

Zooplankton grazing effects on ^{14}C -based phytoplankton production measurements: a theoretical study

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Abstract. A model constructed to describe carbon dynamics of phytoplankton growth during ^{14}C -tracer incubations gives the range of error in estimating specific growth rates and productivity rates caused by zooplankton grazing during the incubation. Error increases with increasing incubation times and higher specific growth rates. The range of these errors can be given as a function of the specific growth rate calculated from measurements. At the low calculated specific growth rates of the oligotrophic Pacific Ocean, 0.2 d^{-1} , errors are $\leq 16\%$. Similar arguments suggest that bacterial uptake of excreted organics would not cause large errors at low oligotrophic ocean growth rates. There are, however, other possible ways that ^{14}C -based productivity estimates could be wrong.

Introduction

Measurement of phytoplankton production continues to be controversial. Among the factors that have been suggested as affecting results are zooplankton and/or bacterial consumption of photosynthesized material in incubation vessels. In this paper I use mathematical models to study primarily the effects of zooplankton but also of bacteria on production estimates.

Primary production in aquatic systems has usually been estimated using the ^{14}C incubation technique (Steemann Nielsen, 1958). First, the environment is sampled by collecting a volume of water, which contains selected plants, animals and bacteria. A known, trace amount of ^{14}C is added to the $\text{CO}_2 - \text{HCO}_3^- - \text{CO}_3^{2-}$ pool in the sample. This carbonate pool is the carbon source for plant photosynthesis. The sample is then incubated under conditions mimicking those from which it was taken. After a fixed time has passed, the incubation is stopped, the sample is filtered, the amount of radioactive tracer caught on the filter is measured, and the total new particulate carbon calculated. The quantities usually worked with are the initial phytoplankton carbon concentration (C_0), obtained from either a total particulate carbon measurement or from microscopic cell counts/carbon content calculations, the new particulate carbon concentration (C^*), and the incubation time (t). Incubation time usually ranges from 3 h to 1 day.

All new particulate carbon is usually assumed to be phytoplankton. Primary production rate (\hat{P}) is calculated as the new carbon concentration divided by the incubation rate (Eppley and Strickland, 1968).

$$\hat{P} = C^*/t \quad (1)$$

Specific growth rate ($\hat{\mu}$) is calculated assuming exponential growth during the incubation,

$$\hat{\mu} = \frac{1}{t} \ln \left| \frac{C_o + C^*}{C_o} \right| \quad (2)$$

Productivity estimates are important in the study of carbon (or energy) flow through an aquatic community; specific growth rate estimates are important to relate physiological and ecological studies.

Phytoplankton productivity and growth rate estimates from this ^{14}C technique for low nutrient marine environments, such as the North Pacific Gyre and the Sargasso Sea, have been quite low, with specific growth rates of $\sim 0.1 - 0.2 \text{ d}^{-1}$ (Eppley *et al.*, 1977). Estimates are higher in coastal areas, typical surface values being $\sim 0.41 \text{ d}^{-1}$ in coastal southern California (Eppley, personal communication).

Workers using different techniques have recently concluded that phytoplankton specific growth rates, and therefore primary production, are much higher than estimates based on the common ^{14}C technique use (Sheldon and Sutcliffe, 1978; Goldman *et al.*, 1979; Gieskes *et al.*, 1979; Shulenberger and Reid, 1981). Phytoplankton specific growth rates as high as 2.8 d^{-1} can be calculated from new ATP-based measurements for the oligotrophic Sargasso Sea (Jackson, 1980; Sheldon and Sutcliffe, 1978); specific growths calculated from ^{14}C uptake over 24 h for a similar oligotrophic region were only 0.2 d^{-1} (Eppley *et al.*, 1977). If the higher growth rate is accurate, then the conventional ^{14}C method yields a value only 8% of actual specific growth rate. This contrasts with the 80–90% accuracy of the ^{14}C method in physiological experiments (Steemann Nielsen, 1958; Mague *et al.*, 1980). Sheldon and Sutcliffe (1978) suggested that the difference between the two techniques was caused by the presence of grazers in incubated field samples which were cropping newly produced carbon. Peterson (1980) suggested that the study of carbon flow among different organisms in incubation vessels is necessary to understand what the ^{14}C method is measuring.

