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Ecosystem respiration and organic carbon processing in a large, tidally influenced river: the Hudson River

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Abstract. We estimated whole-ecosystem rates of respiration over a 40-km stretch of the tidally influenced freshwater Hudson River every 2 to 3 weeks from May through November. We measured in situ concentrations of oxygen over depth at dusk and dawn at 10 stations spaced over this interval. The use of multiple stations allowed for the consideration of the influence of tidal advection of water masses. Respiration was estimated from the decrease in oxygen overnight with a correction for diffusive exchange of oxygen with the atmosphere. We estimated this flux of oxygen to or from the atmosphere using the measured oxygen gradient and a transfer velocity model which is a function of wind velocity.

Integration of the data for the period of May through November yields an estimate of whole-ecosystem respiration of 591 g C m^{-2} (S.E. = 66). That the standard error of this estimate is relatively low (11% of the estimate) indicates that the use of multiple stations adequately deals with error introduced through the advection of water between stations. The logarithm of average daily respiration rate was correlated with average daily temperature ($p = 0.007$; $r^2 = 0.62$). We used this temperature-respiration relationship to derive an estimate of the annual respiration rate of 755 g C m^{-2} yr^{-1} (S.E. = 72). This estimate is moderately sensitive to the estimated flux of oxygen between the atmosphere and water; using the lower and upper 95% confidence limits of our model relating the transfer velocity of oxygen to wind speed gives a range of annual respiration estimates from 665 g C m^{-2} yr^{-1} to 984 g C m^{-2} yr^{-1}.

The river is strongly heterotrophic, with most respiration driven by allochthonous inputs of organic matter from terrestrial ecosystems. The majority of the allochthonous inputs to the river (over 60%) are apparently metabolized within the river. Any change in allochthonous inputs due to changes in land use or climate patterns would be expected to alter the oxygen dynamics and energy flow within this tidally influenced river.

Introduction

In deep turbid rivers, primary production tends to be quite low (Vannote et al. 1980; Lewis 1988), and most large rivers are heterotrophic with

respiration greatly exceeding primary production (Kempe 1982, 1984). This respiration is driven by allochthonous inputs of organic matter from terrestrial ecosystems, from sewage, and from fringing marshes and flood plain wetlands. However, the respiration of large rivers has received surprisingly little study, and their heterotrophic nature is generally deduced from indirect measures such as consistently high pCO_2 (Kempe 1982, 1984). Also, in general the fate of allochthonous inputs to the large rivers of the world is poorly known (Schlesinger and Melack 1981; Telang et al. 1991; Richey et al. 1991; Ittekkot and Laane 1991; Esser and Kohlmaier 1991). Information on the fate of allochthonous inputs is important because rivers are the major conduit for flows of material from the terrestrial environment to the oceans (Schlesinger and Melack 1981; Meybeck 1982; Devol et al. 1987).

The extent to which allochthonous inputs of organic carbon to rivers are composed of labile or refractory materials is subject to much debate, with estimates ranging from 30 to 75% (Richey et al. 1990, 1991; Ittekkot et al. 1985; Ittekkot and Arain 1986; Ittekkot and Laane 1991; Kempe et al. 1991; Spitzy and Leenheer 1991; Telang et al. 1991; Esser and Kohlmaier 1991). Most of these estimates are based only on the chemical composition of organic matter in rivers, and very few are derived from actual measurements of metabolism. The Amazon River is one of the few large rivers where both organic matter fluxes and rates of respiration have been measured (Devol et al. 1987; Richey et al. 1990, 1991). However, an extensive flood plain, the remoteness of the river, and its huge size have resulted in large uncertainties in the carbon budget there (Richey et al. 1991).

The tidally influenced Hudson River presents an excellent opportunity for studying the fate of allochthonous inputs and respiration rates in a relatively large and deep river. The boundaries to the river are well defined, the river is of moderate size and easily accessible, fringing wetlands are minimal, and there is no seasonally flooded flood plain. The tidally influenced, freshwater Hudson stretches south from a dam at Troy, NY, some 130 km before encountering saline waters in the Hudson River estuary in the vicinity of Newburgh, NY, about 100 km north of New York City. Primary production is light limited and low; phytoplankton production estimated by ^{14}C assimilation averages 80 g C m^{-2} over the ice-free season of the year (Cole et al. 1991). In contrast, allochthonous organic matter inputs from terrestrial ecosystems are some 740 g C m^{-2} yr^{-1} (Gladden et al. 1988; Howarth et al. 1991). Sewage inputs are much smaller and contribute only some 30 g C m^{-2} yr^{-1} (Fruci and Howarth 1989). That allochthonous inputs may be significant to the food webs of the river is suggested by the high rate of bacterial production compared to net primary production (Findlay et al. 1991a).

