5,640	40	80	180	10,220
	20	nd	1,080	1,980	nd	—	20	120
biomass (mm^3/m^3)	0	nd	.375	2.888	.625	.663	1.363	.526
	10	nd	2.538	3.525	.025	.050	.113	6.388
	20	nd	.675	1.238	nd	—	.013	.075
	$\bar{x}$	nd	1.532	2.794	id	.191	.401	3.344
COCCOLITHOPHORES								
cells/liter	0	nd	5,500	7,040	—	—	—	—
	10	nd	1,500	10,000	—	500	—	—
	20	nd	2,500	1,600	nd	—	—	—
biomass (mm^3/m^3)	0	nd	.715	.915	—	—	—	—
	10	nd	.195	1.130	—	.065	—	—
	20	nd	.325	.208	nd	—	—	—
	$\bar{x}$	nd	.358	.846	id	.033	—	—
MONADS & FLAGELLATES								
cells/liter	0	nd	20,500	27,500	5,500	6,000	5,000	12,100
	10	nd	15,500	15,000	5,000	5,000	55,000	24,580
	20	nd	7,500	22,000	nd	9,500	2,000	8,020
biomass (mm^3/m^3)	0	nd	1.333	1.788	.358	.420	.325	.787
	10	nd	1.008	.975	.325	.325	3.575	1.598
	20	nd	.488	1.430	nd	.618	.130	.521
	$\bar{x}$	nd	.960	1.292	id	.415	1.902	1.127
Production mg C/m^3 at	10m	1.9	8.2	9.4	10	52	32	24
Zooplankton ml/1000 m^3		50	*17	54	6	5	226	48

APPENDIX TABLE 1. (Continued)

		1957						
STATION		**57**	**58**	**59**	**60**	**61**	**62**	**63**
DATE	**meters**	**2/25**	**3/12**	**3/21**	**4/10**	**4/22**	**5/6**	**5/20**
Temperature °C	0	22.7	23.6	24.1	24.4	25.8	26.9	28.3
	10	21.6	22.7	20.3	nd	25.2	25.2	27.7
	20	18.4	19.2	19.1	22.6	22.0	22.5	27.5
Salinity ‰	0	34.07	34.11	34.40	34.23	34.25	34.07	32.05
	10	34.04	34.20	34.40	34.27	34.23	34.25	32.43
	20	34.38	34.41	34.49	34.52	34.60	34.52	32.63
Density, σ_t	0	23.34	23.11	23.18	22.96	22.55	22.07	20.10
	10	23.62	23.43	24.24	nd	22.72	22.73	20.59
	20	24.72	24.54	24.62	23.70	23.93	23.73	20.80
Oxygen, ml/l	0	4.56	5.42	6.06	6.34	6.08	5.26	4.91
	10	5.52	3.81	4.97	6.33	6.21	5.57	5.26
	20	2.55	2.50	2.58	2.06	4.78	3.07	5.03
Oxygen, % saturation	0	94.6	114.1	128.9	138.4	132.8	116.9	109.6
	10	112.4	78.9	99.0	nd	134.1	120.3	116.9
	20	49.1	48.9	50.5	42.4	98.4	63.6	111.5
Phosphate, μg at/L	0	0.08	0.33	0.14	nd	nd	0.36	0.05
	10	0.10	1.06	0.48	nd	nd	0.55	0.02
	20	2.71	2.15	2.25	nd	nd	2.63	0.14
	mg at/m^2	85.90	76.42	74.53	nd	nd	85.27	12.00
Secchi Disc (meters)		4.5	8.8	7	7	15	12	29
Wind (miles):								
True North		455.3	595.2	380.2	567.4	321.4	516.2	—
True South		9.2	—	5.0	—	57.1	—	266.8
DIATOMS								
cells/liter	0	4,620,865	3,728,640	960,700	1,252,980	107,120	19,160	47,300
	10	2,331,700	1,097,240	1,020	1,124,600	176,460	64,560	25,340
	20	441,820	20,940	3,160	7,000	1,880	1,120	2,700
biomass (mm^3/L)	0	12.301	2.711	.633	5.880	.459	.100	.443
	10	7.386	.962	.001	5.488	.786	.318	.041
	20	1.579	.044	.021	.025	.015	.002	.021
	$\bar{x}$	7.163	1.170	.164	4.221	.512	.185	.137
DINOFLAGELLATES								
cells/liter	0	4,920	13,720	—	5,140	4,800	580	1,040
	10	41,500	11,700	2,000	1,720	16,580	7,760	1,220
	20	1,880	6,600	340	100	680	40	80
biomass (mm^3/m^3)	0	3.075	8.575	—	3.123	3.000	.363	.650
	10	25.938	7.313	.125	1.075	10.363	4.850	.763
	20	1.175	4.125	.213	.063	.425	.025	.050
	$\bar{x}$	14.032	6.832	.116	1.357	6.038	2.522	.557
COCCOLITHOPHORES								
cells/liter	0	11,500	—	500	—	500	—	—
	10	2,000	—	500	—	—	500	—
	20	—	—	—	—	—	—	—
biomass (mm^3/m^3)	0	1.495	—	.065	—	.065	—	—
	10	.260	—	.065	—	—	.065	—
	20	—	—	—	—	—	—	—
	$\bar{x}$	.504	—	.049	—	.017	.033	—
MONADS & FLAGELLATES								
cells/liter	0	5,500	1,000	1,500	33,020	8,000	5,500	19,120
	10	77,000	8,500	1,000	11,000	26,500	28,500	1,020
	20	13,500	4,500	500	3,500	26,500	8,500	11,020
biomass (mm^3/m^3)	0	.358	.065	.098	2.146	.520	.358	1.243
	10	5.005	.553	.065	.715	1.723	1.853	.066
	20	.878	.293	.033	.228	1.723	.553	.716
	$\bar{x}$	2.812	.366	.065	.951	1.423	1.155	.523
Production mg C/m^3/day at	10m	10	26	2.5	31	26	6.9	10
Zooplankton ml/1000 m^3		53	15	16	20	17	23	140

APPENDIX TABLE 2A. Results of the phytoplankton enumeration at stations 1, 3, 5, 6, 7, 10, 13, 14, 15, 16 sampled from 29 November 1954 to 11 July 1955 (cells per 10 ml)

STATION	1			2		3		
DEPTH (m)	0	10	20	0	20	0	10	20
DIATOMS								
Bact. delicatulum	—	—	—	—	—	65	20	—
Bact. elegans	1.2	—	2.4	.4	.2	—	—	—
Bact. hyalinum	—	—	—	—	—	45	—	50
Bact. hyalinum var. princeps	5.4	2.2	.4	.4	.6	—	—	—
Bact. varians	—	—	—	—	—	10	.8	—
Cerataulina bergoni	.8	—	—	—	—	—	—	—
Chaet. affinis	6.2	2.8	.4	—	.6	.2	.8	—
Chaet. brevis	—	—	—	70	.8	85	135	185
Chaet. compressus	10	15	3.2	50	.4	1670	1010	540
Chaet. constrictus	—	—	—	—	—	—	2.4	300
Chaet. costatus	—	—	—	—	—	—	110	2350
Chaet. curvisetus	—	—	6	—	—	40	10	260
Chaet. decipiens	1.2	—	1.2	.8	—	40	60	5
Chaet. densus	—	—	—	—	—	—	—	—
Chaet. didymus	—	—	—	—	—	20	60	160
Chaet. didymus var. anglica	2.4	.6	—	.8	—	10	—	40
Chaet. didymus var. protuberans	—	—	—	—	—	—	—	90
Chaet. laciniosus	—	—	—	—	10	340	—	205
Chaet. laevis	5.8	—	1.2	10	—	25	—	—
Chaet. lorenzianus	1.6	—	—	1.2	—	110	150	45
Chaet. socialis	—	—	—	—	—	—	—	—
Chaet. subsecundus	—	—	—	—	—	—	—	—
Ditylum brightwelli	.2	—	.8	—	.4	.2	—	—
Eucampia cornuta	—	—	1.2	—	—	35	10	—
Guinardia flaccida	—	.6	—	—	—	—	—	.8
Hemiaulus hauckii	—	—	—	45	—	25	5	5
Hemiaulus membranacea	2.2	4.6	—	.2	—	.4	.8	—
Hemiaulus sinensis	.2	.6	—	.2	—	—	—	—
Lauderia annulata	—	—	—	—	—	.8	1.6	65
Leptocylindrus maximus	—	—	—	—	—	—	1.2	—
Leptocylindrus minimus	—	—	—	—	—	15	—	105
Nitzschia closterium	—	—	—	—	—	—	5	5
Nitzschia delicatissima	5	—	45	10	—	65	230	75
Nitzschia longissima	—	—	—	5	—	15	—	20
Nitzschia pacifica	—	—	—	50	—	45	45	40
Nitzschia pungens var. atlanticus	—	—	6.8	4.4	—	1.6	4	155
Rhiz. alata f. genuina	—	—	—	1.6	.6	.2	.8	1
Rhiz. alata f. indica	—	—	—	.6	.6	.4	.2	.2
Rhiz. delicatula	—	—	—	35	—	20	—	—
Rhiz. fragilissima	—	—	—	—	—	—	5	—
Rhiz. setigera	—	—	.6	.2	—	—	1.1	.2
Rhiz. stolterfothii	—	15	1.2	5	25	105	270	250
Skel. costatum f. tropicum	—	—	2.4	4.4	26.8	120	270	24.5
Thalassionema nitzschioides	.8	—	30	3.8	8.2	1.2	1.6	36
Thalassiothrix mediterranea var. pacifica	.2	—	—	1.8	.2	.8	2.4	.2
DINOFLAGELLATES								
Ceratium spp.	.4	.2	—	.4	—	1	—	.2
Exuviaella baltica	10	5	—	5	—	—	25	—
Glenodinium lenticula f. minor	—	—	.8	.2	.4	2.2	1.2	2
Goniaulax spp.	.2	.4	—	—	.4	2.4	.8	—
Gymnodiniaceae	—	—	—	—	—	5	—	5
Oxytoxum spp.	—	—	10	—	5	—	—	—
Oxytoxum variabile	—	—	5	—	5	—	—	—
Peridinium spp.	12.4	.2	.8	.4	1	8.4	4.4	3.4
Peridinium globulus var. quarnerense	.2	—	—	.2	.8	5	.4	1.8
Prorocentrum spp.	3.4	—	—	1.8	1.6	1	—	.2
Prorocentrum micans	—	—	—	1.2	1.2	.4	—	—
COCCOLITHOPHORES								
Coccolithus huxleyi	40	—	5	—	—	.5	—	—
Gephyrocapsa oceanica	—	10	30	30	5	.5	—	—

APPENDIX TABLE 2A. (Continued)

STATION	5			6			7		
DEPTH (m)	0	10	20	0	10	20	0	10	20
DIATOMS									
Bact. delicatulum	60	20	—	—	65	—	—	—	—
Bact. elegans	—	—	—	—	—	—	—	—	—
Bact. hyalinum	2	.8	—	110	80	—	—	.6	—
Bact. hyalinum var. princeps	.8	—	—	—	—	—	—	—	—
Bact. varians	—	—	—	—	—	—	—	—	—
Cerataulina bergoni	—	—	—	—	—	—	—	—	—
Chaet. affinis	1.2	—	—	70	60	.4	—	1	—
Chaet. brevis	20	60	—	15	120	5	—	.8	—
Chaet. compressus	235	90	—	250	450	—	—	—	—
Chaet. constrictus	50	—	—	40	85	—	—	—	—
Chaet. costatus	25	—	35	15	—	—	—	—	—
Chaet. curvisetus	—	.4	—	—	—	—	—	3.6	1.8
Chaet. decipiens	160	—	—	35	20	—	3	.4	—
Chaet. densus	—	—	—	—	—	—	42.6	205	—
Chaet. didymus	—	—	—	.8	—	—	—	—	—
Chaet. didymus var. anglica	—	—	—	1.6	—	—	—	—	—
Chaet. didymus var. protuberans	65	40	—	—	—	—	—	—	—
Chaet. laciniosus	190	75	35	195	290	—	—	—	—
Chaet. laevis	75	—	—	—	5	—	—	20	—
Chaet. lorenzianus	145	15	—	15	35	.4	—	.4	—
Chaet. socialis	—	—	—	—	—	—	50	—	—
Chaet. subsecundus	—	—	—	—	135	—	—	—	—
Ditylum brightwellii	—	—	—	.2	.4	1.2	—	.6	.6
Eucampia cornuta	20	—	—	30	30	5	—	20	—
Guinardia flaccida	—	1.8	15.8	14.2	4.2	1.4	112	162.75	1
Hemiaulus hauckii	45	—	—	.2	.4	—	—	—	—
Hemiaulus membranacea	.2	—	—	—	4.2	—	—	—	—
Hemiaulus sinensis	35	—	—	—	—	—	—	—	—
Lauderia annulata	.4	—	—	2.4	1	2.2	11240	15230	1440
Leptocylindrus maximus	—	1.8	15.8	—	—	—	48	69.75	.4
Leptocylindrus minimus	60	—	—	—	—	65	—	—	—
Nitzschia closterium	20	.2	.6	20	10	—	—	—	—
Nitzschia delicatissima	100	—	—	115	115	—	—	35	—
Nitzschia longissima	—	—	—	—	—	—	—	—	—
Nitzschia pacifica	45	1.2	—	60	—	—	4.2	—	15
Nitzschia pungens var. atlanticus	—	—	—	—	—	.6	18.2	30	—
Rhiz. alata f. genuina	.4	.8	.4	1	1	1.2	5	10	—
Rhiz. alata f. indica	—	.2	1.2	—	.2	—	2	3.8	—
Rhiz. delicatula	95	—	15	1.4	55	—	6.6	15	—
Rhiz. fragilissima	10	4	4	—	—	—	—	—	—
Rhiz. setigera	.6	.2	—	1.2	.6	1.2	.4	3.9	.2
Rhiz. stolterfothii	220	125	470	485	175	55	705	477.5	55
Skel. costatum f. tropicum	15	1.2	—	310	240	—	—	—	—
Thalassionema nitzschioides	1.2	—	—	10.2	1	3.8	.8	1.6	.4
Thalassiothrix mediterranea var. pacifica	1.4	.4	—	.2	—	.2	7.4	28.2	—
DINOFLAGELLATES									
Ceratium spp.	—	—	.4	—	.2	—	—	1	—
Exuviaella baltica	5	5	—	—	—	—	—	—	—
Glenodinium lenticula f. minor	.2	—	.2	—	.2	—	—	.4	—
Goniaulax spp.	1	.2	—	—	.2	—	—	—	—
Gymnodiniaceae	10	.2	50	10	—	20	—	5	—
Oxytoxum spp.	—	—	10	—	—	—	—	—	—
Oxytoxum variabile	—	—	—	—	—	—	—	—	—
Peridinium spp.	1.8	.4	.2	1.2	.4	.6	.6	.8	1.4
Peridinium globulus var. quarnerense	.8	—	.2	1	.4	—	.2	.6	.4
Prorocentrum spp.	—	—	—	.2	.6	—	.4	—	.2
Prorocentrum micans	—	—	—	.2	.2	—	.2	—	.2
COCCOLITHOPHORES									
Coccolithus huxleyi	25	5	15	10	5	—	—	—	—
Gephyrocapsa oceanica	—	—	5	—	—	—	—	10	—

APPENDIX TABLE 2A. (Continued)

