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Planktonic production and respiration in oligotrophic Shield lakes

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Abstract

A precise oxygen method was used to measure primary production, community respiration and to determine the importance of exogenous organic carbon as an energy source to planktonic communities in the epilimnion of 12 oligotrophic to mesotrophic Shield lakes. Median photosynthetic parameters observed with the oxygen method were up to twice as high as those measured with ^{14}C in other oligotrophic Shield lakes. Gross photosynthesis was almost always larger than community respiration, with a median $P:R$ ratio of 1.7. We observed strong relationships between respiration and gross photosynthesis, but could not detect any significant trend between respiration or the $P:R$ ratio and the concentration of dissolved organic carbon (DOC). DOC appeared to depress both photosynthesis and respiration. These results argue against the importance of exogenous organic carbon supply as a significant energy source to freshwater planktonic communities. Previously low $P:R$ ratios reported for oligotrophic fresh waters may be due to the uncertain meaning of ^{14}C production data.

The balance between production and respiration lies at the basis of our understanding of carbon flow and food web structure in marine and freshwater ecosystems. Ecosystems where photosynthesis exceeds total planktonic respiration ($P > R$) are net autotrophic; they are net sinks for CO_2 and net producers of O_2 and organic matter. Conversely, ecosystems where respiration exceeds photosynthesis ($P < R$) are net heterotrophic; they are net sources of CO_2 and net consumers of organic carbon.

The relative importance of primary production and community respiration in oligotrophic waters and the role of exogenous organic carbon as an energy source to planktonic communities are the subject of an ongoing debate in oceanography and limnology. Most ecologists have considered lakes and oceans as net autotrophic systems fueled primarily by planktonic photosynthesis. Our understanding of carbon flow and of the production-respiration balance in oligotrophic aquatic ecosystems is still limited, however. Several studies have suggested that respiration systematically exceeds photosynthesis in the epilimnion of oligotrophic lakes, estuaries, and oceans (Sorokin 1971; Findlay et al. 1992; del Giorgio and Peters 1993, 1994; Coveney and Wetzel 1995; del Giorgio et al. 1997; Duarte and Agusti 1998). In freshwaters, the net heterotrophy hypothesis is further supported by indirect evidence showing that lakes are commonly supersaturated with respect to atmospheric CO_2 (Cole et al. 1994; Dillon and Molot 1997), and that bacteria can metabolize some exogenous organic carbon derived from terrestrial ecosystems (Hessen 1992; Arvola et al. 1996; Reitner and Herndl 1997).

Ideally, gross photosynthesis and community respiration should be compared by measuring the uptake or release of products or substrates common to both reactions (O_2, CO_2). This approach has rarely been used in oligotrophic waters, however, due to insufficient methodological precision. Rather, recent claims of lake and oceanic hetetrotrophy are largely based on indirect comparisons of organic carbon production (^{14}C uptake) with planktonic respiration (dark O_2 consumption), or with estimates of bacterial respiration or production. Recent improvements of the precision of the Winkler method now allow the detection of planktonic photosynthesis and respiration rates as low as 0.5 mgC m^{-3} h^{-1} after 4 h incubations (Carignan et al. 1998). Here, we use high-precision metabolic rate measurements in the epilimion of 12 Canadian Shield lakes to test the heterotrophy hypothesis. We show that in such lakes, gross photosynthesis nearly always exceeds planktonic respiration.

Study site

The 12 lakes are located on the Canadian Shield, 50 to 100 km north of Montreal. The area is underlain by a granitic or anorthosic bedrock covered by 1–5 m of glacial tills. Soils are mostly Humic Cryorthods (U.S. classification) or Orthic Ferro-Humic Podzols (Canadian classification). Catchments are forested (>95%) primarily with sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), beech (*Fagus*

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Table 1. Morphometric and chemical properties of the 12 study lakes. LA = lake area; CA = catchment area; *zm* = mean depth; τ = hydraulic residence time; ϵ_{PAR} is the light (400–700 nm) attenuation coefficient.

Lake	Location	LA (km^2)	CA (km^2)	*zm* (m)	τ (y)	Total P ($mg\ m^{-3}$)	Total N ($mg\ m^{-3}$)	DOC ($g\ m^{-3}$)	ϵ_{PAR} (m^{-1})
Achigan	45°56′N, 74°00′W	5.31	86.89	12.1	1.48	3.9	220	3.30	0.66
`A l'Ours	45°58′N, 74°04′W	0.15	3.26	6.7	0.64	14.0	439	6.64	1.58
Bélair	46°01′N, 74°09′W	0.09	1.91	6.2	0.61	6.3	193	3.35	0.79
Chertsey	46°09′N, 73°49′W	1.32	4.91	10.4	4.66	3.2	169	2.34	0.34
Croche	45°59′N, 74°01′W	0.19	0.88	5.1	1.91	3.8	211	3.52	0.65
Cromwell	45°59′N, 74°00′W	0.10	9.94	2.9	0.06	9.6	313	5.17	1.09
En Cœur	45°58′N, 74°01′W	0.47	1.91	1.6	0.65	7.1	270	3.53	0.65
Masson	46°03′N, 74°02′W	4.02	34.90	7.9	1.73	4.1	248	4.32	0.67
Montagne-Noire	46°12′N, 74°16′W	2.83	12.60	13.0	5.05	5.4	189	2.07	0.37
Pin Rouge	45°58′N, 74°02′W	0.15	7.01	4.9	0.22	9.4	325	6.06	1.17
Raymond	46°00′N, 74°10′W	0.74	371.30	5.0	0.02	14.4	497	3.86	1.16
Violon	45°56′N, 74°05′W	0.15	1.75	7.3	1.26	3.8	171	2.92	0.54

grandifolia), and poplar (*Populus tremuloïdes*). Annual precipitation averages 1,100 mm y^{-1}, with 30% falling as snow. The lakes represent a wide range of conditions encountered in pristine lakes, as well as in lakes slightly impacted by cottage development (Table 1). Most are oligotrophic, with mean total phosphorus (TP) concentrations ranging from 3 to 14 mg m^{-3}. All the lakes have a near-neutral pH (6.5–7.2) and low to moderate alkalinity (40–360 meq m^{-3}). Dissolved organic carbon (DOC) concentrations (2–7 g m^{-3}) are typical of the southeastern Canadian Shield (Dupont 1992; Hudon et al. 1996; Dillon and Molot 1997). Lakes Cromwell, Pin Rouge, and À l'Ours have relatively high DOC and TP concentrations owing to their large drainage ratio and to the presence of extensive wetlands in their watersheds. Lake Raymond has the highest TP, total nitrogen (TN), and dissolved inorganic nitrogen (DIN) concentrations; this lake is a widened section of Du Nord River, has a short residence time (7 d), and receives treated sewage effluents from upstream villages. Lakes Pin Rouge and Cromwell have well-developed (~25% of lake area) macrophyte beds dominated by *Nymphea odorata, Nymphoides cordata, Potamogeton* sp., and *Utricularia vulgaris.*

Methods

Sampling—Water chemistry, epilimnetic production (*P*), and community respiration (*R*) were measured at least three times (usually four) in each lake between May and October of 1997. Water was collected with a 4-liter Van Dorn bottle between 0700 and 1000 h, when the epilimnion was completely mixed. The epilimnion is defined here as the warmer surface mixed layer where the vertical temperature gradient does not exceed 1°C m^{-1}, as measured in early morning, while the epilimnion is undergoing its complete daily circulation period. Water was taken in the upper, middle, and lower epilimnion; pooled in clean 20-liter dark polyethylene containers; and transported to the laboratory within 1 h in coolers to prevent temperature changes.

