INTER-AMERICAN TROPICAL TUNA COMMISSION
COMISION INTERAMERICANA DEL ATUN TROPICAL

Bulletin — Boletín
Vol. IX, No. 7

(Completing the Volume)
(Completando el Volumen)

A QUANTITATIVE ANALYSIS OF THE PHYTOPLANKTON OF THE GULF OF PANAMA

II. ON THE RELATIONSHIP BETWEEN C^{14} ASSIMILATION AND THE DIATOM STANDING CROP

by
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(Con resumen en Español)

La Jolla, California
1965

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by

THEODORE J. SMAYDA[2]

INTRODUCTION

The Inter-American Tropical Tuna Commission has maintained a hydro-biological station in the Gulf of Panama located at 8°45'N, 79°23'W in connection with their ecological investigation of the anchoveta (*Cetengraulis mysticetus*), a tuna baitfish (see Peterson, 1961, for references). The depth is approximately 42 meters at mean low water at this station. Routine hydrographic and biological observations have been made (Schaefer, Bishop and Howard, 1958; Schaefer and Bishop, 1958; Forsbergh, 1963), including the collection of quantitative phytoplankton samples from November 1954 through May 1957 (Smayda, 1959; *unpublished*[3]). The seasonal and regional variations in phytoplankton growth in the Gulf of Panama have also been investigated (Smayda, 1963).

The ecological conditions in the Gulf of Panama have been outlined in an earlier paper (Smayda, 1963). Briefly, a fertile upwelling period occurs from January through April, but occasionally extends into December and May, followed by a relatively unproductive rainy season during the remainder of the year. The average phytoplankton biomass in the upper 20 meters, due primarily to the diatom component, was approximately nine-fold greater during the upwelling season than during the rainy season at 8°45'N, 79°23'W from 1955 to 1957 (Table 1; Smayda, 1959, 1963).

This paper will describe the relationship existing between C^{14} assimilation and the diatom standing crop at 10 meters when the latter is ex-

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[3] Citations to Smayda, *unpublished,* refer to a third paper in this series, A quantitative analysis of the phytoplankton of the Gulf of Panama. III. General ecological conditions, and the phytoplankton dynamics at 8°45'N, 79°23'W from November 1954 to May 1957, which is in preparation.

pressed as cell numbers, cell volume, cell surface area and cell plasma volume. The observations represent 30 experiments (stations) conducted between November 1954 and May 1957 at 8°45′N, 79°23′W (Fig. 1; Appendix Table 1). Forsbergh (1963) has admirably discussed primary production in the Gulf of Panama using the more extensive data available to him. However, his data did not include direct observations of the phytoplankton standing crop.

ACKNOWLEDGEMENTS

The author is deeply indebted to Dr. Milner B. Schaefer, Mr. Izadore Barrett, Mr. William Bayliff, Mr. Eric Forsbergh, Mr. Gerald Howard, Mr. Antonio Landa and Mr. Clifford Peterson of 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. Mr. Forsbergh made available the results of the corrected C^{14} uptake counts. The author is also indebted to Professor Trygve Braarud for providing facilities at the Institute for Marine Biology, Sect. B, Oslo, Norway from 1955 to 1959, and to Mr. Eystein Paasche of that Institute for the many stimulating discussions related to the present effort. Mr. Joel O'Connor kindly advised on and assisted with the statistical analyses. An IBM 1620 computer was employed using the regression program developed by Mr. Richard Cooper of the Narragansett Marine Laboratory.

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

METHODS

Water bottle samples were collected from the surface, 10 and 20 meters, dispensed into 400 ml citrate bottles, preserved with neutralized formalin and shipped to the Institute for Marine Biology, Sect. B, Oslo, Norway. A phytoplankton enumeration was then carried out on 2 ml and 50 ml sedimented sub-samples employing an inverted microscope (Utermöhl, 1931). The *diatom* cell counts were then transformed to estimates of their equivalent cell volume and cell surface area after determining the average cell dimensions for each species, approximating their equivalent geometrical structure and then applying the calculated mean cell volume and cell surface area values to each species. Estimates of cell volume and cell surface area for the entire diatom community were then obtained by summing up the concentration of each species present. A specific weight of 1.0 has been assumed—the units mm^3/L and mg/L are used interchangeably in the text.

It was desirable to obtain a rough estimate of the biomass of the flagellate components of the phytoplankton community (Table 1). Accordingly, all dinoflagellates were assumed to be *Exuviaella baltica,* the domi-

TABLE 1. Mean population density and biomass in the upper 20 meters 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	0.9	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		81,574		5.8:1

BIOMASS (mm^3 per liter)

	Upwelling (A)	% of Total	Rainy (B)	% of Total	A:B
Diatoms	2.1950	96.9	0.2570	98.8	8.5:1
Dinoflagellates	0.0025	0.1	0.0015	0.6	1.7:1
Coccolithophores	0.0008	+	0.0005	0.2	1.8:1
Monads	0.0656	2.8	0.0010	0.4	65:6:1
TOTAL	2.2639		0.2600		8.8:1

nant species encountered, with a volume of 625 μ^3 (derived from a cultured clone), all coccolithophores as the dominant *Coccolithus huxleyi* with a volume of 125 μ^3 (Paasche, 1960), while a standard naked micro-flagellate (monad) of 65 μ^3 (a sphere of 5 μ in diameter) was assumed.

Although dinoflagellates, coccolithophores and micro-flagellates (monads) were usually present in the preserved samples enumerated, diatoms dominated the communities both numerically and, especially, as biomass throughout the year (Smayda, 1959, 1963; *unpublished*). The importance of the diatoms is reflected in their mean contribution of 97 and 99 per cent of the total community as biomass, and 86 and 71 per cent by numerical abundance during the upwelling and rainy seasons, respectively (Table 1). The relative importance of the naked micro-flagellates is undoubtedly underestimated due to the disruption of many cells beyond recognition accompanying preservation. However, the Utermöhl (1931) technique used here nonetheless permits the detection and enumeration of even considerably damaged cells such that the numerical underestimation of micro-flagellates after preservation is not necessarily as severe as commonly believed, although species identification is virtually impossible (see Hasle and Smayda, 1960). It is difficult to state precisely to what extent the micro-flagellate population was underestimated, although scattered observations from other investigations provide some hint. For example, Pratt (1959) found an average micro-flagellate population density of 811 cells per ml in Narragansett Bay over a five-year period based on counting unpreserved samples using the Sedgwick Rafter chamber. Hasle and Smayda (1960), counting preserved samples by the Utermöhl technique,

found a mean micro-flagellate density of 245 cells per ml in the Oslofjord at Drøbak over an annual cycle. While these two areas and methods of enumeration are not directly comparable, there are sufficient similarities in species composition and abundance to suggest that the enumeration of preserved samples by the Utermöhl technique underestimates the actual micro-flagellate population by less than ten-fold.

The solitary occurrence of a large (1950 μ^3) unidentified green flagellate in great abundance (1.7×10^6 c/L) at station 35 during April significantly influenced the mean values presented in Table 1. Excluding this flagellate, the mean monad population density and biomass during the upwelling season would be 23,557 c/L (cells per liter) and 0.0015 mm^3/L, respectively. Both the regional surveys (Smayda, 1963) and the study from November 1954 to May 1957 at the permanent hydro-biological station (Fig. 1; Smayda, *unpublished*) indicate that the micro-flagellate population in the Gulf of Panama is considerably less than that occurring in Narragansett Bay (Smayda, 1957; Pratt, 1959), Danish fjords (Grøntved, 1958), Oslofjord (Hasle and Smayda, 1960) and the Sargasso Sea (Hulburt, Ryther and Guillard, 1960). This sparse monad population, coupled with their small size, suggests that even if the monad population were underestimated by 100-fold the diatom biomass would still significantly exceed that of the monads (Table 1; Appendix Tables 1, 2). Thus, while the apparent overwhelming numerical importance of the diatoms may be partly attributable to the use of preserved samples, especially during the rainy season, their dominance by biomass appears to be real (Table 1).

The non-diatomaceous groups were not included in the C^{14} assimilation—standing crop comparisons. For example, inclusion of the dinoflagellates would require the difficult task of calculating cell volumes and cell surface areas for this very heteromorphic group (107 species and varieties encountered) as well as making highly subjective visual separations between autotrophic and heterotrophic species. The general importance of micro-flagellates in primary production remains largely unknown, although Grøntved (1958) has determined that in some Danish fjords, where he has occasionally encountered more than 4×10^6 c/L in *preserved* samples, this group may account for more than 50 per cent of the total phytoplankton community production at certain times. The micro-flagellates were not included in the C^{14} assimilation—standing crop comparisons because of the great difficulty in distinguishing between autotrophic and heterotrophic cells, a probable deleterious bottle effect on their response during the production experiments (Smayda, 1957), and their minor standing crop importance when based on biomass or cell surface area (Appendix Tables 1, 2). In a study of the population changes occurring during dark and light bottle oxygen production experiments, Smayda (1957), counting unpreserved samples, observed that the micro-flagellates decreased in cell numbers by 10 and 26 per cent per day, on the average, in the light and dark bottles, respectively. An average diatom light bottle increase of 53 per

cent per day and a dark bottle decrease of 1.2 per cent per day occurred. If these results are applicable to the Gulf of Panama experiments, then the diatom response might be expected to exceed significantly that of the micro-flagellates irrespective of their initial population densities. Finally, the diatom biomass usually exceeded that of the micro-flagellates by 100- to 1000-fold at the stations used in the C^{14} assimilation—standing crop comparisons (Appendix Tables 1, 2). Thus with the possible exception of station 35, characterized by the green flagellate population noted above, exclusion of the micro-flagellate standing crop in the C^{14} assimilation—standing crop comparisons when based on biomass and cell surface area (Figs. 4-9) would not appear to be a serious error.

Thus it is felt that the effort required to include the sparser flagellate groups, especially when based on biomass, plasma volume and surface area, in the C^{14} assimilation—standing crop comparisons was not commensurate with their apparent role. The evidence further suggests that the diatoms provide an adequate quantitative index of the total phytoplankton standing crop and fluctuations (Table 1; Appendix Tables 1, 2; Smayda, *unpublished*).

In all, the average cell volume and cell surface area for 110 diatom species and varieties were determined (Table 2). Some species, notably *Ditylum brightwelli, Eucampia cornuta, Guinardia flaccida, Rhizosolenia bergonii, Rhizosolenia stolterfothii,* and *Skeletonema costatum* f. *tropicum* were especially variable in cell size from station-to-station requiring separate estimates of their cell volume and cell surface area at those stations (Table 2). This, coupled with the relative sparsity of some species, accounts for the considerable variation in the number of cells measured for the different species in deriving their mean cell volume and cell surface area (Table 2). It is difficult to assess how representative the mean diatom cell size data presented in Table 2 are in general. Their reliability is influenced by the number of cells measured per species, inherent errors in cell size measurement and, especially, subsequent geometric approximation, and the degree of intra-specific variation in cell size associated with auxospore formation. A few species, as noted above, exhibited considerable intra-specific variation in cell size, the others tending to be less variable. During the present investigation a serious attempt was made to minimize these various sources of error, contributing significantly to the approximately four months required to complete the calculations. Perhaps a guide to the application of the mean cell size data elsewhere would be to consider their reliability as tending to be directly related to the number of cells measured (Table 2), as well as considering the conclusions based on the data presented in Table 4. Lohmann (1908), Bogorov (1959), Paasche (1960), and Vives and Fraga (1961) have also presented data on average cell volume and cell surface area for various plankton algae.

Plasma volume estimates were also made for the diatom community using a slight modification of Lohmann's (1908) procedure, as will be described later.

TABLE 2. Average cell surface area, and cell volume of diatoms collected from the Gulf of Panama.

Species	Number of cells measured	Surface area (μ^2)	Cell volume (μ^3)	A/V (μ^2/μ^3)
Actinoptychus undulatus f. *catenata*	1	2,286	7,960	0.29
Asterionella japonica	5	689	603	1.14
Asteromphalus flabellatus	2	4,461	20,134	0.22
Bacteriastrum delicatulum	5	551	797	0.69
Bacteriastrum elegans	118	1,409	4,017	0.35
Bacteriastrum hyalinum (including var. *princeps*)	147	1,903	6,293	0.30
Bacteriastrum varians	15	1,067	2,471	0.43
Biddulphia alternans	2	3,203	9,717	0.33
Biddulphia dubia	1	3,997	9,185	0.44
Biddulphia mobiliensis	6	2,772	10,990	0.25
Biddulphia sinensis	27	55,820	937,500	0.06
Brenneckella sp.	3	1,522	4,045	0.38
Cerataulina bergonii	48	3,882	17,173	0.23
Cerataulina compacta	3	9,435	46,809	0.20
Chaetoceros affinis	122	936	2,102	0.45
Chaetoceros anastomosans	7	470	722	0.65
Chaetoceros apendiculatus	10	888	1,923	0.46
Chaetoceros atlantidae	18	1,417	3,825	0.37
Chaetoceros brevis	40	1,220	3,242	0.38
Chaetoceros coarctatus	10	3,426	15,015	0.23
Chaetoceros compressus	261	618	1,165	0.53
Chaetoceros constrictus	49	1,732	5,195	0.33
Chaetoceros costatus	92	517	870	0.59
Chaetoceros curvisetus	151	804	1,682	0.48
Chaetoceros debilis	9	696	1,290	0.54
Chaetoceros decipiens	97	983	2,035	0.48
Chaetoceros didymus includes var. *anglica* includes var. *protuberans*	80	1,123	1,639	0.69
Chaetoceros diversus	17	403	594	0.68
Chaetoceros laciniosus	126	1,051	2,454	0.42
Chaetoceros laevis	35	267	332	0.80
Chaetoceros lauderi	2	3,719	16,611	0.22
Chaetoceros lorenzianus	171	1,373	3,609	0.38
Chaetoceros pendulus	1	1,708	5,331	0.32
Chaetoceros peruvianus	3	1,332	3,647	0.37
Chaetoceros rostratus	13	1,980	6,693	0.30
Chaetoceros socialis	34	254	305	0.83
Chaetoceros subsecundus	21	798	1,525	0.52
Chaetoceros teres	3	3,956	19,076	0.21
Chaetoceros van heurckii	30	1,800	5,255	0.34
Climacodium frauenfeldianum	5	4,700	6,873	0.68
Corethron hystrix	10	4,720	20,175	0.23
Corethron pelagicus	8	11,407	87,058	0.13
Coscinodiscus concinnus	23	6,154	36,424	0.17
Coscinodiscus excentricus	20	2,418	8,308	0.29
Cyclotella caspia	6	1,110	2,790	0.40
Cyclotella striata	7	2,204	7,153	0.31
Dactyliosolen mediterraneus	9	779	1,357	0.57
Ditylum brightwelli	67	37,100	520,900	0.07
Range—min.		33,200	500,000	0.07
Range—max.		40,600	602,700	0.07
Ditylum sol	2	55,540	792,500	0.07
Eucampia cornuta	117	1,871	5,181	0.37
Range—min.		1,024	2,396	0.42
Range—max.		3,555	11,061	0.32
Eucampia zoodiacus	7	1,957	5,388	0.36
Guinardia flaccida	159	11,600	78,400	0.15

TABLE 2. (Continued)

Species	Number of cells measured	Surface area (μ^2)	Cell volume (μ^3)	A/V (μ^2/μ^3)
Range—min.		5,800	24,600	0.24
Range—max.		14,700	127,700	0.12
Hemiaulus hauckii	6	720	1,187	0.61
Hemiaulus membranaceus	16	4,035	10,566	0.38
Hemiaulus sinensis	25	1,639	4,331	0.38
Lauderia annulata	154	4,508	23,107	0.20
Range—min.		4,052	19,806	0.20
Range—max.		4,784	23,991	0.20
Leptocylindrus danicus	41	1,070	1,840	0.58
Leptocylindrus maximus	27	14,177	95,731	0.15
Leptocylindrus minimus	2	416	326	1.28
Lithodesmium undulatum	9	7,639	37,397	0.20
Nitzschia closterium	7	215	121	1.78
Nitzschia delicatissima	29	273	130	2.10
Range—min.		160	51	3.14
Nitzschia kolaizeckii	1	1,344	1,963	0.68
Nitzschia longissima	3	851	511	1.66
Nitzschia pacifica	27	695	662	1.05
Nitzschia pacifica + *pungens* (intergrade)	51	843	763	1.11
Nitzschia pungens var. *atlanticus*	25	990	863	1.15
Nitzschia seriata	51	843	763	1.11
Planktoniella sol	3	1,529	4,454	0.34
Rhizosolenia acuminata	5	105,000	11,740,000	0.01
Rhizosolenia alata var. *genuina*	182	20,110	65,160	0.31
Rhizosolenia alata genuina + *indica* intergrade	9	15,580	48,940	0.32
Rhizosolenia alata var. *indica*	69	25,700	139,000	0.18
Rhizosolenia bergonii	21	26,340	144,200	0.18
Range—min.		8,720	26,240	0.33
Range—max.		30,300	179,200	0.17
Rhizosolenia calcar avis	83	42,120	261,600	0.16
Rhizosolenia delicatula	98	1,257	2,670	0.47
Rhizosolenia fragilissima	38	1,960	4,040	0.49
Rhizosolenia imbricata var. *shrubsolei*	58	15,700	62,000	0.25
Rhizosolenia setigera	59	7,800	23,000	0.34
Rhizosolenia stolterfothii	955	4,500	14,500	0.31
Range—min.		1,500	3,000	0.50
Range—max.		6,000	28,000	0.21
Rhizosolenia styliformis var. *latissima*	1	173,000	4,376,000	0.04
Rhizosolenia styliformis var. *longispina*	37	18,500	57,700	0.32
Schroederella delicatula	10	2,400	7,100	0.34
Skeletonema costatum f. *tropicum*	1391	560	1,000	0.56
Range—min.		320	430	0.74
Range—max.		680	1,300	0.52
Stephanopyxis palmeriana	2	11,900	99,000	0.12
Stephanopyxis turris	26	8,300	54,000	0.15
Thalassionema nitzschioides	119	460	460	1.00
Thalassiosira aestivalis	5	430	620	0.69
Thalassiosira subtilis	3	1,600	4,800	0.33
Thalassiothrix frauenfeldii	84	2,179	2,969	0.73
Thalassiothrix mediterranea var. *pacifica*	17	11,000	10,000	1.10

TABLE 2. (Continued)
Diatoms for which cell area and volume estimations not made, and their "equivalent" species in size used in the calculations

Species—no estimation made	"Equivalent" species used
Asteromphalus heptactis	*Asteromphalus flabellatus*
Bacteriastrum mediterraneus	*Bacteriastrum elegans*
Chaetoceros aequatorialis	*Chaetoceros peruvianus*
Chaetoceros atlanticus	*Chaetoceros laevis*
var. *audax*	*Chaetoceros laevis*
var. *neapolitana*	*Chaetoceros laevis*
var. *skeleton*	*Chaetoceros laevis*
Chaetoceros dadayi	*Chaetoceros costatus*
Chaetoceros densus	*Chaetoceros rostratus*
Chaetoceros holsaticus	*Chaetoceros laciniosus*
Chaetoceros subtilis	*Chaetoceros apendiculatus*
Chaetoceros tetrastichon	*Chaetoceros rostratus*
Coscinodiscus auguste-lineatus	*Coscinodiscus excentricus*
Coscinodiscus lineatus	*Coscinodiscus excentricus*
Coscinodiscus marginatus	*Coscinodiscus excentricus*
Coscinodiscus stellaris	*Coscinodiscus excentricus*
Coscinodiscus rothii	*Coscinodiscus concinnus*
Coscinodiscus thorii	*Coscinodiscus concinnus*
Thalassiothrix delicatula	*Thalassiothrix mediterranea*

Forsbergh (1963) has described in detail the methodology of the C^{14} experiments conducted in the Gulf of Panama which will only be summarized here. Water samples were collected from 10 meters with a Van Dorn sampler at approximately 0830 hours, placed in 250 ml citrate bottles, kept in the dark for one-and-a-half to two hours until the vessel arrived at the "productivity buoy" located off Taboga Island approximately 16 km northwest of the collection site (Fig. 1). The production bottle was then inoculated with radio-carbon and lowered to 10 meters where it remained suspended from the buoy *in situ* for 24 hours, starting at about 1000 hours. At the termination of the experiment, the sample was filtered under suction through an HA Millipore filter (pore diameter of 0.45 μ), washed with surface sea water, vacuum desiccated and counted. No corrections were made for either dark fixation or isotope effect.

Pyrheliometric measurements of the total daily radiation were made at Curundu, near Balboa (Fig. 1), located about 30 km from the production station. These data were obtained by the Inter-American Tropical Tuna Commission from the U. S. Weather Bureau. The radiation measurements were made from 0700 to 1800 hours, and are expressed as langlies per day (ly/day), where 1 langley equals 1 g cal. per cm^2 (Strickland, 1958).