STATION	10		13		14		15	16		
DEPTH (m)	0	10	10	20	0	10	0	0	10	20
DIATOMS										
Bact. delicatulum	30	—	30	—	—	—	—	—	—	—
Bact. elegans	—	—	5	—	—	—	6.2	—	2.2	1
Bact. hyalinum	—	—	25	5	—	—	—	—	—	—
Bact. hyalinum var. princeps	—	—	—	—	45	5	15.6	—	—	—
Bact. varians	—	—	—	—	—	—	—	—	—	—
Cerataulina bergoni	4.6	.2	—	—	—	—	1.4	—	—	—
Chaet. affinis	3.2	—	40	—	—	—	15.6	.6	2.6	—
Chaet. brevis	105	—	85	20	45	10	2.8	—	—	—
Chaet. compressus	185	145	1	—	—	20	135	30	5	60
Chaet. constrictus	30	—	—	—	—	—	.6	—	—	—
Chaet. costatus	—	—	—	—	—	—	—	—	—	—
Chaet. curvisetus	16.8	355	70	—	3.2	—	3.2	.6	—	—
Chaet. decipiens	135	25	.8	—	—	—	—	—	—	—
Chaet. densus	45	15	—	—	—	—	—	—	—	—
Chaet. didymus	—	—	—	—	—	—	—	—	—	—
Chaet. didymus var. anglica	—	—	—	—	15	—	2	.4	—	—
Chaet. didymus var. protuberans	—	—	—	—	30	15	2	—	.2	—
Chaet. laciniosus	60	20	15	—	—	15	8.4	—	—	—
Chaet. laevis	—	—	20	—	—	15	60	—	60	20
Chaet. lorenzianus	3	10	.8	—	—	8.2	28.6	—	15	2.8
Chaet. socialis	435	—	—	—	—	—	—	—	—	—
Chaet. subsecundus	—	2.6	—	—	—	—	—	—	—	—
Ditylum brightwelli	—	—	—	—	.2	—	.2	—	—	—
Eucampia cornuta	575	290	5	—	—	—	.6	—	—	—
Guinardia flaccida	25.6	1.2	.6	—	—	.6	4.4	—	.8	—
Hemiaulus hauckii	—	—	—	—	—	—	2	—	—	—
Hemiaulus membranacea	—	—	.4	—	.2	—	.8	—	—	—
Hemiaulus sinensis	5	—	—	—	—	—	1.2	—	.8	—
Lauderia annulata	55	—	.8	—	—	—	—	—	—	—
Leptocylindrus maximus	.8	—	—	—	—	—	—	—	—	—
Leptocylindrus minimus	40	145	—	—	—	—	—	—	—	—
Nitzschia closterium	—	—	—	—	—	—	—	—	—	—
Nitzschia delicatissima	290	155	—	—	5	—	45	—	—	—
Nitzschia longissima	—	—	—	—	—	—	.2	—	—	5
Nitzschia pacifica	440	80	—	—	—	—	—	—	—	—
Nitzschia pungens var. atlanticus	—	50	—	—	—	—	—	—	—	—
Rhiz. alata f. genuina	2.4	.8	—	—	—	—	2.2	—	—	—
Rhiz. alata f. indica	1.8	.4	—	—	—	—	.8	—	.4	—
Rhiz. delicatula	430	55	15	5	—	15	2.8	—	—	15
Rhiz. fragilissima	480	30	35	5	—	15	20	—	5	10
Rhiz. setigera	1	1.2	—	—	—	—	.2	—	.4	.2
Rhiz. stolterfothii	4270	1820	175	65	.4	80	40	60	15	15
Skel. costatum f. tropicum	—	130	60	—	—	—	2.2	10	145	60
Thalassionema nitzschioides	.2	—	.2	.2	.4	80	2.2	—	2.2	1.6
Thalassiothrix mediterranea var. pacifica	3.6	.2	—	—	—	—	9.6	—	.6	.6
DINOFLAGELLATES										
Ceratium spp.	—	1	—	—	.2	—	—	—	.6	—
Exuviaella baltica	—	—	—	—	—	—	—	—	—	—
Glenodinium lenticula f. minor	1.6	1.2	—	—	.4	—	—	—	—	—
Goniaulax spp.	.6	8	—	—	—	—	—	—	—	—
Gymnodiniaceae	.2	.2	5	—	5	—	25	5	25	45
Oxytoxum spp.	—	5	—	—	—	—	—	—	—	5
Oxytoxum variabile	—	5	—	—	—	—	—	—	—	—
Peridinium spp.	.8	38.4	.2	—	1.4	—	.4	—	1.6	.6
Peridinium globulus var. quarnerense	.2	.4	—	—	.6	—	.2	—	.6	.2
Prorocentrum spp.	3.4	10.2	—	.2	.6	—	—	—	.2	—
Prorocentrum micans	3.4	10	—	.2	.6	—	—	—	—	—
COCCOLITHOPHORES										
Coccolithus huxleyi	30	—	—	—	—	—	—	—	—	—
Gephyrocapsa oceanica	65	15	—	5	—	5	—	5	—	10

APPENDIX TABLE 2A. (Continued) (cells per liter)

DIATOMS: Actinoptychus undulatus **20** 2b,3b,6b,10t, **40** 3t,7b, **120** 1b; Asteromphalus flabellatus **20** 2s,3b,5s,t,6b,15s,16t,b, **40** 3t,6t; Asteromphalus heptactis **20** 7t; Bellerochea malleus **40** 1b, **680** 15s; Biddulphia mobiliensis **100** 6s; Brenneckella sp. **20** 6b, **220** 2b; Chaetoceros apendiculatus **40** 1b, **3500** 2s; Ch. atlanticus f. audax **3,000** 3b; Ch. atlanticus var. neapolitana **1,000** 16t; Ch. atlanticus var. skeleton **7,000** 15s; Ch. coarctatus **100** 5s; Ch. debilis **10,000** 10s,t; Ch. diversus **1,000** 15s, **2,000** 16s; Ch. gracilis **500** 5s; Ch. holsaticus **26,500** 8s; Ch. lauderi **11,000** 3s; Ch. pelagicus **2,000** 7s, **6,500** 6s; Ch. cf. pendulus **40** 3s; Ch. peruvianus **20** 7t,16t, **40** 1b,10s; Ch. subtilis **2,500** 5s; Ch. teres **20** 5s, **40** 13t, **60** 5b, **4,000** 8s;

Ch. tortissimus **100** 8s; Ch. van heurckii **160** 1s, **260** 1t, **700** 15s; Climacodium frauenfeldianum **120** 3t, **80** 16t; Corethron hystrix **20** 2b,3b,6b,16b, **40** 2s,6s,15s, **60** 1s,t,6t,14t, **80** 1b,3s,13t, **120** 14s, **160** 3t; Cosc. auguste-lineatus **20** 16t, **40** 15s, **60** 10s; Cosc. cf. argus **20** 3b; Cosc. concinnus **20** 6s,t,7b,15s, **40** 5t,16b, **100** 7t, **120** 5b, **1,770** 3b; Cosc. excentricus **20** 1t,7t, **40** 16t, **300** 7b; Cosc. cf. gigas **20** 1s; Cosc. lineatus **20** 10t,16b, **40** 1b,6s,t,16t, **60** 14t, **280** 2b, **355** 3b; Cosc. stellatus **120** 7t, **300** 2b; Cosc. thorii **20** 15s, **40** 11t; Ditylum sol **20** 2s,3b,7b,16t, **40** 1b; Fragilaria cf. nana **500** 6b, **1,000** 2s,3s, **2,500** 5s, **6,500** 1s, **7,500** 15s; Guinardia cf. blavyana **360** 2s; Hemidiscus cuneiformis **20** 3s; Isthmia nervosa **20** 3b;

Leptocylindrus danicus **80** 1s; Navicula membranacea **80** 11t; Planktoniella sol **20** 11b,16t, **40** 3t, **240** 3b, **320** 1b, **660** 6b; Pseudoeunotia doliolus **940** 3b; Rhiz. acuminata **20** 3t; Rhiz. bergonii **20** 1s,3b, 6t,16t, **40** 16t, **60** 15s, **80** 2s; Rhiz. calcar avis **20** 1s,3s,t,5b,16t, **40** 2s,6b, **60** 1b,11t,15s, **80** 6s, **160** 7s; Rhiz. cylindrus **20** 6t,15s; Rhiz. hebetata f. semispina **40** 15s, **60** 2s; Rhiz. imbricata var. shrubsolei **20** 1t,b,3b,6s,15s, **40** 5b, **60** 4s, **180** 7t, **200** 7b, **320** 6b, **360** 7s; Rhiz. robusta **20** 2b,3b,7s, **30** 7t, **60** 15s; Rhiz. styliformis **20** 3s,6t,16t, **40** 5s, **60** 6s, **80** 3t,11t; Rhiz. styliformis var. longispina **40** 2b, **280** 2s; Schroederella delicatula **40** 10t, **60** 15s, **180** 3s,10s, **280** 3t; Stephanopyxis palmeriana **200** 11t, **760** 2b;

Step. turris **40** 7t, **120** 6t, **160** 7s, **520** 3b; Streptotheca thamensis **60** 3b; Thalassiothrix delicatula **60** 7t; Thal. frauenfeldii **20** 3b,10t,16b, **240** 1b, **400** 3t; Thal. longissima **20** 3b; Tropidoneis antarctica **40** 2s; Trop. antarctica var. polyplasta **20** 16s; Trop. lepidoptera **20** 3s.

DINOFLAGELLATES: Amphidinium cf. acutissimum **500** 7t; Blepharocysta splendor-maris **20** 11b; Ceratium extensum **20** 3b,5b; Cer. furca var. eugrammum **40** 1s, **60** 3s; Cer. fusus **20** 16t; Cer. inflatum **40** 10t; Cer. incisum **40** 2s,7t; Cer. kofoidii **20** 3s; Cer. massiliense f. macroceroides **20** 14s,16t; Cer. pentagonum var. subrobustum **20** 1t; Cer. setaceum **20** 6t; Cer. setaceum var. reta **20** 16t; Cer. symmetricum **60** 7t; Cer. trichoceros **20** 5b; Dinophysis caudatum **20** 7t,10s, **40** 11b, **60** 10t; Dinophysis fortii **20** 11b; Dinophysis tripos **20** 14s; Exuviaella compressa **20** 1s,6s,t,11b, **60** 5s, **80** 3t; Goniaulax catenella **640** 10t; Goniaulax scrippsae **20** 5s, **40** 2b, **160** 10t; Goniaulax spinifera **20** 1s, **40** 1t; Goniaulax tamerensis var. excavatum **40** 3s,9s; Ornithocercus magnificus **20** 16t; Oxytoxum gracilis **1,000** 5b;

Peridinium breve **60** 10s; Per. brochii **20** 3s,5t,14t, **120** 3t; Per. claudicans **20** 10t; Per. crassipes **20** 2s; Per. depressum **20** 4s,7s,11b; Per. divergens **20** 6b,7t,9t; Per. excentricum **60** 7b; Per. globulus var. ovatum **40** 10t; Per. grande **20** 16t, **40** 3b; Per. granii **1,940** 10t; Per. heterospinum **20** 14s; Per. minutum **20** 16t, **940** 10t; Per. ovum **20** 10t, **40** 11t; Per. pellucidum **20** 8s, **40** 1b; Per. pentagonum **20** 3s,b,10t; Per. pentagonum var. latissimum **20** 5s; Per. pyriforme **20** 5s,6s,b,7b,8s,14s, **60** 3s,b; Per. steinii **20** 16t, **200** 10t; Per. subinerme **20** 5t,6b,7b, **40** 3b, **220** 3s; Per. trochoideum **20** 7s,8s,14s,15s,16t,b, **40** 3t, **80** 30s, **320** 10t; Phalacroma doryphorum **20** 11b,16t; Podolampas spinifera **20** 6t;

Prorocentrum gracile **20** 3s; Pror. hentschelii **60** 1s; Pror. maximus **20** 4s; Pror. schilleri **20** 7s, **40** 6t; Pror. # 1 **20** 3b, **40** 2b,3s,4s, **60** 2s, **280** 1s; Protoceratium reticulatum **20** 6t.

COCCOLITHOPHORES: Acanthoica cf. monospina **500** 3t; Calciosolenia cf. murrayi **500** 1b; Calciosolenia sinuosa **500** 3t; Coccolithus leptoporus **500** 1t,2s,3b,4s,8s,11t,14s,t, **1,000** 3s; Michaelsarsia elegans **20** 1b, **500** 3s; Syracosphaera mediterranea **500** 3b; Syracosphaera nodosa **500** 3b, **1,000** 1t,b,2b; Tergestiella adriatica **500** 1t,11t,b.

SILICOFLAGELLATES: Dictyocha fibula **20** 2b,6t; Distephanus speculum var. polyactis **60** 2s; Ebria tripartita **20** 2b; Mesocena polymorpha var. binonaria **40** 2b,3b; Mes. polymorpha var. octonaria **40** 3b, **100** 2b.

CYANOPHYCEANS: **r** 1s; Katagnymene spiralis **r** 2s,15t; Oscillatoria cf. nigro-viridis **r** 10t; Trichodesmium thiebautii **r** 2s,3b,16b, **c** 16s,t.

DIVERSE: Chilomonas marina **20** 9s, **500** 5b,10s,t,11t,13b; Euglenaceae **20** 6b, **500** 7t; cf. Phaeocystis **1,000** 7t; Lohmaniella oviformis **40** 7t; Strombidium (Laboea) crassula **80** 16b; Strom. conica **20** 8s; Strom. emergens **20** 5s.

APPENDIX TABLE 2B. Results of the phytoplankton enumeration at stations 27 to 34 sampled from 12 December 1955 to 21 March 1956 (cells per 10 ml)

STATION	27			28			29			30		
DEPTH (m)	0	10	20	0	10	20	0	10	20	0	10	20
DIATOMS												
Bact. delicatulum	—	—	—	—	—	30	230	160	—	10	—	—
Bact. elegans	1.6	16	—	80	170	65	580	10	—	—	—	—
Bact. hyalinum	—	—	—	—	—	—	—	90	15	—	—	—
Bact. hyalinum var. princeps	28.8	—	1.2	.8	40	—	845	265	—	2.4	2.4	2.8
Bact. varians	—	—	—	—	—	.4	115	50	30	—	—	—
Cerataulina bergoni	5	.6	.4	3.6	1	.8	5	110	10	90	20	.4
Chaet. affinis	26.4	55	65	10.8	60	160	435	330	1.8	—	3	1.6
Chaet. atlantidae	—	90	45	.2	—	—	35	3.2	5	—	—	—
Chaet. brevis	—	1.2	75	4	1.2	35	295	510	1	2.2	2.6	—
Chaet. compressus	85	150	90	180	380	410	2295	1855	105	245	190	15
Chaet. constrictus	4.4	1.6	—	5	—	10.4	10.4	1.2	4	3.6	—	—
Chaet. costatus	—	—	—	—	—	—	145	—	—	120	—	—
Chaet. curvisetus	2.2	105	35.8	4	—	2	520	410	175	105	520	450
Chaet. decipiens	6	15.2	3.4	4.4	—	—	450	260	40	250	4.2	1.6
Chaet. densus	—	—	—	1.4	—	—	—	—	2	1	9.4	6
Chaet. didymus	—	—	2.6	2	—	—	—	.6	—	—	1.4	5.2
Chaet. didymus var. anglica	4.2	—	—	5.4	13.6	1.8	320	125	10	—	5.2	—
Chaet. didymus var. protuberans	—	—	1	9	3.6	3.4	—	75	35	.6	—	—
Chaet. laciniosus	25.8	7.2	20	75	2	1.8	285	20	—	—	—	—
Chaet. laevis	40	105	10	135	115	85	55	80	1	—	—	—
Chaet. lorenzianus	25.4	24.4	2	24.6	80	90	325	280	—	2	.6	.6
Chaet. socialis	—	—	—	—	—	—	675	50	—	2865	2530	1810
Chaet. subsecundus	4.2	—	8.4	1.2	1.8	—	140	90	—	.4	.8	.4
Ditylum brightwelli	3.2	.4	1	.4	1.6	.8	12.1	24.4	9.2	.2	50.2	61
Eucampia cornuta	.2	.4	65	1.2	30	30	150	190	10	—	—	85
Guinardia flaccida	—	8.4	.2	—	2	3.4	6.2	4.2	.8	—	—	—
Hemiaulus hauckii	.4	2.8	—	3.4	—	—	—	10	—	—	—	—
Hemiaulus membranacea	.2	.4	—	1.6	2	2.6	10.4	12.6	—	4.8	—	—
Hemiaulus sinensis	1.6	.4	1.2	—	1.6	.4	180	190	—	2.4	1.6	1.4
Lauderia annulata	—	.8	1.2	1	3	—	360	190	30.4	125	240	150
Leptocylindrus maximus	—	—	—	—	—	—	—	—	—	67	1.2	—
Leptocylindrus minimus	—	—	—	—	—	—	55	—	—	—	—	—
Nitzschia closterium	20	10	—	—	—	—	70	10	5	50	10	25
Nitzschia delicatissima	110	70	.4	60	290	50	670	140	30	65	—	—
Nitzschia longissima	—	.4	—	5.8	—	—	40	—	10	—	—	—
Nitzschia pacifica	—	—	—	70	35	—	—	—	—	20	—	—
Nitzschia pungens var. atlanticus	—	80	15	3.8	—	—	—	95	3.6	150	—	.8
Rhiz. alata f. genuina	.2	—	.2	.2	.4	.6	1.4	.2	—	2.6	—	—
Rhiz. alata f. indica	—	—	1	—	—	.2	.4	.8	—	7.6	.2	.2
Rhiz. delicatula	50	70	—	5.4	15	1.6	234	—	—	215	—	—
Rhiz. fragilissima	15	20	5	5	40	25	70	—	5	30	—	—
Rhiz. setigera	1.4	.8	3.4	—	.6	.4	19.2	85	1.2	6.6	.8	.4
Rhiz. stolterfothii	205	70	385	25	110	135	285	440	125	580	90	105
Schroederella delicatula	—	—	55	—	.4	—	6	.6	.6	1.8	.6	—
Skel. costatum f. tropicum	14.6	4	1615	—	80	14.4	1060	1540	340	155	405	55

