

A novel approach for estimating ecosystem production and respiration in estuaries: Application to the oligohaline and mesohaline Hudson River

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Abstract

Most estimates of metabolism in estuaries are based on water samples incubated in bottles. Such approaches may severely underestimate rates of both gross primary production (GPP) and respiration for a variety of reasons, including reduced turbulence, unnatural light fields, respiration of ¹⁴C-labeled organic matter, and altered grazer communities. These problems may be particularly intense in turbid and deeply mixed estuaries. The measurement of metabolism from in situ changes in dissolved oxygen (DO) concentration over a diel time period offers a potential solution to these problems, but complicated patterns of water advection and mixing in estuaries have limited the use of such open-water approaches. Here, we describe a method of using diel changes in oxygen concentrations in the oligohaline and mesohaline Hudson River estuary to estimate GPP, whole-ecosystem respiration (ER), and net ecosystem production (NEP). For this approach, concentrations of DO at any given time for several stations are described as a function of salinity and depth, providing a surface in the three-dimensional space of oxygen, depth, and salinity. The change in this “response surface” for oxygen over time, once corrected for atmospheric exchange, allows the estimation of metabolism rates. The regression procedures used allow an estimate of the standard error associated with the metabolism measures. For the mesohaline Hudson River estuary, these standard errors are reasonably small. Similarly, any potential errors associated with the estimation of atmospheric exchange in oxygen are small for the Hudson. The technique should be useful for estimating GPP, NEP, and ER in other partially mixed estuaries without the biases associated with incubations in bottles.

Since its introduction in the early 1950s (Steemann Nielsen 1951), the ¹⁴CO₂ method has become the dominant way to measure rates of primary production in aquatic ecosystems. Until quite recently, the ¹⁴CO₂ approach has been the only method sensitive enough to measure production in oligotrophic oceanic waters and lakes, but because of its ease of use, the method has also been widely applied to mesotrophic and eutrophic lakes (Jorgensen et al. 1983; Bower et al. 1987; Carpenter and Kitchell 1987; Berman et al. 1995), rivers (Lewis 1988; Cole et al. 1991, 1992), and estuaries (Malone 1977; Carpenter and Dunham 1985; Jensen et al. 1990; Taylor and Howes 1994; Callaway et al. 1995). Unfortunately, the method measures neither net nor gross primary productivity but rather, some rate between these two, because some (but not all) of the ¹⁴C incorporated into cells is respired again during the time of measurement (Peterson 1980; Bender et al. 1987). With short enough incubation times, the ¹⁴C method should approach an estimate for GPP (Collos et al. 1993). However, how short a time period is short enough depends upon characteristics of the ecosystem and is not easily determined. In turbid, light-limited systems such as the tidal freshwater Hudson River, ¹⁴C incubations

of just 2–3 h can yield rates that are one order of magnitude lower than GPP (Cole et al. 1991, 1992; Howarth et al. 1996; Howarth and Michaels in press). The ¹⁴CO₂ method also does not allow the estimation of respiration.

In ecosystems where rates of metabolism are great enough, the change in oxygen concentration in light and dark bottles over time can be used to estimate both rates of GPP and respiration. This light–dark O₂ bottle method is therefore preferable to the ¹⁴CO₂ method where the rate of change in oxygen is great enough to give reasonable precision. The approach has been used since at least the 1920s (Gaarder and Gran 1927) and has had widespread use in both freshwaters and marine systems (Odum and Hoskin 1958; Edwards and Owens 1962; Sirois and Fredrick 1978; Kemp and Boynton 1980). However, in common with the ¹⁴CO₂ method, the light–dark O₂ bottle method suffers from a variety of “bottle effects.” Three bottle effects may be particularly severe in estuaries and rivers: (1) bottles tend to be incubated under constant light (either in the field or in the laboratory), whereas plankton in estuaries and rivers can be mixed rapidly through a wide variety of light intensities (Lewis 1988; Richey et al. 1990; Cole et al. 1992; Howarth et al. 1996); (2) enclosure in a bottle eliminates turbulence, which is often high in estuaries and may have a profound effect on both primary production and respiration (Nixon et al. 1979; Kemp and Boynton 1980; Howarth et al. 1992); and (3) the exclusion of some grazers from bottles may affect rates of metabolism and nutrient cycling pathways (Collos et al. 1993).

Where applicable, estimation of rates of metabolism from in situ changes in concentrations of DO (the in situ diel O₂ approach) is preferable to other methods because natural light fields, turbulence, and grazer communities are maintained and because the approach integrates over space and

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time (Kemp and Boynton 1980; Oviatt et al. 1986; Richey et al. 1990; Howarth et al. 1992; Howarth and Michaels in press). The *in situ* diel O_2 approach is relatively easy to apply in nonflowing systems such as ponds, lakes, or estuarine mesocosms (Odum and Hoskin 1958; Oviatt et al. 1986). Respiration rate is estimated from the rate of oxygen decrease overnight in the dark, and GPP is estimated by adding this respiration rate to the rate of oxygen increase in the light during the day. These oxygen changes need to be corrected for atmospheric exchange of oxygen, but where metabolic rates are high and the water column is deeper than a few meters, the correction for diffusive exchange is relatively minor (Marino and Howarth 1993).

The *in situ* diel O_2 method also has been applied to flowing waters. One approach is to compare oxygen concentrations at an initial time and station with oxygen concentrations at a second station downstream, after the time interval estimated for water to flow from the upstream to the downstream station (Odum 1956; Owens 1969; Nixon and Oviatt 1972). Another approach is simply to apply the *in situ* diel O_2 method to one station, as in a pond, and assume that metabolism along the flowing water is homogeneous enough to allow accurate estimation of metabolism rates (Odum 1956). In tidal systems with complex mixing patterns, the application of an upstream-downstream approach is difficult at best, and there is seldom any reason to assume that metabolism rates are homogeneous in space. A third approach was used by Howarth et al. (1992) in the tidal, freshwater Hudson River: they estimated respiration from the decrease in oxygen overnight at 10 stations along a 40-km transect by simply averaging the data for all stations. They reasoned that there should be no systematic bias in estimating average rates of metabolism by this approach because increases or decreases in oxygen at any station due to advection of water masses should be offset by oxygen changes in the opposite direction at adjacent stations, provided that enough stations are sampled over a large enough transect. For the freshwater Hudson, the standard error for the respiration estimate was only 11% of the mean, indicating rather small differences in metabolism rates among the stations (Howarth et al. 1992).

In saline estuaries, mixing is even more complex than in a tidal freshwater river, such as the portion of the Hudson studied by Howarth et al. (1992), and the application of the *in situ* diel O_2 method for estimating metabolism has proven problematic (Kemp and Boynton 1980). Here, we report on the development of a new technique for using the *in situ* diel O_2 approach in saline estuaries. Our technique is an expansion of the multistation-averaging technique of Howarth et al. (1992), but it explicitly makes use of salinity data as a conservative tracer to provide information on mixing and advection. Although we developed the method for the oligohaline and mesohaline Hudson River estuary and have only applied it there, we believe it may be widely applicable to other partially mixed saline estuaries.