Micro-zooplankton are grazers that are sampled along with phytoplankton in bottle-casts (Venrick *et al.*, 1977). They can be important, if not dominant, consumers of marine phytoplankton at some times and places (e.g., Heinbokel, 1978, 1979; Jackson, 1980). M.Landry (in press) has shown that measured phytoplankton productivity can be increased by diminishing grazing in an incubated sample. Thus, there are experimental reasons to consider the effects of grazing on primary production estimates.

In this paper I examine the extent to which grazers can cause the ^{14}C method to underestimate phytoplankton growth. I develop diagnostics to predict under what conditions grazing – or lack of it – can alter productivity and growth estimates and how large the effect can be.

Methods

My basic assumption is that phytoplankton concentrations in the environment and in incubation vessels are determined by growth at a constant specific growth rate during daylight and by mortality at a constant specific rate at all times. My goal is to estimate the range of errors in estimating growth and productivity rates given the three measured quantities: C_o , C^* , and t .

Models for phytoplankton incubation

Changes in phytoplankton concentration (ϕ) when phytoplankton growth rate and grazing rates are proportional to phytoplankton concentration can be mathematically represented as

$$\frac{d\phi}{dt} = \mu\phi - g\phi \quad \text{during daylight} \quad (3a)$$

$$= -g\phi \quad \text{during night} \quad (3b)$$

where μ = specific growth rate

$g = f\mu$ = specific grazing rate

f = specific grazing rate as fraction of specific growth rate.

These equations represent phytoplankton dynamics in the environment or in an incubation vessel. Changes in zooplankton concentration (Z) during an incubation are then given by

$$\frac{dZ}{dt} = \alpha f\mu\phi \quad (4)$$

where α = conversion efficiency of plant to animal if there is no zooplankton mortality.

After the addition of ^{14}C -tracer to the dissolved carbon pool, new phyto- and zooplankton matter (ϕ^* , Z^*) will accumulate as

$$\frac{d\phi'}{dt} = -\mu f\phi' \quad (5a)$$

$$\frac{d\phi^*}{dt} = \mu(\phi' + \phi^*) - \mu f\phi^* \quad \text{during daylight} \quad (5b)$$

$$= -\mu f\phi^* \quad \text{during dark} \quad (5c)$$

$$\frac{dZ^*}{dt} = +\alpha f\mu\phi^* \quad (6)$$

where ϕ' = non-labeled, 'old', phytoplankton carbon concentration. Note that new material includes all new carbon accumulated, calculated as the amount of ^{14}C present divided by the specific activity of ^{14}C in the dissolved carbonate pool.

Total new particulate carbon (C^*), which is what would be caught on a filter at the end of an incubation, is the sum of that present in phyto- and zooplankton:

$$C^* = \phi^* + Z^* \quad (7)$$

Environmental productivity rate (P) is given by:

$$P = \frac{1}{t} \int \mu\phi dt \quad (8)$$

Environmental growth

Phytoplankton dynamics in the environment can be described by integrating equations 3a,b:

$$\phi = \phi_0 e^{(1-f)\mu t} \quad \text{for } t \leq T \quad (9a)$$

$$= \phi_0 e^{(1-f)\mu T} e^{-f\mu(t-T)} \quad \text{for } T < t \leq 1 \text{ day}$$

$$= \phi_0 e^{\mu(T-ft)} \quad \text{"} \quad (9b)$$

where ϕ_0 = phytoplankton concentration at the beginning of daylight
 t = time after start of daylight
 T = length of daylight.

A phytoplankton population at steady state will have the same concentration of phytoplankton after 1 day:

$$\begin{aligned}\phi_0 &= \phi(t = 1 \text{ day}) \\ &= \phi_0 e^{\mu(T-f)}\end{aligned}\quad (10)$$

When length of daylight is 0.5 d, $f = 0.5$. Phytoplankton concentrations should cycle through the day (Figure 1). Productivity rate, averaged over 1 day, is

$$\begin{aligned}P &= \frac{1}{1 \text{ day}} \int_0^T \mu \phi_0 e^{\mu(1-f)t} dt \\ &= \frac{\phi_0}{(1-f)} (e^{\mu(1-f)T} - 1)\end{aligned}\quad (11)$$

The goodness of a productivity estimate from a ^{14}C incubation is a function of how close it comes to the above value of environmental productivity.