Chemical analyses—Chlorophyll was measured by spectrophotometry after overnight extraction of frozen GF/C filters in cold ethanol (Sartorg and Grobbelaar 1984) and corrected for phaeopigments. Samples for DOC measurements were filtered on washed Gelman Supor 0.45-μm membranes and kept at 4°C. Dissolved organic carbon was measured (Shimadzu TOC-5000) within 48 h by infrared gas analysis after sample acidification and He sparging, followed by Pt-catalyzed oxidation at 700°C. In these lakes, DOC concentrations measured with Supor 0.45-μm membranes are identical, within measurement precision, to those obtained with precombusted GF/C filters. Total phosphorus was measured using the molybdenum-blue method (Stainton et al. 1977), after autoclaving 50-ml samples with 0.5 g of potassium persulfate for 1 h at 120°C. Total nitrogen was measured as NO_3-N (Cd reduction, Lachat 10-107-04-1-B) after alkaline persulfate digestion of 50-ml samples at 120°C. Vertical oxygen and temperature profiles were measured with a YSI Model 55 instrument calibrated in vapor-saturated air. Comparisons between polarographic and Winkler measurements agreed within 0.2 g m^{-3}.

Metabolic measurements—Water used for metabolic rate measurements was distributed in triplicate clear and quadruplicate dark 300-ml pyrex bottles that were placed in a light gradient incubator. The incubator was similar to the one described in Shearer et al. (1985) and was equipped with a Phillips MH1000, 1,000 W metal-halide lamp. It provided six irradiance levels ranging from ~30 to ~1,000 μE m^{-2} s^{-1}, as measured at several points inside replicate bottles with a Biospherical QSL-101 4-π quantum meter calibrated by the manufacturer at the beginning of the study. Incubations were performed within 1°C of in situ temperature and lasted 4 h for production measurements and 4–7 h for respiration measurements. A high-precision ($\pm$ 2μg L^{-1}, SE of triplicate determination) Winkler method was used to determine the net production of oxygen (NP) and community respiration (*R*) from changes in dissolved oxygen in clear and dark bottles during the incubation (Carignan et al. 1998). The detection limits for NP and *R* were 0.7 and 0.5 mgC m^{-3} h^{-1}, respectively. Gross photosynthesis during the incubation (GP) was calculated as NP + *R*, assuming equal dark and light algal respiration; the validity of this assumption is not critical to our conclusions since algal respiration is small (5–15%) compared to GP and community respira-

tion (Bidwell 1977; Stone and Ganf 1981). Volumetric (VR) and areal (AR) 24-h community respiration rates were calculated assuming that respiration rates measured on water collected in the morning (R), were representative of the entire day. The computer model PSPARMS (version 4.0, Fee 1990), was used to estimate the photosynthetic parameters P_m^B (the chlorophyll-specific maximum rate of photosynthesis), α^B (the chlorophyll-specific slope of the P/I curve at low PAR) and I_k (the saturation PAR).

Daily areal epilimnetic photosynthesis rates (AGP, mgC m^{-2} d^{-1}) were computed by numerical integration (DPHOTO, version 4.0, Fee 1990) over depth and time of day, of the P/I curves using the PAR extinction coefficient (ϵ_{PAR}) measured (Li-Cor LI-192 and LI-190 sensors) in each lake at each sampling date. Day-to-day photosynthesis rates vary considerably due to changing cloud cover. Because this study compares R to GP among many lakes, we used an average incident PAR amounting to 66.7% of the maximum cloudless daily PAR in DPHOTO to integrate areal photosynthesis. This fraction corresponds to an average daily PAR of 70.2% received (Li-Cor LI-190) at our study site between 25 May and 15 October 1997, from which we have subtracted 5% to account for reflection losses at the water surface. Volumetric gross photosynthesis rates (VGP) were calculated by dividing AGP by the epilimnion depth (z_{mix}). A photosynthetic quotient (PQ) of 1.25 (mole O_2 per mole C produced or respired) was used to express oxygen production and consumption rates as carbon equivalents. Oxygen units were transformed into carbon units for comparison purposes only. Because both P and R were measured as oxygen changes, the choice of a particular PQ has no incidence on our GP:R ratios. All 2-π PAR sensors used during the study were initially calibrated with a Li-Cor LI-1800–02 calibrator.

Statistical analyses—All regression analyses were performed on normalized ($\log_{10}$-transformed) data using a stepwise forward variable selection procedure with an F-ratio of 4. Unless otherwise noted, all regression parameters are significant at the $p < 0.05$ level. In several regression models presented below, log R is regressed against log(GP), even if both measurements are not independent (GP = NP + R). As a result, apparently significant, but artifactual relationships may arise between log R and log(GP), even in the absence of functional relationship between both variables. Whenever this possibility occurred, we used a permutation method (Legendre and Legendre 1998) to determine the statistical significance of regression slopes and intercepts. Briefly, GP values were generated using random permutations of the observed NP and R values. Ten thousand regression slopes and intercepts of R vs. GP were calculated and t-tests were used to determine whether the slopes, intercepts, and r^2 obtained with nonpermuted data belonged to the populations of regression statistics generated with permuted values.

Results

Photosynthetic parameters—All chlorophyll-specific photosynthesis vs. irradiance curves yielded the maximum photosynthetic rates (P_m^B) expected for nutrient-limited phytoplankton growing in temperate marine or fresh waters (Fig. 1, Table 2). In the 18–22°C range, most light-response curves exhibited a slight (5–10%) photoinhibition above 500 μE m^{-2} s^{-1} (Fig. 1). Photoinhibition was more pronounced, however, and sometimes reached 50% of P_m^B when surface temperatures were below 15°C and when the epilimnion depth exceeded 5–6 m. The median P_m^B (3.5 mgC mgChl a^{-1} h^{-1}) was within the range of median or mean values reported by others (Harris 1978; Côté and Platt 1983; Fee et al. 1992). P_m^B was, however, about 50% higher than the 8-yr average value observed in the ELA lakes (Fee et al. 1987) but close to phaeopigment-corrected values reported for Lake Ontario (Millard et al. 1992). The median α^B (9.2 mgC mgChl a^{-1} E^{-1} m^2) was nearly twice as high as median values reported for ELA and other Shield lakes (Fee et al. 1987, 1992). Median I_k (119 μE m^{-2} s^{-1}) corresponded to the range of values (100–160 μE m^{-2} s^{-1}) compiled (Harris 1978) between 15 and 20°C for marine and fresh waters. P_m^B and I_k were significantly related to temperature, DOC, and z_{mix} (Table 3, models 1 and 2). Temperature alone explained 53% and 63% of the variance of P_m^B and I_k, respectively (models 3 and 4), with a Q_{10} value of 2.5 in the 11–23°C range, as usually observed (Bindloss 1976; Harris 1978). As expected, α^B was not related to temperature; it was, however, weakly (r^2 = 0.08, $p < 0.03$) related to a combination of two variables, ϵ_{PAR} and z_{mix}, determining light availability in the water column.