Site description and sampling protocol

From April 1993 to December 1995, we measured DO depth profiles over diel time periods in oligohaline and me-

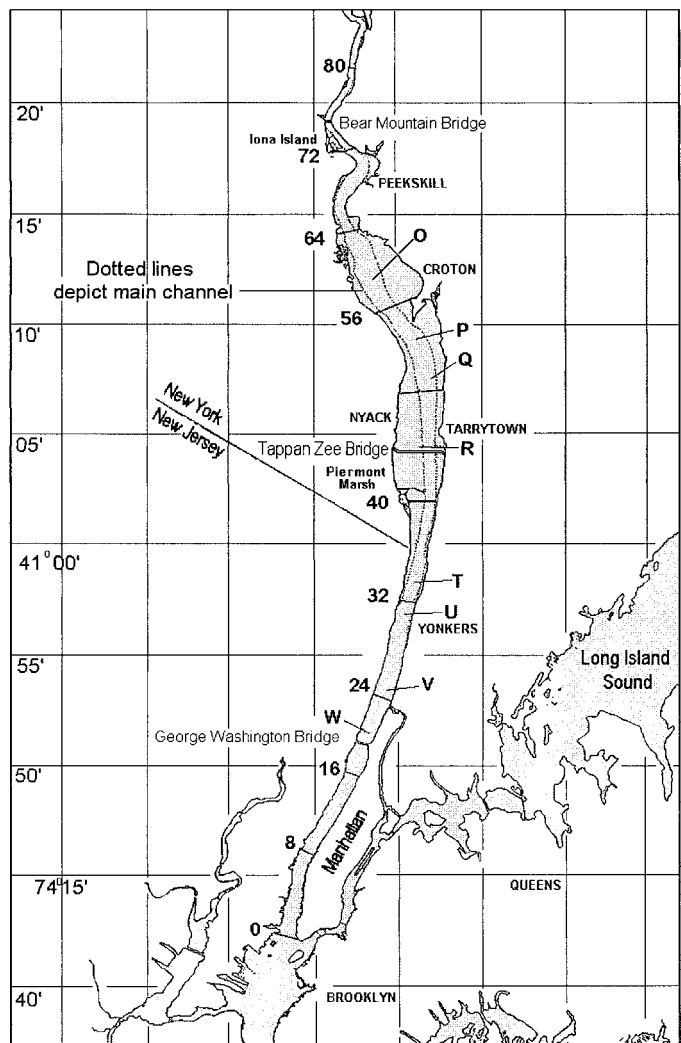


Fig. 1. Map of the Hudson River showing sampling stations.

sohaline sections of the Hudson River along a transect from upper Haverstraw Bay (river km 59) to the George Washington Bridge (river km 19; Fig. 1), with the objective of estimating GPP, ER, and NEP. This section of the river is considered a partially stratified estuary where there is complex, tidally induced mixing (Abood 1974). The upper half of this section, represented by Sta. N-S (Fig. 1), is oligohaline and has a main channel depth of 9.5 m bordered by much shallower areas (approximately 3 m). The lower section from Sta. T to W is mesohaline, deeper, and narrower, with a main channel depth of 11 m and very little shallow water area. The mean water-column salinities range from 0 to 5 ppt and from 7 to 14 ppt in the spring for the oligohaline and mesohaline sections, respectively. In summer and early fall, with much lower freshwater discharge, mean salinities range from 4 to 7 ppt and from 9 to 15 ppt for the oligohaline and mesohaline sections, respectively.

In 1993, we sampled Sta. N-S (Haverstraw Bay through the Tappan Zee [HTZ]), each located near the main channel of the river. In 1994 and 1995, we continued to sample Sta.

O–R in HTZ and added Sta. T–W in the Palisades section further downriver (PAL).

Each year, we made measurements at roughly 3-week intervals between April and May or June and November. For most sampling trips, we began sampling near midday and made subsequent measurements at dusk and dawn and at midday on the following day (or as near as possible to these times). On some trips, the initial or final midday sampling was omitted because of logistical problems. For each diel period, we were constrained to three–four visits per station by the travel time required to traverse the 40-km transect; even with a relatively fast boat, transect sampling time was 2–2.5 h.

Percent oxygen saturation was measured with a YSI model 58 DO meter accurate to 0.3% of saturation (YSI 1989) at 0.5-m intervals through the top 3 m of the water column and at 1-m intervals in the remainder of the water column to the bottom. This compares to measured changes in DO between sampling times at individual stations on the order of 4–6% of saturation. The meter and probe were carefully calibrated in water-saturated air at in situ surface-water temperatures, as in Howarth et al. (1992). Calibration at 100% saturation was checked for drift after each station profile and, in most cases, varied by <1%. Percent oxygen saturation values were corrected for bias after each sampling run (i.e., if the mean calibration was greater than or less than 100%).

Temperature and salinity were measured simultaneously using an Orion model 140 conductivity meter. Temperature, salinity, and percent oxygen saturation data were used to calculate oxygen concentrations in mass units (APHA 1992).

Representative DO and salinity profiles

Vertical profiles of DO may change over the day in partially mixed estuaries such as the Hudson in response to variation in stratification associated with tidal flow, riverine metabolism, and atmospheric diffusion at the surface. Moreover, these effects may vary significantly with distance from the river mouth. Significant changes in DO profiles were evident between midday and dusk (see Fig. 2a) at Sta. P in the HTZ reach during a summer sampling date (3–4 July 1995). The profile exhibits a decrease in DO, with depth characteristic of unstratified (or weakly stratified) water, and an increase over time consistent with daytime positive NEP. The corresponding salinity profiles (Fig. 2b) indicate a slight increase with depth and an increase over time, indicating the effect of an incoming tide. The DO profiles for the same period at Sta. U (Fig. 2c), approximately 22 km downstream, show a sharper decline with depth in the upper 6–8 m but level off in the lower layer, consistent with greater stratifi-