APPENDIX TABLE 2B. (Continued)

STATION	27			28			29			30		
DEPTH (m)	0	10	20	0	10	20	0	10	20	0	10	20
DIATOMS (Continued)												
Thalassionema nitzschioides	16.4	14.8	25.6	19.8	120	24	—	22.8	70	.4	51	43.6
Thalassiosira aestivalis	—	—	—	—	—	—	420	85	—	—	170	180
Thalassiothrix frauenfeldii var. panama	—	—	—	21.2	3.8	4.2	242.4	64.8	16.8	22.2	44	72
Thalassiothrix mediterranea var. pacifica	2	.8	—	1.8	1.2	3.4	40	25.8	1.4	24.4	4.4	2.2
DINOFLAGELLATES												
Ceratium spp.	.8	.8	.2	.4	.8	.4	.6	—	—	1.4	—	—
Exuviaella spp.	—	.4	25.2	.4	15.2	5	—	—	—	—	—	—
Exuviaella baltica	—	—	25	.2	15	5	—	5	—	—	—	—
Glenodinium lenticula f. minor	—	1.6	.2	—	.2	—	.2	—	—	.4	—	—
Goniaulax spp.	1.6	.6	.4	.4	—	—	.4	.2	—	5.4	—	—
Gymnodiniaceae	—	5	25	—	15	—	20	15	—	—	—	—
Oxytoxum spp.	10	—	—	15	5	5.2	—	—	—	—	—	—
Oxytoxum variabile	10	—	—	—	—	—	—	—	—	—	—	—
Peridinium spp.	.4	1.2	1	1.4	1	.2	1.2	2.2	.6	12.8	—	—
Peridinium globulus var. quarnerense	—	.8	.2	1.4	.6	.2	.4	.2	—	—	—	—
Prorocentrum spp.	1	—	.2	.6	.2	—	1.2	.4	.2	1.8	—	—
Prorocentrum micans	—	—	—	—	—	—	1.2	—	—	1.2	—	—
COCCOLITHOPHORES												
Calciosolenia sinuosa	—	—	—	—	—	—	15	—	5	—	—	—
Coccolithus huxleyi	—	—	—	—	30	105	10	5	—	20	—	5
Gephyrocapsa oceanica	—	—	—	120	40	50	40	40	5	65	—	—

STATION	31			32			33			34		
DEPTH (m)	0	10	20	0	10	20	0	10	20	0	10	20
DIATOMS												
Bact. delicatulum	—	—	—	30	55	—	—	1.2	—	—	—	—
Bact. elegans	—	—	.8	12.2	2.6	—	—	—	—	—	.2	—
Bact. hyalinum	—	—	—	10.8	—	—	—	.2	—	—	—	—
Bact. hyalinum var. princeps	1.4	—	—	—	10.2	.4	—	—	—	—	—	—
Bact. varians	—	—	—	—	—	—	—	—	—	—	—	—
Cerataulina bergoni	.8	—	—	30	2.2	1.6	—	—	6.2	.8	3	—
Chaet. affinis	.2	—	—	5	11.8	2.4	—	2	1.4	3.8	1.8	—
Chaet. atlantidae	—	—	—	—	—	—	—	—	—	—	—	—
Chaet. brevis	—	—	—	5.8	10	1.2	1.6	8.4	4.4	7	5	—
Chaet. compressus	—	.8	—	325	180	145	—	110	250	160	—	—
Chaet. constrictus	—	—	—	4.2	3.2	—	.8	3.6	—	—	—	—
Chaet. costatus	—	—	—	4.4	4.2	—	1870	305	60	1.4	3	—
Chaet. curvisetus	.4	—	—	11.4	38.8	20	—	110	14.8	2.6	—	—
Chaet. decipiens	2.2	1.2	—	7.4	17.8	.8	190	95	5.6	4.4	9.2	—
Chaet. densus	—	—	—	1.2	3	.4	—	8.2	.8	—	—	—
Chaet. didymus	—	—	—	2	9.2	3.4	25	—	40	5	1	—
Chaet. didymus var. anglica	1.6	—	—	6.2	—	—	1.4	—	—	—	—	—
Chaet. didymus var. protuberans	—	—	—	—	2	2.6	—	—	—	1.2	—	—
Chaet. laciniosus	—	—	—	4	3.4	1.6	60	100	25	—	.8	—
Chaet. laevis	—	—	—	.8	30	.8	—	—	—	—	—	—
Chaet. lorenzianus	1	—	—	17	6.6	3.2	.6	4	.8	1	—	—
Chaet. socialis	—	—	—	15	370	—	—	405	120	140	—	—
Chaet. subsecundus	—	—	—	11	6.4	2.6	—	2.2	—	—	—	—
Ditylum brightwellii	—	—	—	—	—	—	—	.2	—	—	—	—

APPENDIX TABLE 2B. (Continued)

STATION	31			32			33			34		
DEPTH (m)	0	10	20	0	10	20	0	10	20	0	10	20
DIATOMS (Continued)												
Eucampia cornuta	—	.4	1	1	18.8	10.4	40	13.2	7.8	9	35	—
Guinardia flaccida	.8	.4	—	.4	5	.2	—	12.2	.8	2.6	—	.2
Hemiaulus hauckii	—	—	—	1.6	—	—	—	—	—	—	—	—
Hemiaulus membranacea	—	—	—	—	—	.4	—	.8	—	—	—	—
Hemiaulus sinensis	1.6	—	—	10	2	—	—	—	—	—	—	—
Lauderia annulata	—	.2	.2	4.6	4.2	1.8	.8	3.6	.6	.8	1.2	—
Leptocylindrus maximus	—	—	—	—	—	—	—	—	—	—	—	—
Leptocylindrus minimus	35	—	—	55	—	—	—	1.2	2	—	—	—
Nitzschia closterium	20	—	—	65	40	10	45	60	9	45	75	5
Nitzschia delicatissima	25	25	40	95	70	15	120	25	2.4	1330	825	.6
Nitzschia longissima	.4	—	.2	.6	.8	—	—	—	—	—	—	—
Nitzschia pacifica	.6	—	—	—	1.4	20	—	3.2	.6	90	—	20
Nitzschia pungens var. atlanticus	—	—	—	3.6	15	2.6	50	50	.8	80	105	.4
Rhiz. alata f. genuina	.6	—	—	.2	—	—	—	—	—	4.8	.6	—
Rhiz. alata f. indica	—	—	—	.4	.4	.6	—	.8	—	—	.6	—
Rhiz. delicatula	20	5	—	1040	265	30	—	50	10.2	305	255	.4
Rhiz. fragilissima	—	.2	.2	30	3.2	.8	.8	24	8.4	—	120	.2
Rhiz. setigera	.6	.2	.2	2.8	3.8	.6	.8	3.8	4.6	.2	.2	—
Rhiz. stolterfothii	3.2	1.8	2.4	280	595	105	250	270	60	1825	750	10
Schroederella delicatula	—	—	—	.8	2	—	.6	—	—	—	—	—
Skel. costatum f. tropicum	65	15	5	110	540	35.2	—	4	7.4	3	8.8	—
Thalassionema nitzschioides	2.8	1.6	—	—	3.4	2.2	.6	—	—	—	—	—
Thalassiosira aestivalis	—	—	—	—	—	—	—	—	—	45	40	—
Thalassiothrix frauenfeldii var. panama	—	—	—	—	—	—	1.8	—	—	—	—	—
Thalassiothrix mediterranea var. pacifica	—	.2	.4	.8	4.2	—	.8	5.4	—	1.2	1.2	—
DINOFLAGELLATES												
Ceratium spp.	—	5	—	—	.2	—	—	.4	—	.2	.2	—
Exuviaella spp.	—	—	—	—	—	5	55	50	—	15	20	20
Exuviaella baltica	—	—	—	—	—	5	55	50	—	15	20	20
Glenodinium lenticula f. minor	—	—	—	—	.2	—	—	.6	—	.8	—	—
Goniaulax spp.	—	—	—	—	—	—	—	—	—	—	—	—
Gymnodiniaceae	—	5	15	40	80	30	35	115	—	—	35	110
Oxytoxum spp.	—	10	5	—	20	10	5	1.2	—	—	—	—
Oxytoxum variabile	—	—	5	—	15	—	5	1.2	—	—	—	—
Peridinium spp.	4.2	.6	.8	2.6	8.6	2.4	1	7.4	1	.4	1.4	27
Peridinium globulus var. quarnerense	—	—	—	.2	.4	1.4	—	—	.4	—	.4	—
Prorocentrum spp.	1.8	—	—	1.4	2	—	1	4	—	—	3	.2
Prorocentrum micans	1	—	—	.2	1.4	—	.4	—	—	—	—	—
COCCOLITHOPHORES												
Calciosolenia sinuosa	—	—	—	40	20	—	—	40	—	—	—	—
Coccolithus huxleyi	—	105	10	340	520	145	—	75	5	260	310	45
Gephyrocapsa oceanica	—	60	105	415	350	280	220	10	15	190	130	—

APPENDIX TABLE 2B. (Continued) (cells per liter)

DIATOMS: Actinoptychus undulatus **20** 27b; Actin. undulatus var. catenata **80** 29b; Asterionella japonica **280** 30t, **500** 29s; Asteromphalus flabellatus **40** 28t,31t, **60** 27s,28s,b, **80** 29s, **120** 27t; Aster. heptactis **20** 34t; Bacteriastrum mediterraneum **2,000** 28b; Bellerochea malleus **20** 28b,30b, **40** 31b, **80** 30t, **180** 27b,30s, **460** 29t, **1,180** 29s; Biddulphia alternans **60** 32b, **100** 29t, **120** 27b, **1,000** 30b; Bidd. longicruris **120** 27b; Bidd. mobiliensis **20** 29b,30s,34b, **40** 27t, **60** 33t, **80** 27b,32b,33b, **100** 29s, **120** 29t, **160** 30t, **200** 30b; Bidd. sinensis **20** 28b,30s, **40** 29s, **80** 27b,30b, **380** 29t, **840** 29b; Brenneckella sp. **60** 29b,30t, **320** 27b; Cerataulina compacta **280** 33b; Chaetoceros aequatorialis **20** 32s; Ch. affinis var. willei **420** 30s;

Ch. anastomosans **1,500** 32b, **6,500** 28b, **15,500** 32s, **20,500** 32t; Ch. atlanticus var. neapolitana **40** 27b; Ch. coarctatus **200** 28t; Ch. dadayi **60** 27s; Ch. debilis **440** 27b; Ch. dichaeta **20** 30b; Ch. difficilis **2,500** 27t; Ch. diversus **40** 32s, **120** 28b, **160** 28s; Ch. eibenii **60** 28t, **300** 28s; Ch. gracilis **20** 27s,28t,30s,t, **500** 28s, **1,500** 31s; Ch. lauderi **80** 31t; Ch. cf. messanensis **40** 27s; Ch. pelagicus **3,000** 32t; Ch. perpusillus **1,500** 31t; Ch. peruvianus **20** 31t,32t,b, **40** 27b,29t, **120** 28b, **160** 27t,28t, **240** 28s,29s, **340** 27s; Ch. pseudocrinitus **400** 32s; Ch. rostratus **200** 27s; Ch. seiracanthus **80** 28b; Ch. simplex var. calcitrans **1,000** 28t; Ch. subtilis **1,000** 32t,34s; Ch. tetrastichon **120** 33b, **240** 33t; Ch. teres **60** 31b,32s, **200** 30s; Ch. vixvisibilis **320** 32t; Climacodium frauenfeldianum **180** 33t;

Corethron hystrix **20** 29s,30s,34b, **40** 28t, **80** 28b, **100** 27s,30t,b, **180** 28s, **240** 29s, **320** 27b,29t, **840** 27t; Corethron pelagicum **80** 28t, **160** 27s,b, **680** 29s; Coscinodiscus auguste-lineatus **20** 33b; Cosc. centralis **40** 29s; Cosc. concinnus **20** 30t,33t; Cosc. excentricus **40** 31t,33b,34t, **60** 30s, **120** 29b,32b, **140** 29s, **160** 29t, **180** 30b, **420** 30t, **1,360** 27b; Cosc. granii **20** 27s,b,28b; Cosc. cf. lacustris **20** 30b; Cosc. lineatus **20** 28t,30s, **40** 30b, **60** 31b, **120** 29s; Cosc. marginatus **60** 28s; Cosc. perforatus var. pavillardi **20** 30s,b; Cosc. radiatus **20** 29b,31t,32t, **40** 30t, **80** 29t; Cosc. stellatus **100** 28s; Cosc. thorii **40** 28t,b,30s, **60** 29b, **100** 29s, **120** 30t,b, **240** 29t, **3,000** 27b; Cosc. wailseii **20** 29b; Cyclotella striata **40** 27t; Dactyliosolen antarcticus var. laevis **780** 27s; Dact. mediterraneus **180** 32b, **260** 30b;

Ditylum sol **20** 30b, **40** 27t,28b, **60** 30t, **140** 27b, **240** 28s; Fragilaria cf. nana **500** 30s,t, **2,000** 27s, **3,500** 31b, **4,000** 32s, **5,000** 31t, **15,500** 31s; Fragilaria norma **20** 29s,31s,t, **40** 32s, **120** 28b; Leptocylindrus cf. adriaticus **40** 28s; Lithodesmium undulatum **60** 28s, **320** 29t, **640** 30b, **680** 29s, **840** 29b, **1,040** 30t; Nitzschia sigma var. indica **20** 29s; Opephora pacifica **20** 34s; Planktoniella sol **20** 34s, **40** 30t; Rhiz. alata f. gracillima **20** 28s; Rhiz. bergonii **20** 27s,b,28t,b,30t,b,32s,34s, **40** 29t,33s, **60** 29s, **160** 33t, **280** 30s; Rhiz. calcar avis **20** 27t,30b,32s, **40** 30t,32t, **80** 28s, **100** 28t, **120** 28b, **240** 27s, **380** 30s, **420** 29s, **480** 29t; Rhiz. cylindrus **20** 27b,32s; Rhiz. hebetata f. semispina **20** 28s; Rhiz. imbricata **20** 27t;

Rhiz. imbricata var. shrubsolei **60** 28s, **200** 29s, **240** 29b, **280** 27b,30b, **680** 29t,30t, **780** 30s; Rhiz. robusta **20** 27b,29t, **80** 29s; Rhiz. styliformis **20** 30t, **40** 31b,33t, **60** 28t, **100** 29s, **180** 30s, **280** 31s, **300** 30b; Rhiz. styliformis var. longispina **20** 28t,b,29s, **40** 29t; Skeletonema costatum **5,500** 34s, **8,500** 34t; Stephanopyxis palmeriana **80** 30t, **120** 27b,30b **160** 29t; Step. turris **20** 31t, **40** 30t,b,32t, **60** 30s, **280** 27b, 29s, **580** 29t; Thalassiosira subtilis **160** 32t, **3,080** 30t; Thalassiothrix delicatula **20** 28b,29s,32s,t,b, **40** 27s,28s,t; Thal. frauenfeldii **60** 32t; Tropidoneis antarctica **40** 27t, **140** 27b; Trop. antarctica var. polyplasta **40** 27b,28s; Trop. lepidoptera **20** 33b, **40** 27b, **80** 33t.

