

Turbid waters and clarifying mussels: their moderation of empirical chl:nutrient relations in estuaries in Prince Edward Island, Canada

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ABSTRACT: Coastal eutrophication has been identified as an important ecological problem in many regions. Yet simple, generalizable models, such as those available for the management of lake eutrophication, do not exist for estuaries. As a first step in the development of estuarine eutrophication models, we generated chlorophyll *a*:nutrient regression models for 15 estuaries in Prince Edward Island, Canada. Total phosphorus and total nitrogen account for 65 and 72% of the variance in chlorophyll (chl), respectively. However, when these models are compared to similar models for lakes, the yield of chl per unit nutrient is between 1 and 2 orders of magnitude lower in estuaries than in lakes. As herbivory and turbidity are likely contributors to this low yield, we used a mass-balance approach to model phytoplankton biomass as a function of primary production and losses due to flushing, sedimentation and herbivory. In the 6 estuaries with mussel aquaculture, 45 to 88% of the chl deficit could be accounted for by herbivory. In the remaining 9 estuaries, turbidity accounted for 35 to 75% of the chl deficit. Considering both herbivory and turbidity, the mass-balance accounted for on average 68% of the chl deficit for the 15 estuaries. We also generated an empirical model predicting the deficit as a function of herbivory and turbidity; this model accounted for 50% of the variation in the deficit. The analysis suggests that chl:nutrient relations can be generalized across fresh and estuarine aquatic systems if turbidity and herbivory are considered.

KEY WORDS: Coastal eutrophication · Regression · Phosphorus · Nitrogen · Iron · *Mytilus edulis* · Aquaculture

INTRODUCTION

Coastal eutrophication is recognized as an important ecological problem in many regions [e.g. U.S. Atlantic coast (Bricker et al. 1995) and the Baltic (Rosenberg et al. 1990)]. Nutrient loading to coastal waters resulting in increased phytoplankton biomass has been linked to increased incidence of toxic phytoplankton blooms (Paerl 1995) and increased anoxia both locally (Cooper 1995) and on the continental shelf (Turner & Rabalais 1994). Concern over coastal eutrophication is reflected in the U.S. Estuarine Eutrophication Survey (Bricker et al. 1995), and 2 primary journals have dedicated issues to the topic (Nixon 1990, Vollenweider et al. 1992).

Because eutrophication is defined as an aquatic system's response to nutrient loading (Edmondson 1991), identification of the key nutrient controlling coastal

phytoplankton biomass is considered essential. Based on the stoichiometric work of Redfield (1958), phosphorus (P) has been considered a key limiting nutrient in marine systems. Moreover, P control of phytoplankton biomass in many freshwater systems and similarities in phytoplankton physiology and nutrient requirements in both coastal and freshwater systems (Hecky & Kilham 1988) make P control of coastal systems intuitively appealing. Nevertheless, following Ryther & Dunstan's (1971) influential work, nitrogen (N) is generally seen as the limiting nutrient in coastal systems and has received the bulk of research interest. A review of the 1995 to 1997 biological abstracts shows that, of 596 articles on estuaries and nutrients, 52% consider only nitrogen, 32% refer to both nitrogen and phosphorus, and 16% consider only phosphorus.

Despite the preponderance of research on N, the evidence for general N limitation of coastal systems is weak compared to the evidence for general P limita-

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tion of freshwater systems. In their comparative review of nutrient limitation in aquatic systems, Hecky & Kilham (1988) argued that, although N may well be the key limiting nutrient in coastal waters, the evidence is inconclusive as it is mostly derived from bioassays and observations of inorganic nutrient concentrations. Since this review, a series of mesocosm experiments on N versus P limitation have been conducted (e.g. Oviatt et al. 1995, Tamminen 1995). However, whole system experiments such as those of Schindler (1977) that provided such convincing evidence of P limitation in lakes are absent in coastal areas. Coastal and marine ecologists have also generally eschewed the comparative approach of limnologists (e.g. Dillon & Rigler 1974), which has been instrumental in establishing the generality of P limitation in lakes. Although limited examples of comparative work in the coastal literature exist (cf. Nixon 1981, Monbet 1992, Boynton et al. 1996), the relative strength of patterns between phytoplankton biomass and total N (TN) and total P (TP) in estuaries has not been tested.

To evaluate patterns between phytoplankton biomass and nutrients, the following hypotheses were tested: (1) estuarine phytoplankton biomass [measured as chlorophyll *a* (chl)] is primarily a function of bottom-up nutrient control; (2) chl:nutrient relations can be established using a comparative, empirical approach; (3) the relation between chl and TP is stronger than that between chl and TN; and (4) chl responds to total nutrient concentrations similarly in estuaries and lakes. We also examine the role of herbivory and turbidity in moderating the relation between nutrients and coastal phytoplankton biomass.

METHODS

Study location. This analysis is based on data from 15 estuaries in Prince Edward Island (PEI), Canada. PEI is a small island (575 000 ha; Environment Canada 1990) located in the Gulf of the St. Lawrence River, approximately 15 km from the New Brunswick coast (Fig. 1). Maximum salinity surrounding PEI is approximately 29‰, reflecting the strong influence of the Gulf of St. Lawrence. The island is heavily bisected by rivers flowing into approximately 25 coastal embayments along a 1600 km coastline (Environment Canada 1990). These embayments include coastal plain estuaries (Fairbridge 1980) as well as lagoons that form behind barrier sandbars on the Island's north shore. Tides are semi-diurnal with a mean high tide of 0.9 m and mean low tide of 0.2 m on the north shore and a mean high tide of 2.4 m and mean low tide of 0.5 m on the south shore (Department of Fisheries and Oceans 1996).

