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Comparative and Experimental Approaches to Top-Down and Bottom-Up Regulation of Bacteria

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Abstract. The regulation of bacterial community biomass and productivity by resources and predators is a central concern in the study of microbial food webs. Resource or bottom-up regulation refers to the limitation of bacteria by carbon and nutrients derived from allocthonous inputs, primary production, and heterotrophic production. Predatory or top-down regulation refers to the limitation of bacteria below levels supportable by resources alone. Large scale comparative studies demonstrate strong correlations between bacterial productivity and biomass, suggesting significant resource regulation. Comparisons of the abundances of heterotrophic flagellates and bacteria, however, imply that in some cases there may be top-down regulation of bacteria in eutrophic environments. Experimental studies in lakes support the importance of resource regulation and reveal little top-down control from protozoans. Increases in bacterial abundance and production with nutrient enrichment were limited in enclosure experiments with high abundances of the cladoceran, *Daphnia*. Regulation of bacteria by *Daphnia* may occur in many lakes seasonally and prevail in some lakes throughout the year where these animals sustain dense populations. In most situations, however, bacteria appear to be limited primarily by resources.

Introduction

The function of bacteria is a central issue in the study of aquatic food webs. Numerous studies have documented that bacteria utilize a large fraction of the carbon that flows within aquatic ecosystems [10]. Bacteria also serve as food for protozoans and some metazoans [24]. In some systems a significant fraction of the carbon produced by bacteria moves up to higher trophic levels [51], but in other cases bacterial carbon is largely respired within a microbial food web [15]. Bacteria may also either regenerate or consume limiting nutrients such as nitrogen and phosphorus depending on the C:N and C:P ratios of available substrates [5]. When bacteria act as nutrient sinks, consumers of bacteria become a primary vector for nutrient recycling [5]. Bacteria, therefore, not only account for a large fraction of the carbon flow through ecosystems, they also play a variable role in nutrient recycling depending on resource availability and trophic structure.

Given the importance of bacteria, factors regulating the productivity and biomass of these communities are of interest. The availability of resources and consumption by predators have been considered key controls of the dynamics of bacterial communities. Regulation by resources and/or predators are often referred to as bottom-up and top-down control [25,26], but these concepts require some clarification when applied to bacteria. Limiting resources for bacteria are, typically, labile carbon substrates as well inorganic and organic N and P. If resource regulation is important, increases in the loading of nutrients or increases in labile carbon from, for example, phytoplankton blooms should increase bacterial biomass and productivity.

Bacterial resources, however, are not just derived from primary production and allocthonous loading. Food web interactions, including nutrient recycling and labile carbon production from feeding, excretion, and egestion by consumers, may all be important processes generating resources for bacteria. We use the term bottom-up regulation in this paper to refer to resource regulation in general, recognizing that bacterial resources have multiple origins.

The concept of top-down control also requires further clarification because this term has been used in the ecological literature in at least three ways. Top-down regulation is often used to describe how apical predators structure ecosystems via cascading predator–prey interactions that propagate down the food web [7]. More loosely, top-down regulation may simply refer to regulation by an upper trophic level some distance from the trophic group of concern [27]. Finally, top-down regulation may be applied more narrowly to mean direct control by predators. In the case of bacteria, the latter meaning (predator-control) is most common, and we will use the term top-down regulation in this way.

One way to visualize the regulation of bacteria by top-down and bottom-up forces is to consider how biomass and growth rates change along a resource gradient at low and high levels of predatory mortality (Fig. 1). As resources increase, we might expect a wider scope of bacterial biomasses and productivities depending on predatory pressure which might vary within and among ecosystems. If predation is relatively unimportant in regulating bacteria, we would expect a tight relationship between increases in resources and increases in bacteria along the upper line (equalling low mortality) in Fig. 1. In this case, bacterial regulation is determined primarily by changes in resources while predatory mortality remains low and relatively constant across the gradient. If predatory regulation is paramount, we would expect bacterial biomass and productivity to increase only slowly or not at all across resource gradients as illustrated by the lower line (equalling high mortality) in Fig. 1. Our model assumes and we provide evidence below that bacterial biomass and productivity covary. We also consider mechanisms that may lead to the uncoupling of biomass and productivity.

