

COMMENT

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Reply to the note by Chavez et al.

In our earlier paper (Dickson and Wheeler 1993), we question the existence of a latitudinal gradient in integrated chlorophyll *a* (Chl *a*) concentrations between subtropical and subarctic waters. Our results indicate that a significant fraction of the Chl *a* in subtropical waters passed through the GF/F filters but was retained by 0.2- μm Nucleopore filters. Comparison of the calculated gradients in integrated Chl *a* (Table 1) shows that the relatively steep latitudinal gradients observed for Chl *a* retained on GF/C and GF/F filters are diminished when results are calculated for Chl *a* retained on 0.2- μm filters.

Chavez et al. (1995) repeated the comparison of Chl *a* trapped on GF/F and 0.2- μm filters in the equatorial divergence, low latitude subtropical gyres, and higher latitudes of the North Pacific and found little difference. Most of their samples had Chl *a* concentrations $>0.1 \mu\text{g liter}^{-1}$ and at these higher concentrations their filter comparison results are similar to ours. The discrepancy between our two data sets is only found for samples with $<0.1 \mu\text{g Chl } a \text{ liter}^{-1}$. Although the Chavez et al. results for waters with low concentrations of Chl *a* disagree with our subtropical data set, other published data confirm differential and poor retention characteristics of GF/F filters in subtropical waters. Taguchi and Laws (1988) presented the largest data set for the comparison of GF/F and 0.2- μm trapped Chl *a* in the subtropical North Pacific. They found a large variance in Chl *a* passing GF/F filters but trapped on 0.2- μm filters (their fig. 2). Although the median value of Chl *a* passing through the glass-fiber filters is $\sim 0.02 \mu\text{g liter}^{-1}$, 20% of the data fall in the range of 0.05–0.15 $\mu\text{g liter}^{-1}$. If evenly distributed through a 150-m water column, this GF/F “missing fraction” of Chl *a* would contribute 7.5–21 mg m^{-2} to estimates of integrated Chl *a*. These data suggest that *at times* a significant fraction of Chl *a* is missed by standard GF/F filtration protocols.

We have carefully reviewed our protocol for filtering, extracting, and measuring Chl *a* and can find nothing that indicates the presence of a systematic error. Indeed, we were concerned enough about the large fraction of Chl *a* not captured by the GF/F filters on the southern end of the NOAA transect, and the implications of these results, to further test our procedures. To rule out the possibility of increased filter porosity (due to precombustion) or the effect of vacuum pressure used for filtration, we made appropriate comparisons and reported them in table 1 of our paper. We found no evidence that the low concentrations of Chl *a* measured with GF/F filters resulted from the combustion of filters or the applied vacuum pressure. In addition, the $F_o:F_a$ ratio was high (1.8–2.0) in the

mixed layer for both GF/F and 0.2- μm filters, indicating that most of the pigment was from healthy phytoplankton and not due to degradation products. Robust conclusions on filter retention efficiency should be based on samples collected at the same time and place and treated similarly. Our GF/F and 0.2- μm filter comparisons were conducted on parallel, equal volume samples collected at the same time and place, using identical methods for extraction and fluorometric analysis of Chl *a*. Thus, we do not believe that our GF/F measurements were compromised. Instead, we suspect that differences between our results and the data of Chavez et al. (1995) reflect the natural variability inherent in the ocean.

Integrated Chl *a* from the HOT site varies by a factor of three (from 14.8 to 45.6 mg m^{-2}) with a mean concentration of 23.3 mg m^{-2} . Causes of this magnitude of variation are not known, but it is noteworthy that the lowest concentrations were prevalent from June 1990 to March 1991 (Winn et al. 1991, 1993) which encompasses the time when our samples were collected. Other recent studies indicate two–threefold variations in Chl *a* standing stocks in the subtropical Pacific on diel (Hayward et al. 1983, 7.4–18.8 mg m^{-2}) and longer time scales (e.g. DiTullio and Laws 1991, 7.0–21.5 mg m^{-2}).

