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Abstract

Plankton biomass, material fluxes, e.g. ^{14}C uptake, and specific growth rates are related quantities. In the course of comparing various methods of measuring these properties in September 1982 off Oahu, Hawaii, we found specific growth rates of $1–2 \cdot d^{-1}$. Such rates approach the maximum expected values observed in laboratory cultures.

Plankton production is reported to be low in subtropical oceanic gyres compared with coastal waters at similar latitudes (Steemann Nielsen 1955; Koblentz-Mishke et al. 1970). Standing stocks, e.g. chlorophyll concentrations, are lower in the gyres, and plant nutrient levels are scarcely detectable by standard methods. We report here on a preliminary comparison of methods using, wherever possible, the same water samples and trace-metal-clean techniques. Although the experiments were done in coastal waters off Hawaii, the orientation is toward the subtropical oceanic gyres where later studies will be carried out and where discrepancies between measurements of plankton productivity are greatest.

Because primary production is the product of standing stock and specific growth rate, either low growth rate or low standing stock can lead to low production. We know that standing stocks are low in the gyres but there is disagreement on growth rates. The

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historical ^{14}C primary production values, normalized to chlorophyll biomass, could provide growth rate information if one knew both the C:Chl ratio of the phytoplankton and whether the photosynthetically produced organic matter was conserved during the experiment. In general, neither of these is known; thus the observation that the productivity index is lower (1–3 g $C \cdot g^{-1}$ Chl $a \cdot h^{-1}$) in subtropical gyres than inshore (Curl and Small 1965) only suggests that growth rates are also lower in oligotrophic waters than inshore. The low ambient nutrient concentrations, the evidence of incipient nitrogen deficiency (Thomas 1970), and other indirect evidence about physiological states are consistent with such a supposition, however. Furthermore, estimates of plankton standing stock from microscopy and ATP (Beers et al. 1975, 1982), combined with ^{14}C production estimates, also suggest lower growth rates in the North Pacific gyre than in inshore California coastal waters (Eppley et al. 1973; Sharp et al. 1980).

Recent information provides a new perspective on the idea of low growth rate for phytoplankton in the gyres (Peterson 1980). First, it is unlikely that the photosynthetic product is conserved in the 6–24-h experiments used for production measurements with ^{14}C. Much of the carbon appears to enter a microplankton food web contained within the experimental bottles and may be recycled on a time scale of hours. This microplankton food web most likely consists of phagotrophic nanoplankton, bacteria, and ciliate protozoa along with cyanobacteria and nanoplanktonic algae as the chief photosynthetic forms. Screening out the macrozooplankton, such as copepods, may not remove the chief herbivores, which are now thought to be the phagotrophic flagellates (Pomeroy 1974; Sieburth et al. 1978). Second, ambient nutrient concentrations, even if undetectable by standard analytical methods, need not imply low growth rates; N-limited chemostat cultures of phytoplankton display undetectable ambient N levels at growth rates as high as approximately 0.85 of maximum possible rates (Goldman and McCarthy 1978), and growth rates $> 1.0 \cdot d^{-1}$ have been measured in surface waters depleted of nitrate (Herbland and Le Bouteiller 1983). It is not the ambient nutrient level but the rate of supply that regulates production (Menzel and Ryther 1961). Such microplankton food webs may be important inshore as well as in the oligotrophic subtropical gyres, but their activity compared to that of diatom-copepod food chains is probably less, on an annual average, than in the gyres.

The subtropical gyres make up about 40% of the surface area of the ocean (Koblentz-Mishke et al. 1970). Because of the interdependence between primary productivity and the sinking flux of biogenic organic particles and the geochemical importance of the sinking flux, it becomes important to determine accurate values for the primary production of these large oceanic regions. This becomes especially urgent when indirect approaches suggest severalfold higher values for oceanic production than were obtained in the 1950s and 1960s by the ^{14}C method (Shulenberger and Reid 1981; Jenkins 1982; Postma and Rommets 1979; Tijssen 1979). Furthermore, measures of photosynthesis with trace-metal-clean ^{14}C methods suggest that the older data could be as low as 40% of true values solely because of metal contamination (Fitzwater et al. 1982).

