The Uptake of Inorganic Nutrients by Heterotrophic Bacteria

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Abstract. It is now well known that heterotrophic bacteria account for a large portion of total uptake of both phosphate (60% median) and ammonium (30% median) in freshwaters and marine environments. Less clear are the factors controlling relative uptake by bacteria, and the consequences of this uptake on the plankton community and biogeochemical processes, e.g., new production. Some of the variation in reported inorganic nutrient uptake by bacteria is undoubtedly due to methodological problems, but even so, uptake would be expected to vary because of variation in several parameters, perhaps the most interesting being dissolved organic matter. Uptake of ammonium by bacteria is very low whereas uptake of dissolved free amino acids (DFAA) is high in eutrophic estuaries (the Delaware Bay and Chesapeake Bay). The concentrations and turnover of DFAA are insufficient, however, in oligotrophic oceans where bacteria turn to ammonium and nitrate, although the latter only as a last resort. I argue here that high uptake of dissolved organic carbon, which has been questioned, is necessary to balance the measured uptake of dissolved inorganic nitrogen (DIN) in seawater culture experiments. What is problematic is that this DIN uptake exceeds bacterial biomass production. One possibility is that bacteria excrete dissolved organic nitrogen (DON). A recent study offers some support for this hypothesis. Lysis by viruses would also release DON.

While ammonium uptake by heterotrophic bacteria has been hypothesized to affect phytoplankton community structure, other impacts on the phytoplankton and biomass production (both total and new) are less clear and need further work. Also, even though bacteria account for a very large fraction of phosphate uptake, how this helps to structure the plankton community has not been examined. What is clear is that the interactions between bacterial and phytoplankton uptake of inorganic nutrients are more complicated than simple competition.

One feature of the microbial loop that has revolutionized our view of aquatic ecosystems is the high uptake of inorganic nutrients by heterotrophic bacteria. Although we typically think that this inorganic nutrient uptake by bacteria was first observed relatively recently, uptake of at least one major inorganic nutrient was known to be important long before the term “microbial loop” was coined by Azam et al. [1]. Citing the work of Johannes [31], Pomeroy [58] pointed out that “aerobic bacteria tend to take up all available phosphorus” and went on to sketch the role of bacteria versus protozoa in remineralization, a picture that is still accepted today.
Pomeroy's review goes on to discuss the preferential use of \( \text{NH}_4^+ \) by phytoplankton, how \( \text{NH}_4^+ \) inhibits \( \text{NO}_3^- \) uptake, and the importance of new and regenerated production [14]. But heterotrophic use of \( \text{NH}_4^+ \) was not mentioned until 1977 by Eppley et al. [15].

We now know that heterotrophic bacteria can account for a large fraction of uptake of both orthophosphate (Pi) and dissolved inorganic nitrogen (DIN), principally \( \text{NH}_4^+ \). I review here studies of that uptake, discuss how relative uptake by bacteria varies, and explore its importance to phytoplankton and community structure of freshwater and marine ecosystems.

I do not have enough space to say much about the role of bacteria in the mineralization of organic matter to \( \text{NH}_4^+ \) and Pi. Pomeroy's review in 1970 has it right anyway, as I already mentioned. Protists are probably more important than bacteria in the regeneration of both Pi and \( \text{NH}_4^+ \), and the contribution of heterotrophic bacteria to net regeneration is probably small. However, Tupas and Koike [72] showed that bacteria can mineralize dissolved organic nitrogen (DON) to \( \text{NH}_4^+ \) even when net \( \text{NH}_4^+ \) uptake by these bacterial assemblages is high. This process has been shown to be important in ecosystem models (e.g., [16]), but it is not well understood.

**Uptake of Phosphate and Ammonium by Bacteria**

Uptake of Pi by heterotrophic bacteria in freshwaters has been examined quite extensively, probably motivated by the recognition of the importance of P in limiting freshwater primary production. Several size fractionation studies have shown that heterotrophic bacteria are responsible for a large proportion of Pi uptake in lakes, usually at least 50% of total uptake (Table 1). The fraction is usually also quite high in marine systems, ranging from 5% in Peruvian coastal waters [25] to >90% in the Rhode River [17].

In addition, heterotrophic bacteria can account for a large fraction of total \( \text{NH}_4^+ \) assimilation in marine systems and in at least one freshwater lake (Table 2). The percentage attributable to bacteria ranges from insignificant uptake in the Delaware Bay [29] and Chesapeake Bay [21] to 78% in waters off Sapelo Island, Georgia [74].

Heterotrophic bacteria appear to account for a much greater fraction of total Pi uptake than \( \text{NH}_4^+ \) uptake (Fig. 1), the median for Pi being 60% vs. 30% for \( \text{NH}_4^+ \). This difference should not be overemphasized, given the large variability in these percentages and various methodological problems. Also, only one study [65] has examined \( \text{NH}_4^+ \) uptake in lakes, and so any apparent differences between Pi and \( \text{NH}_4^+ \) may really be due to differences between marine and freshwaters; in fact, Lebo [48] found that relative Pi uptake did differ with salinity in the Delaware estuary. However, generally, Pi uptake in marine systems is just as high as in freshwaters (Table 1). Also, there are good biochemical reasons to expect Pi and \( \text{NH}_4^+ \) uptake to differ, as discussed below.

The first step in understanding these percentages is to consider the ratio of bacterial to primary production (BACT:PRIM), which is usually expressed in carbon units. This should be instructive because nearly all of N and P assimilation has to be associated with biomass production eventually. The canonical BACT: