CHAPTER 7

Respiration in lakes

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Outline

This chapter reviews, from a quantitative perspective, estimates and models of planktonic and benthic respiration in lakes, as derived from bottle and core incubations. Using data gleaned from the literature, empirical models of planktonic and benthic respiration are presented in which respiration is shown to depend primarily on lake trophic conditions and, secondarily, on temperature and other factors such as dissolved organic carbon loading and community structure. The possibilities and limits of alternative methods of measuring lake respiration and its components are discussed. Extrapolations of the findings to the globe suggest that about 62–76 Tmol of carbon are respired annually in the world's lakes, exceeding the estimated gross primary production of these ecosystems. Lakes thus contribute significantly to the oxidation of land-derived organic carbon.

7.1 Introduction

Respiration in lakes recycles organic carbon arising from photosynthesis back to inorganic carbon. Prior to this transformation, the organic carbon is potentially available to support secondary production. The efficiency of primary and secondary production relative to respiration is an important feature of lakes and other aquatic ecosystems. The relative rates and locations of primary production and respiration also influence oxygen concentrations. Intensive respiration in sediments and isolated waters, such as the hypolimnion or in ice-capped lakes, often leads to oxygen depletion and even anoxia. Thus, the rates and controls of respiration are of central importance in lake ecosystems.

Respiration affects net balances of carbon in lakes. Many lakes are net heterotrophic, meaning respiration exceeds gross primary production (del Giorgio and Peters 1994). In this case, the partial pressure of carbon dioxide exceeds that in the atmosphere and so carbon dioxide diffuses out of the lake while oxygen is undersaturated and diffuses into the lake (Prairie *et al*. 2002). The loss of carbon dioxide to the atmosphere, however, does not imply that storage of carbon in net heterotrophic lakes is zero. Quite the contrary, lakes accumulate organic matter in sediments (Dean and Gorham 1998). This seeming contradiction that lakes are sources of carbon to the atmosphere and sedimentary sinks for organic carbon is reconciled by respiration of terrestrial organic inputs in lakes (del Giorgio *et al*. 1999). Thus, the carbon that supports respiration in lakes is derived from within-lake primary production as well as allochthonous sources in the watershed. Some lakes are net autotrophic, where gross primary production exceeds respiration. These draw inorganic carbon from the atmosphere and store sediment organic carbon. Thus, both net autotrophic and net heterotrophic lakes are sinks for atmospheric carbon when considered on a watershed scale.

The purpose of this chapter is to summarize measured rates, variation in rates among lakes, and factors regulating respiration in lakes. Methods of

measuring respiration are not reviewed in detail but common approaches are mentioned briefly to give the reader context for the discussion of rates. Rates of planktonic and sediment respiration are presented from literature data on oxygen consumption obtained from studies using bottle and core incubations. The data are used to develop general empirical models of planktonic and sediment respiration as a function of lake trophic conditions. These models are applied to generate a global estimate of respiration in lakes. Anaerobic respiration is also important in many lakes but only considered briefly here. Fenchel (1998) and King (Chapter 2) provide an excellent introduction to anaerobic processes. Wetzel (2001) reviews the general significance of anaerobic respiration in lakes. A limitation of traditional methods for estimating respiration is that changes in oxygen or carbon dioxide of enclosed communities are measured and extrapolated over time and space for an entire lake. Diel cycles of oxygen can be measured using *in situ* instruments. We provide an example of respiration derived from this "free water" approach and compare estimates from *in situ* and enclosure approaches.

7.2 Planktonic respiration

7.2.1 Methods

Consumption of oxygen in dark bottles has been the main approach to measuring planktonic respiration. Alternative methods have been used, including measuring activity of the electron transport system (del Giorgio 1992), changes in the partial pressure of carbon dioxide (Davies *et al*. 2003), and changes in oxygen isotope ratios (Bender *et al*. 1987). We primarily discuss dark bottle oxygen consumption because the data synthesis provided below is based on measurements made with this method. We also briefly consider the application of some of the other methods to lake systems.

In the dark bottle method, plankton communities are enclosed in bottles and replicate measurements of the initial and final concentrations of oxygen are made. Because the method depends on measuring small differences in oxygen concentrations, precision and accuracy are important. Much effort has focused on improving standard oxygen measuring techniques to enhance accuracy (e.g. Carignan *et al*. 1998) and facilitate the ease of replicate measurements in order to improve precision (e.g. Roland *et al*. 1999). In addition, the availability of very sensitive instruments for oxygen measurement, such as dual-inlet mass spectrometry, allows shorter incubation intervals (del Giorgio and Bouvier 2002). With improvements in methods, incubations of a few hours rather than a full day are sufficient to estimate rates even in oligotrophic lakes (e.g. Carignan *et al*. 2000). Short incubation reduces artifacts associated with enclosing microbial communities in bottles and provides results over timescales commensurate with other measures of microbial activity such as primary and bacterial production assays.

Differences in oxygen concentration at the beginning and end of a dark bottle assay represent net oxygen consumption from all processes occurring in the bottle over time. Since bottles are incubated in the dark, it is assumed no oxygen production occurs. Oxygen consumption may arise from abiotic chemical oxidation as well as biotic reactions. Chemical oxidation reactions are primarily light driven. The aggregate of these reactions is referred to as photooxidation, and this process is presumed to cease during dark incubations. Graneli *et al*. (1996) directly compared measurements of photooxidation and dark respiration in Swedish lakes that varied in dissolved organic matter and found that photooxidation was $<10\%$ of dark respiration. Thus, measurements of dark respiration are probably not compromised by oxygen consumption due to photooxidation reactions initiated in the light that might continue during some portion of the dark incubation.

Extrapolations of bottle respiration measurements typically make the assumption that oxygen consumption measured in the dark is equivalent to oxygen consumption that occurs in the light. However, oxygen consumption in the light can be higher than in the dark because of photorespiration, the Mehler reaction (a photoreduction of O_2), and light-stimulation of normal cytochrome oxidase respiration (also referred to as dark or mitochondrial respiration). In addition, a process

known as the alternative oxidase respiration may consume oxygen in the light and the dark (Luz *et al*. 2002, see also Raven and Beardall, Chapter 3). Photorespiration occurs because of oxygen accumulation and a relative decline of carbon dioxide as photosynthesis proceeds such that the primary carbon fixation enzyme (ribulose-1,5-***bis***-phosphate carboxylase/oxygenase) no longer fixes carbon dioxide but instead consumes oxygen (see also Raven and Beardall, Chapter 3). The Mehler reaction involves electron tranport among photosystems 1 and 2 with concurrent oxygen reduction (Falkowski and Raven 1997). Finally, enhanced cytochrome oxidase respiration occurs in the light for actively growing phytoplankton in cultures (Grande *et al*. 1989; Weger *et al*. 1989). The overall effect of these mechanisms that result in light-enhanced oxygen consumption on measurements of respiration is poorly understood and is an area of active research (Luz *et al*. 2002). Underestimates of respiration in dark incubations will likely be related to the relative importance of autotrophs and their growth rate in a given sample as well as to contemporaneous environmental conditions such as light exposure and temperature (see also Williams and del Giorgio, Chapter 1).

