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Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations

Jonathan J. Cole[1] *and Michael L. Pace*
Institute of Ecosystem Studies, Box AB, Route 44A, Millbrook, New York 12545-0129

Stephen R. Carpenter and James F. Kitchell
Center for Limnology, University of Wisconsin, 680 North Park Street, Madison, Wisconsin 53706-1413

Abstract

Net ecosystem production (NEP) is the difference between gross primary production (GPP) and community respiration (*R*). We estimated in situ NEP using three independent approaches (net CO_2 gas flux, net O_2 gas flux, and continuous diel O_2 measurements) over a 4–7 yr period in a series of small lakes in which food webs were manipulated and nutrient loadings were experimentally varied. In the absence of manipulation, these lakes were net heterotrophic according to all three approaches. NEP (NEP = GPP-*R*) was consistently negative and averaged -35.5 ± 3.7 (standard error) mmol C m^{-2} d^{-1}. Nutrient enrichment, in the absence of strong planktivory, tended to cause increases in estimates of both GPP and *R* (estimated from the continuous O_2 data) but resulted in little change in the GPP/*R* ratio, which remained <1, or NEP, which remained negative. When planktivorous fish dominated the food web, large zooplankton were rare and nutrient enrichment produced positive values of NEP by all three methods. Among lakes and years, daily values of NEP ranged from -241 to $+175$ mmol m^{-2} d^{-1}; mean seasonal NEP was positive only under a combination of high nutrient loading and a planktivore-dominated food web. Community *R* is significantly subsidized by allochthonous sources of organic matter in these lakes. Combining all lakes and years, we estimate that $\sim$26 mmol C m^{-2} d^{-1} of allochthonous origin is respired on average. This respiration of allochthonous organic matter represents 13 to 43% of total *R*, and this fraction declines with increasing GPP.

Primary production and respiration are the major metabolic pathways by which organic matter is produced and destroyed. Gross primary production (GPP) is the gross fixation of inorganic C by photosynthesis. Respiration (*R*) is the remineralization of organic C to CO_2. Net ecosystem production (NEP) is the difference between GPP and ecosystem *R*. NEP, which can be positive or negative, represents the overall metabolic balance of an ecosystem (Howarth et al. 1996). When NEP is positive, GPP exceeds *R*, and the system can export or store organic C (Schindler et al. 1972). When NEP is negative, *R* exceeds GPP and the system respires more organic C than was produced by primary production within the system's boundaries. Sustained negative values of NEP, or GPP/*R* ratios <1, imply that a system's respiration is subsidized by organic matter that was imported from outside of its boundaries.

In aquatic ecosystems we recognize several levels of control for both primary production and respiration but have little expectation for the controls of NEP. Primary production is frequently limited by the supply of plant-limiting nutrients (largely P and N, e.g., Elser et al. 1990). The extent to which this nutrient supply increases algal biomass is under partial control of the food web. When large-bodied zooplankton, particularly *Daphnia*, are abundant, they can crop new primary production, which suppresses blooms and prevents further increases in primary production (Mazumder and Lean 1994). These primary consumers of phytoplankton can in turn be controlled by the size and community structure of their major predators, particularly small fishes. These small fishes are often under strong predatory control from larger piscivores. Thus, the structure of the fish community can indirectly regulate primary production at a given nutrient input rate (Carpenter et al. 1999). The strength of such cascading trophic interactions appears to vary greatly among systems and conditions (Baca and Drenner 1995; Pace et al. 1999)

The light climate, a function of light extinction and mixing depth, can also regulate primary production (Fee et al. 1996). In most lakes, the major light-attenuating agent is colored dissolved organic C (CDOC), which has multiple effects on primary production. CDOC absorbs photosynthetically available light, which makes the water column darker. This light absorption tends to warm and stabilize the surface waters, which results in a squeezing of the photic and mixing zones into a shallow layer. On an areal basis, CDOC therefore tends to reduce primary production (Carpenter et al. 1998) even though algal biomass may remain large in surface waters (Nurnberg 1999).

The regulation of respiration is less well studied but is related, in part, to the supply of labile organic C. Planktonic respiration tends to covary with planktonic primary production (del Giorgio and Peters 1994). Phytoplankton can be a

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[1] Corresponding author (colej@ecostudies.org).

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significant component of planktonic respiration (Pace and Cole 2000), and the metabolism of both zooplankton and bacterioplankton tends to covary with primary production (White et al. 1991). However, aquatic ecosystems receive organic carbon from multiple autochthonous and allochthonous sources potentially uncoupling ecosystem respiration from planktonic primary production (Wetzel et al. 1972; Howarth et al. 1996). Primary production by phytoplankton, macrophytes, and benthic algae within the system form the autochthonous basis of the food web. Terrestrial inputs of particulate and dissolved organic C represent the potential for an allochthonous basis for the food web. Although autochthonous primary production may be readily metabolized, the organic C inputs from the watershed, particularly DOC, are considered to be relatively refractory. There is good reason for this notion. Terrestrially derived DOC represents C that survived microbial attack in the watershed and in the soil system. Bioassays that measure the short-term lability of DOC in lakes suggest that a relatively small fraction ($<15\%$) is labile to microbial use (Sondergaard et al. 1995). In contrast, a number of independent lines of evidence suggest that some of this terrestrial DOC is respired once it enters aquatic ecosystems. In some oligotrophic systems, both total planktonic respiration (del Giorgio and Peters 1994; Duarte and Agusti 1998) and the respiration of the bacterioplankton component (del Giorgio et al. 1997) tend to exceed gross primary production. A majority of lakes and rivers tend to be supersaturated in CO_2 and are net exporters, not consumers, of inorganic C (Kling et al. 1991; Cole et al. 1994; Kratz et al. 1997). This observation is consistent with R in excess of GPP, although other explanations are possible (Cole et al. 1994; McConnaughey et al. 1994). Further, budgets of DOC (Dillon and Molot 1997) models that couple lakes with their watersheds (del Giorgio et al. 1999; Caraco and Cole 2000) both suggest that a considerable fraction of the DOC that enters a lake from the watershed is in fact respired within the lake. Since the loading of allochthonous organic C can greatly exceed autochthonous primary production (Caraco and Cole 2000), the respiration of even a relatively small fraction of it can potentially have a major impact on the metabolic balance of an ecosystem.

In this study, we use three independent approaches to investigate how NEP responds to a set of whole-lake experiments in which we manipulated the supply of exogenous nutrients and fish community structure in a series of small lakes in northern Michigan. We reasoned that nutrient loading, independent of food web structure, would increase the rates of both GPP and R. The experiments allowed us to examine how the relative rates of these processes changed, any consequent shifts NEP, and under what conditions the systems were net autotrophic (NEP > 0) versus net heterotrophic (NEP < 0). We hypothesized that dominance of the food web by planktivorous fish would, through cascading trophic interactions, allow for the accumulation of algal biomass and an increase in NEP.

Methods

Four lakes are included in this study, three of which were manipulated (Table 1). The lakes are all situated within a 1-km radius and are located at the University of Notre Dame Environmental Research Center (UNDERC) near Land o' Lakes, Wisconsin (89°32′W, 46°13′N). Paul Lake, which was not manipulated throughout the study, had significant populations of piscivorous fish (*Micropterus salmoides*) throughout. Few planktivorous fish of any kind appeared, except during brief periods when young of the year *M. salmoides* were abundant (Post et al. 1997). Consequently, large-bodied cladocerans (*Daphnia* and *Holopedium*) were the general dominant macrozooplankters in Paul Lake (Post et al. 1997). The other three lakes received nutrient additions (inorganic P and N) from 1993 through 1997 at several different loading rates (Table 1). In 1998 nutrients were not added to any of the lakes. Because P was the plant-limiting nutrient in the lakes, we express these loads as areal P (μmol P m^{-2} d^{-1}); in all cases nutrients were applied as weekly additions, and inorganic N (ammonium nitrate) was added with the P at atomic ratios of >30 (Carpenter et al. 1998). Nutrient loads, including background ambient loading, varied among years from 8.8 to 194 μg P m^{-2} d^{-1} (Houser 1998; Pace and Cole 2000). With one exception, loads were held nearly constant among the manipulated lakes within each year. In 1995 East Long Lake received a higher load than the other two (Carpenter et al. 1998).

Piscivorous fish were removed in from Peter Lake in 1991, and the lake was stocked with an assemblage of small planktivorous minnows: fathead minnows (*Pimephales promelas*), redbelly dace (*Phoximus pos*), and golden shiner (*Notemigonus chrysoleucas*), which remained the dominant fish throughout the study. Planktivory was intense, and large-bodied *Daphnia* were uncommon. The dominant zooplankters were generally rotifers and small copepods (*Cyclops varicans rubellus*) and small cladocerans (*Bosmina longirostris*), except during brief periods when minnows declined and *Daphnia* outbreaks occurred (Schindler et al 1997; Pace et al. 1998).

