

# Responses of estuarine and coastal marine phytoplankton to nitrogen and phosphorus enrichment

Val H. Smith<sup>1</sup>

Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045

## Abstract

A cross-ecosystem comparison of data obtained from 92 coastal zone ecosystems worldwide revealed a strong positive response of marine phytoplankton biomass to nutrient enrichment that is highly consistent with the general patterns reported previously in the limnological literature for freshwater lakes and reservoirs. Average concentrations of chlorophyll *a* in estuarine and coastal marine systems were strongly dependent on the mean concentrations of total nitrogen and total phosphorus in the water column. Moreover, as is true of freshwater ecosystems, the identity of the primary growth-limiting nutrient for marine phytoplankton appeared to be generally predictable from water-column total nitrogen:total phosphorus (TN:TP) ratios. This similarity in physiological response to nutrients likely derives from the shared evolutionary histories of marine and freshwater phytoplankton.

Much of our current knowledge of eutrophication is derived from research on lake systems in North America and Europe, which led to the development of the predictive frameworks now used worldwide in freshwater management (Smith 1998). However, it is clear that, in many nutrient-sensitive coastal marine waters, eutrophication can cause increased rates of primary productivity, changes in algal and vascular plant biomass, shifts in algal and vascular plant species composition, diebacks of sea grasses and corals, reduced populations of fish and shellfish, reductions in transparency, losses of acceptable aquatic habitats and biodiversity, and oxygen depletion in bottom waters (National Research Council 2000). Coastal marine environmental quality is thus an issue of major global concern (United Nations Environment Programme 1995; Elmgren and Larsson 1997; Rabalais and Nixon 2002; Smith et al. 1999).

It is thus critically important that we understand the quantitative linkages that exist between nutrients and water quality in our surface waters. These linkages allow us not only to assess the risk of eutrophication-related problems in receiving waters but also to quantify the degree to which nutrient loading must be controlled or reduced to maintain desirable water quality. Unfortunately, our understanding of the quantitative linkages that exist between anthropogenic nutrient loading and water quality in estuaries and coastal ma-

rine ecosystems is much less well developed than for freshwater systems. Different paradigms for the nutrient limitation of biological production have emerged for lakes versus oceans during the past 20 yr (Hecky and Kilham 1988; Downing 1997). In addition, marked differences of opinion still persist in the literature concerning the degree to which nutrient loading, water column nutrient concentrations, and marine primary production are linked (e.g., contrast Boynton et al. 1996 with Sharp 2001). A unification of our knowledge of eutrophication is therefore badly needed.

An essential step toward this unification was made by Guildford and Hecky (2000), who presented a comparative study of contemporaneous total nitrogen (TN), total phosphorus (TP), and chlorophyll *a* measurements in freshwater and marine ecosystems. Using data from individual sampling dates from sites located in both lakes and oceans, Guildford and Hecky (2000) revealed a significant correlation between Chl *a* and TP for their marine sites but parallel evidence that marine phytoplankton biomass was controlled by TN was inconclusive. Hoyer et al. (2002), in contrast, found significant correlations between Chl *a* and both TN and TP in Florida's coastal waters. The purpose of this article is to explore further the results from these two studies, using a larger and geographically more diverse dataset compiled from a variety of sources worldwide.

## Methods

*Study areas and data collection methods*—Data on TP ( $\mu\text{mol L}^{-1}$ ), TN ( $\mu\text{mol L}^{-1}$ ), and phytoplankton biomass estimated as concentrations of Chl *a* ( $\mu\text{g L}^{-1}$ ) were obtained from the published literature, open file reports, and personal communications for a total of 335 cases derived from 92 different estuarine and coastal marine sites worldwide (Table 1). TP measurements were made consistently in these studies using standard molybdate-based, spectrophotometric methods. As was true in the data set of Smith (1982), the analytical methods used for TN in these studies ranged from direct spectrophotometric analyses of TN to the summation of independent Kjeldahl nitrogen and inorganic nitrogen measurements. Nitrogen versus phosphorus limitation of

<sup>1</sup> Corresponding author (vsmith@ku.edu).

## Acknowledgments

I thank Richard Boler, Environmental Protection Commission of Hillsborough County, Florida; and George Gibson, U.S. Environmental Protection Agency, for generously providing unpublished data from Tampa Bay and the Mid-Atlantic Bight, respectively. I also thank Mandy Joye and Bob Howarth for co-chairing with me the ASLO Historical Session that led to the creation of this special issue of *Limnology and Oceanography*. Comments from Steve Smith and an anonymous reviewer were extremely helpful during the revision of this article. This article is dedicated to David Schindler in recognition of his tremendous contributions to limnology and eutrophication science.

This research was supported in part by National Science Foundation grants DEB-9520882 and DEB-9815799 to Mathew A. Leibold and Val H. Smith.

Table 1. Coastal marine sites used in model development.

Site	Reference
Adriatic coast	Giovanardi and Tromellini (1992)
Archipelago Sea, Finland	Kirkkala et al. (1998)
Baltic Sea	Meeuwig et al. (2000)
Chesapeake Bay	Price et al. (1985)
Florida Bay	Fourqurean et al. (1993)
Mexican coastal lagoons	Contreras and Kerekes (1993)
Mid-Atlantic Bight	George Gibson, pers. comm.
Peel Estuary, Australia	McComb and Lukatelich (1987)
Potomac estuary	Limno-Tech (1991)
Prince Edward Island	Meeuwig et al. (1998)
Swedish coast	Wallin (1991)
Tampa Bay	Richard Boler, pers. comm.

phytoplankton growth was assessed, where possible, using TN:TP ratios, but, where measurements of both TN and TP were not available, the nutrient limitation status of a given water body was determined from author-reported assessments.