In this paper we evaluate the model of bacterial regulation proposed in Fig. 1 by reviewing a number of comparative studies from the literature and a series of experimental studies that we have conducted. These comparative and experimental studies attempt to test directly the relative importance of top-down and bottom-up regulation. We focus on resources and predatory mortality because these processes have been considered central and have received the most study. At the end of the paper, we discuss how other regulatory processes, such as viral lysis and temperature, might modify our conclusions.

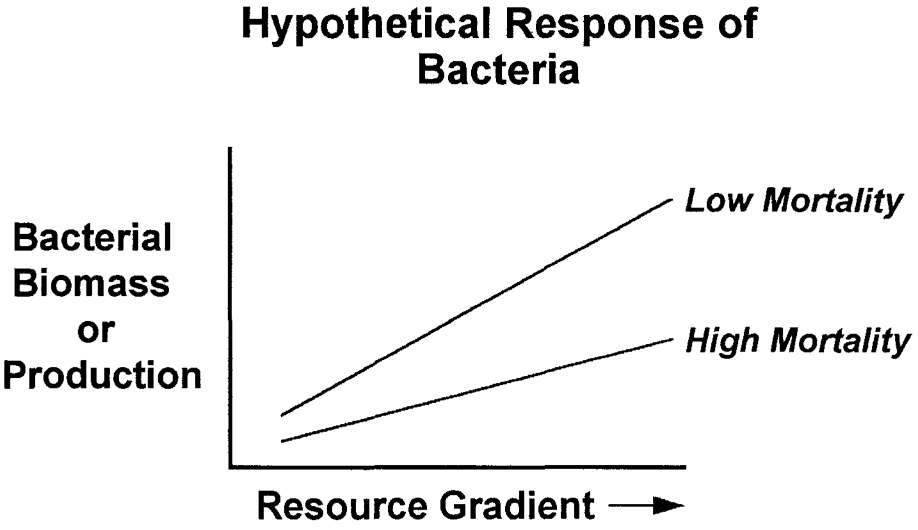

Fig. 1. Hypothetical response of bacterial biomass or productivity across a gradient of increasing resources assuming biomass and productivity are coupled; see text for details. Lines indicate responses at high and low mortality. While relationships are depicted as linear, the response of bacteria may be nonlinear especially at higher resource levels.

Comparative Studies of Bacterial Communities

Comparative studies are analyses of data drawn from a variety of systems to examine general questions about the patterns and correlates of an ecological variable [11, 29]. In the case of bacteria, these studies have demonstrated that abundance and productivity increase across resource gradients as measured by chlorophyll, primary productivity, total phosphorus, and particulate organic carbon (e.g., 4, 8, 10, 13, 45]). These studies provide strong evidence for the importance of resources to bacteria but do not directly address the problem of the bottom-up and top-down control.

Billen et al. [3] argued that the relationship between bacterial production and abundance could be used to evaluate bottom-up and top-down regulation. Since bacterial resources are difficult to measure and always at low concentrations, bacterial production serves as a surrogate measure of resources. Variability in rates of production reflects variability in resource inputs. Regressions of biomass as a function of production should have a steep slope if biomass is strongly determined by resources. Alternatively, there should be no relationship, or at best a shallow slope, between productivity and biomass if other factors such as mortality are most important in regulating bacteria. A complication not considered by Billen et al. [3] is the situation where predation on bacteria is a major mechanism of resource recycling. In this case, increases in mortality might lead to resource regeneration by consumers, resulting in bacterial biomass being partially or completely uncoupled from increases in bacterial productivity.

