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Nutrient and light availability regulate the relative contribution of autotrophs and heterotrophs to respiration in freshwater pelagic ecosystems

Brian J. Roberts[1] *and Robert W. Howarth*
Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York 14853-2701

Abstract

In this study, two main hypotheses were addressed. (1) Bacteria contribute proportionally less than autotrophs to ecosystem respiration as trophic status increases. This hypothesis was examined in a pond phosphorus-fertilization experiment and two microcosm nutrient-fertilization experiments. (2) The relative contribution of autotrophs to ecosystem respiration, at a given nutrient availability, increases as light availability increases. This hypothesis was tested in three light by nutrient factorial microcosm experiments. Rates of total plankton community, bacterial (<1 μm fraction), and phytoplankton (total $-$ bacterial) respiration all increased as nutrient availability increased. The contribution of bacteria to community respiration ranged between $\sim$10 and 90%, with the highest contribution occurring under the most oligotrophic conditions. As light availability increased within each nutrient availability treatment, there was a similar decline in the contribution of bacteria to community respiration. Under oligotrophic conditions bacteria are better competitors for nutrients that limit both autotrophs and heterotrophs, but as nutrient availability increases, conditions become increasingly favorable for larger celled phytoplankton that have higher maximal nutrient uptake rates. As light availability increases, the relative contribution of phytoplankton to ecosystem respiration also increases. Light and nutrient availability are important regulators of the relative contributions of autotrophs and heterotrophs to ecosystem respiration, but the observed patterns are primarily driven by changes in phytoplankton production rates.

Introduction

Two of the key parameters in ecosystem energy and mass flow are rates of gross primary production (GPP) and respiration (Howarth and Michaels 2000). These processes link the uptake and production of carbon dioxide (CO_2) and oxygen (O_2) and provide the major biological mechanisms for cycling these important gases on earth. Over the past 30 yr, numerous studies have examined the regulation of GPP in aquatic ecosystems and the consensus has emerged that nutrient availability (Elser et al. 1990), light availability (Cloern 1999), grazing pressure (Cottingham et al. 1997), dissolved organic carbon availability (Jansson et al. 2000), as well as the interaction of these factors (Carpenter et al. 1998*a*) are all important in GPP regulation. Knowledge about factors regulating respiration rates has lagged, even though Pomeroy and Johannes (1968) recognized over 30 yr ago that respiration is the key index of energy use by consumers in an ecosystem (but see Howarth et al. 1992; Mulholland et al. 2001, among others).

In both freshwater and marine ecosystems, some general relationships between autotrophs and heterotrophs have been described (see Cole 1999; Cotner and Biddanda 2002 for recent reviews). In general, planktonic biomass is dominated by heterotrophs in oligotrophic waters and autotrophs in eutrophic waters (Ducklow and Carlson 1992). Similarly, heterotrophs tend to dominate in waters with high organic carbon : inorganic nutrient supply ratios, whereas autotrophs become increasing important in the plankton as the supply ratio decreases (Grover 2000). Although the biomass of both autotrophs and heterotrophs increases along a trophic gradient, heterotrophic bacterial biomass appears to increase more slowly than autotrophic biomass with increasing nutrient status (Cole et al. 1988; del Giorgio et al. 1997).

Although heterotrophic bacterial production (BP) is correlated with net primary production (Cole et al. 1988; Ducklow and Carlson 1992), we lack a similar understanding of any relationship between autotrophic and heterotrophic rates of respiration because bacterial respiration (BR) rates are not frequently quantified (Jahnke and Craven 1995). There is a need for more BR rate measurements because BR is a direct measurement of the importance of the bacterial community in the carbon cycle (Jahnke and Craven 1995). It is therefore important to better understand the regulation of this important community and its contribution to ecosystem respiration.

Few studies have directly examined the relative contribution of autotrophs and heterotrophs to ecosystem respiration along trophic gradients. Cimberlis and Kalff (1998) found that the bacterial fraction accounted for 42% of total planktonic respiration rates, on average, in 14 Canadian lakes. Pace and Cole (2000) found that the ratio of bacterial respiration to total planktonic respiration decreased with in-

[1] To whom correspondence should be addressed. Present address: Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831-6036 (robertsbj@ornl.gov).

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creased fertilization. Biddanda et al. (2001) examined bacteria and total plankton metabolism along a trophic gradient in several Minnesota Lakes and Lake Superior. Bacterial metabolism dominated in oligotrophic lakes but accounted for as little as 10% of total plankton respiration in eutrophic lakes (Biddanda et al. 2001).

The majority of studies examining the relationship between autotrophs and heterotrophs in freshwater and marine ecosystems have been based on cross-system analyses (e.g., Cole et al. 1988). An alternative approach is to conduct experiments varying only the parameters of interest while holding the remaining variables constant in an experimental system.

In this study, two main hypotheses were addressed using microcosms and small ponds. The emerging hypothesis that bacteria contribute less to ecosystem respiration as production increases was addressed through a pond phosphorus-fertilization experiment and two microcosm nutrient-fertilization experiments. Since photoautotrophs require light energy for photosynthesis in addition to nutrients for growth, it was also hypothesized that these nutrient effects will only be manifested at high light availability through their effects on photosynthesis. If either light or nutrients are limiting, the percentage of ecosystem respiration accounted for by phytoplankton will decrease because of lower rates of photosynthesis. This hypothesis was directly examined in three, light (three levels) by nutrient (two levels) factorial-design microcosm experiments. These experiments were conducted by using identical treatments but different source waters to begin to assess the generality of the observed responses.

Materials and methods

Nutrient enrichment gradient experiments—We conducted two types of experiments to examine the relative importance of autotrophs and heterotrophs in ecosystem respiration along nutrient availability gradients. We ran the first type of experiment in conjunction with a whole-pond phosphorus fertilization gradient experiment in 1999 (Chan et al. 2004). We also conducted two microcosm experiments in a growth chamber on the Cornell University campus during August 2000 and September 2001.

