Limnol. Oceanogr., 37(8), 1992, 1608–1617

Can phytoplankton maintain a positive carbon balance in a turbid, freshwater, tidal estuary?

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Abstract

An analysis of phytoplankton primary production in the tidal freshwater portion of the Hudson River estuary suggests that net primary production is strongly limited by light and mixing regime. In this turbid, well-mixed system, cells spend from 18 to 22 h d^{-1} below the 1% light level. Autotrophic dark respiration, conservatively estimated at 5% of P^b_{max}, is of sufficient magnitude to make positive algal growth impossible over much of the river and much of the year. It is particularly difficult to explain the observed increase in algal biomass during blooms in spring and summer. We hypothesize that such blooms can occur only in a small fraction of the river where depth is $\lesssim 4$ m.

Phytoplankton living in a well-mixed water column experience a varying light regime. If the water column mixes to a depth deeper than the photic zone, light will vary from full sunlight to values too low to support photosynthesis. If the duration in darkness is long, respiration of the phytoplankton would begin to exceed photosynthesis and the cell would experience some loss of biomass. Although the first oceanographers to work on primary production were well aware of the effects this dark period could have on organisms (Sverdrup 1953) and calculation of primary production (Ryther 1954; Talling 1957), the problem of algal dark respiration has been generally ignored in studies of primary production (*but see* Cloern 1987; Lewis 1988). Although some models of primary production have included algal dark respiration (e.g. Sverdrup 1953; Wofsy 1983; Peterson and Festa 1984), it is usually aggregated into a combined loss term that includes respiration of the algae as well as that of their consumers and would be analogous to community respiration.

The importance to primary production studies of understanding algal dark respiration is greatest in turbid, well-mixed systems such as most large rivers and unstratified estuaries. We studied the tidal freshwater portion of the Hudson River estuary. This 163-km section of the river accounts for ~72% of the entire length of the river, is freshwater along its course from near Troy, New York, to Haverstraw Bay, and is influenced by tides of ~1 m. The area of this stretch is roughly 165 km^2 and the volume (~70% of the volume of the entire river) is 1,560 km^3. The average depth is 9.4 m (Gladden et al. 1988). The water is nutrient-rich with NO_3 concentrations usually >50 μM and PO_4 concentrations varying seasonally between 0.1 and 1 μM. The water is generally quite well mixed, moderately turbid, and contains a large amount of suspended solids (averaging ~20–50 mg $liter^{-1}$; Cole et al. 1991).

The turbid waters, in combination with the complete mixing, mean that phytoplankton are in dark or dimly lit waters much of the time. In the Hudson, for a daylight period of 12 h, the average phytoplankton would spend from 18 to 22 h below the 1% light level (Cole et al. 1991). Despite these apparently adverse light conditions, phytoplankton biomass in the river varies seasonally with low values near 1 μg Chl *a* $liter^{-1}$ in winter to values >50 μg $liter^{-1}$ in summer (Cole et al. 1991). In this paper, we investigate primary production in the Hudson River in an attempt to understand how phytoplankton maintain a positive carbon balance in this turbid, well-mixed system.

Methods

Field sampling—Two levels of sampling are represented: a seasonal cycle of biweekly measurements at two sites, a deep-water

Acknowledgments

Financial support was provided by the Hudson River Foundation (HRF 003/90A/007).

We thank S. Findlay, R. Howarth, R. Marino, and M. Pace for comments. This paper is a contribution to the Institute of Ecosystem Studies.

station (km 117) and a shallow-water station (km 146), which included 94 station-dates between August 1986 and November 1988; a series of 10 transects over the length of the river at monthly intervals during spring through autumn (e.g. excluding winter) between September 1987 and November 1988 covered six stations between km 220 and km 63 and included 60 station-dates. The "kilometers" are linear kilometers along the spine of the river with km 0 set at Battery Park where the Hudson meets the sea. Additional stations were sampled irregularly through 1992. The map shown as figure 1 of Findlay et al. (1991) presents the general features of the river and highlights our sampling stations.

Samples for chemical analysis and primary production were taken with a peristaltic pump (samples touch no metal) and tubing lowered to the appropriate depth by means of a heavily weighted calibrated line. For chemical analysis, samples were pumped directly into 1-liter polypropylene bottles. Samples for dissolved inorganic C (DIC) were pumped directly into 60-ml BOD bottles. Oxygen profiles were measured in situ with a YSI model 57 oxygen meter. Samples for primary production were pumped into 2-liter polypropylene bottles, which were kept in a dark cooler throughout the sampling procedure to avoid light shock.

Photosynthetically available radiation was measured with a LiCor model LI-193SB 4π sensor with a model LI-1000 data logger at depth intervals of 0.5–1 m, starting 0.05 m below the surface. These data were used to calculate light extinction coefficients for the river.

Primary production measurements—Immediately upon return to the laboratory, 30-ml subsamples were decanted into sixteen 30-ml clear polycarbonate centrifuge tubes. Each tube was spiked with 2 μCi of Na $H^{14}CO_3$ (New England Nuclear; 50–60 mCi $mmol^{-1}$). Two tubes were fixed with 2% Formalin (v/v final concn) to serve as abiotic controls; the remaining 14 tubes were incubated in pairs for 2–3 h under constant illumination at 7–10 different light levels ranging from 0 to 2,000 μEinst $m^{-2}\ s^{-1}$. The light source was twin 500-W quartz floodlamps.

