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Dominance of bacterial metabolism in oligotrophic relative to eutrophic waters

Abstract—Heterotrophic bacteria are a key component driving biogeochemical processes in aquatic ecosystems. In 1998, we examined the role of heterotrophic bacteria by quantifying plankton biomass and bacterial and planktonic respiration across a trophic gradient in several small Minnesota lakes as well as Lake Superior. The contribution of bacteria (<1-μm fraction) to total planktonic respiration ranged from ~10 to 90%, with the highest contribution occurring in the most oligotrophic waters. The bacterial size fraction constituted a substantial reservoir of planktonic carbon, nitrogen, and phosphorus (14–58%, 10–49%, and 14–48%, respectively), being higher in oligotrophic than in eutrophic waters. However, we saw no clear evidence for the selective enrichment of either nitrogen or phosphorus in the bacteria size fraction relative to total plankton. Carbon : nitrogen and carbon : phosphorus ratios in both the total particulate matter and <1-μm fractions were similar and above Redfield values in oligotrophic waters, but approached them in eutrophic waters. Carbon-based bacterial growth efficiencies (BGE) were variable (4–40%) but were lowest in oligotrophic systems and increased in eutrophic systems. BGE varied negatively with carbon : nitrogen : phosphorus ratios, suggesting increased maintenance costs in low-nutrient waters. In oligotrophic waters most of the organic matter is dissolved, supporting a predominantly microbial food web, whereas in eutrophic waters there is an increased abundance of particulate organic matter supporting a food web consisting of larger autotrophs and phagotrophic heterotrophs.

Autotrophs and heterotrophs constitute two of the most

Table 1. Chlorophyll (μg L^{-1}), dissolved organic carbon (DOC), planktonic respiration (PR), bacterial respiration (BR), bacterial contribution to planktonic respiration (BR/PR), bacterial production (BP), and bacterial growth efficiency [BGE = BP/(BP + BR)] for the different water bodies.

Water body	Chlorophyll (μg L^{-1})	DOC (μM)	PR (μM O_2 h^{-1})	BR (μM O_2 h^{-1})	BR/PR (%)	BP (μM C h^{-1})	BGE (%)
Lake Superior September 1998	0.57	110	0.034	0.031	91	0.002	4.8
Lake Superior July 1998	0.73	119	0.023	0.019	82	0.004	13.1
Lake Christmas	1.37	551	0.225	0.221	98	0.039	15.1
Lake Turtle	2.47	600	0.269	0.067	25	0.015	18.1
Lake Minnetonka	3.35	712	0.398	0.120	30	0.042	25.8
Lake Owasso	4.25	695	0.308	0.113	36	0.045	28.5
Lake Round	8.74	537	0.750	0.195	26	0.024	10.9
Lake Josephine	11.57	545	1.083	0.305	28	0.032	9.5
Lake Johanna	20.20	584	1.196	0.147	12	0.038	20.7
Lake Eagle	25.16	643	0.723	0.104	14	0.031	23.2
Lake Medicine	40.49	615	0.849	0.082	9	0.052	38.9
Lake Mitchell	52.70	784	1.742	0.169	9	0.068	28.7

fundamental and complementary functional units in ecosystems. Therefore, understanding the nature of autoheterotrophic processes is central to the study of biogeochemical cycles. The general tendency for biomass domination by heterotrophs in oligotrophic systems and by autotrophs in eutrophic systems is supported by previous observations (Dortch and Packard 1989; Gasol et al. 1997). Because heterotrophic bacteria are now recognized as major consumers of organic matter in natural waters (Sherr and Sherr 1996; Azam 1998), it is necessary to understand the relationship between trophic state and bacterial metabolism.

The bacteria to phytoplankton biomass ratio is greater in oligotrophic waters than in eutrophic waters because bacterial biomass increases somewhat more slowly than phytoplankton biomass along a trophic gradient (Cole et al. 1988; Sanders et al. 1992; Simon et al. 1992). In oligotrophic systems, bacterial production plus respiration can approach that of primary production, decreasing in relative significance in eutrophic systems (Williams 1984; del Giorgio et al. 1997; Cole 1999). Consequently, the relative biomass, as well as the magnitude of carbon flux through bacteria, is expected to be larger in oligotrophic than in eutrophic water bodies (Biddanda et al. 1994).

In this study, we have examined the emerging hypothesis that the contribution of heterotrophic bacteria to total planktonic biomass and metabolic activity is high in oligotrophic systems and decreases along an increasing productivity gradient (Biddanda et al. 1994; del Giorgio et al. 1997). In order to meet this objective, we measured the biomass and activity of autotrophic and heterotrophic plankton in several freshwater systems characterized by a wide range of biomass and productivity.

Materials and methods—During the summer of 1998, we quantified plankton biomass and measured bacterial growth and respiration in 10 Minnesota kettle lakes (0.2–56.7 km^2 surface area; www.dnr.state.mn.us/) and Lake Superior (82,350 km^2 surface area). Lake Superior samples were taken on two R/V *Blue Heron* cruises during July and September of 1998 (maximum depth ~200 m, located on the western arm of the lake at ~47°00′N and 91°30′W). Ten Minnesota kettle lakes located in the Minneapolis–Saint Paul metropolitan area were sampled between June and August 1998. The systems sampled represented a very broad trophic gradient with ~100-fold chlorophyll *a* values that varied from 0.5 (Lake Superior) to 53 μg L^{-1} (Lake Mitchell, Minnesota; Table 1). Along this trophic gradient, dissolved inorganic nutrient concentrations were typically low in low-chlorophyll environments and high in high-chlorophyll environments (0.01–2.61 μM phosphate and 0.6–76.9 μM ammonium). We used chlorophyll values as an index of planktonic primary productivity and autotrophic biomass because it is a commonly used index of aquatic productivity (Falkowski et al. 1998). However, the patterns observed and described here would still be prevalent if we had used total phosphorus, another commonly used indicator of trophic state.

