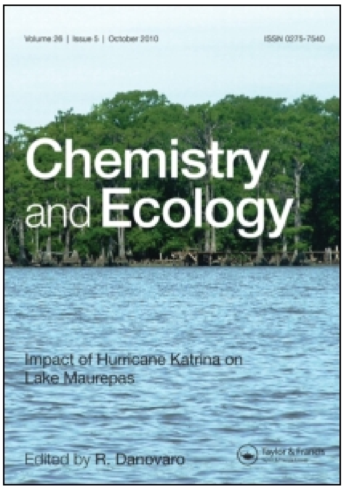

Chemistry and Ecology
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713455114

Do Bacteria Compete with Phytoplankton for Inorganic Nutrients? Possible Ecological Implications

Roberto Danovaro[a]
[a] Cattedra Biologia Marina, Facoltà di Scienze, Università di Ancona, Ancona, Italy

To cite this Article Danovaro, Roberto(1998) 'Do Bacteria Compete with Phytoplankton for Inorganic Nutrients? Possible Ecological Implications', Chemistry and Ecology, 14: 2, 83 — 96

To link to this Article: DOI: 10.1080/02757549808035544

URL: http://dx.doi.org/10.1080/02757549808035544

Chemistry and Ecology, 1998, Vol. 14, pp. 83–96
Reprints available directly from the publisher
Photocopying permitted by license only

Amsterdam B.V. Published under license
under the Gordon and Breach Science
Publishers imprint.
Printed in India.

DO BACTERIA COMPETE WITH PHYTOPLANKTON FOR INORGANIC NUTRIENTS? POSSIBLE ECOLOGICAL IMPLICATIONS

ROBERTO DANOVARO

Cattedra Biologia Marina, Facoltà di Scienze, Università di Ancona,
Via Breece Bianche, Monte d'Ago, 60131 Ancona, Italy

(Received 22 July 1997; In final form 30 July 1997)

Bacteria have been usually assumed to play a major role in regeneration processes or in conversion of refractory compounds into bacterial biomass. Recent studies have shown that heterotrophic bacteria can specifically select inorganic nutrients to promote their growth. Bacterial uptake of inorganic nutrients would take place when organic substrates (*i.e.* nitrogen or phosphorus) are limited. Therefore, especially in oligotrophic systems, bacteria would compete with microalgae for inorganic nutrients. However, experimental evidences indicate that bacteria, even in non-limiting conditions, sometimes prefer inorganic nutrients to dissolved organic substrate. This may have significant consequences in terms of adaptive strategies and diversity of bacterial assemblages. The competition between heterotrophic bacteria and phytoplankton for inorganic nutrients implies a strong modification of the classical aquatic food web and new elements to include in the schematic concept of microbial loop.

Keywords: Bacteria; phytoplankton; nitrogen; phosphorus

1. INTRODUCTION

Traditionally, heterotrophic bacteria had been assigned the roles of mineralizer and particle-formers (see Azam *et al.*, 1983 for a review). In the last ten years, several studies demonstrated that they can represent an important food source for zooplankton and deposit-feeders and at the same time may compete with animals for organic detritus by solubilizing POM by hydrolytic exoenzymes (Azam and Smith; 1991, Furhman, 1992).

Bacteria can also enrich detritus (with respect to nitrogen), or utilize it, converting refractory compounds into microbial biomass (*i.e.* resources available to consumers; Fabiano and Danovaro, 1994). Therefore, it seems that bacteria may play several roles. Whether bacteria play one role or its reversal, they will have quite different consequences for biogeochemical dynamics. The most likely explanation for the existence of this "role reversal" is that bacteria may play different roles and respond differently, pending on the changing environmental trophic conditions

This paper summarizes recent findings on the competition between heterotrophic bacteria and phytoplankton for inorganic nutrients and outlines the consequent ecological implications for the food web structure. Perspectives and suggestions for future research on this topic are also presented.

2. EVIDENCE FOR BACTERIAL UPTAKE OF INORGANIC NUTRIENTS

Recent measurements in natural systems, showed that bacteria can utilize inorganic nutrients for their growth and consequently may compete with phytoplankton (Furhman *et al.*, 1988; Horrigan *et al.*, 1988). Horstmann and Hoppe (1981) demonstrated that natural bacterial and phytoplankton communities competed for ammonium uptake in oligotrophic and mesotrophic waters of the Baltic Sea and that bacteria out-compete phytoplankton at low light intensity levels. Wheeler and Kirchman (1986) showed that net growth rate of heterotrophic bacteria was significantly higher after ammonium addition. Other evidences for enhanced heterotrophic bacterial growths were provided using ammonium, nitrate and phosphate supplements (Zweifel *et al.*, 1993).