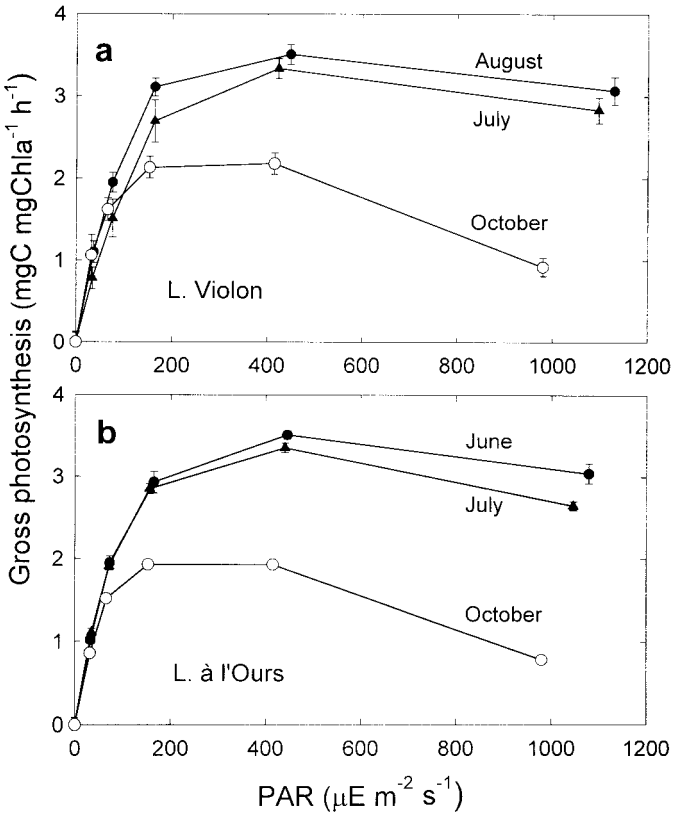

Fig. 1. Typical chlorophyll-specific P/I curves observed between June and October in (a) one of the least productive lakes (Violon) and (b) the most productive lake (Lac à l'Ours). Error bars, when larger than symbols, indicate ±1 SE of triplicate determinations.

Table 2. Physical and chemical properties of the water column, metabolic rates and photosynthetic parameters observed in the 12 study lakes between May and October 1997. Temperature (T, °C); mixed layer thickness ($z_{mix,}$ m); chlorophyll *a* and total phosphorus (Chl *a*, TP, mg m^{-3}); dissolved organic carbon (DOC, g m^{-3}); attenuation coefficient (ϵ_{PAR}, m^{-1}); volumetric production and respiration (VGP and VR, mgC m^{-3} d^{-1}). See text for a definition of the photosynthetic parameters P^B_m, α^B and I_k. Volumetric production and respiration rates can be converted into areal rates by multiplying them by z_{mix}.

Lake	Date	T	z_{min}	Chl *a*	TP	DOC	ϵ_{PAR}	VGP	VR	P^B_m	α^B	I_k
Achigan	25 Jun	20.0	3.75	1.65	4.2	3.19	0.67	91	61±3	4.82	10.0	134
	30 Jul	21.0	5.50	3.03	2.7	3.39	0.65	118	51±9	4.13	11.6	99
	27 Aug	19.5	6.75	1.84	4.6	3.47	0.58	42	29±7	3.05	7.7	110
	24 Sep	15.0	8.75	1.82	4.6	3.35	0.61	27	15±2	2.59	10.0	72
`A l'Ours	04 Jun	16.5	1.75	5.38	14.4	5.91	1.44	222	105±5	3.44	8.9	107
	16 Jul	22.0	2.25	8.35	12.6	7.10	1.72	238	101±7	3.28	9.3	98
	02 Oct	12.0	5.75	8.11	15.2	6.90	1.46	53	44±5	1.93	9.2	58
Bélair	16 Jun	19.0	2.75	1.43	5.3	2.78	0.75	119	104±10	6.56	14.4	103
	28 Jul	22.0	2.75	1.72	7.5	3.55	0.81	101	39±3	5.55	9.4	165
	18 Aug	19.5	4.00	1.88	5.9	3.72	0.81	79	37±2	4.81	10.0	133
	30 Sep	12.5	6.75	1.49	6.4	3.35	0.64	27	12±3	2.54	11.6	61
Chertsey	18 Jun	19.0	4.25	0.69	3.4	2.22	0.37	66	43±3	7.79	12.7	170
	30 Jul	21.0	7.00	0.67	5.1	2.30	0.31	48	11±8	6.86	11.0	173
	27 Aug	19.0	8.75	1.01	2.9	2.44	0.28	35	19±5	3.39	8.3	114
	24 Sep	15.0	10.75	0.79	2.3	2.35	0.33	20	5±6	2.99	11.2	74
Croche	27 May	13.0	2.75	1.40	5.7	3.44	0.69	49	33±3	2.72	6.3	119
	09 Jun	20.0	1.75	0.50	3.4	3.43	0.69	41	41±1	6.57	9.0	203
	25 Jun	21.0	2.50	0.94	3.6	3.42	0.61	65	46±4	5.05	12.9	108
	14 Jul	22.0	3.25	1.27	3.8	3.49	0.63	55	40±6	3.53	8.2	119
	04 Aug	21.0	3.75	1.00	3.5	3.60	0.65	54	34±4	5.27	10.5	140
	06 Aug	21.0	3.75	1.05	3.4	3.57	0.63	53	26±3	4.77	8.9	149
	22 Sep	14.5	5.75	3.60	3.5	3.57	0.61	50	18±4	1.60	9.0	49
Cromwell	27 May	13.0	1.5	2.44	8.2	3.79	0.84	99	58±4	2.98	7.6	109
	09 Jun	20.0	2.25	2.31	8.4	4.43	0.97	140	120±3	5.75	9.3	172
	14 Jul	22.0	2.25	5.01	10.1	5.57	1.24	205	119±4	3.90	8.8	123
	11 Aug	22.5	2.00	2.66	10.3	6.32	1.22	114	106±1	4.59	8.4	153
	22 Sep	14.5	4.75	5.97	10.9	5.73	1.23	72	59±7	2.27	9.5	66
En Cœur	02 Jun	15.5	2.00	1.17	5.6	3.28	0.63	58	48±4	3.61	7.2	140
	16 Jul	22.0	4.25	3.52	6.9	3.60	0.68	117	67±5	3.49	7.5	129
	11 Aug	22.5	4.00	5.03	8.2	3.52	0.64	144	102±3	2.80	6.2	126
	10 Oct	11.5	7.00	4.60	7.8	3.70	0.63	60	30±5	1.83	9.8	52
Masson	11 Jun	20.0	2.75	1.70	4.0	4.20	0.71	66	54±1	3.50	5.6	175
	23 Jul	20.5	4.50	2.48	4.7	4.40	0.65	82	34±5	3.20	7.4	120
	20 Aug	19.5	5.25	1.27	3.9	4.55	0.65	51	28±5	4.53	12.2	103
	28 Sep	13.0	8.25	0.99	3.7	4.15	0.64	13	6±3	2.37	9.9	67
Mont.-Noire	11 Jun	20.0	2.25	0.78	4.8	1.85	0.35	55	36±3	5.26	8.7	169
	23 Jul	20.5	5.25	2.82	5.6	2.14	0.40	118	55±4	3.41	8.0	118
	20 Aug	19.5	7.25	1.66	6.3	2.23	0.37	76	41±3	4.58	11.4	112
	28 Sep	13.0	10.75	1.82	4.8	2.07	0.35	36	13±3	2.43	12.3	55
Pin Rouge	02 Jun	15.5	2.25	2.22	9.3	4.87	0.98	82	66±3	3.55	9.1	109
	21 Jul	21.5	2.50	3.68	10.3	6.78	1.39	101	70±7	3.48	6.3	153
	13 Aug	21.0	2.75	2.37	8.9	6.57	1.13	66	58±7	3.87	7.5	144
	04 Oct	11.0	6.25	6.70	9.3	6.00	1.29	34	16±5	1.41	6.4	61
Raymond	16 Jun	19.0	3.75	4.12	15.4	3.48	1.15	192	256±39	5.97	13.8	120
	28 Jul	22.0	1.50	2.00	16.4	4.20	1.13	146	72±3	6.52	9.8	184
	18 Aug	19.5	5.25	3.36	17.7	4.25	1.19	69	76±5	5.07	8.7	161
	30 Sep	12.5	8.50	4.11	8.0	3.52	1.01	34	22±4	2.42	10.0	68
Violon	04 Jun	16.5	2.25	1.09	3.7	2.79	0.56	62	46±2	4.11	11.2	102
	21 Jul	21.5	4.25	1.61	4.4	3.05	0.53	60	32±3	3.32	6.9	133
	13 Aug	21.0	5.25	1.32	3.5	2.96	0.53	58	31±4	4.23	11.1	106
	02 Oct	12.0	7.25	1.65	3.7	2.88	0.54	27	12±4	2.16	10.3	58