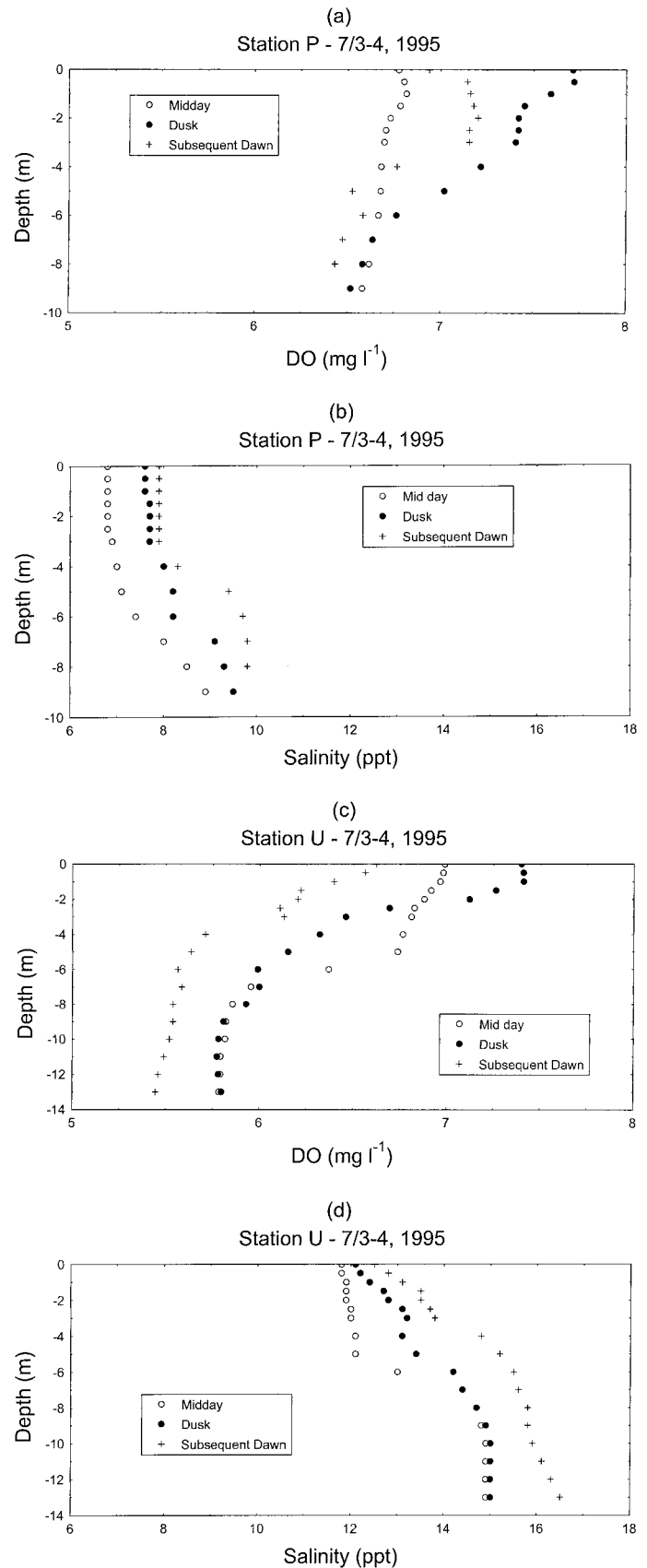
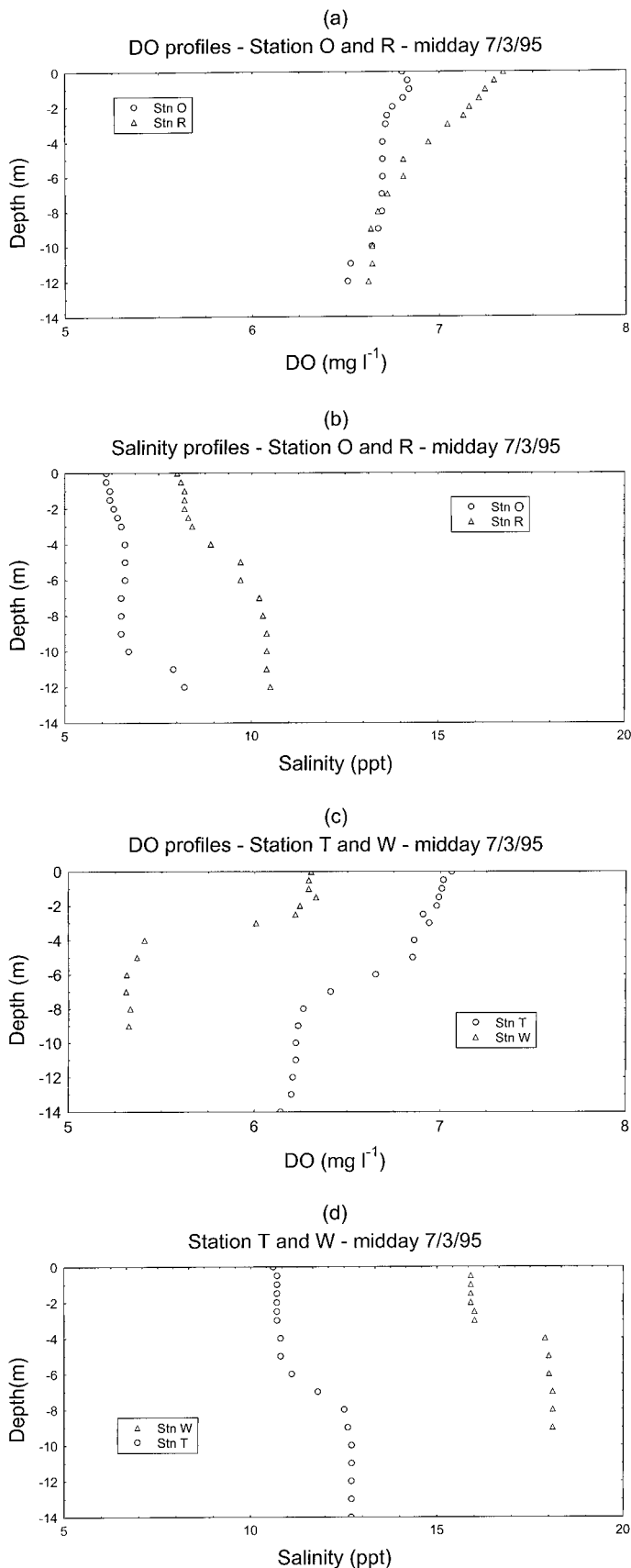


Fig. 2. Typical depth profiles of DO and salinity measured on 3–4 July 1995 at an HTZ (Sta. P) and at a PAL station (Sta. U), which is further downstream and more saline. Profiles for three sample times are shown for each station: (a) DO profiles, Sta. P; (b) salinity profiles, Sta. P; (c) DO profiles, Sta. U; and (d) salinity profiles, Sta. U. Strong negative correlations frequently exist between oxygen and depth and between oxygen and salinity.



ication in this more saline portion of the river. The corresponding salinity profiles (Fig. 2d) support the view that some stratification is occurring here; salinity sharply increases at a depth of 6 m and varies little below this depth.

Strong longitudinal gradients in DO and salinity were also evident in the Hudson River estuary as seen in the midday on 3 July 1995 profiles at Sta. O (upper Haverstraw Bay) and R (lower portion of the Tappan Zee) (Fig. 3b,c). Even stronger gradients are apparent on the same date between the corresponding profiles at Sta. T and W in the deeper downstream portion of the mesohaline Hudson estuary (Fig. 3c,d). Differences between the profiles indicate the strength of the local longitudinal gradient of salinity or DO. The figures show longitudinal gradients >5 ppt in salinity between Sta. T and W (separated by about 14 km) but only about half that across Sta. O and R, also separated by 14 km. A markedly stratified vertical structure of the salinity profile is observed at both Sta. T and W (Fig. 3d), and the difference between the profiles indicates the effect of increased mixing with freshwater as one moves upriver, resulting in a deepening and weakening of the halocline. At both Sta. O and R, the vertical salinity gradients were comparatively weak (Fig. 3b). DO profiles show corresponding characteristics: Sta. T and W showed both strong longitudinal gradients and strong stratification, whereas these features were much reduced at Sta. O and R during the same period. Water at Sta. T–W moved along a relatively strong salinity gradient, presumably through regions of nonuniform production and respiration, and was subject to mixing with other parcels of varying salinity. The metabolism of the water column in this reach of the river should show some effects of stratification (e.g., production confined largely to the surface layer and respiration dominating the lower layer). Water moving through Sta. O–R was subjected to relatively well-mixed conditions, little stratification, and weaker longitudinal gradients; the metabolism of a volume of water in this stretch of the estuary at that time should not exhibit strong spatial variation due to physical factors.

Approach to estimating metabolism—oxygen change over time

Our approach for estimating metabolism can be conceptualized as follows: At any given time, a mathematical relationship is assumed to hold between DO, depth, and salinity. The relationship can be quantified by fitting it to field observations (profiles of DO, depth, and salinity at two or more stations). While the mathematical form of the relationship is assumed to hold over time, parameters of the function (e.g., slope or y-intercept) may change. At a fixed time, the relationship between DO, salinity, and depth can be represented as a plane in three dimensions (Fig. 4). Over time

←

Fig. 3. Depth profiles of DO and salinity at HTZ stations (O and R) and at PAL stations (T and W) illustrating their longitudinal gradient: (a) DO profiles, Sta. O and R; (b) corresponding salinity profiles, Sta. O and R; (c) DO profiles, Sta. T and W; and (d) corresponding salinity profiles, Sta. T and W.