Although bacteria have the potential (*i.e.* high turnover rate) to compete successfully with algae for dissolved inorganic nutrients, several factors may affect the optimal conditions for bacterial growth. The first is that bacterial uptake of ammonium is highly dependent on its concentrations. With increasing ammonium content, a larger fraction goes into larger phytoplankton (Suttle *et al.*, 1990). Bratbak and Thingstad (1985) have reported similar behaviour for phosphorus from observations on *P*-limited mixed bacteria-phytoplankton chemostats. If we consider the kinetics of substratum uptake, this behaviour might be because bacteria have low K_m and low $V_{\max}$ whereas phytoplankton has high K_m and high $V_{\max}$. Therefore, bacteria out-compete phytoplankton at low nutrient levels (*i.e.* in oligotrophic systems) and vice versa at high nutrient levels (meso-eutrophic systems).

These considerations are particularly useful for understanding the fate of the nutrient pulse (opposite to steady, low nutrient concentrations). The presence of pulses (even considered as nutrient patches) would favour nutrient uptake by large phytoplankton rather than by bacteria. This can also be applied to understand predictable and unpredictable fluctuations and different food webs of the high nutrient environments (such as coastal areas) versus low nutrient environments (such as off-shore).

Tupas *et al.* (1994) pointed out a significant ammonium uptake in Antarctic coastal waters during phytoplankton flowering (up to 25%). Similarly high ammonium uptake (27%), apparently due to heterotrophic bacteria, has been reported by Probyn and Painting (1985). Wheeler and Kirchman (1986) determined that about 80% of the ammonium uptake in ≤ 1 μm size organisms was due to prokaryotes and this fraction accounted for 20–60% of ammonium utilization in coastal and Gulf Stream waters off Georgia.

Bianchi (1980), in a polyphasic study carried out with mesocosm experiments on the bacteria-phytoplankton species reported that the addition of nutrients (*i.e.* phosphates, nitrates and silicates) determined a sudden increase of the bacterial diversity. In this case, it is not unlikely to hypothesize that such increase in diversity could be the result of the reduced competition for the available resources (*i.e.* inorganic nutrients). However, this is not the only explanation and the increased diversity could be simply the result of the increase in phytoplankton biomass (*i.e.* increased availability of organic nutrients excreted by phytoplankton). However, this appears, so far, the only study dealing with the effect of nutrient supply on bacterial diversity.

Assuming that heterotrophic bacteria utilize inorganic elements for their growth, several questions remains to be explored. To this regard, little is known about bacterial preference between nitrogen or phosphorus. The experiment carried out by Horrigan *et al.* (1988) with addition of NH_4, NO_3 and PO_4, would suggest that nitrate and ammonium were the major factors responsible for bacterial response but no definitive answer can be drawn.

Zweifel *et al.* (1993) studying changes in bacterial growth in sea water cultures supplied with dissolved organic carbon (DOC), inorganic nitrogen and phosphorus, suggested that heterotrophic bacteria utilized preferentially inorganic nitrogen and phosphorus rather than DOC to support growth on a short time scale (days).

These results are likely to present a new paradox for plankton: heterotrophic bacteria, in certain conditions, prefer inorganic nutrients to organic substrates. Consequently a question arises from this apparent paradox: why bacteria should prefer inorganic sources of these elements (*i.e.* nitrogen and phosphorus)

One possible explanation is that bacteria are characterized by very low C:N ratio (about 4:1) and C:P ratio (about 20:1) when compared to phytoplankton (7:1 and 40–200:1 for C:N and C:P). If we consider that the organic substrate available for heterotrophic metabolism is characterized by much higher C:N and C:P ratios, it is not unlikely that bacteria may require additional supply of these elements to balance their internal stoichiometric equilibrium. Therefore, in presence of "adverse" substrate conditions, bacteria would take up inorganic nitrogen and phosphorus to fulfil their growth demand. The results reported by Tupas *et al.* (1994) in Antarctic waters are consistent with the indication of nitrogen uptake as a food complement. In fact, in the only field study available in literature of bacterial production combined with ^{15}N techniques, demonstrated that ammonium assimilated by bacterial assemblage supplied 35–60% of total nitrogen demand; and a large uptake of ammonia to fulfil 50–80% of bacterial nitrogen demand was reported by Tupas and Koike (1991) in Japanese coastal waters.