In the present study, total community (or planktonic) and bacterial respiration were measured by following changes in dissolved oxygen in sealed BOD bottles during dark incubations of unfiltered and <1-μm water, respectively (Biddanda et al. 1994). The <1-μm water was generated by gently pumping water through a polycarbonate Nuclepore cartridge filter (1-μm pore size). Dissolved oxygen measurements were made with a Mettler DL 21 titrator by automated Winkler titrations based on potentiometric end-point detection (Graneli and Graneli 1991). Measurement of respiration as the decrease in dissolved oxygen concentrations in a given water mass can be directly related to the oxidation of organic matter in aerobic systems (Williams 1984; Hopkinson et al. 1989).

The possibility of artifacts arising from size fractionation of water samples is always a concern. However, a careful study of the results from unfiltered and <1-μm samples indicated no discernable differences in either bacterial abundance or productivity at the beginning of the experiments (time zero). There was particular concern that in waters of high productivity containing filamentous algae and cyanobacteria, the effective filter pore size would be reduced through filter clogging, thereby retaining bacteria. However, our monitoring of bacterial abundance in unfiltered and <1-μm size fraction revealed that >95% of the heterotrophic

bacteria present in the different water samples consistently passed through the filter. Protozoa and autotrophic picoplankton were not usually found in the filtrate. We filtered no more than 20 liters of a given sample through a filter cartridge at a time and took care to back flush and clean the filters with Nanopure water between samples.

For the enumeration of heterotrophic bacteria, a 5-ml aliquot of each water sample was preserved with 2% (final concentration) of 0.2-μm filtered formaldehyde solution. At the end of each day, 1-ml subsamples were acridine orange-stained, filtered onto 0.2-μm black Poretics filters, mounted on slides, and the slides kept frozen until observation by epifluorescence microscopy (Hobbie et al. 1977). Between 20 and 40 fields of view and a minimum of 300 cells were examined for every sample.

Bacterial production was assessed by the dilution culture growth method (Ammerman et al. 1984). Briefly, the method consisted of following the increase in bacterial abundance in a mixture of nine parts $<$0.2-μm water plus one part $<$1.0-μm water in dark incubations over a 24–48 h time period. The slope of a regression of bacterial abundance versus time gives the growth rate. Growth rates obtained as number of cells per unit time were converted to bacterial carbon production rate by using the standard conversion factor of 20 fg C per cell (Lee and Fuhrman 1987). Empirical relationships between [^{3}H] thymidine or [^{3}H] leucine incorporation and increase in bacterial abundance are routinely assessed using dilution culture assays, and are typically linear (Kirchman and Ducklow 1993).

Bacterial growth efficiency (BGE) was estimated as the ratio of production (growth) to production (growth) plus respiration. Net carbon production was estimated from rates of cell increase in dilution cultures. The amount of carbon respired was estimated from oxygen consumption in the $<$1-μm size fraction, assuming a respiratory quotient of one based on the respiration of organic matter having Redfield stoichiometry (Redfield et al. 1963). Bacterial carbon demand (BCD) or carbon flux through the bacteria is equal to gross production or growth plus respiration.

Samples for dissolved organic carbon (DOC) analysis were passed through precombusted Whatman GF/F glass fiber filters (4 h at 450°C) under low vacuum pressure ($<$10 cm of Hg). The filtrate was collected directly in precombusted glass vials (4 h at 550°C), sealed with Teflon-lined caps, and stored frozen until analysis. DOC concentrations were determined by high temperature (680°C) oxidation with a Shimadzu TOC 5000 carbon analyzer (Benner and Strom 1993).

Water samples were filtered onto GF/F filters, and the filters were kept frozen in the dark until analyses for chlorophyll. Pigments were extracted in 90% acetone and fluorometrically analyzed against chlorophyll *a* standards in a Turner Designs 10-AU Fluorometer (Parsons et al. 1984). Particulate matter from unfiltered and $<$1-μm filtered water samples retained on precombusted GF/F glass fiber filters were analyzed for particulate organic carbon (POC) and particulate organic nitrogen (PON) by flash combustion in a Perkin Elmer 2400 CHN elemental analyzer. Particulate organic phosphorus (POP) retained on precombusted GF/F filters was subjected to acid persulfate digestion, and subsequently the released soluble reactive P was analyzed by standard wet chemistry (Parsons et al. 1984).

Herein, we have generally refrained from drawing linear regression lines, but r^2 and p values are reported. Further, we have not attempted to linearize data distributions by means of log–log plots so that the reader may be able to appreciate the actual distribution of the data and the relationships therein including that of the outliers.

Results and discussion—Dissolved organic carbon concentrations and rates of planktonic respiration, bacterial respiration, and bacterial production quantitatively increased along an increasing chlorophyll-productivity gradient (Table 1). Dissolved organic carbon concentration increased an order of magnitude across this gradient. In general, as chlorophyll levels increased over nearly three orders of magnitude, planktonic respiration increased by two orders of magnitude and bacterial respiration increased by only one order of magnitude. The steep decline in the relative contribution of bacteria to planktonic respiration across this productivity gradient suggests that bacteria play a relatively major role in organic matter mineralization in low-chlorophyll environments but their relative importance decreases in high-chlorophyll environments.

Whereas chlorophyll increased three orders of magnitude along this large trophic gradient (Table 1), both bacterial abundance (Fig. 1a) and bacterial production (Fig. 1b) only increased by tenfold, supporting the idea that the relative importance of both bacterial biomass and production to total planktonic biomass and production decreases with increasing trophic state. More (about tenfold higher) bacterial abundance and bacterial production per unit chlorophyll prevailed in oligotrophic waters relative to eutrophic waters (Fig. 1a,b). Such a scenario, where more oligotrophic systems have a higher bacteria : phytoplankton biomass and activity, is in agreement with earlier observations (Cole et al. 1988; Simon et al. 1992; del Giorgio et al. 1997). The underlying cause of this relationship is unclear, but two possible explanations are that bacteria are less relatively abundant at the eutrophic end of the gradient because they are selectively grazed by bacterivores (Fuhrman and Noble 1995), or, alternatively, that bacterial biomass is relatively more abundant in oligotrophic systems because of their ability to acquire nutrients at low ambient concentrations (Sanders et al. 1992). Consequently, along a trophic gradient, both substrate control and bacterivory may be expected to interact to varying extents.

