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Primary production

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Primary production and its regulation in the tidal-freshwater Hudson River

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Abstract

Photosynthesis is the main process by which new organic matter is synthesized. In many aquatic ecosystems, phytoplankton are the major photosynthetic organisms and are responsible for most of the organic C input. In the tidal-freshwater Hudson, primary production by phytoplankton is maintained at relatively low values by a combination of high turbidity and deep mixing (which lowers light availability), advective losses downstream and consumption by grazers. Limitation by nitrogen or phosphorus, the most common plant limiting nutrients, is not an important regulatory factor in the tidal-freshwater Hudson. Respiration by the phytoplankton themselves is the major fate of phytoplankton-derived organic matter (gross primary production), leaving relatively small amounts available to higher trophic levels. Thus, small increases in grazing pressure could have large impacts on phytoplankton. Phytoplankton biomass and gross primary production were dramatically reduced by the 1992 invasion of the zebra mussel, and phytoplankton have not yet recovered to pre-invasion levels. We estimate that phytoplankton gross primary production was  $331 \text{ g C m}^{-2} \text{ y}^{-1}$  in the years prior to the zebra mussel invasion and  $82 \text{ g C m}^{-2} \text{ y}^{-1}$  in the years following. This is from about one-half to one-eighth as large as the input of terrestrial organic C from the watershed.

## Introduction

Primary production is the formation of organic compounds from inorganic building blocks. The energy required to synthesize these organic products may come from sunlight, as is the case in photosynthesis; from chemical reactions, as in the case of chemosynthesis (e.g., ammonia or sulfide oxidation); or a mixture of the two as in some types of anoxygenic bacterial photosynthesis (Brock 1979).

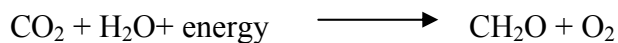
In the Hudson River, as in most aerobic aquatic environments, oxygenic photosynthesis is the by far the major pathway of primary production (but see Kolber et al. 2001). In the tidal-freshwater portion of the Hudson River this photosynthesis is carried out by several functionally different groups of organisms: phytoplankton, (small, often single celled, eukaryotic algae and cyanobacteria suspended in the water column); periphyton (algae attached to various surfaces), submergent macrophytes (higher plants such as Valisneria [water celery] that grow attached to the bottom with leaves that remain within the water column), and floating or emergent macrophytes (higher plants such as Trapa [water chestnut] whose leaves are partially or completely exposed to the air). These differing groups of plants have different consumer organisms, different sets of regulation and constraints and different effects on dissolved gas dynamics in the river.

This chapter focuses on primary production by phytoplankton and its regulation, in the tidal, freshwater portion of the Hudson from Albany south to Newburgh, New York. Further, we compare phytoplankton production in this section of the river into the context of the entire river and other groups of primary producers and compare phytoplankton production in the Hudson to other rivers and estuaries of the world.

Why consider primary production in part of a large riverine estuary? First, the conditions in the tidal, freshwater river are substantially different from those in the saline part of the lower estuary. Thus, phytoplankton experience different regulatory factors in these two sections. Second, the invasion of the zebra mussel in the tidal-freshwater section had dramatic effects on the phytoplankton and provided a great deal of insight into how phytoplankton were regulated. Third, the investigative approaches have differed between the lower estuary and tidal-freshwater river. The lower estuary is covered in the chapter by Howarth et al. (this volume).

### Photosynthesis and respiration

Photosynthesis and respiration can be looked at as the same chemical reaction occurring in opposite directions.



While photosynthesis uses light energy to force the chemical reduction of  $\text{CO}_2$  to the level of a carbohydrate, respiration captures some of the energy released from the oxidation of organic matter back into  $\text{CO}_2$ . Both consumer organisms (secondary producers or heterotrophs) and primary producers (autotrophs) respire.

### Measurement and terminology

To discuss primary production and its measurement, we need to introduce a few terms.

- Gross Primary Production (GPP) is total photosynthesis, including the portion respired by the autotrophs themselves.
- Respiration (R) is the respiration by all organisms. R is the sum of respiration by autotrophs ( $R_a$ ) and heterotrophs ( $R_h$ ).
- Net Primary Production (NPP) is  $\text{GPP} - R_a$ . NPP is the amount of organic matter available to consumer organisms. That is, NPP is the primary production left after plant

respiration has removed that needed to sustain the plants themselves. While NPP is usually  $\geq 0$  it need not be. When NPP is  $< 0$  the biomass of autotrophs must actually be declining over time. That is, phytoplankton are respiring their stored biomass, in excess of new photosynthesis. This condition sometimes occurs for phytoplankton in Hudson River (below).

GPP, or R, or NPP can be studied for a group of organisms (e.g., phytoplankton, macrophytes, etc.) or for an entire community of ecosystem. This chapter focuses on these quantities for phytoplankton.