One approach to resolving this problem is being taken here: several independent investigators work together to measure carbon flow, growth rate, and biomass of the various organisms comprising the microplankton food web—all using the same water samples (Eppley 1982). The experiments yielded high growth rates and high values of the productivity index, characteristic of rich, nearshore waters. Yet the Hawaiian waters were oligotrophic in other respects: they had low standing stocks, deep euphotic zones, and low nutrient concentrations. Values as high as the ones we have found have been observed off Hawaii (Cattell and Gordon unpubl. data; Bienfang pers. comm.) but are unusual in the literature for the area (Bienfang and Szyper 1981; Gunderson et al. 1976). Bienfang et al. (1984) have recently examined this temporal variability and its physical correlates in Hawaiian coastal waters.

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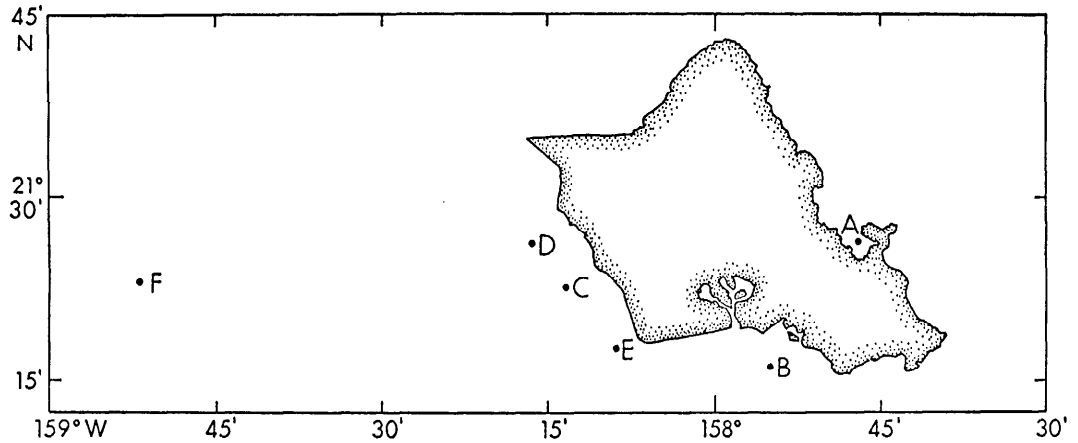

Fig. 1. Station locations off Oahu, Hawaii. Station A was within Kaneohe Bay, Station B was off Honolulu.

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Methods

Six experiments were carried out from 26 August to 23 September 1982 at stations A–F (Fig. 1); station locations were selected at random. The RV *Kila* was used for the work at stations C–F; the RV *Noi'i* at station B. The first trial experiments were done in Kaneohe Bay (sta. A) and off Honolulu (sta. B). As soon as a ship was available operations were moved to coastal waters. We selected quiet-water sites on the leeward side of Oahu (C and E) in order to facilitate the shipboard laboratory work. Following a drogue, the ship drifted to locations D and F about 24 h later. Water was collected in 300-liter polyethylene bags (Burney 1984) near the surface at station A in Kaneohe Bay. At stations B, C, and E water was taken with 30-liter Go-Flo Niskin bottles (specifically cleaned to prevent trace metal contamination) with nylon-coated Kevlar used for hydrographic line (Fitzwater et al. 1982) or, for expediency, with a cleaned all-polyethylene bucket at stations D and F. Two 120-liter polyethylene tubs were filled at each of stations B–F. Water samples were dispensed from the tubs for incubations and analyses. Only one depth was sampled at each station (30 m for stations B and C, surface for stations D and F, and 5 m for station E) so that the same water sample could be used for all measurements. A series of eight samples was also collected at 30 m over 24 h between stations C and D to examine variability in cell counts and particulate matter.