Ponds experiment: Nine ponds (36 m $\times$ 36 m, mean depth = 2 m, initial volume = 1,500 m^3) at the Cornell University Experimental Ponds Facility in Ithaca, New York (see Hall et al. 1970 for complete description of facility) were manipulated in summer 1999. On 10 May, all fish were eliminated from ponds by application of rotenone. Five days after rotenone application, each pond was restocked with 1.8 kg of zooplanktivorous fish (*Pimephales promelas*). Restocking occurred only after complete survival of *P. promelas* placed in minnow traps was observed. Triplicate ponds received either ambient (0 μmol P m^{-3} d^{-1}), medium (66.7 μmol P m^{-3} d^{-1}), or high (266.6 μmol P m^{-3} d^{-1}) levels of P fertilization (as H_3PO_4) over the 14-week period of fertilization. Previous studies at the ponds facility (Morin et al. 1991; Schaffner et al. 1994) demonstrated that the low P addition rate was sufficient to promote planktonic blooms of nitrogen-fixing cyanobacteria. Target phosphorus fertilization rates were achieved by adding H_3PO_4 diluted in approximately 20 liters of water from each respective pond and dispersed from a boat into the middle of each pond twice each week. We collected water for the respiration experiments described below from a depth of 0.5 m in a carboy from the center of three ponds exposed to differing rates of phosphorus fertilization (ambient, low, and high) on three dates (6 September, 21 September, and 6 October) after the final fertilization treatment. Respiration rates of bacteria, phytoplankton, and the total plankton community were then determined by using this water according the protocol detailed below.

Microcosm experiments: We collected water in 25 5-gal carboys from 0.5 m below the surface in the middle of Skaneateles Lake, New York, U.S.A. (mean summer [TP] $\sim$ 0.1 μmol P L^{-1}, mean summer [Chl *a*] $\sim$ 0.3–0.6 μg Chl *a* L^{-1}; UFI 2003) on 13 Aug 2000 and 26 Sep 2001. Eight hundred milliliters of water from each of the 25 carboys was added to a total of 18 different 20-liter microcosm tanks (20 liters total added to each tank). We removed large zooplankton from the collected water by passing it through 70-μm mesh after returning to the laboratory. Microcosm tanks were covered (polycarbonate lids) and exposed to 14 : 10 h light : dark cycle in a growth chamber (equipped with four pairs of 1,000 watt high-pressure sodium and metal halide lamps; Osram Sylvania) at constant T = 22°C for 10 (in 2000) or 8 (in 2001) days. The light program used in all experiments included 1 h each of ''sunrise'' and ''sunset'' achieved by turning each pair of lights on or off sequentially at 20-min intervals. Growth chamber irradiance levels were set at a saturating level of 650 μmol quanta m^{-2} s^{-1} (by placing two layers of 30% shade cloth just below the light diffuser panels in the growth chamber), as determined by photosynthesis-irradiance curves for Skaneateles Lake phytoplankton communities (Roberts 2004). Final nutrient levels were achieved via 10 (in 2000) or 7 (in 2001) days of daily liquid fertilizer additions of N ($NaNO_3$) and P (H_3PO_4) at N : P molar ratio of 5 : 1 (in 2000) or 25 : 1 (in 2001). To avoid CO_2 limitation during the experiment, we added 2.4 mmol L^{-1} HCO_3^- as $NaHCO_3$ to each tank at the beginning of the experiment (as described in Marino et al. 2003), which resulted in higher alkalinity values at the end of the experiments than was in either Skaneateles or Cayuga Lake at the time of water collection (Roberts unpubl. data). Triplicate microcosm tanks were exposed to one of six levels of nutrient addition over the duration of the experiments: ambient, 0.1, 0.5, 1.0, 2.0, or 5.0 μmol P L^{-1}. On day 11 (in 2000) and day 8 (in 2001) of each nutrient manipulation, we collected water to perform linearity test experiments of O_2 consumption (to ensure that substrate limitation was not occurring during incubations; see following). Determination of bacteria, phytoplankton, and total planktonic community respiration rates began on the following day (i.e., after completion of linearity tests).

Light-nutrient interaction experiments—In 2001, three microcosm experiments were conducted to examine the interaction of light and nutrient availability as regulators of bacteria, phytoplankton, and total plankton respiration rates. The 3 $\times$ 2 factorial design microcosm experiments were

conducted using the same growth chamber setup described above and experimental design detailed in Roberts (2004). The experiments used three levels of light availability (achieved by differential layering with 30% shade cloth) and two levels of nutrient fertilization (by daily additions of liquid fertilizer with N : P molar ratio of 25 : 1). The three light levels corresponded to saturating conditions (625 μmol quanta m^{-2} s^{-1}; no shade cloth) and two degrees of light limitation (200 and 100 μmol quanta m^{-2} s^{-1}; two and four layers of shade cloth, respectively) as determined by photosynthesis-irradiance curves for Skaneateles Lake phytoplankton communities (Roberts 2004). The two levels of nutrient fertilization were based on target final TP concentrations corresponding to mesotrophic (0.5 μmol P L^{-1}) and eutrophic (2.0 μmol P L^{-1}) status according to the Vollenweider (1976) scale of eutrophication.

The first two experiments (beginning on 18 Jun and 8 Aug 2001) were again conducted using Skaneateles Lake as a source water, while the third (beginning on 11 Sep 2001) used water collected from mesotrophic Cayuga Lake (mean summer [TP] $\sim$ 0.5 μmol P L^{-1}, mean summer [Chl *a*] $\sim$ 5 μg L^{-1}; UFI 2003). For all three experiments, water was collected from 0.5 m below the surface in carboys at a station in each lake (middle for Skaneateles Lake and at the Remote Underwater Sampling Station [RUSS] at the south end of Cayuga Lake). When water was brought back to the laboratory, three additional tanks were filled according to the procedure above. Water from these carboys was used to determine the initial respiration rates of bacteria, phytoplankton, and total plankton in Skaneateles and Cayuga Lake. The same procedure as described above, for the nutrient enrichment gradient microcosm experiments, was used to determine the final respiration rates.

To make comparisons between the Skaneateles Lake water (SLW) and Cayuga Lake water (CLW) experiments, it was important that the experiments began with the same initial phytoplankton biomass. Because the Chl *a* concentration of CLW collected was 5.0 μg L^{-1} ($\sim$8.3 times greater than SLW), 17.6 liters of 20 liters of CLW added to each tank were passed through Whatman GF/F (0.7 μm nominal cutoff) filters (under low vacuum) in addition to the 70-μm mesh used to remove large zooplankton. This process resulted in similar initial Chl *a* concentrations for all three experiments. Water was collected on day 8 of each experiment to perform linearity test experiments and on day 9 to determine bacterial, phytoplankton, and total plankton community respiration rates (see following).

