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

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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 CO₂ gas flux, net O₂ gas flux, and continuous diel O₂ 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 \(-35.5 \pm 3.7\) (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 O₂ 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 \(-26\) 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 CO₂. 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 shallower 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
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 CO₂ 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 (Phoxinus pos), and golden shiner (Notemigonus chrysopleucas), 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).

<table>
<thead>
<tr>
<th>Lake</th>
<th>Area (ha)</th>
<th>Mean depth (m)</th>
<th>Mixed layer depth (m)</th>
<th>Ground water load (cm d(^{-1}))</th>
<th>DOC (µmol L(^{-1}))</th>
<th>F-Load (µmol P m(^{-2}) d(^{-1}))</th>
<th>Ambient Chlorophyll (a) (µg L(^{-1}))</th>
<th>Mean mixed layer Chlorophyll (a) (µg L(^{-1}))</th>
<th>Mean size crustacean zooplankton (mm)</th>
<th>Fish community structure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Paul</td>
<td>1.74</td>
<td>3.9</td>
<td>1.5±4</td>
<td>9.3</td>
<td>10.3</td>
<td>113±15</td>
<td>3.5</td>
<td>3.5</td>
<td>0.66</td>
<td>2014</td>
</tr>
<tr>
<td>Peter</td>
<td>2.65</td>
<td>6.5</td>
<td>1.4±4.5</td>
<td>128</td>
<td>200</td>
<td>190±7</td>
<td>4.9</td>
<td>4.9</td>
<td>0.44</td>
<td>1995</td>
</tr>
<tr>
<td>West Long</td>
<td>2.21</td>
<td>9.0</td>
<td>1.5±4.5</td>
<td>1128</td>
<td>203±2</td>
<td>200±0</td>
<td>7.8</td>
<td>7.8</td>
<td>0.75</td>
<td>1994</td>
</tr>
</tbody>
</table>

References

Carpenter et al. (1993); Christensen et al. (1996); Pace and Cole (2000).

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,

\[ \Delta O_2 = NEP + D. \]

Diffusion can be positive or negative and is calculated as

\[ D = k(O_2 - O_{2\text{ sat}}), \]

where \(O_2\) is the measured oxygen concentration in the water, \(O_{2\text{ sat}}\) 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 \( (R_{\text{day}}) \) and a value during night \( (R_{\text{night}}) \). Thus

\[
\text{NEP} = \text{GPP} - (R_{\text{day}} + R_{\text{night}}). \tag{3}
\]

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

\[
\Delta O_2 = R_{\text{night}} + D. \tag{4}
\]

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

\[
\Delta O_2 = \text{GPP} - R_{\text{day}} + D. \tag{5}
\]

We can directly measure NEP and \( R_{\text{night}} \). Since we do not have a direct measurement of \( R_{\text{day}} \), both GPP and \( R \) must be estimated by assuming a value for \( R_{\text{day}} \). We assume, in keeping with other literature (see Carignan et al. 2000), that the hourly value of \( R_{\text{day}} \) and \( R_{\text{night}} \) 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, \( \alpha \), which represents the chemical enhancement of diffusion, which occurs at high p\(H\) 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 \( \alpha \).

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 \( (1.03 ± 0.03 \text{ [SD]} \) for Model I and 1.14 for Model II) close to 1.0. For 70% of the measurements, the sonde value was within 10 \( \mu M \) of the Winkler; for only 5% did the values diverge by 30 \( \mu M \) 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-
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 $0.30 \pm 0.4$ (SD) $\mu$mol 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 $<10$ $\mu$M, 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 $\mu$M 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 $R_{\text{day}} = \text{hourly } R_{\text{night}}$) GPP and $R$ for the upper mixed layer. This layer includes the water column to the bottom of the mixed layer ($\sim 1$ 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 ($103 \mu$mol 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.

Weekly CO$_2$ gas fluxes—The weekly measurements of the partial pressure of CO$_2$ ($p$CO$_2$) mirrored the NEP patterns obtained by the continuous O$_2$ data. When $p$CO$_2$ 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, $p$CO$_2$ in the water exceeded $p$CO$_2$ in the atmosphere.
Persistence of net heterotrophy in lakes

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 \( \mu \text{mol P m}^{-2} \text{d}^{-1} \)). Peter Lake was planktivore dominated and was the only lake that lacked large zooplankton.

Fig. 4. (A) \( p\text{CO}_2 \) and (B) \( p\text{O}_2 \) 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 \( \mu \text{atm} \) is the average measured value for \( p\text{CO}_2 \) in the atmosphere at this location. (B) The horizontal line at 0.2 atm represents \( p\text{O}_2 \) in the atmosphere. The start and stop of fertilization is indicated with arrows.