3. IMPLICATION OF BACTERIAL UPTAKE OF INORGANIC NUTRIENTS

There are several important implications of bacterial uptake of inorganic nitrogen or phosphorus; the first is that almost no research acknowledges the possibility of nitrogen uptake by bacteria.

This may certainly have consequences in the investigations carried out to define and quantify the limiting nutrient conditions for phytoplankton development. The significance of the competition between bacteria and algae for nutrients can change with respect to time: bacteria may be out-competed by microalgae in non-limiting conditions that may allow the development of a phytoplankton bloom. However, when the massive nutrient uptake by phytoplankton starts reducing nutrient availability in the photic layer, bacteria may out-compete phytoplankton, determining a rapid but sharp decrease of the nutrient concentrations thus inhibiting, on the short time scale, further phytoplankton growths.

Other consequence of such competition involves the estimation of new and regenerated production. In fact, field measurements of *f*-ratios based on nitrogen uptake (Wheeler and Kirchman, 1986) should include the possibility that part of the nitrogen supplied is sequestered by heterotrophic bacteria (Tupas *et al.*, 1994).

Similarly, indirect calculations of new production based on the difference between expected and actual nutrient concentrations in large water masses (Cota *et al.*, 1990), are biased by the ignorance of the quantitative role of bacteria in the uptake of nitrogen or phosphorus. This would lead to an overestimation of the actual new production, the extent of which is not easy to assess since, among the other factors (such as grazing, bacterial lysis by virus) it depends upon:

1) bacterial densities and activities;
2) bacterial cell size (a relatively large fraction of small size bacteria may pass through the medium pore size of the glass fibre filters used for such measurements and calculations);
3) N/P ratios and nutrient concentrations.

It is sufficient to report some estimates available so far to understand the possible quantitative relevance of the bacterial component. Krempin *et al.* (1981) in Southern California using ^{33}P substrate, reported that bacterioplankton was responsible for 53% of total orthophosphate uptake, whereas phytoplankton accounted only for 47%. Tupas *et al.* (1994) estimated that bacteria are responsible for up to 25.1% of total ammonium uptake in Antarctic waters during a phytoplankton bloom. If we extend these results to other oceans, it appears clearly that primary production based on calculation of theoretical nutrient depletion by phytoplankton may be overestimated by up to more than 50%.

Another consequence of the competition for nutrient involves the applicability of correlation analyses proposed, especially in planktonic systems, to model changes in heterotrophic microbial densities on the basis of the fluctuations in phytoplankton standing stocks (Cole *et al.*, 1988). These analyses, inferring relationships between DOM producers and consumers (phytoplankton and bacteria respectively) are misleading and are confounded by covariation with other variables (such as nitrogen and phosphorus concentrations).

Bacterial utilization of inorganic nutrients may have a significant impact also on the structure of phytoplankton assemblages. For instance, the high bacterial affinity for ammonium may favour the phytoplankton species that utilize other nutrient sources (such as nitrates), or those species with high-affinity uptake for ammonium (more competitive; Koike *et al.*, 1983).

Finally it appears that our conceptual understanding of planktonic pathways of nitrogen and phosphorus flows must be modified. This should be done considering both the existence of a competition for nutrients and the trophic conditions that are in turn favourable to bacteria and algae.

Bacterial incorporation of inorganic nutrients may have important biogeochemical implications. Bacteria attached to the settling particles might sequester nitrogen and phosphorus transferring these pools to the sediments, determining a net loss from the system. Bacteria might affect the phosphorus transport across the sediment/water interface. In fact, it is increasingly evident that bacteria do not only release phosphorus from sediments but also incorporate it and may contribute to the production of organic phosphorus compounds (Gätcher and Meyer, 1993). The conversion of these compounds into refractory organic phosphorus may have different rates in eutrophic and oligotrophic systems. To this regard, Gätcher and Meyer concluded that bacteria in oligotrophic lakes might convert a larger fraction of phosphorus into refractory organic phosphorus compounds than they do in to eutrophic lakes.