In addition, unlike Borum (1996) and Nielsen et al. (2002), attempts were *not* made to modify the total nutrient measurements by subtracting estimates of the phytoplankton's own contributions to TN and TP. This modification was not performed for two major reasons. First, neither the carbon:Chl *a* ratio nor nutrient stoichiometry are constant in marine phytoplankton cells (*see Discussion*), and the use of such constants would add an inconsistent and unpredictable source of error to the database. In addition, this study is intended to expand directly on the results of Guildford and Hecky (2000) and Hoyer et al. (2002), both of which were based on analyses of unmodified TN and TP concentrations.

As in Smith (1982, 1998), the data presented here are derived from arithmetic means of two or more observations obtained from multiple sampling events made during a single calendar year at a specific coastal marine site. Such averaging procedures are inherent in the most commonly used eutrophication modeling frameworks for freshwater ecosystems, as well as in the emerging models that are being developed for marine systems (e.g., Giovanardi and Tromellini 1992; Boynton et al. 1996; Meeuwig et al. 2000; Hoyer et al. 2002).

*Responses of marine phytoplankton biomass to nitrogen*—Unlike the analysis of Guildford and Hecky (2000), a very strong curvilinear relationship was observed between mean phytoplankton biomass and mean total nitrogen for the marine sites at which measurements of both Chl *a* and TN were available (Fig. 1):

$$\log_{10}\text{Chl } a = -3.71 + 4.26 \log_{10}\text{TN} - 0.88(\log_{10}\text{TN})^2, \\ r^2 = 0.84 \quad (1)$$

This strong correlation between algal production and nitrogen availability is consistent with the majority of empirical nitrogen-based models for phytoplankton biomass and productivity that were reported in the literature for marine ecosystems during the past decade (e.g., Hessen et al. 1992; Borum 1996; Kelly 2001; Nielsen et al. 2002), and strong

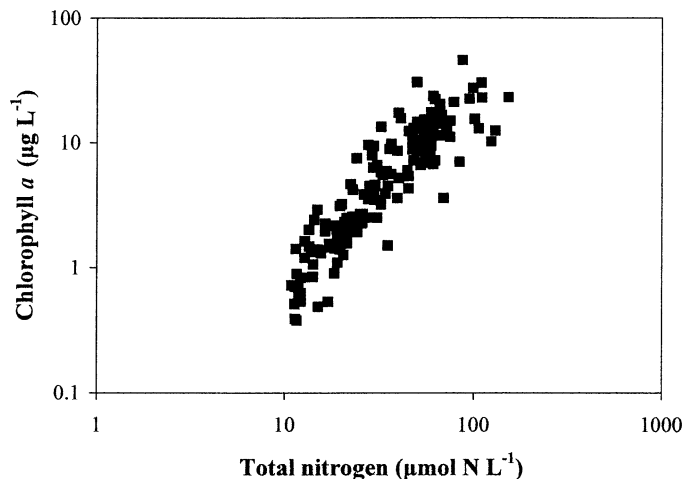


Fig. 1. Relationship between annual mean Chl *a* and annual mean TN concentrations in estuarine and coastal marine ecosystems.

TN-Chl *a* relationships would be expected a priori from the commonly stated assumption that nitrogen is typically the nutrient that is present in the shortest supply relative to algal growth requirements in marine ecosystems (Howarth 1993).

*Responses of marine phytoplankton biomass to phosphorus*—Before the analyses by Guildford and Hecky (2000) and Hoyer et al. (2002), relatively few investigators sought to examine the relationship between phytoplankton biomass and phosphorus availability in marine systems. However, a strong correlation between instantaneous measurements of Chl *a* and dissolved inorganic phosphorus was reported >30 yr ago by Ketchum (1969) in his comparative analysis of data from Atlantic marine ecosystems; early mathematical models of production in the Atlantic and the North Sea were driven by concentrations of inorganic phosphate and *not* by nitrogen (e.g., Riley 1965), and geochemical arguments can be made to argue for P limitation of phytoplankton growth in pristine marine environments (Smith 1984; Downing 1997).

Although more scatter was evident in the data than in the corresponding plot for nitrogen, a strong correlation was found between Chl *a* and TP at the sites for which mean concentrations of both Chl *a* and TP were available (Fig. 3 below).

$$\log_{10}\text{Chl } a = 0.39 + 0.71 \log_{10}\text{TP}, \quad r^2 = 0.60 \quad (2)$$

This regression model broadly confirms the pattern of positive covariance between Chl *a* and TP that was observed by Guildford and Hecky (2000) and Champion and Currie (2000) for individual sampling dates and by Meeuwig et al. (1998, 2000) and Hoyer et al. (2002) using averaged values.

*Nitrogen versus phosphorus limitation of marine phytoplankton biomass*—As has been reported in more geographically restricted analyses (Meeuwig et al. 2000; Hoyer et al. 2002; Nielsen et al. 2002), the evidence shown in Figs. 1 and 2 indicates that phytoplankton biomass appears to be correlated with both TN and TP in marine environments.

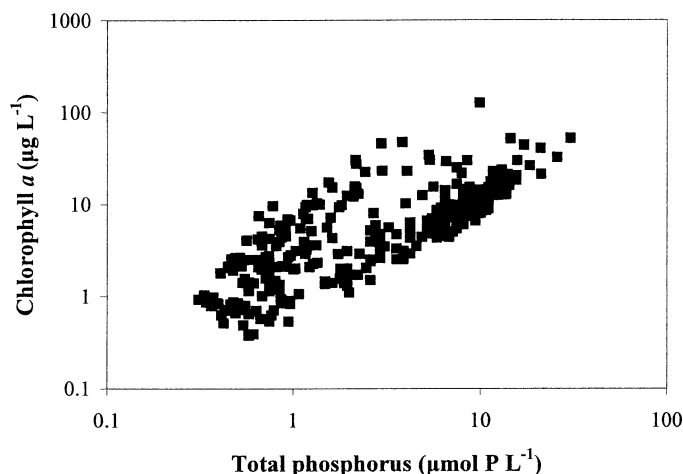


Fig. 2. Relationship between annual mean Chl *a* and annual mean TP concentrations in estuarine and coastal marine ecosystems.