Water was collected before dawn to allow for 0600 starting time for the incubations. However, incubations at station A actually started at 0900 and at B at 1140. Incubations with ^{14}C were in 4-liter polycarbonate bottles, specifically cleaned as noted above. All the incubations were carried out at the temperature of ambient surface seawater, about 27°C, in deck incubators consisting of clear plastic boxes covered with a nickel-stainless screen that transmitted 40% of incident light.

Earlier reports describe the various experimental approaches: preparation of ^{14}C stocks and trace-metal-clean procedures to avoid metal contamination in the ^{14}C studies (Fitzwater et al. 1982); ^{14}C incubations and chlorophyll measurements (Marra and Heinemann 1984); phytoplankton biomass and specific growth measurements using the ^{14}C incorporation into chlorophyll (Redaljc and Laws 1981); phytoplankton biomass values corrected for zooplankton grazing by assuming a balance between phytoplankton

Table 1. Biomass estimates from organism counts.

	Mean No. organisms·liter^{-1}				
	Bacteria ($\times 10^8$)	Cyanobacteria ($\times 10^6$)	Heterotrophic nanoplankton ($\times 10^5$)	Autotrophic nanoplankton ($\times 10^5$)	
Sta.	Picoplankton		Nanoplankton		
B (3)*	6.90±0.31	3.10±0.64	9.92±2.72	4.97±0.73	
C–D (8)†	6.26±0.39	1.36±0.23	6.95±1.51	6.25±0.61	
	Approx biomass as carbon, μM‡				Sum
B	0.58	0.039	0.49	0.25	1.4
C–D†	0.53	0.02	0.35	0.32	1.2

* Number of samples examined for calculation of means.
† Samples were taken from eight discrete bottle casts (30-m depth) over 24 h while drifting between stations C and D.
‡ Assuming cellular carbon contents of 10^{-14} g for bacteria; 1.5×10^{-13} g for cyanobacteria, and 6×10^{-12} g for flagellates. The values are equivalent to the measured cell volumes × 0.15 g C·ml^{-1}.

production and losses due to excretion and grazing; phytoplankton nitrogen demand and relative growth rate from ^{14}C incorporation into protein (DiTullio and Laws 1983); phosphate and ammonium uptake and regeneration (Glibert et al. 1982; Harrison 1983); microbial production (Karl 1981; Karl and Winn in press); phytoplankton growth rate from the time-course of Chl *a* increase in water samples passed through a 3-μm-sized screen to remove grazers (Bienfang and Takahashi 1983); particulate C, N (Sharp 1974), and P (Solórzano and Sharp 1980); epifluorescence microscopy techniques (Haas 1982); and the "dilution experiment" approach to estimating growth and predation rates (Landry and Hassett 1982). The dilution experiment in Kaneohe Bay (station A) is described by Landry et al. (1984).

Results and discussion

Biomass estimates—Microscopic counts of the organisms and carbon/cell information are available for two of the six stations studied (Table 1). Chlorophyll, ATP, and particulate C, N, and P data, although more abundant, are indirect measures of biomass (Table 2). About 60% of the Chl *a* biomass was in the picoplankton size category as evidenced by passage through 3-μm Nuclepore filters.

Only about 25% of the microscopically estimated biomass consisted of photosynthetic forms, cyanobacteria and autotrophic nanoplankton (Table 1). Many of the latter resembled *Chrysochromulina*; the cells were about 4 μm in diameter. At the two locations, bacteria accounted for 41 and 44%, heterotrophic (phagotrophic) flagellates for 35 and 29%, and cyanobacteria for 3 and 2% of the carbon biomass (Table 1). When categorized by size, the picoplankton (bacteria + cyanobacteria) comprised 44 and 46%, the nanoplankton (2–20-μm diameter) 56 and 54% of estimated carbon biomass.

