PLANKTON ENERGETICS OF RARITAN BAY

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ABSTRACT

Plankton production in Raritan Bay is described based on total chlorophyll data and two series of 24-hr dark and light bottle differential oxygen experiments. Maximum chlorophyll (γ) recorded was 663 μg L^{-1} in a bloom of *Massartia rotundata*. Utility of pigment data in estimating productivity or biomass is regarded as dubious: i) 17.3×10^6 chains of *Skeletonema costatum* once corresponded to only trace quantities of chlorophyll; ii) production occurred several times in absence of detectable chlorophyll.

In the first (1957) series of experiments, gross production (π) at 1 ft ranged from 4.8 to 531.6 μg O$_2$ L^{-1} hr^{-1}. Ratios of $\pi\gamma^{-1}$ (when $\gamma > 0$) varied from –0.4 to 14.1 μg O$_2$ L^{-1} hr^{-1} μg^{-1}. Respiration (ρ) at 1 ft ranged from –49.1 to 230.8 μg O$_2$ L^{-1} hr^{-1}, and net production ($\pi - \rho$) from –24.7 to 483.0.

In the second (1959) series at a station 15 ft deep, chlorophyll in the whole water column varied from 14.68 to 173.14 μg cm^{-2} (mean 50.75). The range of π was 1.65–13.90, of ρ 1.42–24.51, and of ($\pi - \rho$) –14.63 to 4.53 cal cm^{-2} day^{-1}. Compensation depths ranged from 0 to 6.3 ft (mean 3.0); compensation points varied from 37.1 to 315.7 cal cm^{-2} day^{-1} (mean 169.3). A model is developed which demonstrates that *compensation* is the critical variable in water mass metabolism, and that determination of this variable is the main reason for experimentation. Gross production per unit light intensity (I) at a given depth z, $(\pi I^{-1})_z$, ranged 0.3–828.6 μg O$_2$ L^{-1} cal^{-1} cm^{-2}. Chlorophyll activity, $(\pi I^{-1} \gamma^{-1})_z$, varied from 0.03 to 6.62 μg O$_2$ L^{-1} cal^{-1} cm^{-2} μg^{-1}. Total production in the water column relative to incident radiation, $\pi_{0 \to z} I_0^{-1}$, ranged from 0.17 to 1.78% (mean 0.88%). Production efficiency relative to amount of light in the water column, $(\pi I^{-1})_{0 \to z}$, was 0.96–28.71 cal kcal^{-1} (mean 9.07 or 0.907%). Thermodynamic cost of energy procurement varied from 0.54 to 2.58 cal cal^{-1} (mean 1.48), indicating a net energy loss during the study. It is concluded that even if this indicated dystrophy is widespread in the upper estuary, sufficient energy is probably introduced from Lower Bay in the form of standing planktonic biomass to bring the system into positive energy balance.

INTRODUCTION

The primary fixation and subsequent utilization of energy by biotic communities is perhaps the most fundamental action performed. Although energy flow pathways through communities are complex (Lindeman 1942; Clarke 1946; MacFadyen 1948; Odum and Odum 1955; Odum 1956, 1957; Teal 1957, 1959; Patten 1959*a*), the overall process is simple. The ecosystem,

itself an aggregation of energy states, continually sacrifices some of its energy to the second law of thermodynamics. Consequently, to preserve its integrity it must procure more energy from the environment. When rate of accrual equals rate of attrition, steady state prevails. When unequal, the system grows or declines, depending upon the direction of the inequality.

This paper is concerned with energy relationships in Raritan Bay plankton. It de-

scribes the annual distribution of chloro-
phyll in the estuary, and reports the results
of two series of light and dark bottle pro-
duction experiments.

METHODS

Total chlorophyll (γ) was determined by
millipore (type HA) filtering a sample,
grinding filtrate and filter with sand in 90%
acetone containing $MgCO_3$, and then ex-
tracting in the dark for at least 12 hr. No
chlorophyll was lost under these conditions
(see Creitz and Richards 1955, Ryther and
Yentsch 1957). The extract was subse-
quently Seitz-filtered to remove sand and
undissolved millipore filter fragments, after
which absorption of light passed through a
#66 filter was determined with a Lumetron
colorimeter. Percentage transmittance was
converted to optical density, and then to
total chlorophyll using a standard curve
prepared from pure chlorophyll a. The
values obtained were corrected for original
volume of water filtered, and total chloro-
phyll expressed as $\mu g\ L^{-1}$.

Two series of dark and light bottle ex-
periments were performed, one in 1957 and
the other in 1959. The series in 1957 was a
pilot study, with emphasis on developing
a feasible field technique. A more elabo-
rate experimental design was employed in
1959.

In the 1957 experiments paired B.O.D. or
citrate bottles were filled with duplicate
samples from different depths, and sus-
pended in situ for as close to 24 hr as
possible, then retrieved and fixed for oxy-
gen titration by the unmodified Winkler
method. Gross production (π), commu-
nity respiration (ρ), and net community
production $(\pi - \rho)$ were computed from
the initial and final dissolved oxygen con-
centrations. When desirable, outputs in mg
$O_2\ L^{-1}$ were converted to cal cm^{-2} based
on a $PQ(+O_2/-CO_2)$ of 1.25 (Ryther 1956).
When chlorophyll was assayed, $\pi\gamma^{-1}$ ratios
were calculated.

The 1959 series was restricted to one
station on the south edge of the ship chan-
nel off Princess Bay, Staten Island (Fig. 1).
Mean low water depth at the station was

about 15 ft. "Master" samples were col-
lected from 1, 5, and 9 ft in an inert con-
tainer and mixed thoroughly to assure
identical communities in replicate bottles.
Samples from each collection depth were
suspended at 1, 5, and 9 ft to compare their
behavior under variable conditions of light
(principally) and temperature. Thus, each
experiment consisted of 9 light bottles and
9 dark bottles: L1-1, L1-5, L1-9, L5-1, ...,
L9-9; D1-1, ..., D9-9, where the number
to the left represents collection depth and
that to the right depth of suspension. Each
experiment was initiated as close to 1200 hr
(EST) as possible, and terminated 24 hr
later.

Incident solar radiation (I_0) was ob-
tained with an Eppley 10-junction pyrheli-
ometer situated less than 10 miles from the
site. Extinction coefficients (η) were de-
termined with the Lumetron colorimeter
using a neutral filter.

CHLOROPHYLL

Chlorophyll assay has developed into one
of the important techniques for estimating
primary production (Ryther 1956). The
method is based on the well-documented
constancy of photosynthesis and chloro-
phyll concentration at any given light in-
tensity (Emerson 1929, Emerson and Ar-
nold 1932, Fleischer 1935, Gaffron and
Wohl 1936, Emerson, et al. 1940, Manning
and Juday 1941, Gessner 1949, Blaauw–
Jansen, et al. 1950, Edmondson 1955, and
Ryther 1956). This constancy is surprising,
really, when one considers: i) the known
loss of efficiency at high concentrations
brought about by high population densities
(Tamiya, et al. 1953, McQuate 1956, Ver-
duin 1959), ii) the occurrence of inactive
chlorophyll (Smith 1954), iii) the associa-
tion of large quantities of chlorophyll and
its degradation products with non-living
detritus (Gillbricht 1951, Krey 1952) and
sediments (Vallentyne 1955, Vallentyne and
Bidwell 1956, Vallentyne and Craston 1957),
and iv) the seasonal variations in ratios of
chlorophyll to phytoplankton organic mat-
ter (Harris and Riley 1956). Ryther and
Yentsch (1957) have developed an empiri-

TABLE 1. *Annual distribution of surface chlorophyll concentration at stations 1–6. The units are µg L^{-1}; t signifies trace quantities (less than 4 µg L^{-1})*