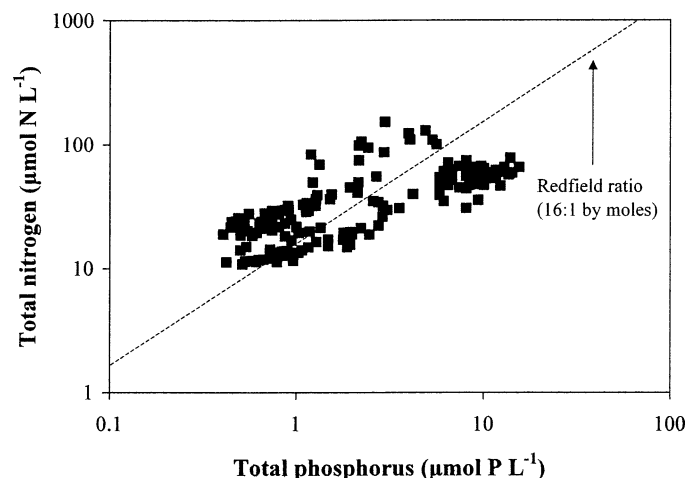


Fig. 3. Relationship between annual mean TN and TP concentrations in estuarine and coastal marine ecosystems.

How then can we discern the identity of the primary growth-limiting nutrient in these ecosystems?

Redfield (1934, 1958) concluded that the particulate N:P ratio in marine organisms averages  $\sim 16:1$  by moles, a value that is now known as the Redfield ratio. This ratio has widely been used to evaluate the nutrient limitation status of many marine ecosystems worldwide where measurements of particulate nutrients, dissolved inorganic nutrients, or total nutrient concentrations are available (Hecky and Kilham 1988; Fisher et al. 1995; Downing 1997), and it provides a useful screening criterion.

A plot of TN and TP concentrations from the coastal marine sites for which both sets of measurements were available revealed a strong positive correlation between TN and TP concentrations (Fig. 3):

$$\log_{10} \text{TN} = 1.38 + 0.41 \log_{10} \text{TP}, \quad r^2 = 0.55 \quad (3)$$

Interestingly, this data set was almost exactly bisected by the Redfield ratio, a conclusion that was further underscored by an analysis of the cumulative frequencies of TN:TP ratios from these sites (Fig. 4). Surprisingly, these plots suggest that  $\sim 50\%$  of the sites analyzed here should show evidence of phosphorus limitation of phytoplankton growth if the Redfield ratio is used as an initial screening criterion.

Similar conclusions concerning the a priori likelihood of N versus P limitation in marine systems can be drawn from other analyses. The TN:TP loading ratio to coastal ecosystems is highly variable, and, as in freshwater ecosystems, this variability in N:P loading ratios can create the potential for differences in phytoplankton nutrient limitation status (Doering et al. 1995; Fisher et al. 1999). For example, Nixon et al. (1986, their fig. 1) plotted the annual nitrogen and phosphorus inputs per unit area to a variety of agricultural, terrestrial, freshwater, estuarine, and coastal marine ecosystems, and the Redfield ratio also approximately bisects their data set. In addition, a more recent plot of annual TN and TP loading rates to estuarine and coastal ecosystems was similarly bisected by the Redfield ratio (Boynton et al. 1996, their fig. 6). Finally, the Redfield ratio approximately bisected the globally diverse data set for water column con-

centrations of TN and TP collected by Downing (1997, his fig. 1). However, the data shown in Fig. 4 provide additional new support for the hypothesis (Howarth et al. 1995; Downing 1997) that more pristine marine environments (annual mean TP  $< 0.8 \mu\text{mol P L}^{-1}$ ) tend to have TN:TP ratios in excess of the Redfield ratio and thus are likely to be consistently P limited. Our data also support their conclusion that heavily nutrient-enriched environments (annual mean TP  $> 8 \mu\text{mol P L}^{-1}$ ) tend to have TN:TP ratios lower than the Redfield ratio and thus are likely to be consistently N limited.

Does the total biomass of the marine phytoplankton communities examined in this study reflect these potential differences in nutrient limitation status? A meta-analysis of marine nutrient enrichment experiments by Downing et al. (1999) suggests that it should: the magnitude of phytoplankton growth responses to N is expected to be highest in nutrient-polluted, low N:P waters, and the magnitude of growth responses to P should be highest in more pristine, high N:P waters. Moreover, Fisher et al. (1999) elegantly demonstrated strong linear relationships between the molar inputs of

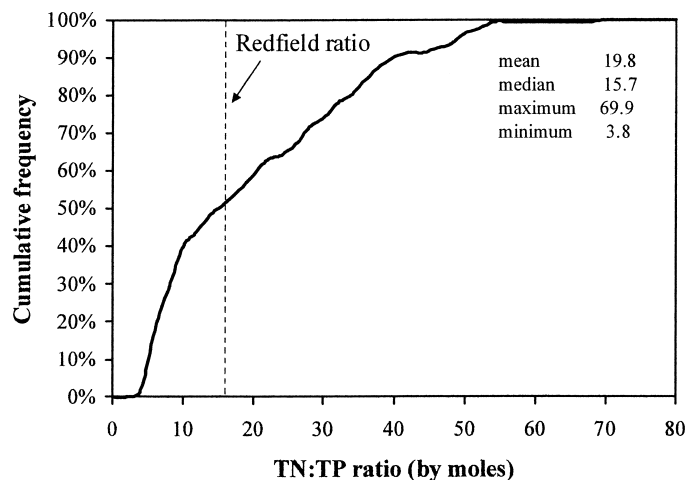


Fig. 4. Cumulative frequencies of TN:TP ratios in estuarine and coastal marine ecosystems.