In terrestrial ecosystems primary production is often assessed by measuring the change in the standing biomass of the species of interest. This approach is occasionally applied to the growth of macrophytes (see Rich et al. 1971) but clearly does not work with phytoplankton or periphyton, which have rapid turnover times. In aquatic systems primary production is usually measured indirectly through changes in dissolved oxygen or dissolved inorganic C (DIC) or, most often, by labeling the DIC pool with  $^{14}\text{C}$  and measuring the incorporation of label into phytoplankton or plant tissue. The various methods do not measure exactly the same quantities (see Williams et al. 1979; Williams and Robertson 1991). From the changes in  $\text{O}_2$  in paired light and dark bottles containing river water, one can measure total planktonic respiration ( $R_a + R_h$  in the dark) and the rate of pelagic NEP in the light. By assuming that R in the dark and light are equivalent we can calculate GPP and R. With the oxygen method, there is no direct way to estimate  $R_a$  and therefore no direct way to estimate NPP. The  $^{14}\text{C}$  method gives, in the light, something between GPP and NPP depending on the length of the incubation, the growth rate of the phytoplankton and the degree of C recycling (Williams et al. 1979). With the  $^{14}\text{C}$  method there is no direct way to estimate any of the components of R. The  $^{14}\text{C}$  method, because of its

high sensitivity, is most widely used and usually reported as “NPP.” Typically results are integrated over depth and during daylight hours, excluding both nighttime and depths with light too low to sustain photosynthesis. To make clear what is, and is not included, we will call this type of estimation Net Daylight Photic Zone Production (NDPZP; Cole et al. 1992) to distinguish it from true NPP.

#### The environment for primary production in the tidal-freshwater Hudson

Riverine environments like the Hudson present certain challenges to photosynthetic organisms (Cloern 1987; Alpine and Cloern 1988). The water column of the tidal-freshwater Hudson is well mixed and turbid. The suspended particles absorb light; the full water-column mixing ensures that organisms suspended in the water are rarely in the surface where light is highest (Fig. 1). At the average depth (9 m) and light penetration for the Hudson, the average phytoplankton spends from 18 to 22 hours in light too dim for net positive photosynthesis to proceed (Cole et al. 1992). The situation differs in the saline parts of the estuary and harbor where the water column is stratified, at least some of the time, leading to shallower mixing depths (Swaney et al. 1999), and concomitantly higher rates of primary production (Howarth et al. this volume). Nevertheless, low light is still a major growth-limiting factor in the lower estuary as well (Garside et al. 1976; Malone 1977).

Attached to the bottom, macrophytes and periphyton are restricted to extremely shallow water (< 1m) due to low light. On the other hand, these attached plants are less affected by advective loss than are phytoplankton. While the net freshwater flow of the Hudson is not very rapid, photosynthesis of suspended organisms needs to exceed the advective losses if biomass is to increase at a given site. During the growing season a typical residence time for water in the tidal-freshwater river is about 30 to 50 d, or 2 to 3% per day. To simply sustain biomass at a

given location then, net growth, after respiratory and predatory losses are subtracted, must be at least this large.

In many aquatic environments the supply of essential nutrients for plant growth, typically phosphorus (P) or nitrogen (N), and some trace metals (iron, selenium e etc.) limits the net growth of phytoplankton. In some rivers and most estuaries, since trace metals are generally high, N and P are the likely limiting nutrients (Howarth 1988; Fisher et al. 1992). Such is not the case in the Hudson. In the tidal-freshwater river, for example,  $\text{NH}_4$  depletes from winter values near  $10 \mu\text{M}$  to fairly low values in mid summer ( $\sim 2 \mu\text{M}$ ).  $\text{NO}_3$  varies seasonally between wintertime highs of near  $50 \mu\text{M}$  and summertime “lows” above  $30 \mu\text{M}$ .  $\text{PO}_4$  values are lowest in spring ( $0.4$  to  $0.5 \mu\text{M}$ ) and increase in late summer (at the peak of phytoplankton biomass) to as much as  $0.8$  to  $1 \mu\text{M}$  (Fig. 2). If either  $\text{PO}_4$  or  $\text{NO}_3$  were limiting one would expect a negative correlation with phytoplankton biomass, which is not seen at all in the Hudson.

That neither inorganic P nor N is low enough for sustained limitation of phytoplankton growth in the tidal-freshwater river can also be examined from a physiological perspective. One can compare the concentration in the water to the kinetic uptake abilities of similar groups of phytoplankton, expressed as the  $k_m$  (the nutrient concentration at which uptake is 50% of maximal) or  $k_s$  (the nutrient concentration at which growth is half maximal). Although there is variance among species,  $k_m$  for  $\text{NO}_3$  for diatoms would be near  $0.5 \mu\text{M}$  (Fisher et al. 1995; Huszar and Caraco 1998), about one-tenth the concentration in the river. For phosphate, an average diatom's  $k_s$  would be about  $0.1$  to  $0.2 \mu\text{M}$ , which is about one-fourth the phosphate concentration in the river during the peak of the growing season, and half during spring. Even  $\text{NH}_4$  is generally higher in the river than the  $k_m$  for phytoplankton ( $0.5$  to  $1 \mu\text{M}$ ). So the likely limiting nutrients are in excess of the  $k_m$  of phytoplankton essentially all the time. While there is

significant spatial variation in the concentrations of the likely limiting nutrients (Lampman et al. 1999), the conclusion that concentrations exceed  $k_m$  values is true for most times and places within the tidal, freshwater river.

