ORGANIC PRODUCTION IN A TROPICAL ESTUARY

BY S. Z. QASIM, S. WELLERSHAUS,* P. M. A. BHATTATHIRI AND S. A. H. ABIDI

(Biological Oceanography Division, National Institute of Oceanography, Ernakulam, Cochin-11, South India)

Received June 17, 1968

(Communicated by Dr. N. K. Panikkar, F.A.SC.)

ABSTRACT

In a highly turbid and polluted estuary the C^{14} assimilation is nearer to net production and the diurnal rhythm in photosynthesis is associated with the increase and decrease in daily illumination. There is no decline in the rate of photosynthesis at peak illumination but the difference between forenoon and afternoon production is significant. Photosynthesis measured in relation to illuminations gave different light saturation optima on different days probably due to highly variable nature of phytoplankton population.

Estimates of gross and net primary production were made for the thin euphotic zone, the latter after computing the respiratory losses occurring during day and night which were large and inconsistent. Seasonal changes in the production rate were not well marked and showed only 3–4 fold increase in certain months. For most of the year, primary production seemed non-existent at depths greater than about 4 metres.

None of the factors such as temperature and nutrients seems to be limiting in the estuary. Monthly variations in total solar radiation are not sufficiently large to affect seasonal changes in production, but the light penetration is greatly reduced which limits column production. Seasonal variations in salinity, primarily induced by the monsoon cycle, initiate a succession of brief pulses of bloom. The stability of the euphotic zone is important for maintaining plant population within the narrow zone of illumination and for favouring production. The range in carbon assimilation to chlorophyll ratio was large which signifies that photosynthesis and chlorophyll maxima are non-synchronous. From the assimilation ratio determined experimentally the estimates of production were made from radiation and chlorophyll data.

---

* Present address: Institut fuer Meeresforschung, Bremerhaven, West Germany.

The interrelationship between carbon assimilation, chlorophyll and detrital material has been discussed and the annual estimates of gross and net production have been given. The efficiency of the environment to convert solar energy into chemical energy was about 0·4%. A general lack of zooplankton grazers in the estuary leaves behind a considerable surplus of unconsumed basic food, much of which seems to be lost by sinking below the narrow euphotic zone.

INTRODUCTION

ALTHOUGH considerable knowledge has been gained in recent years on the organic production of natural bodies of water (*see e.g.*, Yentsch, 1963; Strickland, 1965; Raymont, 1966), practically nothing is known on the productivity of tropical estuaries, backwaters, lagoons and mangrove-swamps. A critical examination of the literature shows that perhaps one of the most intriguing problems of organic production today is to determine the extent to which the environmental factors influence the productivity rhythm. Leaving aside some of the classical controlled experiments where natural phytoplankton populations or laboratory cultures have been used as convenient types for specialized studies on primary production or the theoretical approaches which could be used to predicting changes only in such environments where extremes of hydrographical conditions seldom exist. In this respect a tropical estuary can be considered a unique environment where changes in physical, chemical and biological properties, both in time and space, are really extreme, and the influence of these on primary production though very often difficult to explain, makes it an extremely interesting environment to carry out such studies.

In attempting to present this work, despite the limitations in the knowledge of many environmental factors which are quite apparent, the main emphasis has been not only to determine the daily and seasonal rates of primary production, but to give a critical appraisal of how the observed values arise—which as it is understood now, are because of the interaction of a host of environmental factors (Steele, 1961). Earlier accounts on this estuary have dealt with the estimation of plant pigments (Qasim and Reddy, 1967) and the solar radiation wih its related aspects (Qasim *et al.*, 1968).

PROCEDURE AND METHODS

As shown in Fig. 1, four stations in the upper reaches of the estuary were selected for initiating a programme in June 1965 on the hydrography

and primary productivity. In choosing these stations our interest has primarily been to work in a highly dynamic and typically estuarine condition, rather than moving down to lower regions of the estuary, close to the rivers, where conditions are always nearly freshwater. At these stations which were spread over short distances apart, 3–4 km each, the salinity changes, particularly during the monsoon months (June–September), were considerable.

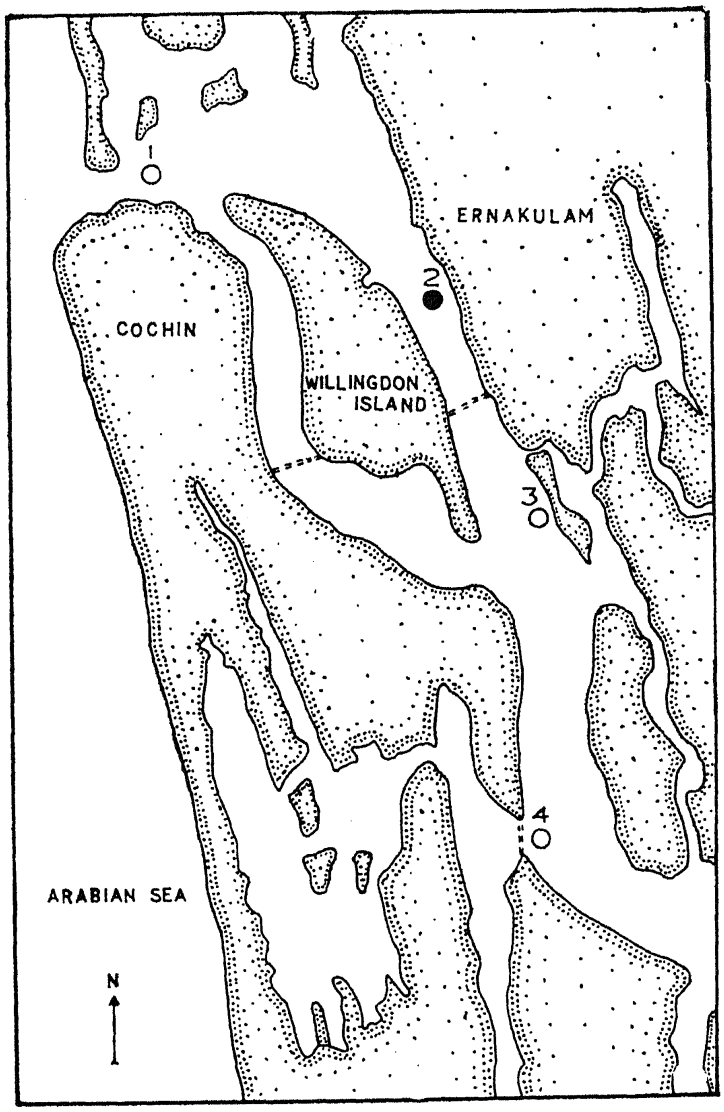

FIG. 1. Map showing the station positions in the upper reaches of the estuary (Cochin Backwater) where data on hydrography were collected. Closed circle indicates station 2 where measurements of primary production were made.

From all the four stations water samples at different depths and phytoplankton and zooplankton at subsurface level were collected at fortnightly intervals throughout the year. As part of the programme the various estimations included the *in situ* measurements of the rate of photosynthesis

(only at station 2), the measurements of physical parameters such as temperature, salinity, light penetration, seston, etc.; chemical features such as alkalinity, pH, nutrients and plant pigments and biological features, namely, the phytoplankton and zooplankton standing crops. Other parts of the same programme included studies on the microbial flora, fish and benthos. A detailed account of the various environmental features demands more space and will be dealt with under separate communications. For the present discussion which follows, the data relevant to organic production were processed in a form suitable to clarify the various points.

THE ENVIRONMENT

Some introductory remarks on the general features of the Cochin Backwater have been made earlier (Qasim *et al.*, 1968). The backwaters, as the name implies, include a system of interconnected lagoons, bays and swamps penetrating the mainland and enclosing many islands in between, whose total area amounts to approximately 500 square kms. The backwater around Cochin is located along Lat. 9° 58′ N and Long. 76° 15′ E. The upper reaches of this backwater are connected with the Arabian Sea by a channel, 450 m wide (Fig. 1). These regions are relatively deeper, with depth ranging 5–15 m, and are marked with flushing of the estuary with flood and ebb tides whose maximum range is about 1 m. The lower reaches of the estuary are shallower (2–5 m deep) with little or no tidal influence and have a markedly low salinity. The permanent sources of freshwater in the estuary are the two rivers, namely, the Periyar on the north, and the Pampa on the south, in addition to several small tributaries, irrigation channels and innumerable drains. The estuary provides an access to all types of boats, country-crafts, ferries, etc., including the ocean going vessels to the Cochin harbour which is situated near the channel on one of the islands called the Willingdon Island (Fig. 1). Because of considerable influence of land and harbour, the portion of the estuary shown in Fig. 1 becomes very polluted.

Table I gives some of the hydrographical features at station 2 whose influence on organic production is discussed in a later section of this paper. It can be seen from Table I that most of the parameters are adapted to an annual rhythm, showing sharp changes during the monsoon months (June-September), with the onset of rain. In the post-monsoon months (October–January), the variations in these parameters remain still well marked, but during the pre-monsoon months (February–May) the conditions become relatively uniform and remain predominantly marine. The most important feature worth noting is the high turbidity in the estuary as is evident from the

TABLE I

Seasonal data on some of the hydrographical features of Cochin Backwater from August 1965 to July 1966

	Depth m	1966							1965				
		J	F	M	A	M	J	J	A	S	O	N	D
Temperature °C	0	29·0	30·2	30·4	31·0	31·8	29·3	28·4	28·9	30·5	30·4	31·3	29·0
	4	29·0	29·8	30·5	30·8	31·6	26·9	25·6	27·0	27·3	29·5	30·2	29·4
	9	29·2	29·8	30·4	30·8	31·2	26·5	25·4	26·0	26·0	29·5	30·1	29·2
Salinity ‰	0	31·46	31·96	32·50	33·51	31·00	12·82	1·40	2·07	6·50	6·40	11·24	20·08
	4	32·14	32·88	32·68	33·33	31·18	31·64	27·52	20·91	23·07	29·61	31·81	23·35
	9	32·05	32·50	32·84	33·33	31·31	31·89	29·57	31·08	32·53	32·81	32·58	31·14
Oxygen ml/l	0	4·819	..	4·620	3·498	3·519	4·600	4·974	5·052	4·789	4·475	4·885	4·731
	4	5·042	4·501	4·726	3·946	4·019	2·650	3·437	3·408	3·276	3·891	4·168	4·706
	9	5·897	5·010	4·673	4·570	4·636	2·623	3·273	3·761	3·961	4·421	4·540	5·072
PO_4-P µg-at/l	0	0·363	0·779	0·785	1·268	1·095	0·707	0·780	0·678	0·629	0·457	0·527	0·556
	4	0·451	0·867	0·649	1·635	1·187	1·482	1·054	1·113	0·945	0·783	0·770	0·737
	9	0·531	0·670	0·881	1·680	1·411	2·108	1·528	1·283	1·016	0·902	0·772	0·774
NO_3-Nµg-at/l	0	0·811	1·230	2·883	1·179	2·510	11·990	39·97	4·312	1·547	4·359	1·226	0·309
	4	0·727	1·776	0·735	1·505	3·342	9·388	33·72	5·764	4·557	1·725	1·226	0·381
	9	1·349	1·016	0·969	1·571	2·714	8·418	39·46	8·666	5·248	1·048	0·890	0·927
SiO_3-Si µg-at/l	0	6·42	11·15	5·00	10·76	20·31	23·46	59·71	49·24	28·64	50·56	31·71	18·55
	4	4·74	8·71	3·93	14·27	19·66	13·40	35·38	24·42	13·30	18·55	8·35	15·42
	9	4·79	7·87	5·25	14·27	21·60	..	35·73	20·33	12·66	9·87	7·63	12·92
Alkalinity mgC/m³	0	25,800	26,254	25,122	23,292	20,032	8,735	2,717	7,364	5,880	7,412	11,092	17,540
	4	26,712	26,819	25,574	23,059	20,730	25,156	15,916	..	19,400	21,325	26,140	19,529
	9	27,156	26,932	26,254	23,059	21,196	25,621	17,392	..	26,500	25,970	27,045	26,140
N:P ratio (euphotic zone)	..	1·89	1·88	2·52	0·92	2·57	9·76	40·17	5·62	3·89	4·91	1·89	0·53
Average solar radiation ly/day	..	532	574	538	504	407	264	307	370	365	390	501	503
Attenuation coefficient (K_{10})	..	0·87	0·90	1·06	1·76	5·54	1·24	1·38	..	1·40	1·19	1·20	1·36
Compensation depth (m)	..	5·34	4·90	4·47	2·77	0·83	3·61	3·32	..	3·00	3·94	3·82	3·20

attenuation coefficients of light (K_{10}) given in Table I. The euphotic zone as determined from the compensation depth (1% of incident illumination) seldom exceeds 4–5 m.

RATE OF PHOTOSYNTHESIS

The rate of photosynthesis was measured by using light-dark-bottle oxygen technique and the radiocarbon (C^{14}) method of Steemann Nielsen (1952). Experiments dealing with the oxygen changes were conducted *in situ* throughout the year by using a float at station 2. In each experiment duplicate or triplicate sets of 100 ml bottles were used at various depths of the euphotic zone which was predetermined by using a submarine photometer (*see* Qasim *et al.*, 1968). All customary precautions were taken to ensure maximum sensitivity of the method (Strickland, 1960). Since the estuary was always characterised by a high phytoplankton crop, an incubation of 2 hours gave a measurable change in the oxygen concentration. However, for all routine observations a 6-hr incubation was considered an ideal time-interval to illustrate the change (*see* below). The factor for converting the oxygen changes to carbon assimilation was (0·375/PQ), where the value of PQ was taken as 1·2 (Strickland, 1960; Antia *et al.*, 1963).