Following increases in carbon dioxide is a feasible means for measuring respiration but is complicated by potential changes in the components of dissolved inorganic carbon (DIC)—aqueous carbon dioxide, bicarbonate, and carbonate. Davies *et al*. (2003) describe a method applicable to lakes for measuring changes in the partial pressure of carbon dioxide (pCO_2) in a headspace created in a sealed sample. The technique involves measuring pCO_2 over time along with at least one measurement of the total DIC. If carbonate alkalinity is constant during sample incubation, DIC can be calculated from pCO_2 for every time point. Respiration is then estimated from the change in DIC over time. This method has not yet been extensively applied, but offers the opportunity to estimate gross primary production, respiration, and net community production (Davies *et al*. 2003) as currently done with light and dark bottle measurements of oxygen. Combining this method with oxygen techniques would, in theory, allow measurement of both carbon and oxygen changes as a consequence of photosynthesis and respiration and provide direct estimates of photosynthetic and respiratory quotients.

Another approach to production and respiration measurements involves spiking samples with $H_2{}^{18}O$. This method has been used in a few lakes (Luz *et al*. 2002). The advantage of this technique is that gross primary production and respiration can be estimated in the light allowing evaluation of the assumption necessary with other methods that respiration in the light equals respiration in the dark. The method is technically demanding and requires measuring oxygen isotopes and estimating fractionation for a number of processes related to biological oxygen consumption and production as well as abiotic exchanges of oxygen (e.g. Luz *et al*. 2002).

7.2.2 Data compilation

We compiled data from the literature for lake studies that reported rates of planktonic respiration based on dark bottle oxygen consumption along with the independent variables chlorophyll *a*, total phosphorus, and dissolved organic carbon. Some studies used other methods to measure respiration such as DIC accumulation in dark bottles (e.g. Graneli *et al*. 1996), and we excluded these to obtain a methodologically consistent dataset. We only used data from studies more recent than those of del Giorgio and Peters (1993) who summarized data from the literature on mean respiration in 36 lakes. We found seven studies that reported mean rates for lakes along with at least some of the independent variables—del Giorgio and Peters (1994), Pace and Cole (2000), Duarte *et al*. (2000), Carignan *et al*. (2000), Biddanda *et al*. (2001), Biddanda and Cotner (2002), and Berman *et al*. (2004). Our search was not exhaustive but was extensive. Keywords in titles and abstracts were searched electronically and numerous individual articles were reviewed. In addition, we visually reviewed all article titles and abstracts over several years in a few journals. A number of the studies noted above measured respiration in multiple lakes and so an aggregate 70 values of mean planktonic respiration were derived from the literature.

The studies were all of north temperate lakes sampled during the May–September period with

the exception of Duarte *et al*. (2000) where lakes in northeast Spain were sampled from December through May. Rates in the literature studies are all derived from surface, mixed-layer samples, and means are based on as few as one sampling time (e.g. Duarte *et al*. 2000), 3–4 samples from approximately monthly observations (e.g. del Giorgio and Peters 1994; Carignan *et al*. 2000), 15–17 samples based on weekly observations (Pace and Cole 2000). Reservoirs and saline lakes sampled by Duarte *et al*. (2000) were excluded from the final data, because respiration in these systems tended to be substantially lower and higher, respectively than in the freshwater lakes. Means from Pace and Cole (2000) were derived from one reference and three lakes manipulated with additions of nitrogen and phosphorus over a number of years. We averaged all data for the reference lake to generate a single mean (years 1991–7). We averaged data for 2 years prior to nutrient loading manipulations for the other three lakes (1991–2) to generate three means and then treated each year of nutrient manipulation (loading rates varied among years) as a separate mean. This generated 19 mean values overall representing 28 lake-years of measurements.

Typically, comparisons of production, nutrient cycling, or biomass among lakes reveal ranges in variation of over a 1000-fold. Mean values of planktonic respiration only varied from 0.029 to 6.73 mmol $O_2\,m^{-3}\,h^{-1}$, a factor of 265. This modest range must underrepresent actual variation among lakes, because of the limited number of studies and the focus on temperate lakes in summer. A more global survey of lakes would probably reveal systems with lower respiration because of low productivity and low temperatures, and some with higher respiration because hypereutrophic lakes (chlorophyll less than 75 mg m^{-3}) are not well represented in the dataset. However, the limited range indicates an important feature of planktonic respiration. Respiration is less variable than other variables measured in aquatic systems.

7.2.3 Models of planktonic respiration

There are few models of planktonic respiration that are comparable to well-developed models of primary production based on photosynthesis—irradiance relationships (Platt and Jassby 1976) as well as approaches that combine photosynthetic parameters with depth distributions of primary producers to estimate rates over large scales such as the global ocean. Models for planktonic respiration are largely empirical and are based on features such as primary productivity as, for example, in the global analysis of aquatic ecosystems inclusive of lakes provided by Duarte and Agusti (1998).

Temperature

Because lake planktonic respiration studies have focused on surface water in summer of temperate lakes, there has been relatively little consideration of the effects of temperature on rates. Nevertheless, Carignan *et al*. (2000) determined a relationship between volumetric respiration and several variables, including temperature. This multiple regression relationship (their equation (10) of table 3) is useful in that it allows one to isolate the influence of temperature on respiration while statistically keeping all other variables constant. Over their observed temperature range of 11–22.5°C, the log–log slope coefficient of temperature is 1.28, implying a Q_{10} of about 2.3 in that temperature range. If this slope coefficient of 1.28 remains valid even for lower temperatures, it would suggest an even higher Q_{10} at low temperatures. This prediction needs to be confirmed by additional observations across a broader temperature range, but the same pattern has been observed for sediment respiration, as discussed below.

Lake trophic conditions and organic matter loading

Plankton respiration (PR) increases in concert with increases in chlorophyll, phosphorus, and dissolved organic carbon (Fig. 7.1). Mean lake chlorophyll *a* accounts for 71% of the variance in respiration (Fig. 7.1(a)). A similar relationship is observed with total phosphorus although r^2 was higher (0.81) for this relationship based on fewer observations ($n = 62$, Fig. 7.1(b)). The equations relating PR (mmol $O_2\,m^{-3}\,h^{-1}$) to chlorophyll *a* (Chl, mg m^{-3}) and total phosphorus (TP mg m^{-3}) are:

$$\log_{10} \mathrm{PR} = -0.81 + 0.56 \log_{10} \mathrm{Chl} \quad (1)$$

$$\log_{10} \mathrm{PR} = -1.27 + 0.81 \log_{10} \mathrm{TP} \quad (2)$$

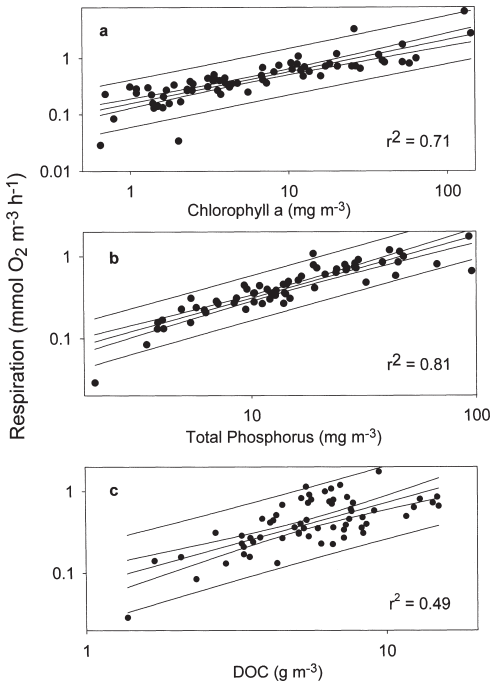

Figure 7.1 Relationships between planktonic respiration and (a) chlorophyll *a* (b) total phosphorus, and (c) dissolved organic carbon (DOC) for lakes. Regressions are model 1 least square plots with 95% confidence intervals for the regression and for individual predictions.