### Composition of Phytoplankton

The Hudson River contains a diverse array of phytoplankton, but diatoms (Baciliariophyceae) are the numerical and biomass dominants and account for the majority of the species identified from the river (Marshall 1988, Smith et al. 1998). Working in the tidal-freshwater river, Marshall (1988) identified 137 species of phytoplankton of which 43% were diatoms, 27% were Chlorophyceae and 15.3% were Cyanobacteria. Other major groups (Cryptophyceae, Chrysophyceae and Pyrrophyceae) are represented in the river but with fewer species and much less biomass (Smith et al. 1998). Earlier work on the taxonomic structure of Hudson River phytoplankton reveals broadly similar conclusions, a dominance of diatoms and the presence of many other groups (Frederick et al. 1976; Sirois and Frederick 1978; Howells and Weaver 1969). The chapter by Strayer (this volume) reviews some of the factors that may regulate the difference in phytoplankton community structure in the Hudson (Caraco et al. 1997; Smith et al. 1998). We have not seen picoplankton (cells  $< 3 \mu\text{M}$ ) in the samples we have counted in the tidal-freshwater portion of the river and know of no published data suggesting that picoplankton are an important component of the Hudson River phytoplankton. Picoplankton have been reported as an important component of other coastal rivers (Kobyashi et al. 2000)

### Biomass of phytoplankton

Phytoplankton biomass is usually reported as the concentration of standing stock of chlorophyll-*a*, a pigment that all phytoplankton have in common. Weekly to bi-weekly measurements of the concentration of chlorophyll-*a* near Kingston, New York (rkm 144-147)

reveal several key features at several time scales about the magnitude and variation of phytoplankton in the Hudson (Fig. 3A).

First, there is an obvious seasonal cycle with peak biomass generally occurring in late spring. While the peak values can be quite high (20 to 50  $\mu\text{g liter}^{-1}$ ), the average level is moderate or low compared to other rivers and estuaries (discussed below). In many estuaries and lakes rapid phytoplankton growth occurs early in the season leading to a “spring bloom” in February to April. In the Hudson River, the bloom is substantially delayed and rarely if ever occurs in the spring. Among all years in Fig. 4A the mean day of peak phytoplankton biomass would be August 14. The earliest peak we have observed was in 1999 (May 12) and the latest in 2000 (October 25). In most years the peak occurs in mid July (Fig. 4A). There is high variance among years of the timing of the rapid growth phase. The day-of-year of peak chlorophyll-*a* is negatively correlated to the average amount of suspended load in the river ( $r^2 = 0.39$ ;  $p = 0.01$ ; Fig. 4B). Suspended load is the major factor controlling light extinction in the river. This correlation, however, explains only a fraction of the variance in the timing of the peak, so other factors are clearly involved.

Second, there are very obvious inter-annual differences in the magnitude of chlorophyll-*a* in the Hudson (Fig. 3A). The largest is the change from moderately high values to low values before and after 1992, the year the zebra mussel first became established at high numbers in the river (Caraco et al. 1997; Strayer et al. 1999; Strayer this volume). Prior to 1992 mean growing season (May-October) chlorophyll-*a* at Kingston averaged  $22.1 \pm 5.9 \mu\text{g liter}^{-1}$ . From 1993-2000 the mean was  $4.4 \pm 1.2 \mu\text{g liter}^{-1}$ . This 80% decline in phytoplankton biomass is consistent with the dramatic increase in water filtration brought about by the zebra mussel (Caraco et al. 1997). Prior to the zebra mussel invasion biological filtration of the tidal, freshwater Hudson occurred

about once in 50 d, and was largely the result of suspension feeding by cladocerans such as Bosmina and copepods (Caraco et al. 1997; Strayer et al. 1999; Pace and Lonsdale this volume). The zebra mussel increased biological filtration so that the entire water column turnover time was as short as 1 to 3 d depending on the year (Fig. 3B).

As in San Francisco Bay, some of the inter-annual differences in the Hudson phytoplankton biomass are related to variation in freshwater discharge among years, which controls the advective loss of phytoplankton (Cloern et al. 1985). Discharge during the growing season varies about 3-fold in the Hudson from 100 to nearly 400 m<sup>3</sup> s<sup>-1</sup> among years. Thus, the residence time of water within the tidal-freshwater region varies with this discharge from about 100 to 25 days. Discharge is negatively correlated to chlorophyll-*a* during the pre-zebra mussel period ( $p = 0.002$ ). During the post-zebra mussel period, this relationship has the same trend, but is not significant ( $p = 0.19$ ) during the post zebra mussel period (Fig. 5). Prior to the zebra mussel invasion, the advective loss term was of comparable magnitude to biological filtration; following the invasion biological filtration greatly exceeds the advective loss term.

### Biomass over space

The variation in phytoplankton biomass over the length of the river is as large as the seasonal variation at a single site (Fig. 6). The spatial structure is complex and has changed dramatically in response to the zebra mussel invasion, as we saw for the seasonal cycle. Even following the invasion, however, there is intriguing spatial structure that we do not fully understand. Clearly a primary determinant is water column depth. Within the tidal-freshwater portion, which is well mixed, the shallower reaches tend to have the highest volumetric biomass. Deeper water column depth causes cells to spend more time in the dark (see Fig. 1). Depth at a given reach interacts with other factors such as input from upstream and advective losses. A

model which includes these factors along with grazing rates and phytoplankton growth rates is able to reproduce the major features of the chlorophyll pattern along the length of the river both before and the first few years after the zebra mussel invasion (Caraco et al. 1997).