Date			Station 1	Station 2	Station 3	Station 4	Station 5	Station 6
July	11,	1957	35.2	–	35.5	52.8	–	53.9
	18		43.6	62.3	104.2	75.0	–	–
	26		20.8	61.3	59.6	49.8	71.3	61.0
Aug	1		48.4	45.6	81.5	67.1	41.3	76.5
	8		0.0	0.0	0.0	7.8	0.0	25.6
	15		37.5	24.5	22.7	22.7	97.0	21.9
	21		58.5	34.7	43.0	55.0	89.1	65.8
	28		–	–	–	–	57.9	49.6
	29		33.4	44.6	64.0	43.7	64.7	62.6
Sept	9		–	–	28.6	7.2	–	–
	12		18.9	7.4	6.8	13.4	20.5	13.4
	23		15.0	12.4	19.5	8.8	25.7	10.9
Oct	8		9.4	17.4	20.5	20.2	19.2	9.5
	15		–	–	2.1	–	–	–
	28		–	–	0.0	–	–	–
	29		t	0.0	t	t	7.9	t
Nov	19		0.0	0.0	0.0	0.0	0.0	0.0
Dec	6		0.0	0.0	0.0	0.0	0.0	–
	17		–	–	0.0	–	0.0	–
	20		0.0	t	–	0.0	–	–
Jan	20,	1958	9.7	t	t	10.0	6.4	t
Feb	6		11.3	t	t	8.4	t	t
Mar	1		9.9	t	t	8.5	t	7.3
	11		t	4.8	4.8	4.6	4.6	4.8
Apr	10		t	t	0.0	4.9	5.3	0.0
	24		26.3	88.5	76.0	94.4	61.5	61.8
May	10		0.0	0.0	0.0	0.0	0.0	0.0
	30		9.5	9.8	10.1	17.2	25.8	18.3
June	23		43.8	22.3	38.2	21.6	34.6	20.4
July	7		33.2	25.4	27.7	162.8	57.7	46.6
	24		27.5	36.6	39.3	29.8	40.0	39.8
Aug	11		34.7	79.2	56.8	95.7	87.6	80.6
	21		8.4	8.2	13.6	22.7	15.0	22.7

cal equation for estimating production from chlorophyll concentration, solar radiation, and visible light extinction based on the assumption of a parallel relationship. Later (1958, Fig. 2) they give data for the continental shelf region southeast of Raritan Bay showing almost a 25-fold variability in production per unit chlorophyll at optimum (sic) light intensities. Verduin (1959) has recently indicated that winter phytoplankton communities are comparably productive to those of summer (which presumably contained more chlorophyll per unit biomass) under light intensities only 1/40 as great. Thus, it would seem that further study is necessary before the efficacy of chlorophyll as an index to productivity becomes unequivocal.

The seasonal aspect of chlorophyll distribution in Raritan Bay is confounded with a daily periodicity (Yentsch and Ryther 1957), making the hour of sampling a consideration. In general, highest chlorophyll concentrations prevailed during the summer, diminishing in September and October to virtual and literal absence in late October, November, and December (Table 1). Traces of chlorophyll began to appear in January, and low levels prevailed throughout the early spring to mid-April. On 24 April, 1958, at the height of the vernal diatom flowering, high chlorophyll levels were recorded throughout the estuary. After the bloom declined, chlorophyll was absent for a period, then gradually increased to late summer maxima.
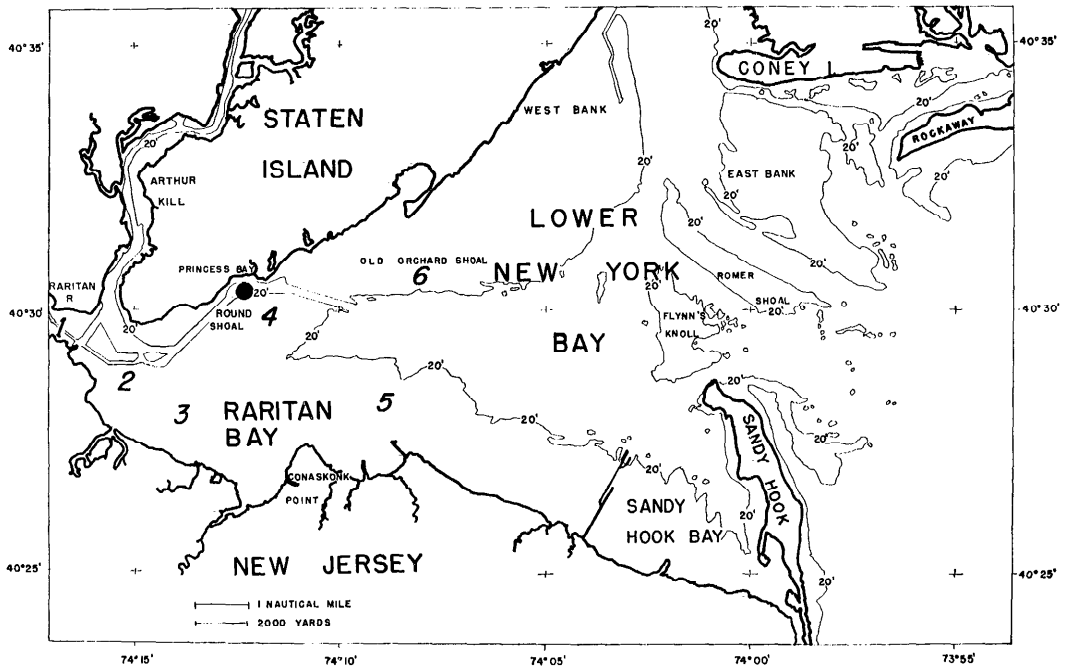
FIG. 1.   Raritan Bay, showing sampling stations (1–6) and dark and light bottle station (●).

Chlorophyll concentrations did not always correlate well with phytoplankton population levels in the estuary. For example, the low autumnal levels did not reflect adequately the high concentrations of colorless chrysoflagellates (especially *Oxyrrhis marina*) dominant during this period. Also, on one occasion during the spring bloom, dominated by *Skeletonema costatum*, 17.3×10^6 units of *Skeletonema* per liter yielded only trace quantities of pigment.

Lowest chlorophyll was generally recorded at stations 1 and 2 at the head of the bay (Fig. 1). The highest levels of summer, 1957, occurred at stations 3 and 5, but in summer, 1958, greatest concentrations were at stations 4, 5, and 6. Red water was encountered in July, 1957; in late May, 1958; and again in June and July, 1959. The principal red tide organism in 1959 was *Massartia rotundata*. Other forms associated as minor constituents were *Eutreptia* sp., *Nannochloris atomus*, *Pyramimonas* sp., *Peridinium trochoideum*, *Gymnodinium* sp., *Skeletonema costatum*, and tin-

tinnids. Chlorophyll levels recorded in the 1957 red tides ranged from 75 to 105 μg L^{-1}. The highest concentration recorded in the bay prior to the summer of 1959 was 162.8 μg L^{-1} at station 4 on 7 July, 1958. Strangely, the water on this occasion did not appear red, possibly because the principal organism was *Nannochloris* (40.6×10^7 units L^{-1}) instead of *Massartia*. The value of 162.8 μg L^{-1} is considerably less than maxima recorded by Riley (1956) of 314 μg L^{-1} in Long Island Sound, and by Pomeroy, *et al.* (1956) of 360 μg L^{-1} in Delaware Bay in 1955. However, during the red water period of 1959, a surface sample was collected on 30 June from center-bay northeast of Conaskonk Pt. which assayed 663 μg L^{-1}. High winds on 1 July completely dispersed this aggregation (*Massartia*) so that no evidence of it remained on 3 July.

Chlorophyll was not usually vertically uniform throughout the water column. Table 2 presents data for some profiles obtained during summer and autumn, 1957. Highest chlorophyll concentration was gen-

TABLE 2. *Vertical distribution of chlorophyll on several dates during summer and autumn, 1957. Chlorophyll concentrations, γ, are given in $\mu g\ L^{-1}$; differentials, $\Delta\gamma$, are also indicated*

Depth (feet)	Station 2 γ	$\Delta\gamma$	Station 3 γ	$\Delta\gamma$	Station 4 γ	$\Delta\gamma$	Station 5 γ	$\Delta\gamma$	Station 6 γ	$\Delta\gamma$
	(SEPT 9)		(SEPT 9)		(SEPT 9)		(AUG 28)		(AUG 28)	
0	–		–				57.9		49.6	
								–7.8		5.6
1	11.7		27.2		8.6		50.1		55.2	
		25.4		–0.4		8.8		–2.7		0.3
3	37.1		26.8		17.4		47.4		55.5	
		–1.3		–8.7		–9.6		–0.2		0.3
5	35.8		18.1		7.8		47.2		55.8	
								–11.0		4.9
7							36.2		60.7	
								10.3		–4.6
11							46.5		56.1	
								–10.1		0.1
15							36.3		50.2	
								0.7		–2.6
17							37.0		–	
19									47.6	
	(SEPT 23)		(SEPT 23)		(SEPT 23)					
0	–		25.7		–					
				1.1						
1	12.4		26.8		10.9					
		–1.5		0.0		–1.6				
3	10.9		26.8		9.3					
		–0.9		–0.5		1.2				
5	10.0		26.3		10.5					
	(OCT 28)				(OCT 28)					
1	trace				0.0					
3	trace				0.0					
5	0.0				0.0					

erally several feet beneath the surface. Vertical homogeneity did occur late in September, associated with the more complete mixing attending breakdown of summer stratification, and also with dominance by non-motile diatoms at that time. Further data on this aspect are presented later which show that motile organisms with highly active (photosynthetically) chlorophyll can maintain a vertical gradient of chlorophyll activity, although not necessarily of concentration.