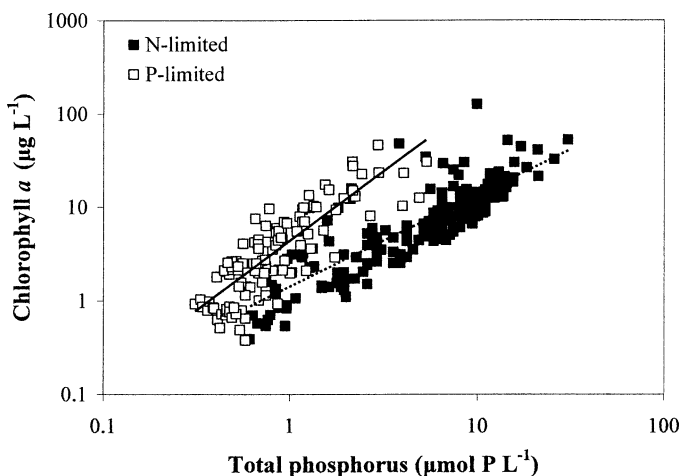


Fig. 5. Relationship between annual mean Chl *a* and annual mean TP concentrations in estuarine and coastal marine ecosystems, coded by inferred nutrient limitation status (see text). Separate regression lines are shown for putatively N-limited (dotted line) and putatively P-limited (solid line) ecosystems.

TN and TP and the average responses of phytoplankton to nutrient addition bioassays performed at five stations in the Chesapeake Bay.

Smith (1982) reported a decreasing yield of Chl *a* per unit of TP as the TN:TP ratio decreased in freshwater lakes, and I hypothesized that a similar effect of N:P ratios would be observed in the marine algal biomass data analyzed here. This hypothesis was tested by coding each case in the data set as being either being N or P limited. For cases in the data set where direct measurements of both TN and TP were available, N- versus P-limited growth was inferred from the mean TN:TP ratio using the empirical boundary of TN:TP < 20:1 by moles proposed by Guildford and Hecky (2000). When only TP measurements were available, I used author-reported assessments of nutrient limitation status to infer N- versus P-limited growth.

When these coded data were plotted in Fig. 5, a remarkable and highly significant discrimination was evident between the putatively N-limited versus putatively P-limited

sites in this data set (Table 2). Moreover, the regression model for putatively P-limited sites

$$\log \text{Chl } a = 1.48 \log \text{TP} + 0.61, \quad r^2 = 0.69 \quad (4)$$

has both a greater slope and a higher intercept from that found for putatively N-limited sites:

$$\log \text{Chl } a = 0.99 \log \text{TP} + 0.11, \quad r^2 = 0.74 \quad (5)$$

The general pattern evident in Fig. 5 broadly resembles the response pattern reported for freshwater lakes, in which the yield of Chl *a* per unit TP is greatly reduced at low TN:TP ratios (Smith 1982). These data thus very strongly support the key conclusion of Guildford and Hecky (2000) that marine and freshwater ecosystems have overlapping TN:TP ratios and that these ratios predict equally well in both sets of environments when N or P can become limiting for phytoplankton growth when available nutrient concentrations are low.

It is important to note, however, that the analyses reported here have relied on *mean* values of both TN and TP to draw inferences concerning N versus P limitation. It is very clear from the literature that many coastal marine environments can exhibit strong seasonality in nutrient limitation (e.g., Fisher et al. 1999) and that individual TN:TP ratios calculated from instantaneous measurements of TN and TP can, in some systems, be an inaccurate indicator of nutrient limitation on that sampling date (e.g., Magnien et al. 1992). I suggest that the use of TN:TP ratios that are based on annual means helps to reduce this type of potential error by suggesting the identity of the most commonly limiting nutrient.

Fig. 5 does raise interesting new questions about the details of N and P limitation in marine versus freshwater phytoplankton assemblages, however. In freshwater lakes, a much more gradual transition is typically evident in Chl-TP plots that is expressed as a slow intergradation between N and P limitation. For example, in his classical analysis of Japanese lakes, Sakamoto (1966) reported strong N limitation if TN:TP < 10:1 by mass (22:1 by moles), strong P limitation if TN:TP > 17:1 by mass (38:1 by moles), and either N or P limitation at intermediate ratios. These approximate boundaries were later confirmed by Forsberg and

Table 2. Summary of regression analysis to examine the effects of nutrient limitation status on the relationship between chlorophyll *a* and total phosphorus. The value of the dummy variable was set to 0 if the case was determined to be N limited, and dummy was set to 1 if the case was determined to be P limited (see text).

Variable	Coefficient	SE	Student's <i>t</i>	<i>p</i>	
Constant	0.03838	0.03179	1.21	0.1749	
Log TP	1.33505	0.07191	18.47	<0.0001	
Log TP <sup>2</sup>	-0.26829	0.06698	-3.85	0.0001	
Dummy	0.57458	0.04212	13.74	<0.0001	
<i>R</i> <sup>2</sup>	0.7432				
ADJUSTED <i>R</i> <sup>2</sup>	0.7408				
Source	df	SS	MS	<i>F</i>	<i>p</i>
Regression	3	53.1450	17.7150	319.27	<0.0001
Residual	332	18.3661	0.0555		
Total	335	71.5111			

Ryding (1980) using algal bioassays and were supported empirically by Smith (1982). The critical value of TN:TP < 20:1 by moles used by Guildford and Hecky (2000) to delimit strong N deficiency is completely consistent with, and likely to be indistinguishable from, the equivalent molar TN:TP ratio of 22:1 that was developed for freshwater lakes by the authors above.