Agriculture is an important economic activity on the island: approximately 35% of the land base is agricultural (MacDougall et al. 1988). The soils are generally acid, well-drained podzols (MacDougall et al. 1988). These podzols erode easily and soil loss can be as high as 40 to 45 tonnes ha⁻¹ yr⁻¹ (Himmelman & Stewart 1979). Because podzols are low in organic matter (<3%; MacDougall et al. 1988) and because of the intensity of agricultural activity, synthetic fertilizers are heavily used (1100 to 1600 kg ha⁻¹ of 13:20:20 N:P:K fertilizer; B. Thompson, Prince Edward Island Department of Agriculture and Forestry, pers. comm.). Nitrogen leaches into ground water through podzols

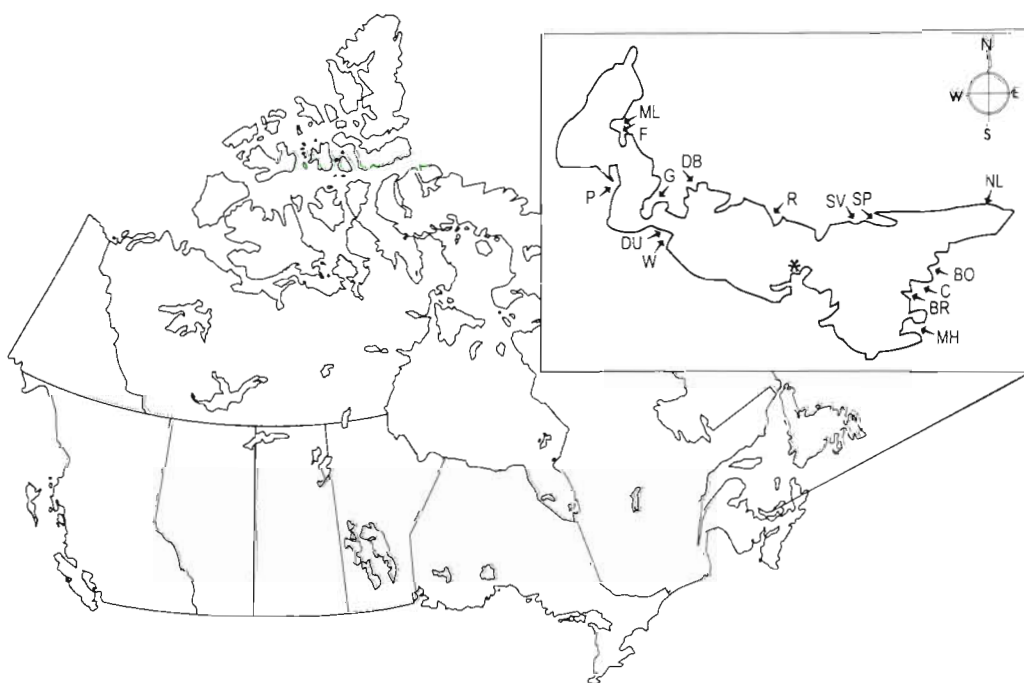


Fig. 1 Location of Prince Edward Island, Canada, and the 15 study estuaries; asterisk indicates the provincial capital, Charlottetown. BO: Boughton; BR: Bruderell; C: Cardigan; DB: Darnley Basin; DU: Dunk; F: Foxley; G: Grand; MH: Murray River; ML: Mill River; NL: North Lake; P: Percival; R: Rustico; SP: St. Peters; SV: Savage Harbour; W: Wilmot

Table 1 Data for 15 estuaries from Prince Edward Island used in this analysis. Mussel weight is in grams dry weight

| Site | Chl (mg m ⁻³) | Total phosph. (mg m ⁻³) | Total nitrogen (mg m ⁻³) | Secchi depth (m) | Mean depth (m) | Volume (× 10 ⁶ m ³) | Residence time (d) | Salinity (‰) | Watershed area (km ²) | Agri- culture (km ²) | Mussel weight (× 10 ⁷ g dw) |
|---------------|------------------------------|---|--|------------------------|----------------------|---|--------------------------|-----------------|---|--|--|
| Boughton | 1.398 | 57.9 | 209 | 3.5 | 18.0 | 140 | 332 | 21.2 | 39.5 | 10.3 | 7.29 |
| Brudenell | 1.952 | 58.8 | 229 | 3.3 | 14.5 | 101 | 44 | 22.2 | 187.0 | 66.5 | 2.03 |
| Cardigan | 1.548 | 55.0 | 241 | 4.1 | 17.6 | 225 | 255 | 21.0 | 80.5 | 21.4 | 6.75 |
| Darnley Basin | 1.369 | 45.8 | 213 | 2.4 | 8.7 | 33 | 129 | 20.5 | 25.1 | 20.4 | 0 |
| Dunk | 5.915 | 85.1 | 481 | 1.2 | 3.1 | 13 | 9 | 16.4 | 202.4 | 140.4 | 0 |
| Foxley | 2.029 | 76.0 | 264 | 2.1 | 7.4 | 39 | 135 | 18.3 | 37.5 | 3.0 | 0 |
| Grand | 1.453 | 45.8 | 241 | 2.5 | 11.2 | 264 | 245 | 20.1 | 110.0 | 44.0 | 0 |
| Murray River | 1.301 | 60.2 | 218 | 3.7 | 10.0 | 351 | 356 | 20.4 | 101.3 | 18.0 | 9.63 |
| Mill River | 3.846 | 89.6 | 367 | 2.0 | 7.7 | 30 | 33 | 18.4 | 117.9 | 56.3 | 0 |
| North Lake | 4.653 | 85.2 | 312 | 1.6 | 2.3 | 2.5 | 6 | 19.9 | 45.6 | 5.1 | 0 |
| Percival | 1.097 | 61.6 | 266 | 1.3 | 5.0 | 60 | 166 | 17.9 | 46.4 | 2.4 | 0 |
| Rustico | 1.988 | 55.4 | 274 | 2.3 | 7.1 | 53 | 83 | 19.8 | 67.4 | 46.6 | 2.70 |
| St. Peters | 1.713 | 68.6 | 298 | 2.9 | 10.3 | 140 | 61 | 18.4 | 292.9 | 75.9 | 6.39 |
| Savage Harb. | 1.571 | 60.1 | 277 | 1.6 | 5.8 | 19 | 74 | 20.5 | 25.6 | 4.7 | 0 |
| Wilmot | 3.475 | 94.8 | 416 | 1.1 | 2.2 | 2.3 | 3 | 19.2 | 206.6 | 65.1 | 0 |
| Mean | 2.354 | 66.7 | 287 | 2.4 | 8.7 | 98 | 129 | 19.6 | 105.7 | 38.7 | 5.80 |
| SD | 1.437 | 15.7 | 79 | 1.0 | 5.0 | 106 | 118 | 1.5 | 81.3 | 38.1 | 2.90 |
| Min. | 1.097 | 45.8 | 209 | 1.1 | 2.2 | 2.3 | 3 | 16.4 | 25.1 | 2.4 | 2.03 |
| Max. | 5.915 | 94.8 | 481 | 4.1 | 18.0 | 351 | 356 | 22.2 | 292.9 | 140.4 | 9.63 |

and it is thus transported to estuaries; phosphorus is transported to surface waters by being adsorbed to particles of the easily eroded podzols.

Data set and analyses. A data set was compiled for 15 estuaries in PEI (Fig. 1) that included water chemistry, shellfish biomass, coastal morphometry, and land-use variables (Table 1). The estuaries were chosen to include a range of size, land-use characteristics and both the presence and absence of mussel aquaculture.