#### Rates of phytoplankton primary production

By varying light in a series of short-term incubations we can see the functional relationship between phytoplankton photosynthesis and irradiance (Fig. 7). The data from the Hudson, as with most other systems, fit a hyperbolic tangent function (Fig. 7). To compare to other systems the photosynthetic parameters are normalized to the amount of biomass (expressed in terms of chlorophyll-*a*). Thus,  $P_{\max}^b$  is the biomass specific rate of photosynthesis at optimum light and  $\alpha_b$  is the biomass-specific initial slope in Fig. 7.  $I_k$  is the value of light at which  $P_{\max}^b$  is first reached. In very clear water systems photosynthesis can be inhibited at high light; in the turbid waters of the Hudson light inhibition is not an important consideration.

$P_{\max}^b$  in the tidal-freshwater Hudson is comparable to values found in other estuarine systems and in the lower Hudson as well (e.g., Cote and Platt 1983; Shaw and Purdie 2001).  $I_k$  is moderately high (and  $\alpha_b$  moderately low) compared to many systems. In chronically low light environments phytoplankton are often adapted to low light by having a very low  $I_k$  and high  $\alpha_b$ , that is, a high affinity for light. The Hudson phytoplankton are not strongly adapted to low light, but are able to grow as rapidly as phytoplankton in other systems at optimum light. In the well mixed water column it is perhaps more reasonable to see the Hudson plankton as adapted to varying light, taking advantage of high light when they are mixed near the surface (see Cole et al. 1992).

It is instructive to compare the photosynthesis-irradiance relationship to the light field in the river. At a typical value of light extinction ( $k_d$  of  $-2 \text{ m}^{-1}$ ; mean for entire data set) light at 0.2

m depth on a cloudless summer day at noon would be about  $1450 \mu\text{Einst m}^{-2}\text{s}^{-1}$ , too low to cause light inhibition based on the measurements we have made. Photosynthesis would operate at  $P_{\text{max}}$  in the upper 0.75 m and fall off sharply with depth. By 3 m light is so low ( $\sim 5 \mu\text{Einst m}^{-2}\text{s}^{-1}$ ) that photosynthesis would be 0. So for the water column as a whole, photosynthesis is strongly light limited (Fig. 1).

Neither the photosynthetic parameters nor light are constant over time. The photosynthetic parameters in the Hudson show strong seasonality and both  $P_{\text{max}}^{\text{b}}$  and  $I_{\text{k}}$  correlate reasonably well with temperature (Fig. 8). Light extinction is largely controlled by the suspended clay and silts in the river and correlates extremely well with suspended weight ( $r = 0.83$ ). Thus, light extinction varies with seasonal variation in suspended weight, which in turn reflects flow and storms. We have also observed some longer-term trends in the photosynthetic parameters. These include a small increase in  $P_{\text{max}}^{\text{b}}$  from the pre- to post zebra mussel period and a much larger increase in  $\alpha$  (40%; Caraco et al. 1997). We do not include these long-term effects in this analysis for the sake of simplicity. Had we included this effect, GPP and NPP in the post zebra-mussel period would be higher than estimated here.

Instantaneous photosynthesis is the product of algal biomass, the photosynthetic parameters and light. Light varies over depth according to light extinction and varies with season and time of day. Algal biomass and the photosynthetic parameters vary, as we have seen (above) with season, flow and in response to the zebra mussel invasion. We can put these pieces together and look at phytoplankton primary production.

#### Daytime photic zone primary production

Traditionally phytoplankton production (NPP, see introduction) is measured by the  $^{14}\text{C}$  method and is integrated over the daylight period and to the depth of the photic zone, and does

not consider respiration. Thus, these values are NDPZP (see introduction). For these calculations we computed primary production for each 0.1-m slice of the water column for each half hour during daylight, for each week for which we have chlorophyll-*a* data. Potential irradiance was calculated from the equations of Iqbal (1983) using an albedo of 10% and the average degree of cloudiness for the region 40% reduction in potential radiation (IES 2001). NDPZP ranges from extremely low values in winter ( $\sim 1 \text{ mmol C m}^{-2}\text{d}^{-1}$ ) to values as high as  $300 \text{ mmol C m}^{-2}\text{d}^{-1}$  during summer bloom conditions (Fig. 9). The seasonal pattern mirrors that of chlorophyll-*a* and shows the dramatic reduction following the invasion of the zebra mussel (Fig. 9).

Since NPP, based on  $^{14}\text{C}$  measurements, does not include an estimate of algal respiration NPP in daylight is potentially smaller than algal GPP by algal respiration in the light. In the dark part of the water column, and at night, algal respiration consumes algal C that is not accounted for at all (Banse 1976). Using the approach outlined in Caraco et al. (1997) if we assume that algal R is proportional to  $P_{\text{max}}^{\text{b}}$  and the  $^{14}\text{C}$  measures net phytoplankton production ( $\text{GPP}-R_{\text{a}}$ ) in the light, we can provide an estimate of algal R and GPP (Fig. 9). In this scenario, we assumed that  $R_{\text{a}}$  was constant at 7% of  $P_{\text{max}}^{\text{b}}$ . Actual estimates of phytoplankton R range from 5 to 25% of  $P_{\text{max}}^{\text{b}}$  (Falkowski et al. 1985; Geider and Osborne 1989; Raven and Beardall 1981).