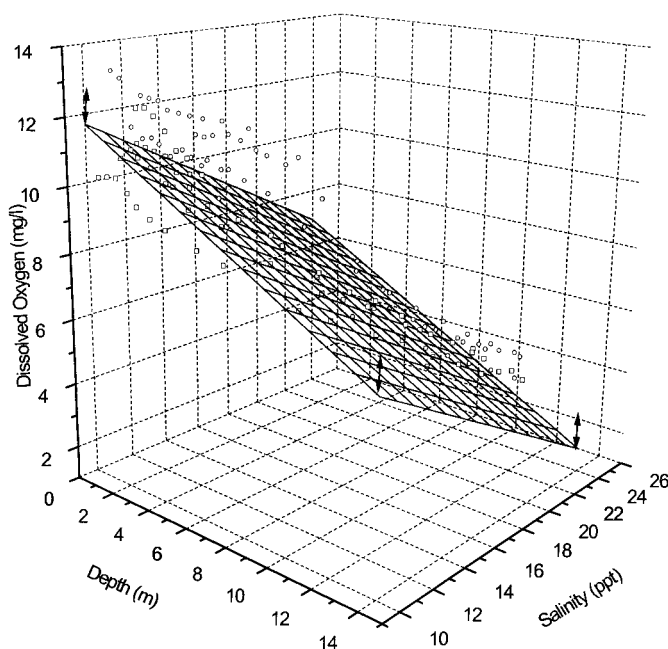


Fig. 4. Response surface of the three-variable regression model used to estimate the rate of change in oxygen. The average difference between the two planes along the DO axis (arrows) represents the average change in oxygen between two sample times across the stations sampled due to estuarine metabolism and diffusion to and from the atmosphere.

during a diel period, this plane will shift vertically and will perhaps rotate as well. These changes can be determined by successively fitting the function at different times over the period of sampling. Our technique can be considered an analysis of the motion of this plane in time; the average movement of the plane in the vertical axis representing DO, if divided by the time between sampling, gives the average rate of change in DO for stations included in the analysis. The estimated rate of change in DO per area associated with ecosystem metabolism is obtained by multiplying by local average depth and correcting the change for atmospheric diffusion, following the basic assumptions of the in situ diel O_2 approach. Because this technique can be envisioned as the difference between different statistical “response surfaces” of DO as a function of depth and salinity at different times (Neter et al. 1990), we refer to it as the “response surface difference” (RSD) technique.

In practice, we found it simpler to incorporate the time between samples directly into the regression calculation than to perform a separate regression calculation for each sampling time. Pooling data from several sampling stations and two sample times, we used linear regression to define the relationship between DO (milligrams per liter); salinity, s (ppt); sample depth, z (m); and time from first sample, t (h), over the sampling period

$$DO = b_0 + b_z z + b_s s + b_t t + \epsilon \quad (1)$$

Here, the coefficients, b_i , represent the change in DO associated with a unit change in each of the independent variables, and ϵ represents the random component of DO not

explained by the independent variables, with mean value = 0. By pooling the data over a longitudinal transect of stations and two sample times, the regression can be used to estimate the regression coefficients, b_i . Equation 1 can be interpreted as a family of parallel plane surfaces corresponding to different times in an oxygen–salinity–depth coordinate system. The addition of cross-terms (i.e., $s \times t$ and $z \times t$) would allow these planes to rotate over time but would not affect the estimate of the average displacement, which is our aim here.

We integrated the regression equation over the range of depth and salinity (s_{\min} to s_{\max}) of the pooled stations to obtain an expression for the average DO as a function of the time interval between measurements for both daytime and nighttime periods. Mathematically, this is of the general form

$$\overline{DO(t)} = \frac{1}{depth} \int_0^{depth} \frac{1}{s_{\max} - s_{\min}} \int_{s_{\min}}^{s_{\max}} DO(z, s, t) dz ds \quad (2)$$

For the linear form of Eq. 1, Eq. 2 yields

$$\overline{DO(t)} = b_0 + b_z \frac{depth}{2} + b_s \frac{s_{\max} + s_{\min}}{2} + b_t t + \epsilon \quad (3)$$

Equation 3 expresses the value of DO in an average parcel of water for the pooled stations at time t in terms of its average depth and salinity and the regression coefficients of Eq. 1. For a parcel of average depth and salinity, the time derivative of Eq. 3 is equivalent to b_t . We interpret this as the local rate of change in oxygen of a parcel moving in the vicinity of the pooled measurement stations of average depth and salinity (see Table 1). From dimensional analysis, it is clear that the units of b_i must be those of DO per time (milligrams per liter per hour). Thus, b_t represents an estimate of the average rate of change in oxygen for the particular interval examined (midday–dusk, dusk–dawn, or dawn–midday)—that is, we can obtain this estimate directly from the regression without doing the arithmetic in Eq. 2.

For the analysis, we used STATISTICA (Statsoft 1998) to obtain values of regression coefficients, their standard errors and statistical significance (P value), and the R^2 of the regression. The R^2 value of the regressions indicates the proportion of the variation explained by the linear model. Most of our sampling times resulted in regressions with relatively high values of R^2 . This is illustrated in Fig. 5a, which gives the frequency of samples associated with a particular value of R^2 over the 3 yr of data ($n = 147$). Overall, 78% of the samples resulted in regressions with an R^2 of $\geq 60\%$. The corresponding P values of the regression coefficient b_t are shown in Fig. 5b. The figure shows that 84% of the time, the regression coefficient is significantly different from zero (alpha = 0.05). Implications of low values of R^2 are discussed below.

Estimates having a P value > 0.05 (i.e., no statistically significant difference from zero rate of change at the 95% confidence level) indicate that oxygen in the water column has reached an approximate steady state between the net change in oxygen due to metabolic processes and that associated with atmospheric exchanges. This often occurs during periods of relatively low metabolic activity associated

Table 1. Range of estimates of volumetric rate of change in oxygen ($\text{mg liter}^{-1} \text{h}^{-1}$) (b_i) derived from regression methods for 1994–1995 together with standard errors, R^2 of the regression used to derive the estimate, and P value of the estimate. The last column indicates whether the estimate is the best or worst estimate for the year as ranked by the R^2 of the regression. P values > 0.05 indicate that the estimate is not significantly different in value from 0.

Date	Estimate	(SE)	R^2	P	Worst case (w)/ Best case (b)
Sta. O–R, nighttime					
29 Jun 94	–0.034	(0.0026)	0.85	$<10^{-6}$	b
24 Aug 94	–0.009	(0.0038)	0.16	0.028	w
25 Apr 95	–0.009	(0.0006)	0.98	$<10^{-6}$	b
28 Nov 95	–0.0058	(0.00089)	0.31	0.0009	w
Sta. O–R, daytime					
29 Jun 94	0.010	(0.0093)	0.65	0.28	b
13 Jul 94	–0.0577	(0.0208)	0.32	0.0064	w
25 Apr 95	0.009	(0.002)	0.98	8×10^{-6}	b
24 Oct 95	0.0188	(0.0023)	0.56	$<10^{-6}$	w
Sta. T–W, nighttime					
19 Oct 94	–0.0118	(0.0015)	0.95	$<10^{-6}$	b
24 Aug 94	–0.0281	(0.0036)	0.86	$<10^{-6}$	w
25 Apr 95	–0.016	(0.001)	0.98	$<10^{-6}$	b
23 Aug 95	–0.094	(0.014)	0.75	$<10^{-6}$	w
Sta. T–W, daytime					
19 Oct 94	0.0692	(0.0066)	0.96	$<10^{-6}$	b
1 Aug 94	0.0409	(0.0131)	0.89	0.0022	w
24 Oct 95	0.00079	(0.0029)	0.98	0.79	b
26 Jul 95	0.07	(0.013)	0.76	$<10^{-6}$	w