Phytoplankton biomass constitutes the largest carbon pool in many eutrophic environments (Simon et al. 1992), whereas bacterial carbon equals or exceeds phytoplankton carbon in oligotrophic waters (Fuhrman et al. 1989; Simon et al 1992). In Florida Bay, a similar relationship was observed for bacteria : phytoplankton biomass ratios along gradients of increasing particulate phosphorus and productivity, suggesting bacterial dominance at low nutrient concentrations and phytoplankton dominance at high nutrient concentrations (Cotner et al. 2000). Other studies (Simon et al. 1992; Gasol et al. 1997) have also documented that oligotrophic waters have a relatively high heterotrophic biomass compared to

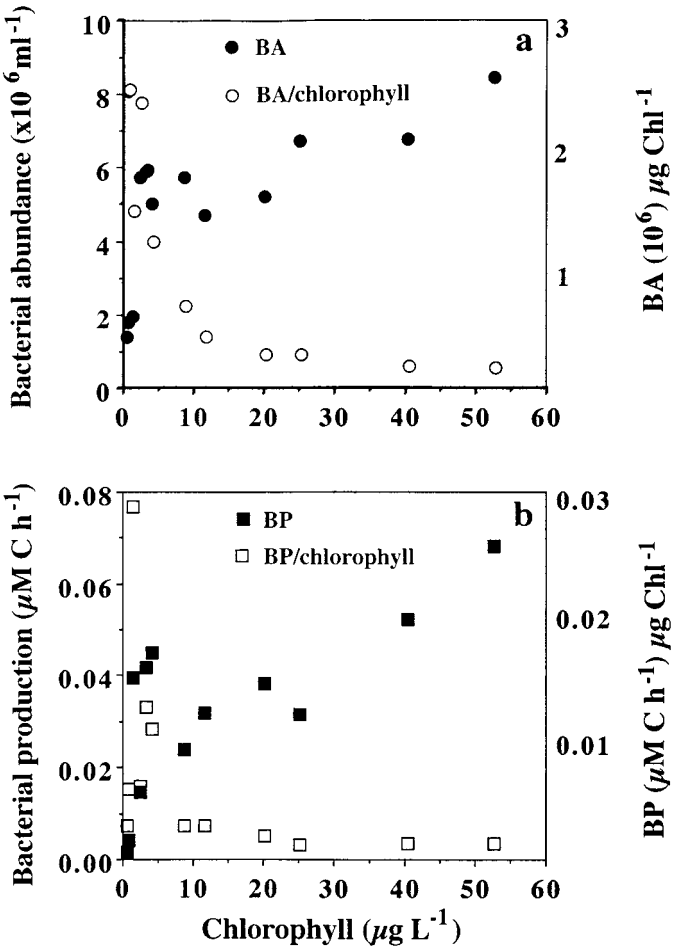

Fig. 1. Relationship of (a) bacterial abundance (BA) and BA normalized to chlorophyll ($n = 12$, $r^2 = 0.557$, $p < 0.01$ and $n = 12$, $r^2 = 0.581$, $p < 0.01$, respectively), and (b) bacterial production (BP) and BP normalized to chlorophyll ($n = 12$, $r^2 = 0.527$, $p < 0.01$ and $n = 12$, $r^2 = 0.227$, $p < 0.1$, respectively) along a chlorophyll gradient.

autotrophs, whereas eutrophic waters have relatively low heterotrophic biomass compared to autotrophs.

Oligotrophic Lake Superior was characterized by the lowest planktonic respiration and bacterial respiration rates in comparison to the mesotrophic and eutrophic Minnesota kettle lakes (Table 1 and Fig. 2a). The range of values measured for bacterial respiration in the present study (~0.02–0.4 μM O_2 h^{-1}) was well within the range of values reported in a recent review of the limnetic and marine literature (~0.01–1.0 μM O_2 h^{-1}; del Giorgio et al. 1997). In the present study, the regression for planktonic respiration versus chlorophyll was statistically significant ($n = 15$, $r^2 = 0.89$, $p < 0.001$). Because planktonic respiration is the closest metabolic counterpart to planktonic primary production (Hopkinson et al. 1989; Williams 1984) such a positive relationship between the two ecosystem parameters is expected—except where nonplanktonic or allochthonous inputs may fuel much of the carbon flux. On the other hand, the relationship between bacterial respiration and chlorophyll did not yield a significant linear regression across the entire trophic gradient.

It is notable that at higher chlorophyll levels, bacterial respiration did not increase at the same rate as planktonic respiration (Fig. 2a). This suggests that as one moves up the productivity gradient, bacterial respiration attains a maximum and then decreases/levels off, whereas the contribution of the remaining plankton (>1 μm) continues to increase. Earlier studies (Biddanda et al. 1994; del Giorgio et al. 1997), have also documented that the contribution of bacteria to plankton respiration is large (approaching or exceeding phytoplankton production) in oligotrophic waters but was relatively small in eutrophic waters. Experimental work from Danish lakes also supports this finding: when phytoplankton biomass and production were increased by nutrient additions, the contribution of bacterial respiration to planktonic respiration declined from ~50% to ~20% (Schwaerter et al. 1988). Whereas eutrophic systems tend to be net autotrophic (del Giorgio et al. 1997), net system heterotrophy has been documented at times (usually in summer) in oligotrophic environments (Biddanda and Benner 1997*a*; Cole 1999).