Determination of bacterial, phytoplankton, and total plankton community R rates—In each of the experiments above, total plankton community and bacterial respiration rates were determined by measuring changes in dissolved oxygen concentration during dark-bottle incubations of unfiltered and filtered (Gelman A/E filters, 1.0 μm nominal cutoff) water, respectively. Eight 300-ml biological oxygen demand (BOD) bottles were filled with water from each treatment by overflowing three times. Half were immediately fixed and the other half incubated (at a depth of 0.5 m for ponds or in growth chamber for microcosms) in the dark for an amount of time determined in preliminary experiments (see following). Dissolved oxygen concentrations in the initial and final samples were determined via the azide modification of the Winkler titration (American Public Health Association 1995). Titrations were performed on 200-ml aliquots that were weighed on an analytical balance to assure accurate volume determinations. End points were determined colorimetrically.

Phytoplankton respiration was subsequently determined by difference (total plankton community respiration minus bacterial respiration). The bacterial (<1 μm) fraction was generated by gently pumping water through 47-mm Gelman A/E filters (1.0 μm nominal cutoff) under low vacuum. To avoid the potential problem of having the effective pore size reduced by filter clogging in highly productive waters, a maximum of 250 ml of water was passed through a given filter in productive waters. To avoid contamination of filtrate, no filters were used for more than a single sample, and the filtering apparatus was backflushed and cleaned with Nanopure water between samples.

Heterotrophic bacteria may have been included in the $>$1-μm-size fractions in our experiments, because small (<1 μm) bacteria attached to phytoplankton and other particles as well as large bacteria may be retained on the Gelman A/E filters (e.g., Lee et al. [1995] found that cells larger than 0.8 μm did not pass through Whatman GF/F, 0.7-μm nominal cutoff, filters). The use of larger (1.0 μm) nominal cutoff filters in the current study minimizes the extent of this problem. Several other studies (e.g., Cimberlis and Kalff [1998] and Biddanda et al. [2001]) have successfully used the $<$1.0-μm-size fraction to quantify heterotrophic bacteria respiration rates. In fact, Biddanda et al. (2001) found that $>$95% of heterotrophic bacteria found in unfiltered samples consistently passed through the 1.0-μm pore-size filters in their study along a trophic gradient in north temperate lakes similar to those in the current study. Because bacterial abundance and biomass were not determined for either size fraction in this study, we consider the respiration rates observed in the $<$1.0-μm-size fraction as conservative estimates of heterotrophic bacteria respiration.

To see whether phytoplankton were being included in the $<$1-μm samples, Chl *a* concentrations were determined on both 1-μm (Gelman A/E) and 0.7-μm (Whatman GF/F) filters. In all cases, measured Chl *a* concentrations on the two filters were not significantly different. Successful removal of autotrophic picoplankton from the filtrate was confirmed through microscopic examination of subsamples.

Because Chl *a* was successfully removed, the filtered samples can be thought to represent conservative estimates (see previous) of heterotrophic bacterial respiration rates (referred to as bacterial respiration below). As a result of this removal of Chl *a* from the bacterial fraction, prokaryotic autotrophs (cyanobacteria) are included in the $>$1-μm fraction and therefore contribute to phytoplankton respiration in this study.

Linearity test experiments to determine duration of dark incubations—An important prerequisite of the oxygen-consumption method is that uptake of dissolved oxygen is linear during the time of incubation (Williams 1981; Pomeroy et al. 1994). To optimize the sensitivity of this approach, it is

Table 1. TP, Chl *a*, and DOC concentrations and planktonic community respiration (CR), bacterial respiration (BR), bacterial contribution to planktonic community respiration (BR : CR), and phytoplankton respiration (PR) for the experimental systems studied in the three nutrient enrichment gradient experiments.

TP (μmol L^{-1})	Chl *a* (μg L^{-1})	DOC (mg L^{-1})	CR (μmol O_2 L^{-1} h^{-1})	BR (μmol O_2 L^{-1} h^{-1})	BR : CR (%)	PR (μmol O_2 L^{-1} h^{-1})
1999 Ponds Experiment						
0.87	4.63	9.06	0.44	0.33	75	0.11
0.87	4.63	9.06	0.52	0.37	71	0.15
2.84	65.60	9.74	1.21	0.53	44	0.68
6.55	84.37	12.16	2.83	0.65	23	2.18
9.52	247.56	11.81	3.78	0.85	22	2.93
2000 Microcosm Experiment						
0.03	2.34	1.62	0.59	0.32	55	0.27
0.1	4.52	1.78	0.77	0.32	41	0.45
0.5	5.59	2.10	1.06	0.34	32	0.72
1.0	12.70	1.92	1.94	0.50	26	1.44
2.0	21.62	1.97	2.38	0.58	24	1.79
5.0	77.36	2.85	3.73	0.69	18	3.04
2001 Microcosm Experiment						
0.03	0.75	1.57	0.44	0.27	62	0.17
0.1	1.07	1.35	0.45	0.22	50	0.22
0.5	4.38	1.33	1.01	0.40	39	0.61
1.0	9.75	1.54	1.39	0.49	35	0.90
2.0	8.95	1.50	1.65	0.57	34	1.08
5.0	11.38	1.51	2.13	0.60	28	1.53

also advantageous to run the incubation for the maximum amount of time that oxygen uptake remains linear. To test for linearity, water was collected from several of the experimental treatments 1 day prior to respiration incubations being performed. At least fifteen 300-ml BOD bottles were filled and triplicate samples were fixed every 4–6 h until all of the samples were consumed. Dissolved oxygen concentrations were determined as above. As a result of these tests, all pond samples were incubated in the pond for 12 h and microcosm tank samples were incubated between 12 h (5.0 μmol P L^{-1} treatments) and 36 h (ambient Skaneateles Lake water).