Water chemistry: The 15 estuaries were sampled from May to August, 1996. All estuaries larger than 4 km² were sampled at 5 stations along a land-sea salinity gradient; the remaining 4 estuaries (Darnley Basin, North Lake, Savage Harbour and Wilmot; Table 1) were sampled at 3 stations. At each station, the location, time of day, maximum depth (Z_{\max}) and Secchi depth (SD) were recorded. Salinity and temperature were measured 0.5 m below the surface and 0.5 m above the bottom. At stations where the maximum depth was less than 1 m, single salinity and temperature readings were taken at 0.5 m depth. Integrated water samples were taken at each station from the surface to 5 m; if the depth was less than 5 m, integrated samples were taken from the surface to 0.5 m above the bottom. Each estuary was sampled 6 times during the sampling season at approximately 2 wk intervals, generating 18 (3 stations per estuary) or 30 (5 stations per estuary) observations per estuary.

Triplicate samples were analyzed for chl, TP and TN. For chl, 0.5 l water was filtered onto Gelman A/E, which were then frozen. Within 6 mo of sampling, the

filters were extracted in 90% ethanol and chl was determined spectrophotometrically following Bergmann & Peters (1980). TP was also determined spectrophotometrically following the persulfate digestion method of Menzel & Corwin (1965). The method was modified in that, after digestion, a 2 ml subsample was taken from each replicate. These subsamples were then frozen to be read on an Alpkem autoanalyzer (Alpkem 1992) within 6 mo of sampling. TN, like TP, was determined on the autoanalyzer using 2 ml subsamples from samples that were digested following Solórzano & Sharp (1980).

Shellfish biomass: The estimated production (total weight in kg yr⁻¹) for the 6 estuaries in which blue mussels *Mytilus edulis* are farmed was provided by the PEI Department of Agriculture, Fisheries and Forestry (unpubl. data; Table 1). Mussel spat are placed in the grow out bags when approximately 3 mo old and 20 to 30 mm long; they are harvested in the 50 to 60 mm size range. A total of 13 km² are under production in PEI (Table 1; Department of Fisheries and Oceans, Halifax, Canada, unpubl. data).

Mussel filtration rates are frequently reported as clearance rates (l h⁻¹) as a function of dry weight (Table 2). We converted all clearance rates to specific filtration rates (f_m ; m³ d⁻¹ g⁻¹ dry wt) using conversion factors calculated from length, total weight, and dry weight measurements for 50 PEI mussels (Table 2).

Coastal morphometry and land use: Coastal morphometry was determined from bathymetric charts published by the Canadian Hydrographic Service

Table 2. Equations used for the calculation of specific mussel filtration rates (f_m ; $\text{m}^3 \text{g}^{-1} \text{dry wt d}^{-1}$), where CR = clearance rate in l h^{-1} , and g_D = grams dry weight

| f_m | Equation | Range of dry wt (\bar{g}) | Source |
|-------------|---|-------------------------------|------------------------------|
| 0.029–0.043 | 0.84–1.25 l h^{-1} for 55 mm animal ^a | 0.7 | Jørgensen (1966) |
| 0.063 | $\text{CR} = 2.410 g_D^{0.74}$ | 0.003–1.186 | Winter (1973) |
| 0.108 | $\text{CR} = 3.90 g_D^{0.6}$ | 0.008–1.0 | Vahl (1973) |
| 0.121 | $\text{CR} = 3.846 g_D^{0.25}$ | 0.5–4.0 | Walne (1972) |
| 0.202 | $\text{CR} = 7.45 g_D^{0.66}$ | 0.011–1.361 | Møhlenberg & Riisgård (1979) |
| 0.427 | Average of data | 0.07–0.39 | Famme et al. (1986) |

^aConversion as follows: a 5 cm long animal weighs approximately 0.7 g dry wt (Widdows et al. 1979, this study)

(1980). Land use information was provided by the PEI Department of Agriculture. For each watershed, land use is divided into area under forest, area under potato crops and 'other', which includes area under hay, grain, and vegetables.

Statistical analyses: chl:nutrient relations were developed using least squares regression techniques (Zar 1984, SAS Institute 1985). Mean values for chl, TP and TN were calculated by averaging the values for the stations for each of the 6 sampling rounds. Means and standard deviations were then calculated from these 6 values to yield growing-season averages. The growing-season averages were log-transformed to stabilize variance.

RESULTS

Chl:nutrient relations

The chl:TP and chl:TN relations are both highly significant, accounting for 65 and 72% of the variation in chl respectively (Fig. 2). The estuarine chl:nutrient relations were then compared to lake chl:nutrient relations. For the TP comparison, we chose the Dillon & Rigler (1974) equation because of the strength of its correlation and the OECD (1982) equation as it was developed for lakes from a wide geographical range (Table 3). For the TN comparison, we used the only 2 lake chl:TN models we could find: Sakamoto (1966) and Prairie et al. (1989) (Table 3).

When the PEI chl:nutrient relations are compared to the lake relations, we see that, although the slopes are similar, the intercepts of the estuarine models are approximately 1 to 2 orders of magnitude lower than those of the lake models (Table 3). Estuarine phytoplankton yield (chl:TP and chl:TN) is much lower in PEI estuaries than in lakes. Assuming that estuarine phytoplankton can respond to nutrients similarly to lake phytoplankton, we calculated a potential chl estimate for each estuary using the observed TP values in

the Dillon & Rigler equation (Fig. 3). The difference between these potential chl values and the observed chl values can be considered to be a 'phytoplankton deficit'. As herbivory and turbidity are 2 possible contributors to this low yield, we then used a mass-balance approach to estimate how much of the phytoplankton deficit could be accounted for by these 2 factors.