Reid's classic comparison of nutrient concentrations and plankton standing stocks in the Pacific Ocean (Reid 1962) sets the stage for the expectation of a positive correlation between nutrient availability and phytoplankton standing stocks. Indeed, early data sets did show a positive gradient in Chl *a* standing stocks between subtropical and subarctic waters in the Pacific (Table 1). Along 145°W, integrated nitrate concentrations between 15°S and 15°N range from 0.4 to 541 mmol m^{-2} (Wilkerson and Dugdale 1992) and reach levels of 1,430 mmol m^{-2} at 50°N (Wheeler 1993). Despite this three order-of-magnitude variation in nitrate concentrations, Chl *a* standing stocks range from 10 to 50 mg m^{-2} with most values falling in the range of 20–35 mg m^{-2} (Chavez et al. 1995). Although latitudinal gradients can be calculated for several of the data sets available for the Pacific Ocean, the magnitude of the slope ranges from 0.174 to 1.655 (Table 1). For the Hayward and McGowan (1985) data, there is a twofold difference in the gradient for 24–44°N compared with the subset of the data for 32–44°N. We found a fourfold difference in the gradient for GF/F vs. 0.2- μm filters for 28–40°N. The full extent to which variations in the gradients are caused by filter type, location, and temporal variations remains to be determined. However, it is clear from the large standard errors and the low correlation coefficients, especially for pooled data sets, that latitude per se is not

Table 1. Latitudinal gradients in integrated Chl *a* in the North and South Pacific Ocean. The depth of integration was 0–175 m for Dickson and Wheeler (1993) and 0–200 m for the other data sets.

Location	Filter type	Gradient	r^2	Source of data
24–44°N	GF/C	0.637±0.180	0.37	Hayward and McGowan 1985
32–44°N	GF/C	1.655±0.043	0.59	Hayward and McGowan 1985
28–48°N	GF/F	0.734±0.293	0.67	Dickson and Wheeler 1993
28–48°N	0.2 μ m	0.174±0.083	0.59	Dickson and Wheeler 1993
22–51°S	GF/F	0.892±0.128	0.75	Chavez et al. 1995

the major variable when integrated Chl *a* concentrations are considered on broad spatial and temporal scales.

A simple relationship between nutrient availability and Chl *a* standing stocks is not supported for mesoscale latitudinal comparisons in the Pacific Ocean. Integrated Chl *a* data (Chavez et al. 1995, their figure 6) confirm that from the equator to 50°N, temporal variability in the data exceeds spatial variability. Chl *a* concentrations around the equator range from 20 to 50 mg m⁻² and show considerable overlap with the HOT data. This high degree of temporal variability relative to spatial variations illustrated by Chavez et al. reinforces our original conclusion that the existence of a latitudinal gradient in integrated Chl *a* “is weak at best” between subtropical and subarctic waters in the North Pacific Ocean. The steep gradient observed in the South Pacific gyre by Chavez et al. is impressive (their figure 6). It will be interesting to see whether the South Pacific gradient is persistent over time as more data become available.

It is intriguing to note the similarity in the latitudinal gradients found in the North and South Pacific Ocean when glass-fiber filters were used (Table 1). The latitudinal gradient between subtropical and subarctic waters from Hayward and McGowan's (1985) data set with GF/C filters is not significantly different from that obtained in our study with GF/F filters. Both these values are slightly lower but similar to that found by Chavez et al. (1995) between 22 and 51°S. Our data indicate that glass-fiber filters introduce an artifact into the evaluation of latitudinal gradients and that gradients are minimized when submicron filters are used. It is interesting that Chavez et al. have two data points for integrated Chl *a* concentrations using GF/F filters that fall on the same line as our 0.2- μ m data for the North Pacific (their figure 7). However, since their data and ours were collected during different seasons and years, the data must be compared cautiously.