At low chlorophyll levels (<15 μg L^{-1}), however, both planktonic respiration and bacterial respiration varied positively with chlorophyll (Fig. 2b; $n = 8$, $r^2 = 0.96$, $p < 0.001$ and $n = 8$, $r^2 = 0.62$, $p < 0.05$, respectively). In this region, both bacteria and phytoplankton may be limited by the same inorganic substrates (phosphorus or nitrogen; Currie 1990; Cotner and Wetzel 1992) or, alternatively, bacteria may be responding to increasing phytoplankton production and release of dissolved organic substrates (Biddanda and Benner 1997*b*). Low-chlorophyll waters supported approximately tenfold higher bacterial biomass, as well as production per unit chlorophyll in comparison to eutrophic waters (Fig. 1a,b), suggesting substrate availability likely controls both biomass and production under oligotrophic conditions. Within this productivity range, planktonic respiration increased at four times the rate of bacterial respiration (Fig. 2b), suggesting that grazer biomass was accumulating faster than bacterial biomass, thereby leading to greater production of larger sized particles. In high-chlorophyll mesotrophic–eutrophic systems, bacterivores are likely to be able to exert greater control over bacterial abundance (Sanders et al. 1992) and consequently mask the effects of enhanced substrate levels and productivity on bacterial respiration. These observations of metabolic activity are also consistent with the prevailing hypotheses that bacterial ecology is largely controlled by substrate availability (bottom-up control) in low-productivity waters and grazing activity (top-down control) in high-productivity waters (Sanders et al. 1992).

There was a negative relationship between planktonic respiration and bacterial respiration per unit chlorophyll and chlorophyll concentration (Fig. 2c), suggesting that the fate of a high proportion of organic matter produced in oligotrophic waters is respiration—consistent with the low fisheries in such systems (Sheldon et al. 1977). Because low-productivity waters tend to support disproportionately high primary production-specific respiratory activity, these systems may approach net heterotrophy (del Giorgio et al. 1997). These observations suggest that a higher proportion of primary production would be mineralized (and therefore recycled in situ) in oligotrophic waters relative to primary production in eu-

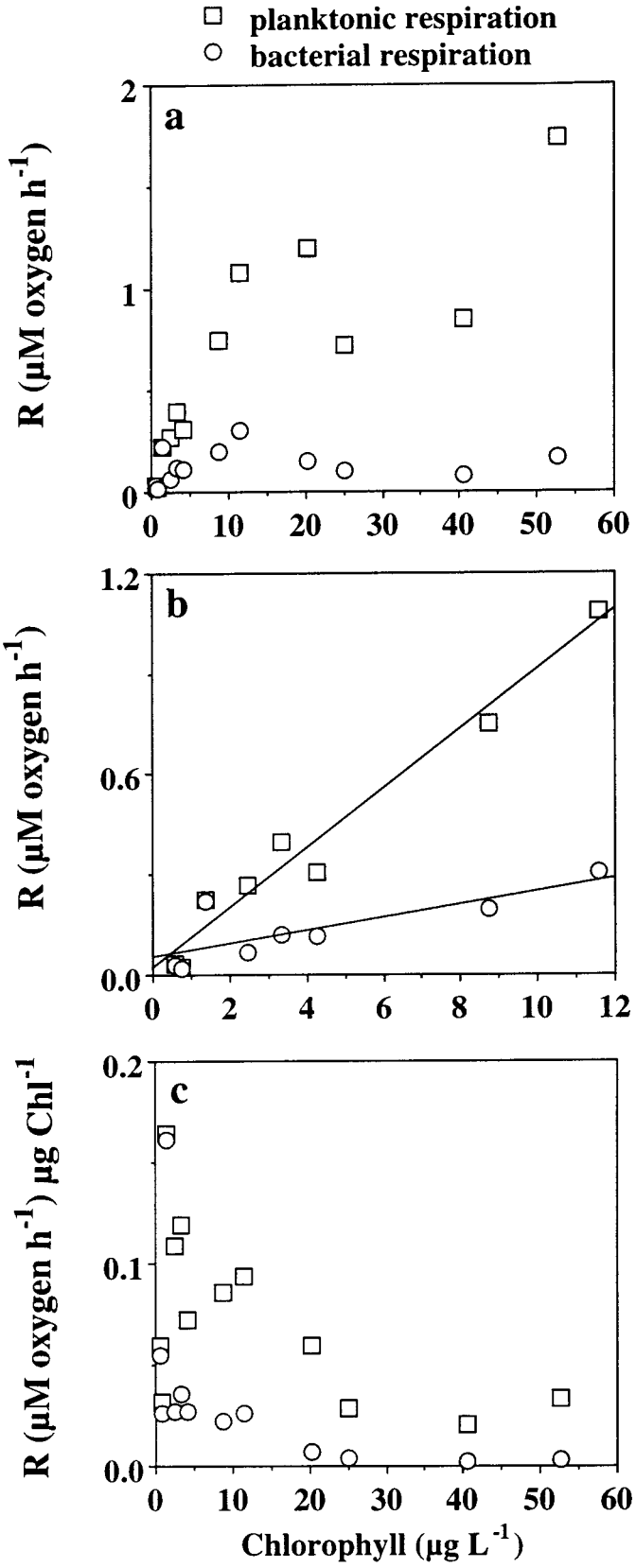

Fig. 2. Relationship of (a) planktonic respiration and bacterial respiration ($n = 12$, $r^2 = 0.697$, $p < 0.001$ and $n = 12$, $r^2 = 0.015$, $p > 0.2$, respectively), (b) planktonic respiration and bacterial respiration in only waters having <15 μg chlorophyll L^{-1} ($n = 8$, $r^2 = 0.966$, $p < 0.001$ and $n = 8$, $r^2 = 0.617$, $p < 0.05$, respectively) and (c) planktonic respiration and bacterial respiration normalized to chlorophyll ($n = 12$, $r^2 = 0.363$, $p < 0.05$ and $n = 12$, $r^2 = 0.251$, $p < 0.1$, respectively) along a chlorophyll gradient.

trophic waters and seem to contradict some recent observations of uniform mass-normalized regeneration rates across a trophic gradient (Hudson et al. 1999). In a review of the literature on respiration in marine environments, Williams (1984) observed that bacterial respiration was a larger proportion of plankton respiration in oligotrophic oceanic waters in comparison to productive nearshore waters. Our published work for Gulf of Mexico (Biddanda et al. 1994) and unpublished results from Lake Michigan and Lake Superior (Biddanda and Cotner pers. comm.) also indicate that bacterial respiration is a major fate of primary production in oligotrophic waters.

