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Nutrient limitation of bacterial growth and rates of bacterivory in lakes and oceans: a comparative study

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ABSTRACT: We conducted a series of dilution bioassay experiments to determine whether limitation of bacterial growth by nutrient elements (N and P) and organic substrates differs in marine and freshwater pelagic ecosystems. We also conducted Landry-Hassett dilution gradient experiments to assess whether rates of bacterivory differ substantially in the 2 ecosystem types. P addition stimulated significant ($p < 0.05$) responses at 5 of 6 marine and 4 of 5 freshwater sites, while N addition stimulated bacteria at 2 of 6 marine sites and 2 of 5 freshwater sites. Organic C (OC, added as glucose) was significant as a main effect in 4 of 6 marine and 2 of 5 freshwater experiments. Significant treatment interactions (N × P, OC × N, OC × P) occurred in several cases. Magnitudes of growth response to addition of the limiting nutrient were consistently greater in freshwater experiments. Rates of bacterivory did not differ ($p > 0.05$) for lake and marine systems sampled although data were extremely limited. Our results support the emerging view that mineral limitation of bacterial growth rates (as well as limitation by organic substrates) is widespread in both marine and freshwater ecosystems. However, differences in degree of response to enrichment and in growth rates in unenriched treatments in our marine and freshwater experiments suggested that severity of nutrient limitation of growth *in situ* was considerably higher for freshwater bacteria than for marine bacteria. While our study was limited in scope and more data are clearly needed, based on these results we propose several hypotheses for the apparent difference in severity of nutrient limitation of bacteria in lakes and oceans.

KEY WORDS: Nutrient limitation · Bacteria · Marine vs freshwater

INTRODUCTION

Planktonic bacteria play a key role in pelagic food webs, both in transfers of organic energy and in cycling of limiting nutrients (Azam et al. 1983). Traditionally, bacteria have been considered primarily as remineralizers ('sources') of nutrients trapped in dissolved and particulate organic matter (Porter et al. 1988). In this view, the primary perspective on the microbial food web is one emphasizing the role of bacteria in scavenging detrital (dissolved and particulate) organic matter for transfer to the 'conventional' food web via consumption of bacteria by bacterivores (Pomeroy & Wiebe 1988). However, studies of bacterial mineral nutrition have suggested that, because of their large surface area to volume ratio, bacteria are also excellent competitors with phytoplankton for nutrient elements such as N and P (Currie & Kalff 1984a, b, Bratbak & Thingstad 1985) and thus can serve as nutrient 'sinks', at least in the short term. These studies imply that one of the crucial impacts of bacterivory [primarily by heterotrophic microflagellate (HMF) grazers; Azam et al. 1983] is to recycle bacteria-bound limiting nutrients, permitting sustained phytoplankton productivity (Bloem et al. 1989, Vadstein et al. 1993, Chrzanowski et al. 1995). Thus, determinations of the intensity of nutrient limitation of bacterial growth and of bacterivory may provide insights into the degree to which bacteria serve as 'sinks' or 'sources' of limiting nutrients in pelagic ecosystems.