In addition to our interest in the fate of allochthonous inputs to a river, we are concerned about the potential for changes in functioning of the Hudson River to lead to hypoxia or anoxia. The tidally influenced freshwater portion of the Hudson River is an important spawning and nursery ground for a variety of migratory fish including striped bass, herring, and shad (Limburg et al. 1986). Even though the watershed of the Hudson River is principally forested, the allochthonous organic inputs reaching the tidally influenced, freshwater portion of the river come primarily from erosion of agricultural lands and from urban and suburban areas (Howarth et al. 1991). Thus, changes in land-use in the watershed could easily increase allochthonous inputs. Is this material readily metabolizable, so that increased inputs might increase respiration sufficiently to result in anoxia or hypoxia? Or do the allochthonous inputs consist largely of relatively refractory material which simply passes through the river without being respired? Although periodic anoxic events occur in portions of the saline Hudson River estuary near New York City (Mearns et al. 1982), present-day oxygen concentrations are higher within the tidally influenced freshwater portions of the river. However, for at least one river, the Ob River, 'natural' occurrences of anoxia have been ascribed to respiration driven by allochthonous inputs of organic carbon from terrestrial ecosystems (Telang et al. 1991).

To address these questions, we measured whole-ecosystem respiration rates in the tidally influenced freshwater Hudson River. We used free-water measurements of oxygen at dusk and at dawn to estimate respiration. This method is preferable to measuring metabolism in closed containers as it seems likely that the greatly reduced turbulence in bottles (relative to conditions in the river) would result in altered, probably reduced, rates of metabolism (Nixon et al. 1979). Richey et al. (1990, 1991) also have argued for the use of free-water techniques over bottle-incubations for measuring respiration in large rivers. Our free-water approach is derived from that used by Odum and Hoskins (1958), Edwards and Owens (1962), Nixon and Oviatt (1972), and Oviatt et al. (1986). We had to modify the approach as outlined below, however, to deal with the large tidal advection of water.

Methods

Site description

We studied a 40-km stretch of the central part of the tidal, freshwater Hudson River extending 20 km north and south of Kingston, NY. We repeatedly sampled stations spaced approximately 5 km apart (Fig. 1).

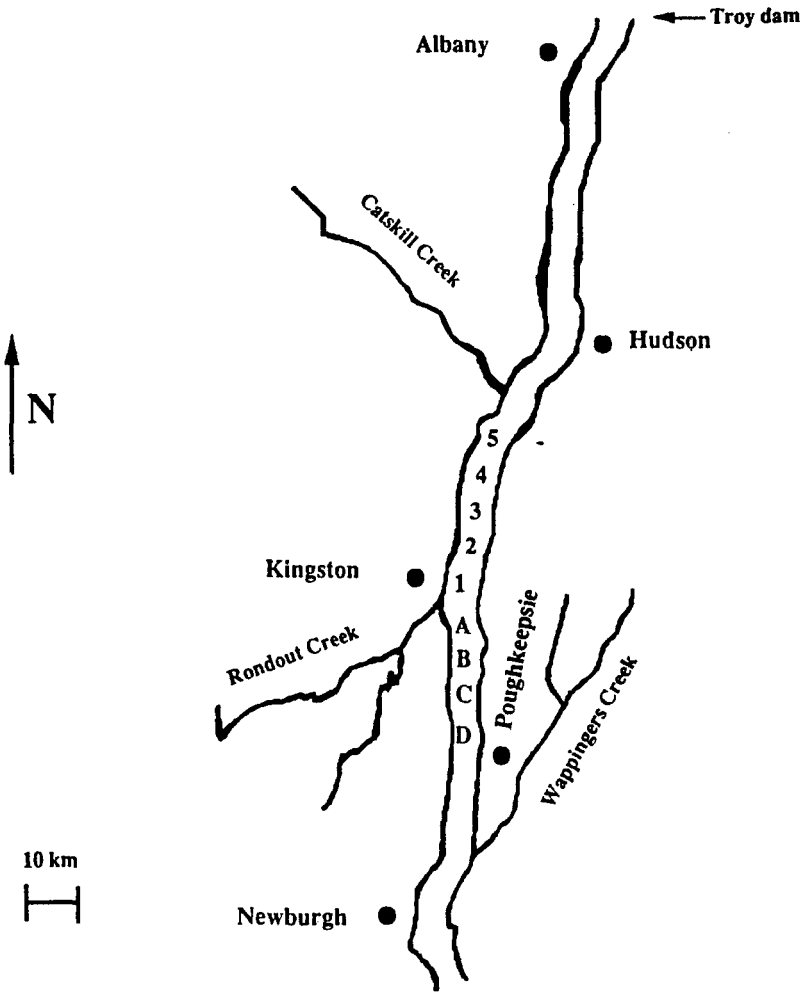

Fig. 1. Location of sampling stations on Hudson River north and south from Kingston, NY. Stations north of Kingston are number 1 through 5. Those south of Kingston are lettered A through D. The tidally influenced Hudson River extends from a dam just north of Albany, NY, south to the salt wedge of the Hudson River estuary, which varies seasonally but is generally just south of Newburge, NY.

The width of the river ranges from 0.5 to 2 km along this reach. Tidal amplitudes range from 0.8 to 1.4 m (Limburg et al. 1986). On average, a water parcel moves north and south approximately 10 km with each tide. Mean tidal current velocities are 0.38 m sec^{-1} (Limburg et al. 1986), although currents much stronger than average are common. Because of the tidal energy, the water column is completely mixed and unstratified.