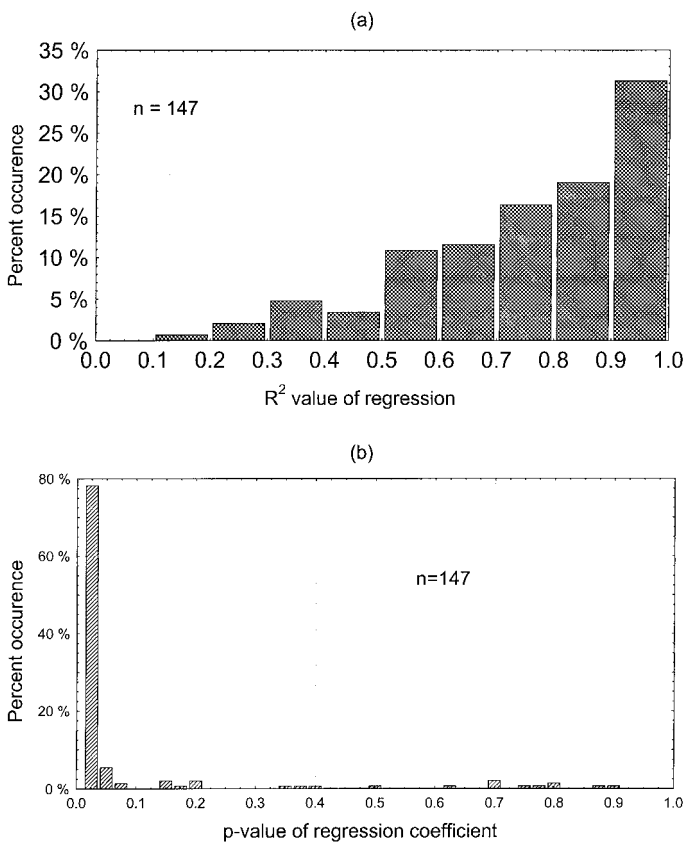


Fig. 5. (a) Frequency distribution of R^2 for the 147 regressions used to estimate the rate of change in DO for Hudson River stations for the years 1993–1995. (b) Corresponding frequency distribution of P values (levels of significance) for the regression coefficient b_i .

with low temperatures or light levels (e.g., at the beginning and end of the sampling season), but it may also occur at other times if the rates of atmospheric exchange are sufficiently high.

The estimates for rate of change in DO seem to be stronger at downstream, mesohaline Sta. T–W than at the less saline Sta. O–R. For Sta. O–R, 75% of the estimates had an R^2 of >0.6 . For Sta. T–W, all of the estimates had an R^2 of ≥ 0.75 . Stronger salinity gradients at Sta. T–W may allow the salinity term in Eq. 1 to explain more of the variability in DO (Figs. 2, 4), yielding higher R^2 values. Daytime regressions (dawn–midday) do not appear to be better or worse than nighttime regressions (dusk–dawn), indicating an equal likelihood of success for estimates of production and respiration.

Another way to examine the significance of the RSD method is to contrast the estimates of rate of change in DO to estimates made by simply averaging over stations at two times and dividing by the time interval between samples (i.e., the multistation-averaging technique; Howarth et al. 1992). Figure 6a,b plots the estimates made using simple averaging against those made using the RSD method for the 1994–1995 sampling seasons (the seasons in which stations were grouped into “upriver” O–R and “downriver” T–W). For the upriver Sta. O–R (oligohaline estuary), a good correlation ($r = 0.85$) exists between estimates made using the two methods (Fig. 6a). The estimates are clustered fairly tightly around the 1:1 line, indicating perfect agreement, with the exception of a few outliers, reflecting the occasional incursion of a tongue of salinity. This is consistent with the notion that for these stations, the influence of salinity is not very strong, and the overall behavior is reasonably well de-

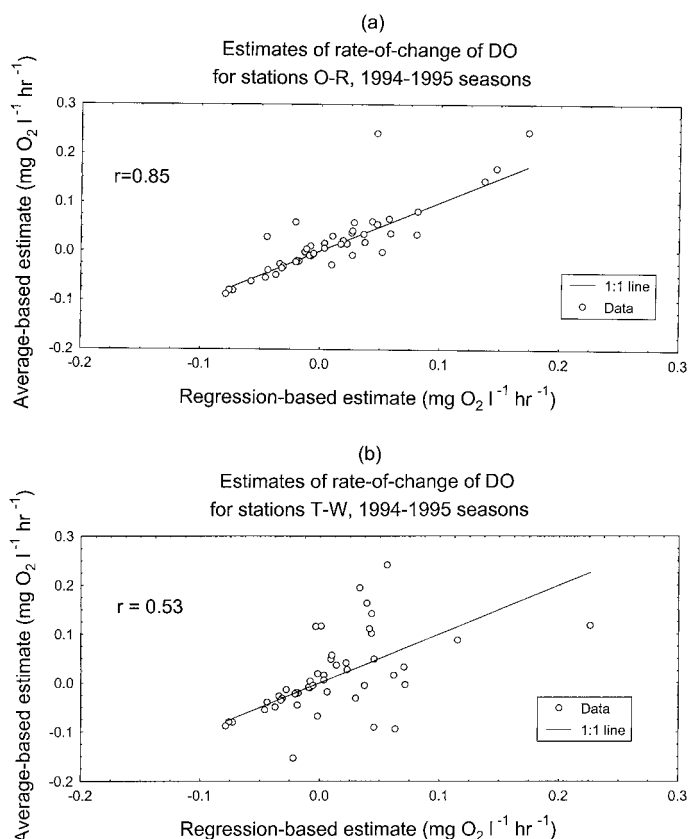


Fig. 6. (a) Plot of multistation-average estimates vs. RSD estimates of DO rate of change for upriver Sta. O-R, 1994–1995. (b) Corresponding plot for downriver Sta. T-W. Agreement is good for Sta. O-R but not for Sta. T-W.

scribed by averaging. However, for Sta. T-W further downriver in the mesohaline estuary (Fig. 6b), the correlation between the estimates is not very high ($r = 0.53$). The deviations between the two estimates do not appear to be biased overall, but they are large. Simply averaging over these stations produces an unreliable estimate of rate of change in DO.

Estimating metabolism from rate of change in DO

DO rates of change are converted to metabolism estimates using conventional assumptions (Howarth and Michaels in press) that are independent of the nature of the estimate of the change in DO. We convert estimates for the rate of change in DO concentrations (milligrams per liter per day) to the rate of change per surface area of water (grams per square meter per day) by multiplying by the mean depth (m) of the estuary for the stations under consideration. This rate of change is due both to metabolism and atmospheric exchange. We estimate the rate of oxygen exchange with the atmosphere from the partial pressure gradient to the atmosphere and from data on wind velocity and temperature (Marino and Howarth 1993). For this analysis, we used hourly wind data from LaGuardia airport in New York City (the closest available meteorological data) acquired from the

Northeast Regional Climate Center at Cornell University. Because wind velocities vary over a diel period and because the rate of oxygen exchange with the atmosphere is a log function of wind velocity, we calculate atmospheric exchanges for each hourly value and then average them over the sampling period.

To correct the rate of oxygen change due to metabolism for atmospheric exchange, we either add the rate of atmospheric exchange to the per-area rate of change in the estuary if oxygen concentrations are below saturation or subtract if concentrations are supersaturated. We can then estimate rates of metabolism directly from these corrected rates of change in oxygen. For ER,

$$ER_h = d(b_t)_{\text{night}} \pm (\text{atm})_{\text{night}} \quad (4)$$

where ER_h is the hourly rate, d is the average depth for the stretch of estuary considered, $(b_t)_{\text{night}}$ is the rate of change in oxygen during the nighttime period (per hour), and $(\text{atm})_{\text{night}}$ is the average exchange in oxygen with the atmosphere during the nighttime period of observation (per hour). Hourly rates are converted to daily rates simply by multiplying by 24, assuming that respiration during the daytime is the same as at night.

Average hourly GPP is estimated from the corrected rate of change in oxygen during the daylight period of observation, the atmospheric exchange, and the rate of respiration:

$$GPP_h = d(b_t)_{\text{day}} \pm (\text{atm})_d + ER_h \quad (5)$$

where $(b_t)_{\text{day}}$ is the hourly rate of change in oxygen during the daylight hours, and $(\text{atm})_{\text{day}}$ is the hourly exchange in oxygen with the atmosphere during the daytime period of observation. For dates on which two daytime estimates of $(b_t)_{\text{day}}$ were available, a time-weighted average was used. Daily rates of GPP are estimated by multiplying the hourly rates by the number of daylight hours for that particular day.

NEP on a daily basis can be estimated from estimates of GPP and ER as follows:

$$NEP_{\text{daily}} = GPP_{\text{daily}} - ER_{\text{daily}} \quad (6)$$

where NEP_{daily} , GPP_{daily} , and ER_{daily} are all rates per day.