Multiplying ATP (Table 2) by 250 (g/g) provides a fairly consistent estimate of total "living carbon" in the plankton (Holm-Hansen 1973). This estimate gave 1.45 μmol C·liter^{-1} for station B and 1.26 for C and D combined, in agreement with the values of 1.4 and 1.2 μmol C·liter^{-1} from microscopy. The "phytoplankton carbon" (Table 2) estimates are from the incorporation of ^{14}C into Chl *a* and the specific activity of the Chl *a* carbon. The values were corrected for the fraction of the particulate ^{14}C estimated to exist in phytoplankton after 24 h of incubation (Table 2). The remaining ^{14}C is in heterotrophic organisms; this amount varied from 10% in the Kaneohe Bay experiment to 28% at station F (Table 2). "Nanoplankton carbon" estimates (Table 2) are derived from total POC measurements (Eppley et al. 1977) yielding 0.58 and 0.45 vs. 0.74 and 0.67 μmol C·liter^{-1} for nanoplankton carbon from microscopy.

Carbon and nutrient flows—Two different measures of carbon flux in the food web are given in Table 3. The first is the ^{14}C measurement of photosynthesis. Values re-

Table 2. Biomass estimates from chemical measurements. Values are means ± SD of the mean; N.D.—no data.

	Station					
	A	B	C	D	E	F
			Particulate measurements			
Chl *a* (μg·liter^{-1})	1.8±0.6	0.082±0.007	0.047*±0.013	0.082†	0.089±0.010	0.075±0.019
Particulate C (μM)	19.8±3.6	3.56±0.08	2.86±0.57	2.75±0.81	2.75±0.17	2.86±0.38
Particulate N (μM)	2.59±0.69	0.48±0.04	0.41±0.06	0.39±0.08	0.39±0.004	0.42±0.05
Particulate P (nM)	193±24	43.9±11.0	14.0±1.6	19.9±3.7	N.D.	N.D.
ATP (ng·liter^{-1})	572±102	69.5±2.8	45.3±8.1	75.7±18.8	50.0±2.8	55.3±12.5
			Derived values			
"Phytoplankton C" (μM)	12.6	0.63	0.27	1.20	0.70	0.48
"Nanoplankton C" (μM)	3.2	0.58	0.45	0.45	0.44	0.46
Particulate N:P molar ratio	13.4	10.9	29.2	19.6	N.D.	N.D.
% particulate ^{14}C in phytoplankton after 24 h	90	78	79	86	79	72

* Samples taken over time from incubating water sample in which Chl *a* decreased over time. Initial value was 0.060.
† Initial sample at beginning of incubation.

ported here are consistent with oxygen measurements (Williams et al. 1983). A second estimate is derived from measures of the rate of DNA synthesis. This flux refers to both autotrophs and heterotrophs because both can use exogenous adenine for DNA synthesis. The flux exceeds the photosynthetic carbon flux (Table 3).

Two estimates of nitrogen incorporation were obtained: the direct incorporation of ^{15}N-labeled ammonium into particulate matter with corrections for isotope dilution

Table 3. Carbon, nitrogen, and phosphorus fluxes over 24 h (units μmol·liter^{-1}·d^{-1}).

	Station					
	A	B	C	D	E	F
			Fluxes			
Photosynthesis						
Particulate ^{14}C	11	0.85	0.35	0.50	0.92	0.86
Dissolved ^{14}C	2.0	0.0	0.053	0.01	0.11	0.16
"Microbial C production" from DNA synthesis	—	3.68	0.52	—	1.0	—
NH_4^+ uptake	1.2	0.41	0.14	0.12	—	—
"Phytoplankton N assim." from ^{14}C → protein	1.1	0.14	0.053	0.12	0.11	0.10
Phosphate uptake	0.22*	0.0086	0.0078	0.0071	—	—
			Derived values			
Productivity index† (g C·g^{-1} Chl *a*·h^{-1})	6.3	15.5	11.5	7.4	10.6	10.4
Photosynthesis: NH_4^+ uptake (C:N molar ratio)	11.1	2.1	2.8	4.1	—	—

* Average of three experiments in Kaneohe Bay.
† Based on initial Chl *a* values, rather than the mean values of Table 2, and photosynthetic carbon assimilation in the light rather than over 24 h.

Table 4. Growth rate estimates, day^{-1}, over 24 h.