DINOFLAGELLATES: Ceratium declinatum **20** 33t; Cer. extensum **40** 27s; Cer. furca var. eugrammum **20** 28t,31b, **40** 29s, **140** 30s; Cer. incisum **40** 27s,t; Cer. massiliense f. macroceroides **20** 34s; Cer. minutum **20** 33t; Cer. trichoceros **20** 32t, **40** 27t; Ceratocorys horrida **20** 28s; Dinophysis fortii **20** 33t; Exuviaella apora **40** 27t; Exuviaella compressa **20** 27b,28s,t; Goniaulax digitale **40** 30s; Gon. cf. gracilis **20** 27b,30s, **40** 28s, **60** 27s,t; Gon. minima **40** 27s; Gon. monacantha **20** 30s; Gon. scrippsae **20** 29t, **40** 29s, **460** 30s; Ornithocercus magnificus **20** 29s; Oxytoxum curvatum **500** 32b; Oxy. gracilis **500** 28t,b,32b, **1,000** 31t, **1,500** 28s; Oxy. scolopax **20** 28b; Parahistoneis karstenii **20** 27s; Peridinium breve **20** 34t; Per. brevipes **160** 33t; Per. claudicans **20** 29t; Per. crassipes **20** 32b; Per. diabolus **20** 34t; Per. excentricum **20** 33t; Per. globulus **20** 27b,29b,32t; Per. globulus var. ovatum **40** 27s; Per. heterospinum **60** 31b; Per. leonis **20** 29b; Per. minusculum **20** 32t,33t,34t, **40** 33b, **2,500** 34b; Per. minutum **20** 32t,34s, **40** 30b, **80** 33t; Per. oceanicum **20** 28t, **40** 30s; Per. ovum **20** 34t, **80** 29s; Per. pellucidum **20** 34b, **200** 33t, **340** 32t; Per. pyriforme **20** 32b,33s,34s,t, **60** 27b; Per. sinaicum **40** 27t,31t; Per. steinii **20** 31s,t,32b, **40** 32s, **100** 30s; Per. subinerme **20** 29t; Per. trochoideum **20** 27b,28t,31b, **40** 33s,t, **60** 31s, **80** 30s, **360** 32t; Prorocentrum hentschelii **20** 27b,28s, **100** 27s; Pror. obtusidens **20** 33t; Pror. rostratus **80** 31s; Protoceratium reticulatum **80** 27t; Pseudophalacroma nasutum **40** 27s; Pyrophacus horologicum **20** 30s.

COCCOLITHOPHORES: Anthosphaera quadricornu **60** 33b, **500** 34s; Braarudosphaera sp. **1,000** 29s, **1,500** 28b; Coccolithus pelagicus **500** 28t, **5,000** 32b; Discosphaera tubifer **500** 28t,b,29t; Halopappus adriaticus **20** 28b, **1,000** 28t; Michaelsarsia elegans **1,000** 31b; Pontosphaera maximus **500** 28b; Tergestiella adriatica **1,000** 29s.

SILICOFLAGELLATES: Dictyocha fibula var. aspera **40** 44s; Dict. fibula var. messanensis **20** 28b, **40** 27s,28s; Distephanus crux **20** 27s; Dist. speculum var. octagonum **20** 28s; Ebria tripartita **20** 29b,33b, **80** 29s; Mesocena polymorpha var. binonaria **20** 29s, **100** 29b; Mes. polymorpha var. octonaria **20** 27b.

CYANOPHYCEANS: ± 28s,32t; Anabaena sp. ± 31t,b; Trichodesmium thiebautii ± 33t,b,34s, **C** 27s,t,b.

DIVERSE: Chilomonas marina **500** 30s,33t,34s, **1,000** 31t,b, **1,500** 27s,32t, **5,000** 32b, **16,000** 27t; Euglenaceae **160** 33s; Lohmaniella oviformis **20** 33s,34s,b, **60** 33t; Strombidium (Laboea) conica **20** 32t.

APPENDIX TABLE 2C. Results of the phytoplankton enumeration at stations 35 to 46 sampled from 2 April 1956 to 24 September 1956 (cells per 10 ml)

STATION	35			37			38	39	
DEPTH (m)	0	10	20	0	10	20	0	10	20
DIATOMS									
Bact. delicatulum	—	—	—	—	—	—	20	—	—
Bact. elegans	—	—	—	—	—	—	—	—	—
Bact. hyalinum	—	—	—	—	—	—	—	—	—
Bact. hyalinum var. princeps	—	—	—	—	—	—	113.6	—	—
Bact. varians	—	—	—	—	—	—	—	—	—
Cerataulina bergoni	—	—	—	—	.8	—	50	—	—
Chaet. affinis	2.8	—	—	—	—	—	42.4	1.4	—
Chaet. atlantidae	—	—	—	—	—	—	—	—	—
Chaet. brevis	80	—	—	.4	.4	.6	.2	—	—
Chaet. compressus	—	—	—	—	—	—	109.4	.6	—
Chaet. constrictus	—	—	—	—	—	—	16	—	—
Chaet. costatus	—	—	—	—	—	—	1.8	—	—
Chaet. curvisetus	1.2	1.2	—	4.2	—	.8	30.4	.8	—
Chaet. decipiens	115	70	—	.6	—	.4	14.8	—	.8
Chaet. densus	—	—	—	—	—	—	1	—	—
Chaet. didymus	—	—	—	—	—	—	—	—	—
Chaet. didymus var. anglica	—	—	—	—	—	—	8	1	—
Chaet. didymus var. protuberans	—	—	—	—	—	—	—	—	—
Chaet. laciniosus	40	10	—	—	—	—	12.4	—	—
Chaet. laevis	—	—	—	—	—	—	2.4	1.2	15
Chaet. lorenzianus	1.2	—	—	—	—	—	4.4	1.4	—
Chaet. socialis	—	—	—	—	—	—	75	—	—
Chaet. subsecundus	—	—	—	—	—	—	6	—	—
Ditylum brightwelli	—	—	—	—	—	—	—	—	—
Eucampia cornuta	.4	100	.4	—	—	—	5.6	—	—
Guinardia flaccida	.4	.8	.2	2.2	.2	.2	5.4	—	—
Hemiaulus hauckii	—	—	—	—	—	—	—	—	—
Hemiaulus membranacea	—	—	—	—	—	—	6.4	1.8	.2
Hemiaulus sinensis	—	—	—	—	—	—	—	—	—
Lauderia annulata	—	.2	—	—	—	—	2.6	—	—
Leptocylindrus maximus	—	—	—	—	1	—	—	—	—
Leptocylindrus minimus	—	—	—	—	—	—	—	—	—
Nitzschia closterium	10	35	—	—	5	—	50	—	—
Nitzschia delicatissima	135	100	.4	300	205	—	150	5	—
Nitzschia pacifica	—	—	—	5	—	270	85	—	—
Nitzschia pungens var. atlanticus	35	—	5	—	95	55	10	—	—
Rhiz. alata f. genuina	35.6	16.8	.2	115	39	4.6	.8	—	.2
Rhiz. alata f. indica	1.2	.8	—	1	1.6	1	—	—	—
Rhiz. delicatula	20	350	.4	—	—	—	690	—	—
Rhiz. fragilissima	—	65	—	—	—	.2	—	—	—
Rhiz. setigera	9.6	5	.8	.4	—	.2	11.2	—	—
Rhiz. stolterfothii	1130	1745	60	—	—	—	245	—	—
Schroederella delicatula	—	—	—	—	—	—	—	—	—
Skel. costatum f. tropicum	—	—	—	15	—	1	6.6	5.6	.6
Thalassionema nitzschioides	1.6	3.2	—	1.6	.6	—	7.2	.8	.6
Thalassiothrix frauenfeldii var. panama	—	—	—	—	—	—	—	—	—
Thalassiothrix mediterranea var. pacifica	2	1.8	—	1	.4	.2	10.2	.8	—
DINOFLAGELLATES									
Ceratium spp.	—	—	—	22.2	.2	.4	.2	.2	—
Exuviaella spp.	—	10	5	.2	15	5	5	10	—
Exuviaella baltica	—	10	5	—	15	5	5	10	—
Glenodinium lenticula f. minor	1.2	1.4	1.2	2.2	1.2	.6	.2	—	—
Goniaulax spp.	—	—	—	—	—	5	—	5	—
Gymnodiniaceae	—	—	—	10	10	5	—	75	10
Oxytoxum spp.	—	—	—	—	—	5	—	5	—
Oxytoxum variabile	—	—	—	—	—	5	—	5	—
Peridinium spp.	.4	.2	.6	155.4	17.2	.8	.6	—	—
Peridinium globulus var. quarnerense	—	—	—	—	—	—	—	—	—
Prorocentrum spp.	1.2	.4	.2	159.2	2	1	1.2	1	—
Prorocentrum micans	.8	.4	.2	4.2	1.8	.6	.6	.6	—
COCCOLITHOPHORES									
Calciosolenia sinuosa	—	—	—	—	—	—	—	—	—
Coccolithus huxleyi	—	10	—	—	—	—	—	—	—
Discosphaera tubifer	—	—	—	—	—	—	—	—	—
Gephyrocapsa oceanica	70	60	—	—	5	—	35	—	35

APPENDIX TABLE 2C. (Continued)

STATION	40		41			42		
DEPTH (m)	0	10	0	10	20	0	10	20
DIATOMS								
Bact. delicatulum	—	—	—	—	—	—	—	—
Bact. elegans	—	—	—	—	—	—	—	—
Bact. hyalinum	—	—	—	—	—	—	—	—
Bact. hyalinum var. princeps	5.4	—	—	—	—	—	—	—
Bact. varians	—	—	—	—	—	—	—	—
Cerataulina bergoni	—	—	—	—	—	—	—	—
Chaet. affinis	20	—	—	—	—	—	40	—
Chaet. atlantidae	—	1.8	3.6	2.4	—	5.4	—	3.8
Chaet. brevis	—	—	1.8	1.4	1.8	15.6	6.2	20
Chaet. compressus	65	65	260	485	130	41.4	185	25
Chaet. constrictus	—	—	—	—	—	11	—	—
Chaet. costatus	—	20	—	—	—	2.4	—	—
Chaet. curvisetus	6.2	15	—	1.4	—	5.6	—	—
Chaet. decipiens	4.8	6.2	1	1.4	—	7.4	2	3
Chaet. densus	—	—	—	—	.8	1.8	.8	—
Chaet. didymus	—	—	1.4	75	—	1	—	1.6
Chaet. didymus var. anglica	—	.4	—	—	—	—	—	—
Chaet. didymus var. protuberans	2.8	1.6	7	4.2	—	17.4	1.8	4.4
Chaet. laciniosus	4.6	2.6	—	40	50	58.6	25	.8
Chaet. laevis	50	10	40	75	10	15.5	4	1.8
Chaet. lorenzianus	—	15	14.8	18	.4	22.8	3.8	3.8
Chaet. socialis	—	—	—	—	—	—	—	—
Chaet. subsecundus	—	—	—	—	—	10	—	—
Ditylum brightwelli	—	—	.2	—	.2	.2	—	—
Eucampia cornuta	—	.2	1.4	.6	—	1.8	.2	—
Guinardia flaccida	—	4.8	.4	.8	—	—	.6	2.2
Hemiaulus hauckii	—	—	—	—	—	—	—	—
Hemiaulus membranacea	—	—	.6	1.2	.4	.8	1.2	—
Hemiaulus sinensis	.4	—	—	.4	—	1.6	.4	1.2
Lauderia annulata	—	.4	—	—	—	1	—	—
Leptocylindrus maximus	—	1.2	1.4	—	—	—	—	—
Leptocylindrus minimus	—	—	—	—	—	—	—	—
Nitzschia closterium	10	—	30	—	—	5	—	10
Nitzschia delicatissima	1.4	30	30	30	—	70	25	5
Nitzschia pacifica	—	2.2	—	—	—	—	20	.4
Nitzschia pungens var. atlanticus	—	.8	50	—	10	—	20	10
Rhiz. alata f. genuina	.4	1.2	.2	.6	.6	1	2.2	.8
Rhiz. alata f. indica	—	—	—	—	—	—	—	—
Rhiz. delicatula	—	65	35	1.2	—	11.2	—	65
Rhiz. fragilissima	—	5	—	—	—	—	—	.2
Rhiz. setigera	.8	.8	.6	.8	.4	.8	.2	1.6
Rhiz. stolterfothii	20	65	—	1.8	—	3.2	60	35
Schroederella delicatula	—	—	7.4	3.8	.6	2	.8	—
Skel. costatum f. tropicum	7.4	25	365	540	225	315	180	40
Thalassionema nitzschioides	1.8	5	25.8	24	3	3.2	1.8	2.6
Thalassiothrix frauenfeldii var. panama	—	—	—	—	—	—	2.6	—
Thalassiothrix mediterranea var. pacifica	1	1.8	.6	2.4	.8	1	—	.4
DINOFLAGELLATES								
Ceratium spp.	1	.2	.2	—	—	8	—	—
Exuviaella spp.	—	15	10	15	15.2	20.2	10	5
Exuviaella baltica	—	.6	.2	.4	1.2	.4	.2	—
Glenodinium lenticula f. minor	.6	.6	.2	.4	1.2	.4	.2	—
Goniaulax spp.	—	—	.2	—	—	—	—	—
Gymnodiniaceae	25	25	25	70	40	15	60	15
Oxytoxum spp.	—	—	—	—	—	—	—	—
Oxytoxum variabile	—	—	—	—	—	—	—	—
Peridinium spp.	.2	.2	.4	.4	1.4	.8	1.4	.2
Peridinium globulus var. quarnerense	—	—	—	—	—	—	1.2	—
Prorocentrum spp.	—	—	1.8	.2	—	.4	.2	—
Prorocentrum micans	.4	—	1.6	.2	—	.2	.2	—
COCCOLITHOPHORES								
Calciosolenia sinuosa	—	15	15	10	5	—	5	30
Coccolithus huxleyi	—	—	—	—	—	—	—	—
Discosphaera tubifer	—	—	5	35	—	.2	10	—
Gephyrocapsa oceanica	60	140	125	140	55	15	35	50

APPENDIX TABLE 2C. (Continued)