According to a report from Texas Instruments (1976), the average depth of the river in the 40-km stretch we studied is approximately 11 m; average depths from bank to bank at each of our stations are reported to range from 5 to 17 m (Texas Instruments 1976). We also estimated average station depths from a navigational chart (N.O.A.A. #12347, 'Hudson River, Wappinger Creek to Hudson,' 25th edition). Depths at 1-m intervals from bank to bank were determined by linear interpolation between soundings. This analysis yielded estimates for average station depths which are generally less than those reported by Texas Instruments (1976), although the estimated depth for one station is considerably deeper. According to this analysis, average depths for our stations range from 2.5 to 24 m. Overall, the average depth for all stations estimated from the N.O.A.A. charts was 8.7 m, 20% less deep that the average derived from Texas Instruments (1976) report.

Oxygen measurements

We measured oxygen concentrations over depth at dusk and the following dawn at 2 to 3-week intervals from May through November, 1988, sampling from a 16-foot boat (the R.V. Muskrat). Measurements generally were made at 0.5 m intervals over depth from the surface to within 0.5 m of the bottom of the river. For our first 5 sampling trips, we only had access to a 10-m long cable for our oxygen electrode, which prevented sampling all the way to the bottom at some stations; for later trips, we used a longer cable (see below). We tried to measure oxygen concentrations at 5 stations for one dusk-dawn sampling and then at another 5 stations on the next dusk and dawn. On several occasions, however, we were unable to sample this entire suite of stations due to adverse weather or mechanical problems. In this paper we report data only for dates when we were able to sample at least 5 stations. Sampling of all stations generally was completed within 1 to 1.3 hours.

We used a Y.S.I. polarographic electrode with a model 58 digital meter to measure oxygen. The digital meter allowed better precision than was possible with an analog meter in a moving boat. We measured oxygen directly as percent saturation to obtain the greatest precision. We also measured temperature to allow the later calculation of oxygen concentrations. The electrode was connected to the meter by a custom-built 30-m cable purchased from Y.S.I. A dacron line calibrated in 0.5-m intervals was attached to the cable, and the bottom of this line was weighted with 5 kg of lead to keep the cable as vertical as possible in the strong tidal currents. We allowed our sampling boat to drift during measurements

both to speed sampling at many stations and to help keep the cable vertical.

The oxygen electrode and meter were carefully calibrated at each station at the in situ water temperature. Calibration was in water-saturated air in a small, insulated chamber. Between stations, we kept the electrode in river water in a cooler to keep the electrode at close to in-situ temperatures; this speeded calibration at the next station. We used thin (0.013 mm) Teflon membranes to improve the electrode response time and performance, especially at colder temperatures.

Estimation of oxygen exchange with atmosphere

Estimates of oxygen transfer between water and atmosphere are necessary to determine metabolism rates by open-water techniques. We estimated oxygen flux using the following basic equation for exchange of an unreactive gas across an air-water interface (Liss and Merlivat 1986; Roether 1986):

$$F = k(C_w - C_a/H)$$

where F is the absolute value of the flux in units of mass per surface area of water, k is the transfer velocity characterizing the resistance in the water phase to gas movement across the interface, C_w is the concentration of oxygen in the water, C_a is the gas concentration in air, and H is the dimensionless Henry's Law constant which relates the gas in air to its solubility in water. Thus, the term $(C_w - C_a/H)$ is the oxygen gradient driving the flux. The transfer velocity, *k*, is in part a function of the molecular diffusivity of the gas, which is a temperature-dependent constant; *k* is also a function of turbulence at the immediate surface of the water.

We used wind as a simple measure by which to estimate the effect of turbulence on k for any given day (Marino and Howarth, submitted). In small rivers and streams, oxygen fluxes often are controlled by turbulence created by interaction of flowing waters with bottom topography (Roberts 1984; O'Connor 1984). However, this is unlikely to be a major control on oxygen fluxes in a large river or estuary with a deep water column where wind is usually the dominant influence (Jirka and Brutsaert 1984). To estimate the influence of wind on the transfer velocity, we both measured oxygen fluxes into a floating dome on the Hudson and compiled data from a variety of other studies (Marino and Howarth, submitted); these other studies used several different techniques, measured a variety of gases, and were made in open ocean waters (Broecker et al. 1980; Smethie et al. 1985; Frankignoulle 1988), lakes (Broecker et al. 1980; Wanninkhof et al.

1985; Roques 1985; Upstill-Goddard et al. 1990), and large estuaries (Hartman and Hammond 1984; Roques 1985). Transfer velocities were converted to those for oxygen at 20 °C using diffusivity data in Broecker and Peng (1974) and Wanninkhof (1985). Wind velocity data were converted to a common height of 10 m above water surface, if necessary, using the relationship in Liss and Merlivat (1986).

Figure 2 illustrates the regression of wind velocity vs. ln k for these data and indicates the 95% confidence limits on the regression line. This regression gives a good, highly significant fit ($r^2 = 0.55$; $p = 0.0001$), particularly in light of the variety of measurement techniques used and the diversity of the natural systems studied. Our data on oxygen fluxes into a floating dome on the Hudson River agree well with the data collected in other systems using other techniques (Fig. 2; Marino and Howarth, submitted). In our compilation, we only used data when the wind velocity was less than 10 m sec^{-1} since breaking waves and bubbles are often formed at higher winds, enhancing gas transfer (Liss and Merlivat 1986; Upstill-Goddard et al. 1990). Wind speeds greater than 10 m sec^{-1} were not recorded for the Hudson during our sampling times.