The other two lakes were formed by placing two curtains in Long Lake in 1991. West Long Lake had piscivorous fish (*M. salmoides* and *M. dolomieu*) and a food web structure that was very similar to the reference lake (large zooplankton, mostly *Daphnia*). East Long Lake became rich in DOC and acidic due to its hydrologic isolation (Christensen et al. 1996). Through most of the study, East Long Lake had few pelagic fish of any type and planktivory was low. Zooplankton were generally dominated by large-bodied *Daphnia* during the period we discuss here (1992–1998). The western curtain was removed after the 1996 field season, which enlarged the area of the West Long Lake basin. East Long Lake was unaffected by this curtain removal.

All four basins are similar in size and hydrology with water residence times near 2 yr (Cole and Pace 1998; Table 1). The lakes are relatively shallow (mean depths from 3 to 5 m) and strongly stratified below a well-defined, isothermal, mixed layer (1.5 to 4 m among lakes and times). Although there are differences in the chemistry of the four basins, all can be characterized as soft water (pH range 5.5 to 8; dissolved inorganic C [DIC] 40–140 μM), moderately rich in dissolved organic C (DOC, 333 to 1,416 μmol C L^{-1}), and poorly buffered (Reche et al. 1999; Pace and Cole 2000).

Table 1. Characteristics of the lakes in this study and their manipulations. Nutrients (inorganic P and inorganic N) were added to three of the lakes during 1993–1997 at weekly time steps. The application rate varied among years but was kept uniform among lakes; N : P ratios always exceeded 30 : 1 (by atoms). *See text* and, for greater detail, Carpenter et al. (in press). For some of the variables we show the value under ambient, premanipulation conditions in 1992 and also in 1996, the fourth year of nutrient enrichment. We also indicate the years of sampling for the dissolved gasses (CO_2 and O_2).

	Paul	Peter	East Long	West Long	References
Area (ha)	1.74	2.65	2.31	3.40	Cole and Pace (1998)
Mean depth (m)	3.9	6	4.9	4.4	Carpenter and Kitchell (1993); Christensen et al. (1996)
Mixed layer depth (m)	1.5–4	1–4.5	1–2	1–2.5	This study
Ground water load (cm d^{-1})					
DOC (μmol L^{-1})	444	506	1128	688	Pace and Cole (2000)
P-load (μmol P m^{-2} d^{-1})					
Ambient 1992	9.3	9.7	20.0	14.2	Pace and Cole (2000)
Fertilized 1996	11.3	196.7	200.0	203.2	Carpenter et al. in press
Mean mixed layer Chlorophyll *a* (μg L^{-1})					
Ambient 1992	4.1	4.9	7.8	4.0	Carpenter et al. (1998); Pace and Cole (2000)
Fertilized 1996	3.5	63.9	28.5	13.6	
Mean size crustacean zooplankton (mm)					
Ambient 1992	0.66	0.44	0.70	0.78	Pace and Cole (2000)
Fertilized 1996	0.58	0.46	0.75	0.89	Carpenter et al. in press
Fish community structure	Piscivore	Planktivore	Few fish	Piscivore	Schindler et al. (1997); Carpenter et al. (1998)
Nutrients added	Never	1993–1997	1993–1997	1993–1997	
Weekly *p* CO_2 measurements	1992–1998	1992–1998	1992–1998	1992	
Weekly O_2 measurements (Winkler)	1991–1998	1991–1998	1991–1998	1991–1998	
Continuous O_2 measurements (Sonde)	1995–1998	1994–1998	1995–1998	1994–1995	

Continuous diel oxygen: We deployed in each basin Endeco-YSI sondes (model UPG-6000) equipped with a rapid-pulsed oxygen-temperature electrode (model 6030). Each week, prior to deployment, each sonde was calibrated in air, with a correction for barometric pressure. This air calibration was checked each 48 h by placing the sondes in water-saturated air for 30 to 60 min before redeploying them. The calibration of each sonde was additionally tested during each deployment by taking discrete dissolved oxygen (DO) samples for Winkler titration (below) during the deployments. The sondes were removed each week for cleaning, maintenance, and recalibration. We programmed the sondes to record DO and temperature every 5 min. During 1995–1998, using two sondes, each basin was monitored for 1 to 2 d of each week during the ~15-week field season (mid-May through early September). During 1994, measurements were made in only two of the lakes (West Long and Peter Lakes), also for 1 to 2 d per week. For the entire period, 373 lake-days of continuous oxygen were successfully recorded. We deployed the sondes at approximately 0.5-m depth near the centers of each lake. The upper mixed layers in these lakes ranged from about 1.5 to 4 m deep (Table 1) and always incorporated the 0.5 m. Note that oxygen and CO_2 (below) in the upper mixed layer are affected by both pelagic processes and benthic processes in the ring of littoral sediments that intersects this mixed layer.

We used the record from the sonde deployment to calculate NEP for each 5-min interval over each 24-h period. The change in DO in each 5-min interval is due to two process, NEP and diffusive exchange with the atmosphere (*D*). We will use positive numbers to denote the addition of O_2 to the system and negative ones for removal. Thus,

$$\Delta O_2 = NEP + D. \tag{1}$$

Diffusion can be positive or negative and is calculated as

$$D = k(O_2 - O_{2\ sat}), \tag{2}$$

where O_2 is the measured oxygen concentration in the water, $O_{2\ sat}$ is what the concentration in the water would be were it in equilibrium with the atmosphere, and *k* is the coefficient of gas exchange for O_2 at a given temperature. In systems, *k* is generally modeled as a function of wind speed (MacIntyre et al. 1995). From 1994 through 1996 we deployed, on a floating raft in the center of the lakes, an anemometer (R. M. Young) connected to a data logger (Campbell 6250). Wind speed was recorded at 2-min intervals 1-m above the lake surface. In 1994 we deployed the raft on a rotating schedule on two of the lakes. Finding no differences among lakes, we deployed the raft on Peter Lake in 1995 and 1996. We assumed a neutrally stable boundary layer and used the empirical equation of Smith (1985) to estimate wind at 10 m above the lake surface. k_{600} (*k* for a Schmidt number of 600) was estimated as a function of wind speed from the low-wind equations of Cole and Caraco (1998). *k* for O_2 and CO_2 (below) was calculated for each temperature and each gas from the estimate of k_{600} and the ratio of the Schmidt numbers according to Jahne et al. (1987).

Rearranging Eq. 1, we computed NEP for each 5-min period and summed these for each 24-h period to produce a daily value for NEP. NEP is also equal to the difference between GPP and total ecosystem respiration, R. Total daily ecosystem respiration consists of a value during the daylight (R_{day}) and a value during night (R_{night}). Thus

$$\mathrm{NEP} = \mathrm{GPP} - (R_{\mathrm{day}} + R_{\mathrm{night}}). \tag{3}$$

During darkness GPP is 0. Thus, at night, the change in O_2 in any 5-min interval (ΔO_2) is caused by respiratory consumption of oxygen (R_{night}) and diffusive exchange with the atmosphere:

$$\Delta O_2 = R_{\mathrm{night}} + D. \tag{4}$$

During daylight the change in oxygen in any 5-min interval is caused by the difference between gross primary production, daytime respiration, and diffusion,

$$\Delta O_2 = \mathrm{GPP} - R_{\mathrm{day}} + D. \tag{5}$$

We can directly measure NEP and R_{night}. Since we do not have a direct measurement of R_{day}, both GPP and R must be estimated by assuming a value for R_{day}. We assume, in keeping with other literature (*see* Carignan et al. 2000), that the hourly value of R_{day} and R_{night} are equal and discuss the consequences of this assumption below.

Static CO_2 flux: Direct measurements of the partial pressure of CO_2 (pCO_2) were made once per week in the surface water of each lake from 1992 through 1998. Samples were taken in the surface water at 0.05-m depth in midmorning (0900–1100 h). We used the head space equilibration method of Cole et al. (1994), in which a large volume of water (2 liters) is equilibrated with a small volume of air (0.05 liters) at ambient temperature in the field. The extracted gas was analyzed on a Shimadzu GC-AIT gas chromatograph with a TCD detector against NBS gas standards. At each sampling, replicate extractions were performed and a sample of the ambient atmosphere was also taken. We calculated the concentration of CO_2 in the water from the measurement of pCO_2 and Henry's constant at ambient temperature; the saturation concentration of CO_2 was computed in the same way using the atmospheric pCO_2. The flux equation for CO_2 is analogous to that of O_2 but includes a factor, α, which represents the chemical enhancement of diffusion, which occurs at high pH and is most significant when the stagnant boundary layer is large (low wind speeds). We used the approach in Wanninkhof and Knox (1996) to compute α.