Water transparency was measured with a Secchi Disc at the *collection site*. The extinction coefficient (k) was calculated from Poole and Atkin's (1929) formula: 1.7/D, where D equals the Secchi Disc disappearance depth in meters. Following Forsbergh's (1963) procedure, the transmission per meter in relation to unity (T) is derived from e^{-k}, and the light intensities at the ten meter depth (I_{10}) of the C^{14} experiments are obtained from the

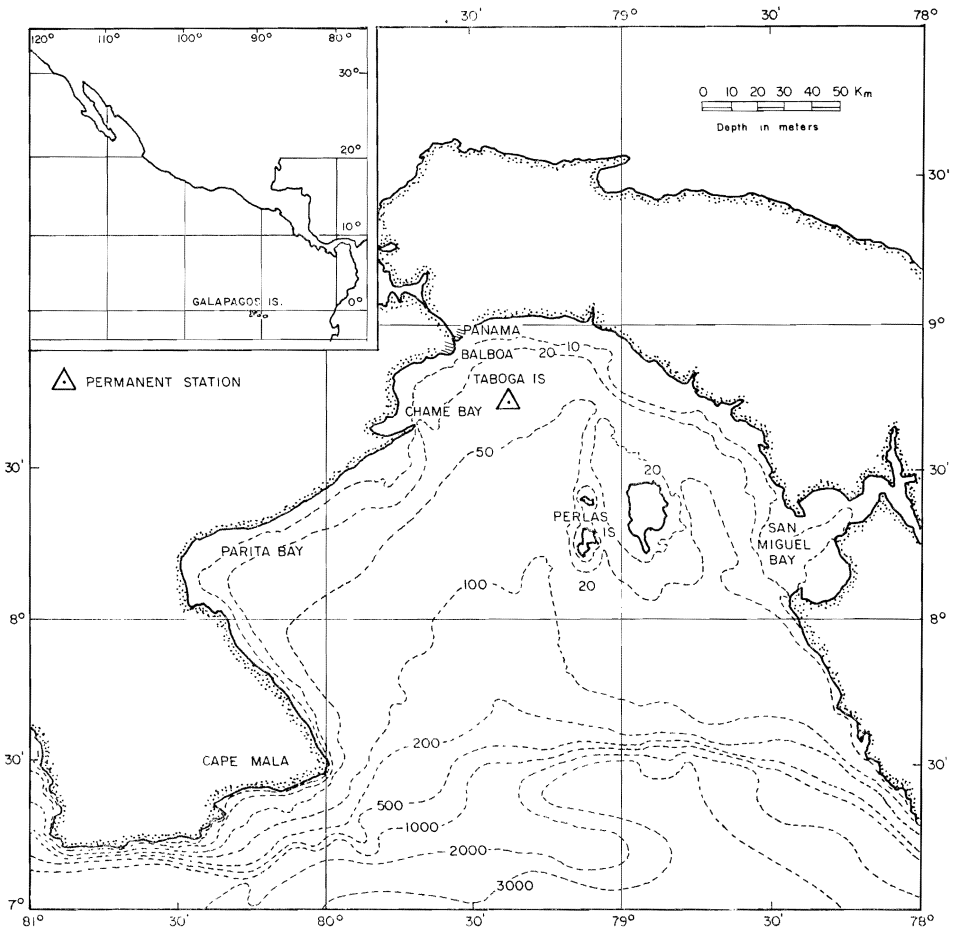

FIGURE 1. Principal features of the Gulf of Panama, including locations of the hydro-biological station maintained by the Inter-American Tropical Tuna Commission, and Taboga Island near which C^{14} experiments were incubated *in situ* for 24 hours.

total incident radiation (I_0) and from the transmission (T) values by the equation:

$$I_{10} = I_0 \times T^{-10} \qquad (1)$$

These radiation data have been applied to the *in situ* incubation station where no Secchi Disc measurements are available for the sampling dates under consideration.

Calculations of log-log linear regressions by the least squares method were made in the assessment of C^{14} assimilation as a function of the diatom standing crop present at ten meters with an IBM 1620 computer.

MICROSCOPICALLY DERIVED ESTIMATIONS OF THE PHYTOPLANKTON STANDING CROP

Although carbon fixation is a measurable attribute of a phytoplankton community, the relationship between size and composition of the standing crop and the rate and magnitude of its organic production is not firmly established. While one generally anticipates that greater, more active standing crops characterize regions and periods of high productivity, as contrasted to less productive situations, it is usually difficult to infer the amount of plant tissue (standing crop) present from the magnitude of its production, or *vice versa.* In part, this reflects several inadequacies in our knowledge and methodology, including those associated with measurements of the standing crop. In addition to standing crop indices based on proximate, gravimetric or pigment analyses, there are four other estimates of the standing crop of a given phytoplankton species or community which are derivable from quantitative microscopic examination—numerical abundance; cell volume; cell surface area; and plasma volume.

Numerical abundance as an expression of standing crop

Enumeration of phytoplankton abundance provides an important and, frequently, indispensable measure of the success, growth and stage of succession, *inter alia,* of a species or community. The importance of such analyses in biological oceanography is well established and need not be justified here. However, it is generally appreciated that a numerical census is of limited value as a measure of the standing crop when considered from the standpoint of production or food chain dynamics. This is attributable, in part, to the considerable inter- and intra-specific variation in cell size characteristics of the phytoplankton (Harvey, 1950). In the Gulf of Panama, for example, the diatom cell volume ranged from 51 μ^3 in *Nitzschia delicatissima* to 11,740,000 μ^3 in *Rhizosolenia acuminata* (Table 2); that is, 230,000 *Nitzschia* cells equalled one *Rhizosolenia* cell in volume.

As Paasche (1960) has pointed out, the use of numerical abundance as a measure of the standing crop also tends to be biased towards the smaller, usually more numerous species in the community thereby underestimating the role of the larger, usually less numerous, species. As an example, of the 300,500 diatom cells per liter representing 28 species observed at station 35 (Smayda, *unpublished*), *Rhizosolenia stolterfothii* accounted for 58 per cent of the population density. Thus, the presumed comparison between the total community numerical abundance and a physiological response such as C^{14} assimilation at this station primarily related the abundance of *Rhizosolenia stolterfothii* to the observed community metabolism. The bias towards smaller cells in such comparisons may be tempered somewhat, however, by the fact that such cells are usually more active metabolically than larger species (Braarud, 1945; Munk and Riley, 1952; Verduin, 1952; Margalef, Durán and Saiz, 1955; Margalef, 1958).

The shortcomings of applying cell count data to certain problems of community dynamics can be frequently remedied by converting such data to their equivalent biomass. The contribution of a given species to community dynamics is clearly influenced by its tissue volume (Margalef, 1958; Rodhe, Vollenweider and Nauwerck, 1958; Paasche, 1960).

Cell volume (μ^3) as an expression of standing crop

Determination of cell tissue volume provides a measure of the "fresh wet weight" or biomass of the phytoplankton and, indirectly, a rough estimate of its potential respiratory demands. The conversion of cell counts to their equivalent cell volumes, however, tends to favor the giant cells over the smaller ones in any subsequent comparisons between the standing crop and a given physiological response, i.e. the converse of that characterizing the cell counts (Paasche, 1960). This is readily demonstrated by the following observation from 10 meters at station 43 (Smayda, *unpublished*). At this station, *Rhizosolenia acuminata* (11,740,000 μ^3) accounted for only 80 cells of the total diatom population of 145,280 cells per liter. However, the wet weight of *Rhizosolenia acuminata* (0.94 mm^3 per liter) comprised approximately 60 per cent of the total diatom biomass of 1.59 mg per liter.

Although biomass estimates are directly applicable to food chain analyses, there is adequate reason to believe that tissue volume by itself does not provide a completely satisfactory estimate of the role of a given species in community dynamics, or the community itself. Many of the larger diatoms contain large vacuoles filled with relatively non-nutritious cell sap, as demonstrated by *Lauderia annulata* (Fig. 2). Such diatoms might be termed "watery" species. In addition, inter- and intra-specific variations in food value (Parsons, Stephens and Strickland, 1961) and respiratory rate (Ryther and Guillard, 1962) occur.

Cell surface area (μ^2) as an expression of standing crop

As for any given cell, a phytoplankton community can be viewed as having a composite surface area. Viewed ecologically, the cell or community surface area is important in that it a). represents the assimilative area (μ^2) through which nutrients must diffuse to meet the physiological demands of the biomass (μ^3), and b). represents the area available for chloroplasts, i.e. the "photosynthetic surface". Significantly, in his outstanding study on the relationship between primary production and standing crop in the Norwegian Sea, Paasche (1960) established that the community cell surface area tended to provide a better measure of phytoplankton standing crop than either cell numbers or tissue volume (biomass). He was unable, however, with the data available, "to produce conclusive statistical evidence that cell surface area is the most adequate measure of standing stock of primary producers."

It is also apparent that a community, as any given cell, can be envisaged as having a cell surface area-to-cell volume characteristic, μ^2/μ^3, based on the composite surface area and cell volume of the individual cells (species) comprising the community. (This characteristic will also be referred to as the A/V or surface/volume ratio in the text to follow). It is pertinent that the rate of cell division of both cultured and naturally occurring phytoplankton species has been observed, in general, to be directly related to their surface/volume characteristic, i.e. smaller species tend to divide faster than larger species (Braarud, 1945; Margalef *et al.,* 1955). Furthermore, respiration (Verduin, 1952) and, on theoretical grounds, nutrient assimilation (Munk and Riley, 1952) have also been reported to be related to the A/V characteristic of phytoplankton cells. Thus, there is ample evidence suggesting that in comparisons between standing crop and a given physiological response the A/V characteristic of the former should be included.

Plasma volume (μ^3) as an expression of standing crop

An estimate of cell volume employed in the determination of biomass includes both the tissue and cell sap contents of the cell. However, Lohmann (1908) long ago communicated that the total cell volume, μ^3, is frequently inadequate as a biomass estimate because of the large quantities of relatively non-nutritious cell sap present in vacuoles. This is especially characteristic of the larger diatoms, as demonstrated here by *Lauderia annulata* (Fig. 2). A thin cytoplasmic layer (pls.), in which the chloroplasts (chl.) are embedded, is observed to line the inner cell wall (cw.) and then continue near the middle of the cell along the pervalvar axis as a protoplasmic bridge (prot. br.) which contains the nucleus (Fig. 2). The bulk of the cell volume comprises the two large vacuoles (vac.) detectable to either side of the protoplasmic bridge. Thus, *Lauderia annulata* might be termed a "watery" species.

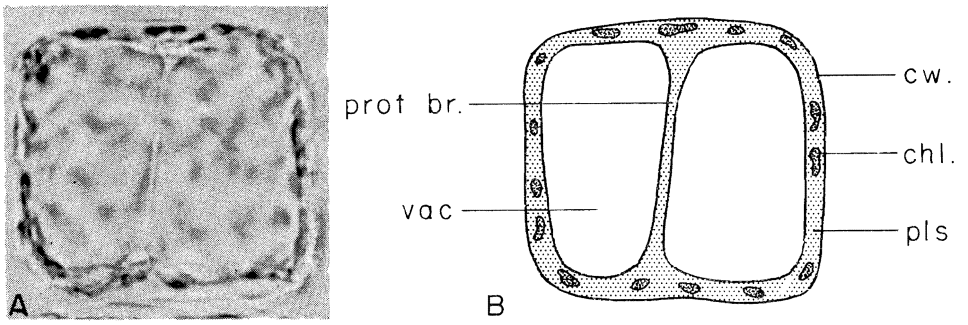

FIGURE 2. **A.** Photomicrograph of the major cytological features of the diatom *Lauderia annulata* Cleve, diameter approximately 30 μ.
B. Schematic presentation, girdle view; cell wall (cw.), cytoplasmic layer (pls.), chloroplast (chl.), protoplasmic bridge (prot. br.), vacuole (vac.).

TABLE 3. Suggested cytoplasmic thickness, in μ, to be used in the calculation of plasma volume (PV) at different surface-to-volume ratios in diatoms.

Surface/Volume (A/V)	Cytoplasmic layer thickness, μ
> 0.90	PV = total volume
0.51 — 0.89	1.0
0.35 — 0.50	1.5
< 0.35	2.0

Lohmann (1908) attempted to correct for such vacuoles by calculating the cell *plasma volume* (PV) which is essentially a measure of total cell volume minus vacuoles. There are three major internal structural elements involved in such calculations: the cytoplasmic layer, the protoplasmic bridge, and the vacuoles (Fig. 2). Lohmann determined that the thin parietal cytoplasmic layer in diatoms (using *Coscinodiscus* and *Rhizosolenia*) was 1 - 2μ thick depending on cell size. A rough estimate of the volume of the protoplasmic bridge, "Kernmantel", is obtained by approximating it to a sphere and then applying the proper mensuration formula. The vacuolar cell sap obviously possesses some nutritional value which Lohmann arbitrarily stated is equivalent to 10 per cent of the volume occupied by the cytoplasmic tissue. Thus, the plasma volume (PV) is estimated by calculating the product of the surface area in μ^2 and parietal cytoplasmic layer thickness (1 - 2 μ), to which is added the volume of the protoplasmic bridge (Fig. 2) assuming it to be a sphere, and then adding 10 per cent of their sum to account for the nutritious portion of the vacuolar cell sap:

$$PV = 1.10\ [\text{(surface area, } \mu^2)\ (1 - 2\ \mu) + \text{(volume of prot. br., } \mu^3)\ ] \quad (2)$$

It has been found that this estimate of the plasma volume can be simplified without serious error as follows:

$$PV = \text{(surface area, } \mu^2)\ (1 - 2\ \mu) + (0.10)\ \text{(Total cell volume, } \mu^3) \quad (3)$$

For example, the plasma volume of *Lauderia annulata* (Fig. 2), assuming a parietal layer thickness of 2 μ, having a volume of 23,000 μ^3 and a surface area of 4,500 μ^2 (Table 2) is: (4,500 μ^2) (2 μ) + (0.10) (23,000 μ^3), or 11,300 μ^3—approximately one-half of the total cell volume.

The actual value used for the parietal layer thickness is subjective, although probably within the limits observed by Lohmann, at least for the larger species. If plasma volume estimations are to be made for species whose surface-to-volume ratio is near unity, then a cytoplasmic layer thickness not exceeding 1 μ must be assumed. Otherwise, plasma volumes greater than the stereometrically calculated volumes will be obtained. For all practical purposes, however, the plasma volume equals the total cell volume in those species having a surface-to-volume ratio of 0.90 or greater. Suggested cytoplasmic layer thickness values to be used for various surface-to-volume ratios are presented in Table 3.

TABLE 4. Variations in cell volume (V), surface area (A) and plasma volume (PV) in diatoms of different size groups.

	Cell volume (μ^3)	Surface area (μ^2)	PV μ^3	Max.V / Min.V	Max.PV / Min.PV	Max.A / Min.A	A/V	A/PV	V/A	PV/A
Guinardia flaccida				5:1	3:1	2.5:1				
Min.	24,600	5,800	14,060				0.23	0.41	4.2	2.4
Max.	127,700	14,700	42,170				0.12	0.35	8.7	2.9
Mean	78,400	11,600	31,040				0.15	0.37	6.8	2.7
Rhizosolenia bergonii				12:1	6:1	5.1:1				
Min.	26,200	8,700	20,020				0.33	0.43	3.0	2.3
Max.	318,000	44,000	120,000				0.14	0.37	7.2	2.7
Mean	144,000	26,300	67,000				0.18	0.39	5.5	2.5
Rhizosolenia stolterfothii				9:1	4.5:1	3.9:1				
Min.	3,000	1,500	2,550				0.50	0.59	2.0	1.7
Max.	28,000	5,800	11,500				0.21	0.50	4.8	2.0
Mean	14,500	4,500	8,225				0.31	0.55	3.2	1.8
Skeletonema costatum f. *tropicum*				3:1	2.2:1	2.1:1				
Min.	430	320	363				0.74	0.90	1.3	1.1
Max.	1,300	680	810				0.52	0.84	1.9	1.2
Mean	1,000	560	660				0.56	0.85	1.8	1.2
Difference between maximum and minimum mean values:										
	144-fold	47-	102-	4-	3-	2.4-	3.7-	2.3-	3.8-	2.2-

The estimation of plasma volume is certainly based on somewhat arbitrary assumptions. However, it would appear to provide a more accurate estimate of "metabolically active" plant tissue than total cell volume, at least for the larger species. (The modified plasma volume calculation, as used here, does not entail much additional work after calculating cell volume.) Paasche's (1960) observations suggesting that the cell surface area is the most adequate measure of the phytoplankton standing crop compared to cell numbers or volume strengthens this opinion. For, as Paasche was aware, the cell surface area provides a fairly good estimate of the plasma volume inasmuch as the latter is primarily a function of the surface area [see equation (2)], as is also evident cytologically (Fig. 2). In fact, *surface area and plasma volume estimates of standing crop size would appear to be interchangeable, either estimate providing a measure of the assimilative and photosynthetic surfaces as well as metabolically active tissue.* On theoretical grounds, therefore, these would appear to be the best of the microscopically derived standing crop estimates.

Plasma volume estimations of diatoms from representative size groups presented in Table 4 demonstrate:

1. *Inter- and intra-specific differences and variations in cell size* (Harvey, 1950; Table 2) *are considerably less when based on plasma volume than on total cell volume.* For example, approximately 27,100 cells of *Nitzschia delicatissima* (51 μ^3) equal one *Rhizosolenia acuminata* cell (1,389,000 μ^3) when based on plasma volume, as contrasted to 230,000 cells when total cell volumes are compared (Table 2).

2. *Inter-specific differences in cell size are least pronounced when based on surface area.* There is only a 47-fold difference in mean surface area of *Skeletonema costatum* f. *tropicum* and *Rhizosolenia bergonii,* the extreme species compared in Table 4, as contrasted to a 102- and 144-fold difference in mean plasma volume and mean cell volume, respectively.

3. *The cell surface area is the least variable of the intra-specific characteristics.*

4. *Intra-specific variations in surface/volume ratio are relatively minor over the entire range in cell size when based on plasma volume, unlike for that on total cell volume.*

5. *Inter-specific differences in surface/volume ratio are less pronounced when based on plasma volume than on total cell volume.*

The ecological significance of these observations will be elaborated upon in a later section.

C^{14} ASSIMILATION AS RELATED TO DIATOM STANDING CROP

In the following section C^{14} assimilation has been related to the diatom standing crop when expressed as cell numbers, cell volume, cell surface area, and plasma volume.

C^{14} assimilation as a function of diatom cell abundance

A direct comparison between phytoplankton standing crop expressed as cell numbers and C^{14} uptake, or any physiological activity, carries the assumption that all cells are of equal importance with respect to average activity per cell, irrespective of their species or size. However, it has been previously shown that comparisons using cell numbers are biased in favor of the smaller, usually most numerous species in the community (Paasche, 1960). Also, reports that physiological responses of phytoplankton cells are related to their area-to-volume characteristics (Braarud, 1945; Munk and Riley, 1952; Verduin, 1952; Margalef *et al.,* 1955; Margalef, 1958) suggest an additional complication in comparing numerical abundance against carbon assimilation. For these reasons, C^{14} uptake (Fig. 3; Table 6) has been compared to both the enumerated diatom abundance as well as to A/V-weighted and V/A-weighted diatom abundance derived as follows:

$$\sum_{i=1}^{m} \frac{A_i}{V_i} N_i = \frac{A_1}{V_1} N_1 + \frac{A_2}{V_2} N_2 + \ldots + \frac{A_m}{V_m} N_m \qquad (4)$$

$$\sum_{i=1}^{m} \frac{V_i}{A_i} N_i = \frac{V_1}{A_1} N_1 + \frac{V_2}{A_2} N_2 + \ldots + \frac{V_m}{A_m} N_m \qquad (5)$$

where m represents the total number of diatom species, i represents species i ($i = 1, 2, \ldots, m$), and N_i represents the number of individuals

TABLE 5. Illustration of procedure used to calculate modified diatom abundance using species A/V and V/A ratios.

Species (i)	A_i/V_i	N_i	$\frac{A_i}{V_i} N_i$	$\frac{V_i}{A_i} N_i$
1	1.0	1,000	1,000	1,000
2	0.5	1,000	500	2,000
3	0.1	1,000	100	10,000
$\sum_{i=1}^{m} N_i$		3,000		
$\sum_{i=1}^{m} \frac{A_i}{V_i} N_i$			1,600	
$\sum_{i=1}^{m} \frac{V_i}{A_i} N_i$				13,000

of species *i*. The recorded number of cells of each species (N_i) was weighted by its surface-to-volume (A_i/V_i) ratio (Table 2) in equation (4) and by its volume-to-area (V_i/A_i) ratio in equation (5), the individual weightings were then summed to obtain the A/V-weighted and V/A-weighted diatom community estimates. The procedure is demonstrated in Table 5.

It is seen that the unmodified cell abundance attributes equal importance to all species irrespective of size; the A/V-weighted diatom abundance estimate favors the smaller species, whereas the V/A-weighted modification favors the larger species (Table 5).