BOTTLE EXPERIMENTS—1957

Criticisms of the Gaarder and Gran (1927) dark and light bottle technique may be grouped into four categories: i)

stagnation of the closed cultures with time (Ryther 1956, Verduin 1956); ii) tendency to overestimate π and ρ because of a) differential development of bacteria in dark and light bottles due to inhibition by light (Steemann Nielsen 1952) or by photosynthesizing phytoplankton (Steemann Nielsen 1955), and b) inordinate bacterial growth made possible by increased surface area of containers (Pratt and Berkson 1959); iii) tendency to underestimate π and ρ with consequent under- or overestimation of $(\pi - \rho)$ due to settling of organisms (Verduin, *et al.* 1959); iv) tendency to underestimate light bottle respiration, hence π, because of differential biomass changes in light vs. dark. Of these criticisms, the

last is most basic because it is insuperably bound to the very thing the experiment endeavors to measure. The other three factors are potentially subject to empirical control.

Ryther and Yentsch (1958), studying the annual productivity of the continental shelf waters off New York, estimated an average 0.2–1.0 g C m^{-2} day^{-1} gross production. This is equivalent to 22.2–111.2 μg O$_2$ L^{-1} hr^{-1}, assuming a photosynthetic quotient (+O$_2$/–CO$_2$) of unity. In the 1957 series of dark and light bottle experiments in Raritan Bay, photosynthesis at 1 ft ranged from 4.8 to 531.6 μg O$_2$ L^{-1} hr^{-1} (Table 3). Gross production generally decreased with depth due to reduced light, but not in every case since more chlorophyll may have been present in some of the deeper samples. Production per unit chlorophyll, $\pi\gamma^{-1}$, was computed whenever possible. These ratios varied considerably from date to date and station to station, although highest values always occurred at the surface. On several occasions positive production was measured in absence of detectable chlorophyll (denoted by $\pi\gamma^{-1} = \infty$ in Table 3). When chlorophyll was present, production per μg ranged from –0.39 to 14.09 μg O$_2$ L^{-1} hr^{-1}, the negative value having been obtained at 7 ft. Respiration rate ranged from –49.1 to 230.8 μg O$_2$ L^{-1} hr^{-1} at 1 ft. The several negative values obtained for respiration suggest either light leakage into the dark bottles or non-photosynthetic production. The $\pi\gamma^{-1}$ ratios of ∞ also indicate the possibility of chemoautotrophic mechanisms. Net community production at 1 ft depth ranged from –24.7 to 483.0 μg O$_2$ L^{-1} hr^{-1}, the maximum value being about four times the maximum offshore gross production recorded by Ryther and Yentsch (1958).

BOTTLE EXPERIMENTS—1959

Hydrography

This series comprised 11 experiments, one each week between 16 June and 25 August. The hydrographic data are summarized in Table 4.

Salinity varied from 24.45 to 26.67‰. Surface water was generally somewhat less saline than mid-depths, and deeper waters slightly more saline. The maximum vertical gradient encountered was only 0.81‰, the mean 0.44‰, and the minimum 0.03‰, indicating a reasonably well-mixed water column.

Temperature varied from 18.00°C on 16 June to 26.32 on 17 August. Maximum vertical gradient was 2.82°C on 8 July, minimum 0.06 on 24 August, and the mean gradient was 0.99°C. Temperature was always greater at the surface, except on 15 July when an inverse gradient was observed, and on 24 August when some surface cooling was in evidence. These temperature patterns also indicate a fairly homogeneous water column.

Secchi disc data proved very unreliable, and showed only little relationship to extinction coefficients obtained by measuring transmittance through a neutral filter. Minimum depth at which the disc disappeared was 45 in. on 16 June, maximum was 82 in. on 17 August, and the mean for the summer was 62 in.

Fate of Solar Radiation

Insolation, I_0, impinges on a water surface directly from the sun and indirectly from the sky. Part of this radiation, I_R, is reflected from the surface or back-scattered. The total loss to I_R is variable, but will be regarded here as 6% of I_0 (see Hutchinson 1957). The remainder, I_A, is transmitted ($I_{0 \to z}$) and absorbed (I_α). The absorption rate is expressed by the extinction coefficient:

$$\eta = z^{-1} \ln \left(I_0 I_z^{-1} \right),$$

where I_z is light intensity at depth z. Calculated values of η were used to compute I_z at several depths, and these figures were then graphed. A typical graph (for expt. I) is provided in Fig. 2, the curve being drawn through the points I_A, $I_{z=1}$, I_5, and I_9. The following areas may be distinguished:

1) ACDF, the potential transmission, I_A, to depth z in absence of an absorbing medium.

TABLE 3. *Summary of 1957 dark and light bottle experiments. Chlorophyll concentration, γ, is in μg L^{-1}; $\pi\gamma^{-1}$ ratios are given wherever the data permitted their calculation; values of ∞ indicate production in absence of detectable chlorophyll*

Station	Depth (ft)	Time (EST) Start	End	Duration (hr)	π	ρ	$\pi - \rho$	γ	$\pi\gamma^{-1}$
				JULY 18–19					
2	1	1310	1245	23.58	–	–	–	62.3	–
	5				89.5	138.3	–48.8	–	–
	7				77.6	64.5	13.1	–	–
3	1	1400	1320	23.67	–	–	83.2	104.2	–
	4				–	–	–171.5	–	–
	7				–	23.7	–	–	–
4	1	1450	1415	23.58	149.7	75.9	73.8	75.0	2.00
	4				38.2	92.0	–53.9	–	–
	7				48.3	337.2	–288.8	–	–
				AUG. 7–8					
2	1	1110	0915	22.10	108.6	25.8	82.8	0.0	∞
	3				46.2	24.9	21.3	0.0	∞
	5				24.4	34.4	–10.0	0.0	∞
5	1	1155	1140	23.67	271.2	95.9	175.3	0.0	∞
	5				81.5	68.0	13.5	–	–
	9				0.0	52.4	–52.4	13.7	0.00
	14				–	–	–	–	–
6	1	1235	1250	24.25	261.4	103.5	157.9	25.6	10.21
	7				113.0	79.2	33.8	–	–
	15				17.5	52.0	–34.6	12.5	1.40
	19				–	–	–	–	–
				AUG. 14–15					
2	1	1045	1350	27.10	7.4	–24.7	32.1	24.5	0.30
	3				38.4	23.6	14.8	–	–
	7				–4.8	15.5	–20.3	12.4	–0.39
				AUG. 20–21					
2	1	0945	1315	27.50	489.0	132.0	357.1	34.7	14.09
	3				293.1	175.3	117.8	–	–
	7				26.2	98.9	–72.7	–	–
	11				–	–	–	34.0	–
				AUG. 28–29					
2	1	1430	1420	23.83	531.6	48.7	483.0	44.6	11.92
	3				139.3	57.5	81.8	–	–
	5				26.9	42.0	–15.1	34.7	0.78
5	1	1000	0950	23.83	148.6	–49.1	197.7	50.1	2.97
	5				–	–	–21.8	47.2	–
	9				–	–	–43.6	37.4	–
6	1	1230	1100	22.50	183.6	16.4	167.1	55.2	3.33
	5				145.8	61.3	84.4	55.8	2.61
	9				40.0	58.7	–18.7	–	–
				SEPT. 9–10					
2	1	1500	1500	24.00	6.7	21.3	–14.6	11.7	0.57
	3				–	13.3	–	37.1	–
	5				–	–	–20.8	35.8	–
between 3 and 5	1	1155	1535	27.67	23.5	10.1	13.4	27.2	0.86
	3				2.9	–15.2	–12.3	26.8	0.11
	5				17.0	20.6	–3.6	18.1	0.94
between 4 and 6	1	1255	1600	27.10	–	–	–24.7	8.6	–
	3				–	–	–22.9	17.4	–
	5				–	–	–	7.8	–

TABLE 3.   (Continued)

Station	Depth (ft)	Time (EST) Start	End	Duration (hr)	π	ρ	$\pi - \rho$	γ	$\pi\gamma^{-1}$
				SEPT. 23–24					
2	1	1230	1430	26.00	–	–	230.8	12.4	–
	3				125.8	28.8	96.9	10.9	11.54
	5				30.8	28.8	1.9	10.0	3.08
between	1	1345	1235	22.83	–	–	42.0	10.9	–
4 and 6	3				23.2	9.2	14.0	9.3	2.51
	5				11.8	18.8	–7.0	10.5	1.12
				OCT. 28–29					
2	1	1400	1630	26.50	10.2	10.2	0.0	0.0	∞
	3				20.0	12.1	7.9	0.0	∞
	5				12.1	6.0	6.0	0.0	∞
4	1	1500	1345	22.75	4.8	14.5	–9.7	0.0	∞
	3				26.4	44.8	–18.5	0.0	∞
	5				8.4	18.9	–9.7	0.0	∞

2) ABEF, the potential transmission not realized at depth z due to absorption.