Static O_2 flux: Direct measurements, using Winkler titrations, of O_2 were also made once per week in the surface water of each lake from 1992 through 1998. Samples were taken in midafternoon (1300 to 1500 h) in the surface water of each lake by peristaltic pump into quadruplicate 300-mL BOD bottles. Winkler titrations were performed on 100-mL aliquots that were weighed on an analytical balance to assure accurate volume determinations, and endpoints were determined colorometrically (Pace and Cole 2000). The coefficient of variation for the quadruplicate determinations averaged <2% (Pace and Cole 2000), which is slightly less precise than using the revised Winkler procedure of Carignan et al. (1998). We used these values to determine the diffusive flux into and out of the lakes using Eq. 2.

In order to translate volumetric measurements (e.g., O_2 concentration) for use with areal-based estimates (CO_2 and O_2 atmospheric exchange), we multiplied the volumetric O_2 change and the depth of the mixed layer, which we estimated from detailed profiles of O_2 and temperature taken at weekly intervals using a YSI model 500 oxygen-temperature probe. The mixed layers (the layer within which both O_2 and temperature were uniform) ranged from 1.5 m to about 4 m. (Table 1).

The methods for other analyses (including chlorophyll, phytoplankton primary production, DOC, etc.) have all been described in detail elsewhere (Carpenter et al. 1998; Pace and Cole 2000, and references therein). Briefly, samples for DOC were filtered through Whatman GF/F filters and measured using an Astro model 2001 (prior to 1994) and Shimadzu model 5000 (1994–1998) TOC analyzer; chlorophyll *a* (Chl *a*) was determined fluorometrically (Holm-Hansen and Riemann 1978); and phytoplankton primary production is based on ^{14}C incubations over depth and a model (Carpenter et al. 1998). The results presented here include much, but not all, of the ice-free season. Sampling began in mid-May, a few weeks after ice out, and ended in mid-September (6 to 8 weeks prior to freezing). In the analyses presented here, when we use seasonal means, these are means of all dates sampled in each field season (mid-May through mid-September). Some of our other publications use a mid-June–August basis, so some values differ slightly (Schindler et al. 1997).

Results

Measurement and fluxes of O_2—Wind and atmospheric exchange: These lakes are low-wind sites with mean hourly wind, corrected to a height of 10 m, of only 1.5 m s^{-1} (Fig. 1A). Wind events above 3 m s^{-1} are rare, occurring <3% of the time. At these low wind speeds, the gas exchange coefficient is low and relatively insensitive to wind speed (MacIntyre et al. 1995). Based on the relationship between wind and k_{600} in Cole and Caraco (1998), k_{600} for the lakes in this study would average 0.48 ± 0.06 (SD) m d^{-1} (Fig. 1B). Because estimated k_{600} is both low and in a very tight range, we used a constant value of 0.48 m d^{-1} as the basis for the calculations. For 1995 and 1996, the years for which we have complete on-the-lake wind measurements, we compare these analyses to the results obtained using the actual hourly wind data (below).

Calibration and sensitivity of sondes: The sondes retained calibration throughout the deployments and reproduced an unbiased estimate of the Winkler titration values. For 176 points for which we have Winkler and sonde values at the same time, the two were well correlated ($r^2 = 0.9$), with a linear regression slope (1.03 ± 0.03 [SD] for Model I and 1.14 for Model II) close to 1.0. For 70% of the measurements, the sonde value was within 10 μM of the Winkler; for only 5% did the values diverge by 30 μM or more. More importantly, the residuals of a sonde vs. Winkler plot are distributed evenly, which demonstrates that Winkler and sonde measurements provide unbiased estimates of each other. Since the calculations for the continuous O_2 record de-

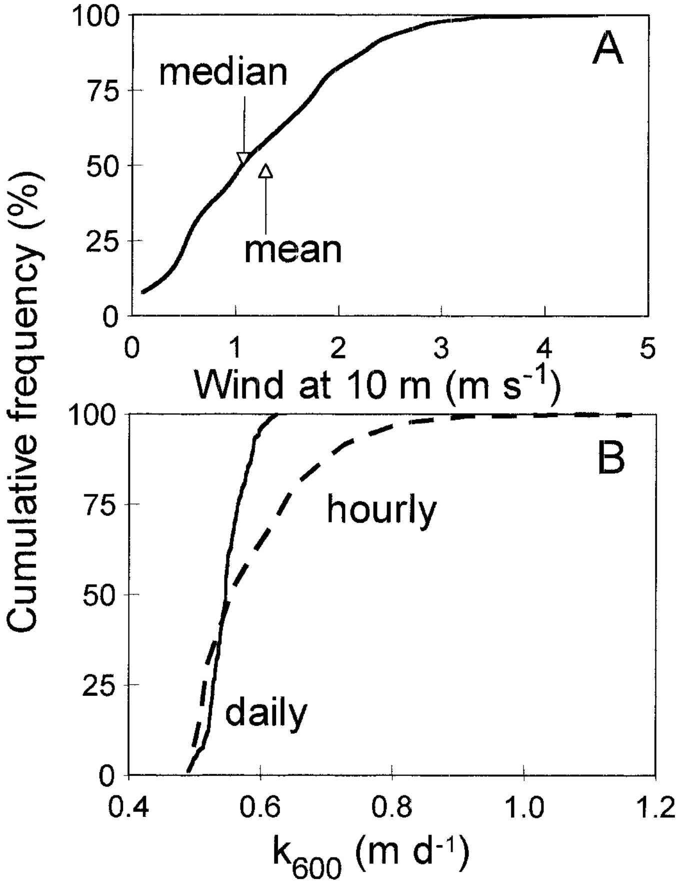

Fig. 1. (A) Cumulative frequency plot of hourly wind speed measured on floating rafts directly on the lakes. (B) Cumulative frequency plot of hourly and daily gas piston velocities (k_{600}) calculated from the equations in Cole and Caraco (1998) and the data in (A).

pend on the entire suite of points, the reasonably good agreement of these spot checks is encouraging.

By comparing the initial air calibration at the start of the deployment with values in saturated air 48 and 96 h into each deployment, we ascertained that electrode drift occurred but was not large. Expressed as a rate of change in water at the appropriate temperature, drift averaged -0.30 ± 0.4 (SD) μmol L^{-1} d^{-1}, which is <5% of mean NEP (below) and a small fraction of the diel excursions of O_2 that we measured.

Diel excursions of O_2 were evident on nearly every deployment, even in the lakes that were not fertilized (Fig. 2A). In Paul Lake (unmanipulated, Table 1), for example, although the difference between the O_2 minimum (generally just postsunrise) and maximum (generally just postsunset) was only <10 μM, clear and consistent increases of O_2 during light and decreases during darkness were seen due to the large amount of data recorded (288 points in 24 h). Under a regime of fertilization, these diel excursions tended to be amplified. In the example shown in Fig. 3B, Peter Lake O_2 changes by about 25 μM between dusk and dawn.

Epilimnetic NEP: From the sonde deployments (e.g., Fig. 2) we can directly compute in situ NEP and estimate (assuming that hourly R_{day} = hourly R_{night}) GPP and R for the upper mixed layer. This layer includes the water column to the bottom of the mixed layer (~1 to 4 m depending on lake and time; Table 1) and the ring of sediments, above the thermocline, intersected by this depth. In Fig. 3, we show the results of the 1997 deployments, expressed volumetrically, for each lake. During 1997, the three manipulated lakes were receiving additional nutrients (N plus P) at a high rate (103 μmol P m^{-2} d^{-1}). In the unfertilized reference lake (Paul) GPP and R tended to be the least variable over the season. Since measured NEP was negative, daily (24 h) R exceeded GPP on nearly every deployment, resulting in GPP/R ratios consistently <1. Fertilization (East Long, West Long, and Peter Lakes) resulted in greater seasonal variance and increased amplitude in both GPP and R. Intriguingly, NEP was also generally negative in West and East Long Lakes, despite the large nutrient enrichment. NEP was positive in 1997 only in Peter Lake, which had a planktivore-dominated fish community and lacked large zooplankton.