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Little is known about differences or similarities in the role of bacteria in pelagic nutrient cycling in marine and freshwater ecosystems. Are the frequency and severity of nutrient limitation of bacterial growth equivalent in lakes and oceans? Does the identity of the primary limiting resource for bacteria (e.g. N, P, organic C) differ between lakes and oceans? Are rates of predation on bacteria similar? While ecologists have recently acknowledged the need for comparative studies of diverse ecosystem types within unified conceptual frameworks (Cole et al. 1991), marine and freshwater ecosystems have largely been studied separately and thus answers to these questions remain uncertain. The limited literature comparing the ecology of lakes and oceans is largely based on subjective reviews of other literature or compilations of diverse data sets (e.g. studies in Nixon 1988) and not on specific, cross-system studies. For example, based on overviews of accumulated literature, both Porter et al. (1988) and Hobbie (1988) concluded that there are no fundamental functional differences in the basic ecology of bacteria in marine and freshwater pelagic ecosystems. Other comparative studies of bacterial ecology in marine and freshwater have been more quantitative. For example, Cole et al. (1988) and Sanders et al. (1992) compiled published studies of bacterial production and relative abundance of bacteria and heterotrophic protozoa, respectively. Both studies concluded that variation in bacterial ecology was more related to trophic status (eutrophic vs oligotrophic) than to ecosystem type (marine vs freshwater). On the other hand, an analysis of compiled data sets by Simon et al. (1992) concluded that relationships of bacterial C and phytoplankton C were similar in lakes and oceans, but that lacustrine systems sustain more bacterial biomass relative to phytoplankton biomass than do marine systems. As for many meta-analyses (Cole et al. 1991), patterns reported in these studies were broad but extremely noisy, reflecting both real ecological variability but also the myriad of factors that introduce variation to studies performed by diverse investigators (e.g. differences in sampling techniques, experimental procedures, calibration methods, statistical assumptions). The purpose of our study was to directly compare bacterial nutrient limitation and rates of bacterivory in marine and freshwater pelagic ecosystems using standardized experimental and sampling procedures in order to determine if there are fundamental differences in bacterial nutritional ecology in lakes and oceans. While rather limited in scope (only 8 lakes and 6 marine pelagic sites were sampled), our study has the advantage of eliminating the uncertainties surrounding comparative studies that involve qualitative or quantitative surveys of published literature.

MATERIALS AND METHODS

This study was part of a larger comparative study of the ecological stoichiometry of N and P in marine and freshwater ecosystems; selected results of that study have been published elsewhere (Elser & Hassett 1994). For our study, 8 lakes in the vicinity of the Northern Lakes Long-Term Ecological Research site in north-central Wisconsin, USA, were sampled (5 for enrichment bioassays and 3 others for dilution gradient experiments) during August 1993. Epilimnetic water was collected from the surface mixed layer, filtered in the field using 125 µm mesh Nitex to remove macrozooplankton, and returned within 2 to 3 h to a central laboratory for further processing. Marine data for our study were obtained for 2 primary locations: the southeast Pacific Ocean (2 stations sampled in early June 1993: 26° 31' 277" N, 123° 1' 120" W, and 27° 12' 80" N, 121° 4' 117" W) and the Gulf Stream in the western Atlantic Ocean (4 stations sampled in early July 1993, 4 to 40 km off Melbourne, Florida, USA). As for lake sampling, seawater was obtained from the surface mixed layer, immediately passed through 125 µm Nitex, and promptly processed on-shore (Atlantic experiments) or shipboard (Pacific experiments).

To test for nutrient limitation of bacterial growth rates, dilution bioassays (Sterner 1994) employing factorial amendments of NH_4, PO_4, and organic C (as glucose; OC) were performed. Water from each site was diluted 1:9 with filtered sample water (whole water to 0.2 µm filtered water). Dilution water was prepared by gentle gravity filtration of sample water through 0.2 µm high capacity capsule filters (Gelman #12117). High dilution reduces microconsumer grazing (Landry & Hassett 1982), permitting a closer determination of actual bacterial growth rate (Chrzanowski et al. 1995). Triplicate assay bottles were spiked with C (glucose, 220 µM), N (NH_4Cl, 16 µM), and P (NaH_2PO_4, 9 µM) in all possible combinations. All chemicals used were A.C.S. grade to minimize potential microcontaminant effects. Triplicate unenriched bottles served as controls. Bottles were incubated for 24 h at moderate light intensity at a temperature matching that of the site sampled. Incubations were performed under natural light conditions to minimize perturbations of the phytoplankton-bacteria interaction. For example, dark incubation would prevent phytoplankton photosynthesis and potentially reduce release of labile DOC (dissolved organic C) compounds by phytoplankton, thus exaggerating the role of DOC in constraining bacterial growth. As nutrient uptake in phytoplankton is largely light-dependent, dark incubation would also profoundly alter potential competitive relationships between bacteria and phytoplankton for mineral resources.