Production and respiration—Daily areal gross photosynthesis rates (AGP), ranged from 73 to 719 mgC m^{-2} d^{-1}, with a median of 282 mgC m^{-2} d^{-1} (Table 2). These values are similar to ^{14}C production rates previously reported for Shield lakes (Shearer et al. 1987; Fee et al. 1992). Areal respiration rates ranged from 51 to 962 mgC m^{-2} d^{-1}, with a median of 150 mgC m^{-2} d^{-1}. The chlorophyll-specific community respiration rate exhibited a positive temperature dependence (Table 3, model 5) and had a median value of 0.85 mgC (mgChl *a*)$^{-1}$ h^{-1}.

Table 3. Linear regressions models ($n = 51$) relating photosynthetic parameters, production, and respiration to water column properties. The ± symbol denotes the standard errors of the regression parameters. Independent variables appear in a decreasing order of explained variance. r^2 and SE correspond to the proportion of the variance explained and to the standard error of estimates, respectively.

Model	Dependent variable	Regression	r^2	SE
1	log P^B_m	$-0.31^* \pm 0.25 + 1.03 \pm 0.16$ log $T - 0.44 \pm 0.11$ log(DOC) $- 0.26 \pm 0.07$ logz_{mix}	0.68	0.08
2	log I_k	$1.03 \pm 0.20 + 1.05 \pm 0.13$ log $T - 0.22 \pm 0.09$ log(DOC) $- 0.30 \pm 0.05$ logz_{mix}	0.77	0.08
3	log P^B_m	$-1.06 \pm 0.22 + 1.29 \pm 0.18$ log T	0.53	0.12
4	log I_k	$0.34^* \pm 0.19 + 1.35 \pm 0.15$ log T	0.63	0.10
5	log(VR/Chl *a*)	$-1.65 \pm 0.48 + 2.36 \pm 0.38$ log T	0.43	0.26
6	log(VGP)	$0.80 \pm 0.22 - 0.67 \pm 0.07$ log $z_{mix} + 0.75 \pm 0.06$ log(Chl *a*) $+ 1.30 \pm 0.15$ log $T - 0.77 \pm 0.13$ log(DOC)	0.90	0.09
7	log(VGP)	$1.32 \pm 0.11 + 0.65 \pm 0.14$ log(TP)	0.30	0.23
8	log(VGP)	$1.69 \pm 0.05 + 0.43 \pm 0.11$ log(Chl *a*)	0.23	0.24
9	log(VGP)	$-0.01^* \pm 0.37 - 0.34 \pm 0.10$ log $z_{mix} + 0.56 \pm 0.10$ log(TP) $+ 1.28 \pm 0.25$ log T	0.70	0.15
10	log(VR)	$0.67^* \pm 0.39 - 0.94 \pm 0.11$ log $z_{mix} + 0.77 \pm 0.10$ log(Chl *a*) $+ 1.28 \pm 0.26$ log $T - 0.64 \pm 0.22$ log(DOC)	0.81	0.15
11	log(VR)	$-0.22^* \pm 0.46 - 0.58 \pm 0.13$ log $z_{mix} + 0.71 \pm 0.12$ log(TP) $+ 1.29 \pm 0.30$ log T	0.73	0.18
12	log(VR)	$-0.03^* \pm 0.22 + 0.99 \pm 0.09$ log(VGP) $- 0.30 \pm 0.10$ log z_{mix}	0.85	0.14
13	log(VR)	$-0.51 \pm 0.14 + 1.16 \pm 0.08$ log(VGP)	0.82	0.15
14	log(VR)	$0.91 \pm 0.14 + 0.89 \pm 0.17$ log(TP)	0.34	0.28
15	log(VR)	$1.44 \pm 0.06 + 0.50 \pm 0.15$ log(Chl *a*)	0.19	0.31
16	log(VGP : VR) log(AGP : AR)	$0.07 \pm 0.05 + 0.20 \pm 0.09$ log $z_{mix} - 0.22 \pm 0.11$ log ϵ_{PAR}	0.27	0.13
17	log(AGP)	$0.82 \pm 0.22 + 0.75 \pm 0.06$ log(Chl *a*) $- 0.77 \pm 0.13$ log(DOC) $+ 1.30 \pm 0.15$ log $T + 0.32 \pm 0.07$ log z_{mix}	0.82	0.09
18	log(AR)	$0.15^* \pm 0.22 + 0.87 \pm 0.09$ log(AGP) $+ 0.35 \pm 0.10$ log ϵ_{PAR}	0.70	0.14
19	log(AR)	$0.02 \pm 0.24 + 0.90 \pm 0.09$ log(AGP)	0.63	0.15
20	log(NP : R)	$0.56 \pm 0.24 + 0.68 \pm 0.25$ log(Chl *a*) $- 1.76 \pm 0.51$ log(DOC)	0.21	0.39

* Not significant at the $p < 0.05$ level.