We compared, on several occasions, results from the artificial illumination incubations to samples incubated in sunlight, attenuated with layers of neutral density screening. For both artificial and natural illumination, temperature was held constant and was within 2°C of ambient in the river.

Upon termination of the incubations, samples were filtered through 25-mm, 0.45-μm Gelman GN-6 filters, and both particulate and dissolved material was examined for radioactivity by liquid scintillation counting. For particles, filters were fumed for 12 h in HCl, dissolved in 1 ml of ethylene glycol monomethyl ether, and then counted in Scintiverse II with a Beckman LSC-1801. Quenching was determined by H number against NBS certified [^{14}C]toluene (New England Nuclear). [^{14}C]DOC was measured by acidifying 10-ml subsamples of the filtrate to pH < 2 and bubbling vigorously with air (30 ml min^{-1}) for 20 min to remove inorganic ^{14}C (Cole et al. 1982). Samples (1–5 ml) were counted as above.

Chemical analyses—DIC was measured for every station and date for which primary production was measured by the method of Stainton (1973) with a Shimadzu gas chromatograph (GC-AIT) and a thermal conductivity detector. Algal pigments (Chl *a* and pheopigments) were determined by fluorescence in methanol extracts by the method of Holm-Hansen and Riemann (1978) and checked against Chl *a* measurements made with high-performance liquid chromatography on a series of subsamples from a range of stations and dates. Total suspended solids were measured gravimetrically with dried (40°C) 0.4-μm, pretared Nuclepore filters.

Net primary production—The equation for primary production is

$$P_g = P_n + R_a$$

where P_g is gross photosynthesis, which is the sum of net photosynthesis (P_n) and autotrophic respiration (R_a). The ^{14}C uptake measurements provide a value intermediate between P_g and P_n for the time period during which the lights are on (Peterson 1980). To provide a maximum estimate of P_n, we assume that the uptake of $H^{14}CO_3$ is a measure of net rather than gross primary pro-

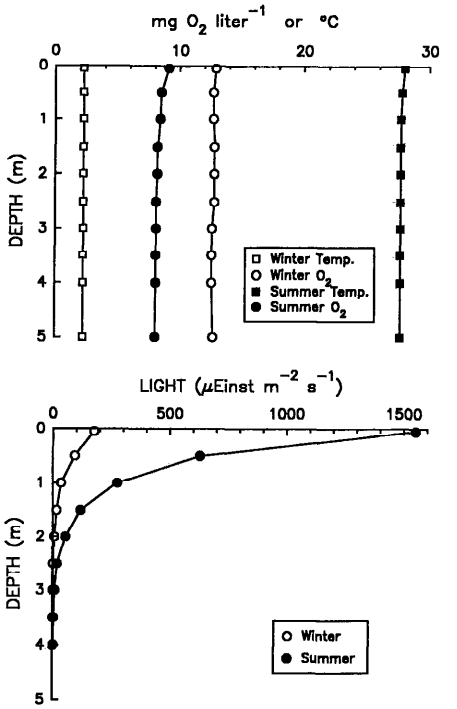

Fig. 1. Representative profiles of temperature, dissolved oxygen, and light (at midday) for winter and summer conditions in the Hudson River.

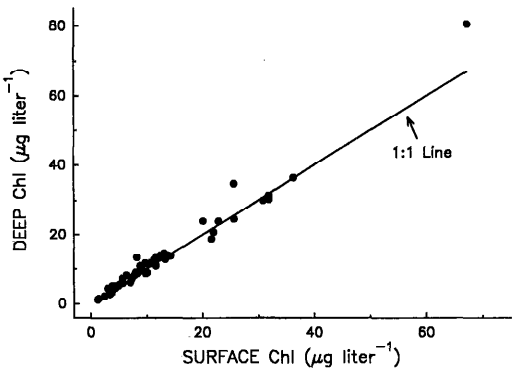

Fig. 2. Concentration of Chl *a* in samples of surface water plotted against samples from deep water. Surface samples were always collected at 0.5 m below the surface; deep samples were collected at least 1 m above the sediments. Depth of the deep samples varied from 5 m to >10 m depending on station depth (*see Fig. 10*). The 1 : 1 line (surface Chl = deep Chl) is shown for comparison.

duction, even though our incubations were relatively brief. Thus, as long as ^{14}C uptake is positive, we assume that it measures $P_g - R_a$. Using the parameters of the production vs. irradiance curves, the chlorophyll content of the water, an estimate of potential sunlight at the surface (I_0), and the extinction coefficient for each station and date, we computed P_n in time steps of 15 min and depth steps of 0.1 m for each station-date in the river.

Potential sunlight was calculated from sun angle and insolation times for the latitude of the river at 15-min time steps for each date. We did not include the effect of cloud cover in this calculation and assumed that albedo was constant at 0.10. This computation provides us with a value of net production, integrated to the base of the photic zone, during the daylight hours or NDPZP (net daytime photic zone production: Cole et al. 1991). We make this calculation because it is generally reported in the literature on primary production in estuaries, including the Hudson (Sirois and Fredrick 1978). Although the use of NDPZP may be appropriate in stratified environments such as the lower Hudson harbor (e.g. Malone 1977, 1982), it is very clearly an overestimate of primary production in well-mixed environments.

In the dark (either at night or when cells are deep in the water) P_g becomes zero, and P_n would be negative. Negative values of P_n obviously cannot be measured with the ^{14}C technique. To compute P_n in the dark, we assumed that R_a was a constant fraction of P^b_{max} and, in different simulations, varied it from 1 to 50% of P^b_{max}. Using this approach, we could calculate P_n integrated for a full 24-h day and for the full depth of the water.