This approach yields estimates of metabolism that are averaged over the pooled stations for whatever set of stations is included in the analysis. For the Hudson River estuary, we group data for Sta. O-R in the oligohaline estuary (HTZ) and for Sta. T-W in the mesohaline estuary, further downriver. This grouping is based not only on similarity in salinity but also on similarities in mean depths (5.4 m for Sta. O-R and 9.2 m for Sta. T-W) and the extent of shallows (which represent 60% of the surface area for the O-R stretch of the estuary and <10% for the T-W stretch of estuary).

Because the estimates of ER, GPP, and NEP are based on linear combinations of independent random variables (the b_t and $[\text{atm}]$ values), their standard errors are directly calculable from the standard errors of the individual variables (Netter et al. 1990).

Estimates of metabolism

Estimates of GPP, ER, and NEP for 1993–1995 for the two stretches of the estuary are shown in Figs. 7–9. Standard

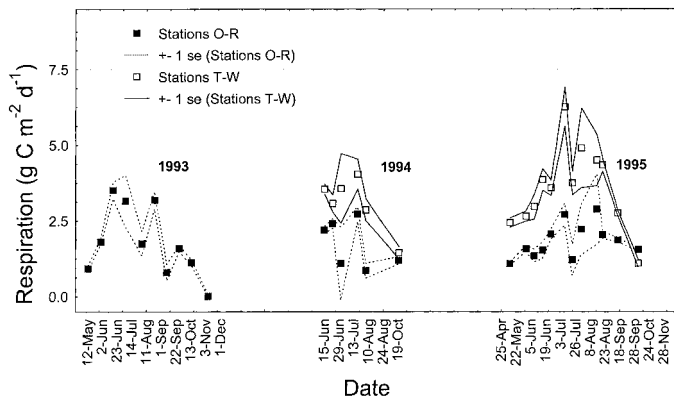


Fig. 7. GPP over time for the 1993–1995 sample period derived from the regression estimates, corrected for wind-driven atmospheric diffusion. Black squares indicate Sta. O-R (HTZ); open squares indicate Sta. S-W; dashed lines indicate ± 1 SE for Sta. O-R; solid lines indicate ± 1 SE for Sta. S-W.

errors above and below the means are shown by the lines that envelop the mean values, shown by symbols. It is clear from the figures that at most times of the year, the standard errors of the estimates of respiration and GPP are much smaller than their means. Some of the variability of the standard errors is due to the contribution of the variance of the atmospheric exchange correction, which we assume to be independent of the variance of the regression coefficients and therefore additive. Even including this source of error, the envelope defined by the standard errors above and below the means tracks the seasonal variability of the means themselves, indicating a robust seasonal variation of the variables.

In quantitative terms, the standard errors of the estimates result in relatively low average coefficients of variation (C.V.) for the variables (0.25 for respiration and 0.29 for GPP). The relative variability of the estimates of respiration and GPP is somewhat higher in the oligohaline estuary (Sta. O-R) than in the mesohaline estuary (Sta. T-W). This is because the regression relationships tend to be stronger for the stations subject to stronger salinity gradients, resulting in smaller standard errors (relative to the mean) of the regression coefficient, b_r .

The average C.V. for NEP is higher than for the other measures (0.57), largely because it is strongly biased by two sample dates (24 August 1994 and 8 August 1995) for which the mean values of NEP at Sta. T-W were close to zero, and the corresponding C.V.s were 4.0 and 5.7. Also for this reason, the average C.V. of NEP for Sta. T-W is increased relative to Sta. O-R. For such variables, it may make more sense to compare the standard error to the range of the mean values. The largest value of the standard error of NEP, around $1.4 \text{ g C m}^{-2} \text{ d}^{-1}$, is only about 12% of the range of variability of NEP seen over the season.

Rates of GPP are correlated with chlorophyll concentrations measured over the same period in 1995 (Howarth et al. unpubl. data). In the mesohaline estuary, GPP showed very strong correlations with chlorophyll *a* (Chl *a*): ($r^2 = 0.90$; $P < 10^{-6}$); in the oligohaline estuary, GPP–Chl *a* correlations were not as strong but were still highly significant ($r^2 = 0.62$; $P = 0.0014$).

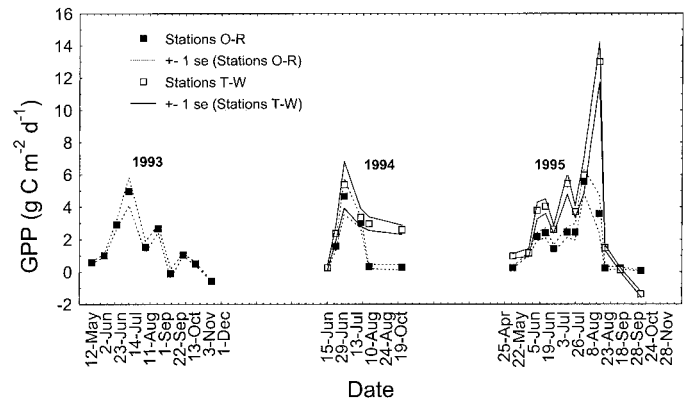


Fig. 8. ER over time for the 1993–1995 sample period. Symbols as in Fig. 6.

Comparison with earlier production estimates

Two earlier studies estimated “primary production” in or near the same area of the Hudson River. Sirois and Fredrick (1978) used a combination of in situ bottle measurements of oxygen taken at 1-m depth in June 1972 and chlorophyll measurements taken in 1972–1973 to estimate GPP along a transect of stations from the mouth of the Hudson to Poughkeepsie (river km 121) in 1972 and 1973. Malone (1977) used carbon 14 uptake to estimate productivity at four stations between the Upper Bay and the northern end of Manhattan. He reported estimates of primary productivity for Sta. A3, just south of the PAL. Table 2 compares these earlier semiannual production estimates to those made here. Estimates of GPP from 1993 to 1995 made with the RSD approach are substantially higher than those of both earlier studies at both HTZ and PAL. Much of this discrepancy could be attributed to changes in river metabolism in the intervening 20 yr. However, for the reasons outlined in the introduction (also, *see* Howarth and Michaels in press), the methods are sufficiently different that the estimates should not be comparable.

By contrast (and not surprisingly), the seasonal variation of NEP and GPP using the RSD approach appears qualitatively similar to the patterns reported by these previous in-

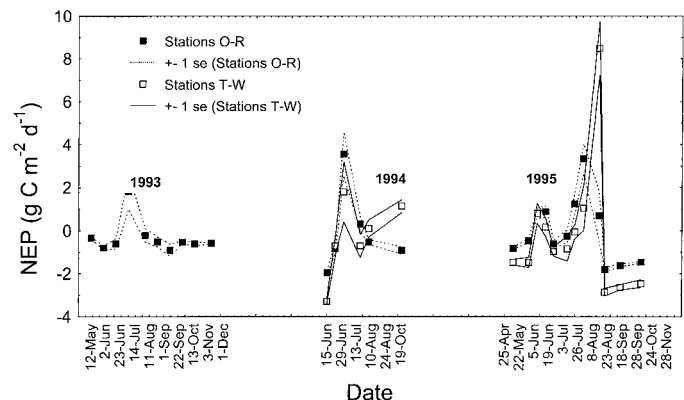


Fig. 9. NEP over time for the 1993–1995 sample period. Symbols as in Fig. 6.

Table 2. Comparison with previous estimates of semiannual productivity in or near the HTZ and PAL reaches of the Hudson (May–Oct, g C m⁻² 180 d).