The C^{14} method was used concurrently with the oxygen method at all depths. In each experiment 60 ml (pyrex) light and dark bottles were inoculated with 0·4 μc C^{14} (4μc Danish ampoules diluted with 170 mg/l $NaHCO_3$ solution; taking the strength of the diluting $NaHCO_3$ almost the same as in sea-water), and incubated *in situ* for a period of 6 hours under natural illumination. Trial experiments conducted earlier with various concentrations of the ampoule showed that because of excessive particulate matter present in the water, the accuracy in the results was greater when the incubations were made in small bottles with ten times dilution of the ampoules. The presence of inert material in the water increased the dark fixation of radioactive carbon (adsorption effect). The percentage occurrence of dark uptake when calculated as a percentage of carbon assimilation in about 100 experiments was found to be $<1\%$ in 7% experiments, 1–5% in 62% experiments, >5–10% in 15% experiments, >10–25% in 10% experiments and >25–50% in 6% experiments. Since in the light bottle the adsorption effect would be similar to that of the dark bottle (blank), this effect will be self-cancelling when the counts are corrected. In turbid conditions, another important factor to be considered is the self-absorption, as the thickness of the particulate matter deposited on the filters would contribute to this effect. To a large extent, the self-absorption could be

minimised by using small volumes of incubating samples (40 ml in 60 ml bottles). The maximum values of seston (total suspended material) recorded in the backwater, only on few instances, were of the order of 100 mg/l Allowing the counting rate in 20 mg/cm² thickness as 10% in terms of zero thickness (Strickland and Parsons, 1965), the loss of activity by self-absorption in 100 mg/l will be as follows:

Filtering area	= approximately 25 mm circle when 35 mm diameter filters are used
or	= 5 cm.²
If seston	= 100 mg/l
and sample filtered	= 40 ml/l
the seston on the filter	= 4 mg or 0·8 mg/cm²
Therefore, the loss of activity at the rate of 90% per 20 mg/cm²	= 3·6%.

This loss corresponds to the maximum value of suspended material. Normally, for most of the year, the seston values range between 5–30 mg/l, and therefore, at these concentrations the loss of activity due to self-absorption would be about 1% or less. This assumption, however, does not take into consideration the self-scattering of β-radiation, which, according to recent findings (Steemann Nielsen, 1965), may cause substantial error in counting even at 0·5 mg/cm² thickness.

All experiments were carried out at about the same time during the day, 0600–1200 hours. After the completion of the incubation the samples were filtered through Göttingen membrane filters. The filters were washed with filtered sea-water, dried in special holders and counted using a thin window gas flow proportional counter. The counts were corrected for background, dark-bottle uptake and for isotope effect (factor 1·05 was used) and the rate of photosynthesis in mgC/m³/h was calculated by the usual method. The total activity of the ampoule was determined by scintillation counting.

It has generally been thought that the C^{14} method gives a measure of net production (Ryther, 1956 *a*; Antia *et al.*, 1963), at least when the incubations are prolonged (Strickland, 1960), or somewhere between gross and net productions but nearer to net production (Steemann Nielsen, 1964), or lower than net production (McAllister *et al.*, 1964). In the present investgation, since the estimates of gross and net production by the O_2 method were available it was considered worthwhile to compare these with the C^{14} values.

Figure 2 *a* and *b* show the gross and net values as a function of C^{14} uptake. It can be seen from the figure that in both cases there is a considerable scatter in the points. However, in each case the scatter is less when the production values are low, and increases with the increase in the rate of photosynthesis. The ratios between gross production (O_2) and C^{14} ranged from 0·17 to 8·37, average = 1·99 with S.D. $\pm$ 1·61. The range in the ratio between O_2 (net) and C^{14}, on the other hand, was relatively less, 0·25–7·09, average = 1·86 with S.D. $\pm$ 1·45. This was largely because of the losses through respiration or excretion, the former, as will be shown later, varied considerably from month to month. It can therefore be concluded that the C^{14} method gives an estimate of production which is nearer to net than gross.

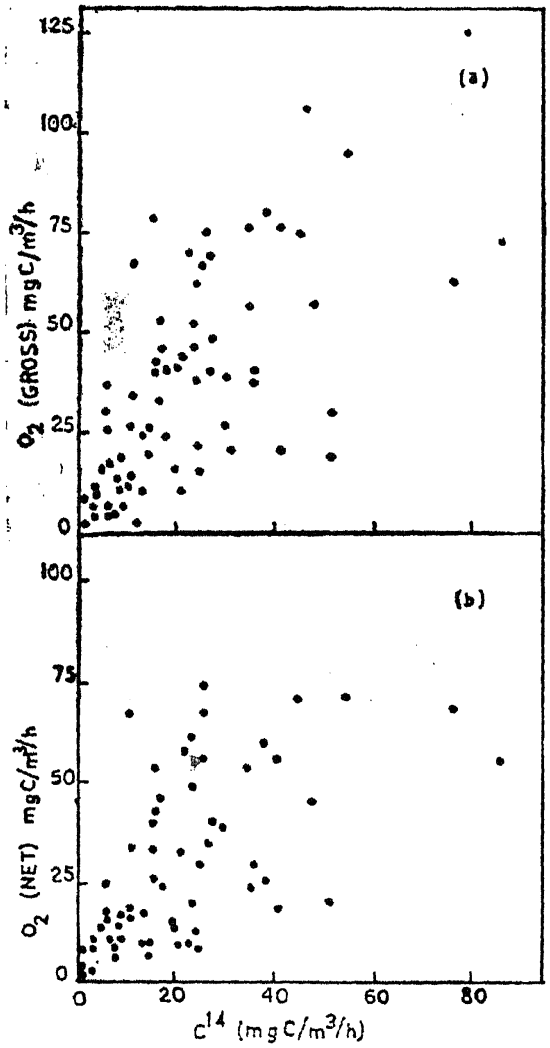

FIG. 2. The relation between rate of photosynthesis measured by O_2 and C^{14} methods (*a*) gross production *vs.* C^{14} uptake; (*b*) net production *vs.* C^{14} assimilation.

INCUBATION TIME AND DIURNAL RHYTHM

In an attempt to determine a most suitable incubation time for estimating the primary production over a day, several series of experiments were

carried out using oxygen and C^{14} techniques for different periods of incubation. For each series, suitable aliquots were taken from the surface water collected in a plastic bucket during the early hours of the morning. These were immediately inoculated and suspended in replicates from a float at 0600 hours under natural illumination. After every 2 hours the bottles were withdrawn and analysed. The difference between two successive readings gave a two-hourly production. The results of four experiments conducted in June and July 1965 are shown in Fig. 3. It can be seen from the

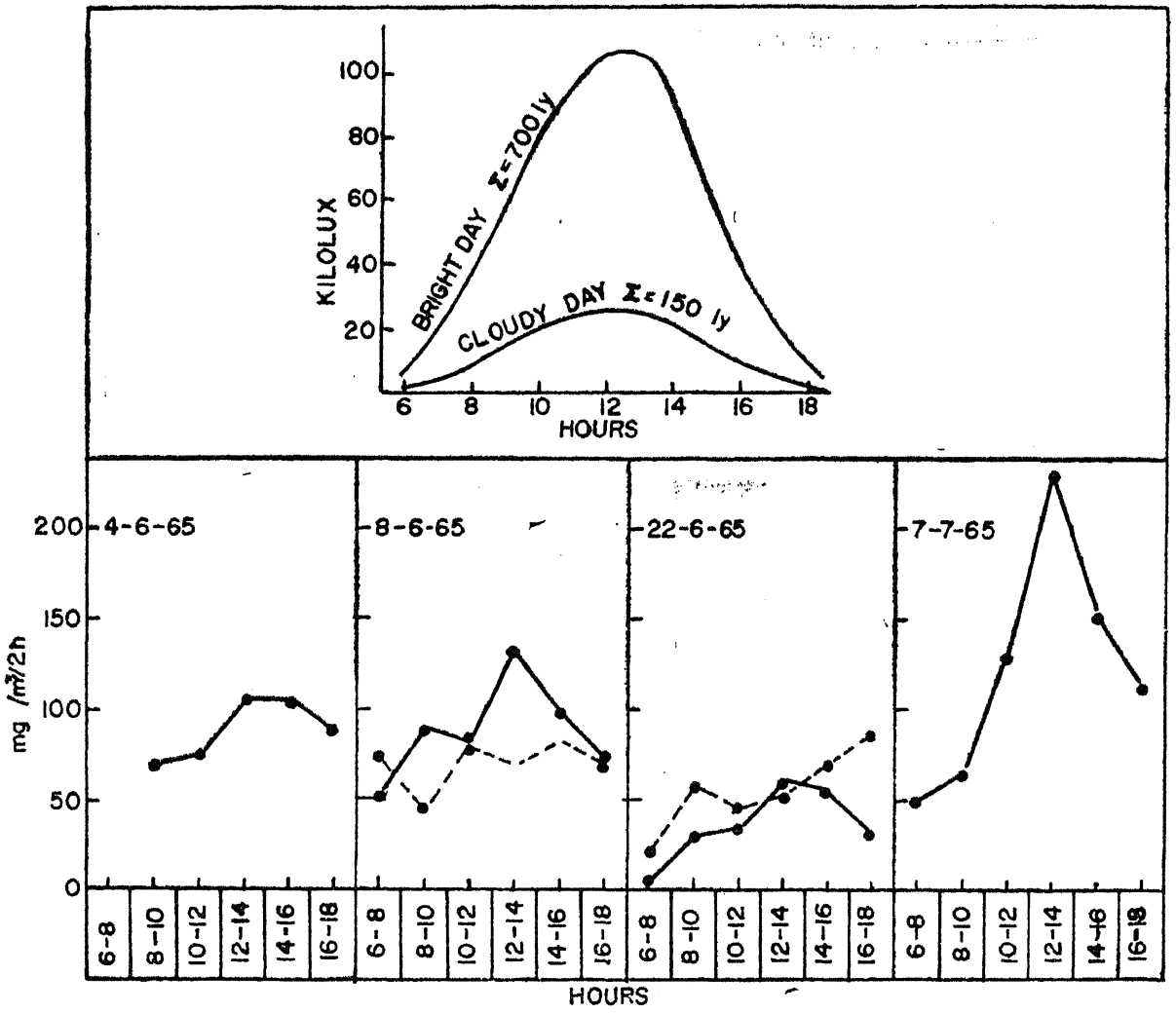

FIG. 3. Diurnal variations in the photosynthetic activity in each of the four experiments ; C^{14} uptake (solid lines), net O_2 production (broken lines). Top figure shows two extreme conditions of diurnal illumination.

figure that the rate of photosynthesis measured by C^{14} and O_2 methods showed wide discrepancies. The oxygen values though still measurable were inconsistent, presumably because of the lack of sensitivity inherent in the method when the incubation time was initially kept short. The C^{14}

method, on the other hand, under similar conditions was found to be more sensitive and gave consistent results. In all the four experiments, the nature of diurnal rhythm was very similar. The values progressively increased upto 1400 hours and then declined sharply. In Fig. 3 are also shown two extreme conditions of daily illumination, namely, a uniformly bright day and a uniformly dull and cloudy day. Under normal weather conditions the daily solar radiation is generally found in between these two extremes (for details *see* Qasim *et al.*, 1968). A comparison of diurnal rhythm in photosynthesis with daily illumination will reveal that the production rates were strictly dependent upon the increase and decrease in the daily illumination. Maximum values of photosynthesis between 1200 and 1400 hours corresponded to peak illumination which under normal weather conditions invariably occurs during the early hours of the afternoon.

Earlier evidences on the daily periodicity of natural phytoplankton populations in clear oceanic waters (Doty and Oguri, 1957; Shimada, 1958) showed that the diurnal fluctuation was because of an endogenous photosynthetic rhythm. This has been found to be associated with similar changes in chlorophyll *a* (Yentsch and Ryther, 1957; Shimada, 1958). Peak values generally occurred during the forenoon and lowest during the late afternoon. The decline in the photosynthesis has been found to be associated with high illumination, exceeding optimal at mid-day or early afternoon (Verduin, 1957), because of a similar decline in chlorophyll due to photo-oxidation of pigments at increased light (Yentsch and Ryther, 1957).

In contrast to the findings noted above, no decline in the photosynthesis was noticed at high light intensities in the backwater. This may be because of highly turbid conditions prevailing in the estuary throughout the year and more particularly during the monsoon months when these experiments were conducted. The light penetration in these months is generally reduced to less than 25% of the incident radiation within 1 m (Qasim *et al.*, 1968) which will be well within the range of optimal light saturation intensity (*see* Table II).