Results

Physical and chemical environment—At all times, the depth profiles of temperature and oxygen were essentially constant from top to bottom, indicating relatively complete mixing (Fig. 1). Similarly, chlorophyll concentrations were usually identical in surface and bottom water (Fig. 2). Some samples showed a slight increase of chlorophyll near the bottom which we interpret as resuspension (Fig. 2). Light was always extinguished rapidly with depth, and light extinction coefficients varied seasonally with

highest values (typically near 4 m^{-1}) in winter and lowest values (~1–2 m^{-1}) in summer. Light extinction was highly correlated with the total suspended load but not with Chl *a*, suggesting that much of the turbidity was due to suspended particles other than algal cells (Cole et al. 1991; Stross and Sokol 1989). Light extinction was greatest (10 m^{-1}) during spring runoff.

Photosynthetic parameters—The photosynthesis vs. irradiance (*P* vs. *I*) curves that we obtained fit the hyperbolic tangent model of Jassby and Platt (1976) with high fidelity. Light inhibition was observed only on a few dates and only at irradiances >1,500 μEinst m^{-2} s^{-1}. Due to turbidity, such high light levels occur only in the uppermost few centimeters of the water (Fig. 1). Thus, we did not consider light inhibition in our model.

For our data set of 129 station-dates sampled, P^b_{max} (the light-saturated rate of primary production per unit of algal biomass) averaged 0.32±0.015 μmol C (μg Chl *a*)$^{-1}$ h^{-1} (± SE) and varied seasonally with lowest values in winter [0.025 μmol C (μg Chl *a*)$^{-1}$ h^{-1}] and maximal values in summer [0.3–0.5 μmol C (μg Chl *a*)$^{-1}$ h^{-1}]. P^b_{max} was significantly correlated to Chl *a* and water temperature ($P < 0.00001$), but these relationships explained little of the combined annual and spatial variation in P^b_{max} ($r^2 = 0.33$). α [the slope of the *P* vs. *I* curve in the initial (nonlight-saturated) region] showed a seasonality similar to that of P^b_{max}, varying about an order of magnitude between winter and summer and highly correlated to P^b_{max} ($P < 0.00001$; $r^2 = 0.64$). α averaged (± SE) $9.7 \times 10^{-4} \pm (0.4 \times 10^{-4})$ μmol C (μg Chl *a*)$^{-1}$ h^{-1} (μEinst m^{-2} s^{-1})$^{-1}$. For any given season, neither α, nor P^b_{max} showed significant spatial variation along the length of the river, although the variance over time was substantial (Fig. 3).

Natural vs. artificial light—On several occasions, we compared *P* vs. *I* curves measured under artificial light to curves measured in natural sunlight. Estimates of P^b_{max} were identical under both types of illumination (Fig. 4). Estimates of α tended to be slightly lower (by 10–20%) under natural light than under artificial light. Thus, our estimates of primary production, especially at low light, would be lower than we report had we used natural light.

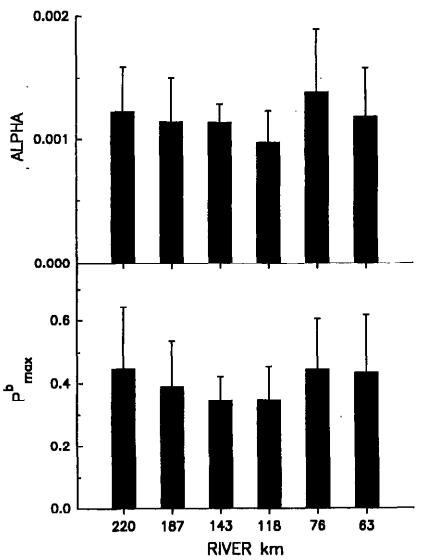

Fig. 3. Longitudinal variation in α and P^b_{max}. Samples for each station are means of seven dates during the growing season (May–October); error bars represent 95% C.L. Units for α are μmol C (μg Chl *a*)$^{-1}$ h^{-1} (μEinst m^{-2} s^{-1})$^{-1}$; units for P^b_{max} are μmol C (μg Chl *a*)$^{-1}$ h^{-1}. River km are kilometers upstream from Battery Park (0).

Variable light—The phytoplankton in a well-mixed, turbid river experience varying amounts of light and dark over time. We compared, on several occasions, the effect of varying, short-term, light and dark periods on *P* vs. *I* curves. In all cases, production per unit time was decreased by any period of darkness. However, production per photon was nearly constant, even in cases where the dark period lasted up to 25 min (Fig. 5).

Algal biomass—Like the photosynthetic parameters, Chl *a* showed strong seasonal variation with highest values (20–40 μg liter^{-1}) in summer (Cole et al. 1991). Winter values were generally 1–2 μg liter^{-1}. Chl *a* increased dramatically over the course of early spring, achieving actual rates of increase of 0.2–2.0 μg Chl *a* liter^{-1} d^{-1}, depending on station (Fig. 6). Some stations showed a decrease in early summer, followed by a second bloom in late July or August. These midsummer realized rates of increase were on the order of 0.5–1.7 μg Chl