Using data collected with common methods from a variety of aquatic systems, Billen et al. [3] found that bacterial biomass was a strong positive function of bacterial production, supporting the hypothesis of resource regulation. Ducklow

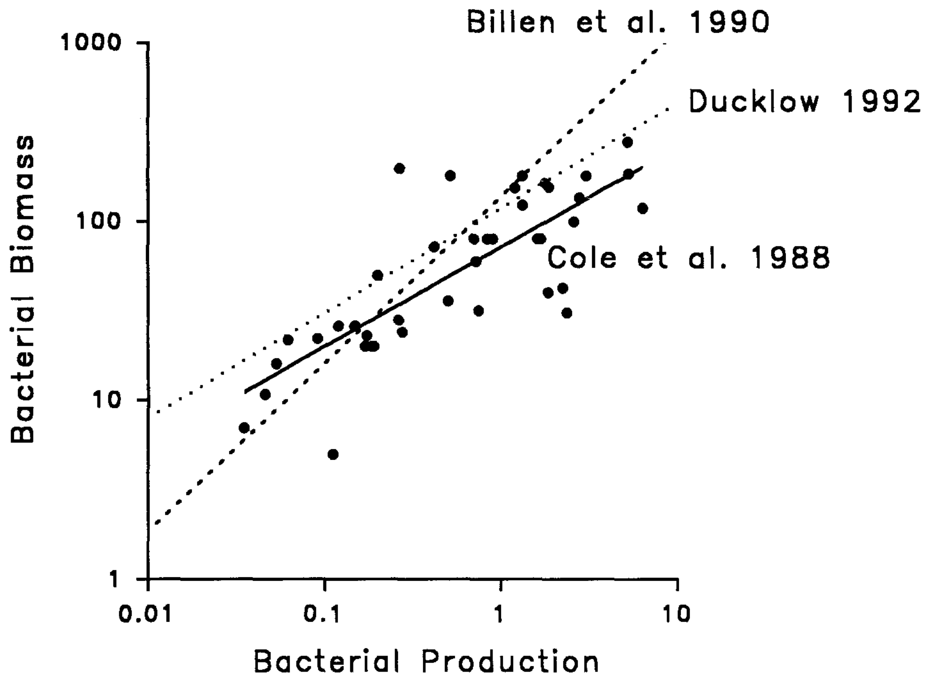

Fig. 2. Relationships between bacterial productivity and biomass from Billen et al. [3], Ducklow [14], and Cole et al. [10]. Points represent means from 40 systems summarized by Cole et al. [10]. Units are μg C liter^{-1} h^{-1} for bacterial production and μg C liter^{-1} for bacterial biomass. Note log scale.

[14] arrived at similar conclusions using data derived from the Chesapeake Bay and oceanic communities. Figure 2 presents the productivity–biomass relationship derived from data we summarized in an earlier review where we were able to obtain mean values of bacterial production and abundance for 40 systems [10]. We converted cell abundances presented in Cole et al. [10] to biomass by using a constant factor (20 fg C cell^{-1}) [22] to make our analysis comparable to Ducklow's [14]. Billen et al. [3] measured cell size and abundance to estimate biomass. The higher slope of the relationship probably reflects the larger cell sizes they observed in eutrophic systems. The three relationships overlap as illustrated in Fig. 2. These relationships between productivity and biomass imply that large-scale differences in resource supply are a crucial determinant of bacterial biomass in aquatic systems.

The increase in bacterial biomass with bacterial productivity is consistent with a model where growth is determined by substrate supply below saturating levels, and mortality is first order with respect to biomass [3]. Under these conditions, biomass at steady state is a direct function of substrate production [3]. The productivity–biomass relationships (Fig. 2) are not consistent with a second model where steady-state bacterial biomass is a function of predatory mortality [3].

These relationships, however, are not as strong when considered at smaller scales. Ducklow [14] analyzed his data further by comparing biomass and productivity relationships for different regions of the ocean as well as seasonally for specific sites within the ocean. These regressions were often weak, implying that bottom-up regulation may be less significant at local scales and may vary seasonally within sites [14]. We suggest that at these smaller scales, the productivity–biomass relationships are weak because bacterial resources have multiple origins. Resource variation at these scales may be related to recycling from other food web constituents as well as to the inputs of new resources from outside the food web. A significant part of the recycling of resources may also derive from bacterial mortality [9], a mechanism that would further uncouple biomass from productivity.