A direct relationship exists between C^{14} assimilation and the various estimates of diatom abundance, the regressions accounting for 40 to 45

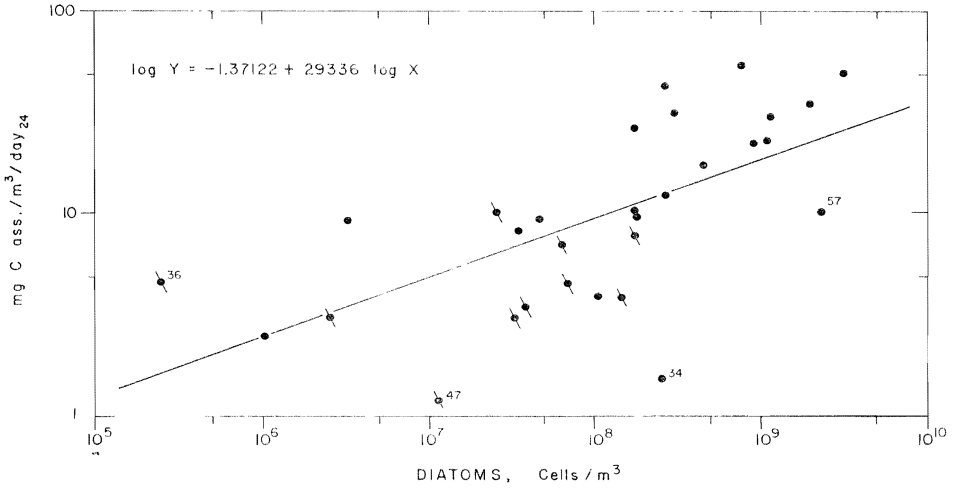

FIGURE 3. The relationship between C^{14} assimilation and diatom cell number. Significance of the numbered stations explained in the text. Symbol ◥ represents a rainy season station.

TABLE 6. Regression equations, C^{14} assimilation as a function of diatom standing crop.

Y = mg carbon assimilated per m^3 per day

X =	Regression equation	% Variation explained by regression	Probability	Standard error of estimate	D.F.
Cells per m^3 $(\sum_{i=1}^{m} N_i)$	$\log Y = -1.37122 + 0.29336 \log X$	42	0.001	0.064	28
$\sum_{i=1}^{m} \frac{A_i}{V_i} N_i$	$\log Y = -1.85591 + 0.35741 \log X$	45	0.001	0.062	28
$\sum_{i=1}^{m} \frac{V_i}{A_i} N_i$	$\log Y = -1.57111 + 0.30500 \log X$	40	0.001	0.065	28
Biomass, mg per m^3	$\log Y = 0.27792 + 0.26960 \log X$	36	0.001	0.068	28
Surface area, cm^2 per m^3	$\log Y = 0.03160 + 0.30103 \log X$	42	0.001	0.066	28
Plasma volume, mg per m^3	$\log Y = 0.26008 + 0.29871 \log X$	41	0.001	0.067	28

per cent of the variation (Fig. 3; Table 6). Interestingly, the regression on A/V-weighted diatom abundance provided the best fit with 45 per cent of the variation being explainable, whereas the V/A-weighted diatom abundance gave the poorest regression (Table 6). These slight differences must be considered as trends only inasmuch as they are probably not statistically significant because of the limited number of observations available.

C^{14} assimilation as a function of diatom cell volume (biomass), surface area and plasma volume

Regressions of C^{14} uptake on surface area and plasma volume did not differ significantly from those based on cell numbers (Figs. 3-5; Table 6). The regression on cell volume (biomass), however, explained only 36 per

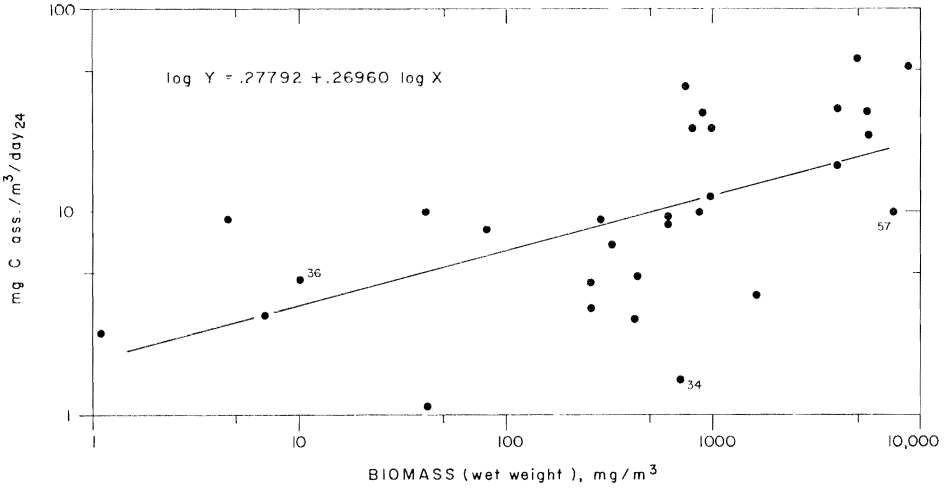

FIGURE 4. The relationship between C^{14} assimilation and diatom total biomass.

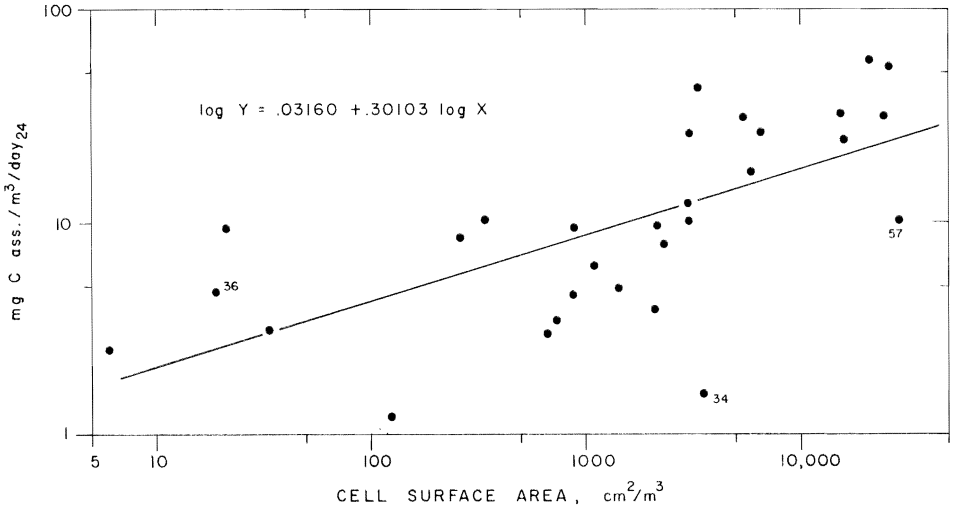

FIGURE 5. The relationship between C^{14} assimilation and diatom cell surface area.

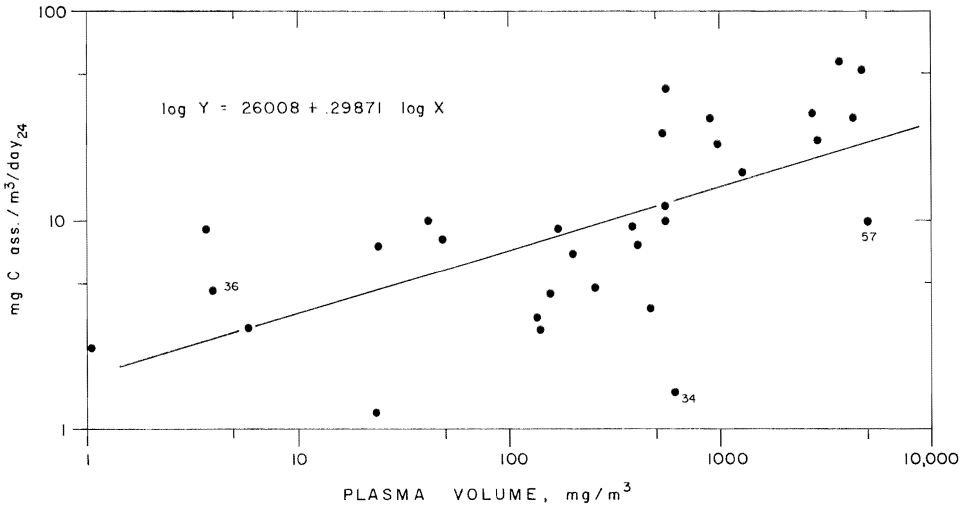

FIGURE 6. The relationship between C^{14} assimilation and diatom plasma volume.

cent of the variation suggesting that of the standing crop indices used, C^{14} assimilation is least related to biomass. It is recalled that the larger cells are favored in the estimation of standing crop based on cell volume or V/A-weighted diatom abundance (Table 5).

Relationship between C^{14} assimilation and diatom standing crop, omitting certain stations

Although it is apparent that C^{14} uptake is related to the standing crop (Figs. 3-6; Table 6), the regressions exhibit considerable scatter. The re-

gressions include the 30 stations for which both C^{14} assimilation and cell count data are available (Appendix Table 1). However, the inclusion of certain stations in the analysis warrants closer examination.

The lowest diatom population occurred at station 36 where only 240 pigmented cells per liter (c/L) were found based on the 52 ml sub-sample examined microscopically, i.e. five-fold less than the next lowest population density at station 59 (Fig. 3; Appendix Table 1). Considerably greater errors of population estimates relative to those at the other more populous stations can be expected in enumerating such low sub-sample volumes at times of great phytoplankton paucity (Hasle, 1959; Lund, Kipling and LeCren, 1958). More important, the station 36 sample was also heavily contaminated with active bacteria which probably caused a more significant source of error. In addition to the 240 pigmented cells per liter present, 2,450 c/L of chlorotic and empty diatoms were also observed. It is unknown to what extent the condition of these cells was attributable to bacterial decomposition after "preservation". Additionally, 3,500 c/L of an unidentified organism intermediate in habitus between *Fragilaria nana* and the bacterial contaminants were observed. Since there is considerable uncertainty as to the exact diatom population at this station (it might have been 6,200 c/L), it seems justifiable, therefore, to withhold station 36 from subsequent regression analyses.

Stations 34, 47 and 57 are characterized by rather low rates of carbon assimilation despite the presence of large standing crops (Fig. 3; Appendix Table 1). There is no floristic evidence to suggest that the response at station 47 is an artifact, however. A very dense population of the small, thinly silicified *Chaetoceros socialis* occurred at station 34 preventing enumeration other than to designate it as being AA (very abundant). Thus the discrepancy at station 34 is even greater than depicted (Figs. 3-6). If only because of the significant underestimation of the diatom standing crop at this station, it seems justifiable to exclude it from subsequent regression analyses.

The response at station 57 is an enigma. Intense growth produced the maximum diatom population observed during the investigation, approximately 4.6×10^6 c/L at the surface (Smayda, *unpublished*); 2.3×10^6 c/L were recorded at 10 meters (Appendix Table 1). Yet, although the diatom population at station 57 was 2.5- to 3-fold greater than that at stations 56 and 58, its measured C^{14} uptake rate was approximately 60 per cent lower (Appendix Table 1). Furthermore, significantly higher rates of C^{14} assimilation were obtained at stations 54 and 55 where the diatom populations approximated that at station 57.

The deviant diatom - carbon assimilation responses at stations 34 (in addition to the standing crop underestimation) and 57 might be attributable to either experimental error or the presence of senescent populations.

TABLE 7. Regression equations, C^{14} assimilation as a function of diatom standing crop (omitting stations 34, 36 and 57).

Y = mg carbon assimilated per m^3 per day

X =	Regression equation	% Variation explained by regression	Probability	Standard error of estimate	D.F.
Cells per m^3 $(\sum_{i=1}^{m} N_i)$	$\log Y = -2.17698 + 0.39733 \log X$	61	0.001	0.055	25
$\sum_{i=1}^{m} \frac{A_i}{V_i} N_i$	$\log Y = -2.18433 + 0.40677 \log X$	63	0.001	0.053	25
$\sum_{i=1}^{m} \frac{V_i}{A_i} N_i$	$\log Y = -2.31005 + 0.39696 \log X$	56	0.001	0.058	25
Biomass, mg per m^3	$\log Y = 0.23203 + 0.30236 \log X$	44	0.001	0.065	25
Surface area, cm^2 per m^3	$\log Y = -0.11259 + 0.35905 \log X$	56	0.001	0.058	25
Plasma volume, mg per m^3	$\log Y = 0.16823 + 0.35283 \log X$	54	0.001	0.059	25

The occurrence of large, relatively unproductive phytoplankton standing crops has been recorded from nature (Ryther *et al.,* 1958). However, the communities present at stations 34 and 57, where intense upwelling was occurring, were robust and well-pigmented, being dominated by *Nitzschia delicatissima* + *Rhizosolenia stolterfothii* + *Chaetoceros socialis,* and *Eucampia cornuta,* respectively. Their appearance contrasted sharply with the well-defined empty or chlorotic condition of senescent cells so common in tropical phytoplankton communities (Allen, 1939; Osorio Tafall, 1943; Occhipinti, Magliocca and Teixeira, 1961; Smayda, *unpublished*). Indeed, the persistent abundance of senescent cells, estimates of which were facilitated by their ease of recognition and enumeration, suggests a minimum natural daily mortality rate of 10 to 15 per cent of the Gulf of Panama standing crop (Smayda, *unpublished*). The diatom communities at stations 34 and 57, therefore, do not appear to have been senescent. Thus, there is reason to believe that the anomalous diatom - carbon assimilation responses at stations 34, in part, and 57 were significantly influenced by experimental error in the carbon uptake estimates. These stations, as well as station 36 for the reasons outlined above, are therefore omitted in the subsequent regression analyses (Table 7). These stations are identified in Figures 4-9.

Substantial improvement in the regressions of carbon assimilation on the various standing crop estimates results. From 44 to 63 per cent of the variation can now be accounted for by the regressions, representing a 10 to 19 per cent improvement over that when all 30 observations are included (Tables 6, 7). The continued significantly poorer regression on biomass (only 44 per cent of the variation explainable) is noteworthy, suggesting again that of the standing crop estimates used carbon assimilation is *least* related to wet weight (biomass). This is also partly reflected in the regression on V/A-weighted abundance (Table 7). On the other hand, 61 per cent of the variation could be explained by the regression on unmodified diatom abundance. This contrasts with Paasche's (1960) observations

in the Norwegian Sea which suggested that cell number was less related to phytoplankton "production capacity" than either cell volume or cell surface area. The continued good correspondence between carbon uptake and A/V-weighted diatom abundance is notable (Table 7).

There is probably no good reason to expect a positive relationship between C^{14} uptake and any index of cell abundance. That fair relationships were obtained (Tables 6, 7; Figs. 3-6), might be interpreted as indicating only that the communities were in similar dynamic states at the time of sampling. It might be further argued that the relationships were therefore naturally improved when diatom communities with different dynamics, such as might be indicated by low cell counts (station 36) or possibly senescent cells (station 57), were excluded from the analysis. This is not the case, however. Diatom populations of widely different species composition which exhibited a range in dynamics from varying degrees of senescence up to vigorous growth under the considerable range in the environmental conditions accompanying the upwelling and rainy seasons (0.02 - 2.24 μg-at/L PO_4-P; 16.83 to 28.17 C; and 28.41 to 34.53 ‰) are included in the regressions (Appendix Table 1). For example, one-third of the stations (identified in Figs. 3, 7) were sampled during the rainy season (May-November) when unfavorable growth conditions are present (Appendix Table 1; Smayda, 1963; *unpublished*). Although this matter will be reconsidered in the Discussion, it is important to bear in mind that the regressions are based on significant station-to-station differences in the dynamic state of the populations, species composition and environmental conditions.

INFLUENCE OF THE DIATOM COMMUNITY AREA-TO-VOLUME RATIO ON THE RELATIONSHIP BETWEEN C^{14} ASSIMILATION AND DIATOM STANDING CROP WHEN EXPRESSED AS SURFACE AREA AND PLASMA VOLUME

The procedure thus far has been to establish the extent of the relationship, if any, between C^{14} assimilation and the diatom standing crop as a necessary preliminary to the evaluation as to whether this relationship, and possibly other community responses, might be influenced by the community A/V ratio. Since a fair relationship exists (Tables 6, 7; Figs. 3-6), the role of the diatom community A/V ratio on this will now be examined. Although carbon assimilation tends to be better related to unmodified and A/V-weighted diatom abundance than to the other standing crop estimates used (Table 7), such numerical estimates are not suited to a more quantitative treatment. For this reason, the relationship between carbon uptake and standing crop will be probed further using plasma volume and surface area as an index of the latter. These two indices, unlike biomass, are reasonably well related to carbon assimilation, accounting for 54 to 56 per cent of the variation (Table 7).

TABLE 8. Illustration of the procedure used to calculate diatom community area-to-volume (A/V) ratios.

Species (i)	N_i	A_i (μ^2)	V_i (μ^3)	A_i/V_i (μ^2/μ^3)	N_iA_i (cells) (μ^2) $n \times 10^5$	N_iV_i (cells) (μ^3) $n \times 10^5$
1	3,000	250	250	1.00	7.5	7.5
2	2,000	600	1,200	0.50	12.0	24.0
3	100	1,500	6,000	0.25	1.5	6.0
			$\sum_{i=1}^{m} N_iA_i$		..... 21.0×10^5	
			$\sum_{i=1}^{m} N_iV_i$			..... 37.5×10^5
			A/V $= \sum_{i=1}^{m} N_iA_i \Big/ \sum_{i=1}^{m} N_iV_i = 21 \times 10^5 \Big/ 37.5 \times 10^5 = 0.56$			

As stated previously, a phytoplankton community can be envisaged as having an area-to-volume (A/V) ratio, just as any given cell. For a community this represents the ratio of the cumulative cell surface area, represented by the individual cells present, to their cumulative volume. Furthermore, one might also expect that the community area-to-volume ratio influences its dynamics, just as it does at the species level with respect to cell division, (Braarud, 1945; Margalef *et al.*, 1955), respiration (Verduin, 1952) and nutrient assimilation (Munk and Riley, 1952). For this reason, community A/V ratios were calculated [utilizing the notations as given for equations (4) and (5)] as follows:

$$\text{Total diatom area} = \sum_{i=1}^{m} N_iA_i = N_1A_1 + N_2A_2 + \ldots + N_mA_m \qquad (6)$$

$$\text{Total diatom volume} = \sum_{i=1}^{m} N_iV_i = N_1V_1 + N_2V_2 + \ldots + N_mV_m \qquad (7)$$

Then:

$$\text{diatom community } \mathbf{A/V} \text{ ratio} = (6) \Big/ (7) = \sum_{i=1}^{m} N_iA_i \Big/ \sum_{i=1}^{m} N_iV_i$$

The procedure is demonstrated in Table 8.

The diatom community A/V ratios ranged from 0.13 to 0.83, and comprised 20 different values (Appendix Table 1). Of the 27 stations used in the analyses, an A/V ratio of 0.43 or greater characterized nine stations; ten stations fell between 0.31 and 0.39, and eight stations had an A/V ratio below 0.31. The frequency distribution of these values does not suggest any sub-groupings of the A/V ratios which might be used in assessing the influence of the diatom community A/V ratio on its rate of C^{14} assimilation.

TABLE 9. Regression equations, C^{14} assimilation as a function of diatom surface area and plasma volume, and as influenced by the community area-to-volume (A/V) ratio.

Y = mg carbon assimilated per m^3 per day

X =	Regression equation	% Variation explained by regression	Probability	Standard error of estimate	D.F.
Cell surface area, cm^2 per m^3:					
$A/V \geq 0.40$	$\log Y = 0.23060 + 0.33077 \log X$	87	0.001	0.064	7
$A/V < 0.40$	$\log Y = -1.01271 + 0.59256 \log X$	75	0.001	0.050	16
Plasma volume, mg per m^3:					
$A/V \geq 0.40$	$\log Y = 0.47961 + 0.33250 \log X$	86	0.001	0.065	7
$A/V < 0.40$	$\log Y = -0.55659 + 0.58034 \log X$	73	0.001	0.052	16

However, the distribution of A/V values in the regressions of C^{14} uptake on diatom standing crop expressed as cell surface area and plasma volume reveals an influence of A/V on this relationship within certain limits (Figs. 7, 8). A consistently greater rate of C^{14} assimilation occurred at those stations where the A/V was 0.43 and greater, than at those stations characterized by an A/V ratio of 0.39 and lower over the entire range in standing crop abundance encountered. (There were no A/V values from 0.40 to 0.42.) A further influence of diatom community A/V ratio on C^{14} assimilation could not be detected either within the above A/V subdivisions, i.e. 0.13 to 0.39, and 0.43 to 0.83, or by taking the data as a whole. On the basis of the data at hand, therefore, two groups of diatom communities can be distinguished: a). those with an A/V ratio equal to or exceeding 0.40, and b). those with an A/V ratio of less than 0.40 (Figs. 7, 8; Table 9; Appendix Table 1).

The regression analyses of C^{14} uptake on plasma volume and cell surface area indicate that 73 to 75 per cent of the variation can be explained, respectively, by the regressions for those communities with an A/V ratio of < 0.40 (Table 9). For communities with an A/V ratio ≥ 0.40, from 86 to 87 per cent of the variation can be explained by the regressions (Table 9). Application of Student's t-test indicates that these regressions are significant to the 0.001 probability level. It is apparent that partitioning of the communities on the basis of their A/V characteristics results in a considerable improvement in the regressions over that when the data are lumped (Tables 7, 9).