The mechanism(s) that may be responsible for creating the much clearer apparent distinction between N versus P limitation in this marine data set than in comparable global datasets from freshwater lakes and reservoirs (e.g., Smith 1982; McCauley et al. 1989; Organisation for Economic and Cooperative Development 1982; Prairie et al. 1989) are unknown. However, it can be hypothesized that this difference in behavior may reflect differences in the abilities of marine and freshwater systems to correct nitrogen deficiencies via dinitrogen fixation.

In freshwater ecosystems, N deficiency frequently selects for phytoplankton dominance by heterocystous cyanobacteria, which can contribute large quantities of new nitrogen to the water column via their nitrogenase activity. This critically important biogeochemical mechanism allows many nitrogen-limited freshwater ecosystems to restore conditions of phosphorus limitation (Schindler 1977). In marine ecosystems, however, dominance by cyanobacteria in the water column is much more rare—planktonic dinitrogen fixation is much less commonly observed, and measured rates of  $N_2$  fixation are typically much lower in magnitude than in freshwater systems of comparable fertility (Vitousek and Howarth 1991; Paerl and Zehr 2000). The much more restricted ability of many marine ecosystems to restore conditions of phosphorus limitation thus may be at the heart of the pattern shown in Fig. 5. Many shallow coastal zone ecosystems are likely to have a very strong potential for sediment denitrification (e.g., Flemer et al. 1998), leading to losses of inorganic nitrogen that can drive water-column N:P ratios away from Redfield stoichiometry.

*Direct comparisons between coastal marine and freshwater ecosystems*—Hoyer et al. (2002) observed a highly significant difference in the response of Chl *a* to TP in coastal marine versus freshwater systems, noting that nearshore coastal Florida data typically fell well below the values predicted for Florida lakes. However, the generality of this apparent difference in algal biomass yield has not yet been examined for other regions. As can be seen in Fig. 6A, a similarly striking difference was also observed when the entire coastal marine database from Table 1 was compared with the global freshwater lake data set of Smith (1982). The amount of Chl *a* produced per unit of TP thus tended to be lower in coastal marine waters than in freshwater lakes, irrespective of their geographical location. Moreover, this difference in yield was conserved both for N-limited (Fig. 6B) and P-limited sites (Fig. 6C).

Hoyer et al. (2002) proposed that one mechanism that could account for the difference in behavior between these two sets of aquatic ecosystems may be the lower average Chl *a* content per unit of algal biovolume that has been reported for marine versus freshwater phytoplankton. Another equally plausible mechanism, however, may relate to differ-