Monitoring of biological, chemical, and physical parameters—Total nitrogen (TN) and phosphorus (TP), nitrate (NO_3^-), soluble reactive phosphorus (SRP), dissolved organic carbon (DOC), water color, and Chl *a* concentrations were monitored weekly throughout the pond experiment and on four dates for each of the microcosm experiments. Water samples for SRP, NO_3^-, and DOC concentrations were filtered through precombusted (4 h at 500°C) Whatman GF/F glass fiber filters under low vacuum pressure. The filters were immediately frozen in liquid N_2 and kept frozen in the dark until analyzed for chlorophyll and pheopigment concentrations. Pigments were extracted in absolute methanol and analyzed fluorometrically (Holm-Hansen and Riemann 1978) on a Turner Designs 10-AU Fluorometer as in Marino et al. (2003) and Chan et al. (2004). The fluorometer was standardized spectrophotometrically using methanol solutions of pure Chl *a* (Sigma Chemical) and the equations of Porra et al. (1989). SRP concentrations were determined colorimetrically using the molybdate-blue method (Murphy and Riley 1962) on a Beckman DU-50 Spectrophotometer. Nitrate concentrations were analyzed colorimetrically by flow injection (Johnson and Petty 1983) on an Alpchem 500 Series Autoanalyzer (Alpkem 1992). TN and TP were measured colorimetrically as nitrate plus nitrite (Johnson and Petty 1983) and soluble reactive phosphorus (Murphy and Riley 1962) after simultaneous persulfate oxidation (modified from D'Elia et al. 1977). DOC concentrations were determined by high-temperature platinum combustion on a Shimadzu model 5000 TOC analyzer as in Perakis (2000). In most cases, chemical analyses were performed within 24–48 h of collection, otherwise, samples were frozen until analysis. Irradiance levels were monitored daily in the center of the water column of each microcosm tank using a Li-Cor LI-193A spherical quantum sensor.

Results and discussion

Nutrient enrichment gradient experiments—Chl *a* concentrations and rates of plankton community respiration (CR), bacterial respiration (BR), and phytoplankton respiration (PR) increased with nutrient enrichment in whole-pond and microcosm experiments (Table 1). In contrast, DOC concentrations did not show a consistent pattern as TP concentrations increased (Table 1). In general, as TP increased along trophic gradients (maximum TP concentration of 9.5 μmol TP L^{-1} in ponds and 5 μmol TP L^{-1} in microcosms): Chl *a* concentrations increased by over an order of magnitude, CR increased between 5 and 6 (microcosms) and 9 (ponds) times, BR increased between 2 and 2.5 times, and PR increased between 9 (2001 Microcosms) and 27 (ponds) times

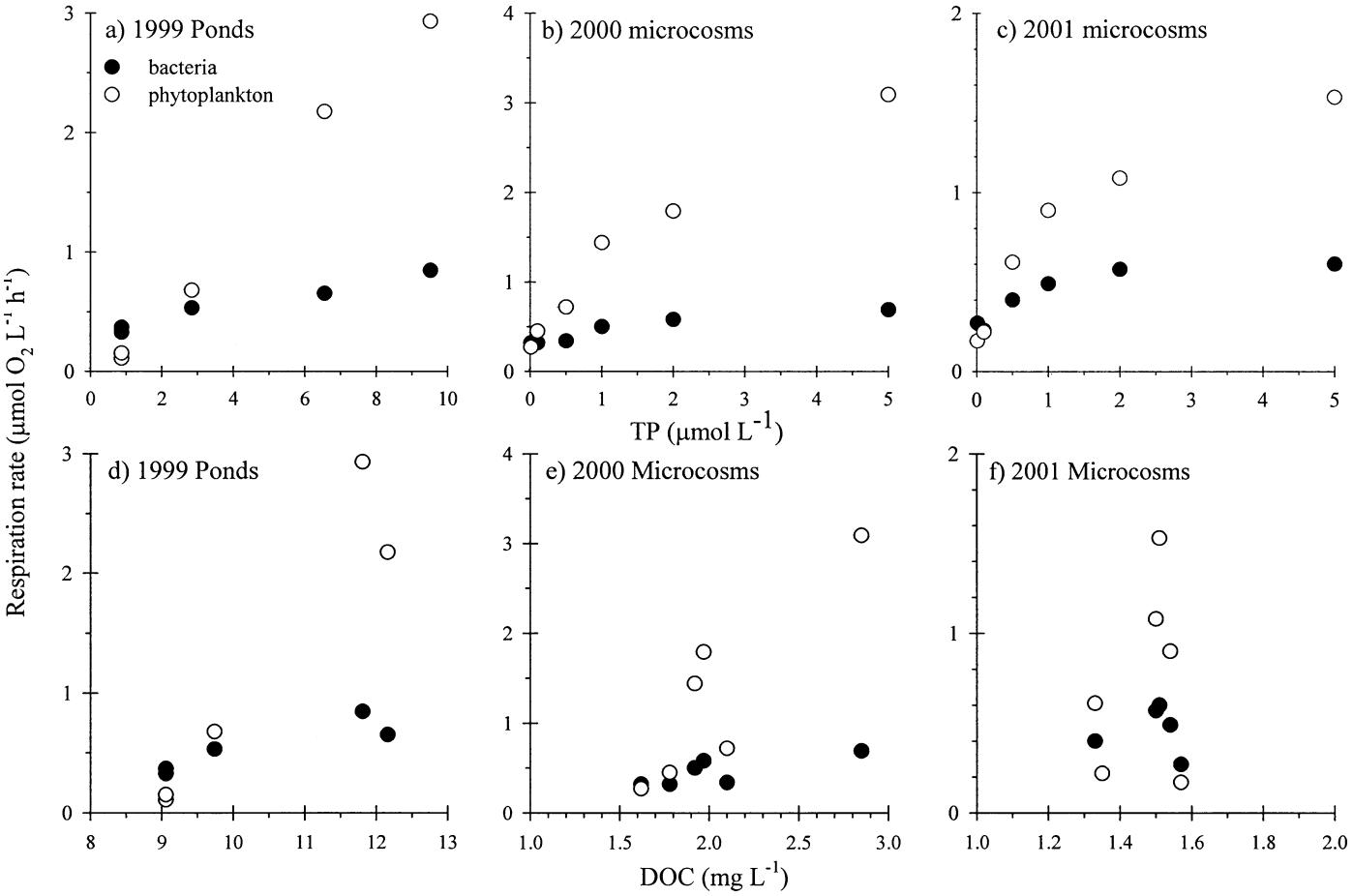

Fig. 1. Relationship between bacterial respiration and phytoplankton respiration rates and total phosphorus concentration in 1999 ponds experiment (a), 2000 microcosm experiment (b), and 2001 microcosm experiment (c). Relationship between bacterial respiration and phytoplankton respiration rates and DOC concentration in 1999 ponds experiment (d), 2000 microcosm experiment (e), and 2001 microcosm experiment (f).