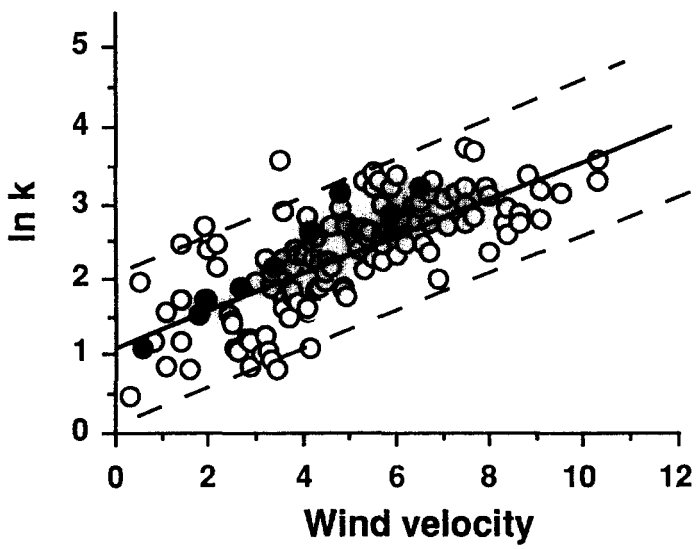

Fig. 2. Regression of the wind velocity (m sec^{-1}) at 10 m height above water surface vs. the natural logarithm of the transfer veloctiy (cm hr^{-1}) for oxygen at 20 °C. Dark solid line is best fit of the data ($r^2 = 0.55$). Dashed lines represent 95% confidence limits of the linear regression. Data are compiled from a variety of published studies of gas transfer in natural systems (open symbols) and our measurements of oxygen fluxes into a floating dome on the Hudson River (filled symbols). Based on analysis of Marino and Howarth (submitted).

We obtained hourly data on wind velocity at 10 m for our sampling dates from the Dutchess Country Airport in Poughkeepsie, NY, near the river at our furthest south station. They do not report wind velocities lower than 1.5 m sec^{-1}, so we assumed a velocity of 0.5 m sec^{-1} whenever they reported velocity as less than 1.5 m sec^{-1}. The daily average wind speed was used to estimate the transfer velocity (k) for each sampling date. This value and the surface oxygen gradient ($C_w - C_a/H$) were then used to calculate the atmospheric diffusive fluxes (F) for each station and date. The oxygen gradient was estimated for each station and date by averaging the measured dawn and dusk oxygen concentrations at the surface.

Estimation of respiration rates

Respiration was calculated as the decrease in oxygen overnight at each station, corrected for oxygen exchange with the atmosphere (F). When oxygen was undersaturated, the estimated oxygen flux from atmosphere to the water (calculated as outlined above) was added to the observed overnight decrease in oxygen. When oxygen was supersaturated, the estimated oxygen flux from water to the atmosphere was subtracted from the overnight decrease in oxygen. To determine daily estimates of respiration, we assumed that night-time rates of respiration held during daylight periods as well. We converted oxygen metabolism rates to carbon metabolism by assuming a 1:1 stoichiometry between O_2 and C.

In calculating respiration rates, we treated the water column as if it were stationary at each station. This is of course not true as the average tidal excursion of a water mass is about 10 km, or twice the distance between stations. Nonetheless, we reasoned that increases or decreases in oxygen at a given station resulting from sampling different water masses should tend to be offset by changes in the opposite direction at the adjacent stations. There should be no systematic bias in estimating average rates of metabolism on any date by this appraoch providing enough stations are sampled, although estimates for any given station may well be in error.

We measured oxygen concentrations in the main channel of the river at each station. For whole-system metabolism rates, however, we wanted estimates which accurately reflect the average depths of the river, and not merely the deepest points. Therefore, for each station we integrated the oxygen change from dusk to dawn over the entire depth of water sampled and adjusted these to the average cross-sectional depth at that station. For example, if the average cross sectional depth at a station were 11 m and we had oxygen data for this station to a depth of 13 m, we would integrate

the entire set of data, divide this by 13 m, and multiply it by 11 m. The diffusive flux correction was then made to these depth-corrected oxygen integrations. Alternative approaches to scaling the data to the average station depths yielded results which are within 4% of the respiration rates we report in this paper. Average depths were assumed to be as reported in Texas Instruments (1976). We also tested the sensitivity of our respiration rate to depth-averaging assumptions by recalculating respiration rates using the station depth estimates derived from the N.O.A.A. navigational chart instead of using the data from the Texas Instruments (1976) report.