GPP is useful to know because we can compute the phytoplankton growth rate from GPP and algal biomass (Fig. 10). In the Hudson this growth rate ( $\mu$ ) ranges from about 0.05 to  $0.4 \text{ d}^{-1}$  and is much slower than these taxa are capable of. If we compute the growth rate the phytoplankton would have without light limitation (growth at  $P_{\text{max}}^{\text{b}}$ ) we see the  $\mu_{\text{max}}$  is much higher than  $\mu$  ranging from 0.4 to more than  $1.75 \text{ d}^{-1}$ , about as fast as these organisms grow in culture. Averaged over the entire data set  $\mu_{\text{max}}$  is 5.9 times faster than actual  $\mu$ . Looking closely at the plot of actual  $\mu$  we generally see slightly faster growth rates in the post zebra mussel years

than in the pre-zebra mussel years, at least during the summer. Presumably the high filtration rate of the zebra mussel selects for phytoplankton species that are faster growing. We have seen a significant change in species composition of the phytoplankton in response to the invasion (Smith et al. 1998), perhaps reflecting this grazing pressure.

From GPP and R we can also estimate phytoplankton net production (GPP-R), which is an interesting quantity since it is the C available to be consumed or exported. Note that NPP is much smaller than GPP or  $^{14}\text{C}$ -based estimates of primary production (NDPZP), rarely exceeding  $30 \text{ mmol m}^{-2}\text{d}^{-1}$ , and is occasionally negative (algal  $R > \text{GPP}$ ). On an annual basis, GPP-R is about ten times larger than measured  $^{14}\text{C}$  primary production. Had we assumed that  $^{14}\text{C}$  in the light measured gross rather than net production, or had we used a higher value for algal respiration, GPP-R would be even smaller (Cole et al. 1992). The very large difference between GPP-R and net daytime photic zone primary production is due to the deeply mixed water column. In the Hudson phytoplankton spend a great deal of time in the dark. For the deeper-water parts of the river, Poughkeepsie for example, algal R would frequently exceed GPP (Cole et al. 1992). The inference is that phytoplankton, as they pass through these deeper regions, must lose biomass due in part to their own respiration. This is consistent with the observed pattern of less algal biomass in the deeper regions of the river, as long as the water column is well mixed (Fig. 6). We do not know the actual rate of algal R so these calculations are only illustrative of what is likely. However, it is unlikely that algal R is much lower than 7% of  $P_{\text{max}}^{\text{b}}$  (Beardall and Raven 1990; Geider and Osborne 1989). It is also possible that R is neither constant nor always proportional to  $P_{\text{max}}^{\text{b}}$  (e.g., Laws 1975; Stone and Ganf 1981). The major point here is that in the well-mixed and dimly lit water column of the Hudson River, algal respiration is a large and important fate of algal gross primary production. This condition is likely true in other well-

mixed turbid rivers and estuaries but has only been considered in a few of them (Peterson and Festa 1984).

Since the net production of phytoplankton ( $GPP - R_a$ ) and growth rates of the Hudson River phytoplankton are low, a small change in a loss term (advection, predation, etc.) can be extremely significant. Even without considering the respiration of phytoplankton, the growth rate of phytoplankton based on GPP is only  $0.3 \text{ d}^{-1}$  at its peak. The biological filtration of the water column by zebra mussels is about this magnitude, 30% of the water column filtered each day. If  $R_a$  is proportional to  $P_{\text{max}}^b$ , as we have modeled it, phytoplankton respiration consumes on the order of 80 to 90% of GPP. Thus a change in removal rates of on the order of 5 to 10% of the water column per day would still significantly impact the phytoplankton of the tidal-freshwater Hudson. The major crash in phytoplankton biomass in response to the zebra mussel invasion is indeed consistent with this reasoning (Caraco et al. 1997)

#### The tidal-freshwater Hudson in comparison to other systems

In comparison to rivers and estuaries of the world, the tidal-freshwater Hudson, depending on the location, was fairly eutrophic prior to the invasion of the zebra mussel in 1992. That is, mean growing season chlorophyll-*a* at Kingston, New York was higher than more than 75% of the rivers and estuaries for which we have data. Similarly, the Kingston region had high chlorophyll in comparison to down river sites within the Hudson. Following 1992, (post-) chlorophyll-*a* in the mid Hudson would be considered moderately low in comparison to other river or estuarine systems (Fig. 11).

As we pointed out GPP is rarely measured in most systems, making comparison limited. However, we can compare our estimates of phytoplankton GPP to estimates of GPP made on the saline part of the Hudson River Estuary, many of which are reviewed in Howarth et al. (this

volume) and Swaney et al. (1999). Howarth et al. (this volume) suggests that GPP for the mid 1990's is about  $850 \text{ g C m}^{-2}\text{y}^{-1}$  in the saline part of the estuary and  $450 \text{ g C m}^{-2}\text{y}^{-1}$  for the oligohaline section. Both estimates are considerably higher than we estimate for the freshwater portion of the river of  $330 \text{ g C m}^{-2}\text{y}^{-1}$  for the pre-zebra mussel period and  $82 \text{ g C m}^{-2}\text{y}^{-1}$  post zebra mussel. On the other hand, the estimates reported by Howarth et al. (this volume) for the mid 1990's are roughly 2 to 4 times higher than prior estimates from the 1970's for the saline and mesohaline sections, respectively. So, prior to the zebra mussel GPP in the tidal-freshwater portion of the estuary was somewhat lower than for the oligohaline region and less than half that for the saline portion. Following the invasion, GPP in the tidal freshwater was only about 25% of that in the oligohaline region and roughly one-tenth the estimates for the saline portion.