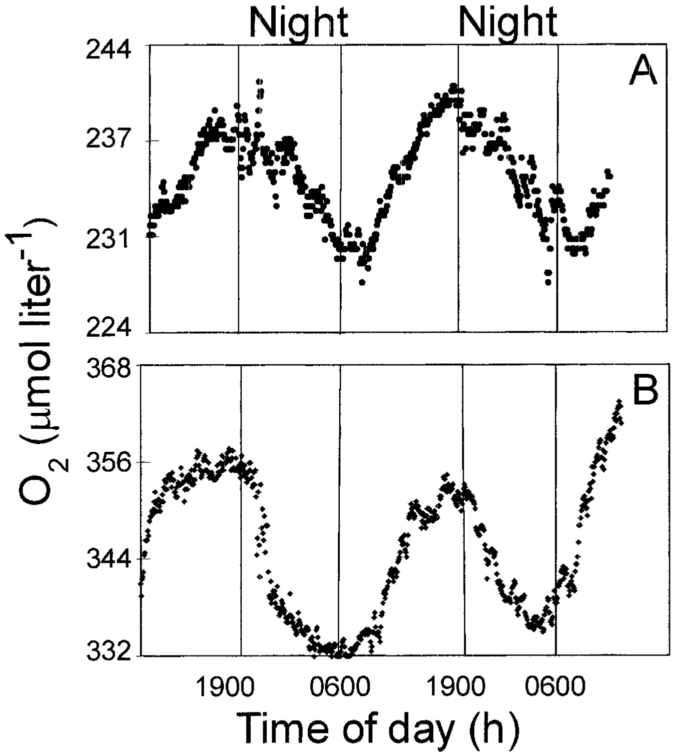

Fig. 2. Diel excursions of dissolved oxygen measured by in situ deployment of sondes on two representative dates, in July 1997, in (A) Paul Lake (unmanipulated) and (B) Peter Lake (planktivore food web and nutrient additions—*see text*). Note the scale differences.

Weekly CO_2 gas fluxes—The weekly measurements of the partial pressure of CO_2 (pCO_2) mirrored the NEP patterns obtained by the continuous O_2 data. When pCO_2 in the water is greater than that in the overlying atmosphere, the lake is a net source of CO_2 to the atmosphere, a condition that is consistent with net heterotrophy (negative NEP). As expected, pCO_2 in the water exceeded pCO_2 in the atmosphere

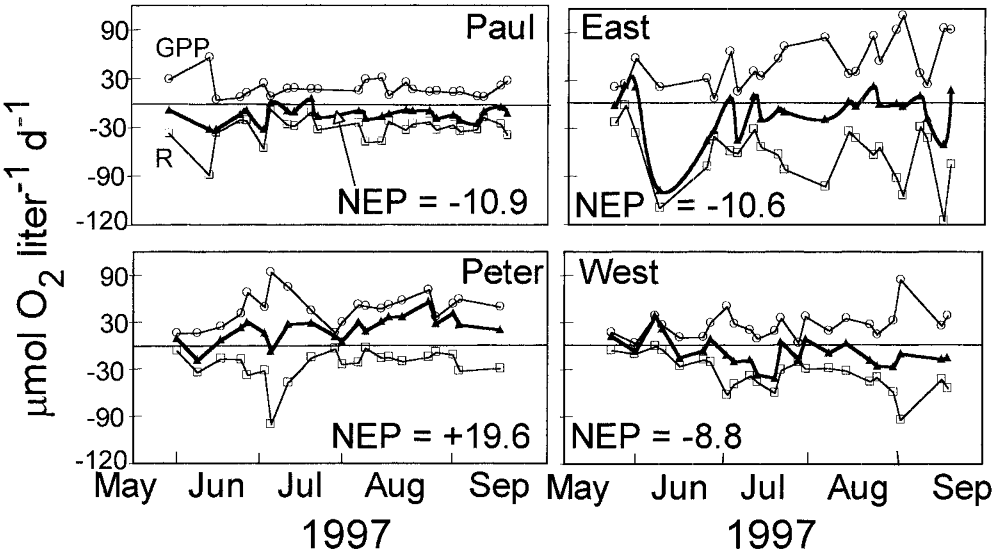

Fig. 3. Estimates of volumetric GPP (open circles), R (open squares), and NEP (filled triangles, heavy line) in all four lakes during 1997. All values are corrected for atmospheric exchange (*see text*). R is presented as a negative number to facilitate plotting on the same graph as GPP. Seasonal mean values for NEP for each lake are given on the graph. Negative values of NEP mean the lake consumes more oxygen in respiration than it produces by gross primary production (net heterotrophy). During 1997 Paul Lake was not manipulated and piscivore dominated; the three other lakes received N plus P (103 μmol P m^{-2} d^{-1}). Peter Lake was planktivore dominated and was the only lake that lacked large zooplankton.

when the lakes were not manipulated (Paul Lake all years, all lakes 1992 and 1998; Fig. 4A) or when nutrients were added in the absence of strong planktivory (East and West Long Lakes 1993–1997; Fig. 4A). In the surface water of the unmanipulated lake the partial pressure of CO$_2$ (pCO$_2$) exceeded the value in the atmosphere nearly every time the lake was sampled, ranging from about 600 μatm to 1,500 μatm over the seasonal cycle (Fig. 4A). Under a regime of high nutrient loading and a planktivore-dominated food web, pCO$_2$ was strongly undersaturated with respect to the atmosphere, consistent with the net autotrophy (positive NEP) obtained by the continuous O$_2$ approach. During the years of high fertilization (1995, 1996, and 1997), only a single measurement in Peter Lake exceeded the atmospheric equilibrium value (Fig. 4A). In both East and West Long Lakes, pCO$_2$ was slightly more variable but consistently more supersaturated than undersaturated (Fig. 4A). These trends expand the pattern reported by Schindler et al. (1997) for the first 3 yr of the experimental manipulations.

Weekly O$_2$ fluxes—The weekly measurements of O$_2$ obtained by Winkler titration matched the pattern of NEP shown by the continuous O$_2$ data and mirrored the pCO$_2$ record (Fig. 4B). When the partial pressure of O$_2$ (pO$_2$) in the water is lower than that in the overlying atmosphere, the lake is a net sink for O$_2$ from the atmosphere, a condition that is consistent with net heterotrophy (negative NEP). pO$_2$ in the water was consistently below the atmospheric value when the lakes were not manipulated (Paul Lake all years, all lakes 1992 and 1998) or when nutrients were added in the absence of strong planktivory (East and West Long

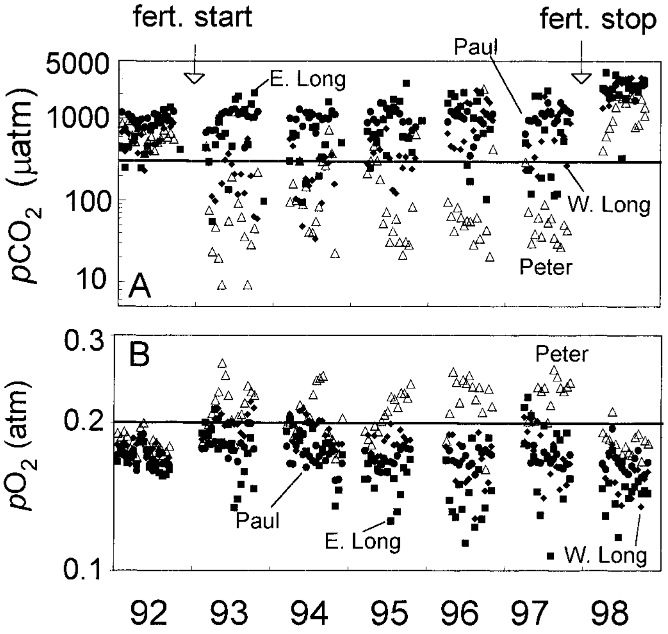

Fig. 4. (A) pCO$_2$ and (B) pO$_2$ in the UNDERC lakes from 1992 through 1998. In both panels, weekly values are shown for Paul Lake (filled circles), East Long Lake (filled squares), Peter Lake (open triangles), and West Long Lake (filled diamonds). Note log scale. (A) The horizontal line at 380 μatm is the average measured value for pCO$_2$ in the atmosphere at this location. (B) The horizontal line at 0.2 atm represents pO$_2$ in the atmosphere. The start and stop of fertilization is indicated with arrows.