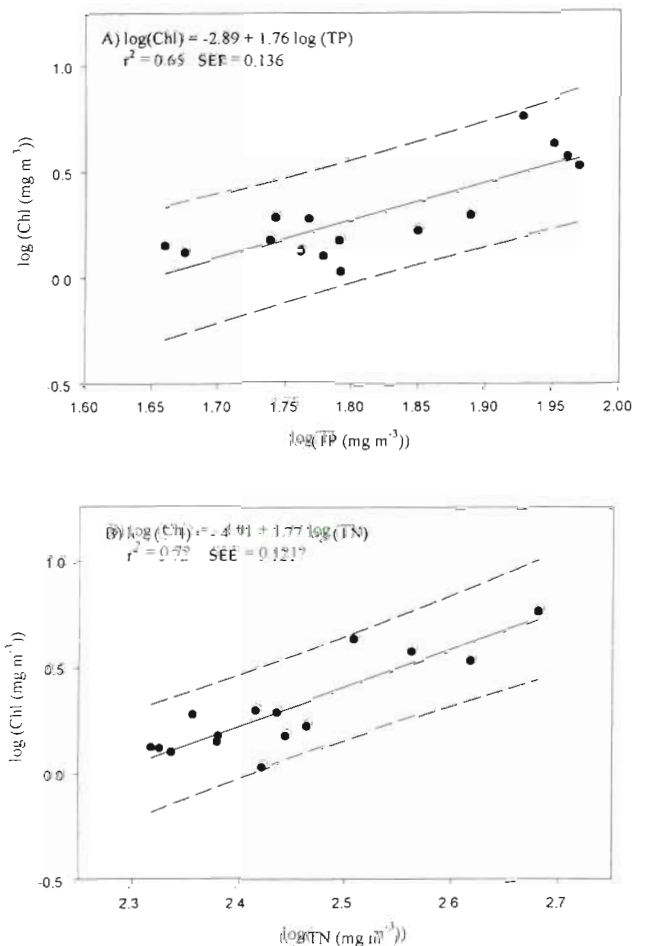


Fig. 2. Chl:TP and chl:TN relations for the 15 PEI estuaries. SEE: model standard error of the estimate

Table 3. A comparison of lake chl:nutrient relations from other studies for the 15 PEI estuaries. SEE: model standard error of the estimate. Nr.: not recorded

| Model | Slope | Intercept | n | r ² | SEE | Source |
|-----------------------|-------------|---------------|-----------|----------------|--------------|------------------------|
| Log chl:log TP | 1.449 | -1.136 | 77 | 0.96 | 0.214 | Dillon & Rigler (1974) |
| Log chl:log TP | 0.96 | -0.553 | 77 | 0.88 | 0.251 | OECD (1982) |
| Log chl:log TP | 1.76 | -2.890 | 15 | 0.65 | 0.136 | This study |
| Log chl:log TN | 1.445 | -3.131 | 133 | 0.69 | nr | Prairie et al. (1989) |
| Log chl:log TN | 1.40 | -2.5 | 21 | nr | nr | Sakamoto (1966) |
| Log chl:log TN | 1.78 | -4.06 | 15 | 0.72 | 0.121 | This study |

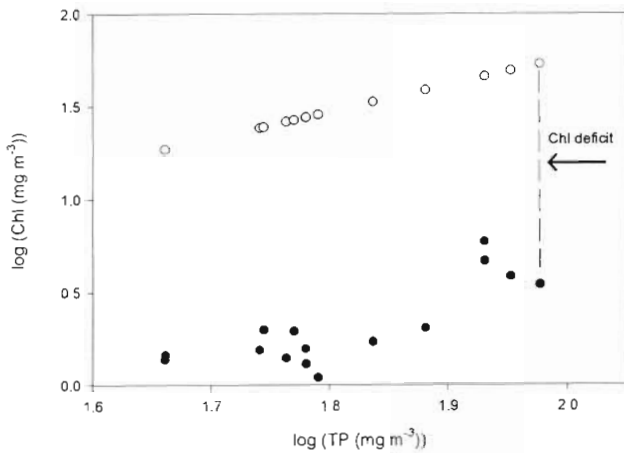


Fig. 3. Chl:TP relations calculated from the Dillon & Rigler (1974) equation (○) and observed for the 15 PEI estuaries (●), demonstrating chl deficit

Mass-balancing phytoplankton biomass

The equation used to model phytoplankton growth is:

$$dB/dt = PP - B \cdot k_L \quad (1)$$

where B is phytoplankton biomass (mg C m^{-3}), PP is primary production ($\text{mg C m}^{-3} \text{ d}^{-1}$) and k_L is the specific loss rate (d^{-1}). At steady state, dB/dt is zero and Eq. (1) can be rewritten as:

$$PP = B \cdot k_L \quad (2)$$

To determine whether we could assume that phytoplankton biomass is at steady state, we plotted biomass as a function of time over the 6 sampling rounds for each estuary and then looked for trends in the data. In almost all the estuaries, chl fluctuated without trend around the mean (Fig. 4). We thus assumed that biomass is at steady state and that we could calculate a steady-state mass balance for phytoplankton.

In our phytoplankton mass balance, the 2 main losses in all 15 estuaries are losses via flushing and sedimentation. Thus Eq. (2) can be rewritten as:

$$B = PP \cdot (k_f + k_s)^{-1} \quad (3)$$

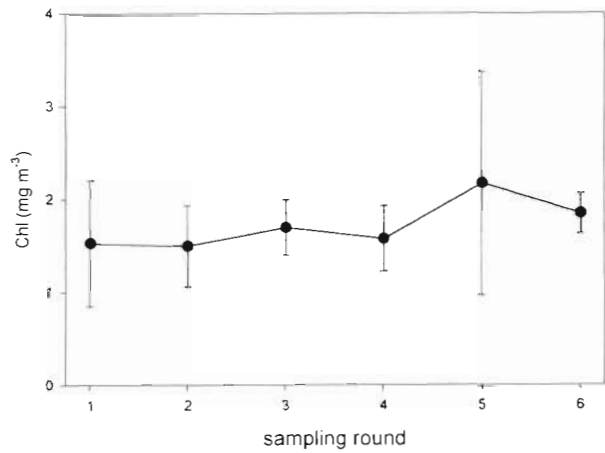


Fig. 4. Variation in chl over time for Boughton Estuary

where k_f and k_s are the loss coefficients (d^{-1}) for flushing and sedimentation. The loss coefficient due to flushing, k_f , is calculated using the salt-water fraction method (Bowden 1980):

$$k_f = Q \cdot V^{-1} \cdot [(S_s - S_m) \cdot S_s^{-1}]^{-1} \quad (4)$$

where Q is the freshwater load ($\text{m}^3 \text{ d}^{-1}$), V is the estuary volume (m^3), S_m is the mean salinity in the estuary (‰) and S_s is the salinity (‰) of open water around the island. For each estuary, the freshwater load was calculated as the product of the average daily rainfall during the period sampled (B. Raymond, Prince Edward Island Department of Fisheries and Environment, pers. comm.) and the area of the watershed. The loss coefficient due to sedimentation, k_s , was calculated from the specific settling rate (0.1 m d^{-1} ; O'Connor 1981) divided by the mean depth of the estuary.