In order to compare planktonic primary production in the tidal-freshwater Hudson more broadly to the saline parts of the estuary and New York Harbor, as well as to other estuaries and rivers, we need to revert to our estimate of DPZNP, which is akin to what most researchers report as "NPP." In the years prior to the zebra mussel invasion, annual DPZNP for the mid Hudson region averaged  $243 \pm 40 \text{ g C m}^{-2}\text{y}^{-1}$ , among year (with 95% CI) a value close to that reported by Malone (1977) for New York Harbor and measured recently at the Verrazano Narrows by Taylor et al. (G. Taylor pers. com). (Fig. 11B). In comparison to other rivers primary production in the tidal-freshwater Hudson was moderately high. Following the zebra mussel invasion (1993-2000) DPZNP for the mid Hudson region averaged  $61 \pm 8.3 \text{ g C m}^{-2}\text{y}^{-1}$ , which groups the Hudson during this period with systems with the lowest reported planktonic primary production for rivers and estuaries in general.

Phytoplankton primary production in context of the Hudson River organic C balance

In Table 1 we show estimates of the major inputs and outputs of organic C to the tidal-freshwater portion of the Hudson River based on the work of many investigators. The C balance of the lower estuary is discussed in the chapter by Howarth et al. (this volume). The balance here is shown for both the pre-zebra mussel period (prior to 1992) and the post-zebra mussel period because of the major impact these bivalves have had on phytoplankton and because they have become an important component of respiration in the system. Unlike a number of large estuaries, phytoplankton production in the tidal-freshwater river is not the dominant source of organic matter. Further, respiration of phytoplankton themselves greatly reduces the amount of organic C of phytoplankton origin that is available to consumers (Table 1). In the post-zebra mussel period primary production from aquatic macrophytes is comparable to that of phytoplankton, especially if we consider the net input (GPP-plant respiration). In both periods, loading of dissolved and particulate organic matter from the watershed is by far the dominant input, and advective losses downstream the dominant output. The net balance shows that the respiration of the known components in the river exceeds primary production, and this difference is more pronounced during the zebra mussel period. Thus, during the pre-1992 period, respiration exceeded GPP by about  $43 \text{ g C m}^{-2}\text{y}^{-1}$  and by about three times this amount ( $153 \text{ g C m}^{-2}\text{y}^{-1}$ ) post 1992. The R in excess of GPP must be supported by the respiration of some of the vast amount of organic material loaded from the watershed.

If it is true that the sum of the components of heterotrophic respiration exceed net primary production, we should be able to measure this net heterotrophy at the ecosystem scale. For example if R exceeds GPP the system will be undersaturated in dissolved  $\text{O}_2$  and  $\text{O}_2$  will invade from the atmosphere. Similarly the system will be supersaturated in  $\text{CO}_2$  and  $\text{CO}_2$  will evade to the atmosphere. Both these conditions are true for Hudson (Raymond et al. 1997;

Caraco et al. 2000; Cole and Caraco 2001). Estimates of these net gas balances are shown in Table 2 and show at least broad agreement to the balance of the known components. While there is a good deal of uncertainty in each individual estimate, all of them indicate that the tidal, freshwater Hudson is net heterotrophic and magnitude is not extremely far from that based on the sum of the components that we outlined in Table 1.

#### Future research

The ecosystem balance concurs with the budget of the components that the respiration of heterotrophic organisms exceeds the input from phytoplankton production. The budget implies that some key heterotrophic organisms must utilize organic matter that was produced outside of the river. For example, the estimate of zebra mussel respiration alone is greater than the net input of organic matter from phytoplankton plus periphyton plus macrophytes. This is also true for pelagic bacteria. Clearly, organic matter of terrestrial origin is an important subsidy for the Hudson River food web. On the other hand, this balance does not imply that phytoplankton are unimportant. In fact phytoplankton are likely a major resources for some components of the food pelagic food web that lead to the production of some fish. In systems, like the Hudson, with multiple types of organic inputs and multiple primary producers, it is often difficult to tease apart the key pathways that lead to the production of important resource species. Stable C isotopes, which offer a hopeful approach in some ecosystems, are not a viable approach in the Hudson because the signals of the phytoplankton terrestrial inputs are nearly identical (see Caraco et al. 1998). Radiocarbon ( $^{14}\text{C}$ ) appears to be a more useful tracer since it was discovered recently that much of the terrestrial input is quite old (500 to 1500 years before present; Raymond and Bauer 2001; Cole and Caraco 2001), but much work remains to be done. Current research, which traces the production of unique fatty acids from either phytoplankton or bacteria

into consumers, has revealed that copepods and some larval pelagic fish are tightly coupled to phytoplankton rather than to terrestrial detritus (K. Limburg and N. Caraco, unpublished data). The decline in some benthic filter-feeding invertebrates in conjunction with the phytoplankton decline brought about by the zebra mussel is also consistent with the idea that phytoplankton were a key element of their nutrition. Future work needs to seek ways to further unravel the importance of phytoplankton to the food web and to key resource species.