These two relationships reflect a typical pattern of lakes where primary production is strongly nutrient limited and closely related to total phosphorus inputs and concentrations. The large-scale comparison in Fig. 7.1 indicates that planktonic respiration is strongly coupled with variation in phytoplankton biomass and primary production.

Equation 1 compares well with the relationship established by del Giorgio and Peters (1993) from earlier literature data. They reported a regression for PR in units of mg C m^{-3} d^{-1} based on chlorophyll *a* with a slope of 0.65 and an intercept of 1.65. Transforming the data underlying equation (1) into commensurable units yields the same intercept of 1.65 observed by del Giorgio and Peters (1993). Thus the two independent relationships overlap closely, differing only slightly in slope (0.65 versus 0.56) and give similar predictions, especially in the range of 0.5 to 5 mg chlorophyll m^{-3}.

Dissolved organic carbon (DOC) in lakes is derived both from watershed sources and within-lake primary production. If allochthonous inputs of DOC are significant to lake carbon cycling and supplement ecosystem metabolism, DOC should be positively related to PR. This is the case for 63 lakes (Fig. 7.1(c)) where there is a positive relationship between DOC (g m^{-3}) and PR ($r^2 = 0.49$).

$$\log_{10} \mathrm{PR} = -1.15 + 1.01 \log_{10} \mathrm{DOC} \qquad (3)$$

The positive relationship of PR with DOC reflects, in part, increased microbial metabolism associated with increased inputs of DOC to lakes. However, DOC is not simply the result of watershed inputs but also arises from phytoplankton and littoral primary producers, the relative contributions of which are still not well known. Hence, the relationship is complex and a more interesting test of the positive effect of watershed-derived DOC on PR would be to compare lakes with differing DOC concentrations (and loadings) but similar levels of total phosphorus or chlorophyll *a*.

Both chlorophyll and DOC are significant variables in a multiple regression ($r^2 = 0.76$, $n = 63$).

$$\log_{10} \mathrm{PR} = -0.92 + 0.41 \log_{10} \mathrm{Chl} + 0.30 \log_{10} \mathrm{DOC} \qquad (4)$$

The *t*-values associated with each variable indicate chlorophyll is highly significant while DOC explains a modest but also significant amount of the residual variation (chlorophyll $t = 7.96$, $p < 0.0001$; DOC $t = 2.35$, $P = 0.022$). Chlorophyll and DOC, however, are correlated ($r = 0.71$, $p < 0.0001$) and so this relationship may be less suitable for predicting PR and associated uncertainty than the single variable relationship with chlorophyll (equation 1).

Other factors influencing planktonic respiration

There have been relatively few detailed studies on respiration and depth in lakes. The primary reason is that respiration becomes difficult to measure at low rates. With the declines in temperature and primary productivity associated with increases depth in lakes, respiration rates probably must also decline. However, bacterial metabolism contributes significantly to respiration and partially compensates for the expected declines with depth. Numerous efforts have been made to partition oxygen consumption in the hypolimnion of lakes among

water and sediments because of the importance of hypolimnetic oxygen deficits during seasonal stratification. These studies either involve modeling (e.g. Livingstone and Imboden 1996) or, when direct measurements of hypolimnetic PR have been attempted, long incubations of organism concentrates (e.g. Cornett and Rigler 1987). Refinements in methods for measuring respiration discussed above provide an opportunity to now make direct measurement over reasonable incubation times.

While planktonic respiration is strongly related to nutrient and organic matter loading as well the biomass of primary producers, food web structure can also influence respiration. Pace and Cole (2000) reported strong food web effects on respiration from a series of whole lake manipulation studies. Fish communities in three lakes were shifted to promote the dominance of either piscivorous or planktivorous fish and then the lakes were fertilized with nutrients. Predator–prey interactions arising from the top of the food web either strongly limited large crustacean grazers or alternatively tended to promote dominance of large zooplankton through trophic cascades (Carpenter *et al*. 2001). Nutrient additions were carried out over 5 years in each lake and dark bottle respiration was measured. Planktonic respiration differed among the fertilized lakes at the same nutrient loading and, over the 15 lake-years represented in this study, was inversely related to the average size of crustacean zooplankton (Fig. 7.2). Gross primary production, system respiration, and net ecosystem production as measured by free water methods (discussed below) were also strongly affected by differences in food web structure in these experimental lakes (Cole *et al*. 2000).

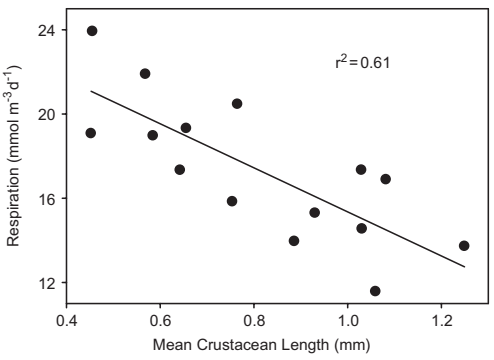

Figure 7.2 Relationship between mean crustacean length and mean planktonic respiration in nutrient fertilized experimental lakes.

7.3 Sediment respiration

The sediment–water interface is the site of some of the most intense biological activity of freshwater systems (Krumbein *et al*. 1994). The large exchange surface area provided by loosely compacted sediment particles, the organic nature of the sediments, and its physical stability all act synergistically to produce an extremely active milieu. In comparison to the water column, sediments are typically 1000-fold richer in both nutrients and carbon, and thereby provide a highly concentrated growth medium for heterotrophic bacteria. Correspondingly, bacterial abundances and production rates are typically about 2–3 orders greater than in the water column, a phenomenon recognized nearly half a century ago (Kuznetsov 1958). Depending on the transparency of the water column above the sediments, the high benthic metabolic activity is differently divided between anabolic and catabolic processes. However, because most of the sediments are below the euphotic zone, respiration is by far the dominant metabolic process in sediments. In his treatise, Hutchinson (1957) argued that oxygen consumption within lake hypolimnia can be accounted for by water column respiration, and therefore, concluded that sediment respiration represented only a minor portion of the hypolimnetic metabolism, a view at odds with recent literature. For example, Lund *et al*. (1963) estimated that about half of the hypolimnetic metabolism of Lake Windermere was benthic, a conclusion upheld by Cornett and Rigler (1987) who found between 30 and 80% of the total hypolimnetic oxygen consumption was attributable to sediment respiration in a series of Québec lakes.