A different perspective is provided by the analysis of Sanders et al. [43], where data from a number of studies on abundances of bacteria and heterotrophic flagellates were summarized. Heterotrophic flagellates are presumed consumers of bacteria; thus the ratio of bacteria to flagellates is an index of grazing pressure [17]. Sanders et al. [43] found this ratio was constant at about 1000:1 across a wide variety of ecosystems. They examined the implications of this ratio by developing a model of bacterial dynamics as a function of substrate supply and flagellate predation. To maintain a constant 1000:1 ratio of flagellates to bacteria, regulation must shift across resource gradients according to their model. In oligotrophic environments, substrate supply controls bacterial abundance, but grazing by heterotrophic flagellates reduces bacteria below carrying capacity in more eutrophic systems [43].

The relationships between bacteria and flagellates may not be as uniform as suggested by Sanders et al. [43]. Gasol and Vaqué [19] collected similar data from a broad range of environments, including rivers, lakes, estuaries, sediments, and open-water marine systems. The ratio of bacteria to flagellates was variable both within and among these systems. Their results indicate that flagellate grazing is insufficient to regulate bacteria in many cases and that other factors such as the presence of large cladocerans in lakes influence the bacteria to flagellate ratio.

In summary, comparative studies generally confirm the importance of resource regulation of bacteria at least at large scales. The models of Billen et al. [3] and Sanders et al. [43], however, disagree on the significance of top-down regulation as do the empirical analyses of Sanders et al. [43] and Gasol and Vaqué [19]. Further, the data evaluated the Ducklow [14] suggest that bottom-up and top-down regulation of bacteria may vary seasonally and perhaps regionally in the ocean. In addition, we suggest that the relationships between resource supply and the productivity, biomass, and mortality of bacteria may be uncoupled within ecosystems because of complex trophic interactions that feed back on bacteria.

Experimental Studies

We have conducted a number of field experiments designed to test the same questions examined above. In these studies either predators, resources, or both predators and resources have been manipulated and the response of the bacterial community observed as changes in abundance and productivity [30–32, Cottingham et al. unpubl. data]. Here, we review these experiments and consider the salient outcomes with regard to top-down and bottom-up controls of bacteria.

Experiments were conducted primarily in Peter, Paul, and Long lakes, located at the University of Notre Dame Environmental Research Center on the upper peninsula of Michigan. These lakes are oligotrophic, brown-water systems that have been extensively described [6]. Some of the experimental work was also done in two eutrophic systems, Tyrrel and Upton lakes, located near the Institute of Ecosystem Studies in Millbrook, New York. We conducted three types of manipulations over increasing scales of time and size, as represented by the experimental containers—bottles (1 liter), buckets (40 liters), and bags (2000 liters).

Bottles

The first set of studies involved the manipulation of zooplankton in short-term bottle experiments. These experiments were designed to address how different zooplankton communities regulate the abundance of protozoans [32]. Because of substantial reduction in protozoans in most of the experiments, we were also able to assess how bacteria respond to changes in protozoan predation. Bottles were filled with lake water filtered through a 150-μm net to remove larger zooplankton. Crustacean zooplankton were added back to one set of bottles at their in situ concentration, while no zooplankton were added to a second set. Bottles were sampled initially and after 24 h, and the microbial components enumerated. Overall, six experiments were done in three lakes with zooplankton communities that differed primarily in terms of the presence or absence of the cladoceran genus, *Daphnia*.

In lakes where the zooplankton were dominated by *Daphnia,* protozoan growth rates were high in the absence of zooplankton and near zero or negative in the presence of zooplankton. In lakes without *Daphnia,* protozoan growth rates were unaffected by zooplankton. Despite large changes in protozoan abundances, bacterial abundance was not different between bottles with and without zooplankton. For example, in Fig. 3, ratios of abundance for the two treatments are plotted for flagellates and bacteria in the four experiments where *Daphnia* were the key constituent of the zooplankton community. Flagellate abundances were much higher after 24 h in treatments without *Daphnia* (ratio > 1). Bacterial abundances were not significantly different between treatments after 24 h (ratios = 1). Overall, bacterial abundances were unaffected by short-term changes in predatory pressure from either flagellates, ciliates, or *Daphnia.* These experiments were done in both eutrophic and oligotrophic lake waters [32]. Short-term changes in protozoan predation on bacteria did not cause differences in bacterial numbers even in the eutrophic lakes, contrary to the hypothesis of Sanders et al. [43] that bacteria should be more strongly regulated by predation in eutrophic systems.