In contrast with previously published $P:R$ ratios (del Giorgio and Peters 1994), gross photosynthesis exceeded community respiration in all but two cases (Fig. 2, $n = 51$). Only one atypical lake impacted by sewage effluents (Raymond), in June and August, consumed more organic carbon than it produced. AGP alone explained 63% of the variance of AR (model 19), and the inclusion of ϵ_{PAR} (Table 3, model 18), or DOC, or z_{mix} explained another 5–7%. Permutation analysis shows that the r^2 statistics of models 13 and 19 are significant at $p = 0.0007$ and $p = 0.03$, respectively. Therefore, models 13 and 19 most probably reflect true statistical relationships between R and GP, even if R is included in GP. Note that this analysis excluded sewage-impacted Lake Raymond. Since the permuted GP values are generated as random combinations of R + NP, two negative NP values observed in Lake Raymond would have generated impossible negative GP values.

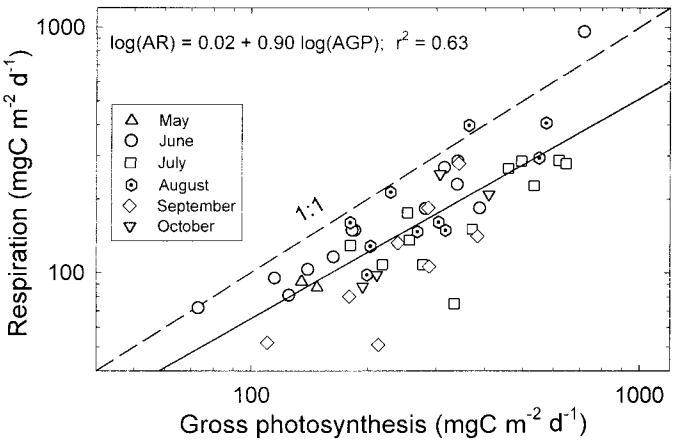

Fig. 2. Areal planktonic respiration vs. areal gross photosynthesis observed in the 12 study lakes between May and October. The dashed line indicates equal metabolic rates. Note the absence of seasonal trend in the AGP : AR ratio.

If exogenous carbon played a significant role in supporting community respiration, AR should be relatively important in the most oligotrophic lakes, and AGP should increase faster than AR as lakes become more productive. In fact, the nonsignificant intercepts and the slopes near unity in the AR models of Table 3 do not support the existence of a basal heterotrophic metabolism independent of in-lake photosynthesis. Instead, models 18 and 19 suggest that AR is, simply, directly proportional to AGP.

We observed positive relationships between VGP or VR and lake trophy, expressed as the concentrations of chlorophyll *a* (Chl *a*) or total phosphorus (models 7, 8, 14, 15). These relationships are weak ($r^2 < 0.35$), however, and their

slopes are not significantly different. del Giorgio and Peters (1994) reported a significant increase of the $P:R$ ratio, with increasing lake trophy expressed as Chl *a* or TP. Except for a weak relationship with ϵ_{PAR} and z_{mix}, (model 16), our data do not show any significant trend in $GP:R$ along the eightfold trophic gradient observed between the least and the most productive lake, nor with any other watershed or in-lake variable, including DOC.

Most of the variance in VGP and VR could be explained by a combination of four significant variables: Chl *a*, temperature (T), z_{mix}, and DOC (models 6 and 10). The negative coefficient of z_{mix} likely appears because photosynthesis is normally light- limited in the lower half of the epilimnion. Among variables appearing in models 6 and 10, Chl *a* and temperature combined explained 64% and 51% of the variance of VGP and VR, respectively. The presence of temperature in models 6 and 10 reflects the dependence of respiration, P_m^B, and I_k on seasonal temperature variations. The similar temperature coefficients in models 6 and 10 indicate that $P:R$ ratios are temperature invariant in these lakes. In models 6 and 10, substitution of total phosphorus for Chl *a* as one of the independent variables yielded slightly lower r^2 values (models 9 and 11).

According to the heterotrophy hypothesis, R and $R:GP$ should increase with the supply of DOC to the lakes (del Giorgio and Peters 1994). Instead, models 6 and 10 suggest a negative effect of DOC on both GP and R. This effect may be due in part to a metabolic inhibition of photosynthesis and respiration by DOC in fresh waters (Jackson and Hecky 1980). Note, however, that DOC strongly reduces light penetration in fresh waters. Because photosynthesis is usually light- limited in the lower epilimnion, the effect of DOC on R may be indirect, through the light- limitation of GP at high DOC concentrations. In these lakes, the PAR absorbance properties of DOC account for about 95% of ϵ_{PAR}. Substitution of DOC by ϵ_{PAR} in regressions 4 and 8 results in r^2 values that are almost as high (0.85 for VGP and 0.76 for VR, not shown in Table 3). The best regression found for VR included VGP and z_{mix} only as independent variables (model 12). Here, VGP alone explained 82% of the variance of VR (model 13).

The representation of metabolic rates per unit of ecosystem area is more meaningful than volumetric rates in terms of ecosystem processes. Areal gross primary production (AGP) was closely related to a combination of four water column properties: Chl *a*, DOC, temperature, and z_{mix} (model 17). Model 17 suggests that epilimnetic production rates in Shield lakes can be estimated empirically with an error of $\pm 45\%$ ($p = 0.05$) from a few chemical and physical properties. As was the case with VGP, substitution of DOC for ϵ_{PAR} in model 17 gave a similar, but slightly less accurate model ($r^2 = 0.78$, not shown). When expressed per unit surface, AR was strongly related to AGP (model 19), with a small additional contribution of ϵ_{PAR} (model 18), as observed for VR. The strong dependence of VR on VGP (model 13), and of AR on AGP (model 19) suggests, again, that in oligotrophic lakes, community respiration is mainly driven by planktonic photosynthesis, and not by exogenous carbon supply.

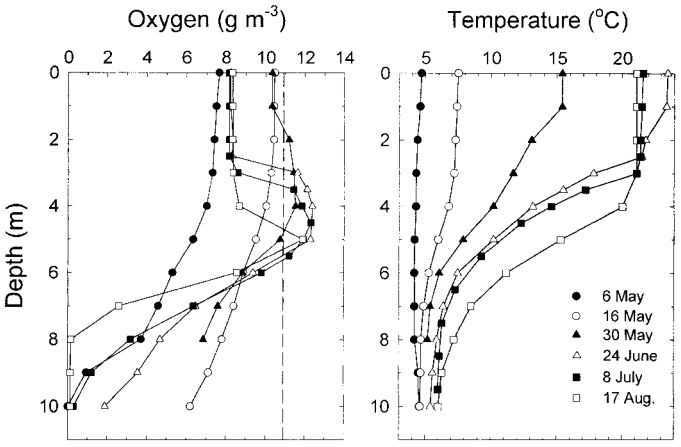

Fig. 3. Seasonal evolution of temperature and of the metalimnetic oxygen maximum in the water column of Lake Croche, 1997. The dashed line indicates the maximum springtime oxygen concentration observed (23 May) by continuous measurement of the O_2 partial pressure at the surface of the lake during the establishment of thermal stratification.