4. CONTRASTING RESULTS

No indication for bacterial utilization of inorganic supplements has been reported, especially in fresh water environments. Currie and Kalff

(1984) demonstrated that bacteria were responsible for a significant fraction of phosphate uptake. By contrast, in streams and in a series of laboratory experiments involving nutrient additions to bacteria and algae at different light levels, Findlay *et al.* (1993) found that both light and inorganic nutrients greatly stimulated algal production but no parallel increase in bacterial abundance or growth rate were observed. The authors concluded that there is not a tight trophic connection between algal and bacterial productivity.

On the light of these results, it appears that bacteria do not always compete for nutrients and that the success of algae in the competition might inhibit bacterial response to nutrient addition.

A potentially confusing point is that several studies have shown that bacteria contribute to the release of nutrients (e.g. ammonium) and this is apparently in contradiction with the data showing bacterial uptake. However these studies deal with total release of ammonium and do not consider the net release. There is the possibility that some bacteria uptake nutrients when others are releasing. For instance, it has been hypothesized that some bacteria may be photo-heterotrophic obtaining energy from sunlight and carbon from organic sources (Tupas and Koike, 1990).

5. BACTERIAL RESPONSE TO INORGANIC NUTRIENT ENRICHMENT IN SEDIMENTS

For sediments, there are no investigations designed specifically to test bacteria uptake and utilization of inorganic nutrients. The only information available derives from "side-studies" designed to test the response of meiofauna and bacteria to the inorganic nutrient enrichment. Wormal and Stirling (1979), in a field study close to a sewage outfall, fed sediments with sea water enriched with inorganic phosphate and nitrate (at maximum levels of 900 g P l^{-1} and 2600 g N l^{-1} and at flow-rates of 1.6 to 3.9 l day^{-1}). They observed that both bacterial and meiofaunal densities declined, as did particulate organic carbon.

More recently, Nilsson *et al.* (1991) investigated the effect of an increased load of inorganic nitrogen and phosphorus on the structural changes of autotrophs, heterotrophic bacteria and meiofauna and their qualitative composition in an experimental system. They found that, 2 to 3 weeks after nutrient enrichment, meiofaunal biomass, primary productivity and bacterial activity increased.

The confusing point of both studies is that experimental variables cannot be isolated and they cannot be clarified whether the reduced bacterial numbers (Wormald and Stirling, 1979) or the enhanced bacterial activity (Nilsson *et al.*, 1991) were the result of the nutrient supply.

Danovaro *et al.* (1994), studying a Mediterranean seagrass (*Posidonia oceanica)*bed system, reported the presence of a significant relationship between pore-water inorganic nutrients (particularly phosphates) and benthic bacteria. These data led the authors to hypothesize that non-limiting concentrations of nitrogen and phosphorus were able to enhance bacterial growth.

6. NEW MODELS FOR THE FOOD WEB

Conceptually bacteria cover a wide range of roles within the food web. It is evident that the traditional approach focusing on evidences of the classical model of interaction between bacteria and algae, lacks the complexity and "flexibility" of the possible roles played by bacteria. Therefore, there is a need for new schematic representations capable to include these new findings with appropriate time and space variables. If bacteria utilize inorganic nutrients as food sources this implies several changes in the conceptual models of the food web.

The main change to report in a conceptual model is that, as already observed in particular environments such as hydrothemal vents and cold, seep bacteria are mixotrophs playing a role as secondary producers (utilizing organic sources) and a primary producer (utilizing inorganic sources).

However, taking into account the flexibility of the bacterial component in the utilization of inorganic sources and therefore in the competition with photoautotrophs, the new conceptual model could include two different trophic conditions:

a) Non-limiting condition: the organic substrate utilized by bacteria as a carbon and energy sources has sufficient nitrogen and phosphorus for growth (non-limiting system), bacteria will use organic nitrogen and phosphorus alone. This system is represented by the classical model reported in Figure 1a.