### Implications for management

To control eutrophication, reducing nutrient load is a key goal of ecosystem management. In systems in which the phytoplankton are strongly nutrient limited, the loading of nutrients (typically N and P) lead to large and often undesirable blooms of phytoplankton (Howarth 1988). The sinking and decomposition of these blooms can lead to oxygen depletion in the sediments and bottom waters in systems in which the water column is physically stratified. The tidal-freshwater Hudson is neither stratified nor nutrient limited. Nutrient concentrations are high, but phytoplankton are limited by the other factors we have discussed here: light; deep mixing; and grazing. Thus lowering the input of these nutrients will not greatly affect phytoplankton or oxygen in this part of the river. On the other hand, if one were to try to manage the Hudson for water clarity by reducing the input of silts and clays, dramatic increases in phytoplankton would be expected (Caraco et al. 1997). If the Hudson River lacked the suspended matter that now absorbs light, phytoplankton would be able to use much of the pools of inorganic N and P that are now exported downstream. In a simulation model of this effect, Caraco et al. (1997) suggested that summertime chlorophyll-*a* would be as high as 70 to 80  $\mu\text{g liter}^{-1}$  (about 20 times the present values) before self shading or P-limitation further limited bloom formation in the mid-Hudson region. Thus while the abatement of turbidity might seem desirable to improve the

river aesthetically and for swimming, it is likely to also lead to dramatic increases in eutrophication.

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	g Cm <sup>-2</sup> y <sup>-1</sup>			g Cm <sup>-2</sup> y <sup>-1</sup>		
	pre 1992			post 1992		
PRIMARY PRODUCERS	GPP	R <sub>a</sub>	NPP	GPP	R <sub>a</sub>	NPP
<u>phytoplankton</u>	331	281	50	82	70	12
<u>macrophytes</u> (1)			30			41
<u>periphyton</u> (2)			2			2
TOTAL NPP			82			55
WATERSHED INPUTS (3)			650			650
Net inputs			732			705
HETEROTROPHIC R		R <sub>h</sub>			R <sub>h</sub>	
<u>pelagic bacteria</u> (4)		116			116	
<u>zebra mussel</u> (5)		0			83	
<u>other benthos</u> (6)		9			9	
TOTAL R <sub>h</sub>		125			208	
GPP-R (ECOSYSTEM) (7)			-43			-153
Net advective outputs (8)			607			497

TABLE 1. Phytoplankton primary production in the context of the organic C budget of the tidal, freshwater Hudson River. The phytoplankton values here are derived from measurements near Kingston-Rhinefluff, New York, and do not take into account spatial variation in biomass and parameters in the freshwater river as a whole, and thus, are not identical to estimates in other papers (see Caraco et al. 1997; 2000). The values of GPP, R<sub>a</sub> and NPP for the phytoplankton are explained in the text. (1) Values for macrophytes from Cole and Caraco (2001); Caraco et al.

2000; Harley and Findlay 1994. We assumed that the values for daily macrophyte net production in Caraco et al. (2000) apply to a 100-d season; we can not estimate macrophyte gross production or respiration from this approach. (2) Periphyton values are approximate and based on biomass data in Bianchi et al. (1993) assuming the same biomass-based photosynthesis as phytoplankton. This is likely an over estimate. (3) Watershed inputs are based on Howarth et al. 1996. (4,5,6) These values come from averages from several sources (Findlay et al. 1998, Roland and Cole 1999, Caraco et al. 2000, Cole and Caraco 2001), and are explained in those sources. Values should be considered approximate only. (7) This is the difference of GPP and R in this table. (8) Net advective outputs are estimated as difference between all inputs (GPP + watershed inputs) – R. In some case we were able to estimate values both prior to the zebra mussel invasion and following it; where we did not have a separate estimate for both periods we used the existing value for both periods.

<u>Net Ecosystem Heterotrophy</u>			
$\text{g Cm}^{-2} \text{y}^{-1}$			
<u>Approach</u>	<u>pre 1992</u>	<u>post 1992</u>	<u>Reference</u>
Component GPP and R	43	153	This study
Annual O <sub>2</sub> influx	44	127	Caraco et al. 2000
Annual CO <sub>2</sub> influx	--	100-190	Raymond et al. 1997
Longitudinal DOC Profile	--	85-185	Cole and Caraco 2001
Diel O <sub>2</sub>	(293)		Howarth et al. 1996
Mean	44	161	

TABLE 2. Net ecosystem heterotrophy (system GPP – system R) for the tidal-freshwater Hudson from several different approaches. Each approach estimates the difference between annual GPP and annual R and is a minimum estimate of the amount of terrestrially derived organic C that must be respired within the river. The approaches and their limitations are explained in the references. See also Findlay et al. (1998). The diel O<sub>2</sub> from Howarth et al. 1996 includes some data in the post zebra mussel period. It is not included in the mean.

Figure 1. Light and water column mixing in the tidal-freshwater Hudson River. The water column of the Hudson is turbid and well mixed. Phytoplankton move with the water from the uppermost, well-lit portion into the deep, dark portion, rapidly and continuously. The heavy line shows the light field which phytoplankton experience over depth, at full sunlight, expressed as percent of incident light. The dashed line shows the effect this light has on photosynthesis, expressed as percent of photosynthesis at optimal light. The respiration of phytoplankton is proportional to their biomass, and thus is nearly constant over depth (thin dotted line). Thus, even at noon on a bright day, phytoplankton respiration in deep water exceeds photosynthesis. At shallower sites, 24-hour photosynthesis can exceed respiration for the entire water column; at deeper sites it cannot.

Figure 2. Twelve years of nutrient concentrations near Kingston, New York (river km 144). Shown are the means, by month (with SD for that month among years) for weekly to bi-weekly data for 14 years 1986-2000. The upper panel shows inorganic N; open circles are  $\text{NH}_4$ ; x's are  $\text{NO}_3$ . The lower panel shows  $\text{PO}_4$ . These data are a summary of nutrient analysis from more than 500 individual dates sampled.