Method	Station A	B	C	D	E	F
	Phytoplankton growth rates					
$^{14}C \rightarrow$ Chl *a*	0.66	1.49	1.42	0.93	1.43	2.00
Photosynthesis/biomass C*						
From microscopy	—	1.37	—	0.92	—	—
From ATP	1.50	1.35	0.89	0.98	1.48	1.29
μ/μ_m from $^{14}C \rightarrow$ protein with $\mu_m = 1.63 \cdot d^{-1}$	1.2	1.3	1.6†	2.1†	1.4	1.3
Chl *a* increase, grazers removed	1.3	—	—	—	1.0	—
	Total microbial assemblage					
NH_4^+ incorp. : biomass N†	0.49	1.1	0.70	0.42	—	—
PO_4^{3-} uptake : biomass P†	1.08	0.49	0.63	0.39	—	—

* When biomass estimates are used with 24-h fluxes to get growth rates, the expression is ln[(biomass + flux)/biomass].
† The high ratio of particulate N:P at these stations suggests growth may have been P-limited, hence the apparent μ/μ_m will be >1.0 with this method and calculated growth rates will be unrealistically high.

over time (Glibert et al. 1982), and the incorporation of [^{14}C]bicarbonate into the protein of the particulate matter (DiTullio and Laws 1983). The latter is primarily a measure of phytoplankton, although heterotrophs will be partially labeled after 24 h if the microplankton food web is active in the incubation bottles. The results of the two methods agreed at stations A and D whereas ammonium uptake exceeded protein labeling at stations B and C (Table 3). Stations B and C also showed low molar ratios of photosynthetic carbon assimilation to ammonium incorporation (Table 3), perhaps suggesting ammonium incorporation by heterotrophs. The mean productivity index was high in these experiments during the photoperiod, ranging from 6.3 to 15.5 g C·g^{-1} Chl *a*·h^{-1} (Table 3). The maximum values expected for phytoplankton should be about 24 in these units (Falkowski 1981).

Growth rate—Several measures of growth rate are shown in Table 4. The most direct of these is from the incorporation of $^{14}CO_2$ into Chl *a* (Redalje and Laws 1981). This measure is not confounded by the flow of labeled carbon into heterotrophs (Welschmeyer and Lorenzen 1984). Values ranged from 0.66 to 2.0·d^{-1} in the different experiments.

The historical estimates of phytoplankton growth rate in the oligotrophic North Pacific are based on the 24-h photosynthetic carbon incorporation and estimates of biomass as carbon. These values average <0.3·d^{-1}, paralleling low productivity indices of <3·h^{-1} (Bienfang and Szyper 1981; Eppley et al. 1973; Gunderson et al. 1976; Sharp et al. 1980). In the present study this approach gives higher growth rates, of 1.37 and 0.92·d^{-1}, based on biomass estimates from microscopy, for stations B and D (Table 4). If we estimate the carbon biomass of photosynthetic forms as 26% of the total and "living carbon" from ATP as it was at stations B and C–D, we then obtain growth rates ranging from 0.9 to 1.5·d^{-1} at stations B–F. The maximum expected growth rate for photosynthetic phytoplankton and cyanobacteria at 27°C and 12-h photoperiod is about 1.63·d^{-1} (equivalent to 2.35 doublings·d^{-1}; *see* Eppley 1972). These growth rates are relatively high and consistent with the high productivity indices.

The incorporation of $^{14}CO_2$ into protein also provides a measure of phytoplankton growth rate, μ/μ_m. If we take 1.63 as μ_m, the results are from 1.2 to 2.1·d^{-1} (Table 4), although the two highest values should be discarded because the experimental μ/μ_m exceeded 1 (*see footnote to Table 4*).

The Chl *a* content of the incubated water samples did not increase to the extent that these growth rates suggest unless phagotrophs (mostly >4 μm long) were removed by prefiltering the water through 3-μm Nuclepore filters. The daytime Chl *a* increases

were then exponential, with specific rates of 1.3 and 1.0·d^{-1} for stations A and E (Table 4).