Bacteria were preserved with 2% (final concentration) filtered formaldehyde and later filtered onto 0.2 µm, predarkened Nuclepore filters and stained with acridine orange (Hobbie et al. 1977) for epifluorescent enumeration at 1000× magnification. Bacterial densities were determined in initial, undiluted sample water (to directly assess the degree of dilution), in initial, 1:9 diluted sample water, and in each sample bottle after the incubation. Apparent growth rate (AGR) in each bottle was calculated assuming exponential growth based on the change in bacterial density during the incubation. Bacterial responses to nutrient amendments were analyzed via 3-way analysis of variance using final bacterial density as the dependent variable.

We employed the dilution gradient method of Landry & Hassett (1982) to measure rates of bacterivory at a limited set of the marine and freshwater sites visited (2 marine sites, 1 at the southeast Pacific site and 1 in the Gulf Stream, and 3 freshwater sites). Sample water collected as described above was enriched with OC, N, and P to saturate bacterial growth rates and then diluted (in triplicate) in the following ratios of whole sample water to 0.2 µm filtered water: 1:0, 3:1, 1:1, and 1:3. A 0:1 dilution (i.e. 0.2 µm filtered water only) was used as a control to assess growth of contaminant bacteria or small bacteria that passed the 0.2 µm filter (Li & Dickie 1985). Bottles were incubated at the appropriate temperature for 24 h, after which bacteria were preserved and counted as described above. The actual degree of dilution applied was determined by comparing initial bacterial densities in undiluted sample water and 0.2 µm filtered sample water. Growth rates at each dilution level were estimated based on changes (from initial density) in bacterial densities at each dilution level, corrected for the contribution of bacteria from 0.2 µm filtered sample water. Plots of AGR versus dilution were examined for nonlinearities indicative of potential deviations from the assumption of the Landry-Hassett method that food levels were below microconsumer incipient limiting concentrations (Elser & Frees 1995). No nonlinearities were observed so simple linear regression was used to calculate bacterivory rates as the slope of the relationship between growth rate and dilution. Mean values of bacterivory rates were compared between marine and freshwater experiments by *t*-test.

RESULTS AND DISCUSSION

Representative growth responses of freshwater and marine bacteria to nutrient enrichment are presented in Fig. 1. In both marine and freshwater assays, P addition significantly ($p < 0.05$) stimulated bacterial growth

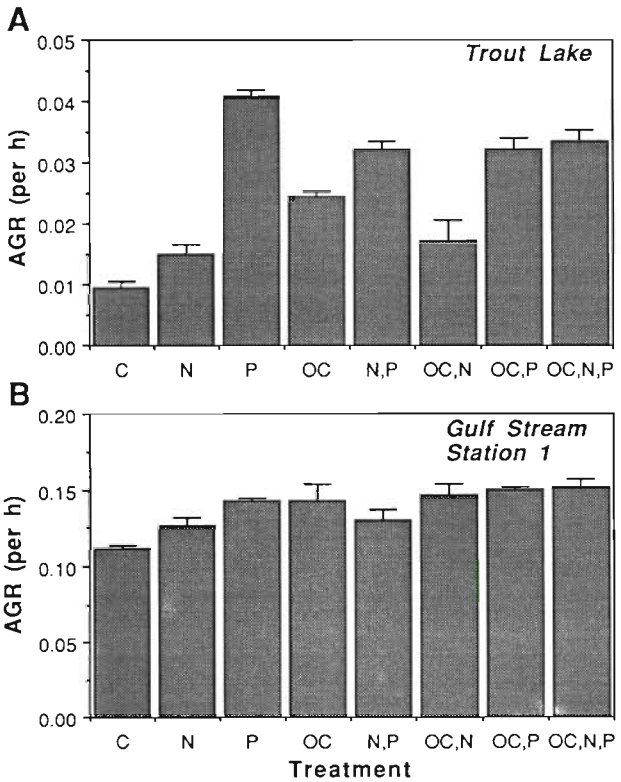

Fig. 1. Representative results of (A) freshwater and (B) marine dilution bioassays. Mean apparent growth rate (AGR, ±1 SE) in each treatment combination in factorial enrichments of NH_4 (N), PO_4 (P), and organic C (OC) is presented