Metalimnetic P-R *Balance*—Although the results presented above strictly apply to the mixed layer, P also exceeds R in the metalimnion of one of the most oligotrophic of our study lakes (Croche), where vertical profiles were routinely collected. Between June and August, a seasonal buildup of O_2 is observed between 3 and 6 m (Fig. 3). In 1997, a maximum O_2 concentration of 10.97 g m^{-3} was measured (Carignan 1998) on May 23, at the beginning of the stratification period, and at a temperature of 9.36°C. Any subsequent increase in O_2 in the physically isolated metalimnion must therefore be due to an excess of production over respiration. The concentrations peaks exceeding 11 gO_2 m^{-3} observed between June and August in the metalimnion of Lake Croche show unequivocally that GP can exceed R, even below the mixed layer, where photosynthesis is light- limited.

Discussion

Photosynthetic parameters—Although our P_m^B, α^B and I_k estimates were within the range of values reported for oligotrophic waters, P_m^B and α^B tended to be higher than long-term mean values found in other Shield lakes (Fee et al. 1987, 1992). Our P_m^B and α^B are not unrealistically high, however, since comparable mean values have also been observed during some years at ELA (Fee et al. 1987). Furthermore, most P_m^B and α^B values published so far for oligotrophic lakes have been obtained with the ^{14}C method. Our values were obtained with the oxygen method and may not be directly comparable to ^{14}C values. In our lakes, the $NP_m^B:GP_m^B$ ratio ranged between 0.48 and 0.93, with an average value of 0.75. Hence, if the ^{14}C method measures net organic C production by the planktonic community, the P_m^B and α^B values found with ^{14}C should be substantially lower than those found with oxygen. Furthermore, our Chl *a* concentrations were corrected for phaeopigments, which amount to 10–20% of the uncorrected values in these lakes (data not shown). Decreasing our P_m^B and α^B values by 20–40% to

account for these methodological differences places them well within the range of reported values usually observed with ^{14}C in oligotrophic Shield lakes.

Production : respiration ratios—Our results show that R is nearly always smaller than, but strongly related to, GP in oligotrophic and mesotrophic Shield lakes. When Lake Raymond, polluted by sewage effluents, is excluded from the data set, our VGP : VR ratios range from 1.0 to 4.5, with a median value of 1.7. Moreover, our data did not reveal any obvious relationship between the GP : R ratio and DOC. These results do not support the idea that exogenous organic carbon plays a significant role as an energy source to the epilimnion of such lakes. In particular, our results contrast with those of del Giorgio and Peters (1994), who found that R was 2 to 8 times greater than ^{14}C production, and that the $P : R$ ratio was inversely related to DOC concentration in 20 lakes of the Eastern Townships located 100–150 km south of our study site. As shown below, this apparent contradiction may just be another manifestation of the old question regarding the meaning of production rates measured with ^{14}C in oligotrophic waters.

We believe that our respiration rates may have been somewhat underestimated. In one of the least productive lakes (Croche), where daily variations of GP and R were monitored, we have observed that although P_m^B and α^B do not change appreciably during daytime, planktonic respiration is always higher (20–30%) at sunset than it is at sunrise (unpubl. data). Since we systematically sampled the lakes in the morning, the daily R estimates of Table 2, extrapolated from morning rates, may be 10–20% too low. This bias is, however, too small to account for the large differences between the $P : R$ ratios reported by del Giorgio and Peters (1994) and those found in this study.

The contrasting $P : R$ ratios appear to arise mainly from the different photosynthesis rates measured in both sets of lakes. A comparison (ANCOVA) of volumetric R values found in both studies, and expressed as a function of lake trophy (TP or Chl *a*), shows a good agreement for respiration measurements (Fig. 4), where the slopes and intercepts of log R vs. log(TP) are not significantly different ($p > 0.1$). Large differences exist, however, in the rates of photosynthesis, with the slopes and intercepts of log P vs. log(TP) significantly different at p levels $=0.03$ and <0.00001, respectively. Below 10 mg m^{-3} TP, photosynthesis rates reported for the Eastern Townships lakes are nearly 1 order of magnitude lower than those observed in the Shield lakes. Note that much of the scatter in the data for Shield lakes in Fig. 4 is due to the temperature dependence of P and R and to the fact that we present individual observations collected at different dates, whereas del Giorgio and Peters reported average values. The contrasting production rates are unexpected, given that both data sets were acquired using methods that were similar in many respects. In both studies, epilimnetic P and R were measured, and a similar incubation method was used to produce the P/I curves. Furthermore, the same software was used to estimate photosynthetic parameters and to integrate daily production rates from the P/I curves, ϵ_{PAR}, and the average incident PAR. The average incident PAR used in both studies was nearly identical (70% of the maximum cloudless PAR assumed in del Giorgio and Peters, compared to 66.7% measured in our study).

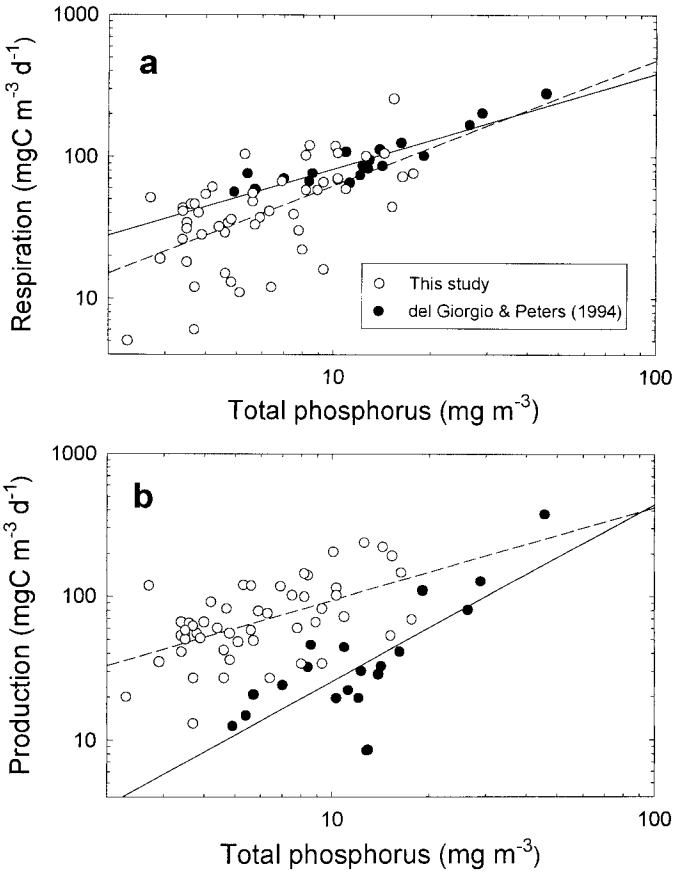

Fig. 4. Least squares fits of (a) volumetric respiration and (b) production vs. total phosphorus (lake trophy) measured in this study (open circles, dashed lines, 51 individual observations in 12 lakes) and by del Giorgio and Peters (closed circles, solid lines, mean seasonal values of 20 lakes).