Results and discussion

During the course of our study, we obtained over 100 paired dusk-dawn sets of oxygen concentration over depth at various stations. Typical data for oxygen decreases from dusk to dawn are shown for three stations in Fig. 3. On a few occasions, the oxygen concentration increased from dusk to dawn at a single station. This is probably due to sampling a different water mass at the same station at dawn; other stations should have correspondingly large decrease in oxygen at these times, reflecting the movement of the water mass with higher than average oxygen. All data were

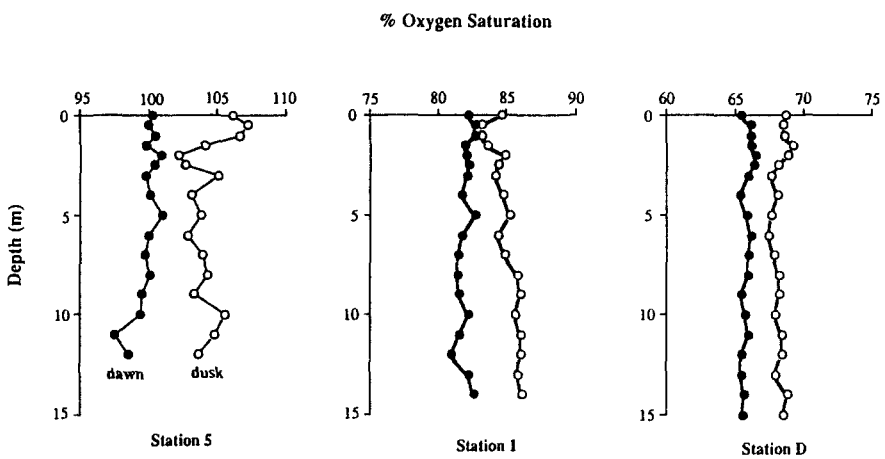

Fig. 3. Typical oxygen concentrations, expressed as percent saturation, over depth at dusk (open circles) and at the following dawn (closed circles) for three representative stations, including the most northern (station 5) and most southern station (station D). On this occasion, oxygen was supersaturated at station 5 at dusk but was undersaturated at other stations.

retained in the analysis for respiration estimation when only one or a few stations showed an oxygen increase overnight. We discarded the data from one date because all stations showed an increase in oxygen overnight from dusk to dawn; this was undoubtedly due to an error in calibrating the oxygen electrode.

Average daily rates of respiration are shown in Fig. 4. Rates ranged from 1.4 g C m^{-2} day^{-1} in November to over 9 g C m^{-2} day^{-1} in August. Integration of these respiration rates over time yields a rate from May 20 through November 18 of 591 g C m^{-2}. We obtained an estimate of the error associated with this estimate of respiration by using SAS (1985) to integrate the full data set, using all the estimates of respiration at each station at each time (weighted for time). The standard error from this integration is 66 g C m^{-2}. That the standard error is relatively small supports our simplifying assumption that it is reasonable to ignore the advection of water among the stations. We believe that any error from water advection is more than made up for by advantages of the open-

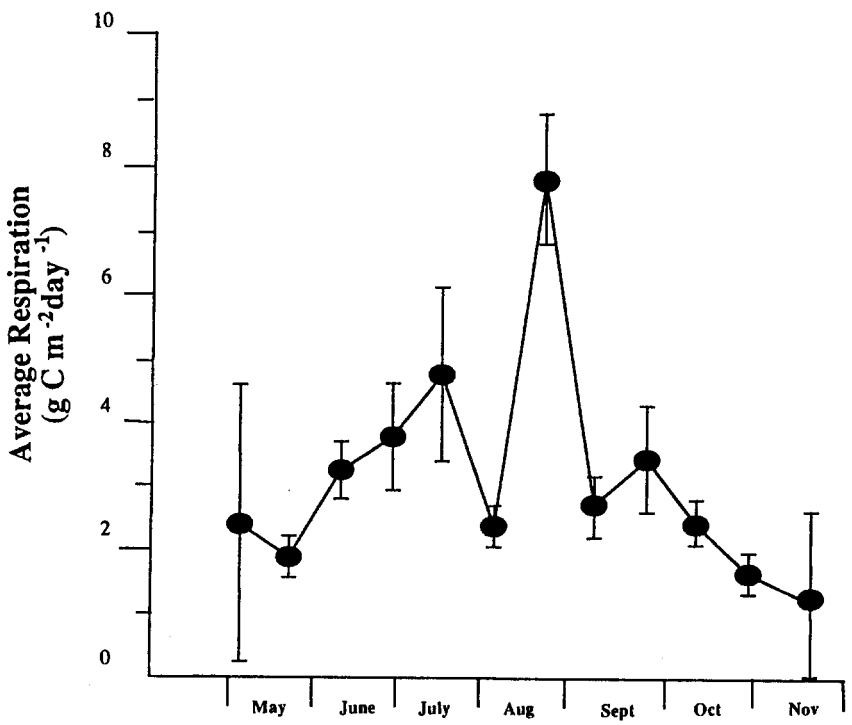

Fig. 4. Integrated rates of respiration per m^2 per day from May though November. Rates are the average for all stations sampled on each date. Standard errors are indicated by vertical bars.

water technique for measuring metabolism. In contrast to measuring metabolism in bottles, the open-water technique inherently integrates over large areas, greatly reducing errors of extrapolation. Bottle incubations suffer additional problems not encountered in the open-water technique, such as artificially lowered turbulence. Richey et al. (1990, 1991) also concluded that open-water techniques provide a better estimate of respiration in the Amazon River than do incubations of confined water parcels.