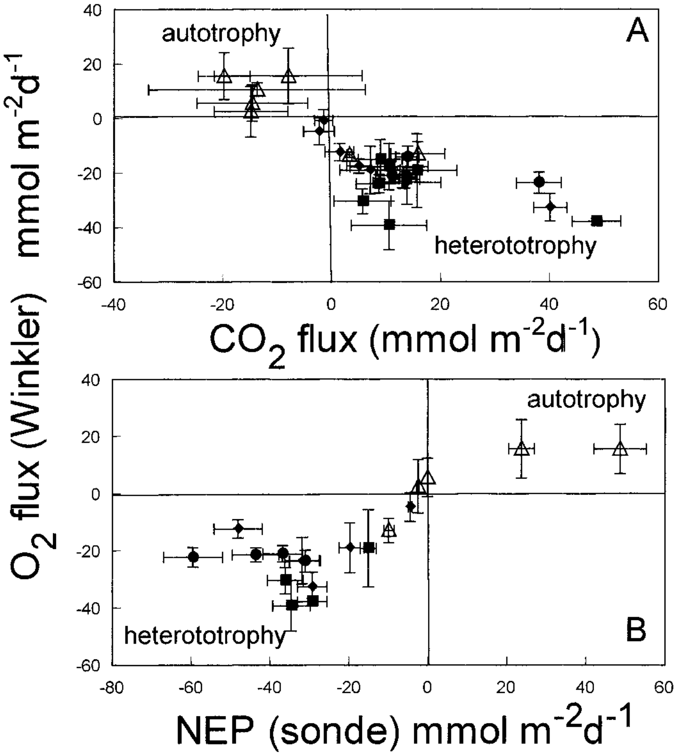

Fig. 5. Comparisons of net ecosystem production (NEP) based on (A) the weekly fluxes of CO_2 and O_2 and (B) continuous diel measurement (sonde) and weekly O_2. In both panels symbols are Paul Lake (filled circles), East Long Lake (filled squares), Peter Lake (open triangles), and West Long Lake (filled diamonds). Plotted are the mean seasonal values (with 95% CI). Positive values denote net gas fluxes from the lake to the atmosphere (net autotrophy for O_2 and net heterotrophy for CO_2). Note that in (A) points are means of weekly values from 1992 through 1998; in (B) sonde measurements started in 1994 in Peter and Long Lakes and 1995 in East Long and Paul Lakes, so there are fewer means in (B).

Lakes 1993–1997). Only the combination of fertilization and strong planktivory (Peter Lake, 1993–1997) resulted in pO_2 in the water exceeding the atmospheric value. In the years of high fertilization, pO_2 in Peter Lake exceeded the atmospheric value on nearly every sampling (Fig. 4B). Considering that these O_2 measurements were taken in midafternoon (1300–1500 h), when O_2 is near its maximal daily value, the persistent undersaturation of O_2 in the other lakes (Paul, East Long, and West Long Lakes) is a very striking result.

From the values of pCO_2 and pO_2 we computed the fluxes of CO_2 and O_2 into and out of the lake using Eq. 2 (Fig. 5A). Seasonal mean CO_2 flux ranged from 50 mmol m^{-2} d^{-1} (out of the lake, negative NEP) in East Long Lake to −15 mmol m^{-2} d^{-1} (into the lake, positive NEP) in fertilized Peter Lake (Fig. 5A). Seasonal mean O_2 flux ranged from −40 mmol m^{-2} d^{-1} (into the lake, negative NEP) in East Long Lake (negative NEP) to +15.5 mmol m^{-2} d^{-1} (out of lake, positive NEP) in fertilized Peter Lake (Fig. 5B). The patterns and magnitudes of net autotrophy and net heterotrophy agreed reasonably well among lakes and years. The fluxes of CO_2 and O_2 were significantly correlated ($r^2 = 0.66$, $p < 0.0001$); the slope [−0.75 ± 0.22 (95% confidence interval), Model II slope = −0.92] shows the magnitudes of the estimates to be comparable. Note that by both the O_2 and CO_2 approaches, Peter Lake (1993–1997) is assigned to the autotrophic quadrant and all other lake-years to the heterotrophic quadrant. The only exception was West Long Lake in 1993 and 1994, which is slightly autotrophic based on CO_2 and slightly heterotrophic based on O_2, but very near NEP = 0 by both measures. Since the CO_2 data were midmorning samples and the O_2 were afternoon samples and were not necessarily taken on the same day each week, the agreement, although not exact, is striking.

We can compare our continuous oxygen (sonde) estimate of NEP to the two weekly flux estimates based on CO_2 or Winkler O_2 for the years for which we have overlapping data (Fig. 5B). Since we have sonde deployments in 1994–1998 for Peter and West Long Lakes and 1995–1998 for Paul and East Long Lakes (Table 1), the plot appears different from that in Fig. 5B. Nevertheless, the sonde-based estimate is well correlated to both the weekly O_2 flux ($R^2 = 0.64$, $p < 0.001$) and to the weekly CO_2 flux ($R^2 = 0.57$, $p < 0.001$) and of comparable magnitude to both. Sonde-based NEP ranged from −59 mmol m^{-2} d^{-1} (net heterotrophy) to +48 mmol m^{-2} d^{-1} (net autotrophy), which is 1.6 to 1.9 times as large as the range seen in the weekly O_2 or CO_2 estimates, respectively. Since the sonde uses continuous diel O_2 data, the larger dynamic range is not surprising. Although the sonde-based NEP ranks the lakes in the same order along a heterotrophy to autotrophy gradient, only Peter Lake (planktivores) during 1996 and 1997 (high fertilization years) averages net autotrophic for the entire season (Fig. 5B). It is again not surprising that midday O_2 and midmorning CO_2 estimates would tend to overestimate net autotrophy compared to continuous diel data.

Patterns of GPP and R—By assuming R_{day} and R_{night} are equal, we can estimate GPP and R from the sonde data. Considering all of the individual deployments together, among lakes and years, R varied from 0.3 to 416 mmol m^{-2} d^{-1}, with highest values occurring in the fertilized lakes. GPP varied over a nearly identical range (0.9 to 418 mmol m^{-2} d^{-1}). Although GPP and R were correlated for the entire data set ($p < 0.001$), the correlation was not strong ($r^2 = 0.35$), in part because the relationship between GPP and R differed under the different manipulations.

Although the absolute magnitudes of GPP and R are sensitive to the assumption that R_{day} and R_{night} are equal, the values of the GPP/R ratio are much less so, and no assumption about R_{day} and R_{night} can alter whether GPP/R is greater or less than 1.0 (*see Discussion*). A frequency plot for the individual deployments shows that in the unmanipulated reference lake (Paul) GPP/R was >1 only 10% of the time, with most ratios between 0.4 and 0.8 (Fig. 6). Nutrient enrichment in the absence of strong planktivory (East and West Long Lakes) resulted in a spreading of these frequencies and an increase in the frequency above 1.0, so that East and West Long Lakes had GPP/R >1 23% and 24% of the time, respectively. Nutrient enrichment in the presence of strong planktivory (Peter Lake) resulted in a very large increase in the frequency of GPP/R > 1 (61%). Note that these fre-

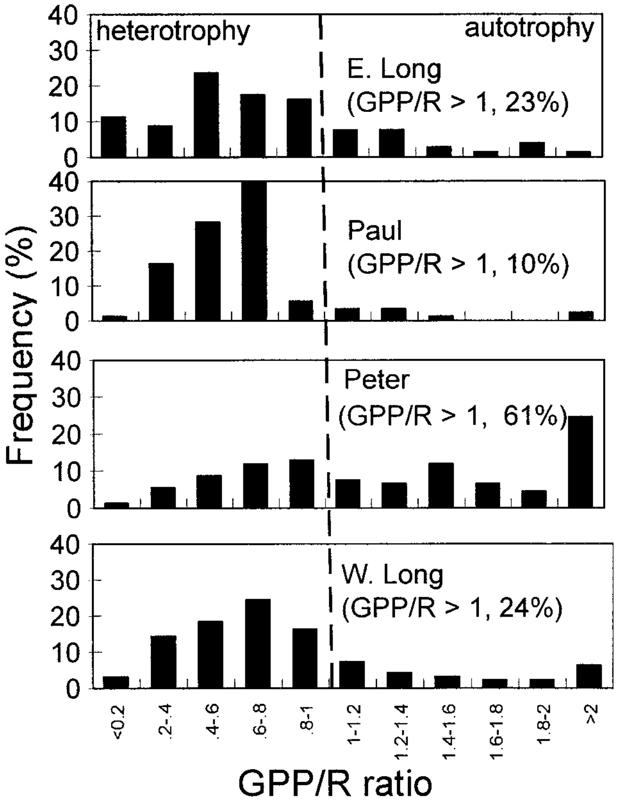

Fig. 6. The ratio of GPP/*R* from the continuous sonde data shown by frequency for each lake. Data for all years are combined in these plots. In this analysis we assume that R_{day} and R_{night} are equal (*see text*).

quency plots include both fertilized and unfertilized years for the manipulated lakes.

Regulation of GPP and R—From the calculated values of NEP and the estimates of *R* and GPP for each year (Fig. 4), we computed seasonal mean values for each lake and year. We show these on a volumetric basis in Fig. 7 plotted against the P load each lake received in each year. Combining all lakes and years, both linear regressions and Spearman rank correlations show that the magnitude of both *R* and GPP increased significantly ($p < 0.01$) with increasing P load. On the other hand, NEP did not track P load for the data set as a whole. NEP remained negative in all lakes and years that had a dominance of large zooplankton (e.g., piscivore food web). NEP was positive only under a planktivore food web and in the presence of large additions of nutrients. Average NEP was never positive in any lake with large zooplankton, even at the highest nutrient loads.