3) BCDE, the amount of light remaining at depth z.

4) ACD'E', the total light, $I_{0 \to z}$, transmitted to depth z where

$$I_{0 \to z} = I_0 \int_0^z e^{-\eta z}\, dz$$

$$= I_0 \eta^{-1}(1 - e^{-\eta z}) \; .$$

5) ABE', the fraction, $I'_{0 \to z}$, of the total transmitted light absorbed.

FIG. 2.   Diagram of fate of solar radiation in a water column (description in text).

6) AE'EF, the total light, I_α, not transmitted to depth z due to absorption ($I_\alpha = I_A - I_{0 \to z}$). In practice $I'_{0 \to z}$ and $I_{0 \to z}$ were always equal at this station since light was always completely extinguished at 15 ft. The quantity $I_{0 \to z}$ is the total energy available for photosynthesis in the water column. Table 5 summarizes the data on I_0, I_R, I_A, $I_{0 \to z}$, $I_{0 \to z} I_0^{-1}$, and η obtained for each of the 11 experiments. I_0 ranged from 277.4 to 953.6 cal cm^{-2} day^{-1}; $I_{0 \to z}$ varied from 309.5 to 1,346.0 cal cm^{-2} day^{-1}.

Chlorophyll Distribution

Initial chlorophyll concentrations, γ, at the beginning of each experiment are reported in Table 6 for each experimental depth. The range at 1 ft was 5.97–135.42 μg L^{-1}, at 5 ft 10.65–106.25 μg L^{-1}, and at 9 ft 10.42–56.70 μg L^{-1}. The vertical distribution is shown to be not uniform. Highest values generally occurred at the surface (8 out of 11 times), and lowest either at 9 ft (6 out of 11) or 5 ft (4 out of 11). Gradients were generally slight at low concentration levels (mean 6.58 μg L^{-1}), but steeper when high concentrations were present (experiments IV and VII, mean 69.93). The maintenance of high γ concentrations in the surface layers may be due in part to motility of the organisms. The principal organism at 1 ft in experiment IV was *Massartia*, associated
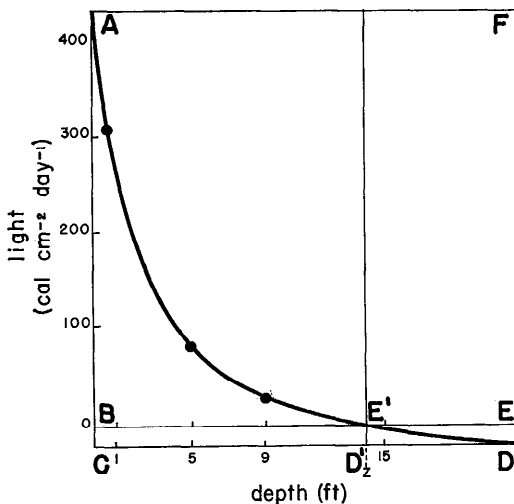
TABLE 4. *Hydrography of the sampling station opposite Princess Bay during the summer of 1959*

Experiment	Dates	Salinity, ‰			Secchi disc (in.)	Temperature, °C						
		1 ft	5 ft	9 ft		Surface	1	3	5	7	9	Bottom
I	Jun 16	–	–	–	45	18.00	–	–	–	–	–	–
	17					–	–	–	–	–	–	–
II	Jun 23	26.47	26.52	26.67	49	19.00	19.00	19.00	18.80	18.55	18.35	–
	24					18.85	18.70	18.65	18.58	18.50	18.45	–
III	Jul 2	26.34	25.80	25.92	61	23.00	22.95	22.93	22.90	22.90	23.00	22.75
	3					23.22	22.98	22.80	22.68	22.62	23.30	22.45
IV	Jul 8	25.04	25.23	25.48	59	25.82	25.40	24.47	23.60	23.60	23.40	23.00
	9					25.15	24.70	24.67	24.23	24.05	23.83	23.45
V	Jul 15	25.24	25.50	25.57	75	23.40	23.48	23.57	23.52	23.50	23.50	23.45
	16					23.40	23.40	23.35	23.30	23.29	23.29	23.24
VI	Jul 20	24.92	25.10	25.60	80	–	–	–	–	–	–	–
	21					25.64	24.84	24.38	24.13	24.10	24.07	23.90
VII	Jul 29	25.60	25.82	26.13	39	25.72	25.50	25.38	25.27	25.05	24.85	23.50
	30					–	–	–	–	–	–	–
VIII	Aug 3	24.87	25.73	25.68	62	25.80	–	–	–	–	–	–
	4					–	–	–	–	–	–	–
IX	Aug 10	24.45	24.61	24.69	62	23.44	23.08	23.00	22.87	22.85	22.56	22.19
	11					–	–	–	–	–	–	–
X	Aug 17	24.68	25.14	25.36	82	26.32	25.97	25.15	25.11	25.10	25.10	25.10
	18					25.70	25.51	25.30	25.25	25.22	25.21	25.21
XI	Aug 24	26.27	26.24	26.27	63	23.34	23.40	23.40	23.40	23.40	23.40	23.40
	25					24.10	24.10	24.08	24.00	23.82	23.50	23.20

with *Eutreptia* and *Pyramimonas*. At 5 ft and 9 ft, however, *Nannochloris* and *Skeletonema*, both non-motile, were dominant, and *Massartia* was entirely absent. In this experiment there was no vertical salinity gradient, but there was a considerable thermal gradient, with the warmer water sharply restricted to the surface (Table 4). In experiment VII, the whole water column was dominated by *Nannochloris* and *Skeletonema*, including the surface, although

Massartia was the third most important species in cell numbers in the upper 1 ft, was rare at 5 ft and absent at 9 ft. In view of what has previously been said about the low chlorophyll content of *Skeletonema*, it seems likely that most of the pigment on this occasion was contributed by *Nannochloris* and *Massartia*, and the gradient resulted from ability of motile *Massartia* to maintain itself at the surface. No salinity gradient existed in experiment VII, but the temperature gradient was considerable,

TABLE 5. *Radiation parameters for each experiment performed during summer, 1959. Values are in cal cm^{-2} day^{-1}. Extinction coefficients (η) are also provided*

Experiment	I_0	I_R	I_A	$I_{0 \to z}$	η
I	457.5	27.5	430.0	567.4	1.16
II	899.0	53.9	845.1	801.9	1.65
III	848.7	50.9	797.8	642.4	1.85
IV	953.6	57.2	896.4	811.1	1.75
V	277.4	16.6	260.8	309.5	1.38
VI	440.7	26.4	414.3	682.1	0.93
VII	551.6	33.1	518.5	342.4	2.43
VIII	944.4	56.7	887.7	1,346.0	1.05
IX	781.3	46.9	734.4	1,083.1	1.05
X	428.8	25.7	403.1	652.0	0.99
XI	331.2	19.9	311.3	572.0	0.81

TABLE 6. *Chlorophyll concentrations, γ_z, at each sample depth, in μg L^{-1}*

Experiment	Sample depths		
	1 ft	5 ft	9 ft
I	15.70	16.17	16.36
II	27.59	21.18	20.55
III	23.03	22.96	22.10
IV	96.84	43.95	35.70
V	17.66	27.88	11.36
VI	5.97	10.73	10.42
VII	135.42	106.25	56.70
VIII	28.27	15.27	16.20
IX	23.21	16.85	20.24
X	21.74	17.66	14.20
XI	13.49	10.65	11.01

TABLE 7. *Vertical temperature profile 150 yards NNE of sta. 3, 19 July, 1957*

Depth (in.)	°C
1	28.5
3	28.8
6	27.6
12	26.2
24	25.4
150	23.6

with warmer water penetrating to a depth of 7 ft (Table 4). The effect of reradiation of long-wave radiation by surface plankton blooms on water temperature is indicated in Table 7, where a gradient of 3°C in 2 ft of depth is noted. The resulting tendency to some degree of thermally-induced stability in the water column is doubtless another factor in the maintenance of red water communities at the surface.