The observation that the importance of heterotrophic bacteria to planktonic respiration is highest in oligotrophic waters gains further support from the data in the present study showing that bacterial respiration declines as a fraction of plankton respiration along the trophic gradient (Fig. 3a). Typically, the most oligotrophic water bodies (Lake Superior and Lake Christmas) had a very high bacterial respiration component (82–98% of planktonic respiration), indicating that perhaps most of the primary production in low-productivity environments is respired by bacteria. Mesotrophic and eutrophic waters were characterized by a much smaller bacterial respiration component in comparison to plankton respiration, leaving the remaining production for other heterotrophs in the food web or for export out of the system.

Knowledge of bacterial growth efficiency (BGE) is critical for estimating the role of bacteria in carbon flow and to know how much of the primary production is processed by bacteria (Biddanda et al. 1994; del Giorgio and Cole 1998). In the present study, measured BGE was positively correlated with chlorophyll (Fig. 3b) and varied between 5 and 39%. These values for BGE fall among the range of values most commonly reported for aquatic ecosystems (del Giorgio and Cole 1998). Similar increases in BGE as one moves from oligotrophic to eutrophic environments have been recorded by earlier studies of both marine and limnetic systems (Hopkinson et al. 1989; del Giorgio et al. 1997). Low BGE and high relative bacterial biomass provide an explanation for the high proportional bacterial respiration observed in oligotrophic systems and support previous observations that bacterial carbon demand can at times exceed phytoplankton productivity in oligotrophic systems (Scavia et al. 1986; del Giorgio et al. 1997).

Several studies have noted that BGE is widely variable under both experimental (Goldman et al. 1987; Biddanda et al. 1994) and natural conditions (Hopkinson et al. 1989; Biddanda et al. 1994). However, Goldman and Dennett (2000) have recently reported somewhat constant and high BGE (~50%) in growth cultures of marine bacteria. Although it is unclear why BGEs are so high and presumably invariant in their study (Goldman and Dennet 2000), it is possible that

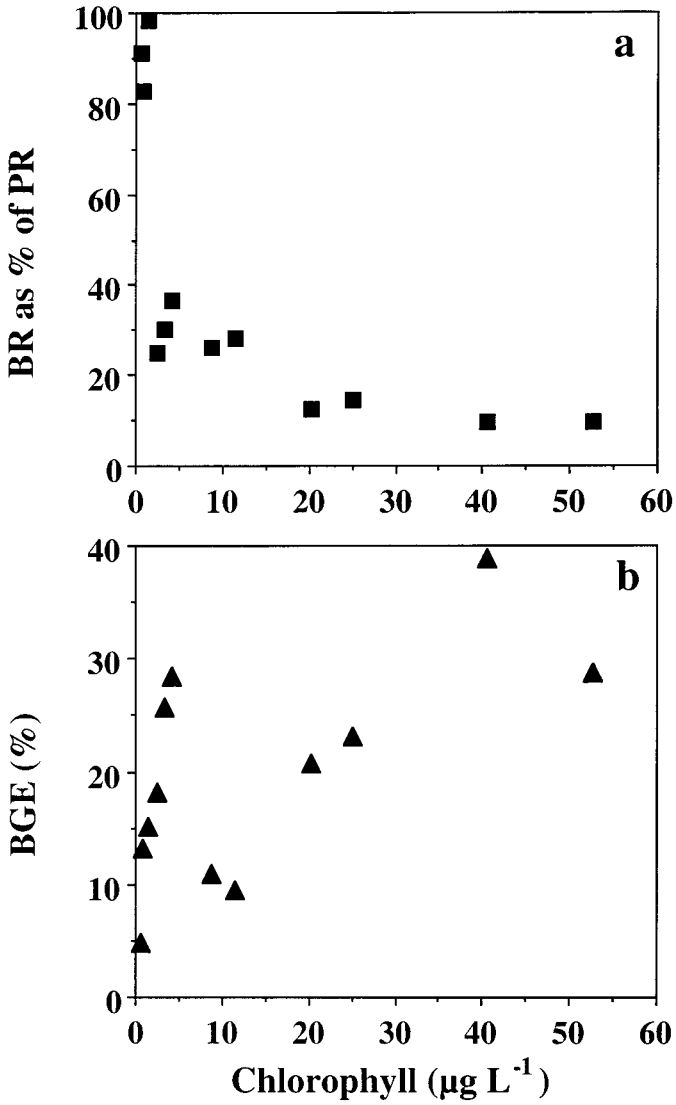

Fig. 3. Relationship of (a) bacterial respiration (BR) as a percent of planktonic respiration (PR) to chlorophyll concentration ($n = 12$, $r^2 = 0.420$, $p < 0.05$) and (b) bacterial growth efficiency (BGE; $n = 12$, $r^2 = 0.414$, $p < 0.05$) to chlorophyll concentration.

their culture conditions mimicked the eutrophic natural systems of our study in terms of substrate availability. Ducklow and Carlson (1992) observed that bacterial production constituted roughly a similar fraction of primary production in systems ranging from oligotrophic to eutrophic environments even though the energetic costs of bacterial growth appeared to be higher in oligotrophic conditions. In order to achieve the same ratio of bacterial production to primary production, indeed greater amounts of primary production must pass through the bacterioplankton in oligotrophic waters (low BGE) than in eutrophic waters (high BGE). Results of the present study where BGE varied from ~4 to 40% along a gradient of increasing productivity show this trend in BGE variability is linked to system primary productivity.