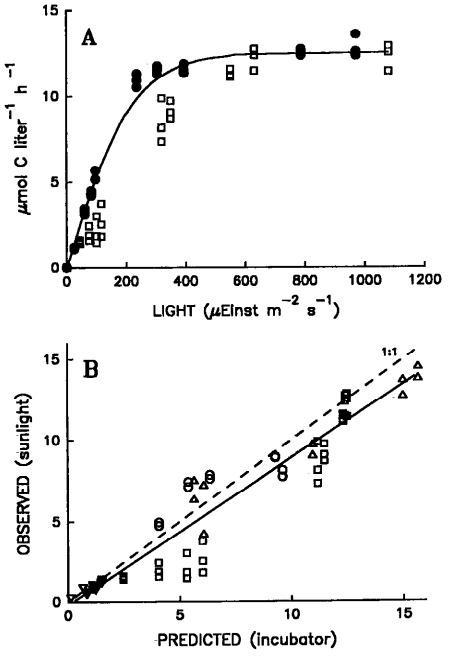

Fig. 4. Comparison of photosynthesis under natural sunlight and artificial light. A. The result of a single comparison from artificial light (●) and natural sunlight (□). The fitted curve is the hyperbolic tangent function for the parameters calculated from the artificial light experiment. Note that the natural light experiment falls slightly under the curve. B. Combined results of several experiments (represented by different symbols) of the type shown in panel A. The *Y*-axis shows the measured amount of photosynthesis in natural sunlight; the *X*-axis shows the predicted amount of photosynthesis based on the parameters calculated from the artificial light incubations. The regression equation is $Y = 0.91X - 0.19$.

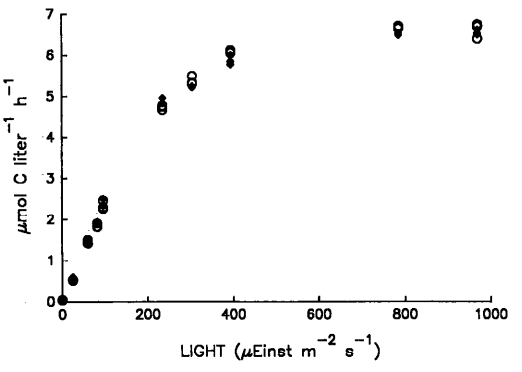

Fig. 5. Photosynthesis of raw river water under constant and variable light regimes. One set of measurements was made under constant illumination (○); the other set, using water from the same sample collection, had the lights on and off as indicated (◆). In all cases, the total amount of irradiance was the same and equivalent to a 1-h exposure under constant light.

a liter^{-1} d^{-1} at different stations. Unlike the photosynthetic parameters, the spatial pattern of chlorophyll over the length of the river varied tremendously (Fig. 7).

Net daytime photic zone primary production—Net primary production during daylight and integrated only to the base of the photic zone averaged ~20 mmol m^{-2} d^{-1} for the year and ~37 mmol m^{-2} d^{-1} for seven dates we sampled in the May–October period and varied seasonally (Fig. 8). Expressed annually, this quantity (NDPZP) varied from ~70 to 220 g C m^{-2} yr^{-1} at the various stations.

24-h water-column production—Primary production, integrated for 24 h over the entire depth of the water column and with an assumed autotrophic respiration equal to 5% of P^b_{max}, was far lower than NDPZP and was actually negative for the deeper stations. For example, at Poughkeepsie, NDPZP averaged ~30 mmol m^{-2} d^{-1}, but 24-h integrated water-column production (WCP) averaged near 0 mmol m^{-2} d^{-1} and was frequently negative (Fig. 8, insert). At Fort Montgomery (km 76), a deeper area in the river, NDPZP was upward of 20 mmol C m^{-2} d^{-1}, and WCP was less than −60 mmol C m^{-2} d^{-1}. These negative values for autotrophic primary production mean that the phytoplankton are respiring more organic C than they produce (Fig. 8, insert).

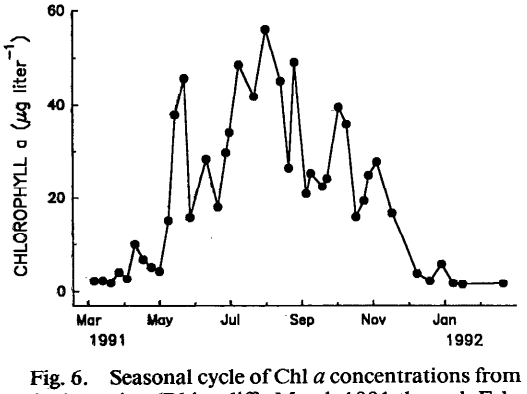

Fig. 6. Seasonal cycle of Chl *a* concentrations from a single station (Rhinecliff), March 1991 through February 1992.

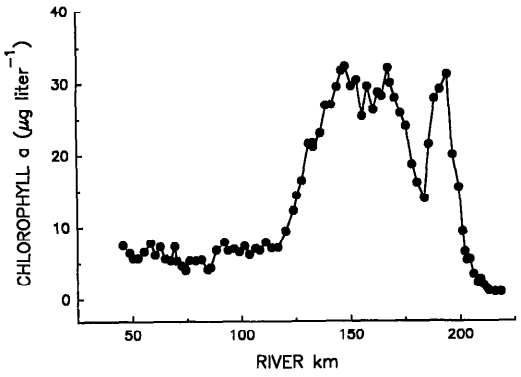

Fig. 7. Spatial variation in Chl *a* concentration along the length of the tidal freshwater river in August 1991. Samples were taken over the course of 2 d. River km are kilometers upstream from Battery Park (0).