STATION	43		44			45		46
DEPTH (m)	0	10	0	10	20	0	10	0
DIATOMS								
Bact. delicatulum	—	25	13.2	—	—	—	—	—
Bact. elegans	—	—	30.8	—	—	121.2	80	20
Bact. hyalinum	—	—	—	—	—	—	—	—
Bact. hyalinum var. princeps	25	445	7.6	—	—	—	30	—
Bact. varians	—	—	.4	—	—	—	—	—
Cerataulina bergoni	—	—	—	—	—	—	.2	—
Chaet. affinis	4	10.6	14.8	14.8	—	19.2	240	10
Chaet. atlantidae	—	4	1.2	—	—	32.6	1	—
Chaet. brevis	—	3.4	1.6	—	1	6.4	3	.8
Chaet. compressus	20	320	48.6	12	—	80	680	15
Chaet. constrictus	—	8.6	—	—	—	—	—	—
Chaet. costatus	—	—	—	—	—	—	—	—
Chaet. curvisetus	—	2.4	6	—	—	13.2	3.4	—
Chaet. decipiens	3.2	6.2	15	17.4	—	15	25	—
Chaet. densus	—	—	—	—	—	—	—	—
Chaet. didymus	4	—	—	—	—	—	—	10.4
Chaet. didymus var. anglica	—	—	—	—	—	12.4	60	—
Chaet. didymus var. protuberans	—	11.8	8.2	—	—	9	105	—
Chaet. laciniosus	—	5	9.4	9.4	—	7.2	1	—
Chaet. laevis	10	50	21.6	—	—	105	195	50
Chaet. lorenzianus	3.4	3.4	17.6	35.2	—	90	170	14.7
Chaet. socialis	15	5	—	—	—	105	35	—
Chaet. subsecundus	—	5.6	4	1.8	—	4.8	—	—
Ditylum brightwelli	—	—	—	—	.2	1.4	1.8	—
Eucampia cornuta	—	.2	.4	.2	—	1.6	.4	—
Guinardia flaccida	.2	1.8	2	—	—	640	700	—
Hemiaulus hauckii	—	—	—	—	—	—	—	—
Hemiaulus membranacea	—	.2	—	—	—	.2	.2	—
Hemiaulus sinensis	—	80	1	.6	—	2.2	1.6	.6
Lauderia annulata	—	—	—	—	—	2	—	—
Leptocylindrus maximus	—	—	—	—	—	—	—	—
Leptocylindrus minimus	—	—	65	—	—	—	—	—
Nitzschia closterium	5	—	10	15	5	5	—	—
Nitzschia delicatissima	40	75	47.6	—	35	150	50	—
Nitzschia pacifica	—	1.6	11.2	5	—	6.4	45	.8
Nitzschia pungens var. atlanticus	20	—	2.4	—	—	5	—	—
Rhiz. alata f. genuina	—	.8	—	.8	—	1.2	1.4	.6
Rhiz. alata f. indica	—	—	—	—	—	—	.2	—
Rhiz. delicatula	—	—	17.2	15	—	6.6	15	—
Rhiz. fragilissima	—	.4	.2	—	—	.2	.4	15
Rhiz. setigera	—	2	1.6	1.6	—	1	.4	.4
Rhiz. stolterfothii	10	75	23	75	5	65	40	.6
Schroederella delicatula	—	3.2	—	—	—	3.4	4.2	—
Skel. costatum f. tropicum	—	70	35	35	2.8	185.2	810	1
Thalassionema nitzschioides	7	8.4	5	5	.4	7.2	21	.4
Thalassiothrix frauenfeldii var. panama	—	—	—	—	—	—	—	—
Thalassiothrix mediterranea var. pacifica	—	.8	.6	.2	—	3	5.4	.6
DINOFLAGELLATES								
Ceratium spp.	—	—	1.6	—	—	1.4	.6	.4
Exuviaella spp.	5	10	5	10	—	5	—	—
Exuviaella baltica	—	.4	—	—	—	—	—	—
Glenodinium lenticula f. minor	—	.4	—	—	—	—	—	—
Goniaulax spp.	—	.2	1.4	—	—	.2	.2	—
Gymnodiniaceae	5	15	10.2	10	5.4	—	—	—
Oxytoxum spp.	—	—	15.2	15	.2	10.4	—	—
Oxytoxum variabile	—	—	—	—	—	5	—	—
Peridinium spp.	—	.4	.4	—	.2	1.4	.4	1
Peridnium globulus var. quarnerense	—	—	—	—	.2	—	.4	—
Prorocentrum spp.	—	.2	1.8	—	.4	1.8	.2	.2
Prorocentrum micans	—	.2	1.6	—	.2	1.8	—	—
COCCOLITHOPHORES								
Calciosolenia sinuosa	—	5	5	—	—	—	—	5
Coccolithus huxleyi	—	—	—	—	—	—	—	—
Discosphaera tubifer	—	5	—	—	—	—	—	—
Gephyrocapsa oceanica	5	15	20	—	25	—	50	10

APPENDIX TABLE 2C. (Continued) (cells per liter)

DIATOMS: Actinoptychus undulatus **20** 45t, **40** 41b; Asterionella japonica f. tropicum **20** 42b, **160** 45s, **180** 42s; Asteromphalus flabellatus **20** 38s, **40** 39t,44s,b,45s, **80** 45t; Aster. heptactis **20** 40s,41s,42b, **40** 40t; Bellerochea malleus **20** 40t; Biddulphia alternans **20** 46s; Bidd. longicruris **40** 41s; Bidd. mobiliensis **20** 38s, **40** 41b; Chaetoceros affinis var. circinalis **60** 44s; Ch. anastomosans **500** 43t, **13,500** 38s; Ch. coarctatus **440** 43t; Ch. convolutus **160** 37b; Ch. dadayi **60** 41t; Ch. danicus **20** 40s; Ch. debilis **140** 35b, **440** 35t, **480** 35s; Ch. diversus **60** 42b, **300** 45t, **360** 44s, **7,500** 43t, **10,000** 41s; Ch. gracilis **1,500** 44s; Ch. holsaticus **1,220** 38s, **2,500** 41b, **5,500** 41t, **16,000** 41s; Ch. perpusillus **4,500** 45s; **20** 40s,41t,45s.t, **40** 39s,41s,44s, **80** 38s,42t,43t, **140** 42s;

Ch. seiracanthus **100** 44s; Ch. subtilis **120** 39t; Climacodium frauenfeldianum **20** 35t, **280** 41t,42t; Corethron hystrix **20** 39t,43s, **40** 38s,40s,t,42t, **60** 41s,42b, **80** 42s,45s, **100** 41t, **120** 41b; Coscinodiscus auguste-lineatus **20** 38s,40t,41s, **40** 35s; Cosc. concinnus **20** 40s,42s,43s,46s, **40** 45s, **60** 42t,b,45t, **80** 41b,t, 44b, **160** 41b; Cosc. excentricus **20** 40s,44b, **40** 37s,t,38s,42s, **60** 35b, **240** 35t, **280** 35s; Cosc. lineatus **20** 41s,42s,43t,46s, **40** 45s, **60** 41t,42b, **120** 42t, **160** 45t; Cosc. marginatus **20** 38s,45s, **40** 44b, **60** 28s; Cosc. perforatus **20** 37t; Cosc. radiatus **40** 40t, **60** 40s; Cyclotella cf. caspia **140** 45s, **220** 45t; Dactyliosolen mediterraneus **20** 44s, **40** 42b, **100** 38s; Ditylum sol **40** 40t; Hemidiscus cuneiformis **20** 44b,45t; Leptocylindrus adriaticus **1,500** 45s;

Nitzschia lorenziana var. incurva **20** 45s; Nitz. sigma var. indica **40** 35s; Rhiz. acuminata **20** 43s,44t, **80** 43t; Rhiz. bergonii **20** 37b,42t,44s,b, **40** 42s,42b.43s,44s,45s.t,46s, **40** 42s,44t, **80** 40t,43t, **100** 41t, **180** 42t,46s, **100** 45t; Rhiz. calcar avis **20** 38s,39b,40s,41b; Rhiz. imbricata **20** 40s; Rhiz. imbricata var. shrubsolei **20** 45s, **40** 35s, **60** 41t,b,46s, **100** 42b, **240** 45t; Rhiz. styliformis **20** 38s; Rhiz. styliformis var. longispina **80** 45s,46s, **180** 44s, **200** 44t, **220** 45t, **420** 43t; Rhiz. styliformis var. latissima **20** 43t; Skeletonema costatum **8,000** 45s; Stephanopyxis turris **80** 44b, **400** 44s; Thalassiosira aestivalis **140** 41t; Thalassiothrix delicatula **20** 42t,45s, **100** 44s; Thal. frauenfeldii **20** 41b,45s, **40** 41s, **60** 40s, **80** 44t, **180** 46s, **240** 44s, **320** 40t,42b, **340** 43t, **360** 42t, **380** 42s, **560** 41t, **720** 45t; Tropidoneis antarctica var. polyplasta **20** 35b,42b, **40** 45t.

DINOFLAGELLATES: Amphidinium minutissima **1,000** 41t, **1,500** 42s, **3,000** 40s; Amphid. cf. oceanicum **20** 44s, **500** 39t,42b,43t; Ceratium deflexum **40** 44s; Cer. furca f. belonoides **20** 37b; Cer. furca var. eugrammum **20** 37b,41s,42s, **2,220** 37s; Cer. humile **20** 37t; Cer. massiliense **20** 39t,40s; Cer. massiliense f. protuberans **20** 38s; Cer. pentagonum **20** 40s,t,42s,44s; Cer. trichoceros **20** 45t,46s; Cer. tripos **20** 40s; Cer. tripos f. semipulchellum **20** 45s; Dinophysis caudatum **20** 36s,37s,b; Exuviaella compressa **20** 37s,41b,42s; Goniaulax minima **20** 39t; Gon. polyedra **20** 45t; Gon. polygramma **20** 45s, **140** 44s; Gon. scrippsae **20** 37b,39b,43t, **40** 39t; Gon. spinifera **20** 41s; Gymnodinium lohmanni **20** 41s; Ornithocercus steinii **20** 44s; Oxytoxum caudatum **500** 41s, **1,500** 44s,t;

Oxy. scolopax **20** 44s; Peridinium brochii **20** 41s,42t, **40** 37s,42s; Per. brochii f. inflatum **20** 38s,43t; Per. diabolus **20** 41t; Per. grande **20** 38s,42s; Per. cf. heterospinum **15,500** 37s; Per. minusculum **1,500** 37t; Per. minutum **20** 35b,38s; Per. ovum **40** 45s, **100** 46s; Per. pyriforme **20** 40s,t,41s,42s, **60** 41b; Per. steinii **20** 35b,44s; Per. trochoideum **20** 35t, **40** 35s; Phalacroma doryphorum **20** 41t; Podolampas bipes **20** 44s,45s; Prorocentrum maximus **20** 37t, **40** 35s; Pror. rostratus **20** 45t,46s; Pyrophacus horologicum **20** 45t.

COCCOLITHOPHORES: Acanthoica lithostratus **500** 38s; Anoplosolenia brasiliensis **500** 44t; Coccolithus pelagicus **500** 40t.

SILICOFLAGELLATES: Dictyocha fibula var. aspera **40** 44s; Dict. fibula var. messanensis **20** 37b; Mesocena polymorpha **20** 40t,44b; Mes. polymorpha var. bioctonaria **20** 45s, **40** 35s, **380** 44b; Mes. polymorpha var. octonaria **20** 41b.

CYANOPHYCEANS: ± 37b,44b, **C** 35s,39t,41s,42t,44s; Oscillatoria cf. bonnemaisonii ± 37s; Oscillatoria cf. niger **20** 41s,45s, **120** 46s; Trichodesmium cf. contortum ± 37b; Trichodesmium thiebautii ± 35s,36b.

DIVERSE: Chilomonas marina **500** 36t,37s,39t,44s,46s, **1,000** 40t, **2,000** 42t; Euglenaceae **225,000** 35b, **911,000** 35s, **1,712,000** 35t.

APPENDIX TABLE 2D. Results of the phytoplankton enumeration at stations 47 to 55 sampled from 8 October 1956 to 29 January 1957 (cells per 10 ml)

STATION	47			48			49			51		
DEPTH (m)	0	10	20	0	10	20	0	10	20	0	10	20
DIATOMS												
Bact. delicatulum	—	—	—	—	—	—	—	—	—	—	—	—
Bact. elegans	7.8	3.6	—	85	80	—	—	2.8	—	4.2	2.8	—
Bact. hyalinum	—	—	—	—	—	—	—	—	—	—	—	—
Bact. hyalinum var. princeps	—	—	—	9.4	110	2	7.8	.8	5.4	.8	.4	.6
Bact. varians	.4	—	—	—	—	—	—	—	.8	—	.4	—
Cerataulina bergoni	.4	—	—	.4	.6	.2	.8	.4	.6	—	.4	—
Chaet. affinis	24.8	45	—	18	9.8	.4	53	14	5	9	2.8	3
Chaet. atlantidae	1.8	—	—	2.4	.2	—	24.6	1.4	1	.6	—	—
Chaet. brevis	—	.8	—	—	1.4	—	—	—	2	—	2	—
Chaet. compressus	15	4.2	—	1.2	255	4	22	2.4	115	225	65	35
Chaet. constrictus	—	.4	—	1	1.8	—	14.8	7	.6	—	—	—
Chaet. costatus	—	—	—	—	—	—	—	—	—	—	—	—
Chaet. curvisetus	1.4	—	—	—	14.2	10.6	13.4	12.2	3.4	.8	—	—
Chaet. decipiens	5	2.8	—	5.8	4	.4	30	4.8	.6	.6	—	—
Chaet. densus	—	—	—	.4	—	—	—	—	—	—	—	—
Chaet. didymus	—	—	—	.4	—	1.2	2.6	—	.8	—	1.6	1.2
Chaet. didymus var. anglica	1.2	—	—	—	1.6	—	.8	1.4	.6	—	—	1.2
Chaet. didymus var. protuberans	—	—	—	4.2	2.4	—	—	5.2	1	2.6	.8	—
Chaet. laciniosus	1.4	—	—	23	14.2	.8	1.8	1	1.8	2	5.2	1.8
Chaet. laevis	35	6.6	—	40	10	1.2	4.8	5.6	4.2	14	16.2	2.4
Chaet. lorenzianus	4.2	4.4	—	65	140	3.8	15.2	8.6	13	14.2	2.2	.8
Chaet. socialis	23	—	—	—	20	—	—	—	—	5	—	—
Chaet. subsecundus	—	—	—	—	2.2	—	—	—	.4	.6	1	—
Ditylum brightwelli	—	—	—	—	.2	1.2	2	.8	.6	—	—	.4
Eucampia cornuta	.8	—	—	.8	1.2	—	—	.2	.2	.2	—	—
Guinardia flaccida	—	—	—	.2	3.4	1	.4	3	1.2	1.4	—	—
Hemiaulus hauckii	—	—	—	—	—	.4	—	—	—	—	—	—
Hemiaulus membranacea	.6	.2	—	.4	.2	—	—	—	—	—	.2	—
Hemiaulus sinensis	.2	—	—	4	3.2	—	—	—	—	—	2.2	—
Lauderia annulata	—	—	—	—	—	—	1.8	—	1.2	—	—	—
Leptocylindrus maximus	.4	—	—	—	.2	—	—	—	—	—	.6	—
Leptocylindrus minimus	—	—	—	—	—	—	—	—	—	—	—	—
Nitzschia closterium	20	5	.2	10	10	10	5	—	—	.2	5	75
Nitzschia delicatissima	30	—	—	25	30	5	—	.8	—	35	40	25
Nitzschia pacifica	10	10	—	75	210	6.8	—	10	—	2	—	6.8
Nitzschia pungens var. atlanticus	10	—	—	—	—	—	2.4	—	—	20	5.2	—
Rhiz. alata f. genuina	.2	—	.6	.2	1.4	1	—	—	—	.4	.2	—
Rhiz. alata f. indica	—	—	—	—	—	1.4	—	—	—	—	.2	—
Rhiz. delicatula	.8	—	—	25	1.8	—	3.2	—	—	—	—	—
Rhiz. fragilissima	.2	—	—	.4	.6	—	1.4	—	—	.6	.8	—
Rhiz. setigera	.2	.2	—	1.4	2.4	.2	.2	.2	.2	1.6	.4	.6
Rhiz. stolterfothii	5.6	.4	—	25	145	50	35	.6	1.4	45	2.6	1.4
Schroederella delicatula	—	—	—	1.2	4.6	.4	—	.4	—	—	.2	—
Skel. costatum f. tropicum	—	6.6	3	34.6	580	10	26.4	23.6	43	3.6	125	27.2
Thalassionema nitzschioides	7.8	1.2	.4	7.6	23	7.8	14.8	23.6	14	4.4	3.4	21.4
Thalassiosira aestivalis	—	—	—	—	—	—	—	—	—	—	—	—
Thalassiothrix frauenfeldii	1.2	2.4	1.8	3.0	4	—	4	—	—	2.8	1.2	.4
Thalassiothrix mediterranea var. pacifica	—	—	—	2.2	2.2	.2	.2	1	.2	2	—	.2
DINOFLAGELLATES												
Ceratium spp.	.4	.2	.2	1.4	.6	—	.4	.2	—	.2	—	.4
Exuviaella spp.	10	15	20	15	—	10	15	10	10.2	—	10	.2
Exuviaella baltica	10	15	20	15	—	10	15	10	10	—	10	—
Goniaulax spp.	—	—	—	.2	—	—	—	—	—	—	.2	—
Gymnodiniaceae	5	5	—	—	15	5	15	5	5	—	25	10
Oxytoxum spp.	—	10	—	5	.6	—	5	—	—	5	5	5
Oxytoxum variabile	—	10	—	5	—	—	—	—	—	5	5	5