There was much scatter in BGE at low chlorophyll levels—perhaps due to bacterial nutrient or organic carbon limitation and/or competition with phytoplankton for nutrients (Currie 1990; Cotner et al. 2000). The increased C : N and C : P ratios found in the total seston and <1-μm fractions in low-chlorophyll waters (Fig. 4a,b) were consistent with the idea that inorganic nutrients were more likely to limit bacterial production in low-productivity systems. Furthermore, communities are likely to be limited by several different nutrients in oligotrophic systems, i.e., the paradox of enrichment (Rosenzweig 1971). Variability in the severity and extent of nutrient limitation, especially in oligotrophic systems, could have important effects on BGE.

Evidence from experiments and models suggests that BGE decreased as the C : N of substrates increased, whereas BGE increased as the C : N of substrates decreased (Goldman et al. 1987; Hopkinson et al. 1989). Results from both Canadian lakes (Cimbleris and Kalff 1998) and the present study (Figs. 1, 2, 3, and 4), demonstrate that the cell-specific respiration of bacteria was elevated in high C : N or oligotrophic waters and reduced in low C : N or eutrophic waters (i.e., respiration per bacterium increased as the C : N ratio of the substrate increased). Indeed, estimates from our study suggest that bacteria in oligotrophic waters were characterized by up to tenfold higher per cell respiration rate compared to their eutrophic counterparts. Seston C : N and C : P ratios were highest in oligotrophic systems (Fig. 4a,b); presumably these particles are the source of substrates for bacterial metabolism. Therefore, such changes in the seston nutrient composition may be expected to be reflected in the BGE.

Particulate carbon (C), nitrogen (N), and phosphorus (P) in the total and <1-μm fractions increased in absolute quantities from oligotrophic to eutrophic waters, but the quantities present in the <1-μm fraction did not increase to the same extent as the total particulate pool along this increasing productivity gradient (Table 2). Consequently, the C, N, and P present in the <1-μm fraction was a much larger proportion of total seston C, N, and P in oligotrophic waters (30–50%) than in eutrophic waters (10–25%; Fig. 4c), similar to our observations on size-fractionated respiration. Both C : N and C : P ratios in the total as well as the <1-μm fractions were above Redfield ratio (106C : 16N : 1P by atoms, Redfield et al. 1963) in oligotrophic–mesotrophic conditions and approached the Redfield ratio in mesotrophic–eutrophic waters. The C : N and C : P ratios of total and <1-μm fractions showed a negative relationship with chlorophyll, indicating that there was some selective enrichment of N and P taking place in the plankton along the productivity gradient (Fig. 4a,b). However, the C, N, and P present in the <1-μm fraction as a percent of that in the total plankton were similar across the entire productivity gradient, suggesting there was no selective enrichment of these key bioelements in the bacterial size fraction (Fig. 4c).

It has been shown that bacteria, because of their high nucleic acid content, are enriched in N and P relative to C (Goldman et al. 1987). Existing data from single cell and dilution cultures on bacterial ratios of C : P (Vadstein et al. 1988) and C : N (Lee and Fuhrman 1987) of bacteria suggest a high N and P content compared to algae (Lee 1993). However, a review of the literature on stoichiometry and productivity reported aquatic bacterial C : P ratios ranging from 25 to 300 that, although more constrained than that of algae,