Incubation dynamics

Short term incubation. Concentration of radioactively-labeled, new carbon during a short, daylight incubation is given by

$$\phi^*(t) = \phi(t_1) [e^{\mu(1-f')\tau} - e^{-f'\mu\tau}] \quad (12)$$

$$C^*(t) = \phi(t_1) \left[\left(1 + \frac{\alpha f'}{1-f'}\right) e^{\mu(1-f')\tau} - \frac{\alpha}{1-f'} + (\alpha-1)e^{-\mu f' \tau} \right] \quad (13)$$

$$\phi(t_1) = \phi_0 e^{\mu(1-f)t_1} \quad (14)$$

where all times are relative to sunrise

t_1 = time at which samples are collected and incubations begins

τ = $t - t_1$ = length of incubation

$\phi(t_1)$ = environmental phytoplankton concentration at $t = t_1$

ϕ_0 = environmental phytoplankton concentration at start of daylight,
 $t = 0$

f = fraction of grazing in environment

f' = fraction of grazing in incubator

α = conversion efficiency from phyto- to zooplankton.

Full day (24 h) incubation. Concentration of radioactively-labeled, new carbon at the end of a 24 h incubation is given by

$$\phi^* = \phi(t_1) e^{-\mu f' D} (e^{\mu T} - 1) \quad (15)$$

$$\begin{aligned}C^* &= \phi(t_1) \left\{ \frac{\alpha}{1-f'} [e^{\mu(1-f')(T-t_1)} - 1 + e^{\mu(T-D)} (e^{\mu(1-f')D} \right. \\ &\quad \left. - e^{\mu(1-f')(D-t_1)})] + (1-\alpha)[e^{-\mu f' D} (e^{\mu T} - 1)] \right\}\end{aligned}\quad (16)$$

where D = day length = 24 h = 1 day

T = daylight length

Results

This model predicts that environmental phytoplankton biomass should fluctuate over a 24 h day, even if phytoplankton are in steady state from day to day (Figure 1). This results from the fact that photosynthesis occurs only during daylight but grazing pressure occurs during the entire 24 h. Under ^{14}C incubation conditions, phytoplankton biomass fluctuations are mirrored in radioactively-labeled phytoplankton carbon and total carbon (Figure 1). A significant amount of this new carbon can be present in the zooplankton under conditions of high grazing and growth rates.

Grazing causes the estimated daily specific growth rate, $\hat{\mu}_D$ (computed from equation 2 with $t = 1$ day), to be underestimated (Figure 2). When there is no grazing during a 24-h incubation ($f' = 0$), $\hat{\mu}_D$ equals the product of the instantaneous specific growth rate, μ , and the daylight length, T ; when grazing intensity during incubation is the same as in the environment ($f' = 0.5$) and the conversion efficiency, α , equals 0.37 (Checkley, 1980), $\hat{\mu}_D$ is less than μT because new carbon respired by zooplankton is uncounted. For an incubation starting at noon ($t_0 = 0.25$) with environmental grazing pressure ($f' = 0.5$) at the high growth rate of $\mu T = 1$, $\hat{\mu}_D = 0.55 \text{ d}^{-1}$. This estimate is almost half what it should be. The relative error of the specific growth rate estimate is less for slower growth rates.

Measured productivity (Figure 1) is less affected by environmental-level grazing pressure (Figure 3): at $\mu T = 1$, measured productivity is 77% of real productivity. Absence of grazing within the incubation container has a greater effect because the phytoplankton population can explode to much higher concentra-

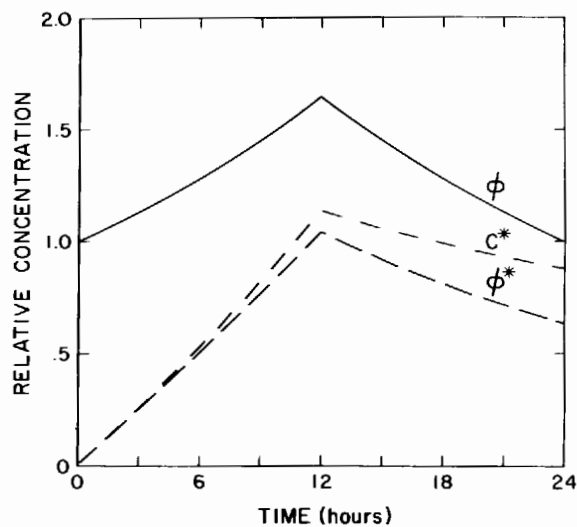


Fig. 1. Daily cycle of total phytoplankton carbon (ϕ), new radioactively-labeled phytoplankton carbon (ϕ^*), and total new radioactively-labeled carbon (C^*). Values in model from equation 9 are: $\alpha = 0.37$, $t_0 = 0$ (incubation starts at dawn), $f' = 0.5$ (environmental levels of grazing), $\mu = 2 \text{ d}^{-1}$, and $T = 0.5 \text{ d}$ (daylight is 12 h). The difference between C^* and ϕ^* is the carbon in the zooplankton.