at the great majority (>80%) of sites sampled (Table 1). These data, while limited, add to accumulating evidence for the occurrence of P limitation of bacterial growth (Coveney & Wetzel 1992, Morris & Lewis 1992, Chrzanowski et al. 1995) and further substantiate the argument that bacteria function in the P cycle not as 'decomposers', remineralizing P, but as short-term sinks for P, with recycling performed instead by bacterivores (Bloem et al. 1989, Vadstein et al. 1993, Chrzanowski et al. 1995). N enrichment significantly stimulated growth at 33% of the marine and 40% of the freshwater sites sampled, while OC was significant as a main effect in 67% of the marine experiments and 40% of the freshwater experiments (Table 1). Thus, the relative importance of N, P, or OC as limiting factors, as judged by frequency of growth response, did not appear to differ for the marine and freshwater sites we sampled.

While the frequency of bacterial growth response to nutrient amendment apparently did not differ for marine and freshwater experiments, the average magnitude of responses to nutrient amendment (AGR treatment/AGR unenriched control) was consistently and considerably higher in the freshwater bioassays

Table 1 Summary of 3-way analysis of variance (main effects, 2-way and 3-way interactions) of nutrient enrichment bioassay experiments. Final bacterial density after 24 h incubation was used as the response variable. Level of statistical significance of each treatment or interaction is indicated by: •••p < 0.001, ••p < 0.01, •p < 0.05, +: p < 0.10 (marginally significant)

Experiment	N	P	OC	N × P	N × OC	P × OC	N × P × OC
Marine							
Gulf Stream Stn 1		+	••				
Gulf Stream Stn 2		•••	•			•••	
Gulf Stream Stn 3		•••					
Gulf Stream Stn 4		•••		••	•	•	•••
Pacific Stn 1	•••	••	•••		••		
Pacific Stn 2	•••	•	•••	+		••	••
Freshwater							
Trout Lake	•	•••				•••	•••
Firefly Lake		••	•••			+	
Bug Lake		•••					••
Littlejohn Jr. Lake	••			•••	••	••	•••
Pauto Lake	••		••		+	+	

we performed (Fig. 2). This observation suggests that *in situ* growth limitation was more severe in the freshwater sites visited. We also compared AGRs in highly diluted, unenriched bioassay controls for marine and freshwater experiments as an additional index of the actual extent of *in situ* growth limitation. In highly diluted samples, bacterivory is minimized and competition for ambient nutrients is greatly reduced. High rates of growth in such unenriched controls when predation is reduced would indicate an ambient supply of nutrients sufficient for substantial bacterial growth, perhaps reflecting high rates of bacterial predation with concomitant nutrient recycling and/or high external nutrient supply rates (such as cross-thermocline nutrient transfers). We found significantly higher ($p < 0.0001$) AGRs in control treatments in marine experiments (mean = 0.095 h^{-1}) than in lake experiments (mean = 0.031 h^{-1}), further suggesting that nutrient limitation was more severe in the freshwater sites we sampled. In the marine experiments these control growth rates approached ~85% of rates in the 'all' treatment (i.e. in the presence of concentrations of P, N, and OC likely saturating to bacterial growth) while control growth rates were generally <50% of rates in the 'all' treatment in the freshwater experiments (Fig. 2).

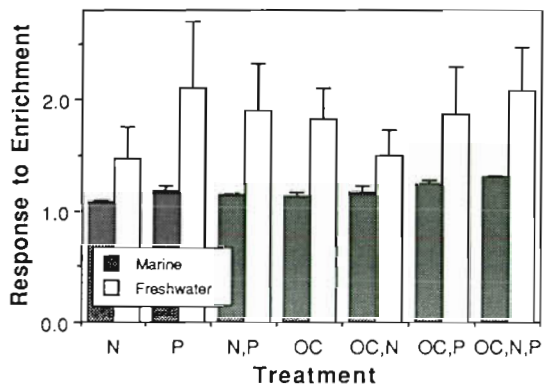

Fig. 2. Summary of relative growth responses to nutrient enrichment combinations (mean growth rate in treatment/mean growth rate in unenriched controls) for freshwater and marine dilution bioassays. Symbols for treatments as in Fig. 1. Mean values (±1 SE) of relative growth response in each treatment are presented for freshwater (n = 5) and marine (n = 6) experiments