However, such diurnal fluctuations in the rate of photosynthesis will undoubtedly affect the estimates of day-primary-production. The order of magnitude of these fluctuations was estimated as follows: Table II shows the day-production values based on 2-hourly readings, as indicated in Fig. 3, in relation to the time of the day. It is clear from Table II that the differences in the estimates based on the time of the day were very large. The lower half of Table II shows the day-production determined from the duration

TABLE II

Primary production computed over a day from two-hourly readings of C^{14} uptake and from periods of incubation lasting 2–12 hours

Day production mgC/m^3	Time of day					
	0600–0800	0800–1000	1000–1200	1200–1400	1400–1600	1600–1800
Experiment 1		412	451	635	631	522
2 ..	317	535	499	798	593	442
3 ..	32	178	329	357	331	187
4 ..	297	388	772	1378	912	676

Day production mgC/m^3	Periods of incubation					
	0600–0800 2h	0600–1000 4h	0600–1200 6h	0600–1400 8h	0600–1600 10h	0600–1800 12h
Experiment 1		503	486	523	545	541
2 ..	317	426	450	537	548	531
3 ..	32	105	140	194	221	215
4 ..	297	342	486	709	749	737

of the incubation. From these data it is clear that while the two-hourly-incubation between 0600 and 0800 hours gave consistently low values, the differences between 4, 6, 8, 10 and 12 hours were progressively reduced when the incubation time was prolonged. However, if the forenoon production (6 hours) is compared with that of a similar time-interval in the afternoon (Table III), it would appear that the latter was always greater than the former. The consistency of these values—for both C^{14} and O_2 methods gave similar results (Table III)—shows that these differences are significant and do not arise merely as an artifact. It is therefore important that the magnitude of these variations must be appreciated and accounted for while calculating daily and seasonal production rates.

TABLE III

Differences obtained between forenoon and afternoon production in C^{14} and oxygen experiments

Date	Fore-noon 6h	After noon 6h	F.N. +A.N. 12h	Calculated from F.N. 12h	Difference %
		Production (mgC/m³) C^{14}			
4–6–1965 ..	243	298	541	486	11
8–6–1965 ..	225	305	530	450	18
22–6–1965 ..	70	115	185	140	32
7–7–1965 ..	243	494	737	486	52
		Production (mgC/m³) O_2			
8–6–1965 ..	202	228	430	404	6
22–6–1965 ..	126	208	334	252	33
10–5–1967 ..	20	30	50	40	25
5–6–1967 ..	614	817	1433	1228	17

The summed values of forenoon and afternoon which give the actual 12-hours day-production are shown in Table III. Also included in the same table are the values computed from the forenoon production alone. The difference between the two fell within a range of 11–52% in C^{14} experiments (mean = 28%) and 6–33% for O_2 method—average of the two = 24%. It is therefore evident that the day-production based on doubling the values of forenoon will be underestimated by about 24%, and similarly from the afternoon values it will be overestimated by about the same magnitude. Since all our incubations were made in the forenoon (0600–1200 hours), to account for this difference it was thought best to calculate the day-production for 14 hours instead of 12 hours. This seemed a reasonable assumption not only because it compensated for the afternoon difference of about 20% but it gave a more realistic picture of the length of a tropical day-which from the annual sunrise and sunset records showed little deviation (about

40 minutes) from the 12-hour average. But when the sky radiation before sunrise (at dawn) and after sunset (at dusk) is considered it will amount to 13–14 hours a day throughout the year. To assume, therefore, as is customary in the literature that photosynthesis will take place only from sunrise to sunset, but nothing before or afterwards in the skylight, even at the surface, would be more unrealistic for the tropics than to assume a uniformly 14-hour day and 10-hour night. For these reasons all our estimates of daily production rates, unless otherwise stated, are based on 14-hour-day.

Photosynthesis as a Function of Illumination

Many direct observations on the rate of photosynthesis of temperate phytoplankton, generally in a light incubator under varying intensities of light, artificial or natural, have shown that at low illuminations the increase in the rate of photosynthesis is linear. This is followed by a less rapid increase upto a saturation point (I_k) from where the 'use' of optimum photosynthesis at light saturation occurs. At high illuminations there is a progressive inhibition in the rate of photosynthesis (Currie, 1962). Earlier experiments have shown that different light optima are required by different groups of phytoplankton to reach saturation intensity (Ryther, 1956*c*). Thus, the plankton occurring at or near the surface, being adapted to high illuminations, exhibit "sun characteristics" and those from deeper layers behave like "shade plankton" (Steemann Nielsen and Hansen, 1959; Yentsch, 1963). Such a behaviour of plant organisms to light has been attributed to differences in their chlorophyll content (Ryther and Menzel, 1959). These features, however, are of a transient nature, for one form of plankton can adapt to changing conditions of light fairly rapidly (Steemann Nielsen, 1962; Steemann Nielsen and Park, 1964). According to Steemann Nielsen (1963) the light saturation intensity of tropical and subtropical phytoplankton organisms is about 20,000 lux.

The results of some of the experiments conducted on freshly collected surface phytoplankton from the backwater by using C^{14} technique have been shown in Fig. 4. These experiments were carried out in a light incubator, very similar to what has been described by Steemann Nielsen (1963). It had a revolving disc placed in a large glass tank with running water. The disc had 10 equal compartments to accommodate bottles and pre-calibrated neutral density filters. Each experiment was conducted for a duration of 2 hours, between 10 a.m. and 12 Noon, on sunny days, using sunlight as a source of illumination. The incubator was kept at an angle to allow full

exposure to sunlight. Before each experiment, the illuminations in various compartments, with or without filters, were checked by a lux-meter (Dr. B. Lange, Type II). The first three experiments were conducted on such days (*see* dates, Fig. 4), when the incident radiation outside the incubator ranged between 50–60 kilolux, but the influence of water in the container and the bottle-chambers reduced it to about 40–45 kilolux. Similarly on March 24th when the fourth experiment was being conducted, at the start of the experiment the incident radiation was about 80 kilolux, but within half-an-hour because of some cloudiness, it was reduced to about 50 kilolux.

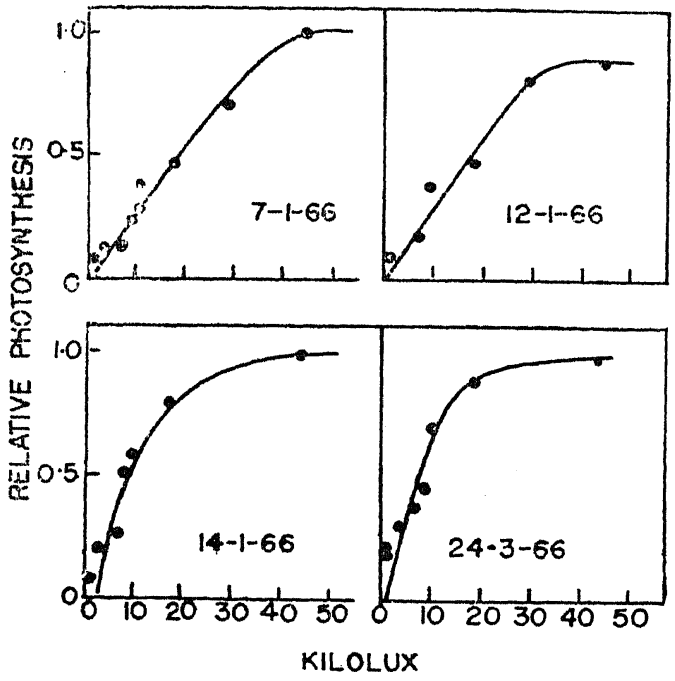

FIG. 4. The relation between photosynthesis and light intensities in surface phytoplankton. Each curve refers to a different experiment.

It can be seen from Fig. 4 that each experiment gave an entirely different result. In the first experiment the increase in the photosynthesis upto nearly 40 kilolux was almost linear. No further increase in the rate occurred after about 45 kilolux which probably indicates that the I_k lies somewhere near this point. In the second experiment the light saturation intensity was reached at about 30 kilolux, but in the third and very clearly in the fourth experiment, the light saturation occurred at about 18–20 kilolux. Such differences in the light saturation optima could not have arisen unless in each experiment a different composition of phytoplankton population was investigated. It is interesting to note that though the time-gap between the first three experiments was only a few days, it does not warrant a consistent and homogeneous picture. It can therefore be con-

cluded that at any given time, even from day to day, a heterogeneity rather than uniformity in the phytoplankton population seems to be the rule.

From these experiments it can also be deduced that within the range of illumination investigated, the light saturation intensity continued until about 50 kilolux and that the surface plankton of the estuary exhibits all characteristics of " sun plankton". It has been reported earlier that on very bright days the total solar radiation may reach approximately 625 g cal/cm^2/day (Qasim *et al.*, 1968). On such days the intensity at about midday exceeds 100 kilolux. It is therefore less surprising to find the saturation intensity of mixed phytoplankton population of the estuary reaching 50 kilolux. In January and March when these experiments were conducted the euphotic zone in the estuary was at its maximum, about 5 m (*see* Table I). In other months it is much reduced and during the monsoon period it is only about 3 m. It would be interesting to know whether in highly turbid conditions the phytoplankton occurring at the base of the euphotic zone, being adapted to much reduced light, will possess characteristics somewhat different from those of the surface plankton. If so, the differences obtained in the light saturation intensity on different days would be easy to explain, for if they were to approach " shade characteristics " these would be constantly mixed due to wind action and tidal influence and therefore the results of any experiment would indicate the relative predominance of one type or the other.

Gross and Net Production

As has already been pointed out the available evidence shows that the C^{14} method of estimating primary production gives a value which is nearer to net than gross. The reason for discrepancy between gross and net is owing to the fact that plant cells lose an appreciable portion of their assimilated C^{14} through respiration and excretion (Ryther, 1956*a*; Fogg *et al.*, 1965). It has however been suggested by Steemann Nielsen (1955) that in experiments involving a short duration, 50–70% of the labelled CO_2 produced by respiration is again photosynthesised, thereby making the respiratory loss, on an average, to about 8% (Steemann Nielsen and Hansen, 1959). On the other hand, "in experiments with duration of 24 hours or more the C^{14} technique must measure net production" (Steemann Nielsen, 1964). Perhaps a serious limitation in the radiocarbon technique is that it does not give any information on the amount of material respired or excreted (Fogg *et al.*, 1965). Steemann Nielsen and Hansen (1959) developed a method of

estimating the rate of respiration from the C^{14} technique by extrapolating the curve of C^{14} uptake as a function of light intensity to a point of intersection along the carbon assimilation axis and multiplying this negative value by a factor 10/6 (Steemann Nielsen, 1963), to allow for a disproportionate absorption of respired CO_2. To obtain theoretically both net and gross productions, Steemann Nielsen (1964) applied 0·96 and 1·06 as correction factors, assuming that the rate of respiration is approximately 1/10 of the maximum photosynthesis. Ryther (1956 *b*), however, considers it unlikely that the ratios between photosynthesis and respiration (PS : R) would remain constant from season to season because of differences in the availability of light and nutrients.

In the present investigation the values of C^{14} assimilation have been taken as net production (Table IV). This seemed a reasonable assumption, for the discrepancies between net production obtained from the oxygen experiments were less with C^{14} assimilation than with gross production (*see* Fig. 2). For comparison the average net and gross values obtained from the oxygen experiments are also included in Table IV. Thus an estimate of net production for the day was obtained both by the O_2 and C^{14} methods. However, in order to determine the potential source of organic matter which is transferred to the next trophic level we must know the 24-hour net primary production. This has been computed as below.

The average values of respiration over a day determined from the oxygen decrease in the dark-bottle during concurrent oxygen and C^{14} experiments at various depths of the euphotic zone have been given in Table IV as their carbon equivalents. These have been taken as the respiratory loss occurring during the carbon assimilation, which when added to the C^{14} (net) values gave another estimate of gross production—called here as *adjusted gross* (Table IV). This method of estimating the respiratory loss had to be based on the usual assumption that the respiration occurring in the dark is the same as that during the corresponding period of light in conjunction with photosynthesis. Brown (1953) using isotopically enriched oxygen (O^{18}) has shown that the respiration is the same in the light as that in the dark. It can be seen from Table IV that the respiratory loss is highly variable from month to month and therefore as pointed out by Ryther (1956 *b*) cannot be corrected by a common factor. Total respiration (day) as a percentage of gross was in no case less than 20% and in one month it reached 45%. Taking the respiration as a process quite independent of photosynthesis and assuming that it occurs at the same rate throughout day and night, the values for the respiratory loss occurring during the night

TABLE IV

Net and gross primary production in the euphotic zone determined from oxygen evolution and C^{14} assimilation. The latter when corrected for respiration gave adjusted gross. Estimates of 24-hours net primary production were made by assuming the respiration to be at the same rate throughout day and night. Net: gross ratios of each pair have also been included

	O_2 production mgC/m²/d (14 h)		Respiration mgC/m²/d (14 h)	Respiration % of gross	C^{14} uptake mgC/m²/d (14 h)		Respiration night (assumed) mgC/m² (10 h)	Adjusted net production mgC/m²/d (24 h)		Net : Gross ratio (14 h)	
	Net	Gross			Net	Gross (adjusted)		O_2	C^{14}	O_2	C^{14}
1966											
January ..	658	829	171	20·6	647	818	122	536	525	0·79	0·79
February	772	1,127	355	31·5	375	730	254	518	121	0·68	0·51
March ..	658	908	250	27·5	442	692	179	479	263	0·72	0·64
April ..	1,211	1,851	640	34·6	883	1,523	457	754	426	0·65	0·58
May ..	485	855	370	43·3	434	804	264	221	170	0·57	0·54
June ..	597	789	192	24·3	343	535	137	460	206	0·76	0·64
July ..	296	543	247	45·5	741	988	176	120	565	0·55	0·75
1965											
August ..	393	556	163	29·3	490	653	116	277	374	0·71	0·75
September	632	1,012	380	37·5	485	865	271	361	214	0·62	0·56
October ..	390	538	148	27·5	692	840	106	284	586	0·72	0·82
November	232	311	79	25·5	270	349	56	176	214	0·75	0·77
December	233	371	138	37·3	266	404	99	134	167	0·63	0·66

(10 hours) have also been indicated in Table IV. These when subtracted from the day-net production, C^{14} or O_2 values, gave an estimate of 24-hours net primary production, which has been termed here as *adjusted net* (Table IV).