7.3.1 Methods

Historically, sediment respiration has been determined mostly using measurements of oxygen consumption (Hayes and Macaulay 1959; Pamatmat 1965) although some early work also used carbon

dioxide accumulation (Ohle 1952). Oxygen consumption and carbon dioxide release are not always well coupled (Rich 1975, 1979), particularly in dystrophic lakes and peat bogs (see Roehm, Chapter 6), and the degree of decoupling is usually attributed to anaerobic respiration pathways (methanogenesis or use of alternate terminal electron acceptors such as sulfates, nitrates, and metal oxides, see also King, Chapter 2). In systems where anaerobic metabolism is negligible, oxygen consumption and inorganic carbon release are both adequate measures of benthic respiration, provided carbon dioxide release and consumption induced by $CaCO_3$ precipitation and dissolution, respectively, are taken into account (Graneli 1979; Andersen *et al*. 1986, and see Hopkinson and Smith, Chapter 6, and Middelburg *et al*., Chapter 11). Most reports of benthic respiration are based on oxygen consumption.

Benthic respiration rates has been estimated by several direct and indirect techniques including: sediment core incubations (Hargrave 1969*a*; Rich 1975; den Heyer and Kalff 1998; Ramlal *et al*. 1993; Schallenberg 1993), benthic chambers (Pamatmat 1965, 1968; James 1974; Cornett 1982), vertical profiles of decomposition products in interstitial sediment water (Carignan and Lean 1991), or as the difference between total and water column metabolism in lake hypolimnia (Cornett and Rigler 1987). Because these methods encompass very different degrees of spatial integration and because of the notorious spatial heterogeneity of lake sediments, it is difficult to compare rates of benthic respiration obtained from these different methods.

James (1974) compared sediment respiration rates obtained from cores and benthic chambers and concluded that cores tended to underestimate respiration rates by an average of 35%, although Campbell (1984) showed that core incubations can estimate whole-lake sediment respiration within 10%. Given that most literature values of benthic respiration were derived from core incubations, models of benthic respiration, therefore, carry the potential bias of being slight underestimates.

A more spatially integrative measure of sediment respiration has recently been proposed by Livingstone and Imboden (1996). The effects of sediment respiration can be observed through the nearly ubiquitous nonlinearities of hypolimnetic oxygen profiles, with lower concentrations near the sediments. The extent of these sharper reductions close to the sediments is largely determined by the increasing area of sediments in the deeper strata of the hypolimnion. Livingstone and Imboden (1996) proposed a simple modeling approach to estimate the relative contributions of benthic and water column metabolism to the total oxygen consumption of the hypolimnion by relating the rate of decline of oxygen at a given depth to the sediment surface area: water volume at that particular depth. Application of this method to a vertical oxygen profile from Lac Fraser (Québec) shows a very strong relationship, the intercept and slope of which correspond to the water column and benthic respiration rates, respectively (Fig. 7.3). If the general applicability of this approach can be firmly established, it may provide a more useful measure of benthic respiration, by implicitly integrating differences in respiration at different depths within the hypolimnion and by avoiding potential experimental artifacts inherent to incubations in closed containers.

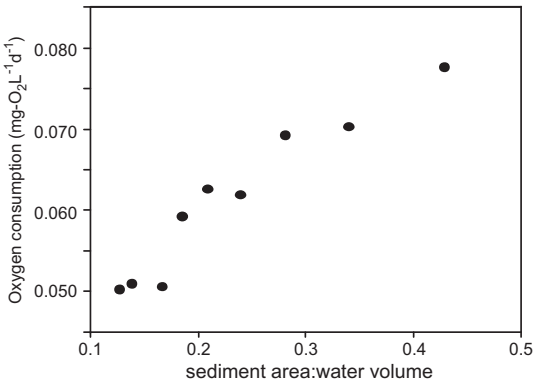

Figure 7.3 Relationship between oxygen consumption as a function of the sediment area: water volume ratio for each 1-m hypolimnetic strata in Lac Fraser, Québec (Canada).

7.3.2 Data compilation

The literature on sediment respiration in freshwater systems is much sparser than for marine or estuarine waters, particularly in recent years. As

for pelagic respiration, we synthesized the published literature and obtained values on sediment respiration rates from a variety of freshwater systems, located mostly in North America or Europe. The lakes spanned the entire trophic range, from the arctic oligotrophic Char Lake (Canada, Welch and Kalff 1974) to eutrophic Lake Alserio (northern Italy, Provini 1975) and encompassed very different types of sediments (organic matter content varied from 10 to 40%). Sediment respiration varied only 20-fold, from 1.6 to 33 mmoles $O_2\,m^{-2}\,d^{-1}$ (average is 10.9), similar to the range observed by den Heyer and Kalff (1998). For consistency, models developed from the literature data were restricted to measurements made in core incubations.

7.3.3 Models of benthic respiration

Existing models of benthic respiration can be broadly categorized as those based on sediment properties and those based on water column or whole system properties. In comparison with models of planktonic respiration, the predictive ability of existing sediment respiration models has been rather poor and their generality tested more regionally.

Effect of temperature

The earliest general model of benthic respiration was originally proposed by Hargrave (1969*a*), who argued that temperature was the main driving variable. Graneli (1978) suggested that temperature and oxygen concentration were more important factors in regulating sediment respiration than differences in lake trophic status and its associated lake primary productivity. Our compilation of sediment respiration rates from the literature gives, at first sight, credibility to this claim. Temperature alone has been shown to induce changes in respiration rates of nearly one order of magnitude (Hargrave 1969*b*; Graneli 1978; Ramlal *et al*. 1993) within the 4–25°C temperature range, in sediments incubated at different temperatures or followed through an annual temperature cycle. Thus, temperature-induced variations in sediment respiration of a given sediment can be nearly as large as among-lake differences (1.5 and 1 orders of magnitude range, respectively). Several authors have shown that the temperature effect is more pronounced at low temperatures than in warm environments (Hargrave 1969*b*; Graneli 1978; den Heyer and Kalff 1998). These relationships are often best described on a double logarithmic scale, and therefore, the relative increase in respiration rate with temperature (i.e. a Q_1) decreases with increasing temperature and can be expressed by the simple function:

$$Q_1 = 1 + b/t \tag{5}$$

where b is the slope of the log–log relationship between respiration rate and temperature (t in °C). An analysis of b values derived from the literature yields an average value of 0.65 ± 1 and Fig. 7.4 illustrates how the relative rate of increase in respiration rate per degree centigrade decreases with temperature. Most of the nonlinearity in this relationship occurs below 10°C, suggesting that changes in temperature are much more important for hypolimnetic sediments than in warm littoral zones. For example, increasing the temperature of hypolimnetic sediments from 4 to 5°C has the same relative effect on benthic respiration as increasing the temperature of epilimnetic sediments from 20 to 25°C. For comparison, Fig. 7.4 also illustrates the inferred influence of temperature on planktonic respiration derived in the previous section. It appears that, at least for warm waters, the influence of temperature on respiration is greater for the plankton than it is for sediments.