Based on our limited measurements, rates of predation on bacteria did not appear to vary substantially in our study sites (Fig. 3). Grazing rates averaged 0.059 h^{-1} in the 2 marine experiments and 0.044 h^{-1} in 3 lake experiments; this difference was nonsignificant ($p \gg 0.05$) but interpretation is problematic due to the extremely small sample. However, given the greater apparent severity of nutrient limitation of freshwater bacteria (e.g. growth rates in control treatments in freshwater experiments were considerably lower than in marine experiments) similar rates of bacterivory between marine and freshwater systems imply that bacterivory is ecologically more significant in regulating bacterial dynamics in the lake habitats we sampled than in the marine systems we studied. This also seems to suggest that a greater proportion of bacterial production passes through bacterivorous microconsumers in lakes than in oceanic systems, and that other sources of mortality (bacterivorous macroconsumers, physical mixing losses) must be higher in marine systems. Our data, however, are extremely limited and only direct comparisons of these processes with a more extensive data set will be able to reach firm conclusions.

Similar to Hecky & Kilham's (1988) comparison of studies of phytoplankton N and P limitation in marine

and fresh water, our study, while limited in scope, provides no evidence for a qualitative difference between marine and fresh waters in the importance of N versus P in limiting bacterial growth rates. The frequencies with which P or N stimulated bacterial growth did not differ in our lake and marine experiments. In addition, P consistently produced significant increases in bacterial growth rate in marine experiments, suggesting that, as Hecky & Kilham (1988) pointed out, P may be more important as a limiting nutrient in marine pelagic ecosystems than the previous paradigm has suggested. A more balanced view of N and P as limiting nutrients in marine ecosystems may be in order.

The most striking pattern in our data is the apparent difference in severity of *in situ* nutrient limitation of bacteria in marine and freshwater habitats, as evidenced by differences in the relative growth responses to nutrient addition (Fig. 2) and in bacterial growth rates in unenriched controls. We propose several non-mutually-exclusive hypotheses to explain the apparent dichotomy in the severity of nutrient limitation of bacterial growth in lakes and oceans:

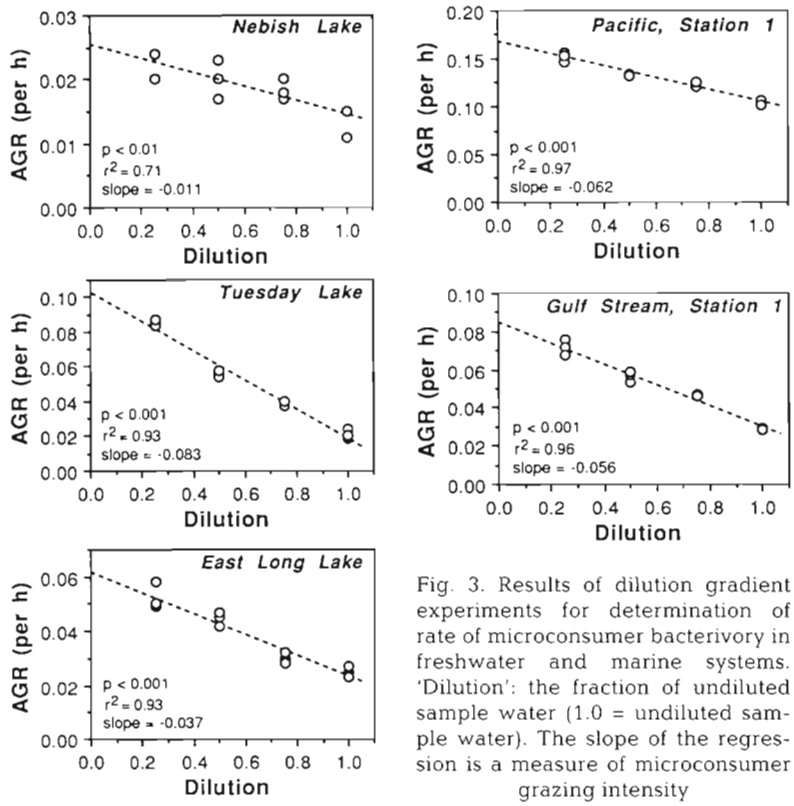

Fig. 3. Results of dilution gradient experiments for determination of rate of microconsumer bacterivory in freshwater and marine systems. 'Dilution': the fraction of undiluted sample water (1.0 = undiluted sample water). The slope of the regression is a measure of microconsumer grazing intensity