Figure 5 shows daily respiration rates (station averages) for all of the sampling times plotted as a function of temperature. The natural logarithm of the respiration is correlated with temperature ($r^2 = 0.62$; $p = 0.007$); the slope of this relationship yields a Q^{10} value of 2.0. We can use this relationship to derive an annual rate of respiration from monthly temperature data if we assume that it holds in the colder months when we were not able to sample. The rate thus derived is 755 g C m^{-2} yr^{-1} with a standard error of the temperature-based predictive model of 72 g C m^{-2} yr^{-1}. We believe this approach is reasonable, and an annual rate of 755 g

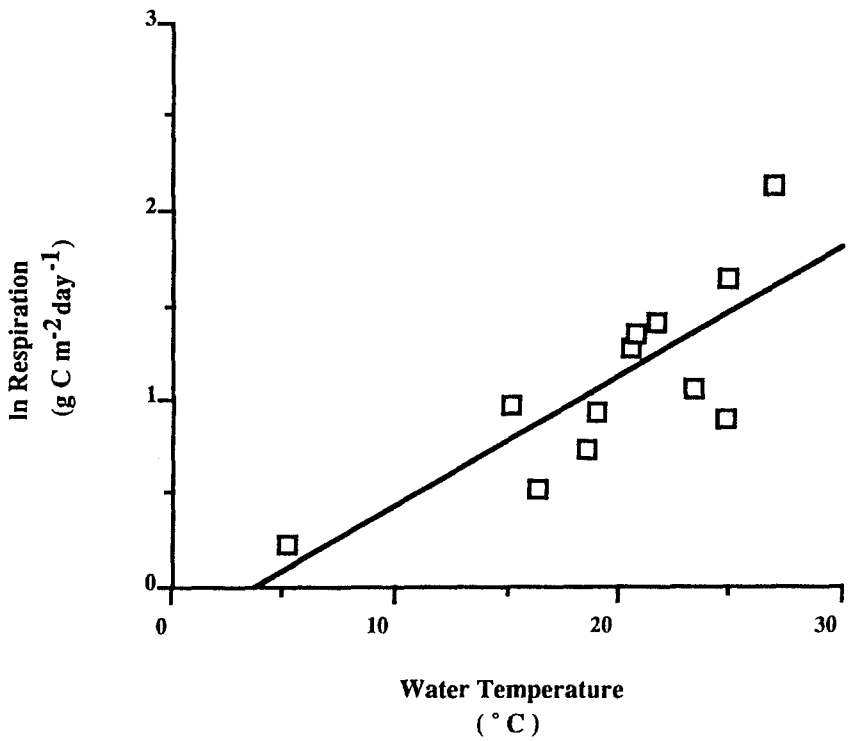

Fig. 5. Natural logarithm of average daily respiration rates plotted as a function of temperature. Regression line is significant ($p = 0.007$; $r^2 = 0.62$). The slope indicates a Q^{10} of 2.0.

C m^{-2} yr^{-1} appears sensible, given a respiration rate of 603 g C m^{-2} between May 20 and November 18. The magnitude of potential errors with this approach can be assessed by comparing the temperature-based model estimate with the actual integration of the respiration data for the period of measurement, May 20 through November 18. The temperature extrapolation yields an estimate for this period of 567 g C m^{-2} yr^{-1} (S.E. = 54), 4% lower than the integration of the actual measured data (591 g C m^{-2} yr^{-1}; S.E. = 66).

Sensitivity analyses of respiration rate

Several assumptions are necessary to estimate respiration from our data set, and we have tested the sensitivity of our estimate to these assumptions by varying one assumption at a time and recalculating the annual respiration using a temperature-based model, as above. First, we tested the effect of assuming a wind velocity of 0.5 m sec^{-1} whenever the reported velocity at Dutchess County Airport was less than 1.5 m sec^{-1}. If we instead assume a velocity of 1.0 m sec^{-1}, the estimate of respiration is increased by 13% (Table 1). If we assume a velocity of 0 m sec^{-1} whenever the reported velocity is less than detectable, respiration is decreased by 4% (Table 1). Unfortunately, our own wind data collected at dusk and dawn are unreliable at wind velocities below 0.5 m sec^{-1}, and we did not collect wind data continuously between dusk and dawn in any event.

Next, we tested the assumption relating atmospheric oxygen fluxes to wind velocities. Rather than using the best fit linear relationship between ln k (transfer velocity) and wind velocity, we used the upper and lower bounds for this relationship defined by the 95% confidence limits for the regression in Fig. 2. Using the upper bound curve to predict k from wind speed increases our annual estimate of respiration by 30% to 984 g C m^{-2} yr^{-1} (Table 1). Using the lower bound decreases the estimate by 12% to 665 g C m^{-2} yr^{-1} (Table 1).