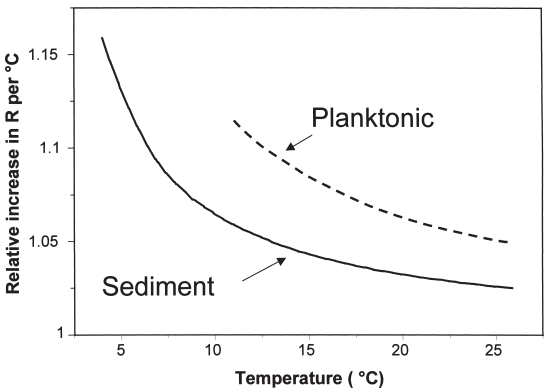

Figure 7.4 Temperature dependence of respiration expressed as relative increase in respiration rate per degree Celsius. Solid line is for sediment respiration, dashed line corresponds to planktonic respiration.

Assuming that the temperature relationship holds generally, sediment respiration (SR) rates can be normalized to a standard temperature (e.g. 10°C) by using

$$SR_{std\ 10°C} = SR/(Temp/10)^{0.65} \quad (6)$$

to allow more direct comparisons among sediments of different systems. Application of this standardization to our data compilation showed that while individual values changed as much as threefold, it affected the overall range of observed benthic respiration rates very little, suggesting that the strong relationship between temperature and benthic respiration rates of Hargrave (1969*a*) may be more the result of cross correlations between temperature and other system properties (such as lake productivity) than only the metabolic enhancement of respiration at high temperatures.

Organic matter loading, primary production, and lake trophic status

Ultimately, benthic respiration below the photic zone is fueled by organic material sinking from the pelagic zone or transported laterally from shallow sediments. Despite this functional coupling, the link between short-term organic carbon flux and sediment respiration has not been well established largely because of the apparent delay between when the organic particles settle and decompose. Indeed, the relative invariance of benthic respiration over the seasons when large changes occur in the organic matter flux has led several authors to argue that benthic respiration is the reflection of the organic matter loading integrated over several years rather than the rapid decomposition of freshly sedimented material (Lasenby 1975; Graneli 1978; Linsey and Lasenby 1985). The implications of this dampening effect of the accumulated surface sediments are important: reductions in lake productivity following eutrophication control measures may only translate into a response in benthic metabolism after several years (Graneli 1978; Carignan and Lean 1991). In lakes with shallow hypolimnia, which constitute the majority of eutrophic lakes (Kalff 2002), sediment respiration is responsible for a large fraction of the total hypolimnetic oxygen consumption (Cornett and Rigler 1987). Hypolimnetic anoxia may, therefore, continue long after nutrient loading reduction targets have been achieved, a phenomenon unfortunately observed in many lake restoration efforts (Sas 1989). Baines and Pace (1994) have shown that organic particle flux is well correlated to lake trophic status as measured by epilimetic chlorophyll concentration. In steady-state conditions, benthic respiration should therefore be well correlated with primary production and its determinants, particularly given that the fraction of the primary production carbon exported to the deeper layers appears only modestly reduced in highly productive systems (Baines and Pace 1994). A closely related hypothesis was first proposed by Hargrave (1973), who suggested that benthic respiration should be expressed as a power function of the ratio of areal primary production (PP) to mixing depth (Z_m)

$$SR = \alpha(PP/Z_m)^{\beta} \quad (7)$$

Graneli (1978) further tested this pattern in a series of five Swedish lakes and showed that while the relationship was strong, Hargrave's model systematically overpredicted the measured sediment respiration. This compound variable (PP/Z_m) is equivalent to the volumetric primary production averaged over the epilimnion, a variable known to be well predicted from phosphorus concentration (e.g. del Giorgio and Peters 1994). Because phosphorus concentration data are more generally available compared to primary production estimates, we further examined the generality of the relationship between sediment respiration and variables indicative of lake trophic status.

The analysis of our data compilation revealed that total phosphorus concentration was a very good predictor of sediment respiration (standardized to 10°C according to equation (6)) explaining 69% of the variance in sediment respiration and yielded the following empirical equation:

$$\log_{10} SR_{std\ 10°C} = 0.17 + 0.58 \log_{10} TP, \quad (8)$$

where SR is in mmoles $O_2\ m^{-2}\ d^{-1}$ and total phosphorus (TP) is in milligram per meter cube (Fig. 7.5). Because total phosphorus is also a well-known predictor of chlorophyll concentrations and primary production in lakes (Dillon and Rigler 1974 among

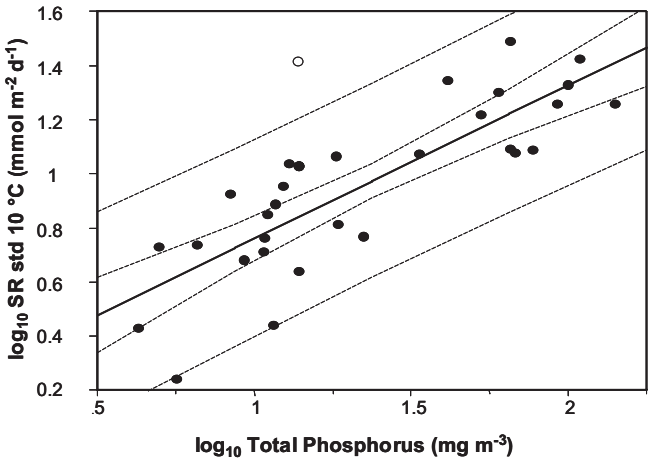

Figure 7.5 Log–log relationship between standardized sediment respiration rates (SR, mmoles m^{-2} d^{-1}) and total phosphorus concentrations (mg m^{-3}). Individual data points were obtained from Provini (1975), Ramlal *et al*. (1993), Schallenberg (1993), Hayes and MacAulay (1959), Graneli (1978), Welch and Kalff (1974), Lasenby (1975), and Hargrave (1972). Open circle (Lake Southport, Hayes and MacCauley 1959) excluded from regression line.

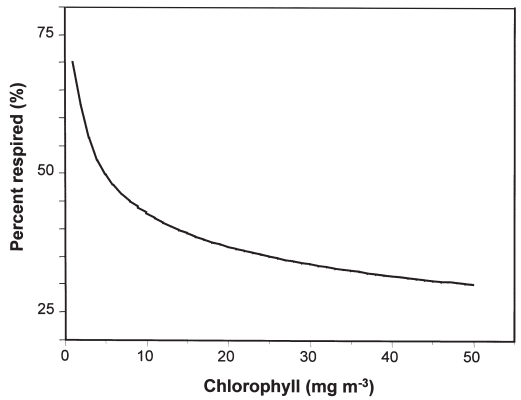

Figure 7.6 Inferred relationship between the fraction of carbon flux (as %) to sediments that is eventually respired, as a function of chlorophyll concentration (mg m^{-3})

many others, Smith 1979, del Giorgio and Peters 1994), sediment respiration can also be expressed as a function of chlorophyll (mg m^{-3}) or primary production:

$$\log_{10} \mathrm{SR}_{\mathrm{std}\ 10^{\circ}\mathrm{C}} = 0.63 + 0.40 \log_{10} \mathrm{Chl}, \qquad (9)$$

$$\log_{10} \mathrm{SR}_{\mathrm{std}\ 10^{\circ}\mathrm{C}} = 0.093 + 0.47 \log_{10} \mathrm{PP}, \qquad (10)$$