Discussion

Sensitivity of calculation of 24-h production—Our study shows that including a term for algal dark respiration in primary production estimates in a turbid, well-mixed environment will result in considerable divergence from a traditional calculation of primary production. Our calculations of 24-h primary production are sensitive to the assumed value of algal respiration and to our measurements of the photosynthetic parameters, P^b_{max} and α. Although our values for P^b_{max} [4–6 mg C (mg Chl *a*)$^{-1}$ h^{-1} during the growing season] are quite typical for reported measurements in the literature, our values of α are near the low end. Keller (1988), reviewing α values, reported that system mean α ranged from ~8.5 to 16.7 mg C (mg Chl *a*)$^{-1}$ Einst^{-1} m^2 and averaged 12 for five coastal and estuarine systems. Converting to the units used by Keller (1988), our values of 9–12 μmol C (μg Chl *a*)$^{-1}$ h^{-1} (μEinst m^{-2} s^{-1})$^{-1}$ are equivalent to 3–4 mg C (mg Chl *a*)$^{-1}$ Einst^{-1} m^2.

α varies quite widely in the literature with some values well below the ones we reported (*see* Gallegos et al. 1983; Cote and Platt 1983). This variation is in part methodological (e.g. 2π vs. 4π light sensors; range

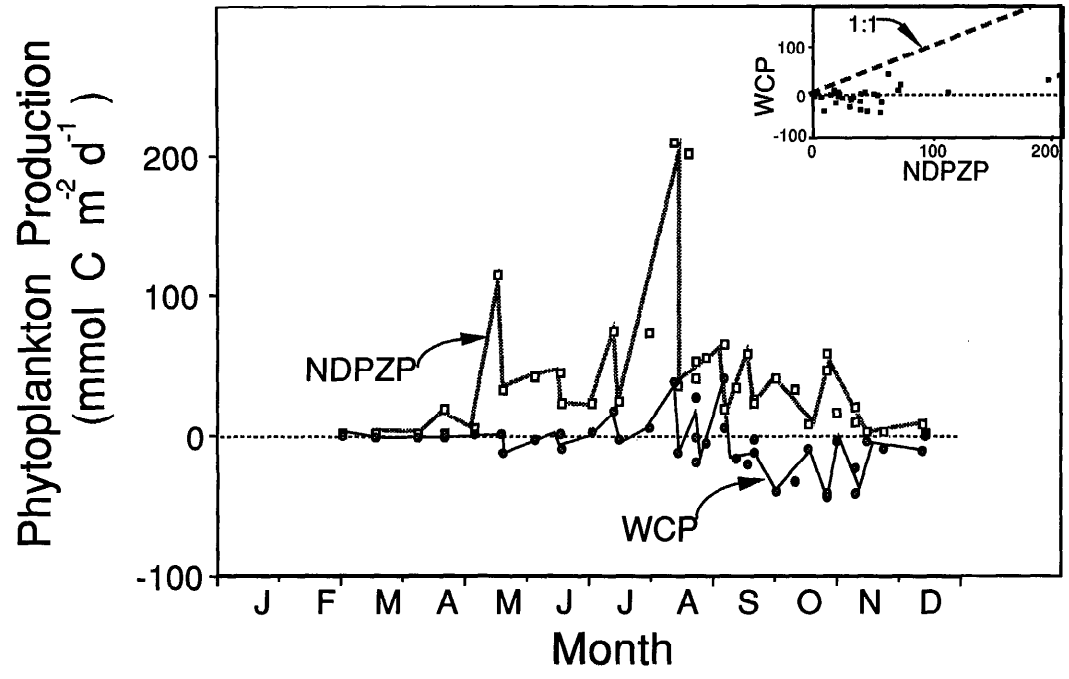

Fig. 8. Annual cycle of primary production (NDPZP) for a single station (Poughkeepsie, km 117). NDPZP is net algal photosynthesis for the daylight period, integrated to the base of the photic zone. WCP is phytoplankton primary production integrated over 24 h for the entire depth of the water column and includes an estimate of algal dark respiration (*see text*). Insert: The same data plotted against each other; both in units of mmol C m^{-2} d^{-1}. The 1 : 1 (WCP = NDPZP) line is shown for comparison.

of light gradient used) and partly due to variable physiology. If the true value of α were lower than our estimate, we would overestimate primary production, a problem that does not affect our argument. If, on the other hand, we underestimated the true value of α, we could underestimate primary production and possibly affect our conclusions.

Although we have no reason to suspect our α values of being too low for methodological reasons, we, nevertheless, tested the effect that higher values would have on estimated 24-h production at a range of assumed values of R_a and depths. First, if the assumed value of R_a is $\geq$20% of P^b_{max} (a common assumption; Coveney et al. 1977; Cloern 1987), 24-h production will be negative at any reasonable value for α at essentially any depth in the river. If the water depth is $\gtrsim$10 m, increasing α by as much as threefold has a negligible effect on 24-h production for any reasonable value of R_a. In shallow water (e.g. our Kingston station), increasing α by threefold increases the calculated 24-h integrated production by ~5–10 mmol C m^{-2} d^{-1}. Thus, if α were substantially higher than we estimate it to be, estimated primary production would be higher in shallow water, but remain low or negative in deep water.

Although the ^{14}C method is not without problems, our tests here indicate that we have not used the method in a way that would necessarily produce low values. First, we used artificial light. We demonstrated however, that, probably due to decreased UV in artificial light, natural light yielded slightly lower estimates of production. Second, we used static light-level incubations. We demonstrated that varying periods of light and dark had very little effect on short-term photosynthesis.