Some previous studies which used in-situ oxygen data to estimate metabolism in other aquatic ecosystems have modeled the gas exchange with the atmosphere as a function of oxygen gradients alone rather than as a function of gradients and wind speed. These studies used a stagnant boundary layer model of oxygen exchange and assumed a constant boundary layer thickness. Lehman and Naumoski (1986) assumed a boundary layer of 200 μ for a lake in Michigan, while Copeland and Duffer (1964) assumed a boundary layer of 32 μ for a river in Oklahoma; the latter is also close to the boundary layer assumed by Kemp and Boynton (1980) for Chesapeake Bay. An assumed constant boundary layer of 200 μ for the Hudson River decreases our respiration estimate by

Table 1. Sensitivity analyses for effect of different assumptions on annual respiration.

	Mean annual respiration rates (g C/m^2 yr)	% Change from standard run[1]
Standard run[1]	755	0
Assumed wind speed of 1.0 m sec^{-1} when < 1.5 m sec^{-1}	856	+13
Assumed wind speed of 0.0 m sec^{-1} when < 1.5 m sec^{-1}	726	−4
Upper bound of transfer velocity model	984	+30
Lower bound of transfer velocity model	665	−12
Constant boundary layer (200 μ)	720	−5
Constant boundary layer (32 μ)	1,237	+64
Depth assumption (N. O. A. A. chart)	590	−22

[1] Standard run was corrected for the effect of wind on oxygen exchange with the atmosphere by using the best fit linear relationship between transfer velocity (k) and wind speed (Fig. 2). When wind speed was reported as less than 1.5 m sec^{-1}, standard run assumed wind speed was 0.5 m sec^{-1}. Station depths for the standard run were taken from Texas Instruments (1976).

5%, while an assumed constant boundary layer of 32 μ increases our respiration rate by 64% to 1,237 g C m^{-2} yr^{-1} (Table 1). This range of boundary layers includes the range of values estimated for the Amazon River using both floating dome and oxygen mass-balance techniques (Devol et al. 1987). We believe it better to let the boundary layer vary as a function of wind velocity whenever possible.

In addition to being sensitive to various assumptions about wind velocity and boundary layer, our respiration rate is sensitive to the average station depth. If instead of using data from Texas Instruments (1976) we use our depth estimates derived from the N.O.A.A. navigational chart, the annual estimate of respiration decreases by 22% to 590 g C m^{-2} yr^{-1} (Table 1).

Relationship of respiration to depth

The average depths of the cross-section of the river at our stations varied

considerably. One might expect respiration rates per m^2 to be greater at the deeper stations merely because the water column contains a larger volume of water in which respiration is occurring. On the other hand, if benthic respiration is a considerable portion of the total ecosystem respiration, there may be few if any differences among stations of different depths. To evaluate this, we used the SAS (1985) general linear models procedure to perform a series of paired comparison tests. All respiration rates on each date sampled were compared on the basis of station depth, resulting in 28 paired comparisons since some stations have the same mean depth. The model indicated a significant relationship between station depth and respiration rate per m^2 ($p = 0.018$; Table 2), with respiration rates higher in the deeper stations.

We evaluated the relationship between depth and respiration further by calculating average rates of respiration per volume of water. These average rates of respiration per volume were calculated by dividing the areal rates of respiration by depth and so include benthic respiration, normalized to the volume of water above the sediments. Paired comparison tests (SAS 1985 general linear models procedure) showed no significant relationship between average station depth and respiration rate per m^3 ($p = 0.30$; Table 2). Among the 28 pairs examined, we found only two paired stations where rates were significantly different (alpha = 0.05; controlling for type I comparisonwise errors); rates at stations with average depths of 11 m and 14 m were greater than the respiration rates at one station with an average depth of 9 m.

The results of these paired comparisons tests, when taken together, strongly indicate that respiration rates tend to be greater at the deeper stations only because there is a greater volume of water in which respiration can occur at these stations. This suggests that respiration in the water column (rather than benthic respiration) dominates whole-ecosystem respiration.

Table 2. Results of SAS general linear models procedure for paired comparison tests of respiration as a function of average station depth.

Model	DF	MS	F	P
Respiration per m^2	7	1.51	2.61	0.018
Respiration per m^3	7	0.81	1.23	0.30

DF stands for the degrees of freedom and MS for the mean square estimates of the model runs.

What is fueling respiration?

Our estimate of respiration includes both heterotrophic organisms and algae. Algal respiration in the same reach of the Hudson River from May through October has been estimated as averaging 0.8 g C m^{-2} day^{-1} (Cole et al. 1991). Our estimate of whole-ecosystem respiration for this period is 591 g C m^{-2}, or an average of 3.2 g C m^{-2} day^{-1}. Subtracting the estimate of algal respiration from the rate of total respiration yields an estimate of average respiration by heterotrophic microorganisms and animals of some 2.4 g C m^{-2} day^{-1}, or roughly 75% of the total rate of respiration. This estimate is similar to the 2.6 g m^{-2} day^{-1} calculated for rates of respiration by bacteria in the water-column of the river from data on tritiated thymidine (Findlay et al. 1991a, corrected for an average water-column depth of 11 m). Although our estimate includes benthic respiration and respiration by animals, we consider our estimate and that of Findlay et al. (1991a) to be in good general agreement given the various assumptions and sources of error. Both estimates indicate that the freshwater, tidally influenced Hudson River is strongly heterotrophic.