where primary production (PP, mg C m^{-3} d^{-1}) is volumetric primary production averaged over the euphotic zone (del Giorgio and Peters 1994). The shallow slopes of all three relationships imply that SR does not increase proportionately with any measure of lake trophic status. The consequences of this disproportionality can be further explored by combining these trends with the work of Baines and Pace (1994) who showed that the vertical flux of carbon can be well estimated ($r^2 = 0.83$) from chlorophyll concentration. Assuming a respiratory quotient of 0.9 (Graneli 1979, although the trend is not affected by the particular choice of RQ), the fraction of the vertical flux of carbon that, at steady-state, will be respired in the sediments ($\%C_{\mathrm{resp}}$) will be a declining function of lake trophic status. Expressed as a function of chlorophyll, the resulting equation is:

$$\%C_{\mathrm{resp}} = 71.4\ \mathrm{Chl}^{-0.22} \qquad (11)$$

This inferred relationship, illustrated in Fig. 7.6 suggests that, in oligotrophic lakes, about 70% of the carbon raining down to the sediments will be respired while this fraction is considerably reduced in more eutrophic systems (to about 40% in lakes with 20 mg m^{-3} chlorophyll). Long-term carbon burial is, therefore, increasingly important in more productive systems, a conclusion also reached by Hargrave (1973).

Other factors influencing sediment respiration

While lake productivity and temperature are clearly the main determinants of sediment oxygenic respiration, other factors are known to influence sediment respiration in lakes, albeit to lesser extents. Sample depth, sediment organic matter content, ambient oxygen concentrations are among the

most cited factors influencing sediment respiration although general tests of their importance are rare. Lake acidification has also been shown to reduce respiration in some instances (Andersson *et al*. 1978).

Unlike water column respiration processes, sediment respiration is suppressed when ambient oxygen concentrations decrease (e.g. Edberg 1976; Graneli 1978; Cornett and Rigler 1984), particularly when they drop below 30–60 mmol O_2 m^{-3} (Anderson *et al*. 1986). This is probably the result of the supply of oxygen to the sediment/water interface becoming limited by the reduced diffusion. Whether this reduced oxygen consumption is fully compensated by increased anaerobic decomposition is unclear (Bédard and Knowles 1991). However, we suggest that the failure of empirical models such as equations (4)–(6) to incorporate this first-order concentration effect may not overly compromise their utility.

The influence of the depth at which sediment cores are taken has also been noted by some authors (e.g. Campbell 1984; den Heyer and Kalff 1998) but the effect appears significant only when comparing sites differing in depth by orders of magnitude. Given that very deep lakes are usually oligotrophic, it may be that the depth effect is a proxy for a trophic status effect. Indeed, variations among depths within individual lakes are nonexistent or modest (Lasenby 1975; Newrkla 1982). In our data compilation, adding site depth as an additional independent variable was not significant ($p > 0.05$) once lake trophic status (as total phosphorus) was entered in the model, providing further indication that the depth acted as a surrogate in earlier models.

7.4 Free water respiration

By frequent *in situ* measurements of oxygen dynamics over diel cycles, it is possible to calculate respiration. This so-called "free water" approach (Odum 1956) has the advantage of not requiring enclosure and incubation. The method also measures the contribution of all components, from bacteria to fish, to total system respiration and oxygen consumption. An open question discussed further below is the vertical and horizontal scales over which the estimate of respiration is made. This technique potentially provides an integrated measurement of pelagic and sediment respiration in lakes.

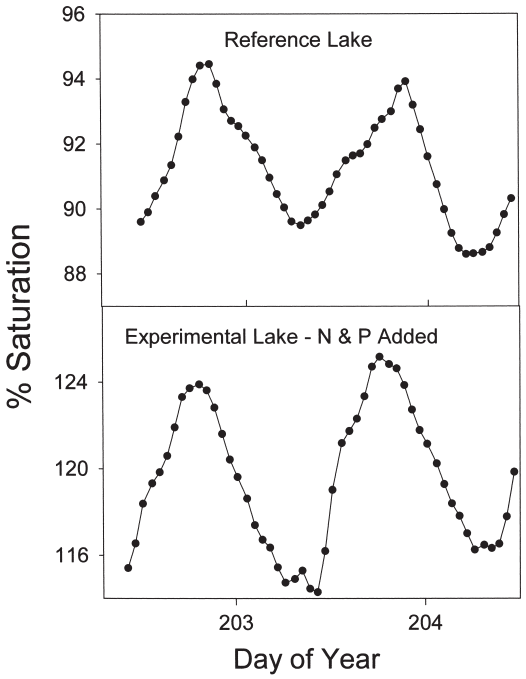

Figure 7.7 Diel oxygen dynamics as percent saturation in a reference and experimental lake (Paul and Peter Lakes, respectively, Michigan, USA). Details in text.

Respiration can be estimated from the night-time decline in oxygen once external exchanges (e.g. with the atmosphere) are accounted for. Figure 7.7 presents an example from a reference lake and an experimental lake fertilized with nitrogen and phosphorus of diel oxygen dynamics measured *in situ* with autonomous instruments such as rapid-pulsed oxygen electrodes (details of study in Cole *et al*. 2000). Oxygen is undersaturated in the reference lake and diel dynamics are modest while in the experimental lake oxygen is ovesaturated and there is a large diel excursion (Fig. 7.7). Under these conditions, the decline of oxygen at night is a function of respiration and net diffusion to or from the atmosphere. Oxygen diffusion at the base of the mixed layer can be ignored (Cole and Pace 1998). Atmospheric gains or losses of oxygen were calculated as the difference between measured and saturated oxygen times a coefficient of gas exchange. The gas

exchange coefficient is either modeled or measured directly (e.g. Clark *et al*. 1995; Cole and Caraco 1998; Wanninkhof and McGillis 1999). Diel cycles of oxygen can also be used to estimate gross primary production based on increases in oxygen during the day and the assumption that night and day respiration are equal.

Respiration calculated from diel oxygen dynamics in the mixed layer of lakes should represent an integrated response of the surface mixed layer and sediments on the edge of the lake that lie within the mixed layer. Hence, the pelagic and sediment respiration are included in the estimate. In the small lakes (1–3 ha) illustrated in Fig. 7.8, free water respiration is greater than dark bottle respiration. For example in the unfertilized, reference lake, weekly measures of dark bottle respiration were made during the same time as diel oxygen dynamics were measured (Fig. 7.8). Dark bottle respiration averaged 8.8 mmol m^{-3} d^{-1} while free water respiration averaged 30.6 mmol m^{-3} d^{-1}. While dark bottle respiration might underestimate planktonic respiration, the free water method indicates that benthic respiration must be about twofold higher than planktonic respiration in the reference lake. Thus, in small water bodies much of the overall system metabolism can occur in sediments, particularly shallow littoral sediments where benthic respiration is stimulated by primary production of macrophytes and periphyton.