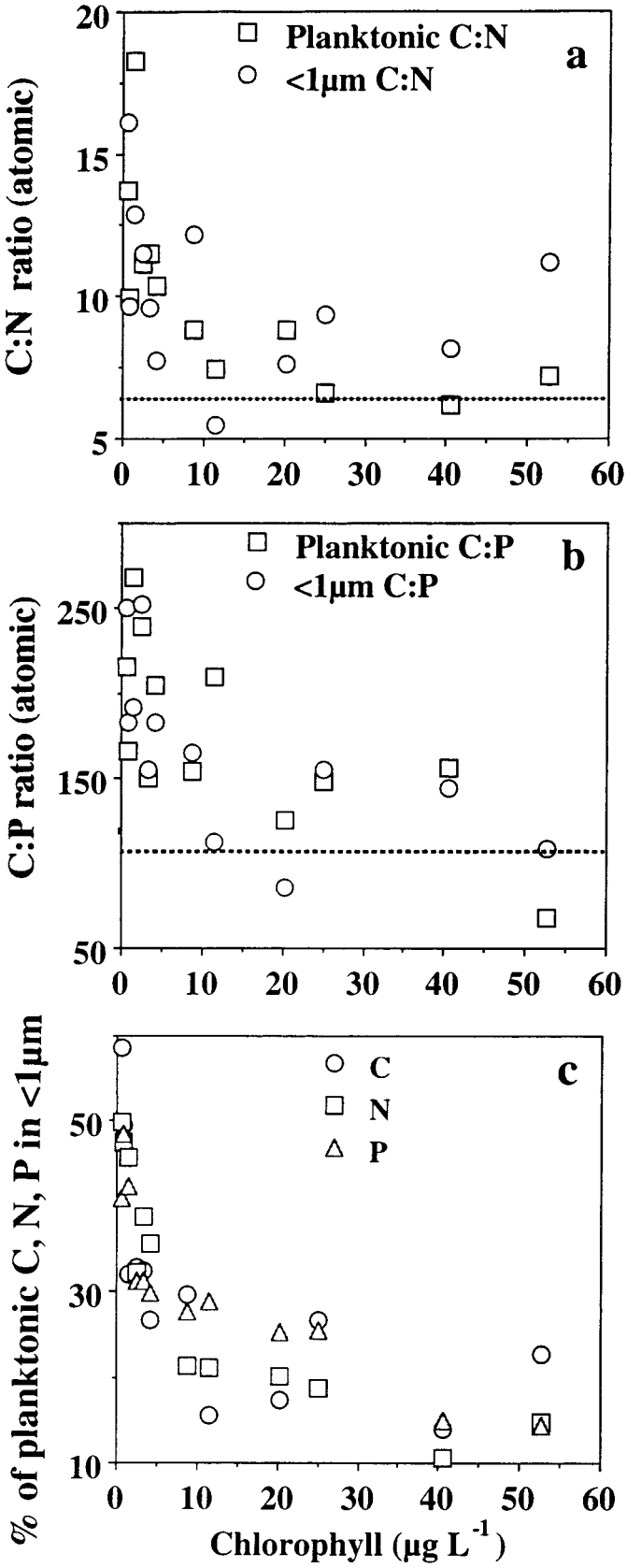

Fig. 4. Relationship of (a) C : N ratio of total plankton and <1-μm size fraction ($n = 12$, $r^2 = 0.438$, $p < 0.05$ and $n = 12$, $r^2 = 0.057$, $p > 0.2$, respectively; dotted line represents Redfield ratio of C : N = 6.6), (b) C : P ratio of total plankton and <1-μm size fraction ($n = 12$, $r^2 = 0.546$, $p < 0.708$ and $n = 12$, $r^2 = 0.382$, $p < 0.05$, respectively; dotted line represents Redfield ratio of C : P = 106) and (c) percentage of planktonic carbon (C), nitrogen (N), and phosphorus (P) present in the <1-μm size fraction ($n = 12$, $r^2 = 0.349$, $p < 0.05$; $n = 12$, $r^2 = 0.660$, $p < 0.01$; and $n = 12$, $r^2 = 0.731$, $p < 0.001$, respectively) to chlorophyll concentration.

clearly overlap with all other plankton groups as well as seston (Sterner et al. 1998). Our study did not distinguish between bacteria and other particulate matter present in the <1-μm fraction and assumed that most of the particulate matter in this fraction was heterotrophic bacteria. Epifluorescence microscopic examinations confirmed that the bulk of the microorganisms present in this <1-μm fraction were heterotrophic bacteria (>95%).

Some recent marine studies have shown significant sorption of DOC onto GF/F filters (Karl et al. 1998). This would compromise our observations only if DON and DOP are sorbed differently than DOC. Further, the presence of detritus would complicate our interpretations if there were selectively more of it in the <1-μm size fraction. The fact that C : N and C : P ratios of this size fraction were essentially the same as bulk seston measurements suggests that this was not the case. The size-continuum theory of organic matter distribution in the ocean states that the smallest size fractions constitute the largest pools (Benner et al. 1997). The abundance of nonliving detrital submicron particles is estimated to be an order of magnitude higher than that of bacterial abundance in the ocean (Koike et al. 1990). It is possible that a large pool of detrital submicron particles that is N and P deplete could have diluted out the N and P replete signals from bacteria. The exact composition of these hard-to-characterize, primarily organic submicron particles (Koike et al. 1990) is not well known. However, POC : PON and POC : POP plots showed no evidence for the presence of enhanced detrital carbon in the <1-μm size fraction relative to total seston in our study (data not shown).

In most natural water bodies, the size of the DOC pool is approximately 10 times that of POC (Wetzel 1984). Although the dominance of DOM pool over POM is common knowledge, the consequences are still not fully appreciated (Williams 1995). For example, ecosystems with different productivities may be characterized by distinct dissolved : particulate resource ratios. Oligotrophic lakes and oceans are characterized by higher DOM : POM ratios compared to eutrophic systems. DOM-dominated oligotrophic lakes and oceans are likely to support a predominantly microbial food web (Azam 1998; Cotner and Biddanda pers. comm.), whereas POM-dominated eutrophic water bodies are likely to sustain a predominantly grazer food chain (Wetzel 1984). Our study deals with planktonic processes only. In shallow productive waters where particle flux to the sediment is likely to be high, the contribution of benthic respiration to system metabolism may be considerable. Because we have limited our considerations in the present study to the comparison of processes within the pelagial, any variable

Table 2. Particulate carbon, nitrogen, and phosphorus concentrations (μM) in whole water (total) and $<1\mu$m fractions.

Water body	Total C	<1 μm C	Total N	<1 μm N	Total P	<1 μm P
Lake Superior September 1998	17.01	10.0	1.24	0.62	0.08	0.04
Lake Superior July 1998	7.98	3.66	0.80	0.38	0.05	0.02
Lake Christmas	53.86	17.25	2.95	1.34	0.20	0.09
Lake Turtle	107.92	35.36	9.66	3.07	0.45	0.14
Lake Minnetonka	57.21	18.52	4.97	1.93	0.38	0.12
Lake Owasso	98.09	26.10	9.44	3.37	0.48	0.14
Lake Round	143.00	42.30	16.19	3.47	0.93	0.25
Lake Josephine	126.93	19.66	17.07	3.60	0.61	0.17
Lake Johanna	167.08	29.05	18.95	3.80	1.33	0.34
Lake Eagle	128.23	34.14	19.32	3.64	0.86	0.22
Lake Medicine	226.40	31.80	36.65	3.89	1.45	0.22
Lake Mitchell	203.80	45.41	28.18	4.14	3.00	0.42

significance of benthic metabolism is not expected to confound our interpretations.

In the present study, the ratio of DOC to POC decreased as expected along the trophic gradient (Fig. 5). The DOM: POM ratio was always greater than one in all the environments studied. Oligotrophic waters contained 5–15 times more DOC than POC, whereas eutrophic waters contained only 2–5 times more DOC than POC. These results provide support for the idea that dissolved organic resources are high in low-productivity environments and particulate resources increase in high productivity environments. Consequently, the different nutrient fields prevailing in oligotrophic and eutrophic waters may be expected to support different types of food webs. Heterotrophic bacteria and autotrophic phytoplankton are the primary osmotrophs in aquatic ecosystems. Therefore, the predominance of dissolved nutrients in oligotrophic systems may select for bacteria as the dominant heterotrophs over phagotrophs (Cotner and Biddanda pers. comm.).