Total chlorophyll in the whole water column was obtained by planimetric integration of the curves connecting γ_z ($z = 1$, 5, and 9 ft), and extrapolating to $z = 0$ and $z = 15$. These values are summarized in Table 8, which shows a range of $\gamma_{0 \to z}$ from 14.68 to 173.14 μg cm^{-2}.

Production Parameters

Table 9 summarizes results for *in situ* π, ρ, and ($\pi - \rho$). Data for depth combinations other than 1-1, 5-5, and 9-9 will be

discussed later. As shown in Table 9, gross production at 1 ft ranged from 24.2 to 625.0, at 5 ft from 3.3 to 48.3, and at 9 ft from 0.4 to 19.2 μg O$_2$ L^{-1} hr^{-1}. The values of π_z ($z = 1\text{-}1$, 5-5, and 9-9) for each date were plotted, and the area under the curves determined planimetrically to obtain $\pi_{0 \to z}$, the total gross production in the whole water column. Values of $\pi_{0 \to z}$, converted from mg O$_2$ L^{-1} to cal cm^{-2} day^{-1}, are given in Table 8. Community respiration, ρ_z, was 15.8–289.6 μg O$_2$ L^{-1} hr^{-1} at 1 ft, 11.3–217.9 μg O$_2$ L^{-1} hr^{-1} at 5 ft, and 11.3–89.6 μg L^{-1} hr^{-1} at 9 ft. As with π, the values of ρ_z were plotted, a curve drawn through the points, and the area under the curve estimated planimetrically to obtain total community respiration in the water column. These values are also presented in cal cm^{-2} day^{-1} in Table 8. Community net production, ($\pi - \rho$)$_z$, also appears in Table 9. The values ranged from –6.7 to 530.8 μg O$_2$ L^{-1} hr^{-1} at 1 ft, –192.5 to 14.2 μg O$_2$ L^{-1} hr^{-1} at 5 ft, and –81.3 to –4.6 μg O$_2$ L^{-1} hr^{-1} at 9 ft, indicating a shallow trophogenic zone, no more than several feet in depth on the average. Even when surface gross production was substantial, as in experiments IV and VII (625 and 352 μg O$_2$ L^{-1} hr^{-1} at 1 ft, respectively), the net product at 5 ft and below was negative. Thus, it appears that the red water organisms involved, in order to maintain a favor-

TABLE 8. *Integrated values of the variables* y = I, γ π, ρ, *and* ($\pi - \rho$), *per 24 hr; i.e.,* $y_{0 \to z} = \int_0^{15} y_z \, dz$.

Radiation and production parameters are in cal cm^{-2} day^{-1}; $\gamma_{0 \to z}$ is in μg cm^{-2}

Experiment	$I_{0 \to z}$	$\gamma_{0 \to z}$	$\pi_{0 \to z}$	$\rho_{0 \to z}$	$(\pi - \rho)_{0 \to z}$
I	567.4	33.38	3.47	4.71	–1.37
II	801.9	45.31	8.41	4.57	3.84
III	642.4	45.67	4.53	7.27	–2.74
IV	811.1	100.31	13.90	9.37	4.53
V	309.5	30.27	2.10	4.30	–2.20
VI	682.1	19.71	1.65	1.97	–0.32
VII	342.4	173.14	9.83	24.46	–14.63
VIII	1,346.0	39.27	7.59	8.50	–0.91
IX	1,083.1	14.68	6.08	9.60	–3.52
X	652.0	32.19	5.76	6.49	–0.73
XI	572.0	24.09	0.55	1.42	–0.87
Means		50.75	5.81	7.50	–1.69

TABLE 9. *Values of* π_z, ρ_z, *and* $(\pi - \rho)_z$, *in* μg O_2 L^{-1}, *obtained in the 1959 experiments*

Experiment	π_z			ρ_z			$(\pi - \rho)_z$		
	1-1	5-5	9-9	1-1	5-5	9-9	1-1	5-5	9-9
I	91.5	19.2	7.7	31.1	21.2	25.4	60.4	−1.9	−17.7
II	233.3	48.3	12.5	45.0	34.2	23.3	188.3	14.2	−10.8
III	120.8	25.4	12.5	45.8	36.3	35.8	65.0	−10.8	−23.3
IV	625.0	42.1	19.2	94.2	79.6	81.3	530.8	−37.5	−62.1
V	51.7	14.2	2.1	25.8	63.8	16.7	25.8	−49.6	−14.6
VI	50.0	3.3	7.1	15.8	11.3	11.7	34.2	−7.9	−4.6
VII	351.7	25.4	8.3	289.6	217.9	89.6	62.1	−192.5	−81.3
VIII	292.1	16.7	5.8	66.3	32.5	44.2	225.8	−15.8	−38.3
IX	210.0	16.3	14.2	67.1	47.1	52.9	142.9	−30.8	−38.8
X	197.5	17.5	1.3	66.3	42.5	37.5	131.3	−25.0	−36.3
XI	24.2	11.7	0.4	30.8	25.8	11.3	−6.7	−14.2	−10.8

able balance between trophogenesis and tropholysis, are inherently restricted to surface layers where light intensity is high. As with π and ρ, $(\pi - \rho)_{0 \to z}$ was also determined. These values are given in Table 8 in cal cm^{-2} day^{-1}.

Total chlorophyll in the water column, $\gamma_{0 \to z}$, varied from 14.68 to 173.14 μg cm^{-2}, with a mean of 50.75 μg cm^{-2} (Table 8). Two pulses in concentration are indicated, experiments IV and VII. Gross production, $\pi_{0 \to z}$, ranged from 0.55 to 13.90 cal cm^{-2} day^{-1}, with a mean of 5.81. Peak photosynthesis occurred in experiments IV and VII corresponding to γ maxima. Community respiration, $\rho_{0 \to z}$, varied from 0.31 to 5.35 cal cm^{-2} day^{-1}, with pulses again in experiments IV and VII. In general, a good visual relationship between γ_z and ρ_z was observed in constructing the graphs. The correlation can be made by comparing the ρ_z values in Table 9 with the γ_z values in Table 6. The second mode of ρ is prolonged through experiments VII–X, with a minor pulse in IX not associated with a γ pulse. The significance of this will be discussed later when $(\rho\gamma^{-1})_{0 \to z}$ ratios are considered. Net community production, $(\pi - \rho)_{0 \to z}$, was negative except in experiments II and IV. The range was from −3.20 to 0.99 cal cm^{-2} day^{-1}, with a mean of −0.37 cal cm^{-2} day^{-1}. Thus, net community production was negative between 16 June and 25 August in spite of consistently substantial photosynthetic rates (mean π_z at 1 ft, 5 ft, and 9 ft, respectively, 204.4, 21.8, and 8.3 μg O_2 L^{-1} hr^{-1}). The reason is that

photosynthesis diminishes exponentially with increased depth, whereas respiration remains more or less constant throughout the water column.

Compensation

As indicated above, estuarine productivity is intimately bound up with depth. The best single criterion of the whole dynamic interplay between light, bathymetry, trophogenesis and tropholysis in a water mass is compensation—either compensation depth (c), where photosynthesis equals respiration, or compensation point (I_c), the light intensity at the compensation depth. All the complexity of trophodynamic action devolves to this single variable, as follows.

From Patten (1961), the biomass energy $B(Q)$ at time t in a homogeneous water column is related to that at time 0 by

$$B_t(Q) = B_0(Q) \exp [(\pi - \rho)/B(Q)]t. \quad (1)$$

If photosynthesis per unit biomass at a given depth may be regarded as a direct function of light intensity:

$$[\pi/B(Q)]_z = \phi I_z = \phi I_0 e^{-\eta z}, \quad (2)$$

then in the whole water column

$$[\pi/B(Q)]_{0 \to z} = \int_0^z \phi I_0 e^{-\eta z} \, dz$$
$$= \phi I_0 \eta^{-1} (1 - e^{-\eta z}). \quad (3)$$

Similarly for respiration:

$$[\rho/B(Q)]_z = \lambda \quad (4)$$

and

$$[\rho/B(Q)]_{0 \to z} = \int_0^z \lambda \, dz = \lambda z. \quad (5)$$

Compensation point, I_c, is related to incident radiation by

$$I_c = I_0 e^{-\eta c}. \qquad (6)$$

At the compensation depth, combining (2) and (4),

$$\lambda = \phi \, I_0 e^{-\eta c}$$

which, substituting (6), yields

$$\lambda = \phi \, I_c,$$

or

$$I_c = \lambda \phi^{-1}. \qquad (7)$$

Thus, I_c summarizes the relationship between the photosynthesis and respiration coefficients. The *cost* in biomass energy to procure a unit of energy from the biotope may be expressed in terms of four variables by making appropriate substitutions of (7) into (3) and (5) and cancelling:

$$(\rho \pi^{-1})_{0 \to z} = \eta z I_c I_0^{-1} (1 - e^{-\eta z})^{-1}. \qquad (8)$$

Substitution of (6) into (8) yields

$$(\rho \pi^{-1})_{0 \to z} = \eta z e^{-\eta c} (1 - e^{-\eta z})^{-1}. \qquad (9)$$

Since η, z, and I_0 can be determined independent of experimentation, it is clear that the whole *raison d'être* of dark and light bottles is to determine I_c (eq. 8) or c (eq. 9). The reason is implicit in equation (7).