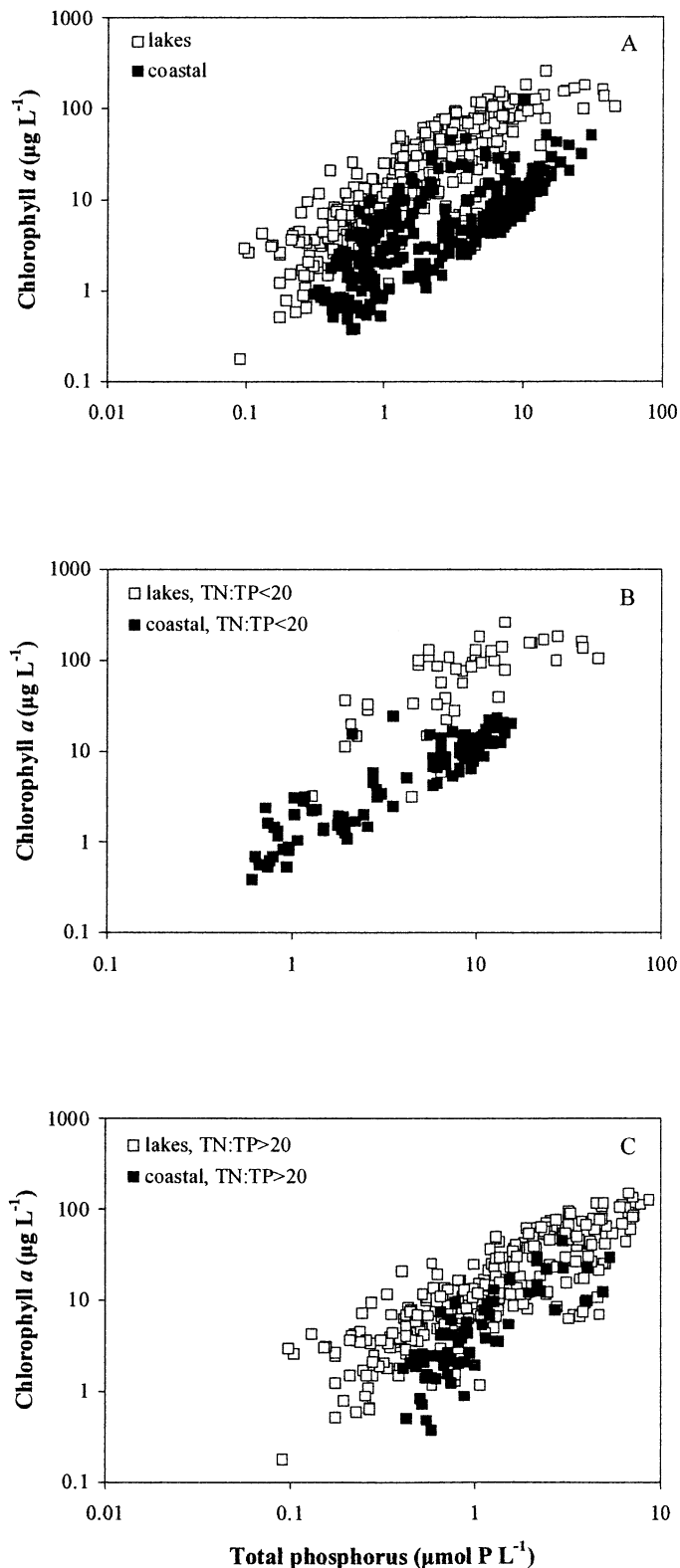


Fig. 6. Relationships between annual mean Chl *a* and annual mean TP concentrations in the freshwater lakes (open symbols) data set from Smith (1982), and in the estuarine and coastal marine ecosystems reported here (closed symbols). (A) All data, (B) N-limited sites, and (C) P-limited sites. Note changes in *x*-axis scaling.

ences in nutrient use efficiency and in the loss rates experienced by marine versus freshwater phytoplankton. In their comparative analyses of photosynthesis and sinking fluxes in lakes and oceans, Baines et al. (1994) found higher chlorophyll-specific photosynthetic rates in marine and freshwater algae, with the greatest differences occurring at the oligotrophic end of the gradient; they also found that carbon sinking rates averaged two- to threefold higher in the oceans than in lakes with similar concentrations of Chl *a*. They concluded that marine and freshwater ecosystems may differ systematically in the efficiency of nutrient recycling processes in the water column and in the nature of the settling material itself.

The observations of Baines et al. (1994) suggest that the per capita growth rate of phytoplankton and, thus, their cellular nutrient quotas, may be higher on average in marine than in freshwater algae. This conclusion is consistent with the suggestion by Goldman et al. (1979) that many marine phytoplankton may be growing at near-maximal rates and that this rapid growth rate is reflected in the phytoplankton's nutrient stoichiometry. High growth rates and assimilation numbers are correlated with high cell nutrient quotas (Rhee 1978; Senft 1978) and, thus, with low nutrient use efficiency. The lower yields of algal biomass per unit of TP in marine ecosystems therefore may reflect differences in their elemental stoichiometry. This hypothesis is consistent with evidence in Sterner and Elser (2002, their figures 3–13) that suggests that cellular C:P ratios are lower on average and exhibit far less variance in marine than in freshwater phytoplankton. The ecological stoichiometry hypothesis is also consistent with the conclusion of Guildford and Hecky (2000) that freshwater ecosystems are more consistently and strongly nutrient deficient than are marine ecosystems. The carbon:chlorophyll hypothesis of Hoyer et al. (2002) and the ecosystem stoichiometry hypothesis presented here can be tested explicitly in the future by making parallel comparisons of the elemental composition of marine and freshwater seston across an equivalent gradient of mixed-layer chlorophyll concentrations.

### Conclusions and practical implications

In a synthesis of our knowledge of coastal marine eutrophication, Richardson and Jørgensen (1996) concluded that there are essential differences between freshwater and marine environments that prevent us from simply applying knowledge gained from limnological studies to the marine environment. They argued that the study of marine eutrophication is a unique scientific discipline that is related to, but distinct from, the study of eutrophication in freshwater ecosystems. Sharp (2001) took a much stronger view, asserting that limnological studies and concepts and observations often lead to incorrect conclusions when they are applied to estuarine and coastal marine waters. Sharp (2001) suggested that, contrary to simple limnological models, nutrient loading to nearshore marine waters often does not support the level of phytoplankton biomass that would otherwise be expected from existing nutrient concentrations.

The comparative marine ecosystem analyses reported here

do not support these views, however. Together with the studies of Guildford and Hecky (2000), Hoyer et al. (2002), and other empirical studies (e.g., Boynton et al. 1996; Meeuwig et al. 1998, 2000), these analyses suggest a remarkable consistency in the response of phytoplankton biomass to nutrient enrichment in marine ecosystems. As in comparable limnological models, these empirical relationships do exhibit a large amount of vertical scatter at any given nutrient concentration, and this variance reflects the influence of additional physical and biotic factors that may be acting to enhance or reduce algal biomass. Nevertheless, these complicating factors could not obscure the overwhelmingly strong responses of phytoplankton to nutrient enrichment in the globally diverse data set analyzed here.

The data presented in Fig. 5 also appear to confirm that phytoplankton algae have a common response to the TN:TP ratio, regardless of whether they are marine or freshwater in origin, as was concluded by Guildford and Hecky (2000). The threshold TN:TP ratio at which strong N limitation of algal growth occurs (TN:TP < 20:1 by moles) appears to be very similar and may be statistically indistinguishable in marine and freshwater ecosystems. As was stressed by Downing (1997), the use of TN and TP pools to distinguish N from P limitation has been very widely applied in freshwater systems, and this approach appears to be equally applicable to marine systems. If photoautotrophic life on Earth first began in the oceans, then observed similarities in the elemental requirements, cellular mineral nutrient composition, and responses to nutrient enrichment by marine and freshwater phytoplankton follow logically from their shared phylogenetic histories. The stoichiometry of N and P supplies to the water column thus has a central and essential control on phytoplankton primary production in freshwater, estuarine, and coastal marine ecosystems worldwide. As was stressed by Redfield (1958) and Reiners (1986), elemental stoichiometry is a fundamental property of life itself, and it has a profound and detectable influence on the behavior of all organisms (Sterner and Elser 2002).