APPENDIX TABLE 2D. (Continued)

STATION	47			48			49			51		
DEPTH (m)	0	10	20	0	10	20	0	10	20	0	10	20
DINOFLAGELLATES (Continued)												
Peridinium spp.	.4	.2	—	2.4	.6	1.2	.6	1.2	.8	.8	1	.2
Peridinium globulus var. quarnerense	—	—	—	.2	—	.4	.2	.4	—	.4	.4	.2
Prorocentrum spp.	—	.6	.4	3.8	—	—	2.8	.2	—	.6	.8	—
Prorocentrum micans	—	.6	.2	3.6	—	—	2.4	.2	—	.2	.2	—
COCCOLITHOPHORES												
Coccolithus huxleyi	—	5	—	—	—	—	—	—	—	10	5	—
Gephyrocapsa oceanica	15	30	10	—	—	—	—	—	—	35	10	15

STATION	52			53		54			55		
DEPTH (m)	0	10	20	0	10	0	10	20	0	10	20
DIATOMS											
Bact. delicatulum	—	—	—	—	—	—	—	2.8	—	—	—
Bact. elegans	220	195	—	125	70	650	230	3.2	—	—	—
Bact. hyalinum	.6	.6	.8	—	—	—	—	—	—	—	—
Bact. hyalinum var. princeps	—	—	—	200	115	60	45	—	2.4	5.4	—
Bact. varians	—	—	.4	—	—	—	35	—	—	—	—
Cerataulina bergoni	1.2	.6	4.6	.2	.2	.2	.8	.4	1.4	65	9
Chaet. affinis	22.6	12.2	2.8	6.2	10	120	65	1	5.6	4.6	—
Chaet. atlantidae	2	2.2	1	—	2.8	1.4	290	2	—	18.8	30
Chaet. brevis	2.4	1.8	5.4	12.6	11.2	—	—	5.6	105	120	—
Chaet. compressus	1220	710	225	430	290	780	440	110	1045	1420	—
Chaet. constrictus	—	—	1.4	—	—	85	—	—	—	—	—
Chaet. costatus	—	—	—	—	—	—	1425	8.2	480	1000	365
Chaet. curvisetus	4.6	2.4	3.8	3.2	3.2	90	2330	30.2	120	210	385
Chaet. decipiens	.8	—	—	—	1.4	180	230	.8	—	.8	.4
Chaet. densus	—	—	—	—	—	—	8.8	2.4	2.2	—	—
Chaet. didymus	—	—	6.2	—	—	—	35	—	—	2.6	1.8
Chaet. didymus var. anglica	10.2	3	—	—	—	10	—	—	—	—	—
Chaet. didymus var. protuberans	8	3.4	7.8	1.8	3.2	75	—	1.4	—	—	—
Chaet. laciniosus	215	35	1.2	12.6	14.6	40	—	—	—	—	—
Chaet. laevis	145	90	10	90	80	125	20	.4	—	—	—
Chaet. lorenzianus	330	210	.8	6.6	5.6	280	120	1.2	440	8.6	—
Chaet. socialis	40	—	—	30	80	—	215	—	—	950	175
Chaet. subsecundus	2	.4	—	1.2	—	45	—	—	—	—	—
Ditylum brightwellii	—	.4	—	.4	—	.4	39.2	4.4	—	7.4	29.6
Eucampia cornuta	.4	.4	.4	.2	—	5.4	420	1	8.4	2390	250
Guinardia flaccida	1	1.8	1.6	2	1.2	.6	1.4	.4	.6	1.2	—
Hemiaulus hauckii	—	—	—	—	—	55	40	—	—	—	—
Hemiaulus membranacea	.2	.2	1	—	—	1	.4	—	—	—	—
Hemiaulus sinensis	2.8	1.6	2	.2	.8	.8	10	—	.2	—	—
Lauderia annulata	—	.4	7.2	—	—	7.6	300	1.6	5	7	10
Leptocylindrus maximus	—	1.6	.2	1	.6	.8	—	—	2.8	1.6	—
Leptocylindrus minimus	—	—	—	—	—	—	—	—	35	1570	930
Nitzschia closterium	10	10	40	10	10	45	440	—	25	840	160
Nitzschia delicatissima	105	85	40	10	80	145	510	—	95	790	70
Nitzschia pacifica	130	30	75	125	75	—	—	—	—	—	—
Nitzschia pungens var. atlanticus	—	.6	6.8	90	55	—	—	—	—	—	—
Rhiz. alata f. genuina	.4	1.4	5	2.4	6	.2	—	.2	—	1.4	—
Rhiz. alata f. indica	.2	.2	1.2	.4	.2	—	.4	—	.8	1.4	—
Rhiz. delicatula	140	55	10	325	—	420	205	2.2	110	910	185
Rhiz. fragilissima	.6	1.4	2.8	135	60	60	70	—	140	70	—
Rhiz. setigera	3	3.4	4.2	1.6	.8	2.8	4.6	1	.4	1.4	3
Rhiz. stolterfothii	115	145	50	310	255	400	770	6	335	920	210
Schroederella delicatula	1.4	2.4	1	—	.6	3	1	—	1.6	3.8	—
Skel. costatum f. tropicum	37.8	23.6	305	25	40	730	19300	1010	—	532	10680
Thalassionema nitzschioides	2.8	2.6	3.8	3.6	.6	10	21	14	.4	48.8	60
Thalassiosira aestivalis	—	—	—	—	—	—	910	75	—	1340	1220

APPENDIX TABLE 2D. (Continued)

STATION	52			53		54			55		
DEPTH (m)	**0**	**10**	**20**	**0**	**10**	**0**	**10**	**20**	**0**	**10**	**20**
DIATOMS (Continued)											
Thalassiothrix frauenfeldii	7.4	.6	10.4	.2	2	1.4	6.4	—	1.6	6	1.6
Thalassiothrix mediterranea var. pacifica	2.2	1.6	.8	.6	.6	2.4	—	.2	.6	1.4	.2
DINOFLAGELLATES											
Ceratium spp.	—	.8	.4	—	.2	—	—	—	—	—	—
Exuviaella spp.	10	35.2	10.2	5	—	—	—	—	10	—	—
Exuviaella baltica	10	35	10	5	—	—	—	—	10	—	—
Goniaulax spp.	.2	—	1.2	—	—	—	—	—	.4	—	—
Gymnodiniaceae	30	10	—	5	—	10	—	—	5	—	—
Oxytoxum spp.	6	5.2	.2	—	.2	—	—	—	—	—	—
Oxytoxum variabile	5	5	—	—	—	—	—	—	—	—	—
Peridinium spp.	1	3.4	4	—	—	.4	.6	—	2.8	1.4	.2
Peridinium globulus var. quarnerense	—	.2	—	—	—	.2	—	—	.2	—	—
Prorocentrum spp.	.2	1.4	.2	—	—	—	—	—	2.8	.4	—
Prorocentrum micans	—	.2	.2	—	—	—	—	—	2.8	.4	—
COCCOLITHOPHORES											
Coccolithus huxleyi	20	35	10	—	—	—	—	—	—	—	—
Gephyrocapsa oceanica	35	30	—	—	—	—	5	—	—	—	—

APPENDIX TABLE 2D. (Continued) (cells per liter)

DIATOMS: Actinoptychus undulatus **20** 48t, **80** 48b; Actin. undulatus var. catenata **40** 54b; Asterionella japonica **3,000** 55s, **11,500** 55t; Ast. japonica f. tropicum **80** 51t, **120** 48b, **240** 54s, **300** 54b, **5,500** 55t, **23,500** 55b, **69,500** 54t; Asterolampra marylandica **20** 51b; Asteromphalus flabellatus **20** 47s,48t, **40** 49s, 52t,55t, **60** 48s,52s; Aster. heptactis **20** 51t, **60** 51s,52t; Bacteriastrum mediterraneum **100** 55t, **200** 54s; Bellerochea malleus **40** 48t,52s, **80** 53s; Biddulphia alternans **40** 47t; Bidd. dubia **260** 54b; Bidd. longicruris **20** 51t; Bidd. mobiliensis **20** 47s,51t,54s, **40** 48s,t,b,55t, **80** 51b,55b, **160** 52b, **9,000** 54t; Bidd. sinensis **60** 49s, **100** 48b, **220** 54b, **360** 54t, **520** 55b; Brenneckella sp. **20** 48s, **60** 52b, **540** 51t, **1,120** 51b; Cerataulina compacta **40** 57s, **60** 49b, **80** 54b, **280** 55b;

Chaetoceros affinis var. circinalis **120** 53t; Ch. apendiculatus **40** 48s,53s,t, **60** 51t, **380** 51b, **940** 49s, **1,000** 54s,b, **2,000** 54t; Ch. coarctatus **20** 52b, **100** 55t, **340** 49t; Ch. dadayi **20** 51s, **40** 52b, **60** 52t; Ch. diversus **40** 47t, **60** 47s,51t, **80** 49b, **140** 51s, **200** 49t, **280** 52s, **300** 52t, **420** 49s, **660** 48s, **1,000** 48t, **1,500** 53t, 54s; Ch. eibenii **100** 47s; Ch. lauderi **140** 49s; Ch. cf. pendulus **20** 48s,55s, **40** 49b, **240** 49t, **660** 49s; Ch. peruvianus **20** 47t, **40** 47s,48b,51s,b, **60** 52t,55s, **80** 52s,b,54s, **140** 48t; Ch. rostratus **40** 52s,54s, **160** 48t; Ch. tetrastichon **40** 54b; Climacodium frauenfeldianum **20** 52t, **100** 53t, **140** 52b, **420** 48t; Corethron hystrix **20** 47s,t,53s,t,55b, **40** 51s,t,52t,55s, **60** 49s,b,52b, **80** 48s, **100** 48b, **140** 51b,52s, **220** 54b, **300** 54s, **800** 48t, **11,000** 54t;

Corethron pelagicum **20** 48t; Coscinodiscus concinnus **20** 48t,49t,53s,54s, **40** 47s,49s, **60** 54b,55t, **340** 52b, **360** 48b,51t, **800** 51b; Cosc. excentricus **20** 47t,48s,52t, **40** 47s, **220** 51t,b, **360** 48b; Cosc. granii **20** 49t; Cosc. lineatus **20** 47b,49s, **40** 47s,49t,b, **60** 47t, **100** 48t, **180** 48b; Cosc. marginatus **20** 47b,49t,52s, 54t, **40** 52b, **60** 48b; Cosc. perforatus **20** 55s; Cosc. rothii **20** 48b; Cosc. thorii **20** 52b; Cyclotella cf. caspia **40** 48t, **60** 54t, **160** 55t,b; Cyclotella striata **60** 49s, **620** 48b; Ditylum sol **20** 48b,51t,53s,t,55b, **40** 49t,52b, **60** 55s, **100** 51b; Fragilaria norma **120** 52s,t; Hemidiscus cuneiformis **100** 47s; Leptocylindrus danicus **1,000** 49s, **4,000** 53s; Lithodesmium undulatum **160** 54b, **200** 55b, **260** 54t; Nitzschia kolaizeckii **20** 52b, **80** 52t; Opephora pacifica **80** 52b, **4,500** 53s;

Planktoniella sol **20** 55t,b, **40** 49b; Rhiz. acuminata **20** 55t; Rhiz. bergonii **20** 47s,48s,51s,52s,t,53t, 54s,55s,b, **40** 51t,53s, **80** 48t, **140** 52b,55t; Rhiz. calcar avis **20** 48b,54t,55s, **40** 48s,52b, **60** 49s,b,53s,54s,55t, **80** 47t,51s, **100** 47s, **160** 48t,52s, **180** 52t, **580** 53t; Rhiz. imbricata var. shrubsolei **20** 49s,t,51t,54t,55t, **40** 52t,b, **60** 48t,51b, **100** 47s, **220** 48s, **340** 53t; Rhiz. styliformis **20** 49t, **60** 55s, **140** 52s; Rhiz. styliformis var. longispina **20** 47t,52b, **40** 51s, **60** 48t, **80** 52t,53t; Stephanopyxis palmeriana **40** 48b,55t, **160** 54b, **520** 54t; Streptotheca thamensis **40** 54t; Thalassiosira subtilis **120** 55b, **160** 55s, **640** 55t, **1,300** 54t; Thalassiothrix delicatula **20** 51t, **40** 48t, **60** 52t; Tropidoneis antarctica **20** 49t,51t,b,54s, **80** 52t, **100** 52s,55b, **120** 52b,54t,55t.

DINOFLAGELLATES: Blepharocysta splendor-maris **20** 49s; Ceratium declinatum **20** 49s,52b; Cer. extensum **20** 52b, **80** 52t; Cer. trichoceros **20** 48s,t; Dinophysis hastata **40** 49s; Epiperidinium sp. **40** 48s; Exuviaella compressa **20** 49b,51b,52t,b; Glenodinium lenticula f. minor **20** 47s,52t,54s; Goniaulax polyedra **120** 52b; Gon. polygramma **20** 48s,51s,52s; Gon. tamarensis var. excavatum **40** 55s; Ornithocercus quadratus f. intermedia **20** 48t; Oxytoxum curvatum **20** 48t,52b; Oxy. caudatum **20** 52t, **100** 52s, **500** 49s; Oxy. scolopax **20** 53t, **40** 48t; Peridinium bipes **20** 55t; Per. brochii **20** 55b; Per. conicum **20** 55s; Per. crassipes **20** 54t; Per. excentricum **20** 55t; Per. globulus **40** 49b; Per. globulus var. ovatum **20** 54t, **60** 52b,55t; Per. longispinum **20** 52b;

Per. nipponicum **20** 54s,t,55t, **40** 49s,t,b,51s, **60** 48s,t, **80** 48b, **120** 52t, **160** 52b; Per. oceanicum var. oblongum **20** 55s; Per. ovum **20** 47t, **40** 47s, **60** 48s; Per. steinii **20** 52b; Per. subinerme **20** 48s, **100** 55s; Per. trochoideum **20** 52t, **40** 48s,49t,55s; Podolampas bipes **20** 48t, **40** 47s; Podol. spinifera **20** 52t, **60** 52s; Prorocentrum maximus **20** 49s; Pror. obtusidens **20** 47b,48s, **40** 51s; Pror. rostratus **40** 51t.