Values of c and I_c are provided in Table 10 for each experiment. Compensation

TABLE 10. *Compensation depths, c (in ft), and compensation points, I_c (in cal cm^{-2} day^{-1})*

Experiment	c	I_c
I	4.6	90.1
II	6.3	37.1
III	3.1	147.4
IV	3.2	174.4
V	1.8	132.3
VI	3.0	188.5
VII	1.6	171.1
VIII	3.4	315.7
IX	2.5	298.2
X	3.8	138.6
XI	0.0	–
Means	3.0	169.3

depth ranged from nil in the last experiment to 6.3 ft, with a mean of 3.0 ft. Compensation point varied from 37.1 to 315.7 cal cm^{-2} day^{-1}. In experiment XI, respiration exceeded photosynthesis even at the surface so that no compensation point existed.

Efficiencies

The following intensive variables were computed: $(\pi I^{-1})_z$, $(\pi I^{-1} \gamma^{-1})_z$; $\pi_{0 \to z} I_0^{-1}$, $(\pi I^{-1})_{0 \to z}$, $(\pi I^{-1} \gamma^{-1})_{0 \to z}$, $(\rho \gamma^{-1})_{0 \to z}$, and $(\rho \pi^{-1})_{0 \to z}$.

1. $(\pi I^{-1})_z$: Efficiency of primary production per unit light available at each depth (Table 11) varied from 0.30 to 828.57 $\mu g \, O_2 \, L^{-1} \, cal^{-1} \, cm^{-2}$. Two periods of

TABLE 11. *The efficiency $\pi_z I_z^{-1}$ for each sample in the 1959 experiments. The figures are in $\mu g \, O_2$ $L^{-1} \, cal^{-1} \, cm^{-2}$*

Experiment	1-1	1-5	1-9	5-1	5-5	5-9	9-1	9-5	9-9
I	7.84	6.65	8.02	3.69	6.65	13.37	4.19	6.78	10.70
II	10.92	27.87	46.81	4.19	16.67	41.49	4.84	19.25	31.91
III	6.36	20.33	62.50	2.85	12.53	152.08	2.15	15.20	62.50
IV	49.44	82.41	136.71	5.21	15.59	62.03	6.64	15.59	58.23
V	7.14	12.90	11.94	4.89	9.97	43.28	1.61	5.28	7.46
VI	3.83	2.53	5.34	1.47	0.78	5.34	1.15	0.49	5.04
VII	33.71	137.50	828.57	13.62	44.85	57.14	15.62	45.59	285.71
VIII	10.85	11.98	14.12	1.64	2.21	3.03	2.06	2.98	2.35
IX	9.46	14.00	11.52	1.88	2.64	6.62	3.98	6.85	8.33
X	15.78	10.11	16.38	5.99	4.52	1.74	5.69	6.02	1.05
XI	2.39	2.22	1.50	1.36	3.11	3.59	1.52	1.56	0.30
Means	14.34	29.86	103.95	4.25	10.87	35.43	4.50	11.42	43.05
Ratios of means	1.00 :	2.08 :	7.25	1.00 :	2.56 :	8.34	1.00 :	2.54 :	9.57

TABLE 12. $\pi_z I_z^{-1} \gamma_z^{-1}$ at the Princess Bay station, summer, 1959. The units are $(\mu g\ O_2\ L^{-1})(cal\ cm^{-2})^{-1}$. $(\mu g\ L^{-1})^{-1}$

Experiment	1-1	1-5	1-9	5-1	5-5	5-9	9-1	9-5	9-9
I	0.50	0.42	0.51	0.23	0.41	0.83	0.26	0.41	0.65
II	0.40	1.01	1.70	0.20	0.79	1.96	0.24	0.94	1.55
III	0.28	0.88	2.71	0.12	0.55	6.62 .	0.97	0.69	2.83
IV	0.51	0.85	1.41	0.12	0.35	1.41	0.19	0.44	1.63
V	0.40	0.73	0.68	0.18	0.36	1.55	0.14	0.46	0.66
VI	0.64	0.42	0.89	0.14	0.07	0.50	0.11	0.05	0.48
VII	0.25	1.02	6.12	0.13	0.42	0.54	0.28	0.80	5.04
VIII	0.38	0.42	0.50	0.11	0.14	0.20 ·	0.13	0.18	0.15
IX	0.41	0.60	0.50	0.11	0.16	0.39	0.20	0.34	0.41
X	0.73	0.47	0.75	0.34	0.26	0.10	0.40	0.42	0.07
XI	0.18	0.16	0.11	0.13	0.29	0.34	0.14	0.14	0.03
Means	0.42	0.64	1.44	0.16	0.35	1.31	0.28	0.44	1.23
Ratios of means	1.00 :	1.50 :	3.40	1.00 :	2.12 :	8.04	1.00 :	1.60 :	4.44

higher efficiency were observed, in experiments IV and VII, associated with higher than average chlorophyll concentrations (Tables 6 and 8). Extremely low efficiencies were recorded in the last experiment suggesting a loss of productive capacity, and signaling decline of the summer phytoplankton. The summer means and their ratios demonstrate two facts: i) samples collected at the surface (1-1, 1-5, and 1-9) were several-fold more productive per unit light intensity than those collected at 5 ft and 9 ft, indicating greater viability of surface communities. However, ii) production efficiency of a given community per unit light, regardless of collection depth, increased with depth, reflecting the well-known adverse influence of higher light intensities upon photosynthesis. This effect was less pronounced under conditions of low incident light (experiments I, V, VI, X, and XI), and was not observed at all in the last two experiments.

2. $(\pi I^{-1} \gamma^{-1})_z$: The amount of photosynthesis per unit light per unit chlorophyll is a good index to the γ activity of a given bottled community. These data (Table 12) appear to equivocate the thesis of unit chlorophyll activity at a given light intensity. Values ranged from 0.03 to 6.62 $\mu g\ O_2$ $L^{-1}\ cal^{-1}\ cm^{-2}$ per $\mu g\ \gamma\ L^{-1}$. The means and their ratios show γ activity to increase with depth, although this effect was manifested principally in the early experiments.

3. $(\pi_{0 \to z} I_0^{-1})$: Gross production efficiency in the water column per unit incident radiation at the surface is given in Table 13 in cal kcal^{-1} (1 kcal = 1,000 cal). To convert these figures to percentages move the decimal one place to the left (e.g., the efficiency in experiment I was 0.758%). The values ranged from 1.66 to 17.82 cal kcal^{-1}, a 10-fold variability; mean efficiency was 8.81 cal kcal^{-1}. These data indicate three peaks in photosynthesis during the summer, experiments IV, VII, and X. The efficiency levels reported are relatively lower than those cited elsewhere in the literature for aquatic ecosystems: various lakes 0.043–0.38% (Clarke 1939), Lake Mendota 0.40% (Juday 1940), Long Island Sound 0.08–0.72% (Riley 1941), Cedar Bog Lake 0.10% (Lindeman 1942), Minnesota pond 0.04% (Dineen 1953), Eniwetok reef 5.80% (Odum and Odum 1955), Silver Springs 1.22% (Odum 1957), and Root Spring 0.20% (Teal 1957). The figures for Raritan Bay are 0.116–1.782%, with a mean of 0.881%.