tions than found in the environment. At $\mu T = 1$, this measured productivity is 120% of real, environmental productivity. Thus, a more important concern is the overestimate of production caused by the absence of grazers.

Samples collected at different starting times will have different measured pro-

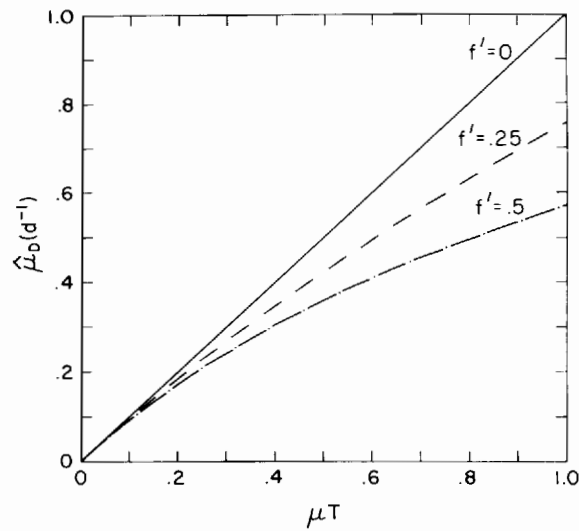


Fig. 2. Estimated daily specific growth rate ($\hat{\mu}_D$) as a function of actual specific growth rate times the daylight length (μT). μ_D is calculated from equations 16 and 2. The incubation is for 24 h starting at noon ($t_0 = 0.25$). Notice that with no grazing ($f' = 0$), $\mu_D D$ equals μT ; grazing decreases amount of new carbon measured, causing equation 2 to underestimate growth rate.

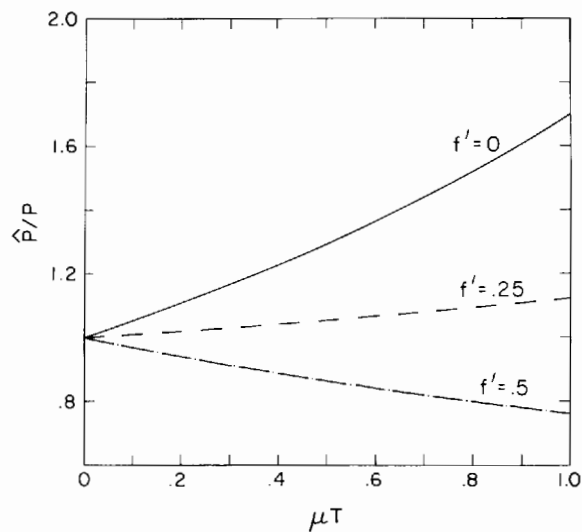


Fig. 3. Relative productivity as a function of T for 24 h incubation starting at noon. No grazing ($f' = 0$) causes the productivity calculated from equations 1 and 16 (\hat{P}) to overestimate the real environmental productivity (P), given by equations 8 and 9; environmental-level grazing ($f' = 0.5$) causes \hat{P} to underestimate P . Best estimate comes from partial grazing — in this case $f' = 0.25$.

ductivities (Figures 3 and 4). Samples collected later in the day have higher productivities because they have higher initial phytoplankton concentrations and because proportionally less new carbon is vulnerable to night time grazing.

Differences between calculated productivity and environmental productivity caused by different start times and grazing intensities is a function of μT (the growth rate) as is the average daily specific growth rate, $\hat{\mu}_D$. Thus, the ratio of calculated to environmental productivity can be used to estimate how great an error could be made using ^{14}C -based productivity estimates. Grazing at environmental intensities ($f' = 0.5$) causes productivity to be underestimated by 20% when $\hat{\mu}_D$ reaches 0.39 d^{-1} for incubations started at dawn ($t_1 = 0 \text{ d}$) and 0.71 d^{-1} for incubations started at dusk ($T_1 = 0.5 \text{ d}$; Figure 5a). No grazing in the incubators ($f' = 0$) causes the calculated productivity to be 20% greater than environmental when $\hat{\mu} = 0.24 \text{ d}^{-1}$ for dusk-started incubations (Figure 5b). Errors are greater for larger values of $\hat{\mu}_D$.