Four stations (51, 54, 55 and 61—represented by the symbol ◕ in Figures 7 and 8) *included* in the regressions calculated for the < 0.40 A/V group have strong "affinities" to the ≥ 0.40 A/V community group. An examination of the species composition at these stations revealed the pres-

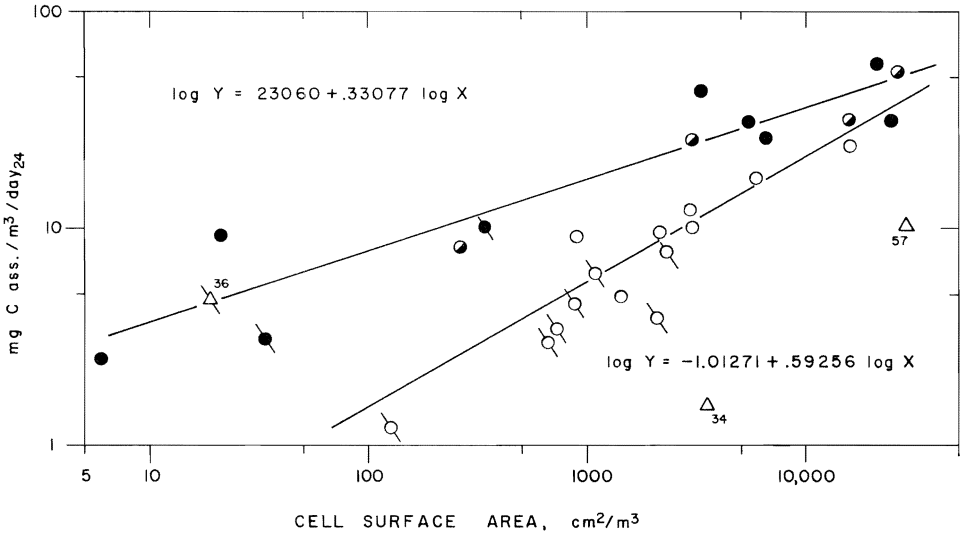

FIGURE 7. Influence of the diatom community cell surface area-to-cell volume (A/V) ratio on the relationship between C^{14} assimilation and diatom cell surface area. Symbols: ● = A/V ratio $\geq$ 0.40; ○ = A/V ratio $<$ 0.40; ◕ = stations included in regression for $<$ 0.40 A/V groups (○) but showing strong affinities to the $\geq$ 0.40 groups (●) as discussed in text; △ stations not included in the regression analyses for reasons given in the text. Symbols with a \ drawn through them, as ⊘, represent rainy season stations.

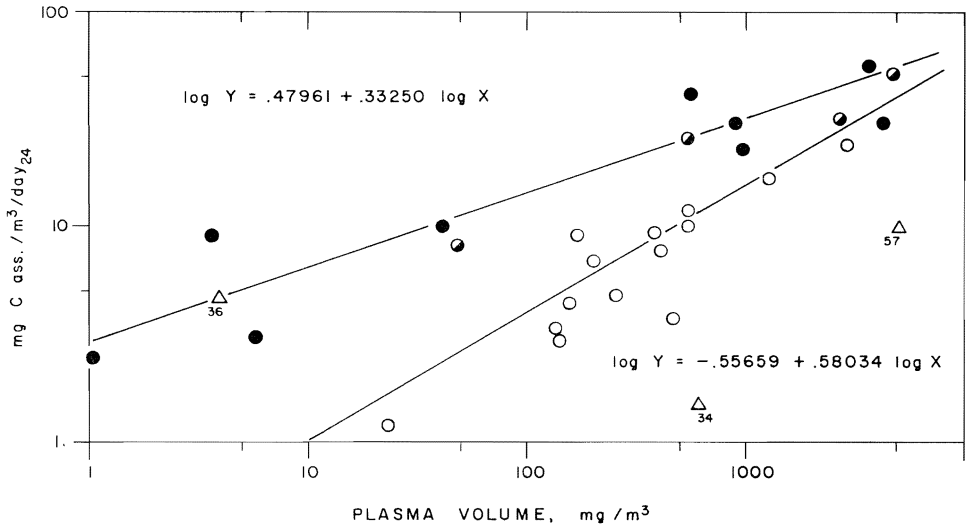

FIGURE 8. Influence of the diatom community cell surface area-to-cell volume (A/V) ratio on the relationship between C^{14} assimilation and diatom plasma volume. Symbols as explained in legend to Figure 7.

TABLE 10. Influence of sparse "giant" diatom species on community area-to-volume (A/V) ratio.

Station	Diatoms c/L	Community A/V ratio	"Giant" diatoms Species	c/L	Per cent of total diatoms	A/V ratio omitting "giant" diatoms
51	35,020	0.33	*Ditylum sol*	20		
			Rhiz. alata f. *indica*	20		
			Rhiz. bergonii	40		
			Σ	80	0.3	0.42
54	3,149,940	0.30	*Ditylum brightwelli*	3,920		
			Biddulphia sinensis	360		
			Σ	4,280	0.1	0.42
55	2,014,260	0.39	*Ditylum sol*	60		
			Rhiz. acuminata	20		
			Σ	80	<0.01	0.41
61	176,640	0.38	*Rhiz. bergonii*	360		
			Rhiz. calcar avis	140		
			Lept. maximus	200		
			Σ	700	0.4	0.42

ence of two to three "giant" species (Table 2) which significantly influenced the community A/V ratio even though they were very sparse, comprising from less than 0.01 to 0.4 per cent of the diatom population as cell numbers (Table 10).

Excluding the "giant" diatom species in calculating the area-to-volume ratio would elevate these stations to the ≥ 0.40 group. While this would not improve the regression analysis for this A/V group, a substantial improvement (from 73 to 75 per cent, *vide* Table 9) in the explainable variation of the regressions on plasma volume and cell surface area to 80 to 83 per cent, respectively, would result for the < 0.40 group. This additional, solely illustrative refinement of the data strengthens the observation that the diatom community A/V ratio, within certain limits, influences the rate of C^{14} uptake.

The following conclusions based on the foregoing regression analyses can be drawn:

1). a strong direct relationship exists between C^{14} assimilation and the standing crop when the latter is expressed either as surface area or plasma volume,

2). the nature of this relationship suggests that the C^{14} experiments provide some measure of the diatom standing crop in the Gulf of Panama, and

3). the rate of C^{14} uptake is related to the cumulative cell surface area-to-cell volume ratio of the diatom community within certain limits, suggesting that this characteristic influences community dynamics as well as individual species responses.

These conclusions will be reconsidered in the Discussion.

TABLE 11. Regression equations, C^{14} assimilation as a function of diatom standing crop based on the least number of species comprising 50 per cent or more of the diatom population as cell numbers.

Y = mg carbon assimilated per m^3 per day

X =	Regression equation	% Variation explained by regression	Probability	Standard error of estimate	D.F.
Cells per m^3 $(\sum_{i=1}^{m} N_i)$	$\log Y = -1.36824 + 0.30096 \log X$	43	0.001	0.064	28
$\sum_{i=1}^{m} \frac{A_i}{V_i} N_i$	$\log Y = -1.15103 + 0.28285 \log X$	36	0.001	0.067	28
$\sum_{i=1}^{m} \frac{V_i}{A_i} N_i$	$\log Y = -1.39729 + 0.29375 \log X$	35	0.001	0.068	28
Biomass, mg per m^3	$\log Y = 0.53448 + 0.21285 \log X$	29	0.001	0.071	28
Surface area, cm^2 per m^3	$\log Y = 0.19079 + 0.28176 \log X$	36	0.001	0.067	28
Plasma volume, mg per m^3	$\log Y = 0.52368 + 0.22993 \log X$	33	0.001	0.069	28

C^{14} ASSIMILATION AS RELATED TO THE STANDING CROP OF THE DOMINANT DIATOMS IN THE COMMUNITY

Phytoplankton communities are frequently dominated by one or more species. For example, of the 103 species recorded at station 3, two species (*Chaetoceros compressus* and *Chaetoceros costatus*) accounted for 47 per cent of the standing crop when expressed as cell numbers (Smayda, *unpublished*). It might be expected, therefore, that a community response such as C^{14} uptake primarily reflects the activity of several dominant species. This possibility has been examined (30 observations) by comparing the community carbon assimilation rate against the standing crop of the least number of diatom species comprising 50 per cent or more of the community based on cell numbers (Table 11). A maximum of five species was represented per station, three or less species obtained for 80 per cent of the 30 stations involved, while only one species was used at eight stations. The dominant species, so defined, represented from 50 to 98 per cent of the cell density of their respective communities.

The regression analyses for the "least number" of dominant diatom species indicate that the regression on unmodified cell abundance compares favorably with that observed with all species included (Tables 6, 11). The regressions on the other standing crop indices, especially biomass, are considerably weaker, however. Nonetheless, it would appear that carbon assimilation is better related to the standing crop of the dominant diatoms than the regressions suggest. For although these data are not as amenable to objective sub-grouping and examination as is possible for the total community, visual observation of potential sub-groupings suggests a substantial improvement in the regressions. However, it remains uncertain whether the dominant species are primarily responsible for the observed community C^{14} assimilation uptake.

DIATOM STANDING CROP DENSITY DEPENDENCE OF C^{14} ASSIMILATION

The foregoing analyses have demonstrated that a). total carbon uptake is directly related to the size of the diatom standing crop when expressed as either surface area or plasma volume, and b). this uptake is also influenced by the community surface/volume characteristic within certain limits. However, the relationship between standing crop size and the *rate* of C^{14} assimilation *per unit of standing crop* has not been established as yet. Figure 9 reveals that the rate of carbon uptake per unit of standing crop surface area is *inversely* related to the size of the standing crop when expressed as biomass. This inverse relation persists if the standing crop is expressed as plasma volume or surface area, or if C^{14} uptake per unit of standing crop biomass or plasma volume is used. A decline in the rate of

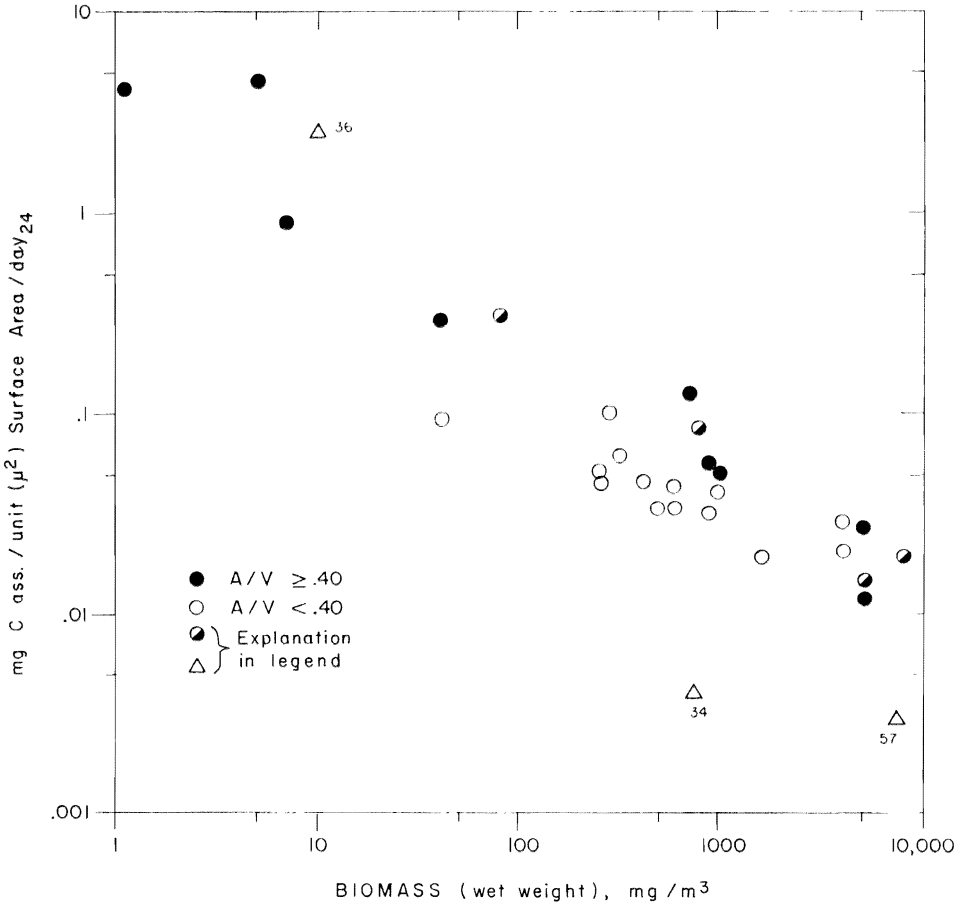

FIGURE 9. The relationship between the daily C^{14} uptake per unit of diatom standing crop cell surface area and standing crop abundance expressed as biomass. Symbols as explained in legend to Figure 7.

carbon assimilation per unit of standing crop as the latter increases has been observed in lakes as well (Rodhe *et al.,* 1958; Wright, 1959, 1960). In general, in those communities with an A/V ratio ≥ 0.40 the rate of carbon uptake per unit of standing crop exceeded that accompanying larger-celled communities (Fig. 9). This suggests that a family of curves based on the A/V ratio and expressing this relationship would be possible, as it would for total carbon uptake as well (Figs. 7, 8), were more extensive observations available. On the basis of the data at hand, however, this relationship appears to be independent of the A/V ratio.

Thus, an additional characteristic of the C^{14} uptake-diatom standing crop relationship in the Gulf of Panama is that the rate of carbon uptake per unit of standing crop decreases as the latter increases; that is, it is dependent upon the density of the standing crop.

RELATIONSHIPS BETWEEN CHLOROPHYLL *a*, C^{14} ASSIMILATION AND STANDING CROP CARBON CONTENT

An evaluation of the standing crop density dependence of carbon uptake (Fig. 9) is facilitated by chlorophyll observations. Although chlorophyll data are available for only nine stations, sampled during the upwelling season, they provide an insight into the carbon uptake-diatom standing crop relationship (Tables 12, 13). The biomass and plasma volume estimates of the diatom standing crop at these stations have been converted to carbon content by the formula:

$$\text{mgC} = \text{F} \times \text{mm}^3 \text{ of algal volume} \qquad (8)$$

where F is taken to be 0.12 (Strickland, 1960), and a specific weight of 1.0 is assumed.

The mean diatom carbon : chlorophyll *a* ratios of 325:1 and 195:1, by weight, based on biomass and plasma volume carbon, respectively, are considerably greater than those summarized by Strickland (1960). This suggests that the carbon : chlorophyll ratio may be greater in tropical phytoplankton communities than in those from other thermal regions. However, the mean Gulf of Panama values have limited, if any, applicability to natural populations in view of the considerable range in ratios from community to community (Tables 12, 13), a situation well known to other investigators.

As with carbon assimilation (Fig. 9), the amount of chlorophyll *a* per unit of standing crop decreased as the latter increased (Tables 12, 13). The diatom carbon : chlorophyll *a* ratios especially demonstrate this inverse relationship (Table 12). The decline in chlorophyll *a* per unit of standing crop as the latter increases (Tables 12, 13) might explain the density dependence of C^{14} assimilation (Fig. 9; Table 13). However, the amount of carbon assimilated per unit of chlorophyll *a* does not exhibit

TABLE 12. Carbon : chlorophyll *a* ratios as a function of diatom standing crop when expressed as total biomass and plasma volume (PV).

Station	Biomass (mg/m^3)	Biomass carbon (mg/m^3)	PV carbon (mg/m^3)	Chl. *a* (mg/m^3)	mg biomass C / mg Chl. *a*	mg PV-C / mg Chl. *a*
59	1.1	0.15	0.05	1.11	0.13	0.04
63	41.3	5.0	2.0	0.41	12.2	48.8
62	317.6	38.0	23.5	0.71	53.5	33.1
52	602.8	72.5	45.5	0.73	99.3	62.3
53	860.0	103.0	65.0	0.75	137.3	86.7
58	962.2	115.5	115.5	0.85	135.9	135.9
55	3981.5	478.0	326.0	1.45	329.7	224.8
56	5560.8	667.5	351.0	0.84	794.6	417.9
54	8671.5	1040.5	567.5	0.76	1369.1	746.7
				MEAN	325.7	195.1

TABLE 13. Relationships between chlorophyll *a*, C^{14} assimilation and diatom standing crop.

Station	Biomass (mg/m^3)	Chl. *a* (mg/m^3)	C^{14} ass. ($mgC/m^3/day$)	mg Chl. *a* / mg Biomass ($\times 10^{-3}$)	mg Chl. *a* / mg PV ($\times 10^{-3}$)	mg Chl. *a* / cm^2 Surface ($\times 10^{-3}$)	mg C^{14} ass./day / mg Biomass	mg C^{14} ass./day / mg PV	mg C^{14} ass./day / cm^2 Surface	mg C^{14} ass./day / mg Chl. *a*
59	1.1	1.11	2.5	1000.0	1100.0	183.0	1.363	2.470	.4166	2.25
63	41.3	.41	10.0	992.0	992.0	1.19	.242	.180	.0290	24.15
62	317.6	.71	6.9	2.23	3.60	.64	.021	.035	.0062	9.72
52	602.8	.73	9.4	1.21	1.92	.34	.016	.025	.0044	12.88
53	860.0	.75	10.0	.87	1.38	.24	.011	.018	.0032	13.33
58	962.2	.85	26.0	.88	.88	.13	.027	.024	.0041	30.59
55	3981.5	1.45	32.0	.36	.53	.09	.008	.011	.0021	22.07
56	5560.8	.84	24.0	.15	.28	.05	.004	.008	.0015	28.57
54	8671.5	.76	52.0	.08	.16	.02	.006	.011	.0020	68.42

any clear relation to the size of the standing crop (*vide* last column in Table 13). This might be expected, however, since the rate of carbon assimilation per unit of chlorophyll is also related to the light intensity (Ryther and Yentsch, 1957). It would not appear to be wholly attributable to the fact that the biomass is calculated on the basis of the diatoms, whereas the chlorophyll is extracted from the entire phytoplankton community (*vide* page 471).

RELATIVE EFFICIENCY, AND NON-MICROSCOPIC DERIVATION OF COMMUNITY A/V RATIO

The influence of light on this relationship has been assessed using a slight modification of Forsbergh's (1963) relative efficiency (RE) calculation:

$$RE = \frac{\text{daily rate of carbon assimilation}}{(\text{amount of chlorophyll } a) \times (\text{illumination in ly/day})} \quad (9)$$

defined as the daily amount of carbon assimilated (as mgC per m^3) per unit of chlorophyll *a* (as mg per m^3) per unit of visible (photosynthetic) radiant energy in langlies : mgC per mg chlorophyll *a* per langley per day. This formulation differs from Forsbergh's equation in that visible rather than total radiant energy is used. The light available for photosynthesis is assumed to represent 50 per cent of the total radiation (Harvey, 1955; Talling, 1957), otherwise applied as described under Methods. The photosynthetically available light ranged from 29.0 to 58.5 langlies per day at the seven stations for which calculations of the diatom standing crop relative efficiency could be made (Table 14).

The relative efficiency (RE) of carbon uptake is directly related to the size of the standing crop (Fig. 10; Table 14). The sample correlation coefficient (r) is 0.96**. This relationship contrasts with the inverse relationships

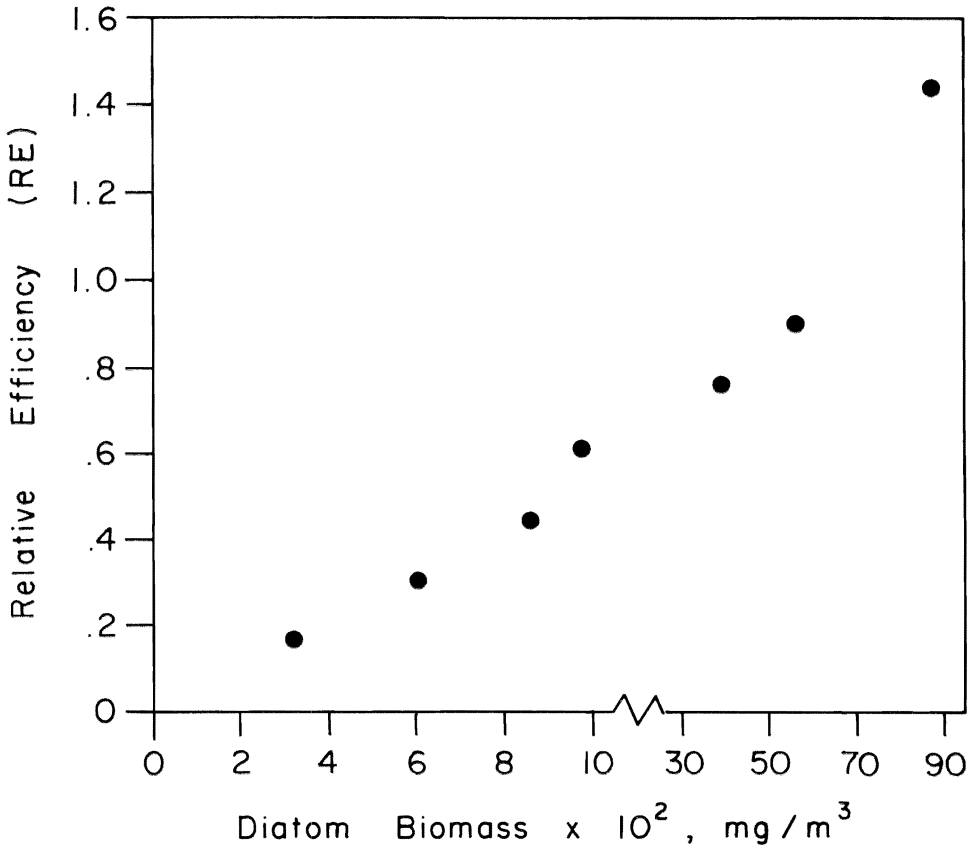

FIGURE 10. The relationship between relative efficiency (RE) as derived by equation (9) and the diatom biomass standing crop; data presented in Table 14. The sample correlation coefficient (r) is 0.96**.