To estimate PP in the estuaries, we collected data for 5 estuaries along the U.S. east coast for PP (Boynton et al. 1982) and chl and TP [United States Environmental Protection Agency (US EPA) unpubl. data, retrieved from STORET (Central Data Repository)]. We calculated the means and coefficients of variation for these 3 variables: while chl varied 6-fold, PP varied by a factor of 2 (Table 4). This is consistent with results from Oviatt et al. (1986) demonstrating that experimental

nutrient additions resulting in a 32-fold increase in nutrients produced only a 3.5-fold increase in PP. Given the small range of chl in the PEI estuaries, it is unlikely that PP varies greatly across the systems. We chose a value of $300 \text{ g C m}^{-2} \text{ yr}^{-1}$ as this approximates the average value of the estuaries represented (Table 4). It also corresponds to mesotrophic status (Nixon 1995), which is consistent with our TP values.

To test whether the mass-balance calculation provides a reasonable estimate of the biomass, B , observed in the estuary, we calculated B for all the estuaries, including only sedimentation and flushing as losses. These mass-balance estimates of B (B_{MB}) should be comparable to the B estimates from the Dillon & Rigler (1974) equation (B_{DR} ; we converted chl to C using a C:chl ratio of 50; Nixon et al. 1986). We plotted the Dillon & Rigler equation and its 95 % confidence bands for a predicted value (Zar 1984). The values of B_{MB} all fall within the prediction bands, suggesting that the values of B_{MB} are no less precise than the B_{DR} estimates (Fig. 5). We thus felt that the phytoplankton mass balance and the chosen parameters adequately estimate B for these estuaries.

Herbivory and mass balance

To estimate how much of the phytoplankton deficit was attributable to mussel herbivory, the impact of mussel aquaculture on phytoplankton biomass was estimated for the 6 estuaries with extensive mussel

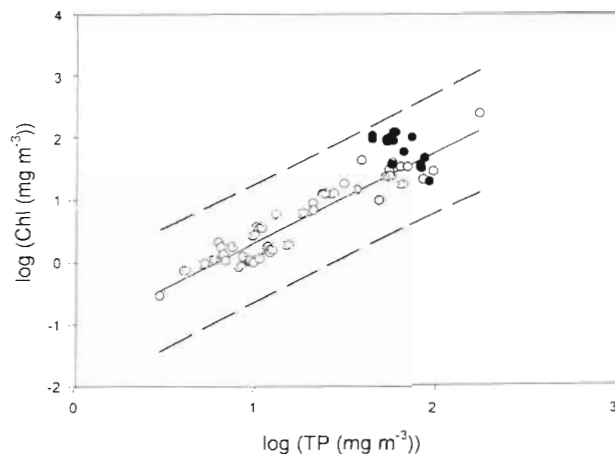


Fig. 5. A comparison of chl estimates from the Dillon & Rigler (1974) equation (solid line) and the mass-balance estimate (●), demonstrating that the mass-balance estimates fall within the 95 % confidence bands for predicted values (dashed lines; Zar 1984). (○) Original data used to fit the model

Table 4. A comparison of primary production (PP; Boynton 1982), chl and TP (US EPA unpubl. data) data for estuaries along the U.S. East Coast

| Estuary | PP ($\text{g C m}^{-2} \text{ d}^{-1}$) | PP ($\text{g C m}^{-2} \text{ yr}^{-1}$) | Chl (mg m^{-3}) | TP (mg m^{-3}) |
|--------------------------|--|---|-------------------------------|------------------------------|
| Narragansett | 0.739 | 270 | 3.31 | 102.4 |
| Chincoteague | 0.553 | 202 | 7.17 | 68.3 |
| Pamlico | 1.256 | 458 | 10.50 | 61.2 |
| Mid-Chesapeake | 0.951 | 347 | 13.00 | 73.0 |
| Neuse | 0.938 | 342 | 20.16 | 162.0 |
| Mean | | 324 | 10.83 | 93.4 |
| Standard deviation | | 96 | 6.36 | 41.4 |
| Coefficient of variation | | 30 | 58.76 | 44.4 |

farms (Table 1). The loss coefficient due to herbivory, k_h , was added to the loss term in Eq. (4). It is calculated as the fraction of the estuary filtered each day by the mussels:

$$k_h = V_F \cdot V^{-1} \quad (5)$$

where V_F is the volume filtered by the mussels per day and is equal to the product of the mussel biomass (g dry wt) and the specific filtration rate, f_m (Table 2). Filtration rates reported in the literature vary over an order of magnitude (0.03 to $0.4 \text{ m}^3 \text{ d}^{-1} \text{ g}^{-1}$ dry wt), depending on the size of the mussels used, the temperature and the experimental design. We chose a value in the middle of the range of $0.108 \text{ m}^3 \text{ d}^{-1} \text{ g}^{-1}$ dry wt (Vahl 1973).

To determine the phytoplankton deficit attributable to mussel herbivory, we recalculated B including the herbivory loss coefficient, k_h , in the mass balance. The difference between the phytoplankton biomass under herbivory, B_H , and that calculated in the absence of herbivory (B_{MB}) is the phytoplankton deficit attributable to herbivory. Herbivory accounts for between 45 and 88% of the phytoplankton deficit (Table 5).

Table 5. Phytoplankton biomass deficit attributable to mussels: observed B (B_o ; mg C m^{-3}), biomass expected from the mass balance (B_{MB} ; mg C m^{-3}) calculated from Eq. (3), where the loss terms are flushing (k_f) and sedimentation (k_s), biomass expected in the presence of mussels (B_H ; mg C m^{-3}), where herbivory (k_h) is included in the loss term of Eq. (4), and percent reduction in the phytoplankton deficit [$100 \times (B_{MB} - B_H) / (B_{MB} - B_o)$]

| Site | B_o | B_{MB} | B_H | % reduction |
|--------------|-------|----------|-------|-------------|
| Boughton | 70 | 5328 | 704 | 88 |
| Brudenell | 98 | 1920 | 1105 | 45 |
| Cardigan | 77 | 4865 | 111 | 78 |
| Murray River | 65 | 6417 | 1936 | 71 |
| Rustico | 99 | 1424 | 1424 | 69 |
| St. Peters | 86 | 1057 | 1057 | 67 |

Turbidity

The estimates of PP used to calculate B_{MB} and B_H above were volumetric and assume that PP occurs throughout the water column. Such an assumption overestimates PP, and turbidity will further decrease the depth to which PP occurs.