Gilmartin (1964) while estimating the 24-hours net primary production of a British Columbia Fjord gives a measure of day and night respiration separately. However, from his data, if the ratios between day and night respiration are calculated, these fall within a range 0·45–2·1, average of

10 values = 1. Therefore the assumption here that the rate of respiration during the night is the same as during the day does not seem unrealistic, although the respiratory losses during day or night do not preclude the respiration contributed by zooplankton and bacteria and therefore may not strictly conform to the phytoplankton respiration alone. The O_2 dark load, because of high microbial population in the backwater (Santhakumary, 1966) would also include the bacterial respiration and this would obviously underestimate the net primary productivity both for the day and 24 hours by a high and variable amount. This probably explains the wide discrepancy in the estimates obtained from the O_2 and C^{14} methods (compare pairs in Table IV, column 1 with 5; 2 with 6 and 8 with 9).

The most interesting feature, however, which emerges from the analyses of these data is the ratio of net: gross production. These have also been included in Table IV for the production rates determined from the O_2 and C^{14} methods. It can be seen from Table IV that the two sets of ratios obtained by the two different methods agree very closely except for some months which probably may be due to some experimental error. This provides a further evidence that the radiocarbon technique measures net production. Ketchum *et al.* (1958) have pointed out that the ratio of net: gross photosynthesis in a healthy population should approach unity if respiration is 5–10% of the total photosynthesis. It also indicates the physiological state of phytoplankton organisms arising due to nutrient deficiency. In such cases the ratio would be nearer to zero.

In the backwater the respiration being 20–45% of gross (Table IV), the ratios fall within a range of 0·55–0·75 in one set and 0·51–0·77 in the other. Their fluctuation within such a limited range probably signifies that the nutrients do not act as a limiting factor. However, the somewhat lower ratios found in some months may be because the backwater receives a considerable amount of organic matter from land. Since its decomposition requires more oxygen it would enhance the values of respiration which in turn will give rise to low net: gross ratio. Probably, a disproportionate distribution of organic matter may be yet another factor which gives rise to discrepancy in the estimates obtained by the O_2 and C^{14} methods (Table IV). Such conditions are always to be expected in turbid and polluted water and therefore the disparity in the results in itself is quite suggestive. It only supports the contention that the two methods, widely different as they are in their analytical approach, are affected differently under particularly adverse environmental conditions prevailing in the estuary, and these effects

would not have been possible to appreciate if one method were to be used in isolation with the other.

Seasonal Changes in Production Rates

Monthly values of gross and net production rates at various depths, 0–3 m, have been shown in Fig. 5. As can be seen from Fig. 5 there is a seasonal cycle in production. High values are recorded from April to August and low values from September to March. The discrepancy between gross and net production is greater at 0 m and 0·5 m than at deeper layers. However, despite the seasonal rhythm in production rates the fluctuations hardly exceed 3–4 times. In this respect the backwater behaves very similar to other tropical areas where production has been reported to go on at a moderate level throughout the year with little seasonal increase

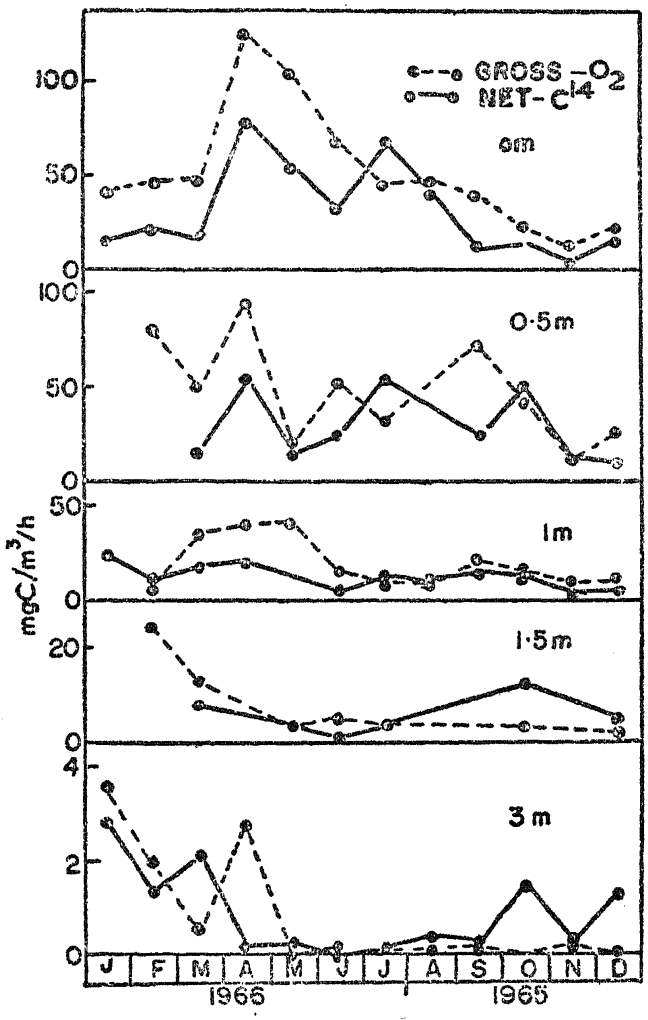

Fig. 5. Seasonal changes in gross and net primary production at different depths; C^{14} assimilation (solid lines), O_2 production (broken lines).

(Hulbert *et al.*, 1960; Menzel and Ryther, 1961 *a*; Prasad and Nair, 1963). This feature, however, is in contrast to higher latitudes where the seasonal amplitude in production during spring and summer may be 50 times or more of the autumn or winter (Raymont, 1966).

Figure 6 shows the production with depths after pooling the values for the entire period of observation into three seasons. Since the changes from month to month were small, each season included 4 months, June–September (monsoon), October–January (post-monsoon) and February–May (pre-monsoon). This division, though arbitrary, fits in well with the changes in light penetration (Qasim *et al.*, 1968). It can be seen from Fig. 6 that nearly 90% of the total production is confined to a narrow zone of 0–1·5 m. During the monsoon and pre-monsoon months when the turbidity is very

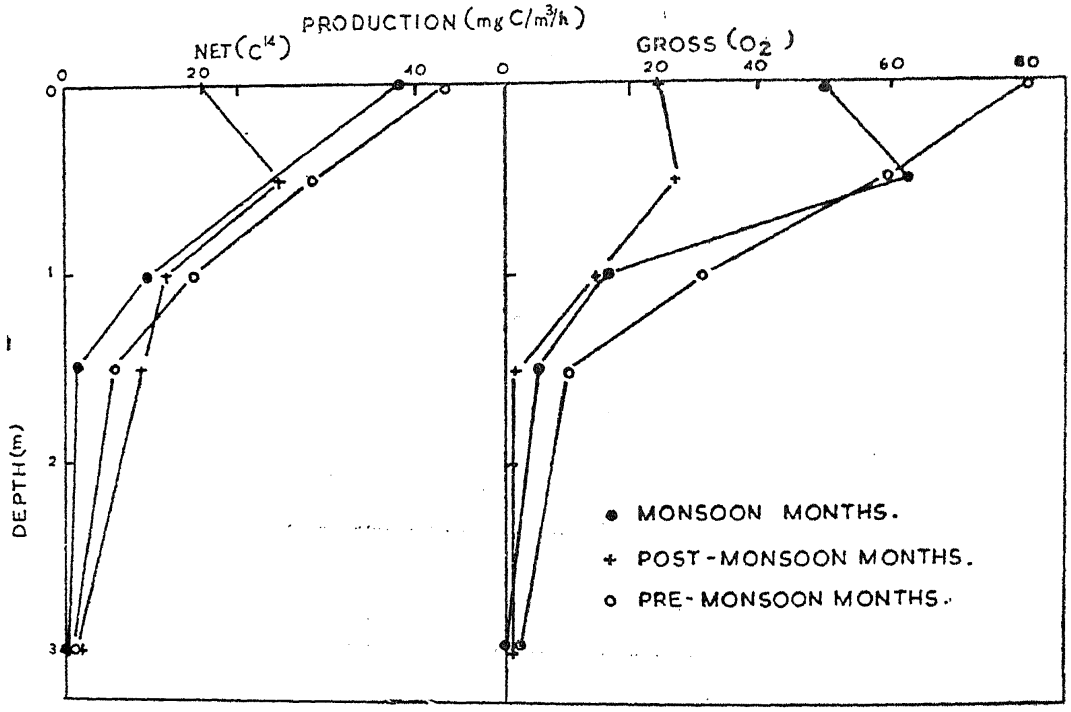

FIG. 6. Gross and net primary production in three seasons in relation to depth.

high, maximum production occurs at the surface, but in the post-monsoon months when the light penetration somewhat improves, maximum production is found slightly below the surface. There was a slight deviation in the picture of gross production which showed a maximum at 0·5 m during the monsoon months.

The column production of the euphotic zone has been shown in Fig. 7 *f*, along with the seasonal changes in some of the hydrographical features whose

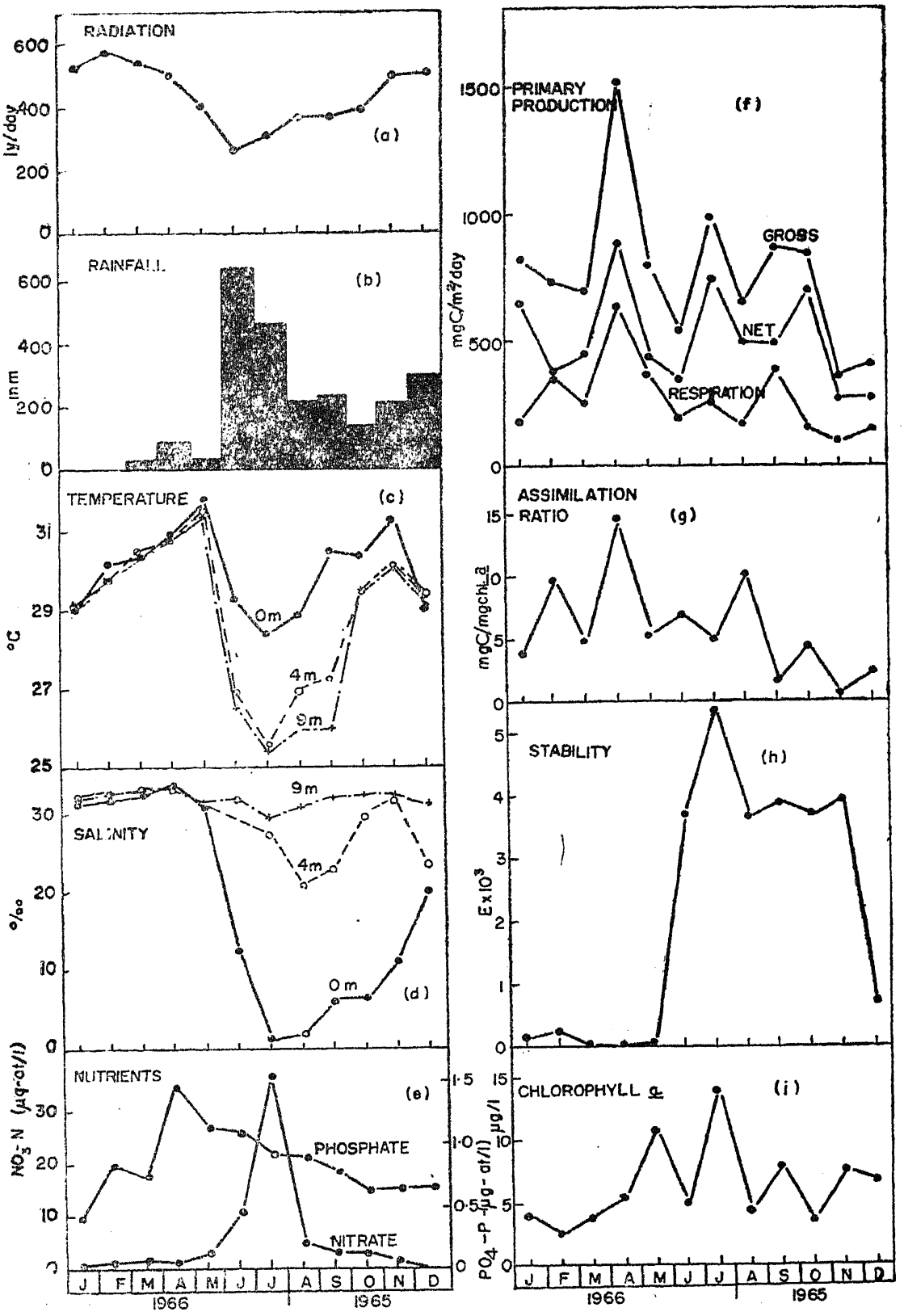

FIG. 7. Seasonal changes in various environmental factors in relation to gross and net primary production. The values of production, respiration, nutrients, assimilation ratio and chlorophyll refer to euphotic zone whereas the stability was calculated for 0–4 m.

possible influence is discussed below. For reasons of greater accuracy in the estimates of column production, we have used only the values of C^{14} uptake and not the estimates based on O_2 production, *i.e.*, the gross production refers to adjusted gross (day) and the day-net production is the actual C^{14} assimilation (Table IV, columns 5 and 6). Also included in Fig. 7 *f* is the average respiration in the euphotic zone (Table IV). It can be seen from Fig. 7 *f* that the annual cycle of production forms three small peaks—one in April, the second in July and the third in October. Here the fluctuations are of a smaller range than those at the surface (Fig. 5). Since the production rates, as will be shown later, are largely dependent on external forces such as monsoon conditions, land drainage, etc., these fluctuations may not be consistent year after and may occur at any time with a correct synchronization of meteorological conditions. The Cochin area, on an average, gets an annual rainfall of 3,200 mm. Of this, nearly 75% occurs from May to September (Fig. 7 *b*). Generally a few spells of rain occur during March-April. These are commonly called the "pre-monsoon showers" which are very often fairly heavy, with 2·5–5 mm of rain within a few hours. This however cannot be regarded as a usual feature, for in March/April 1967 there was practically no rain and several heavy showers occurred in early May. Undoubtedly the first few showers seem important in inducing a brief pulse of bloom in the estuary. This may be because of a sudden increase in nutrients. As can be seen from Fig. 7 *e* and *i*, the phosphorus and chlorophyll values increase sharply in April. Similarly the other peaks in the rate of production seem closely related to the rise in phosphorus and chlorophyll values.