The results presented in this study also have important practical implications. As was noted by Boesch et al. (2000), cross-system comparisons have provided freshwater policy-makers and managers with highly credible tools to deal with important water quality problems. Similarly, when coupled with appropriate watershed nutrient-loading and mass-balance models, empirical phytoplankton-nutrient concentration models such as those presented here can contribute to the development of parallel frameworks to help guide the management of coastal zone water quality. In addition, as is true in freshwater ecosystems, changes in the N:P loading ratio to coastal waters can cause concomitant shifts in water-column N:P ratios and in the phytoplankton nutrient-limitation status (Ærtebjerg et al. 2003). The strong nitrogen-phosphorus interactions reported here support previous arguments (Fisher et al. 1992; Conley 2000; Elmgren and Larsson 2001) that controlling the eutrophication of coastal zone waters will likely require careful basin-specific management practices for *both* N and P. Such nutrient-loading management efforts should provide us with vitally important, new ecosystem-level tests of nutrient limitation that will be sim-

ilar to those that have been so successfully conducted in freshwater lakes (Fisher et al. 1992).

## References

- ÆRTEBJERG, G., J. H. ANDERSEN, AND O. S. HANSEN [EDS.]. 2003. Nutrients and eutrophication in Danish marine waters. A challenge for science and management. National Environmental Institute.
- BAINES, S. B., M. L. PACE, AND D. M. KARL. 1994. Why does the relationship between sinking flux and planktonic primary production differ between lakes and oceans? *Limnol. Oceanogr.* **39**: 213–226.
- BOESCH, D. F., J. BURGER, C. F. D'ELIA, D. J. REED, AND D. SCALIA. 2000. Scientific synthesis in estuarine management, p. 507–526. *In* J. E. Hobbie [ed.], *Estuarine science: A synthetic approach to research and practice*. Island Press.
- BORUM, J. 1996. Shallow waters and land/sea boundaries, p. 179–203. *In* B. B. Jørgensen and K. Richardson [eds.], *Eutrophication in coastal marine ecosystems*. Coastal and Marine Studies 52. American Geophysical Union.
- BOYNTON, W. R., L. MURRAY, J. D. HAGY, C. STOKES, AND M. R. KEMP. 1996. A comparative analysis of eutrophication patterns in a temperate coastal lagoon. *Estuaries* **19**: 408–421.
- CHAMPION, M., AND D. J. CURRIE. 2000. Phosphorus-chlorophyll relationships in lakes, rivers, and estuaries. *Verh. Int. Ver. Theor. Angew. Limnol.* **27**: 1986–1989.
- CONLEY, D. J. 2000. Biogeochemical nutrient cycles and nutrient management strategies. *Hydrobiologia* **410**: 87–96.
- CONTRERAS, E., AND J. KERÉKES. 1993. Total phosphorus-chlorophyll relationships in tropical coastal lagoons in Mexico. *Verh. Int. Ver. Theor. Angew. Limnol.* **25**: 448–451.
- DOERING, P. H., C. A. OVIATT, B. L. NOWICKI, E. G. KLOS, AND L. W. REED. 1995. Phosphorus and nitrogen limitation of primary production in a simulated estuarine gradient. *Mar. Ecol. Progr. Ser.* **124**: 271–287.
- DOWNING, J. A. 1997. Marine nitrogen:phosphorus stoichiometry and the global N:P cycle. *Biogeochemistry* **37**: 237–252.
- , C. W. OSENBURG, AND O. SARNELLE. 1999. Meta-analysis of marine nutrient-enrichment experiments: Variation in the magnitude of nutrient limitation. *Ecology* **80**: 1157–1167.
- ELMGREN, R., AND U. LARSSON [EDS.]. 1997. *Himmerfjärden: Changes of a nutrient-enriched coastal ecosystem in the Baltic Sea*. Report 4565. Swedish Environmental Protection Agency (in Swedish).
- , AND ———. 2001. Eutrophication in the Baltic Sea area: Integrated coastal management issues, p. 15–35. *In* B. von Bodungen and R. K. Turner [eds.], *Science and integrated coastal management*. Dahlem Univ. Press.
- FISHER, R. R., AND OTHERS. 1999. Spatial and temporal variation of resource limitation in Chesapeake Bay. *Mar. Biol.* **133**: 763–778.
- FISHER, T. R., J. M. MELACK, J. U. GROBBELAAR, AND R. W. HOWARTH. 1995. Nutrient limitation of phytoplankton and eutrophication of inland, estuarine, and marine waters, p. 301–322. *In* H. Tiessen [ed.], *Phosphorus in the global environment*. Wiley.
- , E. R. PEELE, J. W. AMMERMAN, AND L. W. HARDING, JR. 1992. Nutrient limitation of phytoplankton in Chesapeake Bay. *Mar. Ecol. Progr. Ser.* **82**: 51–63.
- FLEMER, D. A., E. M. LORES, AND C. M. BUNDRICK. 1998. Potential sediment denitrification rates in estuaries of Northern Gulf of Mexico. *J. Environ. Qual.* **27**: 859–868.
- FORSBERG, C., AND S.-O. RYDING. 1980. Eutrophication parameters and trophic state indices in 30 Swedish lakes. *Arch. Hydrobiol.* **89**: 189–207.
- FOURQUREAN, J. W., R. D. JONES, AND J. C. ZIEMAN. 1993. Processes influencing water column nutrient characteristics and phosphorus limitation of phytoplankton biomass in Florida Bay, US: Inferences from spatial distributions. *Estuar. Coast. Shelf Sci.* **36**: 295–314.
- GIOVANARDI, F., AND E. TROMELLINI. 1992. Statistical assessment of trophic conditions. Application of the OECD methodology to the marine environment. *Sci. Total Environ. Suppl.* **1992**: 211–233.
- GOLDMAN, J. R., J. J. MCCARTHY, AND D. G. PEAVEY. 1979. Growth rates influence on the chemical composition of phytoplankton in oceanic waters. *Nature* **279**: 210–215.
- GUILDFORD, S. J., AND R. E. HECKY. 2000. Total nitrogen, total phosphorus, and nutrient limitation in lakes and oceans: Is there a common relationship? *Limnol. Oceanogr.* **45**: 1213–1223.
- HECKY, R. E., AND P. KILHAM. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. *Limnol. Oceanogr.* **33**: 796–822.
- HESSEN, D., O. VADSTEIN, AND J. MAGNUSSON. 1992. Nitrogen to marine areas, on the application of a critical load concept, p. 201–237. *In* *Critical loads for nitrogen*. Proceedings of a workshop held in Lökeborg, Sweden, 6–10 April 1992. Environment Canada and Nordic Council of Ministers. NORD, 41. Copenhagen.
- HOWARTH, R. W. 1993. The role of nutrients in coastal waters, p. 177–202. *In* *Managing wastewater in coastal urban areas*. Report from the National Research Council Committee on wastewater management for coastal urban areas. National Academy Press.
- , H. S. JENSEN, R. MARINO, AND H. POSTMA. 1995. Transport to and processing of P in near-shore and oceanic waters, p. 323–345. *In* H. Tiessen [ed.], *Phosphorus in the global environment*. Wiley.
- HOYER, M. V., T. K. FRAZER, S. K. NOTESTEIN, AND D. E. CANFIELD, JR. 2002. Nutrient, chlorophyll, and water clarity relationships in Florida's nearshore coastal waters with comparisons to freshwater lakes. *Can. J. Fish. Aquat. Sci.* **59**: 1024–1031.
- KELLY, J. 2001. Nitrogen effects on coastal marine ecosystems. *In* R. F. Folett and J. L. Hatfield [eds.], *Nitrogen in the environment: Sources, problems, and management*. Elsevier.
- KETCHUM, B. 1969. Eutrophication of estuaries, p. 197–209. *In* *Eutrophication: Causes, consequences, correctives*. National Academy of Sciences.
- KIRKKALA, T., H. HELMINEN, AND A. ERKKILÄ. 1998. Variability of nutrient limitation in the Archipelago Sea, SW Finland. *Hydrobiologia* **363**: 117–126.
- LIMNO-TECH. 1991. Evaluation of nitrogen removal eutrophication risk for the freshwater Potomac estuary. Final report prepared for the Metropolitan Washington Council of Governments. Limno-Tech.
- MCCAULEY, E., J. A. DOWNING, AND S. WATSON. 1989. Sigmoid relationships between nutrients and chlorophyll among lakes. *Can. J. Fish. Aquat. Sci.* **46**: 1171–1175.
- MCCOMB, A. J., AND R. J. LUKATELICH. 1987. Nutrients and plant biomass in Australian estuaries, with particular reference to South-western Australia, p. 433–455. *In* P. De Dekker and W. D. Williams [ed.], *Limnology in Australia*. Monographs in Biology, V. 61. Junk.
- MEEUWIG, J. J., P. KAUPPILA, AND H. PITKÄNEN. 2000. Predicting coastal eutrophication in the Baltic: A limnological approach. *Can. J. Fish. Aquat. Sci.* **57**: 844–855.