(Table 1). PR rates increased between 4 (2001 Microcosms) and 11 (ponds) times more than BR rates along the trophic enrichment gradients (Table 1, Fig. 1).

In all three experiments, the regressions for BR, PR, and CR with TP (Fig. 1) were statistically significant (Table 2). These results are qualitatively similar to those of Biddanda et al. (2001) except that, in their study, BR was positively correlated with Chl *a* concentrations only at low (<15 μg Chl *a* L^{-1}) concentrations. Their findings suggested that BR attains a maximal rate along a trophic gradient after which it either levels off or decreases (Biddanda et al. 2001). In contrast, none of our experiments suggested decreased BR at high nutrient enrichment and in only one of our experiments (2001 Microcosms) did the data better fit a nonlinear than a linear model (Fig. 1c). However, the linear regression model for the 2001 microcosm experiment is significant ($p < 0.05$) and explains 68% of the variation in the data (Table 2). The linear regressions for the other two experiments are both highly significant (Table 2) over the entire range (Table 1) despite having greater Chl *a* concentrations (maximum concentrations of ~248 μg L^{-1} [Ponds] and ~ 77 μg L^{-1} [2000 Microcosms]) than any observed in the Biddanda et al. (2001) study (maximum concentration of ~53 μg L^{-1}).

Differences in DOC concentration explained far less of

Table 2. Results of regression analyses (r^2 and *p* values) for DOC versus bacterial respiration (BR) and TP concentrations versus bacterial respiration (BR), phytoplankton respiration (PR), and plankton community respiration (CR) for 1999 ponds experiment and 2000 and 2001 microcosm experiments conducted with Skaneateles Lake water.

	DOC × BR		TP × BR		TP × PR		TP × CR	
	r^2	*p*	r^2	*p*	r^2	*p*	r^2	*p*
1999 ponds	0.79	0.04	0.97	<0.001	0.99	<0.001	0.99	<0.001
2000 microcosms	0.60	0.07	0.85	<0.01	0.97	0.001	0.97	0.001
2001 microcosms	0.13	0.48	0.68	<0.05	0.92	<0.01	0.90	0.01

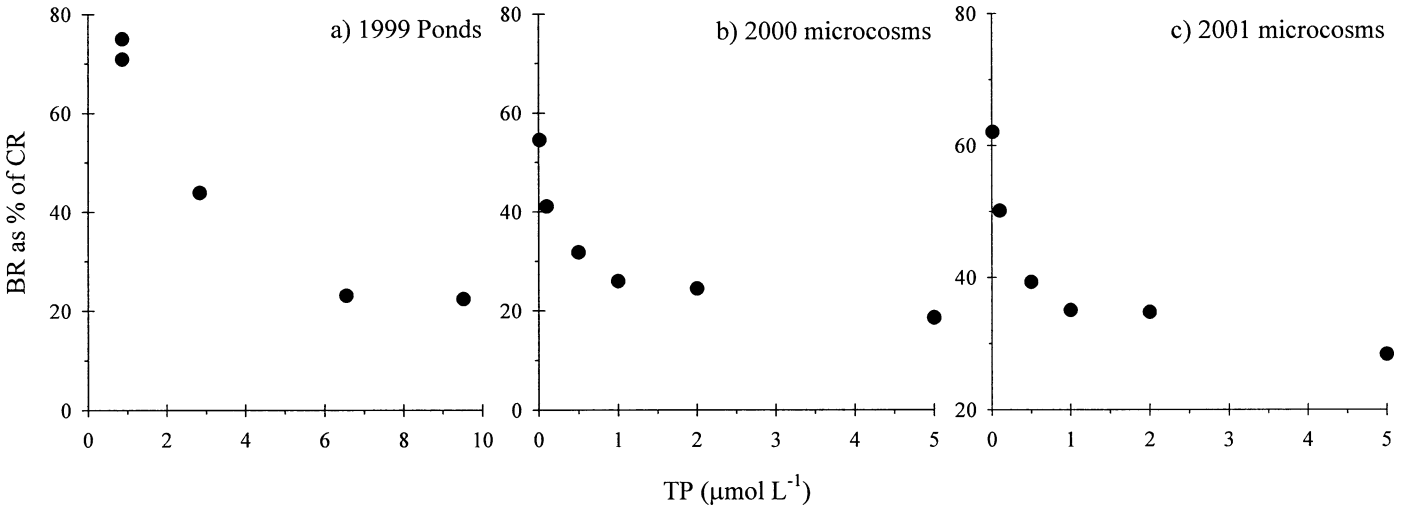

Fig. 2. Relationship between bacterial respiration (BR) as a percent of total plankton community respiration (CR) and total phosphorus concentration (TP) in 1999 ponds experiment (a), 2000 microcosm experiment (b), and 2001 microcosm experiment (c).

the variability in BR rates than did TP concentrations (Fig. 1, Table 2). The regression of DOC with BR was only significant in the pond experiment, where it still explained less of the variability (79%, Table 2) than TP concentration (97%, Table 2). In the 2001 Microcosm experiment, DOC was only able to explain 13% of the variability in BR. The observation that TP concentration explains a greater percentage of the variability in BR than DOC concentration is consistent with heterotrophic bacteria in these systems being more strongly limited by P than DOC availability. However, it is difficult to assess carbon limitation in this study from changes in DOC pool size since most of the DOC measured has a relatively long turnover time whereas the more labile DOC that is consumed by bacteria has a shorter turnover time. Nutrient rather than carbon limitation of heterotrophic bacteria has been a common finding in both freshwater and open-ocean ecosystems (Coveney and Wetzel 1992; Thingstad et al. 1998).

As nutrient availability and TP increased, bacteria accounted for a decreasing amount of plankton community respiration in all three experiments (Fig. 2). Heterotrophic bacteria often account for as much as 80% of plankton community respiration in the oligotrophic systems, but less than 20% in eutrophic systems (Fig. 2). This general pattern was observed under three contrasting nutrient fertilization regimes: phosphorus only (Ponds), low N : P ratio equal to 5 (2000 Microcosms), or high N : P ratio equal to 25 (2001 Microcosms). These results suggest that bacteria will account for a lower proportion of plankton respiration as nutrient availability increases, regardless of whether the phytoplankton community is dominated by N-fixing cyanobacteria (Ponds; Chan et al. 2004) or eukaryotic autotrophs (2000 and 2001 Microcosms; Roberts, unpubl. data).