Secchi depth can be used to estimate the depth of the euphotic zone (Z_E ; Cole 1994), and convention frequently uses a Z_E :Secchi depth ratio of 2 (Dillon & Rigler 1974). However, turbidity and colour can reduce PAR (photosynthetically active radiation) by 66 to 99% within a meter of water (James & Birge 1938 in Wetzel 1982). Thus, for turbid estuaries where Secchi depth was less than 2 m (Dunk, North Lake, Percival and Wilmot), we used a ratio of Z_E :Secchi depth of 1; for the remaining estuaries which were less turbid we used the conventional ratio of 2. The mass-balance equation thus becomes:

$$B = PP_E \cdot (k_l + k_s + k_h)^{-1} \quad (7)$$

where PP_E is the amount of PP occurring in the euphotic zone:

$$PP_E = PP \cdot (Z_E \cdot Z_M^{-1}) \quad (8)$$

where Z_M is the mean depth of the estuary. Recalculating B to include losses due to herbivory and the effect of turbidity, B_T , we find that turbidity accounts for 8 to 35% of the phytoplankton deficit in the estuaries with mussels and 35 to 75% of the deficit in the other estuaries (Table 6).

Table 6. Phytoplankton biomass deficit attributable to turbidity: observed B (B_O ; mg C m^{-3}), biomass expected from the mass balance (B_{MB} ; mg C m^{-3}), biomass expected given reduction in primary production as a function of turbidity (B_T ; mg C m^{-3}), and percent reduction in the phytoplankton deficit [for estuaries with mussels = $100 \times (B_{MB} - B_T)/(B_{MB} - B_O)$; for estuaries without mussels = $100 \times (B_{MB} - B_T)/(B_{MB} - B_O)$]

| Site | B_O | B_{MB} | B_T | % reduction |
|----------------|-------|----------|-------|-------------|
| Boughton | 70 | 5328 | 274 | 8 |
| Brudenell | 98 | 1920 | 503 | 33 |
| Cardigan | 77 | 4865 | 518 | 12 |
| Darnley Basin | 69 | 4913 | 2710 | 45 |
| Dunk | 296 | 1914 | 741 | 72 |
| Foxley | 102 | 5316 | 3017 | 44 |
| Grand | 73 | 5638 | 2517 | 56 |
| Mill River | 192 | 2446 | 1270 | 52 |
| Murray River | 65 | 6417 | 1432 | 8 |
| North Lake | 233 | 1716 | 1193 | 35 |
| Percival | 55 | 6314 | 1642 | 74 |
| Rustico | 99 | 4423 | 922 | 11 |
| St. Peters | 86 | 3042 | 595 | 15 |
| Savage Harbour | 79 | 4606 | 2541 | 45 |
| Wilmot | 174 | 1020 | 510 | 60 |

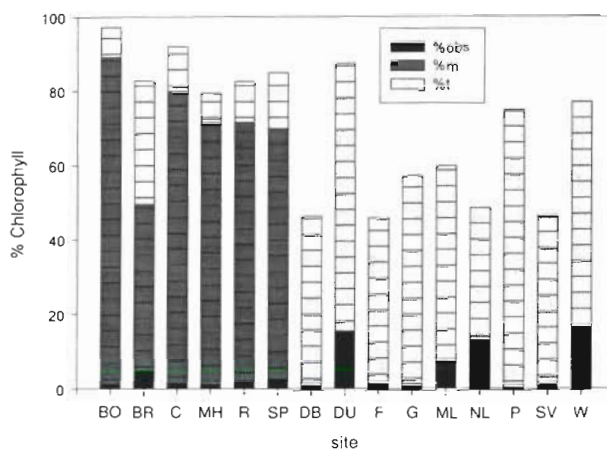


Fig. 6. Proportion of phytoplankton deficit accounted for by herbivory (% m) and turbidity (% t). % obs: proportion observed

Combined effects of herbivory and turbidity in explaining the phytoplankton deficit

The combined effects of herbivory and turbidity account for between 35 and 96% of the phytoplankton deficit (Fig. 6). The average remaining phytoplankton deficit is 32%. The mass balance is most effective in accounting for the phytoplankton deficit in estuaries with mussel aquaculture (78 to 96% of the deficit). In the remaining estuaries, the mass balance accounts for 35 to 75% of the phytoplankton deficit and on average 46% of the deficit remains. The highest remaining deficit (65%) is in North Lake, a very small, shallow estuary that is remarkably clear for its depth, thus the mass balance had little effect.

An empirical alternative to the mass balance

We have argued that the chl deficit is a function of the loss rates (flushing, sedimentation and herbivory) and decreased primary productivity due to turbidity. Thus, it should be possible to predict the deficit empirically as a function of these loss rates and turbidity. We calculated the deficit both arithmetically:

$$Def_A = chl_E - chl_O \quad (9)$$

and geometrically:

$$Def_G = 10^{\log chl_E - \log chl_O} \quad (10)$$

The arithmetic deficit, Def_A , indicates the absolute difference between expected chl (chl_E) and observed chl (chl_O), while the geometric deficit, Def_G , indicates the relative difference in terms of factors. We combined the effects of the loss rates and turbidity as follows:

$$\text{Total losses} = k_{TOT} \cdot (Z_E \cdot Z_M^{-1}) \quad (11)$$

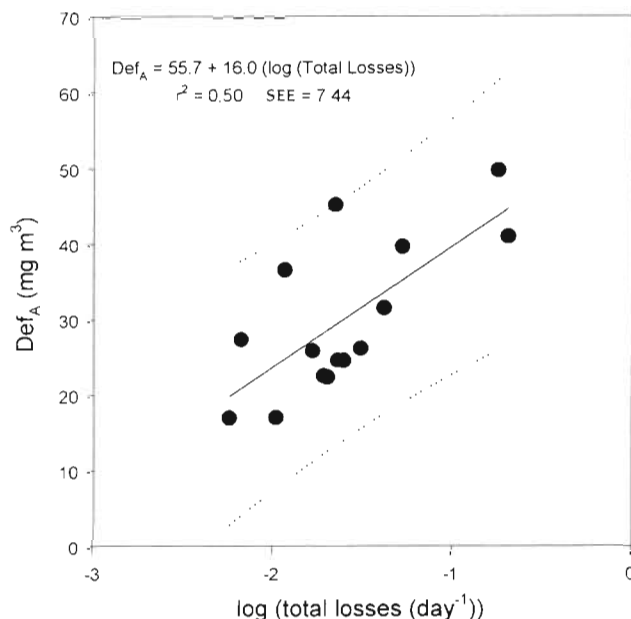


Fig. 7 Empirical model predicting the arithmetic chl deficit (Def_A) as a function of log total losses; dashed lines are 95% prediction intervals

where k_{TOT} is the sum of k_l , k_s and k_h and $Z_E \cdot Z_M^{-1}$ is the ratio of the euphotic depth to the mean depth as in Eq. (8). In other words, if the euphotic depth is half of the mean depth of the estuary, the losses are effectively doubled. We estimated a linear model predicting these deficits as a function of the total loss and were able to fit the model:

$$Def_A = 55.7 + 16.0 \cdot \log(\text{Total losses}) \quad (12)$$

This model accounted for 50% of the variation in Def_A (Fig. 7; $n = 15$, $p < 0.003$). We also fit other linear and nonlinear models, using Secchi depth and other combinations of k_{TOT} and turbidity. None of these models had stable residuals.