COCCOLITHOPHORES: Acanthoica lithostratos **500** 52t; Calciosolenia sinuosa **500** 47b,51s,52s, **1,000** 51b; Discosphaera tubifer **40** 52s, **500** 47t,b,52t; Halopappus adriaticus **40** 52b, **3,000** 52t; Michaelsarsia elegans **500** 51s, **1,000** 52s; Pontosphaera maximus **40** 47b, **60** 53s.

SILICOFLAGELLATES: Ebria tripartita **240** 54t.

CYANOPHYCEANS: ± 47b,48s,49s,51s,t,b,52t, **C** 47s,t,48t,49t,b.

DIVERSE: Chilomonas marina **500** 47b,48s,52t,54s,b, **1,000** 52s,55t.

APPENDIX TABLE 2E. Results of the phytoplankton enumeration at stations 56 to 63 sampled from 11 February to 20 May 1957 (cells per 10 ml)

STATION	56			57			58			59		
DEPTH (m)	0	10	20	0	10	20	0	10	20	0	10	20
DIATOMS												
Bact. delicatulum	15	—	—	—	—	—	—	—	—	—	—	—
Bact. elegans	—	—	—	—	—	—	—	—	—	—	—	—
Bact. hyalinum	—	—	—	—	—	—	—	—	—	—	—	—
Bact. hyalinum var. princeps	2	—	2.6	—	—	—	—	—	—	—	—	—
Bact. varians	—	2	—	—	—	—	—	—	—	—	—	—
Cerataulina bergoni	.8	2.2	6	195	400	175	.8	—	—	—	—	—
Chaet. affinis	350	4	2.2	—	—	—	1.6	—	—	—	—	—
Chaet. brevis	560	325	190	75	—	.4	—	—	—	—	—	—
Chaet. compressus	550	465	—	—	—	—	—	—	—	—	—	—
Chaet. constrictus	—	—	—	—	—	—	—	—	—	—	—	—
Chaet. costatus	205	16.8	—	—	—	—	—	—	—	—	—	—
Chaet. curvisetus	90	230	2.2	—	—	—	—	—	—	—	—	2
Chaet. debilis	60	—	—	—	—	—	—	—	—	—	—	—
Chaet. decipiens	—	1	—	—	—	—	—	—	—	—	—	—
Chaet. densus	—	—	—	—	—	—	—	—	—	—	—	—
Chaet. didymus	55	1.4	.6	—	—	1	—	—	—	—	—	—
Chaet. didymus var. anglica	—	—	—	—	—	—	—	—	—	—	—	—
Chaet. didymus var. protuberans	30	—	6.2	—	—	—	—	—	—	—	—	—
Chaet. laciniosus	35	—	—	—	—	—	—	—	—	—	—	—
Chaet. laevis	—	—	—	—	—	—	—	—	—	—	—	—
Chaet. lorenzianus	465	140	70	—	—	.4	—	—	—	—	—	—
Chaet. socialis	890	675	385	—	—	—	—	—	—	—	—	—
Chaet. subsecundus	—	35	.6	—	—	—	—	—	—	—	—	—
Eucampia cornuta	160	400	150	42136.7	20580	3695	—	—	—	—	—	—
Guinardia flaccida	1.6	4.4	.8	.2	—	—	.2	—	—	—	—	—
Hemiaulus membranacea	2	.6	—	—	—	—	—	—	—	—	—	—
Hemiaulus sinensis	25	2.8	.6	.4	.2	—	—	—	—	—	—	.2
Lauderia annulata	12.4	8.8	1.2	1.6	—	—	1.4	—	—	—	—	—
Leptocylindrus maximus	2.6	4.6	1.2	—	—	1.6	—	—	—	—	—	—
Leptocylindrus minimus	405	1315	95	15	—	—	—	—	—	—	—	—
Nitzschia closterium	130	130	100	40	10	—	10	5	5	—	—	—
Nitzschia delicatissima	150	45	25	301.95	100	35	13390	6600	35	2238.9	—	10
Nitzschia pacifica & pungens	400	195	220	924.7	90	85	19870	3210	150	7243.5	—	.4
Rhiz. alata f. genuina	2.4	2.2	2.8	.2	—	—	—	—	—	—	—	—
Rhiz. alata f. indica	.6	2	1.2	—	—	—	.4	—	—	—	—	—
Rhiz. delicatula	2225	1960	225	1226.5	890	15	1710	330	.8	65	—	—
Rhiz. fragilissima	305	195	70	50	45	5	—	—	—	5	—	—
Rhiz. setigera	2.8	3.8	5.2	1.2	.8	.4	1.6	9.6	.2	3.6	.2	7.8
Rhiz. stolterfothii	1645	1985	255	1075.6	1160	245	1220	430	15	30	—	—
Skel. costatum f. tropicum	485	310	290	60	10	60	35	—	.4	—	—	—
Thalassionema nitzschioides	.6	—	4	5.4	—	1.4	—	1	1	—	—	—
Thalassiosira aestivalis	85	50	50	25	—	75	1000	380	—	20	10	—
Thalassiothrix frauenfeldii	5.4	10.6	1.4	1	—	.2	.6	—	.2	—	—	—
Thalassiothrix mediterranea var. pacifica	5.6	3.2	.8	.4	—	—	3.6	1.6	—	.4	—	.8
DINOFLAGELLATES												
Ceratium spp.	—	—	—	—	—	.2	—	—	—	—	—	.2
Exuviaella spp.	5	45.2	—	10	220	10	45	30	.2	—	25	—
Exuviaella baltica	5	45	—	10	220	10	5	—	—	—	—	—
Exuviaella vaginule	—	—	—	—	—	—	.2	40	30	—	25	—
Glenodinium lenticula f. minor	—	.2	.2	—	1	.6	—	—	.2	—	—	—
Goniaulax spp.	—	—	—	.2	—	—	—	—	—	—	—	—
Gymnodiniaceae	—	45	—	—	35	—	90	35	60	—	—	—
Oxytoxum spp.	—	10	—	5	15	—	—	50	5	—	—	—
Oxytoxum variabile	—	10	—	5	15	—	—	50	5	—	—	—
Peridinium spp.	2	.8	.8	11.4	34.2	2.8	—	.4	—	—	18.4	2.8
Peridinium trochoideum	1.6	.2	—	10.2	—	—	—	—	—	—	18.4	2.6
Prorocentrum spp.	1	1	.2	.4	—	—	.2	—	—	—	.8	—
Prorocentrum micans	—	—	.2	.4	—	—	.2	—	—	—	.4	—
COCCOLITHOPHORES												
Coccolithus huxleyi	—	—	—	65	—	—	—	—	—	—	—	—
Gephyrocapsa oceanica	—	—	—	50	15	—	—	—	—	5	5	—

APPENDIX TABLE 2E. (Continued)

STATION	60			61			62			63		
DEPTH (m)	0	10	20	0	10	20	0	10	20	0	10	20
DIATOMS												
Bact. delicatulum	—	—	—	—	—	—	—	—	—	6.4	5.2	—
Bact. elegans	—	5.6	—	—	—	—	—	—	—	3.6	—	—
Bact. hyalinum	—	—	—	—	—	—	—	—	—	8	—	.4
Bact. hyalinum var. princeps	12.6	—	—	—	—	—	—	—	—	—	2.6	—
Bact. varians	—	—	—	—	—	—	—	—	—	—	—	—
Cerataulina bergoni	11.6	2	—	—	—	—	—	—	—	1.2	1.6	1
Chaet. affinis	48	—	—	—	6.2	—	—	—	—	.4	1.4	—
Chaet. brevis	11.2	9.4	—	3.8	2.8	—	1.6	2.4	—	5.8	1	—
Chaet. compressus	265	85	—	—	—	—	3.2	3.2	—	2.2	1.2	—
Chaet. constrictus	—	—	—	—	1.2	—	—	—	—	—	—	—
Chaet. costatus	—	—	—	—	16.8	1.4	—	—	—	—	—	—
Chaet. curvisetus	295	205	5.4	—	3.2	—	—	1.8	—	3	—	—
Chaet. debilis	30	9.2	10.2	1.6	23.6	3.8	1.6	—	—	.8	—	—
Chaet. decipiens	9.6	—	3.8	—	—	—	—	1	—	—	1.8	—
Chaet. densus	—	1.6	—	—	1	—	—	—	—	1	—	—
Chaet. didymus	4.2	—	—	—	—	—	—	—	—	—	—	—
Chaet. didymus var. anglica	—	—	—	—	—	—	—	—	—	4.2	—	—
Chaet. didymus var. protuberans	—	—	—	—	—	—	—	—	—	—	—	—
Chaet. laciniosus	—	—	—	—	—	—	—	—	—	—	—	—
Chaet. laevis	—	—	—	—	—	—	—	15	—	10	—	—
Chaet. lorenzianus	.8	2.8	.8	—	1	—	3.2	—	—	9	1.2	—
Chaet. socialis	1290	1550	—	—	—	—	—	—	—	—	—	—
Chaet. subsecundus	2	4.4	—	—	2.2	—	—	—	—	—	—	—
Eucampia cornuta	920	533.6	—	—	1.2	.4	.8	3.2	—	5.2	4.8	.4
Guinardia flaccida	1.6	—	—	.4	—	—	—	—	—	21.8	7.2	3
Hemiaulus membranacea	—	—	—	—	—	—	—	—	—	.4	—	—
Hemiaulus sinensis	—	—	—	—	.4	—	1	—	—	1.6	—	—
Lauderia annulata	11	7.2	—	.6	1	—	—	—	—	—	—	—
Leptocylindrus maximus	3.6	—	—	3.2	2	—	—	—	—	—	—	—
Leptocylindrus minimus	—	—	—	—	—	—	—	—	—	—	—	—
Nitzschia closterium	25	—	—	—	—	—	—	10	—	.2	5	5
Nitzschia delicatissima	80	—	—	—	165	—	10	15	—	110	105	10
Nitzschia pacifica & pungens	230	80	15	610	55	1	—	45	10	15	18.2	1.2
Rhiz. alata f. genuina	2.2	—	.2	4.4	3	.2	—	.4	—	1.6	.2	—
Rhiz. alata f. indica	—	.8	—	1.8	8.6	—	—	.4	—	1.8	—	—
Rhiz. delicatula	—	590	1.2	265	1215	2	30	15	—	35	21.2	—
Rhiz. fragilissima	5	20	—	—	2.4	—	40	12.4	—	40	12.4	.8
Rhiz. setigera	—	—	.6	.2	.4	.2	.4	1.2	—	.8	1.2	—
Rhiz. stolterfothii	9160	9530	20	165	225	3.2	45	180	—	165	25.6	1
Skel. costatum f. tropicum	—	—	—	2.4	2.4	—	—	1	—	2.8	3.4	—
Thalassionema nitzschioides	2	—	1.8	—	.4	1.6	—	9	.4	.4	—	—
Thalassiosira aestivalis	—	—	—	—	—	—	25	295	—	—	—	—
Thalassiothrix frauenfeldii	—	—	—	—	—	—	—	—	—	.8	1.6	—
Thalassiothrix mediterranea var. pacifica	3	—	—	.4	2.4	.2	—	.4	—	.4	—	—
DINOFLAGELLATES												
Ceratium spp.	—	—	—	.6	.2	.2	—	—	—	.2	.2	—
Exuviaella spp.	30	10	—	40	125.4	—	5	5	—	—	5.2	—
Exuviaella baltica	30	10	—	40	125	—	5	5	—	—	5	—
Exuviaella vaginule	—	—	—	—	.4	—	—	—	—	—	—	—
Glenodinium lenticula f. minor	4.2	1.6	—	—	.4	1	—	—	—	.4	—	—
Goniaulax spp.	—	—	—	.2	.2	—	—	—	—	1.8	—	—
Gymnodiniaceae	15	—	—	—	35	5	.8	45	—	—	5	—
Oxytoxum spp.	—	5	—	5	—	—	—	10.2	—	—	—	—
Oxytoxum variabile	—	5	—	—	—	—	—	10	—	—	—	—
Peridinium spp.	.2	.4	.4	1.2	3	.4	—	2	.4	2.4	.2	.2
Peridinium trochoideum	—	—	—	—	.2	—	—	1	—	.8	—	—
Prorocentrum spp.	2	.4	.6	.6	1	.2	—	.4	—	5.6	1.6	.2
Prorocentrum micans	1.6	.4	.6	.6	1	.2	—	.2	—	—	1	.2
COCCOLITHOPHORES												
Coccolithus huxleyi	—	—	—	—	—	—	—	—	—	—	—	—
Gephyrocapsa oceanica	—	—	—	5	—	—	—	5	—	—	—	—

APPENDIX TABLE 2E. (Continued) (cells per liter)

DIATOMS: Actinoptychus undulatus var. catenata **40** 57b, **140** 56t; Asterionella japonica f. tropicum **2,500** 56s; Asteromphalus flabellatus **20** 57b,60b,61s,b,63s,b, **40** 58t,b,59s; Aster. heptactis **20** 63b; Bellerochea malleus **60** 56s, **80** 63b, **180** 63t, **600** 63s; Biddulphia alternans **40** 57b; Bidd. mobiliensis **20** 57s,61b, **80** 56s,t; Bidd. pulchella **20** 63s; Chaetoceros aequatorialis **20** 56t; Ch, atlanticus var. neapolitana **5,500** 56s; Ch. atlantidae **180** 56s; Ch, coarctatus **40** 56t, **300** 56s; Ch. diversus **40** 63t; Ch. eibenii **100** 56t; Ch. lauderi **120** 63t; Ch. cf. pendulus **20** 56b; Ch. peruvianus **20** 56t,59s,63t, **40** 56s; Ch. teres **740** 62b;

Corethron hystrix **20** 56s,63b; Coscinodiscus marginatus **20** 56s,t,59b,61t; Cyclotella cf. caspia **20** 58s, **40** 57s,60b, **80** 63t,b, **100** 63s, **160** 60s, **220** 56s; Cyclotella striata **40** 59b; Dactyliosolen mediterraneus **40** 57b, **80** 60b, **240** 61s, **340** 61b, **400** 60s, **820** 59b, **1,340** 61t; Ditylum brightwellii **20** 58b,62t, **40** 56s, **60** 56t,57b, **80** 56b; Ditylum sol **60** 56s,b; Lithodesmium undulatum **40** 56t; Planktoniella sol **20** 56t,62b; Pseudoeunotia doliolus **100** 60s; Rhiz, acuminata **20** 56t; Rhiz. bergonii **20** 56b,62t, **40** 60t, **80** 60s, **220** 56t, **240** 61s, **300** 56s, **360** 61t; Rhiz. calcar avis **20** 57s,61b,62t, **40** 56t,60s,61s,62s, **60** 56s, **100** 63s, **140** 61t; Rhiz. calcar avis var. cochlea **40** 60b, **60** 60s, **160** 60t; Rhiz. imbricata var. shrubsolei **20** 61b, **300** 56s, **360** 56t; Rhiz. robusta **20** 62s,63b, **60** 61s;

Rhiz. styliformis var. longispina **20** 56b,62t,b; Schroederella delicatula **40** 61t, **220** 56s, **280** 56t; Skeletonema costatum **5,500** 60s; Stephanopyxis palmeriana **120** 56t; Step. turris **240** 56s; Thalassiosira subtilis **400** 56s, **1,000** 56b, **5,700** 56t; Thalassiothrix delicatula **20** 61s,t; Tropidoneis antarctica **20** 56b,57b,58t,62t, **40** 56t,57s,t,58s.