Buckets

In a second set of experiments, we manipulated both bacterial resources and predation pressure in microcosms in Peter and Paul lakes [31]. Experiments were conducted in 40-liter buckets that were placed in the lakes, filled with lake water filtered through a 150-μm net, and sampled at the beginning and end of a 4-day period. The experimental treatments were: (1) controls, (2) *Daphnia* additions at densities comparable to those found in the lake, (3) inorganic nutrient additions (10 μmol liter^{-1} N, 1 μmol liter^{-1} P, final concentration), and (4) *Daphnia* plus nutrient additions.

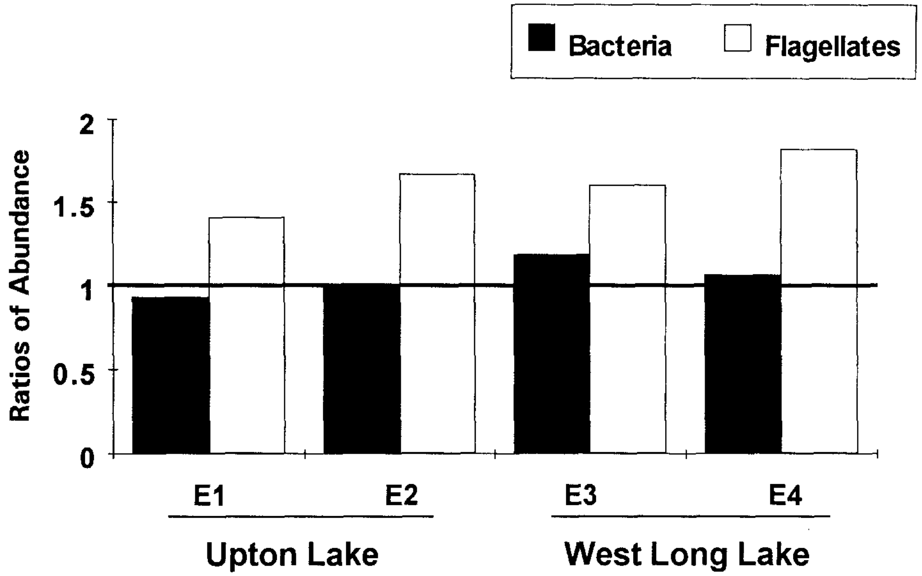

Fig. 3. Ratios of abundance between treatments without and with *Daphnia* at 24 h in bottle experiments. Bacteria were not significantly different between treatments (ratios = 1) while flagellates were more abundant in treatments without *Daphnia* (ratios > 1). *Bars* represent the ratio of the means for four experiments (E1–E4) conducted in two lakes (Upton and West Long).

Table 1. Direction of response (+, increase, −, decrease) and summary of analyses of variance for the Peter and Paul Lakes bucket experiments. The experimental design was factorial. Sources of variance: D, *Daphnia*; N, nutrients; D × N, *Daphnia*–nutrient interactions. Note "flagellates" refers to heterotrophic forms enumerated using epifluorescence microscopy after staining with proflavin. NS, $P > 0.05$; +/−, $P < 0.05$; ++/−−, $P < 0.01$; +++/−−−, $P < 0.001$. Table is modified from Pace and Funke [31]

Lake	Source	Chlorophyll	Bacteria	Flagellates	Ciliates
Peter	D	−−−	NS	−−	−
	N	+++	+++	NS	+
	D × N	−−−	NS	NS	NS
Paul	D	NS	NS	−−−	−−−
	N	+++	+++	+++	++
	D × N	−	NS	−−	NS

Additions of nutrients stimulated, while the presence of *Daphnia* suppressed phytoplankton biomass (Table 1). In nearly all cases, *Daphnia* also reduced the abundance of heterotrophic flagellates and ciliates, relative to treatments without *Daphnia* (Table 1). Bacterial abundance was twice as high in treatments with added nutrients, and the presence or absence of *Daphnia* had no effect on abundance (Table 1). We also observed that bacterial cells were larger in both nutrient-amended buckets, suggesting that bacterial biomass more than doubled with nutrient additions.