The sonde-based estimates of GPP production tracked other measures of eutrophy and primary production in these lakes. GPP was strongly related to the amount of algal biomass (as Chl *a*) on both volumetric ($p = 0.006$) and areal ($p = 0.0001$) bases. The lowest values of GPP (20 μmol L^{-1} d^{-1}) occurred in the unmanipulated lake (Paul) and in the manipulated lakes in 1998 after nutrient additions ceased (all lakes 1998). Highest values (50 to 60 μmol L^{-1} d^{-1}) occurred at high nutrient loading in Peter and East Long Lakes. Our sonde-based measurements of GPP agreed in pattern with ^{14}C-based model estimates of phytoplankton primary production in the same lakes (Carpenter et al. 1998), and the two estimates of primary production were significantly correlated ($r^2 = 0.6$, $p < 0.001$).

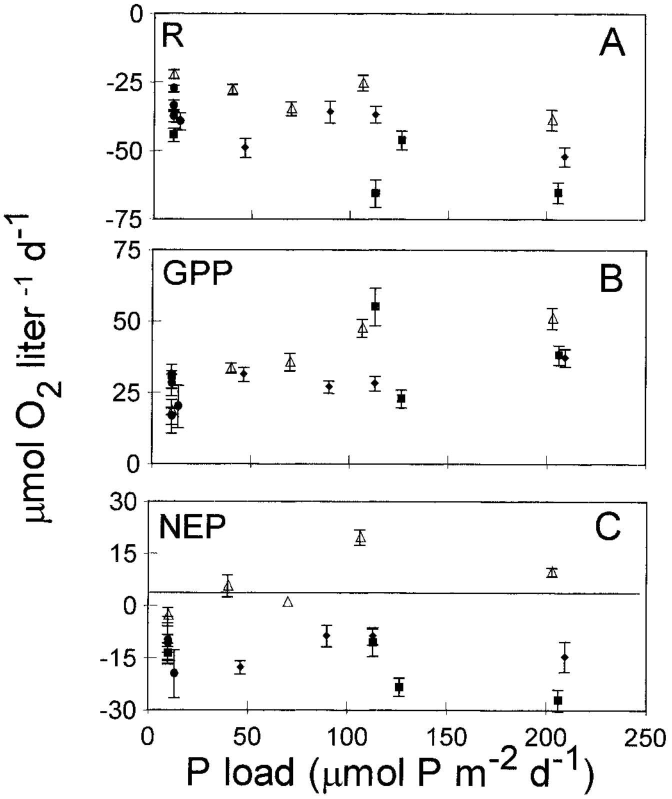

Fig. 7. (A) Respiration, (B) gross primary production, and (C) net ecosystem production for all lakes and years, plotted as a function of nutrient loading, expressed in terms of P. Paul Lake (filled circles), East Long Lake (filled squares), Peter Lake (open triangles), and West Long Lake (filled diamonds). Plotted are the seasonal mean values; the error bars denote 90% confidence limits.

Although respiration tended to increase with increasing algal biomass, it was not related to it in a consistently significant way among lakes ($p > 0.25$, $r^2 = 0.12$). Rather, the magnitude of *R* increased with increasing DOC concentrations ($r^2 = 0.74$, $p < 0.001$). In these lakes, the DOC pool (330 to 1,500 μmol C L^{-1} among lakes; Table 1) is large in comparison to algal biomass (<0.16 μmol C L^{-1} in the unmanipulated lakes and up to 16 μmol C L^{-1} in the most algal-rich lakes), and the loading of DOC from the watershed is large in comparison to autochthonous primary production. Further, much of the respiration measured by the sondes likely occurs in the epilimnetic sediments that would decouple it from measurements of planktonic metabolism alone.

Discussion

Three lines of evidence, net CO_2 gas flux based on weekly measurements, net O_2 gas flux based on weekly Winkler titrations, and continuous diel O_2 measurements (sondes), produce similar views of metabolism in these lakes. In the absence of manipulation, these small, DOC-rich lakes are strongly net heterotrophic. NEP (e.g., GPP-R) is consistently negative and in the range of -20 to -40 mmol C m^{-2} d^{-1}. The net flux of CO_2 is from the lakes to the atmosphere, and this flux is of comparable magnitude to the net flux of O_2 from the atmosphere into the lakes. Although the continuous O_2 data produce a larger dynamic range for NEP than do the weekly data sets, all three are reasonably well correlated.

Nutrient enrichment tended to increase the magnitudes of both GPP and *R;* the food web configuration strongly affects the ratio of GPP to R and the difference between GPP and R (NEP). When large zooplankton were dominant, as in the case of a piscivore food web, the effect of nutrient enrichment on NEP, the GPP/R ratio, or O_2 or CO_2 gas flux was relatively small. That is, GPP and R tend to increase in concert. In the absence of large zooplankton (e.g., under a planktivore-dominated food web) nutrient enrichment leads to a greater increase in GPP than in R, positive values of NEP, GPP/R ratios > 1, an influx of CO_2 from the atmosphere, and a comparable efflux of O_2 to the atmosphere.

Uncertainties and errors: That three lines of evidence lead to similar conclusions about NEP gives us confidence in the patterns and magnitudes of NEP among lakes determined in this study. However, all three measurements are affected to varying degree by assumptions we made.

Groundwater input: We assumed that the net balances of O_2 and CO_2 were governed by metabolism. To the extent that groundwater inputs were significant sources of CO_2-enriched or O_2-depleted water, we would be in error. The loading of groundwater to these lakes has been determined from tracer-derived water budgets, and input rates are fairly low, 0.3 to 0.5 cm d^{-1} (Cole and Pace 1998). CO_2 concentrations in hyporheic groundwater at the nearby North Temperate Lakes LTER site have been measured by Schindler and Krabbenhoft (1998). Averaging the peak concentrations reported by Schindler and Krabbenhoft (1998) at their sites (CO_2 of 215 μM), the input of CO_2 in groundwater (CO_2 concentration × input of groundwater) would account for 0.86 mmol m^{-2} d^{-1} or about 0.6 to 1.5% of the measured CO_2 efflux in the net heterotrophic lakes. Working in the same geographical area, T. Kratz (pers. comm.) measured higher CO_2 concentrations in bog mat pore water, finding CO_2 that was 50-fold atmospheric equilibrium ($\sim$650 μM). If this were the input concentration to our lakes (a high-end estimate) groundwater could bring in as much as 2.5 mmol m^{-2} d^{-1} or 4 to 7% of the measured CO_2 efflux in the heterotrophic lakes. As a boundary condition for the O_2 balance, if the groundwater were anoxic, it would lower the partial pressure (at steady state) of O_2 very slightly and generate an atmospheric influx of 1.1 mmol m^{-2} d^{-1} (at a gas piston velocity of 0.5 m d^{-1}). This groundwater driven O_2 flux is about 2 to 3% of the atmospheric influx we measure in the heterotrophic lakes. Thus, the groundwater inputs are not likely to have a significant effect on our measurements of NEP.

Gas piston velocity—In computing gas fluxes, we treated the gas piston velocity, k_{600}, as a constant because k_{600} computed from measured wind speeds was low and relatively invariant. To what extent does this assumption affect the outcome? We recalculated the entire data set for 1995 and 1996 (the years for which we have continuous on-the-lake wind data) using the actual hourly wind values and the same model relating k_{600} to wind speed (Cole and Caraco 1998). The effect is small. For example, in Peter Lake (the net autotrophic lake) NEP increases (becomes more positive) by 6.8% and in Paul Lake (net heterotrophic) NEP decreases (becomes more negative) by 3.2%. Thus, using real wind data increases the contrast in NEP between the net heterotrophic and net autotrophic lakes and serves to strengthen the observed pattern, albeit by a small magnitude. GPP and R (under any assumption about daytime versus nighttime R, below) are affected by a smaller magnitude, about 2% for both lakes.