Both studies differ on three potentially important points, however. The lakes were not the same; the definition of the epilimion thickness, over which metabolic measurements were integrated, was not identical; and the method used to measure photosynthesis was different (^{14}C vs. O_2). There is little reason to suspect that the lakes were fundamentally different in terms of metabolism. Most of the Eastern Townships lakes studied by del Giorgio and Peters occur on glaciated hilly terrain mainly covered by deciduous forests, except for their eutrophic lakes, which have farmland in their watersheds. Median temperatures (19.5°C) were identical in the two studies. Both sets of lakes had similar or widely overlapping DOC, TP, and Chl *a* concentrations. Our lakes were more oligotrophic, however, with median TP and Chl *a* concentrations of 5.6 and 1.8 mg m^{-3}, respectively, compared to 12.2 and 2.5 mg m^{-3} in del Giorgio and Peters. According to the heterotrophy hypothesis, and contrary to our observations, oligotrophy should have favored GP : R ratios much lower than unity in the Shield lakes. The median drainage ratio is higher (14) in our lakes than in those studied by del Giorgio and Peters (9.5). High drainage ratios and DOC loads should favor net heterotrophy. Yet, with the ex-

ception of Lake Raymond, GP:*R* ratios in our DOC-rich lakes remained substantially above unity (Table 2).

The operational definition of the epilimnion apparently differed in both studies. del Giorgio and Peters collected integrated water between the surface and the thermocline, whereas we collected water from the mixed layer only. We restricted our sampling to the mixed layer in order to study homogenous planktonic communities and to avoid exposing metalimnetic plankton to unrealistic incubation temperatures. Because the median lake area was 1 order of magnitude higher (3.05 km^2) in the Eastern Townships lakes than in the Shield lakes (0.33 km^2), the true epilimnion depth was probably larger in the Eastern Townships lakes. As a result of both factors, the median depth of the water column sampled by del Giorgio and Peters was higher (6.6 m) than in our study (4.0 m). Light limitation of photosynthesis in the lower epilimnion may contribute to the explanation of why volumetric production rates were lower in the Eastern Townships lakes. It is unlikely, however, that this reason alone can explain the large differences in photosynthesis and in *P*:*R* ratios observed between the two sets of lakes. To test this possibility, we recomputed GP and *R* in our lakes after increasing the thickness of the mixed layer by 50%. As a result, our median GP:*R* ratio decreased only from 1.7 to 1.3. Another reason argues against the possibility that the diverging results of both studies arise from differing epilimnion thicknesses. In our study lakes, the *P*-*R* balance remains positive even some distance below the epilimnion, where light is limiting, as shown by the development of a metalimnetic oxygen maximum in Lake Croche between the months of June and September (Fig. 3). The formation of biogenic metalimnetic O_2 maxima is common in lakes (Wetzel 1983; Stefan et al. 1995). Because the metalimnion is a virtually closed system in terms of vertical diffusion of dissolved substances (Quay et al. 1980), such metalimnetic O_2 maxima can develop in this part of the water column only if it is net autotrophic.

Oxygen versus carbon-14—Differences in methods used to measure or estimate metabolic rates probably explain to a large extent why different studies have reached divergent conclusions regarding the *P*-*R* balance of oligotrophic lakes. Although part of the divergence may be due to the particular PQ value (1.25) used to convert oxygen units into carbon units in production measurements, the actual average long-term PQ for phytoplankton communities is not expected to differ by much more than 20% of the assumed value. The relatively small error potentially incurred using a PQ of 1.25 cannot explain the large differences in the *P*-*R* balance found among studies.

It is probably not a coincidence that studies of the *P*-*R* balance in oligotrophic seawater, where the O_2 method was used to measure both GP and *R*, have also concluded to net autotrophy (Williams 1998). del Giorgio and Peters (1994) have compared ^{14}C photosynthesis to O_2 consumption by the planktonic community (*R*). This approach is correct only if ^{14}C uptake measures gross photosynthesis, which is unlikely. Indeed, photosynthesis rates measured with ^{14}C are ambiguous, since they can stand anywhere between gross photosynthesis and the net production of organic C by the plankton community during the incubation, depending on several factors including light and nutrient availability, phytoplankton size, and incubation time (Tilzer et al. 1977; Andersen and Sand-Jensen 1980; Peterson 1980). The meaning of ^{14}C production data is particularly uncertain in oligotrophic waters, where, in some cases, ^{14}C production has been found to underestimate gross photosynthesis by as much as 1 order of magnitude (Peterson 1980). If daily production rates estimated with the ^{14}C technique are close to NP, then *P*:*R* ratios will be underestimated because community respiration is already subtracted from NP.

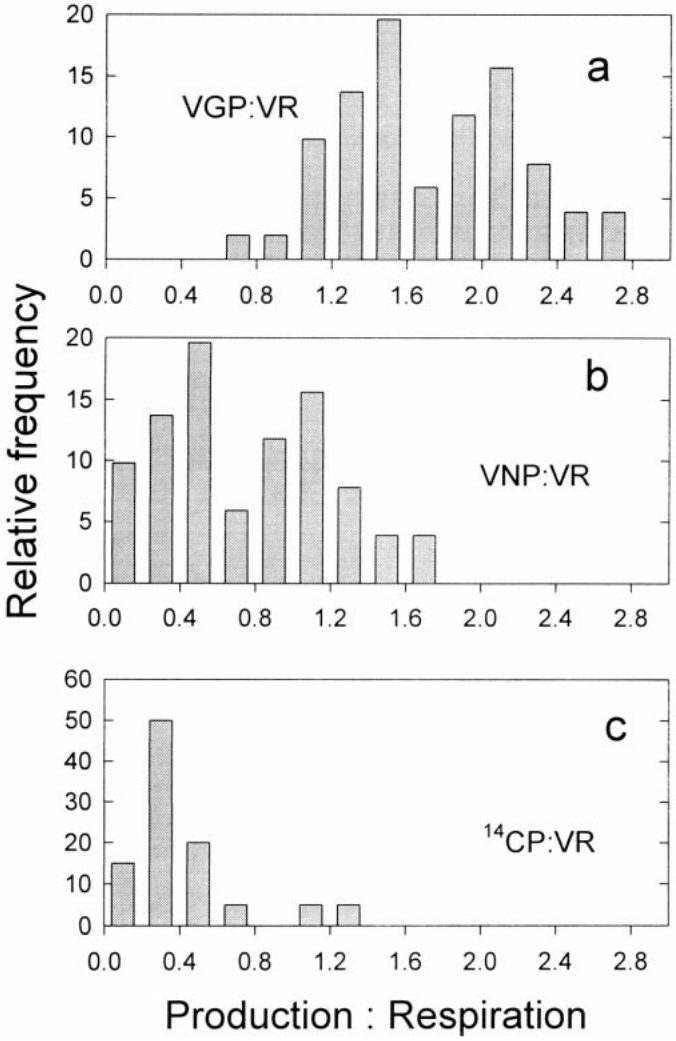

Fig. 5. Frequency distributions of volumetric *P*:*R* ratios calculated as (a) gross photosynthesis over planktonic respiration (this study), (b) net production over planktonic respiration (this study), ^{14}C production over planktonic respiration (del Giorgio and Peters 1994).