As in the bottle experiments, bacteria were unchanged by the shifts in abundance and presumably predation by protozoa and *Daphnia*. The increase in bacterial abundance was similar in the two treatments with nutrients despite the substantial difference in chlorophyll between treatments with nutrients and treatments with nutrients and *Daphnia*. Bacteria, therefore, appeared to be more directly limited by the supply of nutrients than by labile carbon derived from phytoplankton production. Subsequent factorial experiments with additions of glucose, nitrogen, and phosphorus indicated that bacteria are primarily phosphorus-limited in these lakes [30]. Together, these results imply much stronger bottom-up than top-down regulation of bacteria in these lakes.

Bags

A long-term enclosure study was conducted to further test the conclusions derived from our bucket experiments. Enclosures 2 m^3 in volume were placed in Long Lake for a 9-week period. Treatments included three different nutrient loadings and weekly manipulation of the zooplankton community to reduce the relative abundance of *Daphnia*. Nutrients were added daily to establish phosphorus loadings of 0, 0.5, 1, and 2 μg P $liter^{-1}$ day^{-1}. Nitrogen was added at a 20:1 weight ratio to phosphorus. Differing zooplankton communities were established by pulling a 300-μm screen through one set of enclosures each week to remove larger zooplankton. This experiment had 8 treatments (4 nutrient levels × 2 zooplankton community types) and each treatment was replicated 3 times for a total of 24 enclosures. Weekly measurements were made of nutrients, chlorophyll *a*, zooplankton biomass, bacterial abundance, and the incorporation of [^{3}H]leucine by bacteria.

Phytoplankton increased in the enclosures that received nutrient additions. There was, however, a remarkable difference in phytoplankton biomass in enclosures where zooplankton were not removed relative to enclosures where zooplankton were removed weekly [Cottingham et al., unpubl. data]. For example, average concentrations of chlorophyll *a* in the high nutrient loading treatments were 27 μg $liter^{-1}$ in enclosures with unmanipulated zooplankton compared to 10 μg $liter^{-1}$ in enclosures where zooplankton were removed weekly. The primary difference between these two zooplankton communities was the relative abundance of *Daphnia*. Unmanipulated communities had very large populations of *Daphnia*, while the manipulated communities had fewer *Daphnia*.

We observed significant increases in bacterial abundance and production (as measured by leucine incorporation) along the nutrient loading gradient (repeated measures ANOVA: $P < 0.06$ for abundance; $P < 0.03$ for leucine incorporation). Zooplankton community type did not significantly influence bacterial responses (all $P > 0.4$).

Increases in both bacterial productivity and abundance in response to the nutrient manipulations were relatively modest in this experiment. In Fig. 4 we plot the means of bacterial productivity and chlorophyll for all the enclosures, and compare these data to a regression derived from our earlier literature review [10]. Note that while mean chlorophyll concentrations varied from 4.1 to 27 μg $liter^{-1}$, bacterial productivity only varied from 3.4 to 5.7 μg C $liter^{-1}$ day^{-1}. Furthermore, the slope of the regression from the experimental values is much lower than for the literature