A general relationship between k_{600} and wind speed is still somewhat uncertain, especially at low wind speeds (e.g., MacIntyre et al. 1995), so our use of a constant value of k_{600} is probably justified. What if we are wrong about the absolute value of k_{600}? Since we used a constant and relatively low estimate for k_{600}, the true value is likely higher but not likely lower. Both the CO_2 and weekly O_2 flux estimates are linearly sensitive to changes in the value of k_{600}. If k_{600} were 10% larger, CO_2 gas flux (into or out of the lakes) would be 10% larger as well. Thus, increasing k_{600} increases the contrast among lakes and maintains the same pattern we report. For the continuous diel O_2 approach, the relationship between O_2 flux and k_{600} is more complicated. When O_2 is consistently undersaturated with respect to the atmosphere (e.g., Paul Lake, the unmanipulated lake), increasing k increases the estimate of respiration. When the water is supersaturated in O_2 (e.g., Peter Lake, high nutrients, planktivore-dominated), increasing k decreases the estimate of respiration. The magnitude of the uncertainty depends on how far away the lake is from atmospheric equilibrium. As an example, if the 1997 data for Paul Lake are recalculated with k 10% higher than the 0.48 m d^{-1} value we used, respiration increases by 5%. For Peter Lake, the result is an 8% decrease in R. In both cases there is little change in GPP because GPP is calculated from the change in O_2 during daylight plus R. The effect of changing k on daytime net photosynthesis is generally opposite to that on respiration. If the lake is consistently oversaturated or undersaturated, this opposition dampens the sensitivity of the GPP estimate to k. In either undersaturated or supersaturated lakes, the absolute magnitude of NEP is increased comparably to R and the sign of NEP is maintained as k is increased. Thus, increasing k enhances the contrast we report for NEP among lakes and decreases the contrast in R. The magnitude GPP/R ratio is sensitive to k, but k does not affect whether GPP/R is >1 or <1. For example, in Paul Lake, varying k by twofold results in a range of GPP/R from 0.45 to 0.55; in Peter Lake the resulting range is from 1.6 to 2.6.

Daytime *R:* To estimate GPP and R we assumed that R_{day} and R_{night} were equal. NEP and R_{night} are measurements, but to compute R and GPP, we need a value for R_{day}, which we have no independent way to assess. The simplifying assumption that R in the light and dark are equal is widely used for both in vitro incubations and free-water O_2 studies. Where R_{light} has been directly measured (using added ^{18}O for in vitro incubations) it tends to be coequal or larger than R_{night} due to several biochemical pathways (e.g., Bender et al. 1987; Grande et al. 1991). A triple isotopic approach using free-water $^{18}O_2$, $^{17}O_2$, and $^{16}O_2$ has been used in the ocean (Luz and Barkan 2000) and looks promising for unraveling R_{day} and R_{night}. Natural abundance isotopic technique has only recently been applied to free-water situations resembling the lakes in this study, which includes pelagic and benthic respiration. Working in shallow, freshwater ponds, Roberts and Ostrom (pers. comm.) used an ambient ^{18}O approach and found that R_{day} ranged from one to threefold R_{night}.

What would happen if R_{day} were twofold higher than R_{night} in our systems? First of all there would be no effect on NEP or R_{night}. The magnitudes of GPP and R would be increased by equal amounts, and the effect on the GPP/R ratio is proportionately smaller. At representative values of NEP $= -30$ mmol m^{-2} d^{-1} and nighttime R at 3.3 mmol m^{-2} h^{-1}, letting R_{day} increase from 1 to 2 times R_{night} increases GPP from 50 to 96 mmol m^{-2} d^{-1} (1.9 fold), increases total R from 80 to 126 mmol m^{-2} d^{-1} (1.6 fold), and increases the ratio of GPP/R from 0.62 to 0.76 (1.2 fold). Using representative values for the net autotrophic condition of NEP $= 10$ mmol m^{-2} d^{-1}, increasing R_{day} to twice R_{night} increases GPP by 1.4 fold and decreases the ratio of GPP/R by only 4%. Until the measurement of R_{day} can be made routinely, we have to accept some uncertainty in the absolute magnitudes of both GPP and R, less so for their ratio.

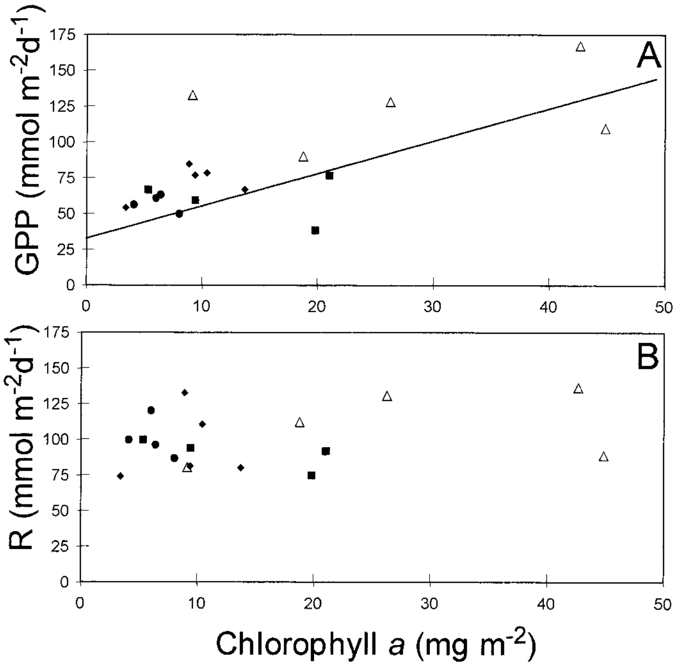

Fig. 8. Mean seasonal measurements of system metabolism plotted against mean areal Chl *a* for each basin. Paul Lake (filled circles), East Long Lake (filled squares), Peter Lake (open triangles), and West Long Lake (filled diamonds). (A) GPP $= 1.8 \times$ Chl $a + 53$, $r^2 = 0.45$, $p < 0.01$. (B) R versus chlorophyll was nonsignificant at $p = 0.05$.

Metabolism of allochthonous organic C: At the weekly time step, GPP and R were well correlated ($r^2 = 0.76$). At the scale of seasonal means, although GPP was strongly related to other independent measures, such as photosynthetic biomass or primary production (e.g., Chl *a*, ^{14}C-primary production), R was not (Fig. 8). Instead, R was best predicted from a combination of DOC and Chl *a*. Thus the interweek variation in system R appears to be related to variation in GPP, but the larger scale variation in R among lakes appears to be controlled by a combination of the loading of organic C from allochthonous sources (DOC) and autochthonous primary production. Further, our measures of system R are both larger than, and not strongly related to, measurements of dark bottle respiration in the same lakes (Pace and Cole 2000). Although these differences may be the result of errors or artifacts in either measure of respiration, the greater magnitude (twofold to fourfold) in system R over bottle (pelagic) R could suggest that the littoral sediments are an important site for system respiration in these lakes (Vadeboncoeur et al. 1996) as is the case in other lakes (den Heyer and Kalff 1999).

System R can be thought of as the sum of two components: (1) the respiration of autochthonous GPP by photosynthetic organisms (phytoplankton, benthic algae, macrophytes) plus the heterotrophic organisms that consume them (zooplankton, bacteria, benthic invertebrates) and (2) the respiration of allochthonously loaded organic C. Caraco and Cole (2000) successfully modeled lake ecosystem respiration in a series of lakes by assuming that a fixed, large percentage (~90%) of autochthonous primary production was respired within the lake (e.g., 10% was buried or exported) and the residual respiration was supported by allochthonous sources. Using that approach here, the best fit (among the lakes and years) to system R occurs when GPP is respired at 90% d^{-1} and the ambient DOC pool (a surrogate for allochthonous C loading) is metabolized 50 times more slowly at 4.5% d^{-1} (Fig. 9A). This estimate of the respiration of DOC is uncertain and may be too high. At steady state for the DOC in the lake, this implies that 4.5% of the DOC pool must be replaced by new inputs from the watershed each day. Using our measured groundwater input rates, the groundwater DOC concentration would need to range from 5 to 10 mmol L^{-1} (60 to 120 mg C L^{-1}) to support this metabolism. This is within, but near the high end, of the range in DOC concentrations reported for pore waters in peat (Yavitt 1994) and interstitial bog fluids in northern Wisconsin (Marin et al. 1990). If GPP is respired at 90% d^{-1}, it implies that about 10% of GPP would either accumulate or sediment out of the epilimnion. This magnitude is consistent with measures of hypolimnetic respiration in these same lakes (J. Houser, pers. comm.).