(1) Some nutrient other than inorganic N, inorganic P, or organic C limits bacterial growth rate in oceans but not in lakes. Thus, bacterial growth rates in marine experiments may not have responded to amendment of N, P, or OC in any combination because growth was limited by another factor. A candidate factor is availability of iron (Martin et al. 1991), a possibility we cannot address because we did not perform metal amendments. However, our marine sampling was primarily from coastal environments where iron limitation is unlikely. In addition, growth rates in our 'all' treatment (combined addition of OC, P, and N) were high and comparable to bacterial growth rates under full nutrient sufficiency (Leick 1968), suggesting that other potential limiting nutrients did not play a role in our experiments.

(2) Higher rates of bacterivory and stronger nutrient regeneration by microconsumers in oceans compared to lakes keeps bacterial growth rate closer to maximum in marine systems. Our grazing experiments do not support this hypothesis but too few data were available to draw any firm conclusions.

(3) Higher rates of disturbance and turbulence in oceans relative to lakes may enhance nutrient supply rates and bacterial mortality, keeping oceanic bacteria growing at high rates.

(4) Lake and ocean plankton systems may lie in different resource (nutrients versus dissolved OC) supply regions mediating the outcome of the alga-bacteria competitive interaction as formalized by Bratbak & Thingstad (1985). In this analysis, bacteria and algae reach a competitive equilibrium in which algal growth is limited by inorganic nutrients (P in the study of Bratbak & Thingstad 1985) but bacterial growth is limited by the availability of organic C (potentially supplied by extracellular release by algae under nutrient stress). Supply ratios of inorganic nutrients and dissolved OC, as well as the rates of loss of bacteria and algae, may differ in lakes and oceans in such a way that both algae and bacteria coexist at growth rates closer to their maximum under the conditions found in marine pelagic zones but at low, resource-limited rates in lake pelagia. These interactions require closer study in both marine and freshwater ecosystems, but the analysis of Bratbak & Thingstad (1985) suggests that under such conditions bacteria should have exhibited stronger evidence of growth limitation by organic substrate supply than we observed. Indeed, given the overall pattern of more severe nutrient limitation of phytoplankton growth in lakes than in oceans found in our larger study (Elser & Hassett 1994) and the higher bacteria:phytoplankton biomass ratio in lakes relative to oceans (Simon et al. 1992), the approach of Bratbak &

Thingstad (1985) would predict more specifically that lake bacteria should have shown less tendency for OC limitation (due to likely higher rates of labile OC release by nutrient-stressed phytoplankton) than marine bacteria. This was not observed but we caution that more work is needed.

While certain aspects of our data from marine and freshwater sites were similar (e.g. there appeared to be no difference in the relative frequency of bacterial response to N, P, or OC in lake and ocean experiments) and thus in agreement with prior conclusions of broad, cross-habitat similarity in bacterial ecology (Cole et al. 1988, Hobbie 1988, Porter et al. 1988, Sanders et al. 1992), we suggest that strong differences between lakes and oceans exist in the *degree* of nutrient limitation of bacterial growth, as marine bacteria are apparently growing at rates much closer to nutrient-saturated rates but lake bacteria appear to be growing at severely nutrient-depressed rates. This is consistent with higher bacterial standing stocks per unit phytoplankton biomass (i.e. higher bacterial nutrient demand) in lacustrine versus marine pelagic ecosystems observed by Simon et al. (1992). We consider our observations suggestive but preliminary due to our study's modest scope. There is a need for more data directly aimed at further characterizing this dichotomy and testing specific hypotheses regarding its potential causes. Such studies will have direct bearing on whether paradigms of microbial ecology developed from study of marine pelagic systems may be validly applied to lakes, and vice versa.

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