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 \( \text{CO}_2 (p\text{CO}_2) \) exceeded the value in the atmosphere nearly every time the lake was sampled, ranging from about 600 \( \mu \text{atm} \) to 1,500 \( \mu \text{atm} \) over the seasonal cycle (Fig. 4A). Under a regime of high nutrient loading and a planktivore-dominated food web, \( p\text{CO}_2 \) was strongly undersaturated with respect to the atmosphere, consistent with the net autotrophy (positive NEP) obtained by the continuous \( \text{O}_2 \) 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, \( p\text{CO}_2 \) 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 \( \text{O}_2 \) fluxes—The weekly measurements of \( \text{O}_2 \) obtained by Winkler titration matched the pattern of NEP shown by the continuous \( \text{O}_2 \) data and mirrored the \( p\text{CO}_2 \) record (Fig. 4B). When the partial pressure of \( \text{O}_2 (p\text{O}_2) \) in the water is lower than that in the overlying atmosphere, the lake is a net sink for \( \text{O}_2 \) from the atmosphere, a condition that is consistent with net heterotrophy (negative NEP). \( p\text{O}_2 \) 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
Lakes 1993–1997). Only the combination of fertilization and strong planktivory (Peter Lake, 1993–1997) resulted in $p_{O_2}$ in the water exceeding the atmospheric value. In the years of high fertilization, $p_{O_2}$ 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 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 $[-0.75 \pm 0.22$ (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.

The seasonal mean $CO_2$ flux ranged from 50 mmol m$^{-2}$ and O$2$ into and out of the lake using Eq. 2 (Fig. 5A). Seasonal mean O$2$ flux ranged from 50 mmol m$^{-2}$ to 15.5 mmol m$^{-2}$ d$^{-1}$ (out of 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 $[-0.75 \pm 0.22$ (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. 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) av-

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%).
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).

Frequency 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 $\mu$mol 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 $\mu$mol 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 ($r^2 = 0.6, p < 0.001$).

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 $\mu$mol C L$^{-1}$ among lakes; Table 1) is large in comparison to algal biomass (<0.16 $\mu$mol C L$^{-1}$ in the unmanipulated lakes and up to 16 $\mu$mol 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 ab-
sence 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 CO₂ is from the lakes to the atmosphere, and this flux is of comparable magnitude to the net flux of O₂ from the atmosphere into the lakes. Although the continuous O₂ 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 O₂ or CO₂ 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 CO₂ from the atmosphere, and a comparable efflux of O₂ 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 O₂ and CO₂ were governed by metabolism. To the extent that groundwater inputs were significant sources of CO₂-enriched or O₂-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). CO₂ 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 (CO₂ of 215 μM), the input of CO₂ in groundwater (CO₂ concentration × input of groundwater) would account for 0.86 mmol m⁻² d⁻¹ or about 0.6 to 1.5% of the measured CO₂ efflux in the net heterotrophic lakes. Working in the same geographical area, T. Kratz (pers. comm.) measured higher CO₂ concentrations in bog mat pore water, finding CO₂ that was 50-fold atmospheric equilibrium (~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 CO₂ efflux in the heterotrophic lakes. As a boundary condition for the O₂ balance, if the groundwater were anoxic, it would lower the partial pressure (at steady state) of O₂ 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 O₂ 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, k₆₀₀, as a constant because k₆₀₀, 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 k₆₀₀ 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 k₆₀₀ and wind speed is still somewhat uncertain, especially at low wind speeds (e.g., Maclntyre et al. 1995), so our use of a constant value of k₆₀₀ is probably justified. What if we are wrong about the absolute value of k₆₀₀? Since we used a constant and relatively low estimate for k₆₀₀, the true value is likely higher but not likely lower. Both the CO₂ and weekly O₂ flux estimates are linearly sensitive to changes in the value of k₆₀₀. If k₆₀₀ were 10% larger, CO₂ gas flux (into or out of the lakes) would be 10% larger as well. Thus, increasing k₆₀₀ increases the contrast among lakes and maintains the same pattern we report. For the continuous diel O₂ approach, the relationship between O₂ flux and k₆₀₀ is more complicated. When O₂ 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 O₂ (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 O₂ 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 O2 studies. Where \( R_{\text{night}} \) has been directly measured (using added \(^{18}\text{O}\) for in vitro incubations) it tends to be coequal or larger than \( R_{\text{day}} \) due to several biochemical pathways (e.g., Bender et al. 1987; Grande et al. 1991). A triple isotopic approach using free-water \(^{18}\text{O}_2\), \(^{17}\text{O}_2\), and \(^{16}\text{O}_2\) has been used in the ocean (Luz and Barkan 2000) and looks promising for unraveling \( R_{\text{day}} \) and \( R_{\text{night}} \). 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 \(^{18}\text{O}\) approach and found that \( R_{\text{day}} \) ranged from one to threefold \( R_{\text{night}} \).

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

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 \( a \), \(^{14}\text{C}-\)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 allochthonous 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 Heye 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% \text{ d}^{-1} \) and the ambient DOC pool (a surrogate for allochthonous C loading) is metabolized 50 times more slowly at 4.5% \text{ 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% \text{ 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 \(^{18}\text{O} \) 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 $R = 0.9 \times \text{GPP} + 0.045 \text{ d}^{-1} \times \text{DOC}$. The regression line: predicted $R = 0.98 \times \text{measured } R$ ($p < 0.001$, $r^2 = 0.24$). (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.

Fig. 10. (A) 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/$R = 0.048 \pm 0.0006$ $\times$ 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/$R = 0.017 \pm 0.0026$ $\times$ GPP $- 0.28 \pm 0.23$, $r^2 = 0.71, p < 0.0001$. The thin horizontal line denotes GPP $= R$.

Thus, the food web actually influences the GPP/$R$ ratio and NEP (Schindler et al. 1997).

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 $25.7 \pm 7 \text{ mmol C m}^{-2} \text{ d}^{-1}$. 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$^{-1}$ ($60 \text{ g C m}^{-2} \text{ yr}^{-1}$) 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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