FACTORS INFLUENCING ORGANIC PRODUCTION

While considering the influence of some factors on the organic production it seems important to point out that although one single factor has been dealt at a time, it is the collective influence of various factors that gives rise to a particular value of organic production. Some of these parameters may directly affect the physiology of the plants while others may either accelerate or inhibit production. There may very well be many more variables which are yet unknown or are adequately studied. Therefore, whatever is said here may only be regarded as a close approximation of the tangle of events during the period to which the data on organic production refer.

Light—Average monthly values of solar radiation falling on the water surface have been given in Fig. 7 *a*. A comparison of these with the monthly

values of production rates would reveal that the peaks in the production cycle are independent of high or low illuminations. The peaks occur in April, July and October when the values of illumination are very different. Evidently, the monthly variations in total radiation are never a limiting factor for maximum photosynthesis. Steemann Nielsen (1963) made similar remarks on the solar radiation of the tropics. The opacity of water, on the other hand, reduces the light penetration considerably. During the monsoon months, the underwater illumination is reduced to about 20% of the incident radiation within 1 m and 1% at 3 m. Similarly, during the post- and pre-monsoon months the reduction in light is about 30% at 1 m and 1% at 4 m (Qasim *et al.*, 1968). With such limitations in the light penetration it seems unlikely that, despite the adaptations in increasing the photosynthetic efficiency under subdued light, such as are known in phytoplankton organisms (*see* Ryther, 1962), the primary production will exist at depths greater than 4 m. If at all, it would only be in January–March, during which period the euphotic zone extends as far as 5 m. It can therefore be concluded that while the solar radiation falling on the water surface remains unlimited, the underwater illumination acts as a serious limiting factor for maximum photosynthesis in the estuary.

Temperature.—Seasonal changes in the surface temperature are not well marked in the estuary (Fig. 7 *c*). These hardly exceed 3–4° C and generally fall within a range of 28–31° C. There seems no direct effect of temperature on organic production, except that the uniformly high temperature will affect the rate of metabolism of the organisms and thus will induce a rapid turnover and increased respiration. The net production much lower than the gross, as has been found in the estuary, may be because of the overall effect of higher tropical temperature in conjunction with other parameters.

Salinity.—Among the physical factors salinity is yet another important factor to be considered in the estuary. Figure 7 *d* shows the variation in salinity at different depths. It is clear from Fig. 7 *d* that from June–December, typically brackish water occupies the entire euphotic zone. A comparison of the annual cycle of production with the salinity changes will indicate that except for April, productivity peaks occurred during a period when the surface salinity was very nearly minimum, approximately 2–20‰ within the euphotic zone. This obviously calls for a mechanism in plant organisms not only to be sufficiently euryhaline, but also to have their range of photosynthesis, very nearly optimum, at low salinities. The predominant phytoplankton crop in the estuary consists of diatoms and dinoflagellates

in addition to numerous unidentified nanoplankton organisms very similar to the "small forms", described by Ryther (1954), which bloom intensely in certain months. Several earlier studies have shown that some diatoms and dinoflagellates have wide limits of salinity tolerance. Thus with *Skeletonema*, optimum photosynthesis occurs at salinities ranging from 15 to 20‰ (Curl and McLeod, 1961) while many dinoflagellates reproduce faster at low salinities and have their optimum range of photosynthesis in between 8–12‰ (Braarud, 1961; Provasoli and McLaughlin, 1963). In addition to these, the "small forms" seem to thrive in brackish water, for they are well adjusted to low salinities (Ryther, 1954; Prakash, 1967). The sharp fall in salinity and its corresponding gradual rise thereafter may therefore introduce what has been referred to in the literature as " species succession " in phytoplankton (Strickland, 1965; Raymont, 1966). This probably explains the abundance and flowering of many phytoplankton organisms at low salinities.

Stability.—As has been shown earlier due to high turbidity, primary production exists only in a narrow water column near the surface. It would therefore to a large extent be dependent on the amount of plant population which is maintained at this favourable zone of illumination. While a considerably large portion of the plant life is constantly removed from this layer due to turbulence, the stability of this water column is important for favouring primary production in certain months. Figure 7 *h* shows the seasonal changes in the stability of water column 0–4 m. A comparison of the stability curve with the seasonal production rate will reveal that while the production peak in April occurred when the water was well mixed and was probably initiated due to some such factors as sudden influx of nutrients, the other two peaks in July and October coincided with a period of greater stability. The reduced salinity during July–November was the main factor involved in increasing the stability in these months. In an oceanic environment prolonged stratification is known to restrict the vertical movement of nutrients to the euphotic zone, where because of continued photosynthesis, these become a limiting factor (Steele, 1958). In the shallow backwater where the nutrient supply seems to be largely dependent on external sources (rivers, land runoff, tidal influence, etc.), such a limitation would not arise.

Nutrients.—Average monthly values of the concentrations of two important nutrients, nitrate and phosphate have been shown in Fig. 7 *e* for the euphotic zone. Silicate in the estuary was always excessive (Table I) and seems to be associated with the freshwater influx and land runoff. The N: P ratios by atoms were found to be highly variable from the normal ratio of 16: 1. During the monsoon months the ratios were remarkably

high reaching 40: 1 in July. In other months they were extremely low, the minimum being in December (0·53: 1). Ketchum *et al.* (1958) recorded similar variations in the N: P ratios from the tropical North Atlantic. Similarly Jeffries (1962) reported highly erratic ratios from an estuary despite the fact that the phytoplankton organisms showed remarkable consistency. A close examination of Fig. 7 *e* and *f* will reveal that while there is a close correlation between the cycles of phosphorus and organic production in the backwater, the nitrogen cycle is completely unconnected with the productivity rhythm, for most of the year there is little or no nitrate–N. In April when the carbon assimilation reaches its maximum, the N: P ratio was 0·92: 1. Similarly the highest ratio in July (40: 1) did not lead to any abnormal rise in the carbon assimilation. Currie (1958) found no significant increase in the rate of photosynthesis when the water samples were enriched with inorganic nitrogen and phosphorus.

A direct plot of nitrate–N by atoms against carbon assimilation as has been shown in Fig. 8 *a* further revealed no correlation ('r' = − 0·17). Similarly no significant relationship was obtained between nitrate–N and carbon assimilation [Fig. 8 *b* ('r' = 0·41)]. On the contrary, the relationship between phosphorus and carbon assimilation (Fig. 8 *c*) was somewhat more definite ('r' = 0·79). This signifies that there must be an alternative source of nitrogen (*e.g.*, ammonia) to be utilized by the plants. Probably like temperature and salinity the changing ratios of N: P may also introduce a succession of organisms which are adapted to a particular range of the ratios, for it is known that the basic nutrient requirement of all organisms would not be the same (Ryther, 1954) and the growth of diatoms will not decrease immediately even when the nutrients have been exhausted (Spencer, 1954). Probably the explanation given by Ryther and Guillard (1959) for the Sargasso Sea that in warmer waters the instantaneous concentration of nutrients is not as important in affecting productivity as the rate with which these elements are regenerated and absorbed in forms other than the inorganic salts, seems to be true for the estuary.

Carbon assimilation: chlorophyll ratio.—Photosynthesis to chlorophyll *a* ratios were determined in three different ways: (1) from the average monthly values of carbon assimilation and chlorophyll *a* taken from different water samples on different days; (2) from the chlorophyll content of the same water sample which was used for estimating the rate of photosynthesis by C^{14} ; and (3) from the chlorophyll concentrations before and after 6 hours of exposure to *in situ* natural illumination, concurrent with C^{14} fixation.

TABLE V

Photosynthesis: chlorophyll 'a' ratios in 22 experiments conducted on different days of the year. Net and gross values refer to C^{14} uptake uncorrected and corrected for respiration

Date of experiment	Assimilation ratio mgC/mg Chl/hr	
	Net	Gross
8–11–1965	4·5	6·7
17–11–1965	3·5	3·6
1–12–1965	1·8	2·9
19– 1–1966	3·4	5·5
2– 2–1966	7·9	—
6– 3–1966	4·1	6·2
17– 3–1966	4·1	5·8
6– 5–1966	2·2	2·9
19– 5–1966	3·9	4·4
7– 6–1966	2·5	2·7
29– 6–1966	2·5	2·7
22– 8–1966	8·2	10·7
do.	7·6	9·0
do.	2·5	5·8
13– 9–1966	5·4	7·1
30– 9–1966	3·4	5·8
18–10–1966	2·2	3·2
29–10–1966	2·7	5·4
18–11–1966	1·6	2·1
29–11–1966	1·1	1·2
15–12–1966	3·7	6·8
30–12–1966	1·0	2·1

In the first case the range in the ratio obtained was considerable, 0·6–15 between net assimilation and chlorophyll *a* (Fig. 7 *g*). This gives a further evidence that the phytoplankton populations are highly variable and that no constancy in the ratio under varying hydrographical conditions is to be expected. Seasonal fluctuations in the ratio very often fell in accordance with a similar rise and fall in the production rates, but in some months these were quite independent of carbon assimilation. It is therefore apparent that the variability in the ratio cannot be explained in terms of changes in the nutrient supply, for there was no close correspondence between the seasonal changes in production rates and the N: P ratios (Fig. 7 *e* and *f*).

In the second case the ratios of 22 experiments ranged between 2·7–10·7 (mean = 4·89) for gross production and 2·4–7·9 (mean = 3·66) for net production (Table V).

In the third situation the range in the ratio, as given in Table VI, was fairly limited, 3·3–7·36 for gross assimilation (mean = 5·56) and 2·09–3·56 for net assimilation (mean = 2·86).

TABLE VI

Assimilation ratios determined from increase in chlorophyll after 6 hours of exposure to in situ *illumination*

Date	Initial chlorophyll mg/m³	Final chlorophyll after 6 hr mg/m³	C^{14} assimilation mgC/m³/hr		Assimilation ratio mgC/mg chl/hr	
			Net	Gross (adjusted)	Net	Gross
18–10–1966	1·40	2·90	3·14	4·54	2·09	3·03
29–10–1966	2·20	3·82	5·93	11·93	3·66	7·36
29–11–1966	5·70	8·40	5·76	18·76	2·13	6·95
30–12–1966	1·60	8·50	24·64	33·84	3·56	4·90

Several earlier authors have found the carbon assimilation: chlorophyll ratios to vary seasonally and these have generally been attributed to nutrient deficiency (Anderson, 1964; Curl and Small, 1965). Steele and Baird

(1961), however, do not consider that fluctuations in the ratio could arise because of nutrient deficiency alone. In the backwater the variability in the ratio may largely be due to the fact that the entire observed chlorophyll may not be photosynthetically active. It may also depend upon the physiological state of the plankton organisms which due to changing conditions in the estuary may not have their photosynthesis and chlorophyll optima phased at the same time.

ESTIMATION OF PRODUCTION FROM RADIATION AND CHLOROPHYLL

Based on the general principle that when the rate of photosynthesis of a phytoplankton population is a function of light intensity, the concentration of chlorophyll at optimum light should give a close approximation of carbon assimilation, Ryther and Yentsch (1957) formulated a new method of estimating gross production from radiation and chlorophyll. This method, simple as it is, has found a fairly important place in the literature. For calculating the production rates, Ryther and Yentsch give a working ratio of carbon assimilation: chlorophyll as 3·7 gC/hr/g chl. This value was determined from their own measurements of *gross* photosynthesis by using light-dark-bottle oxygen technique and from the evidences collected from the literature. In a recent communication, however, Curl and Small (1965) while giving a critical appraisal of the ratio 3·7 have found, in waters off the Oregon coast, the average *net* carbon assimilation: chlorophyll ratio as 8·6, which they used for computing production rates from light and chlorophyll. They also suggest that for such calculations an empirically determined assimilation ratio, specific to the environment in question, should be used.