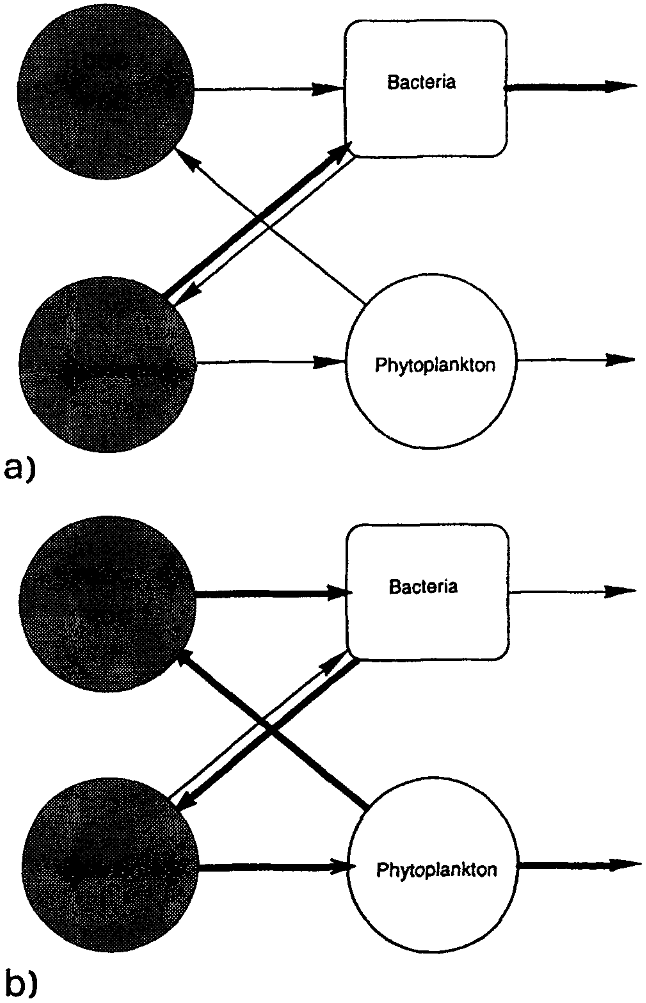

FIGURE 1 Conceptual model of inorganic nutrient (reported as nutrients) uptake by heterotrophic bacteria and phytoplankton in a) oligotrophic and b) eutrophic conditions. The arrow dimensions indicate, on arbitrary scale, the flux importance and direction.

b) Limiting condition: if there is insufficient nitrogen and phosphorus in the organic substrate, bacteria will take up inorganic nutrients to fulfil their needs.

A modification of the classical model including the role of bacteria as competitors for nutrients is reported in Figure 1b.

7. AN HYPOTHESIS FOR DEEP-SEA ENVIRONMENTS

Researches in deep-sea sediments, because of a lack of any competition with autotrophs, may provide important answers to these questions. In these environments bacteria largely dominate total biomass and their relative significance with respect to the other metazoan compartments (meio- and macrofauna) increases with depth.

Deep seas are generally characterized by increasing nutrient concentration at the sediment/water interface. Another characteristic is that deep-sea sediments show an increase of the refractory fraction of the organic matter with increasing water depth. Despite low quantities of available (*i.e.* labile or readily digestible) organic matter, large bacterial biomass and suprisingly high frequency of dividing cells (FDC as index of the bacterial activity) have been demonstrated (Danovaro *et al.*, 1993).

If bacteria, beside their ability to utilize refractory organic compounds, are able to cope with the limited food source of inorganic nutrients (complementing nitrogen and phosphorus content of the highly refractory organic carbon), they would be extremely competitive with respect to metazoans and their advantage would increase with water depth.

Therefore, the fact that bacteria often drive protozoan and metazoan assemblages would be better explained. In this case, bacteria could contribute to stabilize the deep-sea environments in terms of food supply. However, if heterotrophic bacteria may utilize inorganic nutrients also in the deep-sea sediments another strong modification of the classical concept of the food web (relative to the benthic microbial loop) would be required.

8. CONCLUSIONS

Bacteria are competitors with metazoans for organic carbon sources and specifically select those compounds rich in nitrogen or phosphorus in order to keep their low C:N and C:P cellular ratios. In environmental conditions characterized by limiting concentrations of these substrates, bacteria use of inorganic nitrogen and phosphorus as supplements and, thus, as a result, be in competition with phytoplankton. Moreover, there is evidence that bacteria, even in non-limiting conditions, may prefer inorganic nutrients to DOC on a short time scale.

In terms of adaptive strategies, free-living bacteria may take advantage of utilizing inorganic nutrients as a food source and/or as complements because they then have greater possibility to escape predation with respect to bacteria attached to POM.

