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Why measure bacterial production? A reply to the comment by Jahnke and Craven

In their comment, "Quantifying the role of heterotrophic bacteria in the carbon cycle: A need for respiration rate measurements," Jahnke and Craven (1995) make a number of important points. Certainly, their overall plea that the addition of respiration measurements would improve our understanding of microbial carbon cycling is inarguable. Clearly, their comment was not intended as a direct criticism of the measurement of bacterial biomass production (BBP) in general. Their conclusion, p. 439, that ". . .without the additional constraints that would be provided by concurrent respiration rate measurements, [measurements of BBP] will probably provide only marginal improvements in our understanding of the role of this community in the aquatic carbon cycle" does warrant a response, however, about the general utility of measurements of BBP.

It is our intention to argue that BBP has been and continues to be an important rate to measure with or without the addition of respiration measurements, that despite numerous uncertainties and methodological problems estimates of BBP are converging as we gain an understanding of the factors that regulate it, and that growth efficiencies may be known well enough to at least put reasonable boundaries on estimates of bacterial respiration (BR) where BR can be constrained by other information. Additionally, we make the case that the direct measurement of BR is problematic and uncertain.

From an ecological viewpoint the production of biomass of heterotrophic bacteria is secondary production (Fuhrman and Azam 1980). Like herbivores and carnivores, bacteria convert existing organic molecules into their own biomass (e.g. bacterial production) and oxidize some of these to final metabolic endproducts (e.g. bacterial respiration). Unlike most other heterotrophic organisms that consume mostly particulate packages of food, bacteria have remarkable capabilities to assimilate dissolved organic molecules from the environment. BBP, then, converts dissolved organic C (DOC), which would be lost to other members of the food web, into particulate packages (bacterial cells) that are then potentially available to some consumers. This microbial "recovery" of DOC (Paerl 1978) is significant in that it represents a "link" between DOC and higher consumers (Pomeroy 1974). Pomeroy's question of whether the microbial loop functioned more as a respiratory sink for DOC or as a link to higher trophic levels has certainly sparked important research into microbial ecology (Hobbie and Williams 1984; Ducklow et al. 1986).

To examine the link, one needs to know how large BBP is and to what extent it is consumed by higher trophic levels. Further, the magnitude of this link need not be large in comparison to the sink term (BR) to be significant. Bacteria can be the primary diet item of specifically bacteriovorous organisms (Sherr and Sherr 1988; McManus and Fuhrman 1988); understanding the ecology of these organisms requires a knowledge of the production of biomass rather than the respiration rate of their prey. Work on the balance between the production of bacterial cells and their fate as prey has, in turn, raised questions about the mechanisms of bacterial mortality (*see* Pace 1988) and has led to studies of additional agents of mortality such as viruses (Proctor and Furhman 1990), autolysis, or even bacteria themselves (Cole and Caraco 1993). The causes of bacterial mortality in nature, is now an active area for research (*see* Hobbie 1993). The measurement of BBP was essential to gain these insights.

From a biogeochemical and thermodynamic viewpoint one could argue, as do Jahnke and Craven, that the state change from DOC to bacterial biomass (particulate organic C, POC) is not a useful thing to know in and of itself, because it is unconstrained. It is respiration, after all, and not secondary production, that is necessarily constrained by organic matter supply (Strayer 1988). That is, the total amount of respiration in a community (the sum of the respiration of all autotrophs and all heterotrophs including bacteria) cannot exceed the input of organic C from primary production, allochthonous inputs, and changes in standing stocks. With sufficiently long food chains and high growth efficiencies, secondary production can theoretically exceed this "primary" carbon supply (Strayer 1988). Since bacterial production is not theoretically constrained to be less than primary production, it

is intriguing that estimates of pelagic BBP across a wide range of marine and freshwater ecosystems generally converge around 0.1–0.3 times planktonic net primary production (*see* Cole et al. 1988; White et al. 1991). With a few notable exceptions in the literature (Scavia and Laird 1987), the ecosystems in which pelagic BBP is in excess of pelagic net primary production are known to be dominated by allochthonous inputs of organic C and are decidedly heterotrophic (e.g. Findlay et al. 1991). The proposed mechanisms that produce the reasonably strong correlations between BBP and algal primary production among ecosystems are diverse (Currie 1990; Cole et al. 1988; Billen et al. 1990) and an active area of research. Measurements of BR would not have revealed these trends.