4. $(\pi I^{-1})_{0 \to z}$: This efficiency is more indicative of biological capacity for production than $(\pi_{0 \to z} I_0^{-1})$ because it is based on actual light available. The values obtained are also given in Table 13. The range observed was 0.96–28.71 cal kcal^{-1}, with a mean of 9.07 (0.907%). So, even in terms of actual light available, the Raritan estuary was able to convert only about 1% to

TABLE 13. *Summary of various efficiency relationships in the total water column at the Princess Bay station during summer, 1959*

Experiment	$\pi_{0 \to z} I_0^{-1}$ (cal/kcal)	$(\pi I^{-1})_{0 \to z}$ (cal/kcal)	$(\pi I^{-1}\gamma^{-1})_{0 \to z}$ (cal/kcal/μg γ)	$(\rho\gamma^{-1})_{0 \to z}$ (cal/μg)	$(\rho\pi^{-1})_{0 \to z}$ (cal/cal)
I	7.58	6.12	0.18	0.14	1.36
II	9.35	10.49	0.23	0.10	0.54
III	5.34	7.05	0.15	0.16	1.60
IV	14.58	17.14	0.17	0.09	0.67
V	7.57	6.79	0.22	0.14	2.05
VI	3.74	2.42	0.12	0.10	1.19
VII	17.82	28.71	0.17	0.14	2.49
VIII	8.04	5.64	0.14	0.22	1.12
IX	7.78	5.61	0.38	0.65	1.58
X	13.43	8.83	0.27	0.20	1.13
XI	1.66	0.96	0.04	0.06	2.58
Means	8.81	9.07	0.19	0.18	1.48

producer biomass. Peak efficiencies occurred in experiments IV and VII, with the lowest value in experiment XI.

5. $(\pi I^{-1}\gamma^{-1})_{0 \to z}$: This ratio measures chlorophyll activity relative to amount of light transmitted through the water column. The range (Table 13) was from 0.04 to 0.38 cal kcal^{-1} μg^{-1} γ, with a mean of 0.19. The table shows highest γ activity in experiments IX and X and next highest in II and V. The lowest value was recorded in XI, tending to substantiate the idea that deteriorating communities were extant at this time.

These data demonstrate rather clearly that the hypothesis of constant γ activity at unit light intensity is not tenable, presumably because of differences in community composition and variability in physiological state. In the Raritan, chlorophyll collected at 1 ft was usually 2–7 times more active photosynthetically than that found at greater depths (Table 14). This attests further to the vigor of surface communities postulated earlier, and suggests that organisms at deeper levels are older and moribund. Thus, it is concluded that biological stratification in excess of hydrographic stratification can become established and persist in a water column when the flora is dominated by motile flagellates.

This maintenance of a vertical gradient requires a steady energy supply. Because of the shallow compensation depths, any loss in vitality would result in sinking and

ultimate retrogression. That such a vitality decrease is marked by γ activity reduction is aptly demonstrated. This occurs, presumably, before final metabolic failure, as indicated by general uniformity of respiration at all depths. Toward the end of the summer, populations of motile *Massartia* began to subside in favor of increased dominance by non-motile forms, *Nannochloris* and *Skeletonema*. This change in composition was reflected in loss of higher surface γ activity in experiments X and XI (Table 14).

6. $(\rho\gamma^{-1})_{0 \to z}$: As indicated previously, ρ_z and γ_z generally correlated rather well (compare Tables 6 and 9), suggesting a steady relationship between chlorophyll content and quantity of metabolizing plant biomass. Gillbricht (1951) estimated 1 μg

TABLE 14. *Relative γ activity of samples collected at various depths and resuspended at 1 ft. The ratio used was $\pi_z I_z^{-1}\gamma_z^{-1}$*

Experiment	Collected 1 ft	Collected 5 ft	Collected 9 ft
I	2.3	1.0	1.2
II	2.6	1.0	1.2
III	3.0	1.3	1.0
IV	5.8	1.0	1.4
V	4.4	3.0	1.0
VI	3.3	1.3	1.0
VII	2.5	1.0	1.1
VIII	6.6	1.0	1.3
IX	5.0	1.0	2.1
X	1.8	1.0	1.3
XI	1.4	1.0	1.1

of chlorophyll to correspond to 34.8 μg dry organic matter, or 13.6 μg carbon if a 2.5:1 ratio between dry matter and carbon is used. Atkins and Parke (1951), however, indicated considerable variation in number of cells of different species required to yield a chlorophyll unit. Even within the genus *Chlamydomonas*, where organic matter per cell is probably similar, *Chlamydomonas* I and II had, respectively, 202×10^6 and 109×10^6 cells equivalent to 1 mg chlorophyll. If a constant relationship between γ and phytoplankton biomass were found, then $B(Q)$ could be estimated readily by a simple conversion factor.

Data for $(\rho\gamma^{-1})_{0 \to z}$ are given in Table 13. In general, variability was not great, the range (excluding experiments VIII, IX, and X) being 0.06–0.16, mean 0.12 cal μg^{-1} γ. Correcting this for a modicum of zooplankton catabolism, we can employ an arbitrary value of 0.10 cal μg^{-1} γ as the criterion for a reasonably vigorous phytoplankton community. Values less than this might be considered to indicate loss of vigor while higher values would denote a younger, more robust aggregation. The least value obtained from the declining communities of experiment XI was 0.06. If we use $|-0.04|$ as the maximum limit of positive departure from 0.10 for a phytoplankton community of utmost vitality, then 0.14 cal μg^{-1} γ represents an arbitrary index of maximum phytoplankton vigor. Values in excess of 0.14 may then be considered due to zooplankton respiration. Applying this criterion, a small zooplankton pulse was evident in experiment III, and a major pulse in experiments VIII, IX, and X. A maximum of 0.66 cal μg$^{-1}\gamma$ occurred in experiment IX. The associated grazing is undoubtedly instrumental in bringing about demise of the summer phytoplankton crop.

7. $(\rho\pi^{-1})_{0 \to z}$: This efficiency (cost) expresses net community production intensively, and reflects the dynamic state of communities, as follows:

$$\rho/\pi = 1 \quad \text{(steady state)}$$
$$\rho/\pi < 1 \quad \text{(growth)}$$
$$\rho/\pi > 1 \quad \text{(regression)}$$

Cost data appear in Table 13. The range

observed was from 0.54 to 2.50 cal cal^{-1} (mean 1.48). Thus, the plankton at this sampling station appear to have sustained a net energy loss during the summer of 1959.

DISCUSSION

The validity of the foregoing results is contingent upon the efficacy of the light and dark bottle method, some of the criticisms and potential limitations of which have been outlined. Based on i) subsequent experiments employing an identical technique now in progress in the York River, Virginia, which indicate positive net production for an even deeper water column, and ii) circumstantial indications that the bacterial problem may be nominal (note decline of respiration with depth, Table 8), the Princess Bay station will be regarded here as truly dystrophic during the period of study. This means that the energy losses must be obviated at some other time and/or place if the system is not to fall stagnant.

The experimental site stands in relation to the general circulation as follows. According to Ayers, *et al.* (1949), flushing is accomplished by mixing resulting from reversing tidal currents, by net translations of water masses due to inequalities between flood and ebb, and by fresh-water flow to the sea. Numerous shoals produce eddies which reduce and deflect tidal currents and inhibit flushing. The normal drift may also be altered by winds which move surface waters before them. The main fresh-water source is the Raritan River. Salt water flows into the bay between Sandy Hook and Romer Shoal (Fig. 1). This water is the uniformly mixed sea water plus Hudson River water of Lower Bay. A sluggish eddy at Old Orchard Shoal impedes exchange between Hudson River and Raritan Bay. On flood tide, salt water from Lower Bay moves westward into the Raritan along the Staten Island shore, then thrusts southwesterly in the vicinity of Princess Bay to a point just west of Conaskonk Point. This tongue of water is presumed to accelerate the seaward movement of fresher water along the south shore while damming back
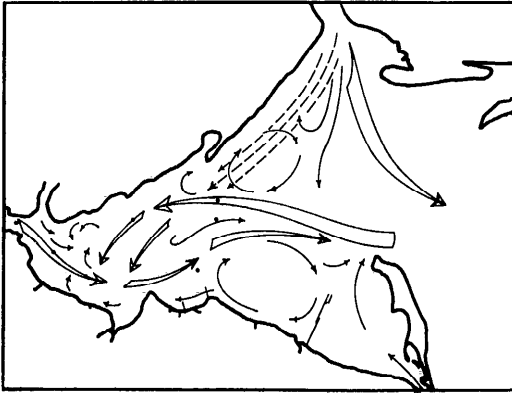
FIG. 3. Schematic diagram of the general circulation of the Raritan–Lower New York Bay system.
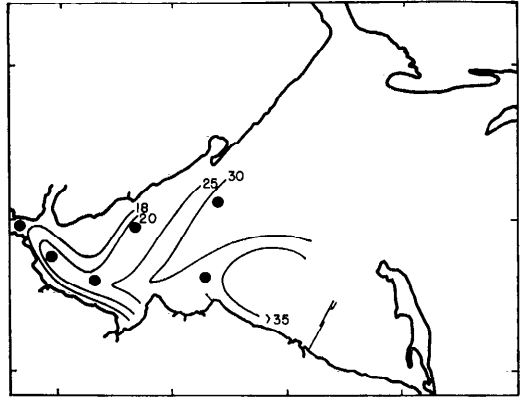

FIG. 4. Mean diversity of net phytoplankton in Raritan Bay between July, 1957 and September, 1958, based on results obtained at the six stations shown. (The diversity index employed was the Shannon (1948) information function

$$H = -N \sum_{i=1}^{m} p_i \log_2 p_i, \text{ where } H \text{ is diversity,}$$

and p_i is the probability for occurrence of the i-th of m species in the aggregation and N is the number of organisms of all kinds per liter. The units are bits $\times 10^{-3} L^{-1}$.)

low salinity water accumulated at the head of the bay. These general relationships are shown in Figure 3.