Bacterial assemblages may also increase in diversity as the result of nutrient supply because of the reduced competition for the available substrate. However, further studies on bacterial diversity (more than a simple series of morphological and physiological tests) should be carried out on a molecular approach (Pedrós-Alió, 1993).

Evidences for bacterial growth stimulated by inorganic nutrients presented here, must be considered with caution since information is extremely limited and some inconsistencies have been observed (see experimental studies in streams; Findlay *et al.*, 1993). Indeed, it is not clear if these inconsistencies are due to the trophic states of the environments (fresh *vs.* sea water, especially with respect to the limiting nutrient sources) or are simply masked by the effects of the competition with phytoplankton.

Finally, a misleading point is due to the overlap in classes of particle size of cyanobacteria (or pico-phytoplankton, functionally part of phytoplankton component) from heterotrophic bacteria. A distinction between these two groups is necessary in order to gather reliable estimates of heterotrophic uptake of inorganic nutrients. Studies *in situ* carried out in deep-sea environments may clarify if, in absence of competition with autotrophs, bacterial productivity is stimulated by inorganic nutrient supply.

The points listed here should be viewed only as a working hypothesis, but should put forward the case that there is an urgent need for the development of further investigations in order to understand:

1) if there is a preference for nitrogen or phosphorus and if such a preference changes in relation to different limited factors (*i.e.* organic nutrient sources);
2) if nutrients may be utilized as complete food source or just as food complements;
3) if all heterotrophic bacteria or just specific strains uptake nutrients;
4) if the nutrient concentrations (oligotrophic vs. eutrophic conditions) determine the successful competition of bacteria vs. phytoplankton;
5) if there are differences in terms of rate and specificity of nutrient uptake by bacteria between fresh water and sea environments and between water column and sediments.

Acknowledgments

Prof. Mauro Fabiano, Dr. Antonio Pusceddu, Dr. Antonio Dell'Anno, Dr. Angela Fara (University of Ancona) and Dr. Gehard Herndl (University of Vienna) are greatfully acknowledged for their comment and suggestions on the early draft of the manuscript.

References

Azam, F., Fenchel, T., Field, J. G., Gray, J. S., Meyer-Reil, L.-A. and Thingstad, F. (1983) The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series*, **10**, 257–263.

Azam, F. and Smith, D. C. (1991) Bacterial influence on the variability in the ocean's biogeochemical state: a mechanistic view. NATO ASI Series **27** *Particle Analysis in Oceanography*. Demers S. Ed., Springer-verlag Berlin Heidelberg, pp. 213–236.

Bianchi, M. A. (1980) Polyphasic study of the microbial ecology of bacterial-phytoplankton interactions. *Microbiology, American Society for Microbiology*, 372–376.

Bratbak, G. and Thingstad, T. F. (1985) Phytoplankton-bacteria interactions: an apparent paradox? Analysis of a model system with both competition and commensalism. *Marine Ecology Progress Series*, **25**, 23–30.

Cole, J. J., Findlay, S. and Pace, M. L. (1988) Bacterial production in fresh and saltwater ecosystems: a cross-system overview. *Marine Ecology Progress Series*, **43**, 1–10.

Cota, G. F., Anning, L. R., Harris, W. G., Harrison, W. G. and Smith, R. E. H. (1990) Impact of ice algae on inorganic nutrients in seawater and sea ice in Barrow Strait NWT Canada, during spring. (Antarctica). *Journal Fishery Aquatic Science*, **47**, 1402–1415.

Currie, D. and Kalff, J. (1984) Can bacteria outcompete phytoplankton for phosphorus? *Microbial Ecology*, **10**, 205–216.

Danovaro, R., Fabiano, M. and Della Croce, N. (1993) Labile organic matter and microbial biomasses in deep-sea sediments (Eastern Mediterranean Sea). *Deep-Sea Research*, **40**, 953–965.

Danovaro, R., Fabiano, M. and Boyer, M. (1994) Seasonal changes of benthic bacteria in a seagrass bed (*Posidonia oceanica*) of the Ligurian Sea in relation to origin, composition and fate of the sediment organic matter. *Marine Biology*, **119**, 489–500.

Fabiano, M. and Danovaro, R. (1994) Composition of organic matter in sediments facing a river estuary (Tyrrhenian Sea): relationships with bacteria and microphytobenthic biomass. *Hydrobiologia*, **277**, 71–84.