Most of our assumptions err on the side of overestimation rather than underestimation of primary production. We assumed the ^{14}C uptake in the light represents net uptake even though our incubations were only 2 h. Weger et al. (1989) has suggested that light respiration can be a significant sink for C. By ignoring light respiration, we overestimated net production by an unknown amount. We also ignored light inhibition and cloud cover (e.g. our calculation assumes a cloudless sky at all times). Including either of these parameters would clearly lower our estimate of both NDPZP and 24-h integrated production (WCP). Further, our calculation assumes that algal dark respiration is only 5% of P^b_{max}, a value at the low end of the reported values (5–50% of P^b_{max}; Raven and Beardall 1981). Finally, we have ignored all losses to algal biomass other than respiration, a clear underestimate of losses.

Maintenance of algal biomass—Light is a critical variable controlling phytoplankton production and distribution, especially in nutrient-rich waters. The phytoplankton in turbid, high-nutrient systems, such as many rivers, may be particularly light limited (e.g. Cloern and Cheng 1981; Wofsy 1983). Wofsy (1983) noted that in these riverine systems, the ratio of mixing depth to depth of light penetration was especially high (nearly twice the values found in other eutrophic systems). How, then, are populations of phytoplankton maintained in well-mixed, turbid rivers? Wofsy suggested three possibilities: dark respiration by phytoplankton could be especially low in these systems; removal of phytoplankton by zooplankton grazing might be especially low as the high suspended load could interfere with feeding; and the phytoplankton may, in fact, not be self-sustaining in some very turbid systems and phytoplankton biomass would be maintained by exogenous inputs.

In the case of the Hudson we can clearly eliminate low zooplankton grazing as an important mechanism. It is true that zooplankton grazing in the river is low (Pace et al. 1991), but even if we assume it were zero as we did in our calculations, calculated phytoplankton growth, corrected for algal dark respiration is much too low to account for the observed increases in algal biomass. Our analysis of primary production in the Hudson differs from analyses in which algal respiration and the respiration of heterotrophs were not separately analyzed (e.g. Sverdrup 1953; Wofsy 1983). Our results are in agreement with work in San Francisco Bay and in the Orinoco River, which indicate that algal respiration alone can exceed photosynthesis in well-mixed turbid

environments (Alpine and Cloern 1988; Lewis 1988).

The validity of algal dark respiration as a mechanism is less clear due to our lack of knowledge about its absolute rate and to what it is actually related. Perhaps R_a is far less than 5% of P^b_{max} or is unrelated altogether to maximum photosynthetic capacity (e.g. P^b_{max}). Instead R_a may covary with growth rate (Peterson and Festa 1984). When we computed R_a based on allometric relationships between size and metabolic rate (Robinson et al. 1983), the values were up to 10-fold higher than the equivalent of 5% of P^b_{max}. Further, although there is uncertainty in R_a, we used the lowest values reported in the literature range of 5–50% of P^b_{max} (Raven and Beardall 1981). Finally, our own preliminary measurements of R_a for the phytoplankton community of the Hudson suggest values between 5 and 10% of P^b_{max} (Peierls et al. unpubl.).

It is possible that algal biomass is maintained in the Hudson by a special case of the exogenous input mechanism; that is, net positive growth occurs in shallow areas and this biomass is imported into deeper areas where net positive growth is not possible. Just how shallow the depth must be to support net positive growth depends on the assumptions made for algal dark respiration (Fig. 9). For example, for a reach in which the mixed depth is <4 m deep in summer, when the photic zone is ~2 m deep, a positive carbon balance would be possible at respiration values up to 25% of P^b_{max}. On the other hand, at 20-m depth, a positive carbon balance is possible only if algal dark respiration is <2% of P^b_{max}. In winter, turbidity is greater and light penetration lower. In this case, a positive carbon balance is essentially impossible at 20-m depth and only possible at 5- or 10-m depth if we assume that dark respiration is <5% of P^b_{max}. If we take the tidal freshwater river as a whole, the average depth is ~9.4 m. In winter, then, a positive C balance would be possible only if autotrophic dark respiration were <1 or 2% of P^b_{max}. In summer, a positive C balance is possible, even if R_a is as large as 10% of P^b_{max}.

There are two periods of rapid increase in algal biomass, one in late spring and another in early summer (Fig. 6). The actual rate of increase of algal biomass can be as great as 0.5–2 μg Chl *a* liter^{-1} d^{-1} (Fig. 6), which would translate to an aerial net production rate of ~20–80 mmol C m^{-2} d^{-1} for the average 9.4-m depth of the stretch. At an assumed respiration of 5% of P^b_{max}, calculated water-column production would be only 1 or 2 mmol C m^{-2} d^{-1} at best; even at a respiration rate of 1% of P^b_{max} production would not be sufficient to account for the increase we observed either in spring or during much of summer (Fig. 9). Under spring conditions of temperature and turbidity, the average depth would have to be 3.3 m for growth to reach 20 mmol m^{-2} d^{-1}; a very small fraction of the river has average depths this shallow (Fig. 10).