Figure 3. The biomass of phytoplankton in the mid-Hudson region. Shown in A are weekly to bi-weekly data for chlorophyll-*a* near Kingston, New York (river km 144). In B we show means for the May-October period for each year (hatched bars, errors are SD). The solid line (right-hand Y-axis) shows the water filtration rate of the zebra mussel (Caraco et al. 1997; Strayer this volume). The filtration rate is expressed as volume per area per time ( $\text{m}^3/\text{m}^2/\text{d}$ ), which is the same as  $\text{m}/\text{d}$ .

Figure 4. Timing of the phytoplankton “bloom” in the tidal freshwater Hudson. Shown in the upper panel is the day of year (1 Jan is DOY 1) of peak chlorophyll for 14 years of observation. Note that peak chlorophyll occurs in mid to late summer (DOY 120-200) rather than in spring. The lower panel shows the relationship, by year, between day of year peak chlorophyll and mean suspended weight for that year. The regression line has an  $r^2$  of 0.39 but is highly significant ( $p < 0.001$ ).

Figure 5. Relationship between phytoplankton biomass (as chlorophyll-*a*) and freshwater discharge, both averaged for the period from May 15 through October 1; error bar is SD. The solid circles are for the period from 1986-1991, prior to the introduction of the zebra mussel (“Pre”). The open circles are for the period 1993-2000 (“Post”) and the open triangle is for 1992, the transitional year (see text).

Figure 6. Representative variation in phytoplankton biomass over the length of the tidal-freshwater Hudson. Shown are transects from the Tappan Zee Bridge (river km 40) to Albany (river km 240) taken in August of three different years (labeled). River km are km north of the southern tip of Manhattan (river km 0).

Figure 7. Result of a primary production versus irradiance measurement for the tidal-freshwater Hudson River. The Y-axis shows primary production measured as the assimilation of  $^{14}\text{C-HCO}_3$  into organic matter as a function of light (X axis). In this example the organic matter includes both particulate and dissolved components (POC plus DOC). The actual data points, with SE are shown as open circles and the line represents the fit hyperbolic tangent function fit to these data.

The photosynthetic parameters ( $P_{\max}$ ,  $\alpha$ , and  $I_k$ ) are derived the equation for the fitted line (see text). These data are for Hudson, New York, on Sept 12, 1998.

Figure 8. Seasonal variation in photosynthetic parameters shown as a function of temperature. Shown as A are  $P_{\max}^b$  ( $\mu\text{mol C } [\mu\text{g chl}] \text{ h}^{-1}$ ) and as B  $I_k$  ( $\mu\text{Einst m}^{-2}\text{s}^{-1}$ ) for 129 incubations made from various locations and dates in the tidal freshwater Hudson. The lines in both A and B are linear regressions.

Figure 9. Phytoplankton primary production over time at Kingston, New York. From weekly measures of chlorophyll-*a* and the photosynthetic parameters (Fig. 9) three aspects of phytoplankton primary production were calculated. In A, we show photosynthesis, integrated over the entire daylight period and integrated to the depth that below no photosynthesis occurs. This is daytime net photic zone primary production. In B, we applied a biomass-specific value of phytoplankton respiration (*R*; see text) and calculated both phytoplankton respiration (plotted as a negative value to simplify the figure) gross primary production. In C we plot GPP-*R*, or true 24 h net phytoplankton production integrated for the entire depth of the water column. Note the expressed this way, NPP is occasionally negative and is much smaller than GPP or NDPZP.

Figure 10. Growth rate of phytoplankton in the tidal freshwater Hudson. The solid circles labeled “actual” show the growth rate calculated from GPP (Fig. 10) and biomass. The thin line shows the growth rate at optimum light (“potential”), with no light limitation. In this scenario the light level was  $1000 \mu \text{Einst. m}^{-2}\text{s}^{-1}$  throughout the water column for 12 h each day.

Figure 11. Phytoplankton biomass (A) and primary production (B) in comparison to other rivers (filled circles) and estuaries (open circles). Each point is for a different riverine or estuarine systems and the systems are ordered by chlorophyll values from low to high. Biomass is mean chlorophyll-a for the growing season. For the tidal-freshwater Hudson this is given for both prior to the zebra mussel invasion (“pre-”) and following it (“post-”). Several other sites for the saline estuary are also shown. These are NYH – New York Harbor (Malone 1975; Malone 1977), and HW – Haverstraw Bay and VB – Verrazano Bridge (both from G. Taylor, pers comm.) and are data from the mid-1990’s.

For primary production values are net daytime photic zone production for the mid Hudson. For other systems we assumed the “NPP” was equivalent to our NDPZP. Values are expressed as daily means for the entire year. Non Hudson data are from Cadee and Hegeman 1974; Cloern 1984; Cloern et al. 1985; Cole and Cloern 1984; Bonnetto 1983; Frey et al. 1984; Cadee 1986; Ertl 1985; Fisher et al. 1982; Flint et al. 1986; Gopinathan et al. 1984; Harding et al. 1986; Levasseur et al. 1984; Pennock and Sharp 1986; Scott 1978; Sinada and Karim 1984; Shehata and Bader 1985; Stockner and Cliff 1979; Turner et al. 1979; Baker and Baker 1979; Flemer 1970; Furnas et al. 1976; Gilmartin 1964; Haines and Dunstant 1975; Keller 1988; Kuparinen 1987; Randall and Day 1987.