Such discrepancies between littoral and pelagic respiration can create spatial heterogeneities in gas concentrations that must be contended with. Thus, while the free-water method offers a greater integration of all the respiring components than bottle measurements, the approach is not without difficulties. For instance, continuous mapping of surface Pco_2 shows that the spatial heterogeneity in the distribution of respiration can be substantial, even in small lakes. Figure 7.9 illustrates the spatial distribution of the night-time increase in surface Pco_2 in a small embayment (0.53 km^2) of Lake Memphremagog (Québec). Over the bay, the increase averaged a modest 28 μatm Pco_2 but some littoral areas increased by as much as 140 μatm. As expected, the amplitude in the daily variation is much greater in the shallow littoral zones. Clearly, horizontal diffusivity is not sufficiently large to homogenize gas distribution at the scale necessary to use the free-water method without consideration of spatial heterogeneities. More interestingly, the night-time increase was significantly smaller in the deepest zone of the bay where samples are normally taken or autonomous sondes deployed. Thus, significant biases may be incurred if the autonomous sondes are placed only in the deepest area of the lake, because the metabolism originating from the more active littoral areas does not completely homogenize even over small horizontal areas.

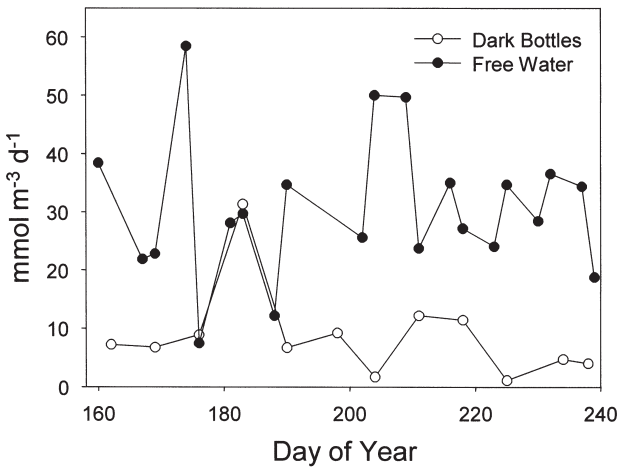

Figure 7.8 Comparison of free water and bottle estimates of respiration over the summer season in Paul Lake (Michigan, USA). Details in text.

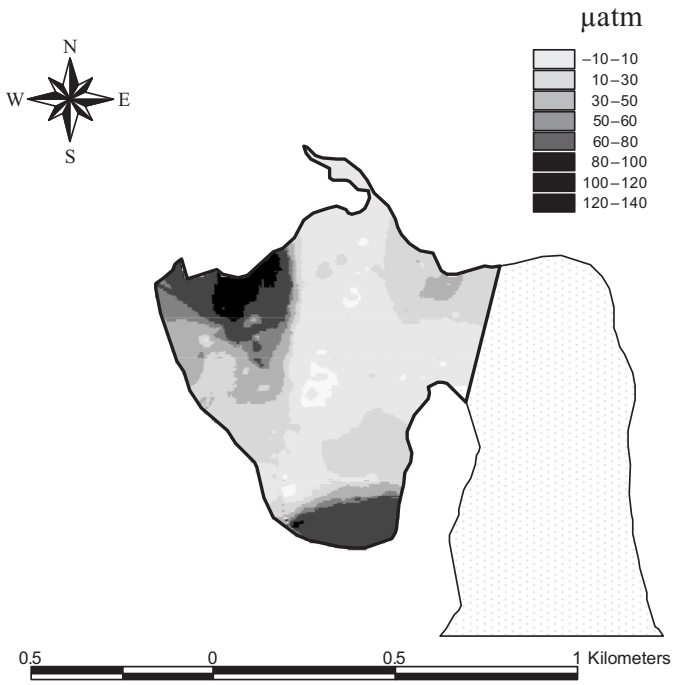

Figure 7.9 Spatial distribution of the night-time increase in pCO_2 in a small bay of L. Memphremagog (Québec) showing large heterogeneities.

7.5 Global estimate of lake respiration

Although freshwater systems occupy a small area relative to the surface area of the world's oceans, freshwaters are comparatively more productive, leading to higher pelagic and sediment respiration rates per unit volume and area, respectively. In addition, lakes have a much larger relative contact area with surrounding terrestrial ecosystems than oceans, and substantial terrestrially derived organic matter is oxidized during its freshwater transit (e.g. Richey *et al*. 2002). The planktonic and sediment respiration models presented above can be used to roughly estimate annual carbon processing in lakes at a global scale. While such calculations are necessarily fraught with large uncertainties and untested assumptions, they can nevertheless provide order-of-magnitude estimates useful for casting the role of freshwaters in the larger context of global carbon cycling.

Our calculations are based on several simple allometric relationships with lake surface area. Lake size is negatively related to lake abundance (Meybeck 1995) and positively related to average depth (Patalas 1984). Large lakes also tend to have longer water residence times (Kalff 2002), a variable associated with reduced productivity on average (del Giorgio and Peters 1994). Figure 7.10 depicts changes in lake abundance, depth, and production (as chlorophyll *a*) across the logarithmic lake size classes of Meybeck (1995). While about two-thirds of the total lake surface area is occupied by lakes less than 320 km^2, more than 70% of total volume is in very large lakes (>320 km^2). This asymmetry has large implications for the distribution of respiration across the lake size classes.

For shallow lakes (less than or equal to 15-m mean depth), we calculated total water column respiration as the product of mean depth and the volumetric respiration rate estimated from the chlorophyll values (equation 2), to which we added sediment respiration, also a function of chlorophyll (equation 9). For large and deep lakes (greater than 15-m mean depth, we integrated planktonic respiration only for the upper 15 m, because respiration deeper in the water column is considerably lower than respiration

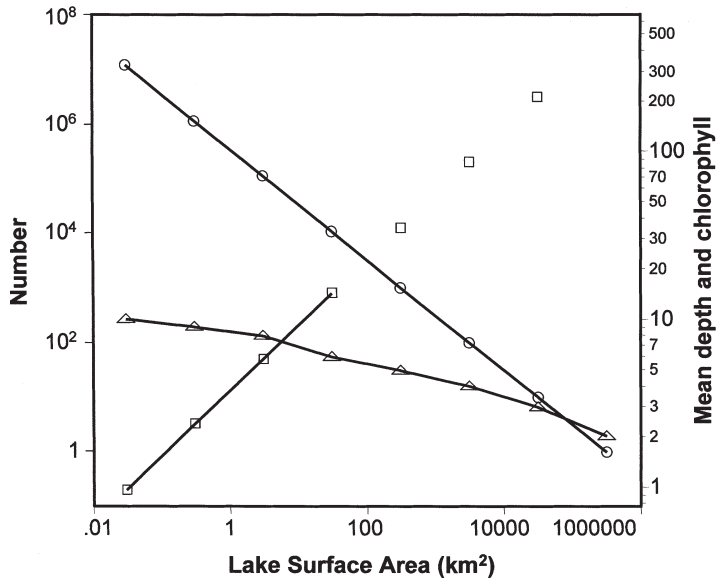

Figure 7.10 Global distribution of lake surface areas (km^2) used in the global estimate of lake respiration. Lake surface areas are arranged in logarithmic size classes following Meybeck (1995) and its relationships are shown, on the left axis, with lake total abundance (open circles, in numbers), and on the right axis, with lake mean depth (open squares, in m), and chlorophyll (open triangles, in mg m^{-3}), as used in our model estimates of global respiration. Note the line break for mean depth indicates that for large lakes unconnected mean depths points in the figure were not used in the calculations, see text for details.

in the uppermost layers. For example, in the deep (100 m) central basin of Lake Memphremagog, epilimnetic plankton respiration has been measured at 10.5 mmol m^{-3} d^{-1} (del Giorgio and Peters 1994) and average hypolimnetic plankton respiration at about 0.4 mmol m^{-3} d^{-1} (Cornett and Rigler 1987). Thus, our method of estimation, while empirical, has the advantage of providing a conservative estimate of respiration by not inflating respiration in the vast volume of water contained in the deep, cold layers of the relatively few very large lakes that dominate global lake volume (e.g. Lake Baikal). This is, however, a poor assumption in a number of ways as we discuss further below and results in what is almost certainly an underestimate.