DISCUSSION

The strong relations between chl and total nutrients (Fig. 2) support our initial hypotheses that estuarine phytoplankton biomass is tightly correlated with bottom-up nutrient factors and that the relations can be captured using a comparative empirical approach. The applicability of the comparative approach to estuarine systems is encouraging as this approach has provided simple ecological models that have contributed to effective lake management (e.g. OECD 1982). In contrast, there have been few ecological models available to support coastal management efforts and those that exist are frequently estuary-specific, information-

intensive and expensive (cf. Linker et al. 1993, Bricker & Stevenson 1996).

These results also demonstrate that this empirical approach can successfully identify simple patterns across estuaries. Such cross-system relations require that each system, whether a lake or an estuary, can be represented by 'characteristic' values. This requirement has meant that researchers implicitly assume that the systems are at steady state and are relatively homogenous in order to minimize sampling effort. Estuaries have complex hydraulic regimes, are considered spatially heterogeneous and generally have shorter water residence times than lakes due to their relatively open exposure to the sea (Bowden 1980). These characteristics could constrain the use of empirical approaches. However, with a slightly more intense sampling regime than that typically used in lakes, representative values for estuaries can be estimated (T. Nayar & J. J. Meeuwig unpubl.).

The strength of the relations also appears insensitive to residence time, which ranged between 3 and 356 d. Provided the residence time exceeds the specific growth rate of phytoplankton, patterns between chl and nutrients are possible. This result is consistent with those of Basu & Pick (1996), who demonstrated a strong relation between chl and TP ($r^2 = 0.76$) in rivers with residence times ranging between 3 and 19 d.

That the relation between chl and TN is marginally stronger than that between chl and TP (Fig. 2) suggests that TN, rather than TP, limits estuarine chl, and thus our third hypothesis should be rejected. This interpretation reflects the assumption that the relative strength of patterns indicates the relative importance of their respective independent variables to the dependent variable (Smith 1979). The average TN:TP ratio of 4.5 also supports the argument for TN as the key limiting nutrient in these estuaries.

Despite the general applicability of a limnological approach to estuaries, the relations between chl and nutrients differ in lakes and estuaries. While the slopes of the chl:TP and chl:TN relations are similar in lakes and estuaries, the intercepts of the estuarine nutrient models are approximately 1 to 2 orders of magnitude lower than those of lake nutrient models. Thus, the yield of chl per unit TP or TN is much lower in these estuaries. This result was unexpected as a chl:TP relation developed for estuaries in North and South Carolina (US EPA unpubl. data) is indistinguishable from lake relations (Fig. 8), suggesting that estuarine phytoplankton can respond to nutrients similarly to lake phytoplankton.

Other researchers have also noted a lower phytoplankton yield in coastal waters (cf. Contreras & Kerekes 1993, Boynton et al. 1996) on the order of a 2- to 8-fold discrepancy. A discrepancy on the level of 2

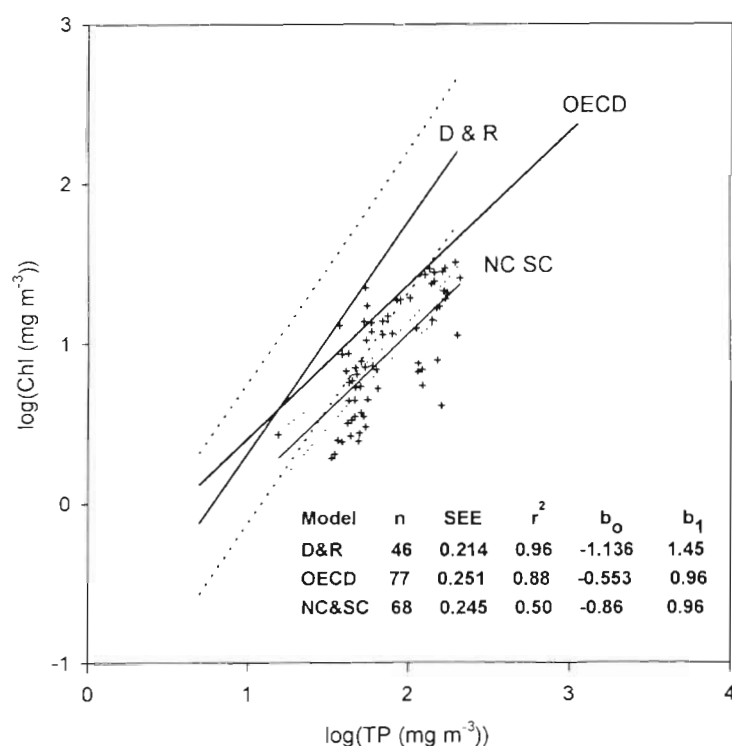


Fig. 8. Chl:TP relations from Dillon & Rigler (1974) (D&R), OECD (1982) and North and South Carolina estuaries (NC&SC) (US EPA unpubl. data)

orders of magnitude was unexpected as phytoplankton element requirements are fairly similar in lakes and estuaries (Hecky & Kilham 1988). The result cannot be attributed to estuarine flushing as this would result in a general dilution with low concentrations of both phytoplankton biomass and nutrients rather than a low yield. Herbivory as a top-down control of phytoplankton biomass or light limitation as a function of turbidity are the 2 most likely explanations.