It is uncertain how representative the Princess Bay station is of the estuary at large. Mean water depths are comparable. Production rates at the primary level are equally high, as indicated by comparison of the 1957 and 1959 series of experiments. Chlorophyll levels at Princess Bay were not unlike those at other stations during the same season of other years. Consequently, this station probably fairly represents the trophodynamics of mid and upper bay. The following interpretations are based on this assumption.

The Raritan estuary is polluted by both domestic and industrial wastes. Although nutrient levels are high as a result, there occurs a drastic reduction in phytoplankton diversity proceeding upbay from Lower Bay (Patten 1959b) following a pattern strikingly similar to that of the general circulation (compare Figures 3 and 4). This suggests an adverse effect of pollution originating, for the most part, at the head of the estuary. During the early part of this study, the Raritan River was so highly polluted that brackish plant species, which normally contribute to diversity and productivity of upper estuaries, were completely non-existent. Consequently, the main contribution to primary production was from the high salinity flora from Lower Bay. The upper estuary is marginal in

many respects for these forms, and the indicated dystrophy may be considered to reflect the dying-out of high salinity, pollution-intolerant floras from Lower Bay as they are thrust into the upper reaches of the Raritan.

This does not necessarily imply lack of production at higher trophic levels. To the contrary, Jeffries (1959) has shown the Raritan to sustain a rich and varied planktonic fauna, and an extensive survey of the benthos by Dean (personal communication) also signifies no lack of energy flow to benthic consumers. Thus, there may be postulated a division of labor in the greater New York Bay ecosystem whereby a polluted segment, the Raritan, maintains high biological quality in the pollution-tolerant upper trophic levels, though incapable of any net organic production at the pollution-intolerant primary level. The main energy flux into the Raritan would appear, then, to be not positive net trophogenesis, $(\pi - \rho)$, but rather standing crops, $B(Q)$, from Lower Bay. The lower part of this system may be regarded as having an agrarian

function with respect to the whole; it grows food which is subsequently transported to the upper segment. In return, it may receive from the latter several services which collectively enhance its productive capacity. Adverse pollutants are localized and diluted, while associated nutrients may be transported downbay. Regenerated nutrients may also be transported downbay to help make possible repetition of the cycle.

This differentiation of function at an epiorganismic level suggests for the ecosystem considerable capacity to become organized for optimum biological activity under conditions of environmental adversity. The degree to which the established relationships will be altered by the lifting of pollution from the Raritan River should provide an interesting area for further investigation against the background provided here.

ACKNOWLEDGMENTS

APPENDIX

The model of information flux in plankton presented earlier (Patten 1961) contained some errors which it is the intent of the following remarks to correct.

In Table 1, flow data were presented which were to represent fluxes in the whole water column (from surface to 15 ft). Instead, the data actually are for *mean* fluxes at any depth. To obtain totals for the whole water column, the figures given for $I_{0 \to z}$, $\pi_{0 \to z}$, $\rho_{0 \to z}$, and $(\pi - \rho)_{0 \to z}$ should be

multiplied by 4.572, which is the depth in meters.

In equation (14), biomass information in a water column at time t was related to that at time 0 by

$$[B_t(I)]_{0 \to z} = [B_0(I)]_{0 \to z} \exp \{ \phi\, I_0 \delta^{-1} [\tfrac{1}{2}(1 + e^{-2\delta z}) - e^{-\delta z}] - \lambda z \} t, \qquad (14)$$

in which the exponent expresses net production from surface to depth z, that is,

$$\int_0^z [\phi\, I_0 e^{-\delta z}(1 - e^{-\delta z}) - \lambda]\, dz. \qquad (i)$$

In (i) the left term is gross production and the right term respiration per unit biomass at depth z.

Developing equation (15), it was stated that the exponent of (14) must vanish at the compensation depth, c. This is erroneous. It is net production *at* this depth which vanishes:

$$\phi\, I_0 e^{-\delta c}(1 - e^{-\delta c}) - \lambda = 0, \qquad (ii)$$

not, as given in (15), the total net production integrated from surface to c. The depth at which the condition of (15) prevails may be termed the *equivalence depth*, ϵ, and is that depth at which total gross production of the water column above is exactly matched by the total respiration, *i.e.* $\pi_{0 \to \epsilon} = \rho_{0 \to \epsilon}$. Under the assumption of vertical biological homogeneity upon which the model was constructed, $\epsilon < z$ would signify that the community must experience a net information loss in the water column since $\rho_{\epsilon \to z} > \pi_{\epsilon \to z}$. Similarly, $\epsilon > z$ implies, by definition of ϵ, a net information gain to the community as a whole.

The model from equation (16) on can be made valid by replacing c by ϵ. This invalidates the comparison which was made between model and Raritan Bay data because compensation depths rather than equivalence depths were employed in the computations. Since compensation depths are easily obtained experimentally while equivalence depths are not, it is desirable to express the variables of equations (17–20) in terms of compensation rather than equivalence. This may be accomplished

beginning with (ii) above, from which λ may be expressed as

$$\lambda = \phi\, I_0 e^{-\delta c}(1 - e^{-\delta c}). \qquad \text{(iii)}$$

Substituting into (14), we obtain instead of (16)

$$[B_t(I)]_{0 \to z} = [B_0(I)]_{0 \to z} \exp$$
$$= \{\phi\, I_0[\delta^{-1}(\tfrac{1}{2}[1 + e^{-2\delta z}] - e^{-\delta z}) - z e^{-\delta c}(1 - e^{-\delta c})]\}t, \quad \text{(iv)}$$

where gross production in the water column is

$$\pi_{0 \to z} = \phi\, I_0 \delta^{-1}[\tfrac{1}{2}(1 + e^{-2\delta z}) - e^{-\delta z}][B(I)],$$

and respiration is

$$\rho_{0 \to z} = \phi\, I_0 z e^{-\delta c}(1 - e^{-\delta c})[B(I)].$$

Since, from (iii),

$$\phi = \lambda\, I_0^{-1} e^{\delta c}(1 - e^{-\delta c})^{-1},$$

and, from (8),

$$B(I) = \rho\lambda^{-1},$$

the expressions for $\pi_{0 \to z}$ and $\rho_{0 \to z}$ may be written

$$\pi_{0 \to z} = \rho\delta^{-1} e^{\delta c}[\tfrac{1}{2}(1 + e^{-2\delta z}) - e^{-\delta z}] \cdot$$
$$[1 - e^{-\delta c}]^{-1} \qquad \text{(v)}$$

and

$$\rho_{0 \to z} = \rho z. \qquad \text{(18)}$$

Net production in the water column becomes

$$(\pi - \rho)_{0 \to z} = \rho\{\delta^{-1} e^{\delta c}[\tfrac{1}{2}(1 + e^{-2\delta z}) - e^{-\delta z}] \cdot$$
$$(1 - e^{-\delta c})^{-1} - z\}, \qquad \text{(vi)}$$

and the cost is

$$(\rho\pi^{-1})_{0 \to z} = z\delta e^{-\delta c}(1 - e^{-\delta c}) \cdot$$
$$[\tfrac{1}{2}(1 + e^{-2\delta z}) - e^{-\delta z}]^{-1}. \qquad \text{(vii)}$$

Expected costs were computed from (vii) and compared with the empirical results from Raritan Bay employing the Kolmogorov–Smirnov test as before. The observed values were found to differ significantly from those predicted by the corrected model.

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