It is however not clear from the literature whether *gross* or *net* carbon assimilation: chlorophyll ratio should form a basis of calculating production rates from the light and chlorophyll method which is essentially intended to give a measure of *gross* production (*see* Ryther and Yentsch, 1958; Menzel and Ryther, 1961 *a*). This may not be important in such areas where losses through respiration are small, but in the backwater where respiration is high this may lead to large discrepancies. As can be seen from Table VII the estimates made by using 4·89 as gross-assimilation ratio and 3·66 as net-assimilation ratio (*see* above) were somewhat different. In general, the gross-assimilation-ratio gave estimates which were somewhat comparable to gross production and similarly the estimates obtained from net-assimilation ratio gave an approximation of net production rates. The variability between each pair of observed and computed values as given in Table VII

TABLE VII

Production rates computed from radiation and chlorophyll data by using different assimilation ratios and the measured values by C^{14} assimilation

	Production mgC/m²/d			
	Calculated		Observed	
	Net	Gross	Net	Gross
1966—				
January	368	495	647	818
February	232	313	375	730
March	330	444	442	692
April	274	370	883	1,523
May	633	853	434	804
June	293	394	343	535
July	1,684	2,269	741	988
1965—				
August	289	389	490	653
September	629	847	485	865
October	172	232	692	840
November	774	1,043	270	349
December	931	1,254	266	404

appears to be large and random. Probably the uncertainty in the photo-synthesis-chlorophyll ratio or some error in the determination of attenuation coefficients of highly turbid waters may be the reason of discrepancies in the estimates.

PRODUCTIVITY IN RELATION TO PARTICULATE MATTER

As has been pointed out earlier the estuary is always characterised by large quantities of particulate matter. These include living organism

plus considerable quantities of dead or detrital matter whose composition and proportion vary from time to time and from one part of the estuary to the other. Besides large quantities of suspended solids (sand, gravel, etc.) brought to the estuary by the rivers and land runoff, it may also include decomposition products of plants, wastes and refuse of all types from the adjacent land and harbour. Since a chemical analysis of the dead material seems difficult to make, the other possible method would be to show the interrelationship of some such parameters which have a direct bearing on productivity.

Figure 8 *d* gives the relationship between seston and phytoplankton counts. It can be seen from Fig. 8 that there is no relationship between the two ('r' $= -0{\cdot}16$). In other words, the phytoplankton organisms which form a small fraction of the particulate matter, occur quite independently of the other suspended matter. Figure 8 *e* shows the relationship between the phytoplankton counts and chlorophyll *a*. It is evident from Fig. 8 that despite much scatter in the points, it is possible to conclude that there is some relationship between the two ('r' $= 0{\cdot}45$). This indicates that chlorophyll largely comes from the phytoplankton organisms. However, if no chlorophyll is contributed from particulate matter other than plant organisms, one would expect no relationship between seston and chlorophyll. On the contrary, a plot of chlorophyll against seston (Fig. 8 *f*) gives some evidence that an increase in seston is followed by a corresponding increase in chlorophyll. A considerable scatter in the points and a low correlation coefficient value ('r' $= 0{\cdot}25$) are probably because the figures includes data of all seasons. If these were to be plotted on a seasonal basis as has been done in the case of chlorophyll to particulate carbon (Steele and Baird, 1961) or between particulate carbon, nitrogen and phosphorus (Menzel and Ryther, 1964), the slope of the regression which may be different in different seasons, would have probably shown better. From this relationship it seems likely that some chlorophyll does come from the non-living material. This probably confirms the findings reported earlier from the Cochin Backwater (Qasim and Reddy, 1967). Moreover, some evidence towards the amount of dead or inactive chlorophyll present in the samples can also be obtained by plotting the rate of photosynthesis against chlorophyll *a*. These have been shown within the limits of available data, for three different seasons in Fig. 9 *a*, *b* and *c*. It can be seen from Fig. 9 that the slope of the regression is different in the three seasons. The regression for January–March intercepts very near the origin whereas those related to May–June and August–December extrapolate to positive values of chlorophyll. In the first case the relationship suggests that the proportion between carbon

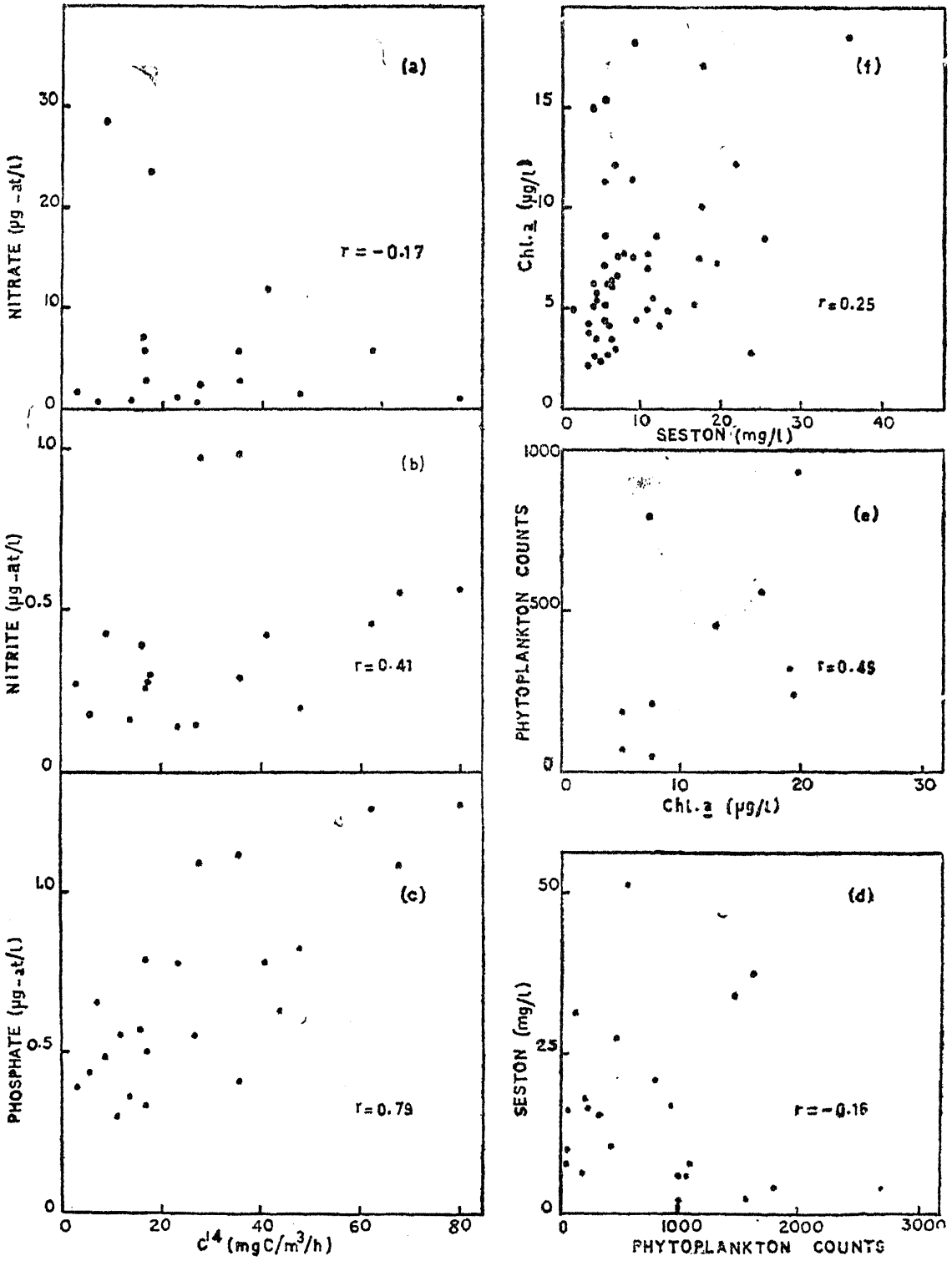

FIG. 8. The relation between net primary production (C^{14}), nutrients, phytoplankton counts, seston and chlorophyll; '*r*' denotes the correlation coefficient.

assimilation and chlorophyll is very nearly the same and that practically all chlorophyll present took part in the photosynthesis. In the other two

cases the intercepts of carbon assimilation suggest the presence of some detrital chlorophyll during these seasons (*see* Steele and Baird, 1961).

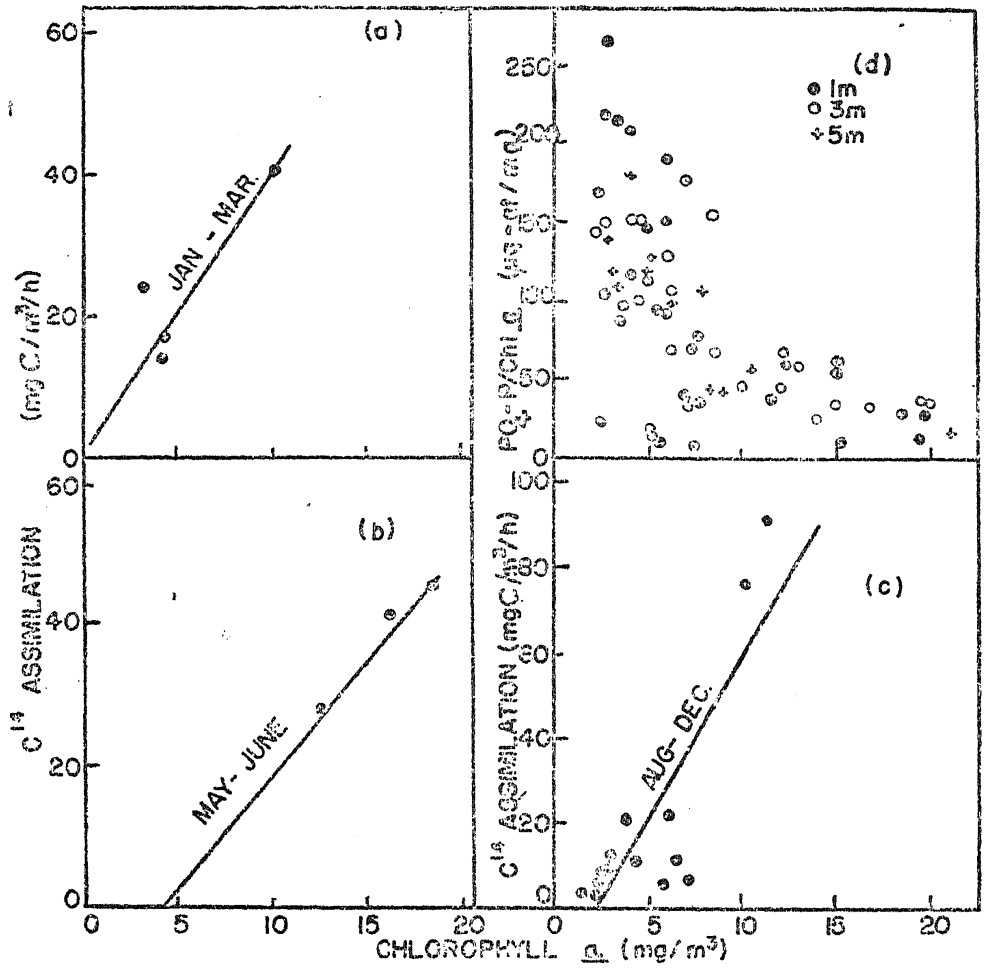

FIG. 9. The relation between C^{14} assimilation and chlorophyll *a* obtained by grouping the values given in Table V into three seasons (*a*, *b* and *c*). Ratio of phosphorus per chlorophyll *a* as a function of chlorophyll *a* (*d*).

If this evidence is to be accepted it would appear from Fig. 9 that the quantity of inactive chlorophyll was somewhat larger in May–June when the suspended matter in the estuary was maximum and the light penetration minimum. It continued to occur from August–December in smaller proportions until practically no dead chlorophyll was left during January–March when the light penetration was maximum. Probably the inactive chlorophyll was in the form of phaeophytin whose formation in darkness has recently been demonstrated (Yentsch, 1965 *a*). The change in the slope of regression in the three seasons gives the relation of carbon assimilation to chlorophyll as 8 : 1 in August–December, 4 : 1 in January–March and 2·2 : 1 in May–June. This offers supporting evidence to the statement made earlier that photosynthesis and chlorophyll synthesis may not have their maxima at the same

time. Some valid explanation of the two processes very often being non-synchronous has been given by Yentsch (1965 *b*).

In oceanic waters from the regression analysis of chlorophyll and phosphorus on nitrogen and carbon, Menzel and Ryther (1964) deduced that chlorophyll and organic phosphorus compounds are quickly decomposed and denatured leaving behind the detrital residue composed mainly of carbon and nitrogen. It seems certainly true of oceanic waters where the detritus primarily includes dead material of plants and more particularly of animal origin (Parsons and Strickland, 1960), which, at greater depths remains more or less constant at any one time of the year in what has been termed as "old waters".

In an environment like the backwater where the water masses are constantly renewed, there is probably a rapid turnover of cellular material. The decomposition of chlorophyll and its regeneration therefore becomes a continuous process. Due to high turbidity the transformation of chlorophyll into phaeophytin also seems a process of simultaneous occurrence. The denaturing of chlorophyll and its removal from the scene may therefore occur at a much later stage. The fate of phosphorus, on the other hand, seems easier to explain. The relationship of phosphorus per chlorophyll *a* as a function of chlorophyll *a* (Fig. 9 *d*) was very similar to what has been previously shown by Ketchum *et al.* (1958). At low chlorophyll concentrations the ratio was very large (40–250) but at high chlorophyll concentrations it ranged between 20–40 μg-at-P/mg chl *a*. The explanation given by Ketchum *et al.*, that " the pigment is quickly decomposed as the cells die, but the phosphorus remains bound, for some time afterwards, to the organic detrital material," seems to be applicable to the backwater.