Findlay, S., Howe, K. and Fontvieille, D. (1993) Bacterial-algal relationships in streams of the Hubbard Brook Experiment Forest. *Ecology*, **74**, 2326–2336.

Furhman, J. (1992) Bacterioplankton roles in cycling of organic matter: the microbial food web. **In**: *Primary Productivity and Biogeochemical Cycles in the Sea.* Falkowski, P. G., Woodhead, A.D. Eds., Plenum Press, New York, 361–383.

Furhman, J. A., Horrigan, S. G. and Capone, D. G. (1988) Use of ^{13}N as tracer for bacterial and algal uptake of ammonium from seawater. *Marine Ecology Progress Series*, **45**, 271–278.

Gätcher, R. and Meyer, J. S. (1993) The role of microorganisms in mobilization and fixation of phosphorus in sediments. *Hydrobiologia*, **253**, 103–121.

Horrigan, S. G., Hagström, Å, Koike, I. and Azam, F. (1988) Inorganic nitrogen utilization by assemblages of marine bacteria in seawater culture. *Marine Ecology Progress Series*, **50**, 147–150.

Horstmann, U. and Hoppe, H. G. (1981) Competition in the uptake of methylamine/ammonium by phytoplankton and bacteria. *Kieler Meeresforsch. Sonderh.*, **5**, 110–116.

Koike, I., Redalje, D. G., Ammerman, J. W. and Holm-Hansen, O. (1983) High affinity uptake of an ammonium analogue by two marine microflagellates from the oligotrophic Pacific. *Marine Biology*, **74**, 161–168.

Krempin, D. W., McGrath, S. M., Beeler-SooHoo, J. and Sullivan, C. W. (1981) Orthophosphate uptake by phytoplankton and bacterioplankton from Los Angeles Harbor and Southern California coastal waters. *Marine Biology*, **64**, 23–33.

Moriarty, D. J. W. and Boon, P. I. (1989) Interactions of seagrasses with sediment and water. **In**: *Biology of Seagrasses.*. Larkum A. W. D., McComb A. J. and Shepherd S. A. Eds, pp. 500–535.

Nilsson, P., Joensson, B., Swanberg, I. L. and Sundbaeck, K. (1991) Response of a marine shallow-water sediment system to an increased load of inorganic nutrients. *Marine Ecology Progress Series*, **71**, 275–290.

Pedrós-Alió, C. (1993) Diversity of bacterioplankton. *Trends in Ecology and Evolution*, **8**, 86–90.

Probyn, T. A. and Painting, S. J. (1985) Nitrogen uptake by size fractionated phytoplankton populations in Antarctic surface waters. *Limnology and Oceanography*, **30**, 1327–1332.

Suttle, C. A., Fuhrman, J. A. and Capone, D. G. (1990) Rapid ammonium cycling and concentration dependent partitioning of ammonium and phosphate: Implications for carbon transfer in planktonic communities. *Limnology and Oceanography*, **35**, 424–433.

Tupas, L. M. and Koike, I. (1990) Amino acid and ammonium utilization by heterotrophic marine bacteria grown in enriched seawater. *Limnology and Oceanography*, **35**, 1145–1155.

Tupas, L. M. and Koike, I. (1991) Simultaneous uptake and regeneration of ammonium by mixed assemblages of heterotrophic marine bacteria. *Marine Ecology Progress Series*, **70**, 189–199.

Tupas, L. M., Koike, I., Karl, D. M. and Holm-Hansen, O. (1994) Nitrogen metabolism by heterotrophic bacteria assemblages in Antarctic coastal waters. *Polar Biology*, **14**, 195–204.

Wheeler, P. A. and Kirchman, D. L. (1986) Utilization of inorganic and organic nitrogen by bacteria in marine systems. *Limnology and Oceanography*, **31**, 998 – 1009.

Wormald, A. P. and Stirling, H. P. (1979) A preliminary investigation of nutrient enrichment in experimental sand columns and its effect on tropical intertidal bacteria and meiofauna. *Estuarine Coastal Marine Science*, **8**, 441 – 453.

Zweifel, U., Norrman, B. and Hagström, Å. (1993) Consumption of dissolved organic carbon by marine bacteria and demand for inorganic nutrients. *Marine Ecology Progress Series*, **101**, 23 – 32.