Errors associated with shorter incubations are smaller (Figure 6). Maximum error under the range of conditions examined for 3 h incubation was a 28% production overestimate for a sample with no grazers, started 3 h before sunset. Short incubation times do not allow development of large differences in phytoplankton concentrations or allow significant zooplankton grazing. The most important variable determining range of possible errors is again the instantaneous specific growth rate, μ .

Discussion

Previous theoretical studies of ^{14}C incubations have focused on the temporal evolution of phytoplankton specific activity (Hobson *et al.*, 1976; Buckingham *et al.*, 1975; Marra *et al.*, 1981). None of these studies included day-night effects; few included grazers. Buckingham *et al.* (1975) and Hobson *et al.* (1976) were in-

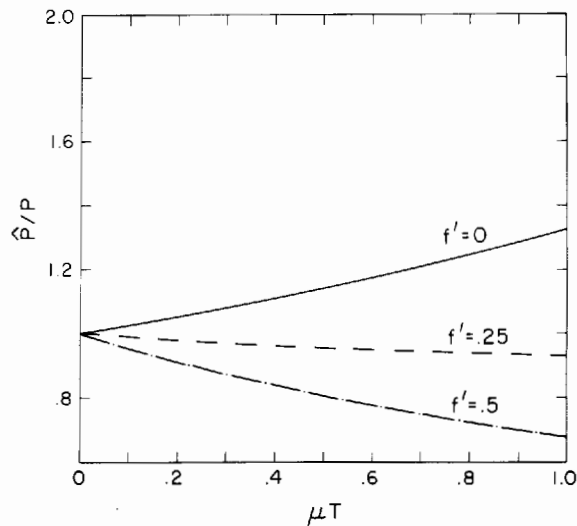


Fig. 4. Relative productivity with a dawn start time ($t_0 = 0$) for a 24 h incubation. Notice all values are less than for noon start time (Figure 3).

terested in the extent that the ^{14}C assay measures net primary production. These authors found that short incubation times overestimated net primary productivity because respiration uses mostly non-labeled carbon at low specific activities. They recommended that incubation for net production be longer than phytoplankton turnover times. Savidge (1978) suggested that a combination of long

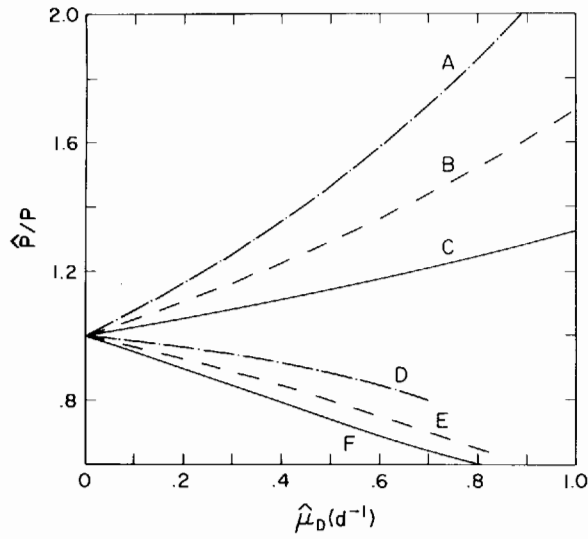


Fig. 5. Range of relative production as function of calculated $\hat{\mu}_D$ for a range of starting times and grazing rates. Range of f' values is the maximum likely. The fact that $\hat{\mu}_D$ is calculated from incubation data allows one to estimate potential errors in productivity estimate. $f' = 0$ for A, B, C; $f' = 0.5$ for D, E, F; $t_0 = 0$ for C, F; $t_0 = 0.25$ for B, E; $t_0 = 0.5$ for A, D. Incubations are for 24 h.