Study	Year	Site	
		HTZ	PAL
Sirois and Fredrick (1978)	1972	177*	151†
Malone (1977)‡§	1973–1974	—	160
This study§	1993	328	—
"	1994	310	508
"	1995	367	680

* Average of Sta. 7–11; see table 6 in Sirois and Fredrick (1978).
 † Average of St. 4–6; see table 6 in Sirois and Fredrick (1978).
 ‡ Sta. A3; see fig. 4b in Malone (1977)
 § Average daily value from May to October multiplied by 180 d⁻¹.

vestigations. In 1993 and 1994, we observed peak productivity in mid-July at both the HTZ and PAL sites, as did Sirois and Fredrick (1978) in 1972. In 1995, we observed peak productivity at PAL sites in September and at HTZ sites in August. Malone (1977) observed peak production south of the PAL in August 1974. Other variations throughout the season observed in these studies and ours can be associated with the effects of both physical and biological variables, such as ambient light levels and grazing (Malone 1977), which we will address in a forthcoming paper.

Sensitivity analysis for atmospheric exchange

The effect of the correction for atmospheric exchange on the estimates of metabolism can be seen in Tables 3 and 4. Table 3 shows seasonally weighted averages for GPP, ER, and NEP calculated both with a wind-based correction for atmospheric exchange and a correction assuming zero wind. Weights for each sample are equal to the average of the intervals between the previous and next sample, divided by the interval between the first and last sampling dates; the weighted values are summed to obtain the seasonal weighted average. The differences that exist between the wind-based and zero-wind corrections are small and not statistically significant. Similarly, Howarth et al. (1992) found that for their estimates of respiration in the tidal, freshwater Hudson, potential errors associated with the correction for atmospheric exchange tended to be quite small. Note, however, that the importance of atmospheric exchange can be greater in shallower ecosystems (Marino and Howarth 1993). The corrected and uncorrected GPP estimates agree best because they result from daytime and nighttime processes in which diffusion tends to occur in opposite directions; the associated corrections tend to cancel.

To examine the sensitivity of the atmospheric correction under extremes of metabolic activity, the maximum and minimum estimates of GPP, ER, and NEP for the 3 yr studied are shown in Table 4, calculated both with the standard, wind-driven correction and with a zero-wind velocity correction. As with seasonal averages, the ER and NEP estimates are most sensitive to the diffusion correction, especially early and late in the season when metabolism tends to be relatively low, and diffusion tends to be increased by

Table 3. Sensitivity of seasonal average metabolism (g C m⁻² d⁻¹) estimates to atmospheric correction. The “wind-corrected” values are our normal estimates, and they include the effect of a wind-driven transfer coefficient in the atmospheric exchange of oxygen, based on the procedure of Marino and Howarth (1993). “Zero-wind” values assume atmospheric exchange of oxygen under no wind (velocity = zero) and are thus a worst-case analysis of potential errors with the approach used to estimate the atmospheric correction.

	ER (SE)	NEP (SE)	GPP (SE)
Sta. N–R—1993			
Wind corrected	1.90 (0.20)	−0.28 (0.23)	1.62 (0.25)
Zero wind	1.59 (0.25)	−0.08 (0.23)	1.50 (0.24)
Sta. O–R—1994			
Wind corrected	1.52 (0.41)	0.095 (0.36)	1.62 (0.39)
Zero wind	1.48 (0.35)	0.086 (0.45)	1.56 (0.32)
Sta. O–R—1995			
Wind corrected	1.88 (0.28)	−0.10 (0.25)	1.77 (0.26)
Zero wind	1.49 (0.22)	0.33 (0.23)	1.82 (0.24)
Sta. T–W—1994			
Wind corrected	2.92 (0.43)	0.20 (0.51)	3.12 (0.53)
Zero wind	2.48 (0.31)	0.64 (0.45)	3.12 (0.48)
Sta. T–W—1995			
Wind corrected	3.58 (0.32)	−0.33 (0.32)	3.25 (0.34)
Zero wind	3.18 (0.30)	0.26 (0.31)	3.44 (0.33)

seasonally higher winds (15 June 1994 was the first date sampled in 1994; 28 November 1995 and 1 December 1993 were the last dates sampled in these years). As with the seasonal averages, the maximum GPP estimates made with zero-wind atmospheric correction are quite close to the correction estimates based on actual wind data. The minimal (negative) estimate of GPP appears to be an artifact of the RSD method on 28 November 1995 and 1 December 1993, or it is perhaps due to sampling inaccuracies associated with cold conditions. The diffusion correction may also be invalid, because the wind speed on these dates frequently exceeded the range of validity of the correction (Marino and Howarth 1993).

There are no significant differences between the maximal values of ER, NEP, and GPP calculated with the wind-based correction and the no-wind correction; it is the minimal val-

Table 4. Values of maximum and minimum estimates of metabolism (g C m⁻² d⁻¹) over the 3 yr studied, calculated (1) using the standard wind-based correction for exchange of oxygen with the atmosphere, and (2) assuming no wind forcing (“zero wind”).

Date	Location		Estimate as normally estimated (SE)	“Zero-wind” value (SE)
GPP				
18 Sep 95	Sta. T–W	Max	13.0 (1.26)	13.2 (1.25)
28 Nov 95	Sta. T–W	Min	−1.4 (0.16)	−0.8 (0.14)
NEP				
18 Sep 95	Sta. T–W	Max	8.5 (1.25)	6.7 (1.25)
15 Jun 94	Sta. T–W	Min	−3.3 (0.12)	−2.2 (0.12)
ER				
18 Sep 95	Sta. T–W	Max	4.9 (1.31)	7.1 (1.18)
1 Dec 93	Sta. O–R	Min	0.01 (0.03)	−0.3 (0.03)

ues of metabolism that show the greatest differences. This is not surprising, because it is precisely under these conditions that an accurate diffusion correction is required and that an inaccurate assumption of zero wind would yield the greatest error.

Discussion

Why should this approach work? We can make three alternative arguments (or interpretations) for why a simple linear relationship between DO, salinity, depth, and time should yield reasonable results. Our reasoning follows mathematical, physical, and biological lines.

First, mathematically, even if the relationship between oxygen, salinity, depth, and time is not simply linear (as we have assumed), a linear relationship represents a “first-order approximation,” which should hold locally and capture much of the variation of oxygen (as it appears to in the Hudson). While more complex relationships could be assumed—and should, if warranted by the evidence—Occam’s razor dictates using the simplest reasonable statistical relationship between the variables.

Second, physically, in a partially mixed estuary, both salinity and oxygen can be considered passive tracers (C), described by a standard mass balance equation of the following form (cf. Fischer et al. 1979; Thomann and Mueller 1987):

$$\frac{\partial C}{\partial t} = \nabla \cdot (D\nabla C - vC) + P \quad (7)$$

The rate of change in concentration, C (grams per cubic meter), is the sum of transport terms (characterized by D [D_x , D_y , and D_z , $m^2 d^{-1}$] and v [v_x , v_y , and v_z , $m d^{-1}$], the dispersion coefficients and transport velocities, respectively), and a production term, which for salinity is assumed to be zero (no local source of salt) and for oxygen, is the local NEP (or at night, ER) (grams per cubic meter per day). In addition, at the water surface, there is a zero-flux boundary condition for salinity and a boundary condition for oxygen stating that the flux in or out is proportional to the saturation deficit/surplus. If the dispersion coefficients and velocities are the same in both mass balances, and salinity satisfies its mass balance equation, it follows that a linear function of salinity, depth, and time (i.e., Eq. 1) satisfies the mass balance equation for oxygen, which includes the additional average production term, $P = b_3 + v_z b_2$. The second term represents a component of change due to vertical gradients of oxygen not associated with corresponding salinity gradients. We assume that v_z , the vertical component of velocity averaged over the water column and over the sampling period, is negligible, so that $P = b_3$. Measured during the day, this provides an estimate of daytime net production, and at night, it provides a measure of respiration, uncorrected for atmospheric exchange. The atmospheric diffusion correction reconciles the effect of the different boundary conditions for salt and oxygen at the water surface. (Here, we assume the average values of D and v in Eq. 7 hold in the vicinity of the stations sampled to obtain a regression relationship; the parameters may be different for other groups of stations.)