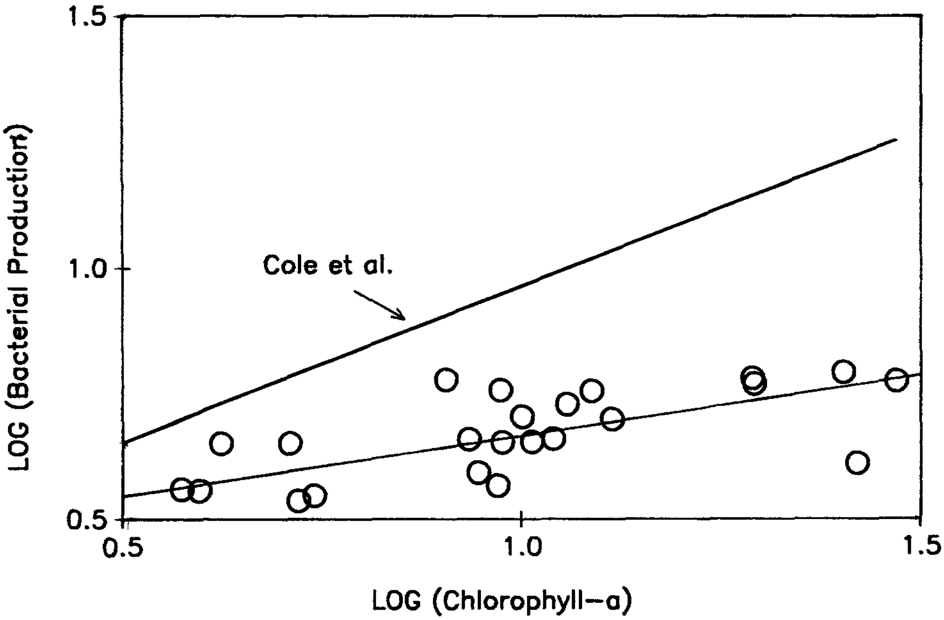

Fig. 4. Relationships between chlorophyll *a* and bacterial production from literature review of Cole et al. [10] and 23 enclosure experiments conducted in central Long Lake. Units are μg liter^{-1} for chlorophyll *a* and μg C liter^{-1} day^{-1} for bacterial production.

data. The trend in the experimental data resembles the pattern suggested for variations across resource gradients when bacterial mortality is high (Fig. 1).

The modest increase in bacterial productivity and biomass across the resource gradient created in this experiment was either the result of higher bacterial mortality in all the enclosures or inadequate resources. Additions of nutrients with stimulation of phytoplankton should have significantly increased resources available to bacteria. The site of this experiment was central Long Lake from which fish have been removed as part of an ongoing series of whole-lake manipulations. Zooplankton biomass in the enclosures varied from about 0.2 to 1 mg dry wt liter^{-1}, and these levels resemble those found in eutrophic lakes (e.g., [28]). Estimation of filtering rates by *Daphnia* suggest consumption of bacteria was on the order of 0.3–0.6 day^{-1}, and these values exceed our estimates of specific growth rates (all <0.3 day^{-1}). We infer that *Daphnia* consumption of bacteria was important in all enclosures and severely limited the response of bacteria to increases in resources. Unlike our previous experiments, this study suggested strong top-down regulation of bacteria. The degree of top-down regulation observed in this case may represent an end-member, given the high biomasses of *Daphnia*. These biomasses were much higher than in our bucket experiments which more closely resembled in situ conditions for the study lakes. Grazer control of bacteria by *Daphnia*, however, may occur in many lakes seasonally during *Daphnia* blooms (e.g., [34]) and may prevail in some systems where high densities of *Daphnia* are found throughout the year (e.g., [20]).

Discussion

Comparative and experimental studies confirm the importance of resource regulation of bacteria. Over large scales the best predictors of bacterial biomass and productivity are factors related to the total resource level in an ecosystem such as phosphorus, chlorophyll, and primary productivity. Within lakes, our experiments reveal that bacteria respond strongly to manipulations of resources, especially phosphorus. Effective models of the dynamics of bacterial communities and the consequences of bacterial activity (i.e., respiration, nutrient cycling, trophic transfer) require a better understanding of the interactions between bacteria and their resource pools, including labile carbon substrates, slowly metabolized carbon substrates, and nutrients. In addition, bacterial resources are probably influenced by food-web interactions, and feedback on bacteria from these processes requires further investigation.

Sometimes predators also regulate bacteria. In freshwater, large *Daphnia* can be effective grazers of bacteria not because of efficient consumption mechanisms [33, 35], but rather the high populations these animals can obtain [34]. *Daphnia* can have strong impacts on the microbial food web because of their ability to feed across a broad spectrum of particles that encompasses the major groups of autotrophic and heterotrophic microbes [46]. In lakes with large populations of *Daphnia,* grazing by this organism focuses production by the entire microbial community. Inefficient microbial loops are broken, and production by the smallest autotrophs and heterotrophs can be transferred to higher predators [34, 41, 45, 51].