This pattern is qualitatively similar to that found by Biddanda et al. (2001) along a chlorophyll concentration gradient that included Lake Superior and a series of small Minnesota lakes. Similarly, Williams (1984), in a review of literature on respiration in marine ecosystems, found that bacteria accounted for a larger portion of plankton respiration at oligotrophic oceanic sites than in productive nearshore waters.

Differences in efficiency of inorganic nutrient acquisition between bacteria and phytoplankton are likely to play a role in this pattern. Heterotrophic bacteria often account for a large proportion of inorganic nutrient (PO_4^- and NH_4^+) uptake in both freshwater and marine ecosystems (Currie 1990; Kirchman 1994) at low ambient nutrient concentrations. Heterotrophic bacteria and other small cells have a higher surface-to-volume ratio than eukaryotic phytoplankton cells resulting in a higher affinity (lower apparent half-saturation constant, K_m) for inorganic nutrient uptake (Cotner and Biddanda 2002). There is a growing consensus that bacteria have a higher P content (lower C : P) than phytoplankton (Vadstein et al. 1989; Sterner and Elser 2002). Bacteria appear to compensate for this high nutrient content by acquiring nutrients more efficiently than phytoplankton in oligotrophic systems. Several experiments have shown heterotrophic bacteria to exhibit higher uptake rates of both inorganic and organic P than phytoplankton when P is in limited supply (Vadstein and Olsen 1989; Cotner and Wetzel 1992; Thingstad et al. 1993, among others). Although phosphorus was strongly limiting in all of our experiments (final DIN : SRP ratios were >50 in all treatments of all experiments; Roberts, unpubl. data), it is important to recognize that evidence for higher rates of NH_4^+ uptake by heterotrophic bacteria when N is limiting also exists (Suttle et al. 1990). This high affinity for both organic and inorganic nutrients is largely a result of the high surface-to-volume ratio in heterotrophic bacteria.

Drakare (2002), however, has demonstrated that the outcome of competition for phosphate between heterotrophic bacteria and phytoplankton is not simply size dependent, as heterotrophic bacteria dominated P uptake in the presence of picoplanktonic cyanobacteria when organic carbon was in sufficient supply. This is consistent with findings that heterotrophic bacteria have higher specific growth rates than an equal-sized phytoplankton (Raven 1999). This has been sug-

gested to be the result of phytoplankton investing large amounts of energy to construct the photosynthetic apparatus (Raven 1999).

The delivery of nutrients to lakes and coastal waters is often intermittent through time (Carpenter et al. 1998*b*). Many aquatic ecosystems can receive the majority of their nutrient load during these intermittent pulses (Suttle et al. 1987). This pulsed delivery of a potentially limiting nutrient leads to a strong selection for large cells that can maintain uptake of that nutrient (i.e., have a relatively high V_{max}) and store it internally for later growth (Suttle et al. 1987). While the high surface-to-volume ratio of bacteria results in a high affinity for nutrients, the small cell size leads to little capacity for storing nutrients internally. In contrast, phytoplankton are expected to sequester an increasing fraction of available nutrients with increasing trophic state as a result of their larger cell size (Cotner and Biddanda 2002). Several studies have demonstrated that the ability of phytoplankton to take up P and accumulate higher intercellular P levels is either comparable (Vadstein et al. 1989) or superior to the ability of bacteria (Suttle et al. 1990; Cotner and Wetzel 1992; Thingstad et al. 1993).

Although competition between bacteria and phytoplankton for dissolved nutrients is likely to play a large role in explaining why oligotrophic ecosystems tend to have higher bacteria : phytoplankton biomass and activity, other hypotheses (not addressed in this study) have also been proposed (see Cotner and Biddanda [2002] for a recent review). Some have argued that the observed decrease in bacterial biomass and activity with increasing trophic state is a result of increases in the consumption of bacterial biomass by protozoan grazers (e.g., Sanders et al. 1992). It has also been proposed that bacterial mortality increases with trophic state as a result of increased viral lysis (Weinbauer and Peduzzi 1995). Fuhrman and Noble (1995) found that bacterial mortality attributed to viral lysis was about equal to mortality due to grazing by protists in coastal seawater.

The results of the experiments presented here are consistent with the notion that heterotrophic bacteria dominate ecosystem respiration under low nutrient conditions, but phytoplankton account for a larger proportion of ecosystem respiration as nutrient availability increases. These observed differences in the relative contributions of heterotrophic bacteria and phytoplankton to ecosystem respiration with changing nutrient status can largely be explained by competition and differences in the nutrient uptake kinetics of the two groups. Heterotrophic bacteria dominate nutrient uptake at low nutrient concentrations due to a higher affinity for nutrients, but at high nutrient concentrations phytoplankton dominate due to a higher maximum nutrient uptake capacity. However, it is likely that in many systems, both substrate control and bacterivory, are likely to interact in regulating the relative contribution of bacteria and phytoplankton to biogeochemical processes along trophic gradients.

Light-nutrient interaction experiments—Skaneateles Lake versus Cayuga Lake: Cayuga Lake exhibited higher concentrations of Chl *a* and DOC than Skaneateles Lake (see Initial tanks in Table 3). Rates of plankton CR, BR, and PR were also greater in Cayuga Lake (Table 3). BR accounted for a smaller percentage of CR in Cayuga Lake (75%) than in Skaneateles Lake (90–93%) (Table 3; solid lines in Fig. 3). These results follow the pattern exhibited in the nutrient enrichment gradient experiments described above, where the lake with higher TP (Cayuga Lake) had higher rates of CR, BR, and PR with bacteria accounting for less of CR than the lower TP lake (Skaneateles Lake).

The effect of nutrients on plankton community respiration: Within irradiance treatments in all experiments, Chl *a* concentrations and rates of CR, BR, and PR increased with increasing nutrient status (Table 3). In contrast, DOC did not show a consistent pattern with increased nutrient availability (Table 3). This, in part, is because labile DOC is probably consumed in bacterial R. As total nutrient availability and TP increased in the microcosms, PR showed a stronger response than did BR (Table 3). These results are consistent with the changes in CR, BR, and PR observed in response to nutrient enrichment in the experiments described above.