This simple model suggests that allochthonous DOC supports a significant fraction of system R in most of these lakes and most years. Among lakes and years the respiration supported by allochthonous DOC would average 28 ± 8% of total respiration; it ranges from 13% to 43%, decreasing in importance as GPP increases (Fig. 9B). Using an $^{18}O_2$ approach to quantify GPP/R ratios, Quay et al. (1995) calculated that allochthonous organic matter supported from 0 to

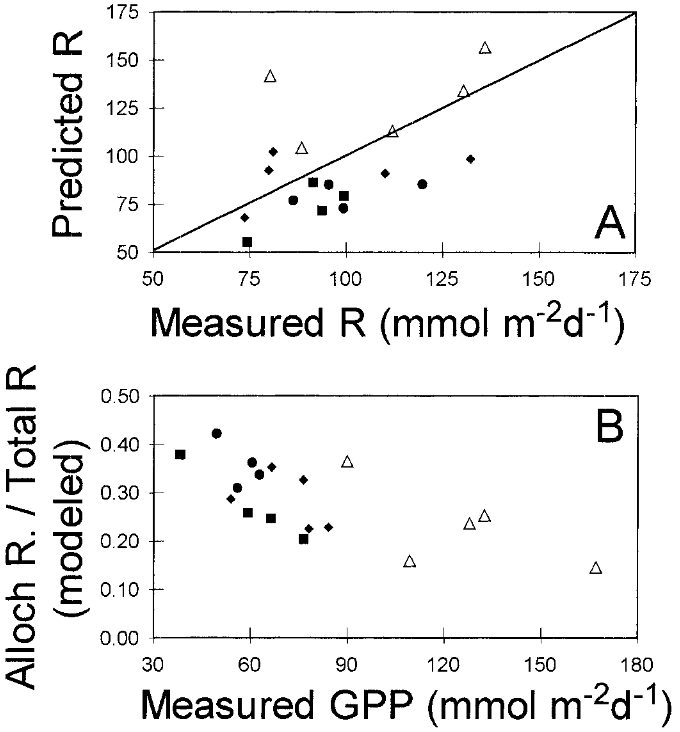

Fig. 9. A Predicted and measured R among lakes and years. Best fit occurred when $R = 0.9 \times \mathrm{GPP} + 0.045\ \mathrm{d}^{-1} \times \mathrm{DOC}$. The regression line: predicted $R = 0.98 \times$ measured R ($p < 0.001$, $r^2 = 0.24$). (B) The fraction of total R supported by allochthonous organic C as a function of measured GPP. In both figures the symbols are as in Fig. 8.

44% of R in a series of Amazonian lakes, a range similar to our results here.

Because DOC varies among the lakes independently of the food web and nutrient manipulations, it creates some uncoupling between GPP and R. Although it is likely that there is a direct food web effect on the fraction of GPP that is respired in the epilimnion, we have not included that in this overly simple illustration.

Several studies suggest that for aquatic systems in general R exceeds GPP at either low rates of primary production (Quay et al. 1995; del Giorgio et al. 1997; Duarte and Agusti 1998) or low algal biomass (del Giorgio and Peters 1994). Our study lends support to these ideas. The ratio of GPP/R tracks Chl *a* in a manner very similar to that seen by del Giorgio and Peters (1994; Fig. 8), who suggested that GPP/R will be <1 when Chl *a* is $<\sim 17\ \mu\mathrm{g\ L}^{-1}$. For our data set, when the mean seasonal Chl *a* is below about 20 mg m^{-2} (10 to 30 μg Chl *a* L^{-1} depending on the mixed layer depth), GPP/R is <1, and the lake has a net heterotrophic C balance. When Chl *a* is above $\sim$20 mg m^{-2}, GPP/R tends to be >1 (Fig. 10A). In our experimental lakes, cascading trophic interactions lead to reduced phytoplankton biomass under a piscivore food web at comparable levels of nutrient loading (Carpenter et al. 1998). The consequence for system metabolism is that GPP/R is <1 except when planktivory is intense and *Daphnia* are grazed to very low abundances, which allows phytoplankton to escape grazer control (Fig. 10A). Thus, the food web actually influences the GPP/R ratio and NEP (Schindler et al. 1997).

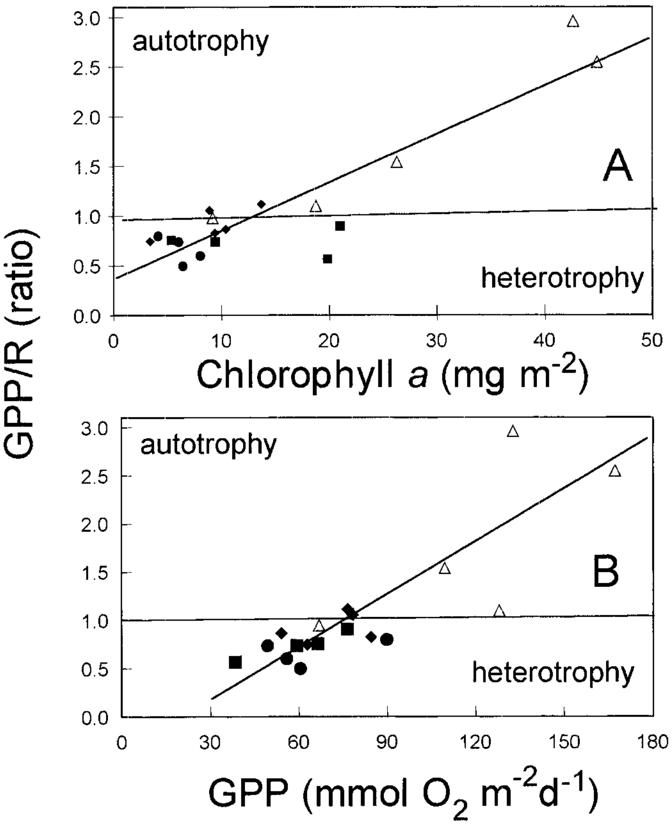

Fig. 10. The relationship between the GPP/R ratio and areal Chl *a* (A) and GPP (B) in the UNDERC lakes. In both panels we show average values for each season; symbols are as in Fig. 8. The thin horizontal line denotes GPP = R. The regression line is GPP/$R = 0.048\ (\pm 0.0006) \times \mathrm{Chl}\ a + 0.35\ (\pm 0.11)$, $r^2 = 0.81$, $p < 0.0001$). In (B) we plot the GPP/R ratio against GPP. The regression line is GPP/$R = 0.017\ (\pm 0.0026) \times \mathrm{GPP} - 0.28\ (+\ 0.23)$, $r^2 = 0.71$, $p < 0.0001$). The thin horizontal line denotes GPP = R.

As Duarte and Agusti (1998) report for aquatic systems in general, we observe that GPP/R increases with increasing GPP in these experimentally manipulated lakes (Fig. 10B). Combining lakes dominated by both piscivores and planktivores, we see that GPP/R ratios are significantly <1 unless primary production is quite high. At GPP $< \sim 1$ g O$_2$ m^{-3} d^{-1} (or $\sim$140 mmol C m^{-2} d^{-1} depending on mixing depth), the GPP/R ratio is consistently <1 in these lakes. Assuming a 200 d ice-free season, we would expect GPP and R to balance when GPP reached roughly 330 g C m^{-2} yr^{-1}, a productivity value in the eutrophic range. Our present study, and prior work, suggests that rates of GPP this high will not occur in these lakes unless the lakes both receive high rates of exogenous nutrients and piscivorous fish have been eliminated.

Allochthonously supplied organic C supports some of the system R we measure in all of our experimental lakes. As a fraction of total respiration, this allochthonous subsidy declines in importance as GPP increases (e.g., Fig. 9B) but is still quite significant across the entire gradient. Even in the most productive lakes, with GPP/*R* ratios >1, we estimate that at least 13% of total system *R* is supported by allochthonous organic C. Although this allochthonous subsidy is most obvious in lakes that have negative NEP, it occurs at comparable absolute magnitudes in lakes with positive NEP as well. Combining all lakes and years, we calculate that the respiration of allochthonous C averaged 25.7 ± 7 mmol C m^{-2} d^{-1}. Assuming 200 ice-free days, this rate suggests that the watershed is the source of roughly 5 mole C m^{-2} (of lake area) yr^{-1} (60 g C m^{-2} yr^{-1}) of organic C that is respired in these lakes at steady state. This allochthonous subsidy of respiration is large in comparison to GPP in these lakes in the absence of nutrient additions. At this point, we know that this allochthonous material must be respired in the lakes. We do not yet know to what extent allochthonous C supports the secondary production of higher trophic levels.

Through cascading trophic interactions, planktivorous fish reduce the abundance of large-bodied zooplankton, which, in the presence of exogenous nutrients, allows phytoplankton populations to increase. Increased phytoplankton abundance leads to greater GPP and pushes the ecosystem toward net autotrophy and changes the lake from a net CO_2 source to a net CO_2 sink (Schindler et al. 1997). In the absence of strong planktivory, large-bodied zooplankton dominate and impede increases in phytoplankton biomass. Although both GPP and *R* increase in response to nutrient additions when large zooplankton dominate (as in the case of a piscivore-dominated food web), they do so more or less in concert in these lakes and net heterotrophy is maintained.

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