Since Carpenter et al. (1985) defined their trophic cascade model, interest in top-down control of phytoplankton biomass has increased. Mazumder (1994) demonstrated that the chl:TP relation is weaker in lakes where large filtering *Daphnia* are present than in lakes lacking *Daphnia*, and that the yield of chl per unit TP is lower in lakes with *Daphnia* by approximately a factor of 3. Quiros (1990) also demonstrated that herbivory by macrozooplankton in Argentinean lakes and reservoirs strongly decreased the intercept of his chl:TP relation by almost an order of magnitude (-1.9 to -2.6). Mellina et al. (1995) showed similar results for zebra mussels *Dreissena polymorpha* in Lake Erie, Lake St. Clair and experimental aquaria. Our mass-balance calculation of the impact of mussel farms on the standing stock of algae suggests that phytoplankton biomass in the 6 estuaries with mussel farms has been reduced by 45 to

88% (Table 5). This level is similar to that found in an enclosure study in which *Mytilus edulis* reduced phytoplankton biomass by 54 to 90% of controls (Riemann et al. 1988). It is likely that suspension feeders are also exerting pressure on the phytoplankton biomass in the other 9 estuaries as all support natural clam and oyster *Crassostrea virginica* populations. For instance, the Dunk and Wilmot estuaries, in particular, provide 60 to 70% of the 1.6×10^6 kg annual oyster harvest. Estimating total biomass from Sephton & Bryan (1989), and using a filtration rate of $0.002 \text{ m}^3 \text{ d}^{-1} \text{ g}^{-1}$ dry wt (Bacher et al. 1995), an additional 29% of the phytoplankton deficit in Dunk can be explained.

The turbidity analysis suggests that a small euphotic zone can sufficiently decrease PP to account for 6 to 79% of the phytoplankton deficit (Table 6). Light limitation as a function of turbidity appears feasible, particularly in the deeper estuaries such as Grand and Mill River. These estuaries show no evidence of stratifying with respect to salinity and temperature; thus, it is likely that the phytoplankton spend time below the euphotic zone.

Generally, herbivory and turbidity account for the deficit between observed phytoplankton biomass and that expected from lake mod-

els, with an average deficit of 32% remaining. This is as accurate as we can expect because PP itself has a coefficient of variation of approximately 30% and we cannot estimate *B* with greater accuracy than PP. In comparison, the empirical model left 50% of the deficit unexplained. These 2 approaches to explaining the deficit complement each other: the mass-balance model allows a more refined breakdown of the loss rates but requires an estimate of PP; the empirical model is a black box in terms of loss rates but does not require an estimate of PP. Because both approaches demonstrate the importance of herbivory and turbidity, together they make a strong case for the deficit as a function of these 2 factors.

The effectiveness of the mass-balance model suggests that once herbivory and turbidity are included in the analysis, lakes and estuaries show similar patterns between phytoplankton biomass and nutrients. Although the approach is particularly effective in the estuaries where herbivory is a dominant factor, it is less effective in the estuaries in which no mussel aquaculture occurs, decreasing the deficit by only 54% on average. It is particularly ineffective in very small estuaries (e.g. North Lake) and in the very shallow, turbid estuaries (e.g. Dunk, Percival, Wilmot). In these shallow, turbid estuaries, a decrease in PP due to light lim-

itation seems less feasible than in the deeper estuaries because these shallow estuaries support a large biomass of the benthic alga *Ulva lactuca* despite the very high turbidity. If light were limiting, it is unlikely that *U. lactuca* would be thriving to this extent.

Thus, although we have argued that turbidity indicates light limitation, it may be a surrogate for another variable controlling phytoplankton biomass. We speculate that this variable is iron. Iron is most usually thought of as a limiting nutrient in certain areas of the ocean (Martin & Fitzwater 1988). However, in areas of excess iron, iron scavenging of phosphorus may make phosphorus unavailable to phytoplankton and thus limit phytoplankton biomass (Froelich 1988). Natural clays with iron hydroxides adsorb phosphorus under acid conditions such as those found in the iron-rich soils of PEI (MacDougall et al. 1988). Soil particles with P adsorbed to them would then be transported into the estuaries where this P may remain relatively unavailable to the phytoplankton. Thus, TP values which do not discriminate between available and unavailable P may result in a low yield in systems where an unusually high proportion of P is unavailable to the algae. As the correlation between particulate TP and particulate iron is strong ($r = 0.95$; Eyre 1994), the proportion of unavailable P should be constant and a function of iron and thus of turbidity.

Control of P availability by iron was considered by Schindler (1981), who suggested that P limitation in lakes might in fact be a function of high iron concentrations recycled from the sediments as a result of the reducing conditions of the hypolimnion. In coastal systems, Krom et al. (1991) also invoked adsorption of P by iron resulting in P limitation of the eastern Mediterranean, which receives high levels of iron-laden dust from the Sahara.

Iron control of P may thus partly account for the low chl yields in turbid estuaries where the mass-balance analysis accounted for only a small proportion of the phytoplankton deficit. Iron control of P may also account for the tight correlation between chl and nutrients. In the absence of nutrient limitation, the pattern between chl and nutrients should only occur if the variable that limits phytoplankton biomass covaries with nutrients. It is likely that iron covaries with nutrients in the PEI estuaries: iron is correlated with turbidity as it enters the estuaries on soil particles and turbidity is correlated with nutrients (Secchidepth:TN, $r = -0.68$; Secchi depth:TP, $r = -0.57$). If iron controls the amount of P available to phytoplankton, an excess of iron would result in a reduced phytoplankton yield and lead to effective P limitation irrespective of the TN:TP ratio.

Indirect P limitation via excess iron would contradict the earlier conclusion that these estuaries are N lim-

ited. However, the evidence for N limitation is not that compelling. First, the coefficient of determination for the chl:TN relation ($r^2 = 0.72$) is only marginally greater than that for the chl:TP ($r^2 = 0.65$) and it is unclear whether such a small difference is sufficient to indicate the relative importance of N and P in limiting chl. Moreover, because TN and TP covary ($r = 0.82$), chl will be strongly correlated with both nutrients. Second, the low TN:TP ratios (3.1 to 8.7) that suggest N limitation may be a function of the loading ratio of N and P to the estuary rather than a function of phytoplankton uptake. Given the relatively short residence times of the estuaries, it is unlikely that ambient nutrient ratios are determined by phytoplankton uptake (Smith 1984). Such indirect control of phytoplankton biomass has been suggested by other researchers as well; Smith & Hollibaugh (1989) argue that carbon control of net heterotrophic systems is masked by an apparent N limitation.

In conclusion, strong patterns can be identified between chl and total nutrients in estuaries. However, the relative strength of these patterns and the TN:TP ratio cannot be used to infer which nutrient is limiting phytoplankton biomass. Thus, although such models are useful tools for coastal managers to predict phytoplankton biomass from nutrient concentrations, they cannot be used to support decisions with respect to single nutrient reduction strategies. The low yield of chl per unit nutrient points to the importance of other factors such as herbivory and turbidity, and potentially to indirect control by iron, in determining phytoplankton biomass. The comparison of these estuaries to lakes, and the use of mass-balance and empirical models to account for the deficit, suggests that, once the effects of herbivory and turbidity are accounted for, phytoplankton response to nutrients is similar in lakes and estuaries.

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