In oligotrophic waters, a microbial food web consisting of autotrophic picoplankton and heterotrophic bacteria and protozoa dominates the flux of carbon (Hagstrom et al. 1988; Fahnenstiel et al. 1998). Most of the biomass in oligotrophic waters may be composed of autotrophic and heterotrophic prokaryotes, whereas the prokaryotes gradually give way to eukaryote dominance in eutrophic systems (Karl 1999). It is not well understood why heterotrophic bacterial activity does not keep up with increasing primary production as system productivity increases, although concurrent increases in BGE may be part of this explanation. Presumably, bacterial growth and respiration can be limited by nitrogen, phosphorus, or other nutrients in the environment when organic carbon is plentiful (Cotner and Wetzel 1992; Pomeroy et al. 1995), and losses from bacterivory by protozoa and viruses may be substantial at high bacterial abundances (Fuhrman and Noble 1995; Sanders et al. 1992). In eutrophic environments, larger eukaryotic algae respond quickly to allochthonous inputs of nutrients, increasing the contribution of larger organisms (large phytoplankton and herbivorous zooplankton; Peinert et al. 1989) to plankton respiration. Thus, increased system productivity may not only dictate a shift in organism size from microorganisms to larger organisms, but also select for eukaryotes over prokaryotes.

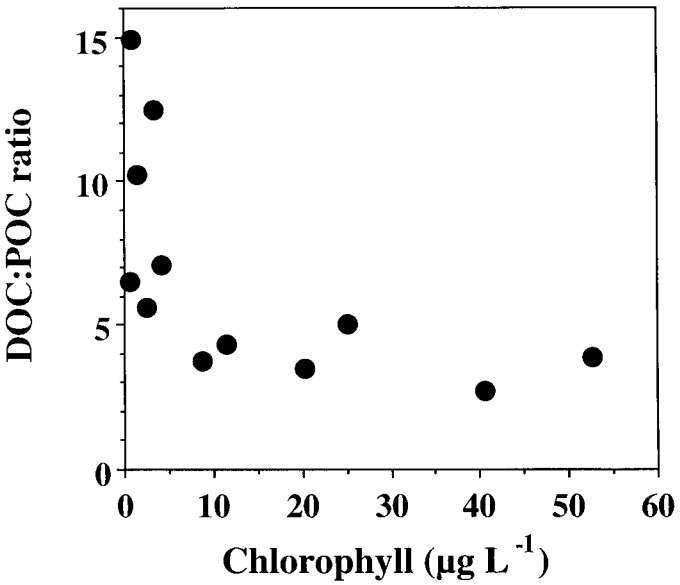

Fig. 5. Relationship of DOC: POC ratio ($n = 12$, $r^2 = 0.35$, $p < 0.05$) along a chlorophyll gradient.

Based on the results of the present study, we propose a conceptual picture of the relationship between autotrophic and heterotrophic processes across the productivity gradient (Fig. 6). Along a gradient of increasing aquatic primary productivity, dissolved nutrients, bacterial C, N, P, and respiration decrease, whereas particulate nutrients, nonbacterial C, N, P, and respiration increase as a proportion of the total. The causes of these phenomena are not as clear to us as are the consequences. Productivity, allochthonous inputs, variable nutrient limitation, and bacterivory appear to be important regulators of bacterial ecology along this gradient. The ecological consequences of such a trend are several: oligotrophic lake and ocean waters are dominated by a nonsinking, osmotrophic, prokaryotic, microbial biomass and activity where autrophic production and heterotrophic respiration tend to be in balance (Williams 1998). On the other hand, eutrophic lakes and nearshore marine environments tend to be dominated by larger organisms (eukaryotic autotrophs and phagotrophic heterotrophs) with an increased potential for export production (Peinert et al. 1989).

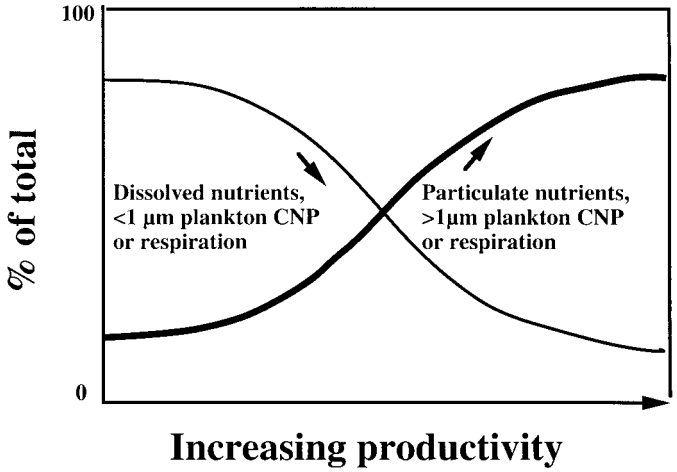

Fig. 6. Conceptual diagram of the relative importance of small and large organisms to planktonic biomass and metabolism across a gradient of primary productivity in natural waters. Autotrophic and heterotrophic processes are in near balance in low-productivity environments that are relatively dominated by dissolved nutrients and microorganisms (there are little or no losses from such systems because microbial respiration is comparable to primary production). Autotrophic and heterotrophic processes are not in balance in high primary productivity environments dominated by particulate matter and larger plankton (there are substantial losses from the system).

In the present study, the contribution of heterotrophic bacteria to planktonic biomass as well as metabolism varied systematically across a trophic gradient in natural waters. There is emerging evidence in the recent literature for the existence of a systematic variability in the role of autotrophs and heterotrophs, prokaryotes and eukaryotes, and microbes and metazoans along natural gradients of productivity (Cotner and Biddanda pers. comm.). The ecophysiological context underlying the intriguing preponderance of microbial prokaryotes in oligotrophic but metazoan eukaryotes in eutrophic environments needs to be clearly defined in terms of cross-ecosystem properties. Oligotrophic waters were clearly dominated by dissolved nutrients, microbial biomass, and microbial activity, whereas particulate matter and larger autotrophic and heterotrophic plankton were relatively more important in eutrophic systems. Recognizing the prevalence of such a trend in biomass distribution and activity among autotrophs and heterotrophs across trophic gradients is likely to have important consequences for our understanding of food web interactions, carbon flow, and nutrient cycling in nature.

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