Growth rate of the total microbial assemblage can be estimated in at least two ways, from the carbon flow rate derived from DNA synthesis measurement and from the total microbial biomass from microscopy (this rate was 1.3·d^{-1} at station B); the ammonium uptake data can also be assumed to represent most of the microbial assemblage. With a nitrogen biomass taken as microbial carbon divided by the Redfield ratio of C:N (6.62 by atoms: Redfield et al. 1963), the ammonium uptake rates gave lower specific growth rates, 0.4–1.1·d^{-1} (Table 4). The phosphate uptake data give growth rates >1.0·d^{-1} at station A, but <1.0 at all other stations (Table 4).

Landry et al. (1984) reported on experiments in Kaneohe Bay (station A) performed a week or so later in which biomass was determined by microscopy (categories in Table 1) and growth and mortality rates of each of those categories were determined separately by a "dilution technique" (Landry and Hassett 1982) with in situ diffusion cages used as incubation chambers. Biomasses were somewhat different but the growth rates were similar to those of Table 4. Specific growth rates were 1.2–1.9·d^{-1} for bacteria, 1.4–2.0·d^{-1} for cyanobacteria, 0.9–1.3·d^{-1} for heterotrophic flagellates, and 1.6·d^{-1} for total chlorophyll.

These results, specifically the rate measurements, the biomass estimates, and the dilution experiment, are consistent with the operation of a microplankton food web inside the experimental containers. Mass balance arguments require that heterotrophic consumption not exceed autotrophic production; therefore, the product of heterotrophic biomass and its specific rate of consumption should not exceed the product of autotrophic biomass and its specific rate of production. The ideal of preparing such a mass balance was not achieved. Nevertheless, chlorophyll measurements in incubations with grazers removed (by 3-μm screens) or not removed suggest that a mass balance exists; no increase is observed unless grazers are removed.

We can compare the products of autotrophic and heterotrophic biomass and growth rate approximately by taking the growth rate estimates of the total microbial assemblage to represent that of heterotrophs. Using biomass data for station B and stations C–D combined (Table 1) and mean growth rates at those stations from Table 4, we can calculate that the flow of carbon into heterotrophs exceeds that into autotrophs by 1.9-fold and 1.3-fold, respectively. The reverse was true in the Kaneohe Bay dilution experiment (Landry et al. 1984).

In the last decade the disparity among estimates of plankton production seems to have grown and differences of 10-fold–100-fold for oligotrophic areas of the ocean now exist (Williams et al. 1983). Such large differences for oceanic areas previously considered to be fairly homogeneous, with less temporal and spatial variability than coastal waters, have brought the methodology itself into question. It is our conviction that related measures of biomass, material flux, and specific growth rates must be consistent if the production estimates are to be considered valid. This stringent criterion remains to be met in any existing study; it may be in fact beyond our reach unless we define the word consistent rather loosely. For example, the present growth rate estimates are "consistent" only to a factor of approximately three (Table 4). Nevertheless, a threefold range is considerably smaller than the range of values in the literature (e.g. *see* the comparison of growth rates compiled by Goldman et al. 1979).

It is not clear that the present results are typical either of Hawaiian coastal waters or of the vast subtropical gyres. The ship consistently drifted at 50–100 cm·s^{-1} with the current west of Oahu. Shears associated with velocity gradients in such currents could be substantial in promoting atypically high rates of nutrient input into the surface waters from below, but we lack information on the vertical structure of the currents or their temporal variability. Estimates of vertical eddy diffusivities, K_z, based on the slope of the increase in nitrate with depth in the nitracline and the rate of nitrate uptake measured with ^{15}N (King and Devol 1979; Eppley et al. 1979) suggest values off Hawaii of

2.8 ± 1.3 $cm^2 \cdot s^{-1}$. These are about three orders of magnitude greater than in the central North Pacific subtropical gyre where K_z was 2.1 (± 1.0) $\times$ 10^{-3} $cm^2 \cdot s^{-1}$, using similar calculations. It remains unclear whether production in the gyres varies primarily because of biomass changes alone or because of changes in both biomass and growth rate. On the basis of the present results, it seems possible to answer that question with similar studies in the subtropical gyres.

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