TABLE 14. Relative efficiency calculations (RE and R'E') using equations (9) and (10).

Station	Biomass (mg/m³)	Chl. *a* (mg/m³)	mg Chl. *a* / mg Biomass ($\times 10^{-3}$)	C^{14} ass. (mg/m³)	mg C ass. / mg Chl. *a*	ly/day	RE	A/V	R'E'	Ratio of R'E' to RE (%)
62	317.6	0.71	2.23	6.9	9.72	58.5	.17	0.35	.20	118
52	602.8	0.73	1.21	9.4	12.88	43.5	.30	0.35	.27	90
53	860.0	0.75	.87	10.0	13.33	30.5	.44	0.35	.29	66
58	962.2	0.85	.88	26.0	30.59	50.0	.61	0.66	.40	66
55	3981.5	1.45	.36	32.0	22.07	29.0	.76	0.39	.82	108
56	5560.8	0.84	.15	24.0	28.57	31.6	.90	0.45	.53	59
54	8671.5	0.76	.08	52.0	68.42	47.5	1.44	0.30	1.73	120

found between standing crop size and the rate of carbon assimilation per unit of standing crop (Fig. 9), and between standing crop and the amount of chlorophyll *a* present per unit of standing crop (Table 13). These various interactions suggest that the *decline* in the amount of carbon assimilated per unit of standing crop as the latter increases, i.e. density dependence (Fig. 9), may be attributable to the decline in chlorophyll *a* concentration per unit of standing crop also accompanying increasing standing crop (Tables 12, 13, 14). Wright (1960) has attributed a similar density dependence observed in limnetic communities to a decrease in available CO_2. Odum (1956) in his discussion of efficiencies and size of organisms has suggested that under varying light intensities an inverse relationship will exist, in general, between photosynthetic efficiency and community production. "Efficiency" as used by Odum means the "per cent of absorbed light of usable wave length that is converted into organic matter." At low light intensities photosynthetic efficiency will be high, but total production low, the converse holding for high light intensities (Odum, 1956).

A similar inverse relationship between relative photosynthetic efficiency, as defined by equation (9), and community production occurs, provided that the RE is compared to the amount of carbon uptake *per unit of standing crop,* i.e. mgC/mg biomass, or mgC/cm² surface (Table 13). That is, *at high relative efficiencies the rate of carbon uptake per unit of standing crop is low.* Assuming a high relative efficiency (RE), the following generalizations about community behavior can be made (Tables 13, 14):

a). The standing crop will be relatively high.

b). Production will be relatively high.

c). Carbon uptake per unit of standing crop will be relatively low.

d). Chlorophyll *a* concentration per unit of standing crop will be relatively low.

The converse will hold for a low relative efficiency (Tables 13, 14). Forsbergh (1963) found that an increase in relative efficiency accompanies lower light intensities. This is also suggested by the data at stations 56

and 58, and especially stations 52 and 53 where, although the amount of carbon assimilated per unit of chlorophyll *a* is similar at each pair of stations, the light intensity and, hence, RE varies (Table 14).

With the exception of station 55, the concentration of chlorophyll *a* is remarkably similar at the various stations sampled during the 1957 upwelling season (Table 14; Appendix Table 1). The factors responsible for the relative constancy of the chlorophyll *a* concentration irrespective of environmental conditions and standing crop size, and the mechanism(s) enabling an increased efficiency in the utilization of radiant energy with increasing standing crop remain obscure. Perhaps in an increasing population the chlorophyll present becomes distributed over a greater fraction of the community surface area, as suggested by the data (Tables 13, 14), resulting in a greater capture of light per unit of chlorophyll and thereby increasing photosynthetic efficiency. Conversely, the bulk of the chlorophyll present in an increasing population may become associated with a progressively smaller, yet more robust and efficient segment of the community which is primarily responsible for the observed carbon assimilation. The data are too few to permit a satisfactory analysis of this problem, complicated as it is by the unknown influence of light adaptation (Steemann Nielsen and Hansen, 1959) and community A/V ratio. An analogous situation of an increase in photosynthetic efficiency with depth, probably attributable in part to a reduction in light intensity, has been reported (Odum, 1956; Forsbergh, 1963; among others).

Since carbon uptake is related to the size and A/V ratio of the diatom standing crop (Figs. 7, 8; Table 9), an additional measure of the relative efficiency (R′E′) seemed likely. The following empirically derived equation resulted:

$$R'E' = C' \times \frac{\text{mgC assimilated per m}^3}{A/V} \qquad (10)$$

When C′ is a constant with a value of 10^{-2} used to adjust the decimal point permitting direct comparison with the RE values derived from equation (9), and A/V is the community surface/volume ratio derived from equations (6) and (7). The R′E′ values calculated in this way are in remarkably close agreement with those (RE) calculated by equation (9) (last four columns in Table 14; Fig. 11). The sample correlation coefficient (r) is 0.93**.

The strong direct relation existing between carbon uptake and standing crop suggests that if the community surface/volume ratio were known one could estimate the standing crop from a C^{14} experiment (Figs. 7, 8; Table 9). Unfortunately, the community A/V ratio can be determined only through laborious microscopic examination. The close correspondence (Fig. 11; Table 14) between the R′E′ values derived by equation (10) and

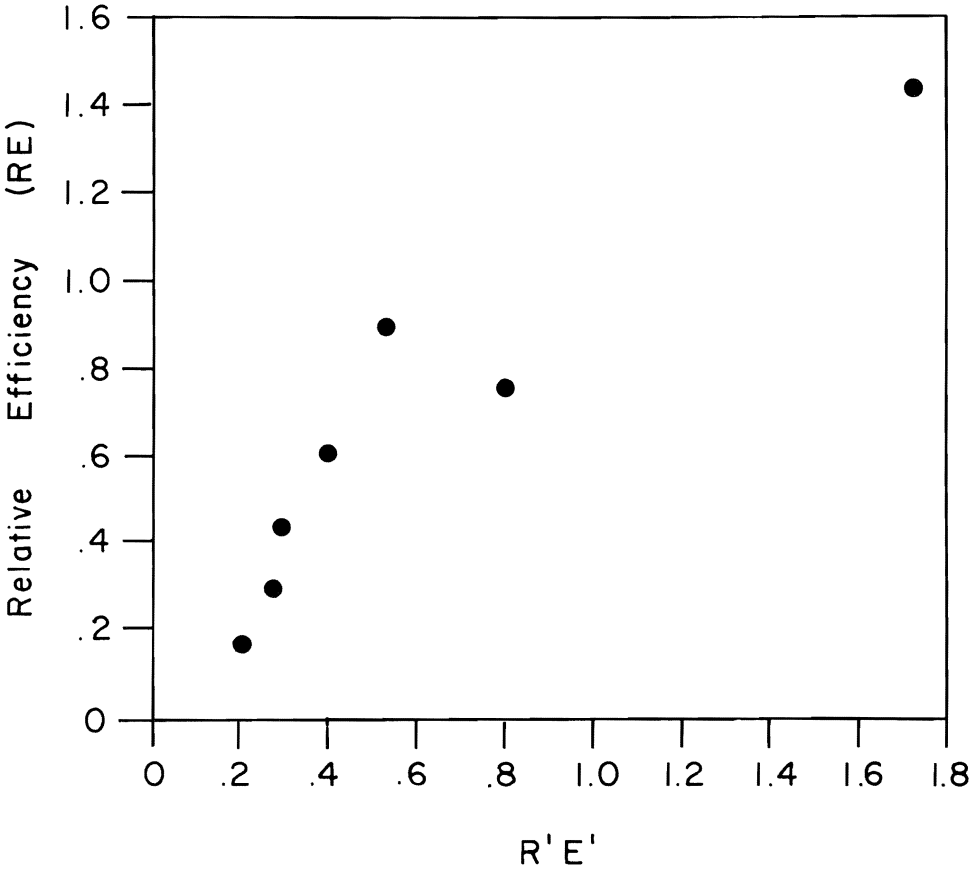

FIGURE 11. The relationship between relative efficiency (RE) as derived by equation (9) and relative efficiency (R′E′) as derived by equation (10); data presented in Table 14. The sample correlation coefficient (r) is 0.93**.

the RE values with equation (9) suggests, however, that an approximation of the community A/V ratio can be obtained from:

$$A/V = \frac{\text{mgC assimilated per m}^3}{100\ RE} \qquad (11)$$

where RE represents the relative efficiency calculated from equation (9). Since equations (9) and (10) can be equated:

$$RE = R'E' \qquad (11A)$$

equation (11) can be simplified to:

$$A/V = \frac{(\text{chlorophyll } a \text{ per m}^3)\ (\text{visible illumination in ly/day})}{100} \qquad (11B)$$

The microscopically derived A/V ratios and those calculated from equation (11) are presented in Table 15. The sample correlation coefficient (r) is 0.37*.

TABLE 15. Comparison of the diatom standing crop surface/volume (A/V) ratios determined microscopically and using equation (11).

Station	A/V ratios, derived by: Microscope	Equation (11)	Ratio of equation (11) to microscopically derived A/V ratios (%)
62	0.35	0.40	114
52	0.35	0.31	88
53	0.35	0.23	66
58	0.66	0.43	65
55	0.39	0.42	108
56	0.45	0.27	60
54	0.30	0.36	120

The regressions of C^{14} uptake on standing crop expressed as plasma volume and cell surface area have been partitioned into two groups: those having an A/V ratio ≥ 0.40 and those having a ratio < 0.40 (Figs. 7, 8; Table 9). Use of equation (11) (or equation 11B) to estimate the A/V ratio would place five of the seven stations (55 and 56 deviant) into the correct size group as derived from microscopic examination (Table 15). The inclusion of station 55 into the higher A/V category would not introduce any significant error in estimating the standing crop from the C^{14} uptake experiment since the presence of two "giant" diatom species accounting for only 80 of the more than 2,000,000 diatom cells per liter present reduces the A/V value to < 0.40 (Table 10) even though this station has the C^{14} uptake-diatom standing crop characteristics of the ≥ 0.40 group (Figs. 7, 8). Thus, *equation (11) provides an approximation of the community A/V ratio permitting an estimate of the standing crop as plasma volume or cell surface area from a given 24 hour* in situ *C^{14} experiment in the Gulf of Panama* (Figs. 7, 8; Table 9).

PRODUCTIVITY INDEX

Strickland's (Strickland, 1960; McAllister *et al.,* 1961) productivity index (PI) has been calculated where possible (11 stations) since this presumably provides a measure of the "production intensity" or "vitality" of a community:

$$\text{PI} = \frac{\text{hourly rate of carbon increase}}{(\text{amount of plant carbon}) \times (\text{illumination in ly/min})} \qquad (12)$$

where carbon production is in mgC per hour per m^3, standing crop as mgC per m^3, and illumination as ly/min visible light. A 12-hour photosynthesis day is assumed. The Gulf of Panama calculations differ from the original formulation of the productivity index in that they are based on production values presumably approaching net carbon uptake rather than the gross production rates called for (Strickland, 1960; McAllister *et al.,* 1961).

In general, relatively high and constant PI values accompanied standing crops of less than about 100 mg biomass C per m^3, whereas lower PI

TABLE 16. Calculation of the productivity index (PI) for standing crop biomass carbon (BM-C) and plasma volume carbon (PV-C) using equation (12).

Station	C^{14} ass. (mgC/m³/hr)	Biomass (mgC/m³)	Plasma volume (mgC/m³)	Visible light (ly/day)	$P\text{-}PO_4$ μg-at/L	PRODUCTIVITY INDEX BM-C	PV-C	A/V	RE
62	0.575	38.0	23.5	58.5	0.55	0.37	0.60	0.35	0.17
48	0.641	72.5	48.5	55.5	0.57	0.23	0.34	0.38	—
52	0.783	72.5	45.5	43.5	0.81	0.36	0.57	0.35	0.30
61	2.166	94.5	64.0	90.0	—	0.36	0.54	0.38	—
53	0.833	103.0	65.0	30.5	1.65	0.38	0.61	0.35	0.44
58	2.166	115.5	115.5	50.0	1.06	0.54	0.54	0.66	0.61
43	0.316	190.5	55.5	29.0	0.71	0.08	0.28	0.13	—
55	2.666	478.0	326.0	29.0	0.60	0.28	0.41	0.39	0.76
60	2.583	658.5	512.0	27.6	0.26	0.21	0.26	0.28	—
56	2.000	667.5	351.0	31.6	—	0.14	0.26	0.45	0.90
54	4.333	1040.5	567.5	47.5	2.24	0.13	0.23	0.30	1.44

values occurred and progressively decreased with increasing standing crops above approximately 200 mg biomass C per m³ (Table 16). Although the PI values are believed to measure the influence of nutritional changes on metabolism (Strickland, 1960), there is no apparent relationship between inorganic phosphate concentration and PI for the data at hand (Table 16).

There is no obvious relationship between the RE and PI for standing crops less than approximately 100 mg biomass C per m³ (Table 16). Above this carbon level, however, the PI progressively *decreases* while the RE *increases* with increasing standing crop. At the maximum standing crop of 1040 mg biomass C per m³ (567 mg plasma volume C) observed at station 54, the PI was 0.13 and the RE 1.44 (Table 16). Forsbergh (1963) states that the relative efficiency is equivalent to Strickland's productivity index; the RE as used here, equation (9), differs from the PI in that chlorophyll *a* concentration is used as a measure of the standing crop rather than carbon content. However, the PI and RE are not equivalent measures as Forsbergh supposed, if only because there is no constant relationship between the amount of chlorophyll present and the carbon content of the standing crop (Table 12). Rather, each index provides a measure of a different aspect of community behavior. The RE measures the "efficiency" of carbon assimilation per unit of chlorophyll *a* present, whereas the PI is an indicator of community "vitality" in that it provides a measure of carbon turnover. Thus, the observed trend of an inverse relationship between the RE and PI for progressively larger standing crops above 100 mg biomass C per m³ (Table 16) is more or less predictable. For, it is consistent with the earlier conclusion (page 497) that at high relative efficiencies (RE) the rate of carbon uptake per unit of standing crop is low (Tables 13, 14). These observations suggest, then, that a relatively low PI and high RE, as at stations 54 and 56 (Table 16), are indicative of communities approaching an asymptote, whereas a relatively high PI and low RE, as at station 58, indicate a vigorously growing community.

Excepting stations 48, 54, 55 and 56, the PI values based on biomass carbon were quite similar to the diatom A/V ratios at the seven other stations (Fig. 12; Table 16). The sample correlation coefficient (r) is 0.71** (Fig. 12). The fact that both the highest PI and A/V values (station 58) and lowest values (station 43) observed (Table 16) coincided at the same stations is especially interesting. The sample correlation coefficient (r) when the productivity index (PI) values are based on plasma volume carbon is only 0.38**.

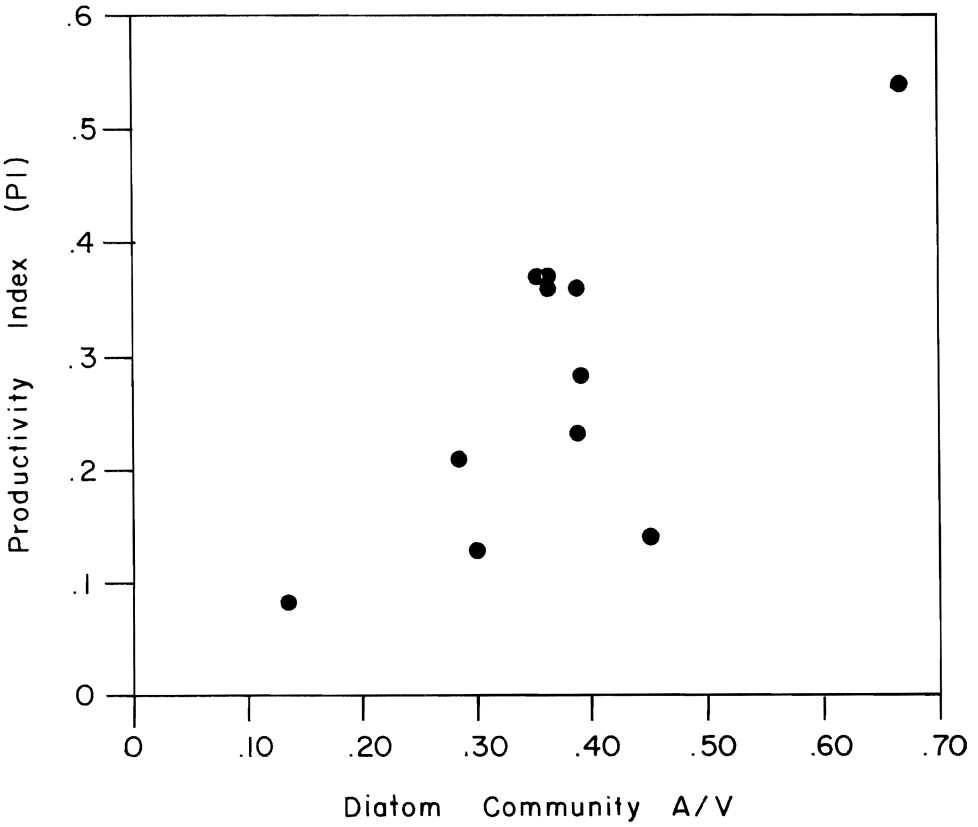

FIGURE 12. The relationship between the productivity index (PI) based on biomass carbon as calculated by equation (12) and the diatom community A/V ratio; data presented in Table 16. The sample correlation coefficient (r) is 0.71**.

The few PI values reported in the literature (Strickland, 1960; McAllister *et al.*, 1961) are generally much higher than those calculated for the Gulf of Panama, and exceed the A/V ratios one would expect to find for natural communities. However, the 24 hour *in situ* C^{14} experiments on which the Gulf of Panama PI calculations are based undoubtedly provide a measure of carbon uptake that is closer to net production than to the

gross production estimate that Strickland's formula, equation (12), calls for (Strickland, 1960, p. 102). This would favor the lower PI values derived for the Gulf of Panama. However, it is unknown whether the general correspondence between PI and the community A/V in this region is fortuitous (Fig. 12) or whether the latter characteristic can be estimated in this way. In view of the role of the surface/volume ratio in influencing community dynamics, the relationship between PI and community A/V merits further investigation.

PRODUCTION COEFFICIENTS

Production coefficients (P_h), defined as the amount of carbon produced per gram of phytoplankton carbon per day (Riley, Stommel and Bumpus, 1949), have been calculated (Table 17) after converting the biomass and plasma volume estimates of the standing crop to carbon content using equation (8).

A considerable range in production coefficients characterizes the Gulf of Panama communities. The median values based on standing crop biomass carbon and plasma volume carbon are 13 and 21 per cent, respectively (Table 17). These values would approximate the mean production coefficients if the exceptionally high values observed at four of the 27 stations (stations 4, 39, 59 and 63) were omitted in deriving the mean (Table 17). The production coefficients are generally much lower than those reported from other marine areas, especially tropical regions (see table VI, Riley *et al.,* 1949, based on dark and light bottle measurements and, apparently, using gross production). The Gulf of Panama coefficients are also generally lower than those reported from Lake Erken, Sweden where 24 hour *in situ* C^{14} experiments were made (Rodhe *et al.,* 1958).

The frequency distribution of the production coefficient values, based on biomass and plasma volume carbon, is presented in Figure 13. For biomass carbon the highest frequency (48 per cent of the 27 observations) occurred within the 0.020 and 0.110 interval; that is, 2 to 11 per cent of the standing crop biomass carbon was fixed per day (Table 17). Based on plasma volume carbon, the greatest frequency (55 per cent) occurred within the 0.050 and 0.230 interval. The range in maximum frequency of biomass carbon fixation (2 to 11 per cent) contrasts to the 16 to 33 per cent of the phytoplankton carbon being fixed per day in Lake Erken [found by converting the "activity coefficients" reported by Rodhe *et al.* (1958) into production coefficients utilizing equation (8)].