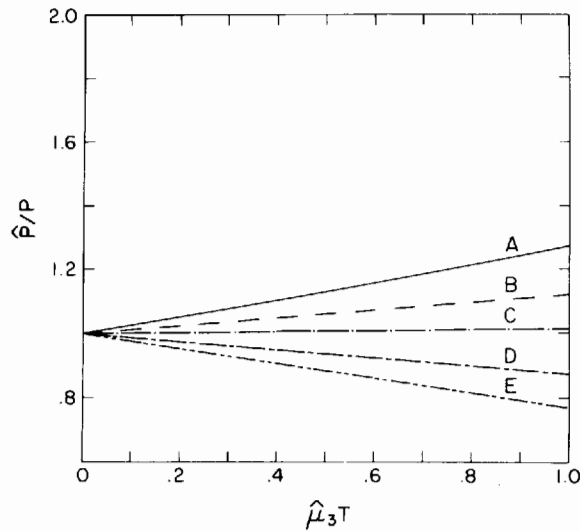


Fig. 6. Range of relative production as a function $\hat{\mu}_3T$ (specific growth rate x daylight length) for 3 h incubations. \hat{P} is four times 3 h C^* value. $\hat{\mu}_3$ is estimated specific growth rate. $f' = 0$ for A, B, D; $f' = 0.5$ for C, E; $t_0 = 0$ for D, E; $t_0 = 0.25$ for B, C; $t_0 = 0.375$ for A.

and short incubations could provide information about phytoplankton respiration and excretion.

Marra *et al.* (1981) examined whether zooplankton grazing or bacterial growth could change ^{14}C productivity estimates. They argued that this would happen when the specific activity of particulate carbon approached that of the dissolved inorganic carbon. They did not look at the size of the effect at a range of specific activities. Their model assumed that total particulate carbon was constant; grazing losses were seen only as part of the general respiration losses. Marra *et al.* (1981) concluded that grazing did not seriously affect productivity estimates.

My model in this paper ignores respiration and concentrates on grazing-growth interactions. The non-constant phytoplankton concentration is an integral part of the interaction. My results show that grazing or lack of it can change productivity results. These results agree with the experimental results of M. Landry (personal communication), showing that a decrease in grazing pressure causes an increase in ^{14}C -labeled carbon.

The role bacteria play in altering phytoplankton productivity estimates can be assessed with the same model. When the model is used to study the effect of bacteria, f becomes the fraction of production excreted by a phytoplankter and taken up by bacteria; α is set to a value of 0.60 to reflect the high efficiency of bacterial uptake (Payne, 1970). It is assumed that bacteria are collected on the same filters as phytoplankton. The results (Figure 7) show that as long as phytoplankton excrete less than $\sim 40\%$ of their production (and zooplankton are not grazing), a 24-h incubation will overestimate phytoplankton production. With estimates of phytoplankton excretion at $\sim 10\%$ (Mague *et al.*, 1980), bacterial uptake should not significantly affect productivity estimates.

The key parameter determining possible deviations of measured ^{14}C production from environmental production is the extent of phytoplankton turnover, expressed as μt , where t is the daylight exposure time during the incubation. This dimen-

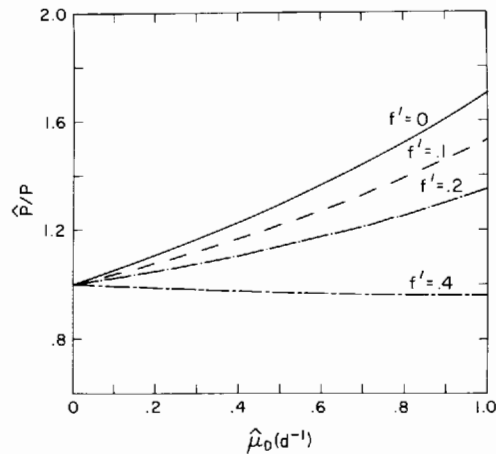


Fig. 7. Relative production with bacterial uptake of excreted organics rather than grazer consumption. Parameters are $\alpha = 0.6$, $t_0 = 0.25$, 24 h incubation. f' is the fraction of primary production excreted and taken up by bacteria.

sionless parameter is important for all incubations because it is a measure of how much the system has turned over. Grazing induced measurement errors for short-term incubations are smaller than for a 24 h incubation. That is, grazers have less time to perturb the system. Values of μ measured in the laboratory under culture conditions are as high as 2.8 d^{-1} (base e) at 25°C (Goldman and Carpenter, 1974). For a 12 h day length in a 24 h incubation, μt equals 1.4; for a 3 h incubation, μt is only 0.35. Thus, short term incubations would appear to be better when specific growth rates are high.