Annual Production

The estimated annual production of the estuary by different methods is given in Table VIII. It is clear from Table VIII that all the methods gave agreeable results. The gross production fell within a range 272–293 $gC/m^2/yr$ (average = 281 $gC/m^2/yr$). Similarly the net production for days ranged from 184 to 202 $gC/m^2/yr$ (average = 195 $gC/m^2/yr$) and the average for days and nights (24 hours) is approximately 124 $gC/m^2/yr$. The estimated net 24 hours production indicates the potential source of organic matter which is available to the next trophic level.

The annual production of the backwater agrees with those of other estuarine environments reported from different geographical regions of the

TABLE VIII

Annual estimates of gross and net primary production by different methods

Method	Annual production gC/m²		
	Gross	Net	
		day	24 hr
O_2 ..	293	198	130
C^{14} ..	279	184	117
Light and chlorophyll	272	202	..
Average ..	281	195	124

world. Thus for the Long Island Sound, the annual gross production is 470 gC/m² (Riley and Conover, 1956) and for the Georges Bank and the Gulf of Maine it is 309 and 270 gC/m² respectively (Riley *et al.*, 1949; Riley, 1941). In a British Columbia Fjord, the annual gross and net production rates are approximately 650 and 450 gC/m² respectively (Gilmartin, 1964) and for Isefjord the gross production is 175 gC/m² (Steemann Nielsen, 1951). A lower annual production of the backwater than some of the other estuaries of the temperate region is because of its shallow euphotic zone. However, as compared to the oceanic waters of different regions, the annual production of backwater is much higher. Ryther (1963) gives the annual estimates of gross production of the temperate and sub-polar waters as 70–120 gC/m² and for tropical oceans (*e.g.*, Sargasso Sea) as 18–50 gC/m², reaching 72 gC/m² off Bermuda. In the Western Indian Ocean the average annual production is 127 gC/m² (Ryther *et al.*, 1966) and for the Antarctic and Arctic Oceans the estimates are 100 and <1 gC/m² respectively.

EFFICIENCY

The efficiency of the ecosystem to convert solar energy into organic matter was determined from the total monthly readings of the solar radiation and the gross production values. The carbon assimilation values were converted into light energies by using the factor 3·5 kcal/gO_2 (Odum and Hoskin, 1957) in terms of carbon equivalents (11·2 kcal/gC). Th

percentage efficiency in each month was calculated from the formula given by Copeland and Dorris (1964) which states

$$F = \frac{11{,}200\ C}{10{,}000\ S} \cdot 100$$

where

F is the per cent efficiency.

C is the gross photosynthesis in $gC/m^2/day$.

S is the visible solar radiation in g cal/cm^2/day and 10,000 is a facto (for converting cm^2 to m^2).

Since only 50% of the incident radiation is photosynthetically active (Ryther, 1959), only one-half of the light energy was taken into consideration. The calculated efficiencies in various months have been shown in Fig. 10 along with the average monthly radiation values. The efficiencies

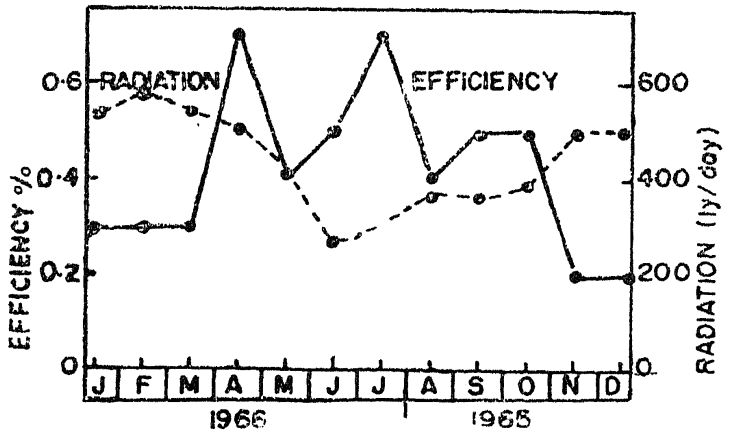

FIG. 10. Average solar radiation falling on the surface in each month and efficiency of fixation of usable light energy by the phytoplankton communities.

range from 0·2 to 0·7%. At low illuminations the photosynthetic efficiency was relatively more than at high illuminations. This probably suggests that excessive solar radiation beyond a certain range does not contribute to the photosynthetic efficiency. A comparison of the efficiency of the backwater with those of the other environments, as given by Ryther (1962), shows that the backwater has an efficiency (0·4%) which agrees very closely to the average for coastal and inshore waters (0·5%). The various factors affecting the photosynthetic efficiency of different marine environments have been discussed by Ryther (1962). Of these, what appears to be the most relevant factor with reference to the backwater, is the absorption of a very large raction of light by non-planktonic particulate and dissolved matter (*see*

Qasim *et al.*, 1968), which leaves behind only a small fraction, perhaps less than the minimal figure of 27% given by Ryther (1962), to be absorbed by the plants.

PRODUCTIVITY IN RELATION TO ZOOPLANKTON

The zooplankton and phytoplankton crops have been shown in Fig. 11 *a* in terms of their carbon equivalents, using the conversion factors, 96 mgC for each ml of zooplankton by displacement (Cushing *et al.*, 1958), and 1·4 mgC for each ml of settled phytoplankton (Sverdrup *et al.*, 1942). The zooplankton abundance in the estuary was predominantly associated with changes in the salinity and thus could be related to the annual monsoon cycle. Maximum zooplankton both in volume and diversity occurred during the period of high salinity (January–March), when its composition was very similar to that of the inshore waters of the Arabian Sea. Besides a variety of crustaceans and molluscan veligers which occurred in varying proportions throughout the year, typically marine forms such as hydromedusae, ctenophores and chaetognaths were also abundant during this season. The following summary which is largely based on the published work of George (1958) will indicate the seasonal abundance of zooplankton in the backwater:

Organisms occurring throughout the year

Copepoda:

(*Acartia* sp.; *Schmackeria tollingeri*)

Cirripedia :

(Barnacle nauplii and cyprids)

Mysidacea:

(*Mesopodopsis orientalis*)

Amphipoda:

(*Corophium trienonyx*; *Photis longicaudata*)

Decapoda:

(Post-larvae of *Metapenaeus monoceros*, larvae of Caridae—*Periclimenes* sp.; *Palaemon* sp.; brachyuran zoea)

Oyster larvae and gastropod veligers:

(*Thais* sp. and *Neretina* sp.)

Polychaeta:

(Pelagic polychaetes—2 species).

Organisms occurring during monsoon and post-monsoon months

Cladocera:

(*Evadne tergestina*)

Ostracoda:

(Several species)

Copepoda:

(*Apseudes* sp.; *Halicyclops* sp.; *Acartia gravelyi*).

Oyster larvae and gastropod veligers

Organisms occurring during pre-monsoon months

Hydromedusae:

(Fairly large numbers)

Ctenophora:

(*Pleurobrachia globosa*)

Chaetognatha:

(*Sagitta enflata*; *S. bedoti*; *S. robusta*)

Copepoda:

(*Paracalanus aculeatus*; *Labidocera pectinata*; *Labidocera kroyeri* var. *gallensis*; *Acrocalanus monachus*; *Eucalanus crassus*; *Canthocalanus pauper*; *Centropages* sp.)

Cumacea:

(*Eocuma* sp.; *Paradiastylis culicoides*)

Isopoda:

(*Sphaeroma* sp.)

Amphipoda:

(*Perioculodes longimanus*; *Grandidierella* sp.; *Hyperia* sp.)

Decapoda:

(Post-larvae of *Metapenaeus dobsoni*; *Penaeus indicus*; *P. carinatus*; adults of *Lucifer hanseni*; *Ogyrides striaticauda*; *Periclimenes indicus*)

Stomatopoda:

(Larvae of *Alima* sp.)

Figure 11 *b* gives the production coefficient which is the ratio of the gross photosynthesis to the carbon content of the phytoplankton (Riley *et al.*, 1949). As can be seen from Fig. 11 the range in the production coefficient is very large (3·7–119) which suggests that the phytoplankton crop

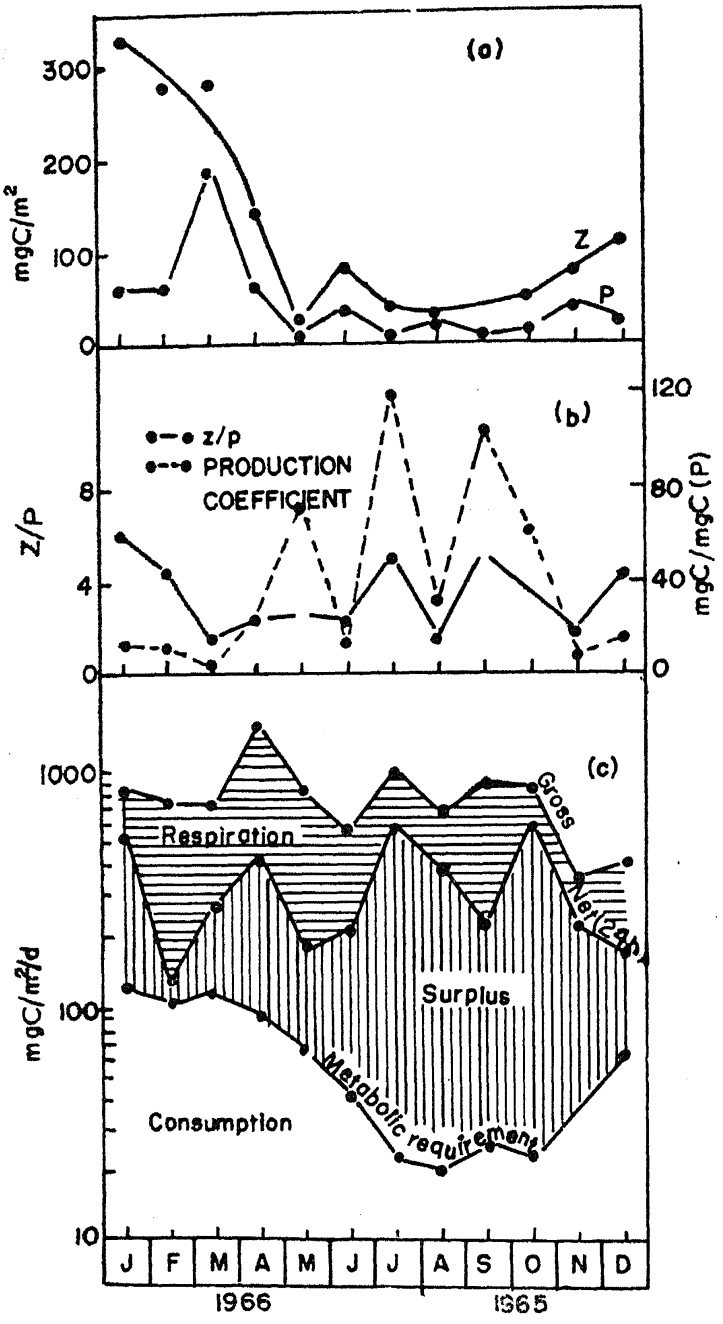

FIG. 11. (*a*) Relation between phytoplankton (P) and zooplankton (Z) taken from parallel hauls on the same day. (*b*) Relation between zooplankton: phytoplankton ratio (Z/P) and production coefficient (Photosynthesis: carbon content of phytoplankton). (*c*) Relation between metabolic requirement of zooplankton and gross and net (24 hrs) primary production. The lower portion shows the approximate consumption of primary production by zooplankton herbivores; the middle portion shows the approximate surplus of basic food and the upper portion hows the average respiration (24 hrs).

sampled by the plankton net comprised only 1 28% of the total carbon assimilation. In certain months when the ratios were high, the crop was dominated by nanoplankton organisms. From November March when the ratios were low the net sampled nearly one-fourth of the total standing crop consisting mainly of large marine diatoms and dinoflagellates.

Seasonal changes in the ratio of zooplankton to phytoplankton, Z/P have been shown in Fig. 11 *b*. The striking correlation between Z/P and the production coefficient suggests that the seasonal variation of the zooplankton population is largely dependent on the type of phytoplankton bloom available in the estuary. Probably the bloom of different organisms at different times of the year fulfils the specific food requirements of the herbivores. An increase in the production (especially at the surface) corresponds to the decrease in zooplankton and to the change from large to small forms. In other words, during the pre-monsoon months the low turbidity is associated with a high zooplankton crop but in the monsoon the reverse seems to be true, with intermediate conditions during the post-monsoon months. This is clearly shown by the fact that although surface productivity (Fig. 5) shows a marked seasonal change, the column production (Fig. 7 *c*) shows a very small range.

Assuming the daily metabolic requirement of zooplankton in terms of carbon as 12% of its dry weight as deduced by Menzel and Ryther (1961 *b*) from the Sargasso Sea, which would perhaps be the nearest for any tropical zooplankton population, the monthly rates of consumption of the primary production by the zooplankton in the estuary have been computed. These have been shown in Fig. 11 *c*, along with gross and net production estimates obtained by the C^{14} uptake for the euphotic zone (*see* Table IV). The average rate of consumption from the daily net production works out as 10% of the production by the plants during the monsoon months, 20% during the post-monsoon months and 46% during the pre-monsoon months. In terms of the estimated annual net production of 124 gC/m^2 given earlier, the total annual consumption by the zooplankton is only about 30 gC/m^2. Evidently, a large surplus of primary production left in the estuary signifies that there is no efficient utilization of the basic food. The lack of zooplankton herbivores in relation to the algal bloom is by no means a rare phenomenon in the tropics. It has been reported in nutrient rich areas of the Western Arabian Sea where sinking of the unconsumed phytoplankton crop below the euphotic zone produces anaerobic conditions (Ryther and Menzel, 1965).