Assuming that heterotrophic respiration comprises approximately 75% of total ecosystem respiration during the entire year, as it apparently does from May through November, we can roughly estimate the annual rate of respiration by all heterotrophs as 566 g C m^{-2} yr^{-1}. This heterotrophic respiration potentially could be fueled by organic matter originating from phytoplankton net primary production, from terrestrial allochthonous inputs, from sewage inputs, and from primary production in macrophyte beds and fringing marshes along the river. Of these sources, it appears that the allochthonous inputs from terrestrial ecosystems dominate. As noted above, the data of Cole et al. (1991) indicate a ^{14}C production rate by phytoplankton in the tidal, freshwater Hudson River of only 80 g C m^{-2} during the ice-free season. These are daytime rates only, and given the high algal respiration rate (Cole et al. 1991) in this deep, turbid and well-mixed ecosystem, net primary production must be significantly lower yet. In fact, Cole et al. (1991) estimate that the compensation depth is usually less than 2 meters, and depth-integrated rates of net primary production by phytoplankton are positive only in shallow waters.

Sewage inputs to the tidal, freshwater portion of the Hudson River contribute only some 30 g C m^{-2} yr^{-1} (Fruci and Howarth 1989). And submerged macrophyte beds in the Hudson appear to be net sinks of carbon, not sources of organic carbon to the main channel of the river; whole-system respiration in macrophyte beds exceeds gross primary production, probably because the beds are trapping particulate organic matter out of the river (Garritt 1990). Although fringing marshes may be export-

ing some detritus to the Hudson (Findlay et al. 1990), these systems too are trapping some particulate organic matter from the river. There is no tendency to observe increased amounts of either dissolved or particulate organic carbon in the waters near the major marshes on the Hudson River (Findlay et al. 1991b). In general, marshes contribute little net organic carbon to adjacent waters (Howarth, in press). Even if the marshes of the Hudson are at the extreme end of export of organic carbon compared with other marshes (Howarth, in press), they would contribute little to the carbon budget of the Hudson because of their relatively small area.

The vast majority of respiration by heterotrophic organisms in the river would appear to be fueled by allochthonous inputs from terrestrial ecosystems. These inputs are estimated as 740 g C m^{-2} yr^{-1} in an average year (Gladden et al. 1988; Howarth et al. 1991). Other net inputs of organic matter input to the river are probably at most 100 g C m^{-2} yr^{-1} (assuming 30 g C m^{-2} yr^{-1} for sewage and much less than 80 g C m^{-2} yr^{-1} for primary production). Thus, assuming these other net inputs are all respired within the river, and assuming the estimate of total respiration by heterotrophs of 566 g C m^{-2} yr^{-1} is valid, at least 63% of the allochthonous inputs to the Hudson River are respired within the river. Given all of the assumptions, this estimate must be qualified, but a sizeable percentage of the terrestrial inputs clearly appears to be metabolized within the river. The same logic but with our upper and lower 95% confidence bounds on the annual respiration rate would suggest that at least 51% to 69% of the allochthonous inputs from terrestrial ecosystems are respired.

A recent review concluded that 30 to 75% of the particulate organic matter inputs to the rivers of the world consists of labile fractions which are likely to be respired within the rivers (Ittekkot and Laane 1991). Most such estimates are based on indirect approaches to determining lability, such as measurements of the carbohydrate and protein content of particulate organic matter in rivers. By assuming that these compose half of the labile matter in the particles, Ittekkot and Laane (1991) estimated that the labile portion represents 35% of the total particulate organic matter transported in the world's rivers.

Our study is one of the very few in any large river in the world where respiration data allow a relatively direct estimation of the percentage of terrestrially derived allochthonous inputs respired within the river. Richey et al. (1990, 1991) have measured respiration in the Amazon River, but the massive scale of that river and difficult-to-quantify exchanges of carbon between the main stem of the river and its floodplain complicate their carbon budget. The moderate size of the tidally influenced Hudson River, the well defined boundaries of the river with essentially no flood

plain, and the tidal advection which may reduce spatial variability in the river make this an ideal site for constructing a reasonably well constrained carbon budget. Also, the whole-ecosystem, open-water technique of measuring respiration provides reasonable precision in extrapolating rates over space. Consequently, we believe we have a very good, relatively direct estimate of what fraction of organic matter inputs are respired within any large — albeit not Amazonian scale — river. Our estimate that at least 63% of the inputs to the Hudson are labile and are respired within the river is at the high end of estimates based on less direct approaches but is probably conservative given our assumptions.

The movement of organic carbon from the landscape to a river in both dissolved and particulate forms is heavily influenced by disturbances and changes in land use (Moore 1989; Howarth et al. 1991; Ittekkot and Laane 1991; Esser and Kohlmaier 1991) and by climate (Gladden et al. 1988; Spitzy and Leenheer 1991; Howarth et al. 1991). Thus, any change in land use or in climate patterns could have a major effect on carbon inputs to the Hudson River. The majority of the allochthonous inputs of organic matter to the Hudson River currently come from erosion of disturbed land such as agricultural and urban and suburban areas (Howarth et al. 1991), and the data presented in this paper indicate that most of these inputs consist of labile, readily respired matter. Consequently, oxygen dynamics and energy flow within the tidally influenced Hudson River are probably quite sensitive to changes in land use and climate.

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