The misinterpretation of ^{14}C data as gross photosynthesis rates can produce *P*:*R* ratios below unity. This is illustrated in Fig. 5, where the frequency distributions of *P*:*R* ratios measured by del Giorgio and Peters (1994) are compared to those calculated from our data as GP:*R* and NP:*R*. As can be seen, the median NP:*R* ratio of our lakes falls below unity, as found by del Giorgio and Peters. Interestingly, al-

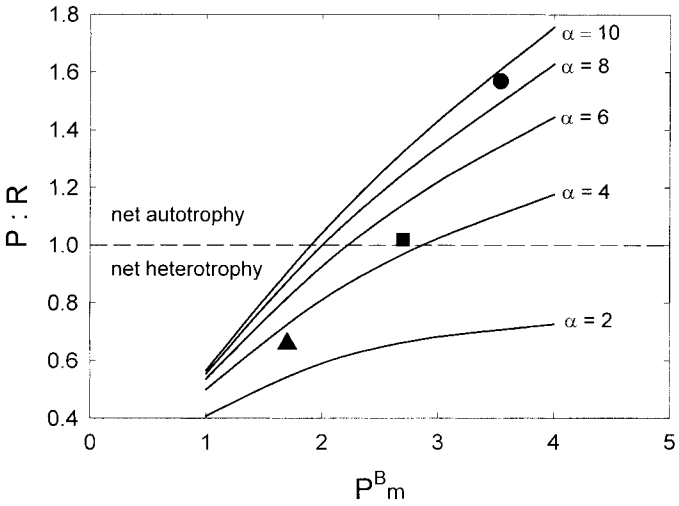

Fig. 6. Midsummer planktonic production : respiration ratio in a water column representing the median conditions (mixing depth, light attenuation, chlorophyll concentration, and planktonic respiration) observed in our study lakes, calculated as a function of P_m^B and α^B. The points compare the contrasting $P:R$ ratios obtained when the daily P integral is calculated (Fee 1990) using P_m^B and α^B values measured with the oxygen method (circle, this study) and measured with the ^{14}C method in other Shield lakes (triangle: median values of Fee et al. [1987]; square: median values of Fee et al. [1992]).

though no relationship could be found between the $GP:R$ ratio and DOC or lake trophy (Chl *a*, TP) in our data set, weak but significant ($p < 0.01$) influences of DOC (negative) and lake trophy (positive) emerge when, this time, the $NP:R$ ratio is considered (Table 3, model 20). In model 20, the intercept and the regression coefficients are comparable to those reported by del Giorgio and Peters. Thus, the results of del Giorgio and Peters can be reproduced, qualitatively at least, if we assume that ^{14}C production is close to NP in oligotrophic lakes. Note, however, that the $P:R$ ratios of del Giorgio and Peters still remain well below our $NP:R$ ratios. In a cross-scale analysis of the $P:R$ ratio of aquatic ecosystems, Duarte and Agusti (1998) concluded that R tends to exceed P in less productive lakes, where VP is smaller than about 1 $gO_2\ m^{-3}\ d^{-1}$ (300 $mgC\ m^{-3}\ d^{-1}$). It should be noted, however, that the oligotrophic O_2 production data used by Duarte and Agusti included, in fact, a large proportion of ^{14}C data (including those of del Giorgio and Peters [1994]) that were transformed into oxygen units.

Photosynthetic parameters and the P : R *ratio*—Photosynthetic light-response curves are usually reported as the chlorophyll-specific parameters P_m^B and α^B, and the chlorophyll-independent I_k. These parameters constitute a convenient way of representing the photosynthetic capacity, the physiological status, and the adaptation of autotrophs to light and temperature conditions. Photosynthetic parameters also allow the estimation of primary production from chlorophyll data and the comparison of production data among studies. Because the ^{14}C method may underestimate P_m^B and α^B, it becomes of interest to explore the effect of these underestimations on $P:R$ ratios. This is illustrated in Fig. 6 for a 4-m-deep water column containing 1.7 $mg\ m^{-3}$ of Chl *a*, with $\epsilon_{PAR} = 0.7\ m^{-1}$. These conditions correspond to median values observed in our study lakes. The $P:R$ isopleths of Fig. 6 were calculated from areal production (DPHOTO) for August 1, at a latitude of 46°N, setting the incident PAR at 66% of the maximum cloudless value. P_m^B and α^B were allowed to vary between 1–4 and 2–10, respectively. Community respiration was set equal to the median value observed in our lakes (164 $mgC\ m^{-2}\ d^{-1}$). The results show, as expected, that P is larger than R when our median oxygen-derived P_m^B and α^B values are used to estimate GP. On the other hand, long-term median ^{14}C-derived P_m^B (1.7 to 2.7 $mgC\ mgChl\ a^{-1}\ h^{-1}$) and α^B (3 to 4.5 $mgC\ mgChl\ a^{-1}\ E^{-1}\ m^2$) taken from Fee et al. (1987, 1992) for Shield lakes yield $P:R$ ratios that lie just above to well below unity. We conclude that much of the debate on the relative size of P and R in oligotrophic lakes may have a purely methodological origin, which resets the focus, again, on the meaning of ^{14}C production data.

Other studies concluding to net heterotrophy have compared ^{14}C photosynthesis (assuming this time to represent NP) with bacterial respiration, as measured from O_2 consumption by the <0.8–2 μm size fraction (del Giorgio et al. 1997). Here, $P:R$ will be underestimated if respiration by the <0.8–2 μm size fraction also includes respiration by photosynthetic picoplankton, which makes up a significant portion of the planktonic community in oligotrophic marine and fresh waters (Stockner 1988; Geider 1997). Furthermore, such results would remain questionable even if they did not include any autotrophic respiration. Indeed, this approach also assumes that ^{14}C-NP measures gross photosynthesis less autotrophic respiration that, in theory, should correspond to the amount of organic C that can be transferred to heterotrophs. In reality, it is likely that some of the net C produced by autotrophs is used by heterotrophs during 2–4-h incubations, particularly in oligotrophic waters, where generation times are short (Peterson 1980). Some reports of low algal to bacterial growth ratios are based on comparisons of ^{14}C NP with bacterial production estimated from ^3H-thymidine or ^{14}C-leucine incorporation (Findlay et al. 1991, 1992). Production : respiration ratios based on this approach are even more questionable, since the conversion factors needed to translate tracer uptake into bacterial growth may not be sufficiently accurate to resolve fine balances between autotrophic and heterotrophic metabolism.

The balance between production and respiration and the role of exogenous organic carbon supply in aquatic ecosystems are fundamental issues that will require further attention. In particular, the validity of using ^{14}C production rates to derive $P:R$ ratios should be closely reconsidered. Our results clearly support the classical view that pelagic food webs are primarily sustained by planktonic photosynthesis. This is confirmed in one of the most oligotrophic of our study lakes (Croche), where continuous high-precision measurements of dissolved gas partial pressures at the water surface (Carignan 1998) during thermal stratification show that the water remains supersaturated with respect to atmospheric O_2 (~1%, on average) despite a persisting CO_2 supersaturation (~50%, on average). The O_2 supersaturation confirms that the epilimnion, including its bottom sediments, must be net autotrophic. The excess CO_2, which is common in lakes

(Cole et al. 1994), likely originates from CO_2-rich groundwaters, which can contain up to 100 times more free CO_2 than lakewaters (Stumm and Morgan 1981). Our conclusions strictly apply to epilimnetic planktonic communities, as observed during the ice-free period, and to metalimnetic communities developing a positive O_2 balance during thermal stratification. Whether entire lake ecosystems are net autotrophic or net heterotrophic on a yearly basis remains to be seen.

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