Extensive regional comparisons are not possible; the limited number of observations indicates that the Gulf of Panama production coefficients are generally *lower* than those reported from other areas (Riley *et al.,* 1949; Rodhe *et al.,* 1958). This suggests that 1). the 24 hour *in situ* C^{14} experiments in the Gulf of Panama may underestimate the actual production oc-

TABLE 17. Production coefficients (P_h) for standing crop expressed as biomass (BM-C) and plasma volume (PV-C) carbon. (g carbon produced per g phytoplankton carbon per day per m^3)

Station	C^{14} ass.	Standing crop		Production coefficients (P_h)	
	mgC/m^3	mgBM-C/m^3	mgPV-C/m^3	gC/gBM-C/day	gC/gPV-C/day
3	12.0	116.5	65.0	0.103	0.185
4	9.2	0.55	0.45	1.673	2.044
5	9.2	34.0	20.5	0.270	0.449
27	4.8	52.0	30.5	0.092	0.157
29	57.0	589.0	437.5	0.097	0.130
30	17.0	473.5	154.0	0.036	0.110
32	42.0	85.5	68.0	0.491	0.618
35	31.0	104.5	104.5	0.297	0.297
39	3.1	0.8	0.7	3.875	4.428
40	3.4	31.5	16.0	0.108	0.212
42	4.5	30.5	19.0	0.147	0.237
43	3.8	190.5	55.5	0.020	0.068
44	3.0	50.5	17.0	0.059	0.176
47	1.2	5.8	2.8	0.240	0.428
48	7.7	72.5	48.5	0.106	0.159
51	8.2	9.5	5.5	0.863	1.491
52	9.4	72.5	45.5	0.130	0.206
53	10.0	103.0	65.0	0.097	0.154
54	52.0	1040.5	567.5	0.050	0.092
55	32.0	478.0	326.0	0.067	0.098
56	24.0	667.5	351.0	0.036	0.068
58	26.0	115.5	115.5	0.225	0.225
59	2.5	0.15	0.03	16.667	125.000
60	31.0	658.5	512.0	0.047	0.060
61	26.0	94.5	64.0	0.275	0.406
62	6.9	38.0	23.5	0.181	0.294
63	10.0	5.0	5.0	2.000	2.000
		Median		0.130	0.212
		Mean		1.046	5.177
		Mean (omitting 59)		0.446	0.569
		Mean (omitting 4, 39, 59, 63)		0.175	0.275

curring (*vide* Strickland, 1960) or, conversely, 2). the calculated amounts of carbon fixed per unit of standing crop carbon are indeed generally less than those reported from other areas. The former possibility can be partially examined by comparing the respiratory demands of the zooplankton standing crop with the amount of net primary production. If the herbivorous zooplankton carbon requirements are consistently greater than available phytoplankton carbon, then one might suspect that the carbon production estimates were in fact too low.

The daily respiratory requirements, as carbon, of the zooplankton standing crop has been assumed to be 12 per cent of its dry weight, as reported for Sargasso Sea populations (Menzel and Ryther, 1961). The amount of daily carbon production per m^2 in the Gulf of Panama at 8°45′N, 79°23′W has been roughly estimated from the equation:

$$gC/m^2/day = F' \times gC/m^3 \text{ at 10 meters} \qquad (13)$$

where F′ is taken to be 13, and is derived from the production data presented for stations 87 through 112 by Forsbergh (Forsbergh, 1963, Ap-

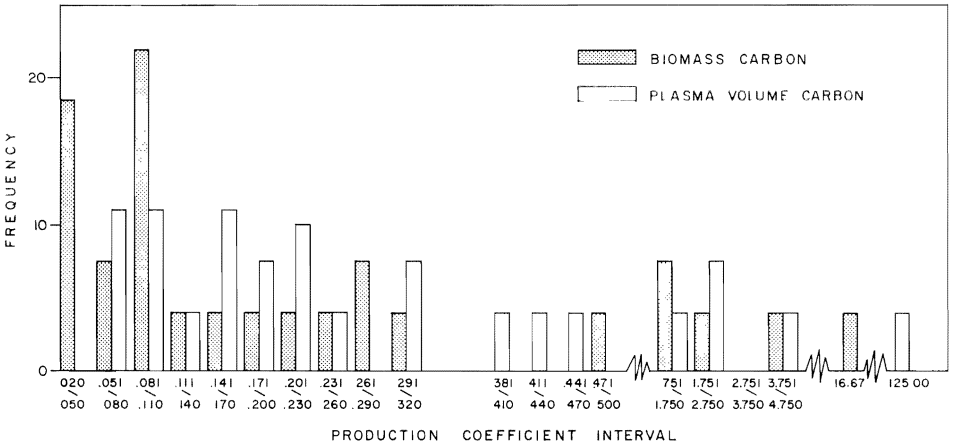

FIGURE 13. Frequencies, in per cent, of the production coefficient values (the amount of carbon fixed per day per gram of phytoplankton carbon) obtained when the diatom standing crop is expressed as biomass carbon and plasma volume carbon.

pendix B). The zooplankton respiratory demands exceeded net primary production on only three occasions (stations 30, 39 and 47); the latter exceeded the daily zooplankton carbon requirement by two- to 50-fold at other times. Although this analysis obviously does not resolve the question of whether the C^{14} experiments underestimated carbon fixation in the Gulf of Panama, it supports the view that the calculated production coefficients are representative of the daily carbon turnover there.

Production coefficients calculated from radiation and phosphate

The influence of environmental conditions on C^{14} uptake can be examined, in part, by calculating production coefficients from certain environmental parameters, as done by Riley *et al.* (1949), and then comparing the observed and calculated results (Tables 18, 19). For example, the observed production coefficients can be compared to calculated coefficients based on light intensity and nutrients using the equation given by Riley *et al.* (1949):

$$P_h = KI_{10}\, v_p \qquad (14)$$

in which P_h is the production coefficient expressed as grams of carbon produced per day per gram of phytoplankton carbon, K is a photosynthetic constant with a numerical value of 2.5, I_{10} is the average daily solar radiation in langlies per minute at 10 meters, and v_p is an index of the amount of reduction of the photosynthetic rate that results from phosphate depletion, and is defined as the ratio of the actual phosphate concentration to the maximum limiting concentration of 0.55 μg-at/L with the added stipulation that this ratio should not exceed unity. Steele (1958) has sug-

TABLE 18. Observed, and calculated production coefficients (P_h) using equation (14), and ratios of observed to calculated P_h for 10 meter diatom standing crops expressed as biomass (BM) and plasma volume (PV) carbon.

Station	Date*	I_{10} (ly/min)	KI_{10}	P-PO_4 (μg-at/L)	ν_p	PRODUCTION COEFFICIENT, P_h Equat. (14)	Observed BM	Observed PV	Ratio of observed to calculated P_h (%) BM	PV
43	13 VIII	.040	.100	0.71	1.00	.100	.020	.068	20	68
48	22 X	.078	.195	0.57	1.00	.195	.106	.159	54	81
52	17 XII	.060	.150	0.81	1.00	.150	.103	.206	69	137
53	1 I	.042	.105	1.65	1.00	.105	.097	.154	92	147
54	14 I	.066	.165	2.24	1.00	.165	.050	.092	30	56
55	29 I	.040	.100	0.60	1.00	.100	.067	.098	67	98
56	11 II	.044	.110	0.26	.47	.052	.036	.068	69	131
58	12 III	.070	.175	1.06	1.00	.175	.225	.225	129	129
62	6 V	.082	.205	0.55	1.00	.205	.181	.294	88	143

* Stations 43 to 52 sampled in 1956, station 53 to 62 in 1957.

gested that a value of 0.40 μg-at/L should be used for the maximum limiting phosphate concentration, a value which will not alter the results calculated here using 0.55 μg-at/L, however, because of the high phosphate levels present (Table 18). The conditions of the equation restrict its application to only nine stations where measurements of both phosphate and radiation are available. (Station 57 has not been included in the analysis for the reasons given on page 486.) The average daily radiation at 10 meters (I_{10}) has been calculated following the procedure outlined under Methods. Six of the nine stations (excepting stations 43, 48 and 62) represent upwelling conditions; the phosphate level was lower than the maximum limiting concentration of 0.55 μg-at/L at station 56 only. Thus, the stations generally represent periods of active phytoplankton growth.

The calculated and observed production coefficient values are in surprisingly good agreement whether based on biomass or plasma volume carbon (Table 18). The sample correlation coefficients are 0.68** and 0.75**, respectively. This agreement contrasts with the observations of Riley *et al.* (1949) in other tropical and subtropical waters where the calculated production coefficients were considerably lower than those observed. These authors found fair agreement in some of the northern waters, however.

Production coefficients calculated from radiation, phosphate and temperature

During the regional survey of the Gulf of Panama (Smayda, 1963), a strong inverse correlation between temperature and mean diatom abundance in the upper 10 meters at depths greater than 50 meters existed during the upwelling season. It is desirable, therefore, to include a term for temperature in calculating production coefficients, which can be done employing the equation given in Riley *et al.* (1949):

TABLE 19. Calculated production coefficients (P_h and P'_h) using equation (15) and equation (16) and ratios of observed P_h to P'_h (equation 16) for 10 meter diatom standing crops expressed as biomass (BM) and plasma volume (PV) carbon.

Station	$\log \nu_p$	$\log I_{10}$	T′	$22.884 + \log \nu_p - \log I_{10} - \frac{6573.8}{T'}$	$\frac{P_h}{KI_{10} - P_h}$	Equat. (15) calculated P_h	A/V	Equat. (16) calculated P'_h	Ratio of observed P_h to P'_h (%) BM	PV
43	0	$\bar{2}.602$	300.9	2.482	303.2	.303	0.13	.039	51	174
48	0	$\bar{2}.892$	300.6	2.092	123.0	.588	0.38	.223	48	71
52	0	$\bar{2}.778$	299.7	2.206	161.0	.453	0.35	.159	65	130
53	0	$\bar{2}.623$	301.9	2.416	261.0	.318	0.35	.111	87	139
54	0	2.820	298.6	2.064	116.0	.498	0.30	.149	34	62
55	0	$\bar{2}.602$	296.1	2.082	121.0	.302	0.39	.118	57	83
56	$\bar{1}.626$	$\bar{2}.644$	296.7	1.666	46.4	.326	0.45	.147	24	46
58	0	$\bar{2}.845$	295.7	1.839	69.1	.524	0.66	.346	65	65
62	0	$\bar{2}.914$	298.2	1.970	93.3	.616	0.35	.216	84	136

$$\log \frac{P_h}{K'I_{10} - P_h} = 22.884 + \log \nu_p - \log I_{10} - \frac{6573.8}{T'} \qquad (15)$$

where K′, the photosynthetic constant, is taken to be 7.6, being derived from Jenkin's (1937) experiments with the large diatom *Coscinodiscus excentricus,* and T′ represents absolute temperature, the other variables having already been explained. The temperature ranged from 22.7 to 27.9 C (Table 19).

The production coefficients calculated by equation (15) are approximately three-fold higher than those obtained with equation (14) and, hence, significantly greater than the observed values (Tables 18, 19). This difference appears to be primarily attributable to the use of 7.6 for the photosynthetic constant K′ in equation (15), a value of 2.5 being used for K in equation (14), and suggests that temperature had little direct effect. This is consistent with the expectation that at the high phosphate levels characterizing most of the stations included in the analysis (Table 18) the influence of temperature on the production coefficient will be relatively minor (Riley *et al.,* 1949). Riley *et al.* found, however, that production coefficients calculated by equation (15) were in better agreement with observed values for tropical and sub-tropical communities than those obtained with equation (14) in which only phosphate and light intensity are considered.

Influence of diatom community A/V ratio in calculating production coefficients

Since the diatom community area-to-volume ratio influences C^{14} uptake (Figs. 7, 8; Table 9), this factor was incorporated into the production

coefficient calculations by multiplying the values (P_h) obtained by equations (14) and (15) by the community A/V ratio:

$$P'_h = (P_h)\ (A/V) \qquad (16)$$

Using the P_h values derived by equation (14), the A/V modified production coefficients (P'_h) derived by equation (16) were 1.7- to three-fold higher than those observed. Fair agreement occurred when based on equation (15), however (see last 3 columns in Table 19). The sample correlation coefficient (r) is 0.87** when based on biomass carbon, and 0.66** when based on plasma volume carbon. It is not apparent, however, whether this agreement resulting from the use of the diatom community A/V ratio in modifying equation (15) reflects a real influence of the A/V on the production coefficient, or whether it merely cancels out the initially high production coefficients relative to equation (14) resulting from the choice of 7.6 for K′ in equation (15). In most instances the A/V ratio was approximately 0.30 (Table 19). It is recalled that the differences in calculated production coefficients between equation (14), which agreed well with observed values, and equation (15) seemed to be attributable to the photosynthetic constants (K, K′) used—the K value of 2.5 used in equation (14) being three-fold lower than that used in equation (15).

All things considered, fairly good agreement occurred between the calculated and observed production coefficients, including those based on plasma volume (Tables 18, 19). Of the environmental factors tested, phosphate and temperature appeared to have little influence on the calculated coefficients, whereas light and, possibly, the A/V characteristic of the community appear to be of greater importance. The correspondence between calculated and observed values is surprising in view of the established density-dependence of photosynthesis and lack of a biomass estimate such as chlorophyll in the equations, variables known to influence the photosynthetic mechanism. An examination of the applicability of the Riley *et al.* (1949) equation (14) based on plasma volume, to other inshore tropical regions is clearly desirable, especially since they reported it to be of little value in the oligotrophic waters of the Sargasso Sea and off the Dry Tortugas.

DISCUSSION

The production estimates obtained by Steemann Nielsen's (1952) C^{14} 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 four to six hour experiments normally conducted using constant, artificial illumination. Thus the opportunity for re-assimilation of C^{14} during respiration (Ryther, 1956) and the secretion of C^{14} labeled organic substances (Fogg, 1958), processes favoring a net production estimate, would appear to be especially great in the Gulf of Panama experiments. Forsbergh (1963) has deter-

mined that the annual primary production in the Gulf of Panama is about 180 g of carbon per square meter of sea surface, 90 g of which are fixed during the January to April upwelling season.

The rate of carbon uptake has been shown to be strongly related to both the surface/volume ratio and abundance of the diatom standing crop when the latter is expressed as either plasma volume or cell surface area (Figs. 7, 8; Table 9). From 73 to 75 per cent of the variation could be explained by the regression of carbon uptake on standing crop for communities with an A/V ratio of < 0.40, and from 86 to 87 per cent of the variation in those communities having an A/V ratio ≥ 0.40. Thus, ***within the Gulf of Panama C^{14} assimilation is related to the diatom standing crop in a manner which suggests that the experiments might permit an estimate of standing crop in addition to providing some measure of primary production.*** A knowledge of the community A/V ratio is required, however, to estimate the standing crop from the C^{14} experiments (Figs. 7, 8; Table 9). The enormously time-consuming task of determining community A/V ratios from microscopic examination makes such standing crop estimates impractical and limits its subsequent use in the Gulf of Panama. Quicker, indirect estimates of the A/V ratio are clearly desirable therefore. Equations (11) and (11B) appear to provide a quick and generally satisfactory estimate of the A/V ratio (Table 15) within the limits of the present analyses. Although the productivity index (PI) is also similar to the A/V ratio under certain conditions (Table 16) a knowledge of the standing crop magnitude is required for its calculation [*vide* equation (12)].

It is unknown whether the observed standing crop - C^{14} uptake relationship is a general one, unique to the Gulf of Panama or represents an experimental artifact. Confirmatory observations from other water masses and with other communities are clearly needed. Paasche's (1960) study of the relationship between "production capacity" [measured by Berge's (1958) modified C^{14} technique] and standing crop in the Norwegian Sea is especially pertinent. He found that the "production capacity" tended to be best related to the surface area of the *total* (including the flagellate groups) community of the three indices of phytoplankton standing crop used—cell numbers, cell volume (biomass) and cell surface area. This led Paasche to suggest that cell surface area might provide the most adequate measure of the phytoplankton standing crop. Although the plasma volume was not determined, he clearly acknowledged that the cell surface area provides an indirect measure of it. Paasche's Norwegian Sea results, therefore, appear to be consistent with the Gulf of Panama observations.

It may be argued, however, that the Panama results represent a "bottle effect" in that considerable exchange or loss of radio-carbon might be expected during the 24 hour incubation period used (Ryther, 1956; Fogg, 1958). There are insufficient data to evaluate properly this possible effect exclusive of the accompanying biological activity, although it would appear

to be of minor overall importance on the basis of the discussion to follow. But even if a significant "bottle effect" should be found to accompany such long term (24 hours) incubation periods and invalidate use of the data as *production estimates,* the possible routine use of such an experimental procedure to estimate *standing crop,* as suggested here (Figs. 7, 8; Table 9), should be further explored.

That cell surface area and cell volume in the form of the A/V ratio influences metabolism is apparent from observations on natural and cultured phytoplankton species that smaller cells assimilate nutrients, respire and divide faster than larger cells (Braarud, 1945; Munk and Riley, 1952; Margalef *et al.,* 1955; Verduin, 1952). That community behavior should likewise be influenced by average cell size is not as obvious, however. In view of the experimental procedure, the observed influence of the diatom community abundance and A/V ratio on carbon uptake might be considered to represent primarily a physical adsorption and/or diffusion of this element rather than active biological uptake. However, if C^{14} uptake resulted primarily from adsorption onto particles, then a much greater scatter of the data than observed (Figs. 3-8) might be expected in response to the considerable seasonal and station-to-station variations in turbidity (Jerlov, 1953; Forsbergh, 1963; Smayda, *unpublished*). Osterberg, Small and Hubbard (1963) found that the adsorption of radionuclides onto the surface of diverse zooplankters was insignificant.

The diffusion of carbon, or any substance, into or out of a cell can be treated as a rheological phenomenon as Eggleton (1952) has done. He (p. 469-470) concluded that as a physical phenomenon "the time scale of a diffusion process is linked to the *square* of the depth through which diffusion has to occur." That is, diffusion into and out of a living algal cell having ten times the diameter of another will take a 100 times longer than in the smaller cell. Thus, viewed strictly as a diffusion phenomenon, a greater rate of carbon uptake would be expected in communities having a higher area-to-volume ratio (smaller cells) than in those comprised of larger cells, even though the standing crop may be similar. This has been observed where such comparisons could be made (Table 20).

Eggleton's conclusion probably does not apply completely to diatoms since diffusion would appear to occur primarily into the thin cytoplasmic layer lining the inner cell wall rather than continuing entirely into the central vacuolar area (Fig. 2). While this might reduce the time scale of the diffusion process, the relative influence of cell size on this rate should remain the same, however.

Although cell size influences the rate of nutrient uptake, it is well established that nutrient utilization is fundamentally a metabolic rather than a physical process. The lower rate of dark fixation of C^{14} compared to that in the light illustrates such biological control. However, observa-

TABLE 20. C^{14} assimilation in communities of equal diatom standing crop as plasma volume (PV) but differing in cell numbers present and A/V ratio.

Station	cells/L	mgC ass./m³	PV (mg/m³)	A/V	mgC ass. / mg PV-C
53	177,560	10.0	543	0.35	0.154
3	264,130	12.0	540	0.30	0.185
61	176,460	26.0	532	0.38	0.406
32	265,960	42.0	567	0.46	0.618

tions of P^{32} (Odum, Kuenzler and Blunt, 1958) and Zn^{65} uptake (Gutknecht, 1961, 1963) by benthic marine algae indicate that significant sorption onto the cell walls occurs without immediate incorporation into the protoplasm. Odum *et al.* (1958) demonstrated that the rates of P^{32} uptake, which were similar in the light and the dark for a given species, and gross production (oxygen method) per gram biomass were directly related to the surface/volume ratio of the seven species used. That is, the rates of P^{32} uptake and gross production increased with increasing A/V. These authors suggest that P^{32} is sorbed at a rate determined by the structural surface area features of an alga in such a way that the rate of P^{32} assimilation (p. 345) "is related to potential production rate and not to the metabolic level occurring at the time of measurement . . . . Therefore, the rate of tracer uptake might be a better index of what the system 'can do' given favorable conditions of light, temperature, etc., rather than a measure of what it 'is doing' at the moment provided there is any sort of consistent relationship between these living surfaces and other sorptive surfaces."

Although Gutknecht (1961, 1963) observed a higher rate of Zn^{65} uptake in the light than in the dark, he concluded that the uptake of this isotope represents primarily a non-metabolic adsorption-exchange related to pH and surface/volume, and secondarily is attributable to photosynthesis. For non-aquatic plants, Steward and Sutcliffe (1959, p. 343) have shown that the rate of uptake of ions of the stable isotopes rubidium and bromide in potato discs is also directly related to the A/V of the slices used.

Since C^{14} uptake occurs during photosynthesis, it is also influenced by the amount of chlorophyll present. Paasche (1960) has demonstrated that the chlorophyll content per unit of cell surface area or cell volume for various species is inversely related to cell size. On the basis of diffusion kinetics (Eggleton, 1952), a greater rate of carbon assimilation per unit of chlorophyll would be expected in these smaller cells or communities than in the larger ones.

This diverse evidence, a possible "bottle effect" notwithstanding, suggests that the observed influence of the diatom community A/V ratio on C^{14} uptake (Figs. 7, 8) is consistent with theoretical and experimental observations reported for physical and biological systems. That C^{14} uptake

is also directly related to the standing crop cell surface area and plasma volume may reflect sorption and photosynthetic activity similar to that described for P^{32} and Zn^{65} uptake (Odum *et al.,* 1958; Gutknecht, 1961; 1963). On the other hand, it may simply confirm that the surface area and plasma volume estimates of the standing crop provide a measure of the assimilative and photosynthetic surfaces, as well as "metabolically active" tissue present. Clearly, further investigations are desirable.

It has been demonstrated that the total community carbon uptake can be satisfactorily related to the diatom standing crop. This may reflect, in part, the relative paucity of the non-diatomaceous groups (Table 1; Appendix Tables 1, 2), notwithstanding the probable underestimation of the micro-flagellates, as discussed earlier. An additional factor may be that predominantly heterotrophic micro-flagellate (see Grøntved, 1958, however) and dinoflagellate (especially the Gymnodiniaceae) populations were present. It is uncertain, however, whether a carbon uptake - standing crop relationship would hold for the flagellate groups in the manner observed for the diatoms. For instance, the plasma volume is virtually equivalent to the total cell volume in the flagellates owing to the absence of, or presence of relatively small, vacuoles (Lohmann, 1908). Furthermore, the forced convection and diffusion of nutrients associated with the motility of these cells may be expected to mask the apparent role of the surface/volume ratio and cell surface in carbon uptake. Therefore, similar observations of the C^{14} assimilation - standing crop relationship in predominantly dinoflagellate or coccolithophore communities would be of interest.