An additional possible explanation for the algal growth we observed could be algal heterotrophy. The Hudson as an ecosystem is heterotrophic in that total system respiration exceeds primary production (Howarth et al. 1992) and bacterial production exceeds primary production (Findlay et al. 1991). Some phytoplankton may be subsidized by heterotrophic activities, either by

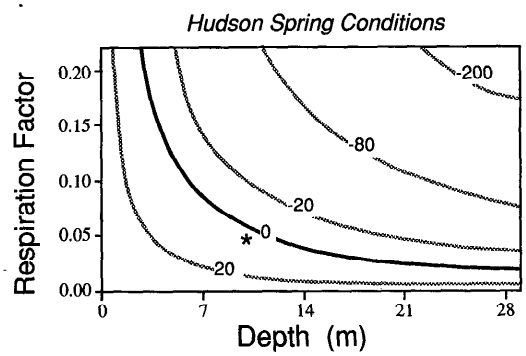

Fig. 9. The relationship between depth, autotrophic respiration, and 24-h integrated primary production for conditions representative of the April–May spring bloom for the tidal freshwater portion of the river. The isolines are values of 24-h integrated primary production (mmol C m^{-2} d^{-1}) and respiration is normalized to P^b_{max} (*see text*). Calculations explained in the text. For these conditions P^b_{max} was set at the average value for spring, 0.24 μmol C (μg Chl *a*) h^{-1}, and Chl *a* = 8 μg liter^{-1}. The isoline of autotrophic C balance (photosynthesis = autotrophic respiration; 0 net production) is solid. Asterisk marks the intersection of the average depth of the tidal freshwater river (9.4 m) and our assumed value of respiration at 5% of P^b_{max}.

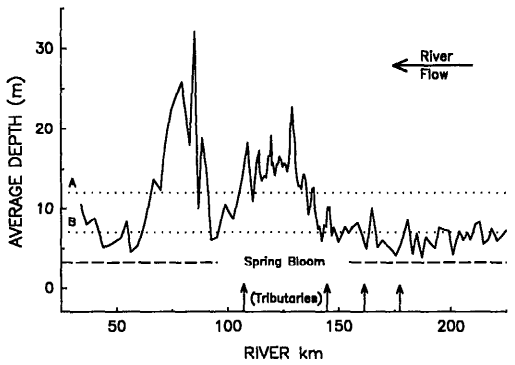

Fig. 10. Variation in average depth along the length of the tidal freshwater portion of the river. River km measured from Battery Park (0) to Troy (250). Average depth is the mean depth, bank to bank, for each stretch of the river indicated. Dotted lines represent depths, under spring conditions, at which algal respiration and photosynthesis would be in balance (zero growth) for assumed dark respiration of 5% (line A) and 10% (line B) of P^b_{max}. Spring bloom line represents the maximum depth at which growth could achieve the measured increases in algal biomass observed during the spring bloom under our conservative assumption that R_a is only 5% of P^b_{max} (*see text*). Locations of tributaries indicated by arrows.

consuming dissolved organic materials (e.g. Bennett and Hobbie 1972) or by direct phagotrophy of bacteria (e.g. Bird and Kalff 1986). Although we cannot rule out the uptake of DOC, phagotrophy would not explain the spring bloom which consists mostly of diatoms.

The ratio of the photic zone to the mixed zone ($Z_p : Z_m$) is probably a major determinant of planktonic primary production in the Hudson, as it is in other nutrient-sufficient systems (Peterson and Festa 1984). If we take the average for the entire tidal freshwater portion in total, $Z_p : Z_m$ would be ~0.05 in winter and ~0.2 in summer. In an analysis of phytoplankton growth in another turbid, well-mixed environment—San Francisco Bay—Alpine and Cloern (1988) suggested that growth would be negative if the ratio $Z_p : Z_m$ were <0.16, close to our maximum seasonal value.

Unlike the case in stratified systems where $Z_p : Z_m$ is controlled largely by changes in light extinction (Wofsy 1983), the variation in $Z_p : Z_m$ in the Hudson is controlled largely by depth. Turbidity varies seasonally and spatially, but the tidal freshwater portion of the river is always turbid. Light extinctions are never <1 m^{-1} and, within a given season, tend to vary slightly along the freshwater portion, with light penetration increasing rapidly in the saline portion (Stross and Sokol 1989). The depth of the river, on the other hand, varies greatly along its course and would be the major determinant of the $Z_p : Z_m$ ratio (Fig. 10). If we accept 5% of P^b_{max} as a reasonable or conservative estimate of algal respiration, then autotrophic net production would vary greatly along these fluctuating depths, from positive values >25 mmol m^{-2} d^{-1} at the shallow stations to values below −100 mmol C m^{-2} d^{-1} at the deepest sites.

Lewis (1988) argued that a positive C balance could not be achieved by the phytoplankton in the main stem of the Orinoco River because R_a exceeded photosynthesis. Increases in biomass in the river were maintained by occasional influxes of phytoplankton from shallow floodplain lakes. The Hudson does not have floodplain lakes, but an analogous situation may be occurring. Although the average depth of the tidal freshwater portion may be too great for the positive C balance we observe, there is a great deal of variation in depth both longitudinally and bank-to-bank (Fig. 10). We hypothesize that it is in these shallow areas that algal growth occurs; through downstream flow and tidal movement, this growth is distributed to the deeper areas where growth otherwise would be negative.

References

ALPINE, A. E., AND J. E. CLOERN. 1988. Phytoplankton growth rates in a light-limited environment, San Francisco Bay. Mar. Ecol. Prog. Ser. **44:** 167–173.

BENNETT, M. E., AND J. E. HOBBIE. 1972. The uptake of glucose by *Chlamydomonas* sp. J. Phycol. **8:** 392–398.

BIRD, D., AND J. KALFF. 1986. Bacterial grazing by planktonic algae. Science **231:** 493–495.

CLOERN, J. E. 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. Cont. Shelf Res. **7:** 1367–1381.