In all probability zooplankton organisms are not the only consumers of the basic food in the estuary. There are always an appreciable numbers

of herbivorous fishes (mullets) and shrimps which are directly dependent on the primary production. Since no estimates have been made of these alternate pathways in the trophic chain, it is difficult to determine quantitatively how much from the surplus crop would be utilized by these consumers. However, from the casual observations made on the gut contents of the mullets it can be inferred that their consumption would be quite substantial. However, the main control of the bloom comes from the small depth of the euphotic zone which increases the sinking rate of a very large proportion of phytoplankton bloom to the bottom, where part of it is probably utilized by the benthic animal communities.

ACKNOWLEDGEMENTS

We are greatly indebted to Dr. N. K. Panikkar, Director, National Institute of Oceanography (India), for his constant interest and encouragement in this work. Sincere thanks are also due to Dr. T. R. Parsons, Dr. John H. Steele and Prof. Charles S. Yentsch for their very constructive criticisms of the manuscript. One of us (S. W.) is thankful to the Ministry of Education (Government of India), for the award of a Fellowship and to Deutscher Forschungsgemeinschaft (German Research Foundation) for the loan of some scientific equipment.

REFERENCES

Anderson, G. C. .. "The seasonal and geographic distribution of primary productivity off the Washington and Oregon Coasts," *Limnol. Oceanogr.*, 1964, **9**, 284–302.

Antia, N. J., McAllister, C. D., Parsons, T. R., Stephens, K. and Strickland, J. D. H. "Further measurements of primary production using a large-volume plastic sphere," *Ibid.*, 1963, **8**, 166–83.

Braarud, T. .. "Cultivation of marine organisms as a means of understanding environmental influences on populations," in *Oceanography*, Edited by Sears, M., A.A.A.S., Washington Publication., 1961, **67**, 271–98.

Brown, A. H. .. "The effects of light on respiration using isotopically enriched oxygen," *Am. J. Bot.*, 1953, **40**, 719–29.

Copeland, B. J. and Dorris, T. C. "Community metabolism in ecosystems receiving oil refinery effluents," *Limnol. Oceanogr.*, 1964, **9**, 431–47.

Curl, Jr. H. and McLeod, G. C. "The physiological ecology of a marine diatom, *Skeletonema costatum* (Grev.) Cleve," *J. mar. Res.*, 1961, **19**, 70–88.

——— and Small, L. F. .. "Variations in photosynthetic assimilation ratios in natural marine phytoplankton communities," *Limnol. Oceanogr.*, 1965, **10** (Suppl.), R-67–R-73.

Currie, R. I. .. "Some observations on organic production in the North East Atlantic," *Rapp. P.-v. Reun. Cons. perm. int. Explor. Mer*, 1958, **144**, 96-102.

——— .. "Productivity," *Proc. R. Soc.*, 1962, **265 A**, 341-46.

Cushing, D. H., Humphrey, G. F., Banse, K. and Laevastu, T. "Report of the Committee on terms and equivalents," *Rapp. P.-v. Reun. Cons. perm. int. Explor. Mer*, 1958, **144**, 15-16.

Doty, M. S. and Oguri, M. .. "Evidence for a photosynthetic daily periodicity," *Limnol. Oceanogr.*, 1957, **2**, 37-40.

Fogg, G. E., Nalewajko, C. and Watt, W. D. "Extracellular product of phytoplankton photosynthesis," *Proc. R. Soc.*, 1965, **162 B**, 517-34.

George, M. J. "Observations on the plankton of the Cochin backwaters," *Indian J. Fish.*, 1958, **5**, 375-401.

Gilmartin, M. .. "The primary production of a British Columbia Fjord," *J. Fish. Res. Bd Can.*, 1964, **21**, 505-38.

Hulbert, E. M., Ryther, J. H. and Guillard, R. R. L. "The phytoplankton of the Sargasso Sea off Bermuda," *J. Cons. perm. int. Explor. Mer*, 1960, **25**, 115-28.

Jeffries, H. P. .. "Environmental characteristics of Raritan Bay, a polluted estuary," *Limnol. Oceanogr.*, 1962, **7**, 21-31.

Ketchum, B. H., Ryther, J. H., Yentsch, C. S. and Corwin, N. "Productivity in relation to nutrients," *Rapp. P.-v. Reun. Cons. perm. int. Explor. Mer*, 1958, **144**, 132-40.

McAllister, C. D., Shah, N. and Strickland, J. D. H. "Marine phytoplankton photosynthesis as a function of light intensity: A comparison of methods," *J. Fish. Res. Bd. Can.*, 1964, **21**, 159-81.

Menzel, D. W. and Ryther, J. H. "Annual variations in primary production of the Sargasso Sea off Bermuda," *Deep Sea Res.*, 1961 *a*, **7**, 282-88.

——— .. "Zooplankton in the Sargasso Sea off Bermuda and its relation to organic production," *J. Cons. perm. int. Explor. Mer*, 1961 *b*, **26**, 250-58.

——— .. "The composition of particulate organic matter in the Western North Atlantic," *Limnol. Oceanogr.*, 1964, **9**, 179-86.

Odum, H. T. and Hoskin, C. M. "Metabolism of a laboratory stream microcosm," *Publs. Inst. mar. Sci. Univ. Tex.*, 1957, **4**, 115-33.

Parsons, T. R. and Strickland, J. D. H. "Oceanic detritus," *Science*, N.Y., 1960, **136**, 313-14.

Prakash, A. .. "Growth and toxicity of a marine dinoflagellate, *Gonyaulax tamerensis*," *J. Fish. Res. Bd Can.*, 1967, **24**, 1589-1606.

Prasad, R. R. and Nair, P. V. R. "Studies on organic production. I. Gulf of Mannar," *J. mar. biol. Ass. India*, 1963, **5**, 1-26.

Provasoli, L. and McLaughlin, J. J. A. "Limited heterotrophy of some photosynthetic dinoflagellates," in *Marine Microbiology*, Edited by Oppenheimer, C. H., Springfield, Ill, Thomas, 1963, 105-113.

Qasim, S. Z. and Reddy, C. V. G. "The estimation of plant pigments of Cochin Backwater during the monsoon months," *Bull. mar. Sci. Gulf Caribb.*, 1967, **17**, 95–110.

———, Bhattathiri, P. M. A. and Abidi, S. A. H. "Solar radiation and its penetration in a tropical estuary," *J. exp. mar. biol. Ecol.*, 1968, **2**, 87–103.

Raymont, J. E. G. .. "The production of marine plankton," in *Advances in Ecological Research*, Edited by Cragg, J. B., Academic Press, London and N.Y., 1966, **3**, 117–205.

Riley, G. A. .. "Plankton studies. III. Long Island Sound," *Bull. Bingham oceanogr. Coll.*, 1941, **7**, 1–93.

——, Stommel, H. and Bumpus, D. F. "Quantitative ecology of the plankton of the Western North Atlantic," *Ibid.*, 1949, **12**, 1–169.

——— and Conover, S. A. M. "Oceanography of Long Island Sound, 1952–54. III. Chemical Oceanography," *Ibid.*, 1956, **15**, 47–61.

Ryther, J. H. .. "The ecology of phytoplankton blooms in Moriches Bay and Great South Bay, Long Island, New York," *Biol. Bull. mar. biol. Lab., Woods Hole*, 1954, **106**, 198–209.

——————— .. "Interrelation between photosynthesis and respiration in the marine flagellate, *Dunaliella euchlora*, " *Nature, Lond.*, 1956 *a*, **178**, 861–62.

——————— .. "The measurement of primary production," *Limnol. Oceanogr.*, 1956 *b*, **1**, 72–84.

——————— .. "Photosynthesis in the ocean as a function of light intensity," *Ibid.*, 1956 *c*, 1, 61–70.

—— and Yentsch, C. S. .. "The estimation of phytoplankton production in the ocean from chlorophyll and light data," *Ibid.*, 1957, **2**, 281–86.

——————— .. "Primary production of continental shelf waters off New York," *Ibid.*, 1958, **3**, 327–35.

——————— .. "Potential productivity of the sea," *Science*, N.Y., 1959, 130, 602–08.

——— and Menzel, D. W. .. "Light adaptation by marine phytoplankton," *Limnol. Oceanogr.*, 1959, **4**, 492–97.

——— and Guillard, R. R. L. "Enrichment experiments as a means of studying nutrients limiting to phytoplankton production," *Deep Sea Res.*, 1959, **6**, 65–69.

——————— .. "On the efficiency of primary production in the ocean," *Proc. 9th Pacific Sci. Congr.*, 1957, 1962, **4**, 188–200.

——————— .. "Geographic variations in productivity," in *The Sea*, Edited by Hill, M. N., Interscience Publ., N.Y., 1963, **2**, 347–80.

——— and Menzel, D. W. "On the production, composition and distribution of organic matter in the Western Arabian Sea," *Deep Sea Res.*, 1965, **12**, 199–209.

——, Hall, J. R., Pease, A. K., Bakun, A., and Jones, M. M. "Primary organic production in relation to the chemistry and hydrography of the Western Indian Ocean," *Limnol. Oceanogr.*, 1966, **11**, 371–80.

Santhakumary, N. .. "Some bacterial characteristics of the Cochin Backwater, *Curr. Sci.*, 1966, **35**, 310–11.

Shimada, B. M. .. "Diurnal fluctuations in photosynthetic rate and chlorophyll "*a*" content of phytoplankton from Eastern Pacific waters," *Limnol. Oceanogr.*, 1958, **3**, 336–39.

Spencer, C. P. .. "Studies on the culture of a marine diatom," *J. mar. biol. Ass. U.K.*, 1954, **33**, 265–90.

Steele, J. H. .. "Production studies in the northern North Sea," *Rapp. P.-v. Reun. Cons. perm. int. Explor. Mer*, 1958, **144**, 79–84.

———— .. "Primary production," in *Oceanography*, Edited by Sears, M., A.A.A.S., Washington Publication. 1961, **67**, 519–38.

———and Baird, I. E. .. "Relations between primary production, chlorophyll and particulate carbon," *Limnol. Oceanogr.*, 1961, **6**, 68–78.

Steemann Nielsen, E. .. "The marine vegetation of Isefjord—a study on ecology and production," *Meddr. Kommn Danm. Fisk.-Og. Havunders Serie. Plankton*, 1951, **5**, 1–114.

———— .. "The use of radioactive carbon (C^{14}) for measuring organic production in the sea," *J. Cons. perm. int. Explor. Mer*, 1952, **18**, 117–40.

———— .. "The interaction of photosynthesis and respiration and its importance for the determination of C^{14} discrimination in photosynthesis," *Physiologia Pl.*, 1955, **8**, 945–53.

——— and Hansen, V. K. .. "Measurement with the carbon-14 technique of the respiration rates in natural populations of phytoplankton," *Deep Sea Res.*, 1959, **5**, 222–33.

———— .. "Inactivation of the photochemical mechanism in photosynthesis as a means to protect the cells against too high light intensities," *Physiologia Pl.*, 1962, **15**, 161–71.

———— .. "Productivity, definition and measurement," in *The Sea*, Edited by Hill, M. N., Interscience Publishers, N.Y., 1963, **2**, 129–64.

———— .. "Recent advances in measuring and understanding marine primary production," *J. Ecol.*, 1964, **52**, (Suppl.), 119–30.

——— and Park, T. S. .. "On the time course in adapting to low light intensities in marine phytoplankton," *J. Cons. perm. int. Explor. Mer*, 1964, **29**, 19–24.

———— .. "On the determination of the activity in ^{14}C-ampoules for measuring primary production," *Limnol. Oceanogr.*, 1965, **10** (Suppl.), R 247–R-252.

Strickland, J. D. H. .. "Measuring the Production of Marine Phytoplankton," *Bull. Fish. Res. Bd Can.*, 1960, No. **122**.

———— .. "Production of organic matter in the primary stages of the marine food chain," in *Chemical Oceanography*, Edited by Riley, J. P. and Skirrow, G., Academic Press, London & N.Y., 1965, **1**, 477–610.

Strikland, J. D. H. and Parsons, T. R. "A Manual of Sea Water Analysis," *Bull. Fish. Res. Bd Can.*, 1965, No. **125**.

Sverdrup, H. U., Johnson, M. W. and Fleming, R. H. "*The Oceans, Their Physics, Chemistry and General Biology*, Prentice-Hall, Inc., N.Y., 1942.

Verduin, J. .. "Daytime variations in phytoplankton photosynthesis," *Limnol. Oceanogr.*, 1957, **2**, 333–36.

Yentsch, C. S. and Ryther, J. H. "Short-term variations in phytoplankton chlorophyll and their significance," *Ibid.*, 1957, **2**, 140–42.

———— .. "Primary production," in *Oceanogr. Mar. Biol. Ann. Rev.*, Edited by Barnes, H., George Allen & Unwin, Ltd., London, 1963, **1**, 157–75,

———— .. "Distribution of chlorophyll and phaeophytin in the open ocean," *Deep Sea Res.*, 1965 ***a***, **12**, 653–66.

———— .. "The relationship between chlorophyll and photosynthetic carbon production with reference to the measurement of decomposition products of chloroplastic pigments," *Memorie Ist. ital. Idrobiol.*, 1965 *b*, **18** (Suppl.), 323–46.

857–69. Printed at The Bangalore Press, Bangalore City, by M. S. Narayana Murthy, Secretary, Published by B. S. Venkatachar, Editor, "Proceedings of the Indian Academy of Sciences," Bangalore