It is especially interesting that a strong relationship should exist between carbon uptake and diatom standing crop *irrespective* of the species composition, environmental conditions, or dynamic state of the communities (Table 21; Appendix Table 1). Considerable station-to-station differences in dominant species were observed. For example, the following diatom species either singly or in combination with two to four others of those listed comprised from 50 to 98 per cent of the community as cell numbers: *Bacteriastrum elegans, hyalinum, varians; Chaetoceros affinis, atlanticus, compressus, curvisetus, laciniosus, laevis, lorenzianus, socialis; Eucampia cornuta; Guinardia flaccida; Hemiaulus membranaceus; Leptocylindus minimus; Nitzschia delicatissima, pacifica, pungens* var. *atlanticus; Rhizosolenia delicatula, stolterfothii; Skeletonema costatum* f. *tropicum;* and *Thalassiosira aestivalis.* Considerable differences in environmental conditions were also observed at the various stations, one-third of which were sampled during the rainy season (Figs. 3, 7). The range in environmental conditions observed at the various stations sampled during the rainy and upwelling seasons was: 0.02 to 2.24 μg-at/L PO_4-P; 16.83 to 28.17 C; 28.41 to 34.53 ‰ (Appendix Table 1).

Both the standing crop and the rate of C^{14} uptake were usually greater at those stations sampled during the upwelling season than during the rainy season (Figs. 3, 7; Appendix Table 1). However, considerable station-to-

TABLE 21. Representative environmental conditions and community structure at 10 meters during various months at 8°45'N, 79°23'W.

Station	30	39	47	58
Date	23 Jan. 1956	19 June 1956	8 Oct. 1956	12 Mar. 1957
Temperature, C	16.83	28.06	28.17	22.7
Salinity, ‰	34.53	29.51	29.36	34.20
σ_t	25.21	18.28	18.13	23.36
O_2 % Sat.	88.2	104.8	100.7	78.9
PO_4 μg at/L	1.23	0.10	0.22	1.06
DIATOMS (cells/liter)	445,900	2,500	11,260	1,097,240
DINOFLAGELLATES	—	9,640	3,100	11,700
COCCOLITHOPHORES	—	—	4,500	—
MONADS	47,500	12,000	19,000	8,500
TOTAL	493,400	24,140	37,860	1,117,440
DIATOMS:				
Chaetoceros affinis	300	140	4,500	—
Chaetoceros compressus	19,000	60	420	—
Chaetoceros curvisetus	52,000	80	—	—
Chaetoceros socialis	253,000	—	—	—
Lauderia annulata	24,000	—	—	—
Nitzschia delicatissima	—	500	—	660,000
Nitzschia pacifica + pungens	—	—	1,000	321,000
Rhizosolenia delicatula	—	—	—	33,000
Rhizosolenia stolterfothii	9,000	—	40	43,000
Skeletonema costatum f. *tropicum*	40,500	560	660	—
DINOFLAGELLATES:				
Exuviaella baltica	—	1,000	1,500	—
Exuviaella vaginula	—	—	—	3,000
Oxytoxum variabile	—	500	1,000	5,000
Gymnodiniaceae	—	7,500	500	3,500
COCCOLITHOPHORES:				
Gephyrocapsa oceanica	—	—	3,000	—

station differences in metabolic condition of the community were observed during both seasons. The population density ranged from 1,020 to approximately 3.2×10^6 c/L during the upwelling season, and from 240 to 176,320 c/L during the rainy season (May to November) (Appendix Table 1). Thus, *variable station-to-station differences in metabolic state ranging from senescent to vigorously growing communities are included in the regression analyses* (Figs. 3-9). Such variable metabolic states, which are probably associated with various degrees of nutrient limitation and the stage of growth (Smayda, 1963), can be expected to influence carbon fixation (Ryther *et al.*, 1958).

Communities belonging to both A/V sub-groups established during the analyses were present during the rainy and upwelling seasons (Fig. 7). One might expect environmentally induced variations in vitality as well as inter-specific physiological differences to contribute to a weaker relationship between carbon uptake and standing crop than actually observed (Figs. 3-8). It is pertinent that this relationship was better correlated when the standing crop was expressed as plasma volume and cell surface area than as total biomass (Figs. 4-8; Tables 6, 7, 9). This probably re-

flects, in part, the fact that these two indices represent the photosynthetic and assimilatory surfaces through which nutrients must diffuse to meet the respiratory demands of the total biomass (μ^3). But of greater importance to the present discussion is the fact that inter- and intra-specific differences in cell size are considerably less when based on plasma volume than on total cell volume, and least when based on surface area (Table 4). For example, there is only a 47-fold difference in mean surface area between *Skeletonema costatum* f. *tropicum* (mean volume of 1,000 μ^3) and *Rhizosolenia bergonii* (mean volume of 144,000 μ^3), as contrasted to a 102- and 144-fold difference in mean plasma volume and total cell volume, respectively (Table 4). A more meaningful comparison, however, is to compare the amount of assimilatory surface (μ^2) available per unit of tissue (μ^3), i.e. the A/V ratio (Table 4). Based on total cell volume, the extreme inter-specific range for species belonging to different size groups is 1.8 to 6.8 μ^3 of tissue per μ^2 of assimilatory surface, i.e. a 3.8-fold difference in the V/A ratio between *Skeletonema costatum* f. *tropicum* and *Guinardia flaccida* (Table 4). There is only 2.2-fold difference when based on plasma volume, however, the range extending from 1.2 to 2.7 μ^3 of tissue per unit (μ^2) of assimilatory area (Table 4). Thus, inter-specific differences in size appear to be relatively *insignificant* when based on their plasma volume-to-cell surface area (PV/A) ratios, or any ratio between surface area and volume (Table 4). This fact, coupled with the apparent role of the surface/volume ratio and chlorophyll in influencing phytoplankton growth, as discussed previously, suggests a mechanism permitting phytoplankton communities, within limits, to respond and be treated as a *physical* system irrespective of the species present in a manner consistent with the observed carbon uptake - standing crop relationship (Figs. 7, 8). A more detailed discussion of information gathering by diatoms is presented elsewhere (Smayda, 1965).

SUMMARY

The relationships existing between C^{14} assimilation as determined by 24 hour *in situ* experiments and diatom standing crop at 10 meters when expressed as cell numbers, cell volume, cell surface area and cell plasma volume have been assessed for 30 observations made between November 1954 and May 1957 at 8°45′N, 79°23′W.

The average cell volume and cell surface area characteristics for 110 diatom species and varieties are presented.

Use of cell numbers as an index of standing crop size in comparisons between community abundance and an associated physiological response is generally biased towards the smaller, usually more numerous species present, whereas use of cell volume (biomass) favors the "giant" species. Use of plasma volume generally provides a more acccurate estimate of

"metabolically active" plant tissue than total cell volume. Use of cell surface area provides a measure of both the assimilative area (μ^2) through which nutrients must diffuse to meet the respiratory demands of the biomass (μ^3), and the area available for chloroplasts, i.e. the "photosynthetic surface".

Plasma volume or cell surface area appears to provide the best estimate of the microscopically derived measures of standing crop abundance for comparisons between community composition + abundance and a physiological response. Surface area and plasma volume estimates of standing crop appear to be interchangeable, either estimate providing a measure of the assimilative and photosynthetic surfaces, as well as "metabolically active" tissue.

Inter- and intra-specific differences and variations in diatom cell size are considerably less pronounced when based on plasma volume than on total cell volume, and are least pronounced when based on surface area. Intra-specific variations in the surface/volume ratio are relatively minor when based on plasma volume than on total cell volume for the range in cell size encountered. Inter-specific differences in the surface/volume ratio are less pronounced when based on plasma volume than on total cell volume.

A direct relationship exists between C^{14} assimilation and the various diatom standing crop indices used, the regressions accounting for 36 to 45 per cent of the variation. The regression on surface/volume (A/V)-weighted diatom cell number provided the best fit, whereas that on total cell volume (biomass) was poorest.

A substantial improvement in the regressions of carbon assimilation on standing crop occurred after omitting three anomalous responses which could be attributed to either enumerative or experimental error. From 44 to 63 per cent of the variation could then be accounted for by the regressions. Carbon uptake was best related to standing crop when expressed as cell numbers and least related to total cell volume (biomass). From 54 to 56 per cent of the variation could be explained by the regressions on plasma volume and surface area, respectively.

The diatom communities could be partitioned into two groups on the basis of their cumulative A/V ratio: a). those with an A/V ratio ≥ 0.40, and b). those with a ratio < 0.40. In the regression analyses of C^{14} uptake on plasma volume and surface area, from 73 to 75 per cent of the variation could be explained, respectively, for those communities with an A/V ratio of < 0.40, and 86 to 87 per cent for the communities ≥ 0.40.

A strong direct relationship exists between C^{14} assimilation and the standing crop when the latter is expressed as total surface area or plasma volume, irrespective of the species composition, environmental conditions or dynamic state of the communities. This relationship suggests that the

C^{14} experiments provide a measure of the diatom standing crop in the Gulf of Panama in addition to some measure of primary production.

The observed influence of the diatom community surface/volume ratio on C^{14} uptake within certain limits also suggests that this characteristic influences phytoplankton *community* dynamics, as has previously been observed for individual species.

The rate of carbon assimilation per unit of standing crop is inversely related to the magnitude of the standing crop, i.e. it is density dependent.

The amount of chlorophyll *a* per unit of standing crop is inversely related to the magnitude of the standing crop. Mean carbon : chlorophyll *a* ratios, by weight, of 325:1 and 195:1 based on total cell volume (biomass) carbon and plasma volume carbon, respectively, were found.

The relative efficiency (RE) of carbon uptake, defined as the daily amount of carbon assimilation per unit of chlorophyll *a* per unit of visible light per day, is directly related to the size of the standing crop ($r=0.96^{**}$).

An index of relative efficiency (R′E′) based on daily carbon assimilation per m^3 per community A/V unit agreed closely ($r = 0.93^{**}$) with the RE calculated from available chlorophyll *a* and visible light intensity.

An approximation of the community A/V ratio could be derived from the relationship: $\frac{\text{mgC assimilated per m}^3}{100\ \text{RE}}$, which would place 85 per cent of the stations in the same size group used in the regression analyses as those based on microscopic measurement.

Above standing crop levels of 200 mg biomass C per m^3 Strickland's productivity index (PI) progressively decreased as the former increased. No obvious relationship was found between inorganic phosphate concentration and the PI. For standing crops greater than about 100 mg biomass C per m^3 the productivity index (PI) progressively decreased while the relative efficiency (RE) increased with increasing standing crop.

The data suggest that a relative low PI and high RE are indicative of communities approaching an asymptote, while the converse signals a vigorously growing community.

The PI values, in general, approximated the microscopically derived community A/V ratios ($r = 0.71^{**}$).

The median production coefficient values (the amount of carbon produced per gram of phytoplankton carbon per day) were 13 and 21 per cent based on biomass carbon and plasma volume carbon, respectively. The maximum frequency of daily carbon turnover was in the range of 2 to 11 per cent based on biomass carbon, and 5 to 23 per cent based on plasma

volume carbon. The production coefficients were generally lower than those reported from other areas.

The observed production coefficients were in good agreement with those calculated by the Riley, Stommel and Bumpus equation: $P_h = KI_{10}\, v_p$.

The calculated production coefficients appeared to be more a function of the available light and, possibly, the A/V characteristic of the community than of the temperature and amount of phosphate present.

The mechanisms contributing to the observed dependence of carbon uptake on the A/V and magnitude of the community standing crop are considered.

RESUMEN

Las relaciones existentes entre la asimilación del C^{14}, determinadas después de 24 horas de experimentos *in situ,* y la cosecha estable de las diatomeas a 10 metros, expresando el número de células, volumen celular, área de la superficie celular y volumen del plasma celular, han sido determinadas por medio de 30 observaciones hechas entre noviembre de 1954 y mayo de 1957, a los 8°45′N, 79°23′W.

Se presenta, para 110 especies y variedades de diatomeas, el promedio de las características del volumen celular y del área de la superficie celular.

El uso del número de células como un índice del tamaño de la cosecha estable al comparar la abundancia de la comunidad y una reacción fisiológica asociada, está generalmente sesgado hacia las especies pequeñas, más numerosas que se presentan, mientras que el volumen celular (biomasa) favorece las especies "gigantes." El uso del volumen del plasma generalmente provee una estimación más acertada del tejido "metabólicamente activo" de la planta que el total del volumen de la célula. El uso del área de la superficie celular proporciona una medida tanto del área asimilativa (μ^2) a través de la cual los nutrientes deben difundirse para satisfacer la demanda respiratoria de la biomasa (μ^3), como también del área disponible para los cloroplastos, esto es, la "superficie fotosintética."

El volumen del plasma o el área de la superficie celular parecen suministrar la mejor estimación de las medidas microscópicamente derivadas de la abundancia de la cosecha estable, cuando se compara la composición de la comunidad + abundancia y una reacción fisiológica. Las estimaciones del área de la superficie y del volumen del plasma de la cosecha estable parecen ser intercambiables, dando cada estimación una medida de las superficies asimilativas y fotosintéticas, como también del tejido "metabólicamente activo".

Las diferencias y variaciones inter e intraespecíficas del tamaño celular de las diatomeas son considerablemente menos pronunciadas cuando se basan en el volumen del plasma que sobre el volumen total de la célula, y son menos pronunciadas cuando se basan sobre el área de la superficie. Las variaciones intraespecíficas en la proporción superficie/volumen son relativamente menores cuando están basadas en el volumen del plasma que sobre el volumen total celular en la amplitud del tamaño de las células halladas. Las diferencias interespecíficas en la razón superficie/volumen son menos pronunciadas cuando se basan sobre el volumen del plasma que sobre el total del volumen celular.

Existe una relación directa entre la asimilación del C^{14} y los varios índices usados de la cosecha estable de diatomeas; las regresiones incluyen del 36 al 45 por ciento de la variación. La regresión de superficie/volumen (S/V)—cantidad ponderada provee el mejor ajuste, mientras que aquella basada en el volumen total celular (biomasa) fue la más deficiente.

Un mejoramiento substancial en las regresiones de la asimilación del carbono sobre la cosecha estable resultó al omitir tres reacciones anómalas que pueden ser atribuidas ya sea al error experimental o enumerativo. De 44 a 63 por ciento de la variación puede entonces ser comprendida por las regresiones. La absorción del carbono se relaciona ventajosamente con la cosecha estable cuando se expresa en número de células, y se relaciona deficientemente con el volumen celular total (biomasa). De 54 a 56 por ciento de la variación puede ser explicada por las regresiones sobre el volumen del plasma y el área superficial, respectivamente.

Las comunidades de diatomeas pueden dividirse en dos grupos en base a su razón cumulativa S/V: a) aquellas con una razón S/V $\geq$ 0.40, y b) aquellas con una razón $<$ 0.40. En los análisis de las regresiones de la absorción del C^{14} sobre el volumen del plasma y el área superficial, puede explicarse del 73 al 75 por ciento de la variación, respectivamente, para aquellas comunidades con una razón S/V $<$ 0.40, y 86 a 87 por ciento para aquellas comunidades con una proporción $\geq$ 0.40.

Existe una relación directa acentuada entre la asimilación del C^{14} y la cosecha estable, cuando ésta última se expresa ya sea como área superficial total o como volumen del plasma independiente a la composición de las especies, condiciones ambientales, o al estado dinámico de las comunidades. Esta relación sugiere que los experimentos del C^{14} proporcionan una medida de la cosecha estable de las diatomeas en el Golfo de Panamá, además de alguna medida de producción primaria.

La influencia observada de la razón superficie/volumen de la comunidad de las diatomeas sobre la absorción de C^{14}, sugiere también que, dentro de ciertos límites, esta característica influye en la dinámica de la *comunidad* del fitoplancton, como se ha venido observando en las especies individuales.

La tasa de asimilación del carbono por unidad de la cosecha estable se relaciona inversamente con la magnitud de la cosecha estable, esto es, depende de la densidad.

La cantidad de clorofila *a* por unidad de cosecha estable está relacionada inversamente con la magnitud de la cosecha estable. Se encontraron las proporciones del promedio de carbono : clorofila *a* por peso de 325:1 y 195:1 basado sobre el volumen total celular (biomasa) y el carbono por volumen de plasma, respectivamente.

La eficiencia relativa (ER) de la absorción de carbono, definida como la cantidad de carbono diariamente asimilado por unidad de clorofila *a* por unidad de luz visible por día, está directamente relacionada al tamaño de la cosecha estable ($r = 0.96^{**}$).

Un índice de la eficiencia relativa (E'R') basado en la asimilación diaria de carbono por m^3 por unidad S/V de la comunidad está muy de

acuerdo ($r = 0.93^{**}$) con la ER calculada de la clorofila *a* disponible y de la intensidad de luz visible.

Una aproximación de la razón S/V de la comunidad puede deducirse de la relación: $\frac{\text{mg C asimilado por m}^3}{100\ \text{ER}}$, lo que colocaría 85 por ciento de las estaciones en el mismo grupo de tamaño usado en los análisis de regresión comparado con aquellos basados en las medidas microscópicas.

Sobre los niveles de la cosecha estable de 200 mg de biomasa C por m^3 el índice de productividad de Strickland (IP) disminuye progresivamente mientras el primero aumenta. No se encontró relación evidente entre la concentración del fosfato inorgánico y el IP. Para una cosecha estable de más de 100 mg de biomasa C por m^3 el índice de productividad (IP) disminuye progresivamente mientras que la eficiencia relativa (ER) aumenta con el incremento de la cosecha estable.

Los datos sugieren que el IP relativamente bajo y la alta ER indican una aproximación de las comunidades a una asíntota, mientras que lo contrario indica una comunidad que crece vigorosamente.

Los valores del IP se aproximan, en general, a las proporciones S/V de la comunidad ($r = 0.71^{**}$) derivadas microscópicamente.

Los valores de los coeficientes de la producción mediana (la cantidad de carbono producido por gramo de carbono del fitoplancton por día) fueron de 13 a 21 por ciento basado en el carbono de la biomasa y en el carbono por volumen de plasma, respectivamente. La frecuencia máxima del ciclo diario de carbono se colocó en orden del 2 al 11 por ciento, basado en el carbono de la biomasa, y de 5 a 23 por ciento basado en el carbono por volumen de plasma. Los coeficientes de producción fueron generalmente más bajos que los que se obtuvieron de otras áreas.

Los coeficientes de producción observados estuvieron bien de acuerdo con aquellos calculados por la ecuación de Riley, Stommel y Bumpus: $P_h = KI_{10}v_p$.

Los coeficientes de producción calculados parecen estar más en función de la luz disponible y, posiblemente de la característica S/V de la comunidad, que de la temperatura y cantidad de fosfato presente.

EXPLANATION OF SYMBOLS

*	significance at P 0.01
**	significance at P 0.001
A	cell surface area expressed as μ^2 or cm^2
A/PV	ratio of cell surface area expressed as μ^2 to cell plasma volume expressed as μ^3
A/V	ratio of cell surface area expressed as μ^2 to cell volume expressed as μ^3
A_i/V_i	ratio of cell surface area to cell volume for the i'th species
BM	standing crop biomass; or wet weight
BM-C	biomass carbon; standing crop carbon content based on wet weight
C	carbon
C′	constant of 10^{-2} used in the derivation of relative efficiency (R′E′)
c/L	cells per liter
D	Secchi Disc disappearance depth in meters
day_{24}	24-hour day
F	factor for converting mm^3 of algal volume to equivalent mg carbon
F′	factor for converting gC per m^3 at 10 meters to gC per m^2 per day
i	i'th species (i = 1, 2, 3, . . ., m)
I_0	incident radiation; or light intensity at the surface
I_{10}	light intensity at 10 meters
K	photosynthetic constant with value of 2.5
K′	photosynthetic constant with value of 7.6
k	vertical absorption coefficient per meter
ly	langley = gram-calorie of radiant energy per cm^2
μ^2	square microns of cell surface area
μ^3	cubic microns of total cell volume; or plasma volume
μ^2/μ^3	ratio of cell surface area to cell volume
N_i	number of cells of the i'th species
P_b	production coefficient of Riley, Stommel and Bumpus (grams carbon produced per day per gram of phytoplankton carbon)

P'_h	production coefficient calculated from the equation: $P'_h = (P_h)\ (A/V)$
PI	Strickland's productivity index: hourly rate of carbon increase per unit of phytoplankton carbon at a standard light intensity of 1 ly/min of photosynthetically active light
PV	cell plasma volume
PV-C	plasma volume carbon; or carbon content based on plasma volume estimation
PV/A	ratio of cell plasma volume to cell surface area
r	sample correlation coefficient
RE	Forsbergh's relative efficiency of photosynthesis based on total radiant energy flux: mgC/mgChl*a*/ly
R′E′	relative efficiency of photosynthesis based on visible radiant energy flux: mgC/mgChl*a*/ly. Also derivable from the equation: $R'E' = \text{mgC assimilated } m^{-3}/100(A/V)$
Sfc. A	cell surface area expressed as μ^2 or cm^2
$\sum_{i=1}^{m} \frac{A_i}{V_i} N_i$	summation of the number of cells of each species (N_i) weighted by their cell surface area-to-cell volume ratio (A_i/V_i)
$\sum_{i=1}^{m} N_i$	summation of the number of cells of each species
$\sum_{i=1}^{m} N_i A_i$	summation of the number of cells of each species weighted by their cell surface area (A_i)
$\sum_{i=1}^{m} N_i V_i$	summation of the number of cells of each species weighted by their cell volume (V_i)
$\sum_{i=1}^{m} \frac{V_i}{A_i} N_i$	summation of the number of cells of each species weighted by their cell volume-to-cell surface area ratio (V_i/A_i)
T	light transmission per meter
T′	absolute temperature
v_p	Riley, Stommel and Bumpus nutrient index: the amount of reduction of the photosynthetic rate that results from phosphate depletion
V	total cell volume expressed as μ^3 or mm^3
V/A	ratio of total cell volume expressed as μ^3 to cell surface area expressed as μ^2
V_i/A_i	ratio of cell volume to cell surface area for the i'th species

LITERATURE CITED

Allen, W. E.
1939 Surface distribution of marine plankton diatoms in the Panama region in 1933.
Bull. Scripps Inst. Oceanogr., Tech. Ser., **4**(7):181-196.