Third, biologically, a partially mixed estuary represents a collection of species suited to different salinity regimes and light levels (and consequently depths), each with corresponding metabolic constraints imposed by their local environment. Even those organisms that are insensitive to particular salinity or depth regimes may be constrained to occupy them in relatively high densities by stratification in areas subject to strong salinity gradients. Thus, it is reasonable to expect a relationship between oxygen levels, salinity, and depth. The “average” metabolism remaining after the trends associated with salinity and depth are removed represents the average ecosystem behavior.

What are the limitations of the method? We have not incorporated a term in the regression to account for lateral variation because we did not observe strong differences between stations in the main channel of the Hudson and stations situated in shallower portions of the river. In some spatially extended systems with significant lateral variability in the distribution of biological communities (such as the Chesapeake Bay), it might be appropriate to extend the method by adding a term for lateral position, though it may be sufficient to rely on a relationship with salinity if lateral salinity gradients exist. Another approach would be to estimate explicitly the lateral variation in metabolism by grouping stations distributed laterally across the estuary into pools associated with particular areas of interest and using the method on each separate group.

The method estimates the average metabolism of the stations grouped for the regression calculations, in effect, using information about variation within the group to remove biases from the estimate of average metabolism. It may appear to sacrifice information about the spatial distribution of metabolism (i.e., alternatively, we could perform the analysis using individual stations, relying on the variation in salinity at individual stations over time to characterize the relationship between DO and salinity, but in doing so, we would lose statistical power). Ultimately, a judgment is required as to the number of stations to pool in the analysis. This should be determined by the experimental question at hand, and we know of no absolute guidelines for determining the number of stations in the pool. For this study, we were most interested in comparing an “upstream” oligohaline region, not subject to strong salinity gradients, to a “downstream” mesohaline region, with frequent strong salinity gradients, and we therefore chose to divide our transect of eight stations into two groups of four. Future studies might dictate alternative groupings of stations.

What does a low R^2 signify? Two possible explanations for low values of R^2 in some regressions are suggested. A large random component of variability (or fluctuations that occur at scales smaller than can be resolved by the sampling interval) is an obvious reason for a low R^2 and is one that cannot be improved by using a different model. If subdiurnal time scales are of interest, more frequent sampling is required, but a large “random” component not captured by the model does not invalidate the estimate of average change in oxygen over the sampling period.

A second possibility is the existence of nonlinear relationships between oxygen and the independent variables. If the data suggest such relationships are appropriate, either

linear models of transformed variables or intrinsically nonlinear models of the relationship between the dependent variables and oxygen could be used, although we found no appreciable difference between overall metabolism estimates made with log-transformed variables and untransformed variables or by the inclusion of cross-terms (e.g., $s \times t$) in the linear regression. If a transformed time variable is used in a linear model, the resulting regression coefficient and its standard error can no longer be simply interpreted as time rate of change in oxygen and its standard error. If a nonlinear model is used, similar concerns apply. However, approximate rates of change and corresponding asymptotic estimates of standard error can be estimated by using the first few terms of a Taylor's expansion of the function. For example, if $f(z, s, t; a_0, a_1, \dots, a_n)$ is a nonlinear function that represents DO in terms of depth z , salinity s , time t , and parameters $a_0 \dots a_n$, with fitted values $a_0^* \dots a_n^*$, then $g(z, s, t; a_0^*, a_1^*, \dots, a_n^*) \equiv \partial f / \partial t(z, s, t; a_0^*, a_1^*, \dots, a_n^*)$ is a first-order estimate of the rate of change in DO, and

$$\sigma^2 = \sum_{i=1}^n \left(\frac{\partial g}{\partial a_i} \right)^2 \sigma_i^2 \quad (8)$$

gives an estimate of the standard error (assuming independence of z , s , and t), where σ is the standard error of the estimate of rate of change in DO (uncorrected for diffusion), and σ_i is the standard error of the i th parameter (Devore 1987). Note that, unlike in the linear model, these estimates may be explicit functions of the dependent variables, so that averaging over the data set may be required to obtain a numeric estimate of the parameter and its uncertainty. Modern statistical software packages use similar procedures to estimate standard errors, σ_i , of the nonlinear regression coefficients (Neter et al. 1985; Statsoft 1998). Confidence intervals on the parameters estimated from these values should be used with caution, especially with small sample sizes, because the standard statistical assumptions may not apply for some nonlinear models.

While there may be partially mixed estuaries where it is inappropriate to apply the method, and diel data are scarce for most estuaries, it is intriguing that we can frequently observe linear relationships between DO, salinity, and depth in the sample profiles from other estuaries. For example, performing linear regressions of DO vs. salinity, depth, and time for three other estuaries, San Francisco Bay (1997–1998 data for 29 cruises from the U.S.G.S. San Francisco Bay water-quality Web site, <http://sfbay.wr.usgs.gov/access/wqdata/>), Delaware Bay (1987–1988 data from five cruises over the saline portion of the bay taken from Lebo et al. 1990), and Chesapeake Bay (1997 data from 41 daily cruise segments taken from the Chesapeake Bay Program Web site, <http://www.chesapeakebay.net/bayprogram/>), we observed R^2 values of >0.90 for 29 times out of 75 data sets, and only four data sets showed R^2 values of <0.50 . These results suggest that at least for some portions of these spatially extensive estuaries, the method might be useful. While there are problems associated with applying this method from a relatively slow-moving ship taking a single sample at each station, as opposed to taking multiple samples over a diel period at fixed stations using a fast boat as we did in the

Hudson, we believe that the RSD method merits further study using cruise-based data.

Conclusion

The RSD technique shows promise for estimating ecosystem metabolism in estuaries. Given a set of oxygen profile measurements at multiple stations and times, the calculations involved in the metabolism estimates are methodologically simple: the data are pooled, regression coefficients are calculated, and diffusion corrections are made. In the Hudson River, an estuarine system that is relatively narrow over much of its length, we collected data along longitudinal transects and used the method to correct for longitudinal variation; the lateral variation of salinity was relatively small compared to the longitudinal variation. For systems of greater lateral extent, such as the Chesapeake Bay, the technique would require that data be collected to reflect lateral variations in estuarine metabolism as well as longitudinal variation. Regardless of geometry, the RSD technique should work to the extent that salinity serves as a “tag” for water that shares the same processes of community production and respiration.

The question of how many stations to sample and how to pool the stations depends in general upon the question being asked and the number of samples taken at each station. In the Hudson, we were interested in comparing the average metabolism of a relatively shallow, upriver reach to a deeper, downriver reach. We sampled four stations three or four times in each reach along longitudinal transects. This gave us a sufficient sample size to see differences in the two sets of stations and relatively strong regression parameter estimates. We could have pooled fewer stations in more groups to give more details of the longitudinal gradients of metabolism along the river, but only at the cost of reduced statistical significance of the estimates (in principle, even individual stations could have been analyzed independently if enough samples had been taken over a tidal cycle to see the full range of effect at each station). Ultimately, the method is limited by the number of stations that can be practically sampled during the day, either from a vessel or from fixed monitoring platforms.

Although, in our opinion, the RSD method eliminates many of the problems associated with estimating metabolism in partially-mixed estuaries, it does not remove the necessity of the atmospheric diffusion correction. In the lower Hudson, we found that the effect of this correction on the metabolism estimates was not strongly dependent upon wind. This is not the same as saying that the diffusion correction is insignificant: the degree of its importance depends directly upon the extent to which the biological processes producing and consuming oxygen are balanced by atmospheric exchange. At steady state, an exact balance is achieved, and the estuarine metabolism has the same magnitude as atmospheric exchange (Stigebrandt 1991; Quay et al. 1995); in the freshwater Hudson, as well as in many other systems, the effect of atmospheric exchange is a relatively minor component of estuarine oxygen dynamics (Howarth et al. 1992; Marino and Howarth 1993).

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