There are probably marine analogues to *Daphnia*. In estuarine systems bivalves might play such a role although direct grazing by bivalves on bacteria has not been extensively investigated (but see [50]). In open water marine systems many pelagic tunicates consume bacteria (e.g., [12, 21]), and large populations of these animals occur in many areas of the sea [1].

Our experimental studies provide no evidence that protozoa effectively regulate bacteria. This finding is counter to the prevailing view that heterotrophic flagellates and ciliates in concert consume most bacterial production and to a large extent regulate the biomass of bacteria (e.g., [2, 24, 42, 44, 49]). Evidence for the importance of protozoa derives primarily from field studies where rates of bacterial growth and protozoan consumption have been measured. Conclusions derived from these studies, however, are based on the difference between two highly uncertain numbers. Questions of precision, and more importantly accuracy, plague the measurement of bacterial growth and mortality, and so these studies must be interpreted cautiously. The key problem may lie in determining when and where protozoan consumption is an important process, as suggested by Sanders et al. [43] in their recent review. Nevertheless, our results lead us to question the overall significance of protozoan predation in regulating bacteria. We suggest that further insights will come from comparative studies of ecologically contrasting systems and from field experiments.

Other regulatory processes such as viral lysis [18] and temperature [40, 48] are likely important in the regulation of bacteria. These factors need to be integrated with resource and predator regulation to develop a more robust view of bacterial dynamics. Models provide a method for this integration, and efforts to simulate the dynamics of bacterial assemblages using models such as those of Fasham et al. [16]

represent an important path for research. Model development is still limited by uncertainties about rates and mechanisms of interaction, and so modeling will need to be conducted in concert with further experimental and observational studies.

We note that Larry Pomeroy's vision of microbial processes derived from an interest in the comparative analysis of ecosystems [36–39]. In considering the future, we must keep in mind that the study of microbial food webs is founded on general questions about ecosystem structure and function. In this spirit it is crucial that microbial studies *not* become a highly specialized discipline solving problems of interest only to microbial ecologists. There is a real danger of this occurring as the complexities of microbial interactions are elaborated and quantified. There is a tendency to assume that learning more about the details of microbial interactions can only enhance our understanding and ability to contribute to the analysis of ecosystem problems. We submit that this view is both impractical and false. First, funding for scientific research is insufficient to allow unfettered explorations of our subject. More importantly, not all microbial interactions will matter equally in illuminating the larger ecosystem problems that are so compelling. We believe the most significant challenge lies in determining how microbial food web processes influence the state and variability of ecosystems and key ecosystem components. This does not mean studies of specific microbial interactions are unimportant. Rather, these studies must continually reflect on and inform the understanding of ecosystem processes and not diverge into ever narrower modes of inquiry.

To keep our field vital and outward in its perspective, we suggest four strategies for future investigations. The first point is the standard, but nonetheless true, mantra that we need to further develop methods to improve our ability to measure microbial activity and interactions. The second strategy, we suggest, is that more studies should be conducted to ask similar questions across a variety of ecosystems. This strategy keeps the research focus on ecosystem level problems and helps identify important similarities and difference among systems that enhance the development of theory. A third need is for careful observations of long time series of microbial processes in selected ecosystems. The value of long-term studies in ecosystem science has been amply demonstrated (e.g., [47]) and will be no less important in illuminating microbial phenomena. Finally, we suggest the need for studies of model systems at several scales, ranging from the laboratory flask through large enclosures to whole ecosystems. Model systems provide excellent tools for examining processes, analyzing budgets, and conducting perturbation experiments. We emphasize that such model systems include ecosystems because perturbations of entire ecosystems have consistently provided insights to the most significant processes determining system behavior [23].

While we believe these research strategies will contribute strongly to advancing the study of microbial food webs, the most important need is, as always, for new ideas. New ideas often develop from evaluation and synthesis of existing information. Pomeroy's 1974 synthesis provided the spark for twenty years of research on microbial food webs. The regulation of bacterial dynamics and processes remains an important focus where new ideas, methodological advances, and synthetic evaluations are required to integrate microbial food web and ecosystem studies.

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