Two questions remain unresolved. First, in subtropical waters are differences in Chl *a* retention of GF/F filters due to methodological differences in sample collection or extraction or due to temporal and spatial variations in phytoplankton assemblages? The second, and more pervasive oceanographic question is whether a consistent relationship exists between nutrient concentrations and phytoplankton standing stocks in oceanic regions. New paradigms have been proposed for high nutrient, low

chlorophyll regions that encompass the role of micro-nutrient limitation and the effect of grazers in maintaining low phytoplankton stocks (e.g. Miller et al. 1991). Do these processes also apply across transition regions? What causes sharp Chl *a* gradients across some regions which are apparently overridden at other locations (or at other times) by dramatic temporal fluctuations? We are pleased that our results have stimulated the publication of a much larger data set by Chavez et al. (1995) and hope that questions of filter efficiency in oligotrophic waters and the broader problem of understanding the causes of variations in phytoplankton standing stocks in oceanic waters will continue to be investigated.

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Quantifying the role of heterotrophic bacteria in the carbon cycle: A need for respiration rate measurements¹

During the past two decades, microbial studies have convincingly demonstrated the existence of a diverse, numerous, and active heterotrophic bacterial community. However, due to methodological uncertainties and limitations, these studies do not accurately constrain the role of the bacterial community in determining the fate of organic carbon in aquatic systems (cf. Pomeroy and Wiebe 1993; Brock 1987). This is, in part, because most studies have focused solely on biomass production as the primary measure of bacterial metabolic activity. In addition, many investigators have not fully appreciated the magnitude of the uncertainties associated with biomass production measurements and respiration rates derived from them. The incorporation of the bacterial community into quantitative models of carbon cycling would be accelerated if future research efforts placed greater emphasis on the determination and interpretation of respiration rates.

Estimates of bacterial biomass production (BBP) are the most commonly reported measure of bacterial activity. Typically, BBP is estimated by measuring changes in cell numbers or POC (particulate organic C) with time or by uptake incubations using various radioactive tracers to estimate synthesis rates of nucleic acids, proteins, or other cellular constituents, followed by extrapolation to BBP via a series of conversion factors. Uncertainties, including catabolism of the tracer compound, nonspecific labeling, unmeasured dilution of tracer by ambient pools and/or de novo synthesis, perturbation of the in situ metabolic rates by nontracer additions, methodological disparities, and other factors, confound the interpretations of these incubations. Even without these uncertainties, however, BBP estimates have important limitations. Unlike autotrophic production, which represents a transfer of carbon from the inorganic to the organic pool, BBP is a transformation solely within the organic pool. Simply put, BBP is a conversion of DOC (dissolved organic C) to POC. Because the DOC may come from many sources including the bacterial community itself, the actual role

of the bacterial community in determining the fate of organic C produced in the euphotic zone based on this measure alone cannot be established.

The latter point is demonstrated by the hypothetical microbial community represented in Fig. 1. This figure is an extension of the model of consumer production presented by Strayer (1988) into which bacteria, interbacterial DOC cycling due to viral lysing, bacterial bacterivory, and leakage (Cole and Caraco 1993), and DOC loss from nonbacterial consumers have been explicitly added (cf. Jumars et al. 1989; Longhurst 1991). In this example, we assume a conversion efficiency (e.g. the percentage of organic C entering the bacterial cell that remains as living carbon) of 50% for all organisms, interbacterial DOC cycling equal to 33% of the BBP rate, and a DOC loss rate from nonbacterial consumers of 10% of the utilization rate. Although these example values are consistent with recent literature, a wide range of values is possible depending on community composition and environmental conditions and we present this calculation simply to illustrate our arguments.

The importance of this figure is to demonstrate that the loss of carbon from the organic pool and the transfer of carbon between bacteria and other consumer levels are not uniquely related to BBP. To estimate respiration from BBP requires independent knowledge of the conversion efficiency. To estimate how much organic carbon is available to non-bacterial consumers requires knowledge of conversion efficiency and interbacterial DOC cycling. Thus, estimates of BBP alone, even without measurement error, cannot unambiguously constrain the role of the bacterial community in determining the fate of organic carbon in the system. This conclusion was also reached by Cole and Caraco (1993) whose case study demonstrated that the percentage of net primary production entering and exported from the bacterial community could be significantly altered by changing the extent of interbacterial DOC cycling, even though BBP remained constant. Thus, in their example, BBP was not uniquely related to the above transfers and could be related to bacterial respiration only through an assumed growth efficiency.

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