The effect of light on plankton community respiration: Within nutrient treatments in all three experiments, Chl *a* concentration increased with increased light availability (Table 3). As light availability increases up to saturation, the biomass-specific rate of photosynthesis also increased (Roberts et al. unpubl. data) because light energy is necessary for photosynthetic electron transport to occur. PR was expected to increase with photosynthetic rate for both physiological and time-integrated reasons. First, PR is expected to increase in response to higher metabolic needs (e.g., nutrient uptake and assimilation), this ''instantaneous'' effect was observed as day : night R increased with ambient light intensity in pond studies (Roberts et al. unpubl.). Second, when nutrient availability is sufficient, this increased rate of photosynthesis can be used to increase biomass. This total gain in biomass is likely to result in an increase in PR that is integrated over time. Strong correlations between Chl *a* and PR were observed in all three experiments (Table 4). Large increases in PR were observed as light availability increased under both mesotrophic and eutrophic conditions in each experiment (Tables 3 and 4). PR : Chl *a* increased significantly with increased light availability in all three experiments (Table 4).

The increase in PR observed over the light availability gradient accounts for the majority of the increases in plankton community respiration (CR) seen in each experiment. However, a smaller ($<2\times$) increase in BR was observed for all three experiments under both mesotrophic and eutrophic conditions (Table 3). This increase is consistent with the notion of bacterial activity being tightly coupled to the extracellular organic carbon released by phytoplankton as a preferred source of labile carbon when P uptake is saturated (Cole et al. 1982). However, it is not clear whether the BR increase observed in this study was due to physiology (higher specific R) or ecology (more bacterial biomass).

Bacterial contribution to plankton community respiration: As nutrient availability increased for a given irradiance level, BR accounted for a decreased amount of plankton CR in all three experiments (Fig. 3, Table 3). This finding supports the notion that, because of their larger size, phytoplankton ac-

Table 3. Irradiance level, Chl *a*, and DOC concentrations and planktonic community respiration (CR), bacterial respiration (BR), bacterial contribution to planktonic community respiration (BR : CR), and phytoplankton respiration (PR) for the experimental systems studied in the three light-nutrient interaction experiments.

Irradiance (μmol quanta m^{-2} s^{-1})	Chl *a* (μg L^{-1})	DOC (mg L^{-1})	CR (μmol O_2 L^{-1} h^{-1})	BR (μmol O_2 L^{-1} h^{-1})	BR : CR (%)	PR (μmol O_2 L^{-1} h^{-1})
Skaneateles Lake Experiment 1						
Initial tanks	0.6	1.48	0.28	0.25	90	0.03
Mesotrophic nutrient level						
100	4.78	1.96	0.34	0.31	91	0.03
200	22.31	1.51	0.56	0.35	63	0.21
625	30.20	1.65	2.53	0.51	20	2.02
Eutrophic nutrient level						
100	5.89	1.64	0.44	0.29	66	0.15
200	43.60	1.61	0.96	0.41	42	0.56
625	125.41	2.96	5.40	0.67	12	4.73
Skaneateles Lake Experiment 2						
Initial tanks	0.6	2.11	0.29	0.27	93	0.02
Mesotrophic nutrient level						
100	2.05	2.13	0.28	0.25	89	0.03
200	3.88	1.69	0.58	0.34	59	0.24
625	8.13	1.70	1.48	0.40	27	1.08
Eutrophic nutrient level						
100	2.25	1.67	0.35	0.27	77	0.08
200	5.66	1.73	1.20	0.45	38	0.75
625	16.86	1.72	3.48	0.50	14	2.98
Cayuga Lake Experiment						
Initial tanks	5.0	2.53	0.44	0.33	75	0.11
Mesotrophic nutrient level						
100	6.31	2.56	0.29	0.18	62	0.09
200	7.32	2.56	1.02	0.25	24	0.77
625	15.43	2.69	2.57	0.36	14	2.21
Eutrophic nutrient level						
100	11.78	2.48	0.67	0.32	47	0.36
200	33.48	2.53	2.58	0.49	19	2.09
625	42.61	2.94	5.88	0.53	9	5.35

quire an increased fraction of the available nutrients as nutrient availability increases (Suttle et al. 1987; Cotner and Biddanda 2002). Under such conditions, the nutrient uptake capacity of small bacterial cells is likely to become saturated. This, in essence, negates their higher affinity for nutrients and allows phytoplankton to take advantage of their higher uptake capacity for nutrients and store them for later growth. Further, these results suggest that, on longer time scales, phytoplankton have a greater capacity to increase their relative biomass, indicating that the ecological factors that limit phytoplankton are more limiting to bacteria.

As light availability increased under both nutrient regimes, BR also accounted for a decreased percentage of CR in all three experiments (Fig. 3, Table 3). This result is consistent with the idea that as light availability increases under nutrient replete conditions, higher rates of photosynthesis will result in an increase in phytoplankton biomass. This increase in phytoplankton community biomass should result in a corresponding increase in the total amount of respiration being carried out by the phytoplankton community (i.e., significant regressions of PR vs. Chl *a* concentrations were observed in all experiments; Table 4). Although BR rate did increase slightly with increased PAR (Table 3), this can only be an indirect effect of light availability on bacterial activity. This is consistent with the notion of bacteria utilizing excreted DOC from phytoplankton as a carbon source during P-saturated conditions.

Because photoautotrophs require light energy for photosynthesis to occur, the direct link between increasing light availability (up to the light saturation point) and photoautotrophic activity is a clear one. In contrast, the role of light in heterotrophic activity is indirect and consequently more complicated to understand. The wavelength of light (ultraviolet [UV] vs. photosynthetically active radiation [PAR]) interacting with components of the water column plays a significant role in determining its impact on heterotrophic organisms.