Measurements of BBP allow assessments of bacterial responses to ecological conditions. In these studies, it may not be necessary to know the absolute values of either BBP or BR. Rather, the interest is in the relative magnitude and direction of the bacterial response. The current methods for measuring BBP are simple to perform and are a convenient way to track the bacterial response over time (Bell and Kuparinen 1984) or changing conditions over depth (Pace and Cole 1994). In enclosures (Riemann and Søndergaard 1986; Hobbie and Cole 1984) and whole ecosystem experiments (Pace 1993), inferences about bacterial responses to food-web structure and nutrient loadings are most easily assessed by measurement of BBP. Some insights into the factors that regulate bacteria can be gleaned from measurements of BBP alone.

If one wanted an analog to primary production (the conversion of inorganic C to organic C) it would clearly be, as Jahnke and Craven state, respiration (the conversion of organic C to inorganic C). However the least ambiguous analog to primary production is community respiration and not bacterial respiration. Community respiration includes the respiration of all heterotrophs and autotrophs and is the back reaction of the photosynthetic equation. Community respiration is directly measurable with a variety of incubation and free-water methods and the sensitivity of these methods has improved greatly in recent years. Community respiration, however, can be considerably larger than bacterial respiration. For example, in a review of a large data set, we estimated that zooplankton respiration is at least as large as that of bacterial respiration across a wide range of trophic conditions (Cole et al. 1988). Further, the respiration of autotrophs is nontrivial. Let's assume that algal respiration is 15% of P_{max} (light saturated photosynthesis), that phytoplankton are growing at 50% of P_{max}, that bacterial production is 20% of phytoplankton production, and that bacteria are growing at a 50% growth efficiency. Given this scenario which is representative of pelagic conditions, BR would be at most 40% of community respiration and less if the respiration of zooplankton and microheterotrophs were important. Our point is that if one is interested in the respiration of heterotrophic bacteria, community respiration may be a poor surrogate because bacterial respiration will be a fraction of community respiration, at least in pelagic systems (Schwaerter et al. 1988). We do

agree with Jahnke and Craven that measurement of community respiration puts an absolute upper limit on the possible range for BR and is useful for that reason.

Unfortunately, direct measurement of BR is problematic because it requires either physical separation of bacteria from other members of the plankton, assumptions about the contribution of bacteria to total respiration, or the use of selective inhibitors. The necessary assumptions or perturbations are not easily constrained or corrected for. Even if we could effect a perfect separation between bacteria and other members of the plankton, one has still perturbed the bacterial community. Does the separation of bacteria from new photosynthate, a potentially significant source of labile organics matter, affect bacterial metabolism? The direct measurement of BR is evolving and its associated problems are still nontrivial despite great strides in the less ambiguous measurement of community respiration. Most microbial ecologists would agree that a knowledge of both BBP and BR is useful. Jahnke and Craven are absolutely correct that a careless application of some "growth efficiency" to a series of BBP estimates can lead to grossly erroneous values for BR. We wholeheartedly endorse the idea that a measure of total community respiration or respiration in some size fraction could be used to at least identify unreasonable values for BR.

The large variation in estimates of growth efficiency pointed to by Jahnke and Craven is probably not random. If the causes of this variation are environmental factors (e.g. nutrient status, type of organic substrate, etc.) there may be a great deal of useful ecological information in the reported variance in growth efficiency. The variation in estimated growth efficiency may be methodological. In that case the studies would have to be stratified by method, length of incubation, type of environment studied, and so on. Further, we need to be clear and consistent about what we mean by growth efficiency. If the measure of growth is the change in bacterial numbers in a "predator-free" fraction, one must be certain that the fraction is indeed predator-free. How should we conceptualize bacterial mortality due to phage or bacteria within this fraction? Obviously growth efficiency needs to be measured on an appropriate and specified time scale and the fate of BBP needs to be accounted for. At very long time scales, apparent growth efficiency will approach zero. Without considering other fates of the cells (e.g. mortality), growth efficiency will be zero at any time scale at which bacterial biomass does not change.