We can determine possible errors for a given 24 h incubation by using the experimental data to calculate the estimated daily specific growth rate, $\hat{\mu}_D$ (Figure 5). Thus, we can ask (and answer) the question of error in past marine productivity estimates.

Sheldon and Sutcliffe (1978) calculated phytoplankton growth rates, using an ATP measuring technique, that were much higher than those calculated from ^{14}C tracer measurements. They suggested that herbivore grazing in incubation bottles biased the tracer calculations. ^{14}C -based values of $\hat{\mu}_D$ are between 0.1 and 0.2 d^{-1} (Jackson, 1980; Eppley *et al.*, 1977). At a value of $\hat{\mu}_D = 0.2 \text{ d}^{-1}$, measured productivity is 0.90 of environmental productivity under the heaviest grazing and worst starting time conditions and 1.16 of measured production for no grazing and optimal starting time (Figure 5). For an incubation starting at noon and heavy grazing ($f' = 0.5$), the actual specific growth rate would be 0.22 d^{-1} . Under these conditions, grazing during the incubation would only cause errors in production and specific growth rates of 10%. Errors in production and growth rate measurements for these oligotrophic waters $>20\%$ must be caused by other factors.

Growth rates can be much higher closer to land: the average $\hat{\mu}_D$ for 11 cruises at a southern California coastal station (SCBS 101) was 0.41 d^{-1} (Eppley, personal communication). If these measurements were made in the presence of heavy grazing, the actual daily growth rate could have been 0.61 d^{-1} (Figure 2), a value almost 50% greater. Actual productivity for this condition would be 25% more than measured. For the case of no grazing in incubators, estimated daily specific growth rate is exact and environmental production is 0.75 of measured production. These values represent the extremes of what might be expected. Grazing at half the environmental rate would cause the bottle and environmental productivities to be much closer.

Conclusion

The small errors in grazing-related productivity estimates for short-term incubations suggest that they are preferable to 24-h incubations. Short-term incubations, however, do lead to greater errors caused by other factors. Any variation in photosynthetic efficiency during daylight hours adds extra variability to the results of short-term incubations which is averaged out in 24 h incubations. Furthermore, the property of short-term incubations that minimizes the effect of grazing, a small value of μt , causes the productivity estimate to overestimate net production (Buckingham *et al.*, 1975; Hobson *et al.*, 1976). In areas where phytoplankton respiration is a large part of the gross photosynthesis, a short in-

cubation to avoid grazing errors could cause greater errors by measuring gross rather than net productivity. A longer incubation may, in fact, be more desirable for a net production measurement, especially if possible errors associated with such factors as grazing can be estimated.

The range of possible errors in phytoplankton productivity estimates is greater for longer incubation times and higher specific growth rates. The overestimate associated with absence of grazers during an incubation can cause greater errors than their presence. At the specific growth rate for oligotrophic reported by Eppley *et al.* (1977) using ^{14}C incubations, 0.2 d^{-1} , the maximum error is 16%. This is too small to account for different estimates obtained using non- ^{14}C techniques. Similar arguments suggest that bacterial uptake of excreted organic carbon is not significant. Therefore other reasons for different values for different techniques must be sought.

This discussion has been based on the assumption that phytoplankton growth rates remain unchanged in an incubation but that biomass accumulation rates change. One possible cause of error in ^{14}C incubations is that phytoplankton growth rates in bottles are different than those in the environment. Carpenter and Lively (1981), Fitzwater *et al.* (1982) and Ortner (unpublished data) have shown that trace metal contamination occurring during water sample handling can change the growth rate of phytoplankton during incubations, either enhancing or inhibiting it. Data show the magnitude of the effect to be quite variable. Trace metal depression of phytoplankton growth in the bottle could intensify the effect of zooplankton grazing during an incubation if the grazers were more tolerant of the trace metals, but the problem would still be trace metal toxicity. In this case the phytoplankton growth rates in bottles would be less than in the environment.

Whatever the errors introduced by using the ^{14}C -tracer technique, they must have causes that can be studied and quantified, mathematically and experimentally. I have presented arguments that zooplankton grazing or bacterial uptake would not change significantly the estimates of phytoplankton growth in the oligotrophic Pacific. This does not prove that growth rates there are slow. Trace metal contamination may or may not be responsible for underestimates of productivity in oligotrophic areas; grazing during incubations is not.

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