Integration of the estimate of respiration over lake size classes yields a value of 62 Tmol C a^{-1}, about one quarter of which occurs in the two largest lake size classes (Fig. 7.11 and Table 7.1). Globally, sediments are responsible for only about 6% of total lake R. Although our global R estimate is rather small when compared to the total respiration of the oceans (del Giorgio and Duarte 2003), the importance of this figure is more revealing when compared to the gross primary production (GPP) that occurs in lakes. There are several published models that relate lake primary production to total phosphorus and chlorophyll. We used the relationship of Carignan *et al*. (2000), because it yields higher values for oligotrophic lakes than all other models, and thus provides an upper estimate of pelagic primary production. Assuming then that water column GPP follows the relationship of Carignan *et al*. (2000) with respect to chlorophyll, and that the depth of the euphotic zone is either equal to the mean depth of small lakes or 15 m for larger lake size classes, global pelagic GPP is estimated to be 51 Tmol C a^{-1}. In all lakes there is some additional primary production from benthic and littoral communities, and this littoral production is especially important in small and oligotrophic lakes (Vadeboncouer *et al*. 2003). If we assume benthic primary production is

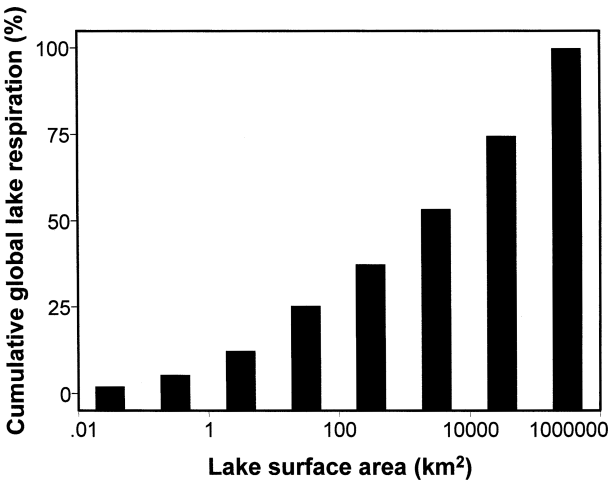

Figure 7.11 Cumulative global lake respiration (%) with increasing lake size classes (km^2).

Table 7.1 Range and averages for planktonic and sediment respiration and of global estimates derived from lake size classes. For the conversion of oxygen to carbon the calculation assumes $PQ = RQ = 1$

	Range	Average (median)
Field observations		
Planktonic respiration		
Volumetric (mmol O_2 m^{-3} d^{-1})	0.7–162	15.7 (10.3)
Areal (mmol O_2 m^{-2} d^{-1})	10–184	71.3 (61.5)
Sediment respiration (mmol O_2 m^{-2} d^{-1})		
Primary data	1.6–32	10.3 (9.7)
Standardized at the rate of 10°C	1.8–31	10.7 (9.2)

Global estimates

Lake surface area (km^2)	Global surface area (10^{12} m^2)	Respiration (Tmoles C a^{-1})		GPP (Tmoles C a^{-1})
		Planktonic	Sediment	
0.01–0.1	0.38	1.3	0.7	1.5
0.1–1	0.37	2.8	0.6	2.9
1–10	0.35	6.2	0.6	5.8
10–10^2	0.34	12.5	0.5	11.4
10^2–10^3	0.33	11.4	0.4	10.3
10^3–10^4	0.32	9.7	0.4	8.9
10^4–10^5	0.30	7.9	0.3	7.5
10^5–10^6	0.29	6.1	0.3	6.0
Sum	2.69	58	3.8	54

half of pelagic primary production in the smallest lakes and diminishes by a factor of 0.5 for successive lake size classes, then we obtain a global estimate of gross primary production of 54 Tmol C a^{-1}. The estimated difference between global lake respiration and global lake production using these assumptions is 8 Tmol C a^{-1}. This value of excess respiration is reasonably close to the 12 Tmol a^{-1} of global lake CO_2 evasion estimated by Cole *et al*. (1994) using the average partial pressure of carbon dioxide in lakes. This correspondence, however, is not fortuitous as we constrained our calculations to fall in the realm of the Cole *et al*. estimate. There are two aspects of comparing our respective estimates that need to be made explicit. The CO_2 evasion from lakes estimated by Cole *et al*. may have other sources beyond excess respiration. This would suggest the excess respiration should be lower than CO_2 evasion. The global lake area used by Cole *et al*. (1994) excluded the very large inland seas (e.g. Caspian, Aral) and is, therefore, not directly comparable with our estimate. Excluding our two largest lake size classes (yielding a total lake area of 2.1×10^{12} m^2 more commensurate with the Cole *et al*. value of 2×10^{12} m^2) further reduces the gap between global lake primary production and respiration in our estimate to 6 Tmol C a^{-1}.

The greatest problem with the assumptions we use is that they exclude respiration in the deeper waters of large lakes. This respiration is probably quite significant. For example, McManus *et al*. (2003) recently estimated the annual respiration for the hypolimnion of Lake Superior as about 0.9 Tmol of C, or 30 mmol m^{-2} d^{-1}. This estimate points to the significance of large lakes in the overall calculation of global lake respiration. If we apply the areal estimate for Lake Superior to all large lakes (the four largest lake size classes), this would increase our estimate of global lake respiration by about 14 Tmol C, to a total of 76 Tmol C a^{-1}. This may be a better estimate, but there are problems with concluding lake respiration is much higher. Indeed, our assumptions tend to provide a realistic but upper limit to global lake GPP because the relationship we used yields very high estimates of pelagic production relative to other models. Thus, greatly increasing respiration would result in an unreasonable excess of respiration over production. One possible explanation is that GPP is too low. We cannot, however, justify a larger value. A second and related problem with increasing the estimate is that the respiration increases mainly in the larger lake size classes. Respiration of >75 Tmol C a^{-1} leads to P : R ratios for large lakes of about 0.65 on an annual scale, which may not be consistent with estimated fluxes and concentrations of O_2 and CO_2. In summary, our calculations cannot at present be completely reconciled. Better global data and models of lake respiration and primary production are needed as well as information on fluxes that can be used to constrain these processes such as carbon dioxide evasion. Our estimates point to the critical lack of understanding of respiration in large lakes and how respiration varies with depth in lakes.

The global fluxes of carbon related to lake respiration are relatively small when compared to rates for the ocean and land. However, inland waters may still be significant as sites of active carbon cycling and carbon losses. Thus, the fluxes of carbon associated with lake respiration need to be accounted for when estimating net ecosystem production and carbon storage as well as evasion of the combined terrestrial and freshwater landscape especially in regions rich in lakes.

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