DINOFLAGELLATES: Ceratium extensum **20** 63t; Cer. furca var. eugrammum **20** 61s; Cer. kofoidii **20** 57t,59b,61s,b; Cer. massiliense f. macroceroides **20** 61s; Dinophysis fortii **20** 57b,61t, **40** 59b, **1,160** 59t; Exuviaella compressa **20** 63t; Ex. marina **20** 56t; Goniaulax polygramma **20** 57s; Gon, tamarensis var, excavatum **180** 63s; Oxytoxum curvatum **20** 63b; Oxy. gracilis **500** 61s; Oxy, scolopax **20** 62t; Peridinium bipes **40** 58t; Per. brochii **40** 63s; Per. depressum **20** 59b; Per. globulus **20** 56b,63s; Per. globulus var. ovatum **20** 60s, **60** 57s, **240** 57b, **3,420** 57t; Peridinium globulus var, quarnerense f. spirale **20** 61b; Per. granii f. mite **60** 57s; Per. heterospinum **20** 61t; Per. leonis **20** 61t; Per. nipponicum **20** 63t,b, **40** 62t,b, **60** 63s; Per, oceanicum **20** 56b; Per. pellucidum **40** 62t, **120** 61t;

Per. pyriforme **40** 56s,t,57b, **60** 56b; Per. steinii **20** 61t,b,62t, **40** 63s; Per. subinerme **120** 61s; Prorocentrum rostratus **100** 56s,t.

COCCOLITHOPHORES: Coccolithus sibogae **500** 57t.

CYANOPHYCEANS: Oscillatoria cf, niger **20** 63b.

DIVERSE: Chilomonas marina **500** 58t,61b,63b, **1,000** 62b, **2,000** 56s,62t, **7,000** 57t; Euglenaceae **8,500** 62t; Halosphaera sp. **20** 56b,60s,63t,b, **60** 63s, **80** 56t, **100** 56s; Strombidium (Laboea) strobila **60** 63s.

APPENDIX TABLE 3. Diatom and dinoflagellate species identified. (See text for coccolithophore, silicoflagellate, cyanophycean and tintinnid species identified)

DIATOMS

CENTRIC FORMS

Actinoptychus undulatus (Bailey) Ralfs
—— —— var. **catenata** (Bailey) Ralfs n. var.
Asterolampra marylandica Ehrenberg
Asteromphalus flabellatus (Bréb.) Greville
—— **heptactis** (Bréb.) Ralfs
Bacteriastrum delicatulum Cleve
—— **elegans** Pavillard
—— **hyalinum** Lauder
—— —— var. **princeps** (Castr.) Ikari
—— **mediterraneum** Pavillard
—— **varians** Lauder
Bellerochea malleus (Brightw.) Van Heurck
Biddulphia alternans (Bailey) Van Heurck
—— **dubia** (Brightw.) Cleve
—— **longicruris** Greville
—— **mobiliensis** Bailey
—— **pulchella** Gray
—— **sinensis** Greville
Brenneckella sp.
Cerataulina bergoni Peragallo
—— **compacta** Ostenfeld & Schmidt
Chaetoceros aequatorialis Cleve
—— **affinis** Lauder
—— —— var. **circinalis** (Meunier) Hustedt
—— —— var. **willei** (Gran) Hustedt
—— **anastomosans** Grunow
—— **apendiculatus** Müller Melchers
—— **atlanticus** Cleve
—— —— f. **audax** (Schütt) Hustedt
—— —— var. **neapolitan** (Schröd.) Hustedt
—— —— var. **skeleton** (Schütt) Hustedt
—— **atlantidae** Müller Melchers
—— **brevis** Schütt
—— **coarctatus** Lauder
—— **compressus** Lauder
—— **constrictus** Gran
—— **convolutus** Castracane
—— **costatus** Pavillard
—— **curvisetus** Cleve
—— **dadayi** Pavillard
—— **danicus** Cleve
—— **debilis** Cleve
—— **decipiens** Cleve
—— **densus** Cleve
—— **dichaeta** Ehrenberg
—— **didymus** Ehrenberg
—— —— var. **anglica** (Grunow) Gran
—— —— var. **protuberans** (Lauder) Gran & Yendo
—— **difficilis** Cleve
—— **diversus** Cleve
—— **eibenii** Grunow
—— **gracilis** Schütt
—— **holsaticus** Schütt
—— **laciniosus** Schütt
—— **laevis** Leudiger-Fortmorel
—— **lauderi** Ralfs
—— **lorenzianus** Grunow
—— cf. **messanensis** Castracane
—— **pelagicus** Cleve
—— cf. **pendulus** Karsten
—— **perpusillus** Cleve
—— **peruvianus** Brightwell
—— **pseudocrinitus** Ostenfeld
—— **rostratus** Lauder
—— **seiracanthus** Gran
—— **simplex** var. **calcitrans** Paulsen
—— **socialis** Lauder
—— **subsecundus** (Grunow) Hustedt
—— **subtilis** Cleve
—— **teres** Cleve
—— **tetrastichon** Cleve
—— **tortissimus** Gran
—— **van heurckii** Gran
—— **vixvisibilis** Schiller
Climacodium frauenfeldianum Grunow
Corethron hystrix Cleve
—— **pelagicum** Brun
Coscinodiscus anguste-lineatus A. S.
—— cf. **argus** Ehrenberg
—— **centralis** Ehrenberg
—— **concinnus** W. Smith
—— **excentricus** Ehrenberg
—— cf. **gigas** Ehrenberg
—— **granii** Gough
—— cf. **lacustris** Grunow
—— **lineatus** Ehrenberg
—— **marginatus** Ehrenberg
—— **perforatus** Ehrenberg
—— —— var. **pavillardi** (Forti) Hustedt
—— **radiatus** Ehrenberg
—— **rothii** (Ehrenberg) Grunow
—— **stellarus** Roper
—— **thorii** Pavillard
—— **wailseii** Gran and Angst
Cyclotella caspia Grunow
—— **striata** (Kutzing) Grunow
Dactyliosolen antarcticus var. **laevis** (Karsten) Heiden & Kolbe
—— **mediterraneus** Peragallo
Ditylum brightwelli (West) Grunow
—— **sol** Grunow
Eucampia cornuta (Cleve) Grunow
—— **zoodiacus** Ehrenberg
Guinardia cf. **blavyana** Peragallo
—— **flaccida** (Castracane) Peragallo
Hemiaulus hauckii Grunow
—— **sinensis** Greville
—— **cuneiformis** Wallich
Lauderia annulata Cleve
Leptocylindrus cf. **adriaticus** Schröder
—— **danicus** Cleve
—— **maximus** n. sp.
—— **minimus** Gran
Lithodesmium undulatum Ehrenberg
Planktoniella sol (Wallich) Schütt
Rhizosolenia acuminata (Peragallo) Gran
—— **alata** f. **genuina** Brightwell
—— —— f. **gracillima** (Cleve) Grunow
—— —— f. **indica** (Peragallo) Ostenfeld
—— **bergonii** Peragallo
—— **calcar avis** M. Schultze
—— **calcar avis** var. **cochlea** Brun
—— **cylindrus** Cleve
—— **delicatula** Cleve
—— **fragilissima** Bergon
—— **robusta** Norman
—— **setigera** Brightwell
—— **stolterfothii** Peragallo
—— **styliformis** Brightwell
—— —— var. **latissima** Brightwell
—— —— var. **longispina** Hustedt
Schroederella delicatula (Peragallo) Pavillard
Skeletonema costatum (Grev.) Cleve
—— —— f. **tropicum** n.f.
Stephanopyxis palmeriana (Greville) Grunow
—— **turris** (Greville & Arnott) Ralfs
Streptotheca thamensis Shrubsole
Thalassiosira subtilis (Ostenfeld) Gran
—— **aestivalis** Gran and Angst

PENNATE FORMS

Asterionella japonica Cleve
—— —— f. **tropicum** n.f.
Fragilaria cf. **nana** Steemann Nielsen
Fragilaria norma n. sp.
Isthmia nervosa Kützing
Navicula membranacea Cleve
Nitzschia closterium (Ehrenberg) W. Smith
—— **delicatissima** Cleve
—— **kolaizeckii** Grunow
—— **longissima** (Bréb.) Ralfs
—— **lorenziana** var. **incurva** (Grunow) Cleve & Grunow
—— **pacifica** Cupp
—— **pungens** var. **atlantica** Cleve
—— **sigma** var. **indica** Karsten
Opephora pacifica (Grunow) Petit
Pseudoeunotia doliolus (Wallich) Grunow
Thalassionema nitzschioides Grunow
Thalassiothrix delicatula Cupp
—— **frauenfeldii** Grunow
—— —— var. **panama** n. var.
—— **longissima** Cleve & Grunow
—— **mediterranea** Pavillard
—— —— var. **pacifica** Cupp
Tropidoneis antarctica (Grunow) Cleve
—— —— var. **polyplasta** Gran and Angst
—— **lepidoptera** (Gregory) Cleve

DINOFLAGELLATES

Amphidinium cf. **acutissimum** Schiller
____ **minutissima**
____ cf. **oceanicum** Lohmann
Blepharocysta splendor-maris Ehrenberg
Ceratium declinatum Karsten
____ **deflexum** (Kofoid) Jørgensen
____ **extensum** (Gourret) Cleve
____ **furca** (Ehrenberg) Claparede & Lachmann
____ ____ f. **belonoides** Jørgensen
____ ____ f. **eugrammum** (Ehrenberg) Jørgensen
____ **fusus** (Ehrenberg) Dujardin
____ **humile** Jørgensen
____ **inflatum** (Kofoid) Jørgensen
____ **incisum** (Karsten) Jørgensen
____ **kofoidii** Jørgensen
____ **massiliense** (Gourret) Jørgensen
____ ____ f. **macroceroides** (Karsten) Jørgensen
____ ____ f. **protuberans** (Karsten) Jørgensen
____ **minutum** Jørgensen
____ **pentagonum** Gourret
____ ____ var. **subrobustum** Jørgensen
____ **setaceum** Jørgensen
____ **symmetricum** Pavillard
____ **trichoceros** (Ehrenberg) Kofoid
____ **tripos** (Müller) Nitzsch
____ ____ f. **semipulchellum** Jørgensen
Ceratocorys horrida Stein
Dinophysis caudata Saville-Kent
____ **fortii** Pavillard
____ **hastata** Stein
____ **tripos** Gourret
Exuviaella cf. **apora** Schiller
____ **baltica** Lohmann
____ **compressa** Ostenfeld
____ **marina** Cienkowski
____ **vaginula** (Stein) Schütt
Glenodinium lenticula f. **minor** (Paulsen) Pavillard
Goniaulax catenata (Lev.) Kofoid
____ **digitale** (Pouchet) Kofoid
____ cf. **gracilis** Schiller
____ **minima** Matzenauer
____ **monocantha** Pavillard
____ **polyedra** Stein
____ **polygramma** Stein
____ **scrippsae** Kofoid
____ **soinifera** (Claparede & Lachmann) Diesing
____ **tamarensis** var. **excavatum** Braarud
____ **lohmanni** Paulsen
Ornithocercus magnificus Stein s. str. Schütt
____ **quadratus** f. **intermedia** Kofoid & Skogsberg
____ **steinii** Schütt

Oxytoxum caudatum Schiller
____ **curvatum** (Kofoid) Kofoid
____ **gracilis** Schiller
____ **scolopax** Stein
Parahistoneis karsteni Kofoid & Michener
Peridinium bipes Stein
____ **breve** Paulsen
____ **brevipes** Paulsen
____ **brochi** Kofoid & Swezy
____ **brochi** f. **inflatum** Okamura
____ **claudicans** Paulsen
____ **conicum** (Gran) Ostenfeld & Schmidt
____ **crassipes** Kofoid
____ **depressum** Bailey
____ **diabolus** Cleve
____ **divergens** Ehrenberg
____ **excentricum** Paulsen
____ **globulus** Stein
____ ____ var. **ovatum** (Pouchet) Schiller
____ ____ var. **quarnerense** f. **spirale** Gaarder
____ **grande** Kofoid
____ **granii** Ostenfeld
____ ____ f. **mite** (Pavillard)
____ **heterospinum** Gaarder
____ **leonis** Pavillard
____ ____ f. **matzenauri** Schiller
____ **longispinum** Kofoid
____ **minusculum** Pavillard
____ **minutum** Kofoid
____ **nipponicum** Abé
____ **oceanicum** Vanhöffen
____ ____ var. **oblongum** Paulsen
____ **ovum** Schiller
____ **pellucidum** (Bergh) Schütt
____ **pentagonum** Gran
____ ____ var. **latissimum** Kofoid
____ **pyriforme** Paulsen
____ **sinaicum** Matzenauer
____ **steinii** Jørgensen
____ **subinerme** Paulsen
____ **tenuissimum** Kofoid
____ **trochoideum** (Stein) Lemmermann
Phalacroma doryphorum Stein
Podolampas bipes Stein
____ **spinifera** Okamura
Prorocentrum gracile Schütt
____ **hentscheli** Schiller
____ **maximum** Schiller
____ **obtusidens** Schiller
____ **rostratum** Stein
____ **schilleri** Böhm
Protoceratium cf. **reticulatum** (Claparede and Lachmann) Bütschli
Pseudophalacroma nasutum (Stein) Jørgensen
Pyrophacus horologicum Stein

APPENDIX TABLE 4. Mean monthly phytoplankton biomass in upper 20 meters (mg m^{-3}) and "3-week winds" (in miles) at Balboa expressed in various ways used in the regression of biomass standing crop on Balboa winds during the upwelling season, as explained in the text. (Phytoplankton data for December 1954 and April 1955 incomplete)

		"THREE-WEEK WINDS" (in miles)											
Month	Mean Biomass (mg m^{-3})	$\Sigma(N)$	$\Sigma(N + NW)$	$\Sigma(N + .1NW)$	$\Sigma(N + NW - S)$	$\Sigma(N + .1NW - S)$	$\Sigma(N + .1NW - 2S)$	$\Sigma(N + .1NW - 3S)$	$\Sigma(N + .1NW - 4S)$	$\Sigma(N + .1NW - 6S)$	$\Sigma(N + .1NW - 8S)$	$\Sigma(N + .1NW - 10S)$	$\Sigma(N + .1NW - 12S)$
Jan. '55	710	630	2122	779	2034	691	603	515	427	251	75	−101	−277
Feb. '55	590	925	2762	1109	2667	1014	919	824	729	539	349	159	−31
Mar. '55	12360	3470	4183	3541	4145	3503	3465	3427	3389	3313	3237	3161	3085
Dec. '55	641	147	1608	293	1476	161	29	−132	−235	−499	−763	−1027	−1291
Jan. '56	3993	1055	3011	1251	2996	1236	1221	1206	1191	1161	1131	1101	1071
Feb. '56	291	437	2621	655	2542	576	497	418	339	181	23	−135	−293
Mar. '56	629	826	3437	1087	3377	1027	967	907	847	727	607	487	367
Apr. a) '56	312	805	2901	1015	2663	777	539	301	63	−413	−889	−1365	−1841
Apr. b) '56	134	876	2956	1084	2652	780	476	172	−132	−740	−1348	−1956	−2564
Dec. '56	337	434	1813	572	1713	672	572	472	372	172	−18	−218	−418
Jan. a) '57	2898	1769	2784	1260	2767	1242	1225	1208	1191	1157	1123	1089	1055
Jan. b) '57	3975	1227	3218	1426	3216	1424	1422	1420	1418	1414	1410	1406	1402
Feb. '57	5719	1326	4155	1609	4146	1600	1591	1582	1573	1555	1537	1501	1483
Mar. '57	667	906	2634	1079	2466	911	743	575	407	71	−265	−601	−937
Apr. '57	2366	821	3276	1067	3187	978	889	800	711	533	355	177	−1