Berge, Grim
1958 The primary production in the Norwegian Sea in June 1954, measured by an adapted ^{14}C technique.
Cons. Explor. Mer, Rapp. Proc.-Verb., **144**:85-91.

Bogorov, B. G.
1959 On the standardization of marine plankton investigations.
Int. Rev. gesamt. Hydrobiol., **44**(4):621-642.

Braarud, Trygve
1945 Experimental studies on marine plankton diatoms.
Norske VidenskAkad., Oslo, I. Mat.-Naturv. Klasse, 1944 (10): 1-16.

Eggleton, P.
1952 Diffusion phenomena in biology, Chapter IX.
In Albert Frey-Wyssling [ed.] Deformation and flow in biological systems. Interscience Publ., Inc., New York.

Fogg, G. E.
1958 Extracellular products of phytoplankton and the estimation of primary production.
Cons. Explor. Mer, Rapp. Proc.-Verb., **144**:56-60.

Forsbergh, E. D.
1963 Some relationships of meteorological, hydrographic, and biological variables in the Gulf of Panama [in English and Spanish].
Inter-Amer. Trop. Tuna Comm., Bull., **7**(1):1-109.

Grøntved, Jul.
1958 Planktological Contributions III. Investigations on the phytoplankton and the primary production in an oyster culture in the Limfjord.
Medd. Danmarks Komm. Havundersög. N. S., **2**(17):1-18.

Gutknecht, John

1961 Mechanism of radioactive zinc uptake by *Ulva lactuca.* Limnol. and Oceanogr., **6**(4):426-431.

1963 Zn^{65} uptake by benthic marine algae. *Ibid.,* **8**(1):31-38.

Harvey, H. W.

1950 On the production of living matter in the sea off Plymouth. J. Mar. Biol. Ass. U. K., **29**:97-137.

1955 The chemistry and fertility of sea waters. Cambridge Univ. Press, London.

Hasle, G. R.

1959 A quantitative study of phytoplankton from the equatorial Pacific. Deep-Sea Res., **6**(1):38-59.

_____ and T. J. Smayda

1960 The annual phytoplankton cycle at Drøbak, Oslofjord. Nytt Magasin f. Botanikk, **8**:53-75.

Hulburt, E. M., J. H. Ryther and R. R. L. Guillard

1960 The phytoplankton of the Sargasso Sea off Bermuda. J. Cons. Int. Explor. Mer, **25**(2):115-128.

Jenkin, P. M.

1937 Oxygen production by the diatom *Coscinodiscus excentricus* Ehr. in relation to submarine illumination in the English channel. J. Mar. Biol. Ass. U. K., **22**:301-343.

Jerlov, N. G.

1953 Particle distribution in the ocean. Rept. Swedish Deep-Sea Exped. 1947-1948, **3**(2):71-98.

Lohmann, Hans

1908 Untersuchungen zur Feststellung des vollständigen Gehaltes des Meeres an Plankton. Wiss. Meeresuntersuch. Abt. Kiel, N. F., **10**:131-370.

Lund, J. W. G., C. Kipling and E. D. LeCren

1958 The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia, **11**(2):143-170.

Margalef, Ramón
1958 Temporal succession and spatial heterogeneity in phytoplankton, p. 323-349.
In A. A. Buzzati-Traverso [ed.] Perspectives in marine biology.
Univ. Calif. Press, Los Angeles.

_____, M. Durán and F. Saiz
1955 El fitoplancton de la ría de Vigo de enero de 1953 a marzo de 1954.
Invest. Pesq., **2**:85-129.

Menzel, D. W. and J. H. Ryther
1961 Zooplankton in the Sargasso Sea off Bermuda and its relation to organic production.
J. Cons. Int. Explor. Mer, **26**(3):250-258.

Munk, W. H. and G. Riley
1952 Absorption of nutrients by aquatic plants.
J. Mar. Res., **11**(2):215-240.

McAllister, C. D., T. R. Parsons, K. Stephens and J. D. H. Strickland
1961 Measurements of primary production in coastal sea water using a large-volume plastic sphere.
Limnol. and Oceanogr., **6**(3):237-258.

Occhipinti, A. G., A. Magliocca and C. Teixeira
1961 Diurnal variation of phytoplankton production and solar radiation in coastal waters off Cananéia.
Bol. Inst. Ocean., São Paulo, **11**(3):17-40.

Odum, E. P., E. J. Kuenzler and Sister Marion X. Blunt
1958 Uptake of P^{32} and primary productivity in marine benthic algae.
Limnol. and Oceanogr., **3**(3):340-348.

Odum, H. T.
1956 Efficiencies, size of organisms, and community structure.
Ecology, **37**(3):592-597.

Osorio Tafall, B. F.
1943 El mar de Cortés y la productividad fitoplanctónica des sus aguas.
An. Esc. Nacional de Cienc. Biol., **3**(1, 2):73-118.

Osterberg, C., L. Small and L. Hubbard
1963 Radioactivity in large marine plankton as a function of surface area.
Nature, **197**:883-884.

Paasche, Eystein
1960 On the relationship between primary production and standing stock of phytoplankton.
J. Cons. Int. Explor. Mer, **26**(1):33-48.

Parsons, T., K. Stephens and J. D. H. Strickland
1961 On the chemical composition of eleven species of marine phytoplankters.
J. Fish. Res. Bd. Canada, **18**(6):1001-1016.

Peterson, C. L.
1961 Fecundity of the anchoveta (*Cetengraulis mysticetus*) in the Gulf of Panama [in English and Spanish].
Inter-Amer. Trop. Tuna Comm., Bull., **6**(2):53-68.

Poole, H. H. and W. R. G. Atkins
1929 Photo-electric measurements of submarine illumination throughout the year.
J. Mar. Biol. Ass. U. K., **16**:297-324.

Pratt, D. M.
1959 The phytoplankton of Narragansett Bay.
Limnol. and Oceanogr., **4**(4):425-440.

Riley, G. A., H. Stommel and D. F. Bumpus
1949 Quantitative ecology of the plankton of the western North Atlantic.
Bull. Bingham Oceanogr. Coll., **12**(3):1-169.

Rodhe, W., R. A. Vollenweider and A. Nauwerck
1958 The primary production and standing crop of phytoplankton, p. 299-322.
In A. A. Buzzati-Traverso [ed.] Perspectives in marine biology. Univ. Calif. Press, Los Angeles.

Ryther, J. H.
1956 Interrelation between photosynthesis and respiration in the marine flagellate, *Dunaliella euchlora.*
Nature, **178**:861-862.

———, and R. R. L. Guillard

1962 Studies of marine planktonic diatoms III. Some effects of temperature on respiration of five species.
Can. J. Microbiol., **8**:447-453.

———, and C. S. Yentsch

1957 The estimation of phytoplankton production in the ocean from chlorophyll and light data.
Limnol. and Oceanogr., **2**(3):281-286.

———, C. S. Yentsch, E. M. Hulburt and R. F. Vaccaro

1958 The dynamics of a diatom bloom.
Biol. Bull., **115**(2):257-268.

Schaefer, M. B. and Y. M. M. Bishop

1958 Particulate iron in the offshore waters of the Panama Bight and in the Gulf of Panama.
Limnol. and Oceanogr., **3**(2):137-149.

———, Y. M. M. Bishop and G. V. Howard

1958 Some aspects of upwelling in the Gulf of Panama [in English and Spanish].
Inter-Amer. Trop. Tuna Comm., Bull., **3**(2):77-130.

Smayda, T. J.

1957 Phytoplankton studies in lower Narragansett Bay.
Limnol. and Oceanogr., **2**(4):342-359.

1959 Some preliminary results from a quantitative analysis of the phytoplankton in the Gulf of Panama.
Preprints, Int. Oceanogr. Cong., New York, p. 901-903.

1963 A quantitative analysis of the phytoplankton of the Gulf of Panama I. Results of the regional phytoplankton surveys during July and November, 1957 and March, 1958 [with Spanish summary].
Inter-Amer. Trop. Tuna Comm., Bull., **7**(3):191-253.

1965 Succession, and a possible mechanism of information gathering by marine diatoms.
Jekyll Island Conference on Estuaries, Proc., (*in press*).

Steele, J. H.

1958 Plant production in the northern North Sea.
Scottish Home Dept., Mar. Res., No. 7, p. 3-36.

Steemann Nielsen, E.

1952 The use of radio-active carbon (C^{14}) for measuring organic production in the sea.
J. Cons. Int. Explor. Mer, **18**(2):117-140.

———, and V. K. Hansen

1959 Light adaptation in marine phytoplankton populations and its inter-relation with temperature.
Physiologia Plantarum, **12**:353-370.

Steward, F. C. and J. F. Sutcliffe

1959 Plants in relation to inorganic salts, Chapter IV.
In F. C. Steward [ed.] Plant physiology. Vol. II. Academic Press, New York.

Strickland, J. D. H.

1958 Solar radiation penetrating the ocean. A review of requirements, data and methods of measurement, with particular reference to photosynthetic productivity.
J. Fish. Res. Bd. Canada, **15**(3):453-493.

1960 Measuring the production of marine phytoplankton.
Fish. Res. Bd. Canada, Bull., No. 122, 172 p.

Talling, J. F.

1957 Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation.
The New Phytologist, **56**:29-50.

Utermöhl, Hans

1931 Neue Wege in der quantitativen Erfassung des Planktons. (Mit besonderer Berücksichtigung des Ultraplanktons.)
Verh. Int. Ver. Limnol., **5**:567-596.

Verduin, Jacob

1952 The volume-based photosynthetic rates of aquatic plants.
Amer. J. Bot., **39**(3):157-159.

Vives, F. and F. Fraga

1961 Producción básica en la Ría de Vigo.
Invest. Pesq., **19**:129-137.

Wright, J. C.

1959 Limnology of Canyon Ferry Reservoir II. Phytoplankton standing crop and primary production.
Limnol. and Oceanogr., **4**(3):235-245.

1960 The limnology of Canyon Ferry Reservoir III. Some observations on the density dependence of photosynthesis and its cause.
Ibid., **5**(4):356-361.

APPENDIX TABLE 1. Summary of the physical and biological conditions at 10 meters at 8°45′N, 79°23′W during the C^{14} experiments. The diatom population given as n × 10^6 cells or units per m^3; biomass (BM), biomass carbon (BM-C), plasma volume (PV) and plasma volume carbon (PV-C) as mg per m^3; cell surface area (Sfc. A) as cm^2 per m^3 or μ^2. The light (I_{10}) values represent photosynthetically (visible) usable radiation. The activity coefficients represent the daily carbon uptake per unit of standing crop per m^3. (Stations 3 - 27 were sampled in 1955; stations 29 - 52 in 1956; stations 53 - 63 in 1957.)

								DIATOM ABUNDANCE (n × 10^6 per m^3)			DIATOM COMMUNITY						ACTIVITY COEFFICIENTS		
Station	Date	Temp. C	$S‰$	PO_4-P μg-at/L	I_{10} ly/day	Chl. *a* mg/m^3	C^{14} mg/m^3	(Cells) m ΣN_i i=1	(A/V-weighted abundance) m $\Sigma(A_i/V_i)N_i$ i=1	(V/A-weighted abundance) m $\Sigma(V_i/A_i)N_i$ i=1	BM mg/m^3	BM-C mg/m^3	PV mg/m^3	PV-C mg/m^3	Sfc. A cm^2/m^3	A/V	mgC/mgBM	mgC/mgPV	mgC/μ^2
3	1/11	26.11	31.99	—	—	—	12.0	264.13	169.57	521.05	972.0	116.5	540.3	65.0	2950.	0.30	.012	.022	.040
4	1/25	26.61	30.67	—	—	—	9.2	3.20	3.87	4.76	4.5	.55	3.6	.45	20.	0.47	2.04	2.56	4.38
5	2/8	26.56	31.52	—	—	—	9.2	46.66	20.31	101.88	283.8	34.0	168.8	20.5	900.	0.32	.032	.055	.101
27	12/12	27.00	28.41	0.72	—	—	4.8	105.88	70.57	210.40	432.9	52.0	255.8	30.5	1420.	0.33	.011	.019	.034
29	1/9	25.33	29.38	0.68	—	—	57.0	795.40	413.20	1704.94	4909.5	589.0	3644.0	437.5	21020.	0.43	.012	.016	.027
30	1/23	16.83	34.53	1.23	—	—	17.0	445.90	306.22	832.89	3946.0	473.5	1283.5	154.0	5830.	0.15	.004	.013	.029
32	2/21	25.50	32.24	0.48	—	—	42.0	265.96	169.62	464.39	711.1	85.5	567.2	68.0	3310.	0.46	.059	.074	.126
34	3/21	19.33	33.76	2.08	—	—	1.5	253.38	282.34	403.85	699.7	84.0	592.9	71.0	3490.	0.50	.002	.003	.004
35	4/2	18.44	34.43	0.59	—	—	31.0	300.50	164.22	614.51	871.3	104.5	871.3	104.5	5430.	0.62	.035	.034	.057
36	5/17	25.28	33.29	0.38	—	—	4.7	.24	.71	1.08	10.2	1.2	3.9	.45	20.	0.18	.460	1.21	2.47
39	6/19	28.06	29.51	0.10	—	—	3.1	2.50	2.25	4.04	6.8	.8	5.8	.7	30.	0.51	.455	.536	.911
40	7/2	28.06	30.44	0.42	—	—	3.4	38.76	23.28	84.96	260.7	31.5	135.3	16.0	730.	0.28	.013	.025	.046
42	7/31	27.72	30.17	0.45	—	—	4.5	67.80	41.08	129.46	253.5	30.5	156.5	19.0	870.	0.34	.018	.028	.051
43	8/13	27.89	30.13	0.71	29.0	—	3.8	145.28	84.24	338.19	1586.9	190.5	464.2	55.5	2040.	0.13	.002	.008	.019
44	8/27	27.78	29.49	0.68	—	—	3.0	32.78	16.54	81.98	419.4	50.5	139.6	17.0	650.	0.16	.007	.021	.046
47	10/8	28.17	29.36	0.22	—	—	1.2	11.26	7.12	20.25	42.3	5.0	23.3	2.8	130.	0.30	.028	.051	.094
48	10/22	27.56	28.48	0.57	55.5	—	7.7	176.32	104.53	351.51	604.2	72.5	405.0	48.5	2300.	0.38	.012	.019	.034
51	12/3	25.72	30.12	0.97	—	—	8.2	35.02	25.39	54.81	80.5	9.5	47.7	5.5	260.	0.33	.101	.171	.310
52	12/17	26.72	28.45	0.81	43.5	0.73	9.4	181.48	101.46	358.95	602.8	72.5	379.0	45.5	2125.	0.35	.016	.025	.044
53	1/2	26.7	28.90	1.65	30.5	0.75	10.0	177.56	104.95	441.81	860.0	103.0	543.2	65.0	3050.	0.35	.011	.018	.032
54	1/14	25.6	32.23	2.24	47.5	0.76	52.0	3149.94	1968.50	6798.89	8671.5	1040.5	4731.0	567.5	25760.	0.30	.006	.011	.020
55	1/29	23.1	—	0.60	29.0	1.45	32.0	2014.26	1663.11	4900.06	3981.5	478.0	2718.5	326.0	15470.	0.39	.008	.011	.021
56	2/11	23.7	32.75	0.26	31.6	0.84	24.0	882.08	594.64	2035.26	5560.8	667.5	2923.8	351.0	15785.	0.28	.004	.008	.015
57	2/25	21.6	34.04	0.10	4.7	0.69	10.0	2331.70	1011.05	5576.16	7385.5	886.5	5047.2	605.5	28720.	0.39	.001	.001	.003
58	3/12	22.7	34.20	1.06	50.0	0.85	26.0	1097.24	2372.19	1230.18	962.2	115.5	962.2	115.5	6330.	0.66	.027	.024	.041
59	3/21	20.3	34.40	0.48	—	1.11	2.5	1.02	.71	14.36	1.1	.15	.6	.05	6.	0.54	1.363	2.470	4.166
60	4/10	—	34.27	—	27.6	—	31.0	1124.60	530.04	2422.44	5488.5	658.5	4265.9	512.0	24850.	0.45	.005	.007	.012
61	4/22	25.2	34.23	—	90.0	—	26.0	176.46	110.15	366.10	786.2	94.5	531.5	64.0	3020.	0.38	.033	.048	.086
62	5/6	25.2	34.25	0.55	58.5	0.71	6.9	64.56	41.68	506.36	317.6	38.0	197.0	23.5	1100.	0.35	.021	.035	.062
63	5/20	27.7	32.43	0.02	—	0.41	10.0	25.34	29.89	34.22	41.3	5.0	41.3	5.0	340.	0.83	.242	.180	.290

APPENDIX TABLE 2. Summary of the flagellate abundance at 10 meters. Cell number given as n × 10^6 cells per m^3, biomass (BM) as mg per m^3, and surface area (Sfc. A) as cm^2 per m^3. (All dinoflagellates have been assumed to be *Exuviaella baltica* (625 μ^3 and 450 μ^2), all coccolithophores *Coccolithus huxleyi* (130 μ^3 and 125 μ^2) and all micro-flagellates as having a mean volume of 65 μ^3 and area of 79 μ^2 in the calculation of tissue volume (biomass) and surface area for these algal groups.)

	DINOFLAGELLATES			COCCOLITHOPHORES			MICRO-FLAGELLATES		
Station	cells	BM	Sfc. A	cells	BM	Sfc. A	cells	BM	Sfc. A
3	3.22	2.01	14.49	1.50	.20	1.88	14.50	.94	11.46
4	1.62	1.01	7.29	1.50	.20	1.88	1.00	.07	.79
5	.58	.36	2.61	.50	.07	.63	10.50	.68	8.30
27	1.04	.65	4.68	—	—	—	34.00	.22	26.86
29	2.28	1.43	10.26	5.00	.65	6.25	85.50	5.56	67.55
30	—	—	—	—	—	—	47.50	3.09	37.53
32	11.08	6.93	49.86	89.00	11.57	111.25	54.52	3.54	43.07
34	5.96	3.73	26.82	44.00	5.72	55.00	26.86	1.75	21.22
35	1.20	.75	5.40	7.00	.91	8.75	1713.00	3340.35	12933.15
36	.02	.01	.09	.50	.07	.63	8.00	.52	6.32
39	9.64	6.03	43.38	—	—	—	7.00	.84	9.48
40	4.10	2.56	18.45	16.02	2.08	20.03	26.00	1.69	20.54
42	7.18	4.49	32.31	9.60	1.25	12.00	51.00	3.32	40.29
43	3.12	1.95	14.04	2.50	.33	3.13	48.50	3.15	38.32
44	3.50	2.19	15.75	.50	.07	.63	11.50	.75	9.09
47	3.10	1.94	13.95	4.50	.59	5.63	19.00	1.24	15.01
48	1.74	1.09	.78	—	—	—	21.00	1.37	16.59
51	4.06	2.54	18.27	1.50	.20	1.88	15.50	1.01	12.25
52	5.64	3.53	25.38	10.00	1.13	12.50	15.00	.98	11.85
53	.04	.03	.18	—	—	—	5.00	.33	3.95
54	.08	.05	.36	.50	.07	.63	5.00	.33	3.95
55	.18	.11	.81	—	—	—	55.00	3.58	43.45
56	10.22	6.39	45.99	—	—	—	24.58	1.60	19.42
57	41.50	25.94	186.75	2.00	.26	2.50	77.00	5.01	60.83
58	11.70	7.31	52.65	—	—	—	8.50	.55	6.72
59	2.00	.13	9.00	.50	.07	.63	1.00	.07	.79
60	1.72	1.08	7.74	—	—	—	11.00	.72	8.69
61	16.58	10.36	74.61	—	—	—	26.50	1.72	20.94
62	7.76	4.85	34.92	.50	.07	.63	28.50	1.85	.81
63	1.22	.76	5.49	—	—	—	1.02	.07	.81