Finally, one can look at Jahnke and Craven's review of growth efficiencies with an optimistic rather than a pessimistic perspective. Yes, the range in estimates is large but there is a strong tendency for these estimates, taken together, to cluster in a relatively narrow range. The midpoints of the ranges they show have a quasi-normal distribution with a peak near 40–50% (Fig. 1A). Of course if each study reported a range of 0–100%, all of the modes would be 50%. Clearly, this is not the case. The means of the low and high ends of the ranges in all of the studies they reviewed span from 30 to 60% (Fig. 1B). So despite variance due to the environment or the type of measure-
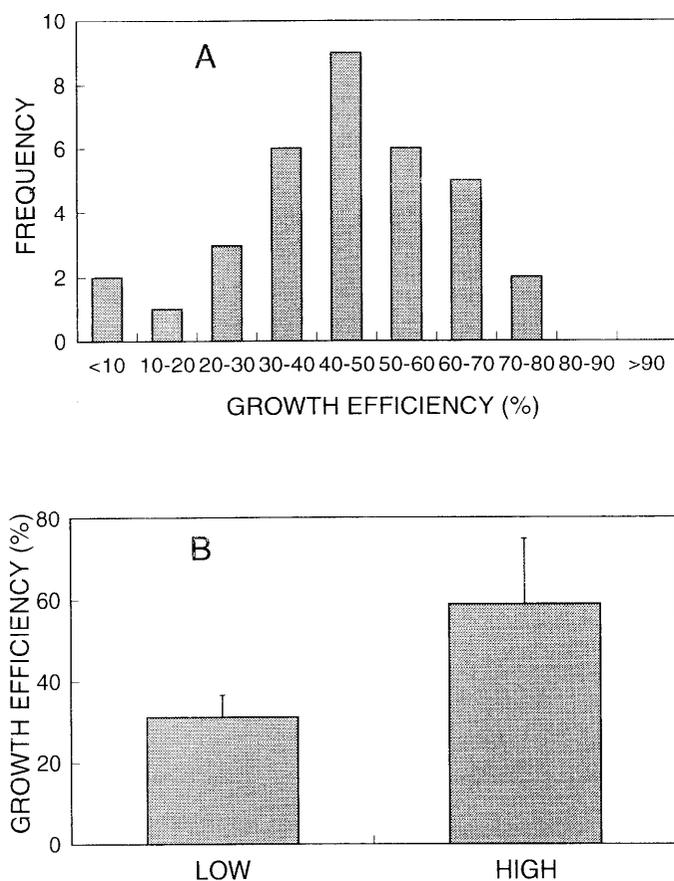
Fig. 1. A somewhat more optimistic look at variation in growth efficiency. A. We took all of the studies reviewed by Jahnke and Craven (1995) and computed the mean value of the midpoint in each growth efficiency range (*X*-axis). These are plotted as a function of their frequency (*Y*-axis) in the studies listed. B. We show the mean (with 95% C.I.) of the low end and high end of all the ranges reviewed by Jahnke and Craven. In both panels, we used all of the studies given by Jahnke and Craven and did not weight them in any way. Looked at either way (A or B), there is a tendency for most values of reported growth efficiency to cluster between ~30 and 60%.

ment we have a strong expectation for growth efficiency to be within a 2-fold range in most of the environments and time scales studied so far. This range, which translates to a 3.5-fold range in BR, may still be too large to accurately assess the role of BR in carbon losses, a point which Jahnke and Craven make. Although a 3.5-fold range sounds large, it translates into very small oxygen changes even at the productivity levels of coastal waters. The uncertainty in the estimated growth yield must be compared with the uncertainty in the respiration rate measurement before deciding whether this uncertainty is too large.

In conclusion we agree that more work is needed on bacterial growth efficiency, and the direct measure of community or size-fractioned respiration may help this effort. We disagree with the notion (p. 439) that further measurement of bacterial production "will probably provide only marginal improvements in our understanding of the role of this community in the aquatic carbon cycle" because there is a great deal of exciting research related to BBP. We look forward to less ambiguous methods for measuring both BR and BBP, but we emphasize that much can be learned with current techniques.

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