———, AND R. T. CHENG. 1981. Simulation model of *Skeletonema costatum* population dynamics in northern San Francisco Bay, California. Estuarine Coastal Shelf Sci. **12:** 83–100.

COLE, J. J., N. F. CARACO, AND B. PEIERLS. 1991. Phytoplankton primary production in the tidal,

freshwater Hudson River, New York (USA). Int. Ver. Theor. Angew. Limnol. Verh. **24:** 1715–1719.

———, G. E. LIKENS, AND D. L. STRAYER. 1982. Photosynthetically produced dissolved organic carbon: An important carbon source for planktonic bacteria. Limnol. Oceanogr. **27:** 1080–1090.

COTE, B., AND T. PLATT. 1983. Day-to-day variations in the spring–summer photosynthetic parameters of coastal marine phytoplankton. Limnol. Oceanogr. **28:** 320–344.

COVENEY, M. F., G. CRONBERG, M. ENELL, K. LARSSON, AND L. OLOFSON. 1977. Phytoplankton, zooplankton and bacteria-standing crop production relationships in a eutrophic lake. Oikos **29:** 5–21.

FINDLAY, S., AND OTHERS. 1991. Weak coupling of bacterial and algal production in a heterotrophic ecosystem: The Hudson River estuary. Limnol. Oceanogr. **36:** 268–278.

GALLEGOS, C. L., T. PLATT, W. G. HARRISON, AND B. IRWIN. 1983. Photosynthetic parameters of arctic marine phytoplankton: Vertical variations and time scales of adaptation. Limnol. Oceanogr. **28:** 698–708.

GLADDEN, J. B., F. R. CANTELMO, J. M. CROOM, AND R. SHAPOT. 1988. Evaluation of the Hudson River ecosystem in relation to the dynamics of fish populations. Am. Fish. Soc. Monogr. **4:** 37–52.

HOLM-HANSEN, O., AND B. RIEMANN. 1978. Chlorophyll *a* determination: Improvements in methodology. Oikos **30:** 438–447.

HOWARTH, R. W., R. MARINO, R. GARRITT, AND D. SHERMAN. 1992. Ecosystem respiration and organic carbon processing in a large tidally-influenced river: The Hudson River. Biogeochemistry. In press.

JASSBY, A. D., AND T. PLATT. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnol. Oceanogr. **21:** 540–547.

KELLER, A. A. 1988. An empirical model of primary production (^{14}C) using mesocosm data along a nutrient gradient. J. Plankton Res. **10:** 813–834.

LEWIS, W. M., JR. 1988. Primary production in the Orinoco River. Ecology **69:** 679–692.

MALONE, T. C. 1977. Environmental regulation of phytoplankton productivity in the lower Hudson estuary. Estuarine Coastal Mar. Sci. **5:** 157–171.

———. 1982. Phytoplankton photosynthesis and carbon-specific growth: Light-saturated rates in a nutrient-rich environment. Limnol. Oceanogr. **27:** 226–235.

PACE, M. L., S. E. G. FINDLAY, AND D. LINTS. 1991. Variance in zooplankton samples: Evaluation of a predictive model. Can. J. Fish. Aquat. Sci. **48:** 146–151.

PETERSON, B. J. 1980. Aquatic primary production and the ^{14}C-CO_2 method: A history of the productivity problem. Annu. Rev. Ecol. Syst. **11:** 359–385.

PETERSON, D. H., AND J. F. FESTA. 1984. Numerical simulation of phytoplankton productivity in partially mixed estuaries. Estuarine Coastal Shelf Sci. **19:** 563–589.

RAVEN, J. A., AND J. BEARDALL. 1981. Respiration and photorespiration, p. 58–82. *In* Physiological bases of phytoplankton ecology. Can. Bull. Fish. Aquat. Sci. 210.

ROBINSON, W. R., R. H. PETERS, AND J. ZIMMERMANN. 1983. The effects of body size and temperature on metabolic rate of organisms. Can. J. Zool. **61:** 281–288.

RYTHER, J. H. 1954. The ratio of photosynthesis to respiration in marine planktonic algae and its effect upon measurement of productivity. Deep-Sea Res. **2:** 134–139.

SIROIS, D. L., AND S. W. FREDRICK. 1978. Phytoplankton and primary production in the lower Hudson River estuary. Estuarine Coastal Mar. Sci. **7:** 413–423.

STAINTON, M. P. 1973. A syringe gas-stripping procedure for gas-chromatographic determination of dissolved inorganic and organic carbon in freshwater and carbonates in sediments. J. Fish. Res. Bd. Can. **30:** 1441–1445.

STROSS, R. G., AND R. C. SOKOL. 1989. Runoff and flocculation modify underwater light environment of the Hudson River estuary. Estuarine Coastal Shelf Sci. **29:** 305–316.

SVERDRUP, H. V. 1953. On conditions for vernal blooming of phytoplankton. J. Cons. Cons. Int. Explor. Mer **16:** 287–295.

TALLING, J. F. 1957. Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation. New Phytol. **56:** 29–48.

WEGER, H. G., R. HERZIG, P. G. FALKOWSKI, AND D. H. TURPIN. 1989. Respiratory losses in the light in a marine diatom: Measurements by short-term mass spectrometry. Limnol. Oceanogr. **34:** 1153–1161.

WOFSY, S. C. 1983. A simple model to predict extinction coefficients and phytoplankton biomass in eutrophic waters. Limnol. Oceanogr. **28:** 1144–1155.

Submitted: 3 October 1991
Accepted: 15 June 1992
Revised: 29 June 1992