Whereas solar UV radiation may play an important role

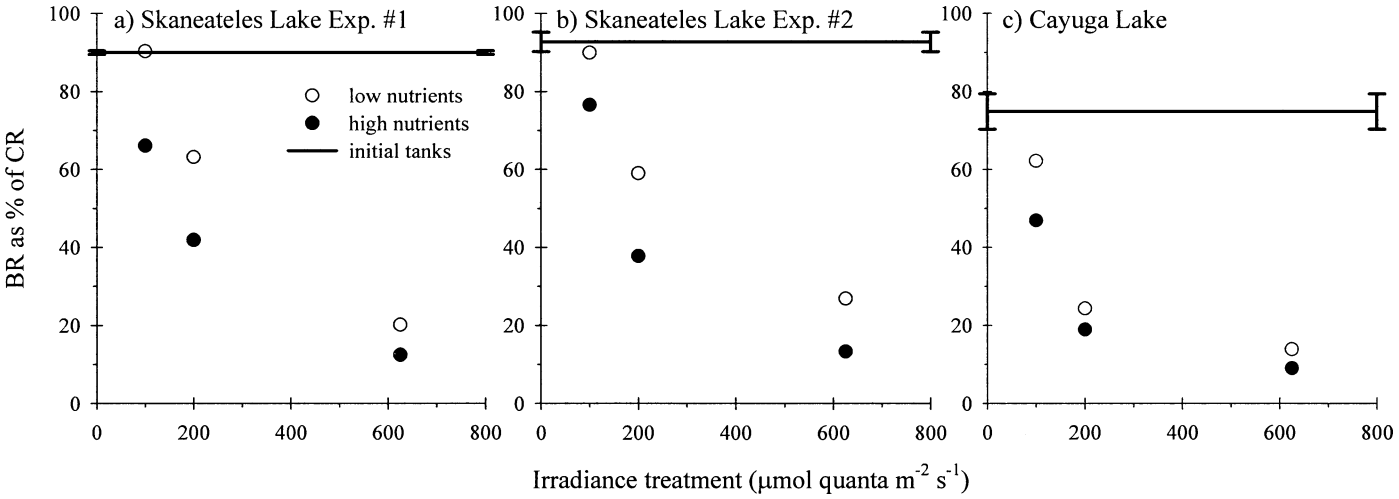

Fig. 3. Relationship between bacterial respiration (BR) as a percent of total plankton community respiration (CR) to irradiance treatment in Skaneateles Lake experiment 1 (a), Skaneateles Lake experiment 2 (b), and Cayuga Lake microcosm experiments (c). Horizontal lines represent value of bacterial respiration (BR) as a percent of total plankton CR for initial tanks for each experiment.

in altering the bioavailability of organic matter in natural ecosystems (Mopper and Kieber 2002), it did not play a role in the microcosm experiments where PAR is of primary concern. As PAR increases (up to a saturating level), biomass-specific rates of photosynthesis will also increase. Extracellular DOC excretion is correlated with increases in particulate primary production or POC production in both marine and freshwater ecosystems (Baines and Pace 1991). Although these broad patterns in DOC excretion rates exist across ecosystem nutrient gradients, mechanistic insights can also be gained by examining the response of extracellular DOC release to changing light availability within a given ecosystem or community. For example, Zlotnik and Dubinsky (1989) found that freshwater and marine algal species, studied in culture, exhibited nearly linear relationships between carbon fixation rate and extracellular DOC release with increased irradiance at or below the light saturation point. At irradiance levels above saturation (i.e., with the onset of photoinhibition), some phytoplankton taxa display a decrease in absolute DOC excretion rate whereas many taxa display further increases in excretion rate (Zlotnik and Dubinsky 1989). The slight increase in bacterial respiration rate observed with increased light availability (from subsaturating to saturating irradiance levels) in the microcosm experiments is consistent with bacteria utilizing the increased amount of DOC released by phytoplankton as a preferred source of labile carbon. Although rates of bacterial respiration did not show significant relationships with DOC concentrations ($p > 0.05$ in all cases), BR rates were significantly correlated with Chl *a* concentrations in all three experiments (Table 5).

Some authors have suggested that nutrient uptake by phytoplankton is light dependent (Lean and Nalewajko 1976), but that uptake by heterotrophic bacteria is not dependent on light availability. As mixed layers become shallower, thus increasing the average light availability in the mixed layer, phytoplankton might be able to better compete with bacteria for available nutrients in the mixed layer. This assertion is consistent with findings that inorganic phosphorus uptake by phytoplankton increased under high-light conditions that occurred when lakes are stratified in summer relative to uptake during unstratified times of the year in Third Sister Lake, Michigan (Cotner and Wetzel 1992). If this logic is carried one step further, as phytoplankton become better competitors for nutrients with increased light availability, bacteria may become more strongly nutrient limited than under lower light conditions (Cotner and Biddanda 2002).

Interaction of light and nutrients as regulators of plankton community R: Phytoplankton require light energy for pho-

Table 4. Results of regression analyses (r^2 and p values) for Chl *a* concentration and light availability versus phytoplankton respiration (PR) and light versus PR : Cha *a* for light-nutrient interaction experiments conducted using Skaneateles Lake water (SLW) and Cayuga Lake water (CLW).

	Chl *a* × PR		Light × PR		Light × PR : Chl *a*	
	r^2	p	r^2	p	r^2	p
SLW 1	0.87	<0.01	0.77	0.02	0.71	0.04
SLW 2	0.99	<0.0001	0.69	0.04	0.69	0.04
CLW	0.80	0.016	0.67	0.04	0.93	0.02

Table 5. Results of regression analyses (r^2 and p values) for DOC and Chl *a* concentration versus bacterial respiration (BR) for light-nutrient interaction experiments conducted using Skaneateles Lake water (SLW) and Cayuga Lake water (CLW).

	DOC × BR		Chl *a* × BR	
	r^2	p	r^2	p
SLW 1	0.58	0.08	0.85	<0.01
SLW 2	0.24	0.33	0.73	0.03
CLW	0.33	0.23	0.92	<0.01

tosynthesis and nutrients for growth. Heterotrophic bacteria require an organic carbon source for energy and nutrients for growth. This fundamental difference between the two groups plays a large role in explaining the observed patterns in respiration. Under low nutrient conditions, bacteria are better competitors for nutrients that limit both autotrophs and heterotrophs. As nutrients become increasingly available in the ecosystem, conditions become increasingly advantageous to larger phytoplankton that have higher maximal uptake rates for nutrients allowing them to achieve higher growth rates and to store excess nutrients for subsequent growth. As an ecosystem increases in light availability, whether via shallowing of the mixed layer or photodegradation of humic substances, phytoplankton should also become an increasingly important contributor to plankton community respiration in the mixed layer. Although previous studies have demonstrated that the organic carbon: inorganic nutrient supply ratio often influences the relative dominance of phytoplankton and bacteria (e.g., Grover 2000), this study demonstrated that PAR availability can be similarly important in determining the autotrophic/heterotrophic balance and phytoplankton-bacterial interactions in pelagic ecosystems. The results from these experiments suggest that the interaction of light and nutrient availability are important parameters in determining the relative contribution of autotrophs and heterotrophs to the important process of ecosystem respiration, but this relationship is driven primarily by changes in phytoplankton production rates.

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