- , J. B. RASMUSSEN, AND R. H. PETERS. 1998. Turbid waters and clarifying mussels: Their moderation of Chl : nutrient relations in estuaries. *Mar. Ecol. Progr. Ser.* **171**: 139–150.
- NATIONAL RESEARCH COUNCIL. 2000. Clean coastal waters: Understanding and reducing the effects of nutrient pollution. National Academy Press.
- NIELSEN, S. L., K. SAND-JENSEN, J. BORUM, AND O. GEERTZ-HANSEN. 2002. Phytoplankton, nutrients, and transparency in Danish coastal waters. *Estuaries* **25**: 930–937.
- NIXON, S. W., C. A. OVIATT, J. FRITHSEN, AND B. SULLIVAN. 1986. Nutrients and the productivity of estuarine and coastal marine ecosystems. *J. Limnol. Soc. South Africa* **12**: 43–71.
- ORGANISATION FOR ECONOMIC AND COOPERATIVE DEVELOPMENT. 1982. Eutrophication of waters: Monitoring, assessment and control. Organisation for Economic and Cooperative Development.
- PAERL, H. W., AND J. P. ZEHR. 2000. Marine nitrogen fixation, p. 387–426. *In* D. L. Kirchman [ed.], *Microbial ecology of the oceans*. Wiley-Liss.
- PRAIRIE, Y. T., C. M. DUARTE, AND J. KALFF. 1989. Unifying nutrient-chlorophyll relationships in lakes. *Can. J. Fish. Aquat. Sci.* **46**: 1176–1182.
- PRICE, K. S., AND OTHERS. 1985. Nutrient enrichment of Chesapeake Bay and its impact on the habitat of striped bass: A speculative hypothesis. *Trans. Am. Fish. Soc.* **114**: 97–106.
- RABALAIS, N. N., AND S. W. NIXON. 2002. Preface: Nutrient over-enrichment of the coastal zone. *Estuaries* **25**: 639.
- REDFIELD, A. C. 1958. The biological control of chemical factors in the environment. *Am. Sci.* **46**: 205–222.
- . 1934. On the proportions of organic derivatives in sea water and their relation to the composition of plankton, p. 176–192. *In* James Livingstone Memorial Volume. Univ. of Liverpool.
- REINERS, W. A. 1986. Complementary models in ecology. *Am. Nat.* **27**: 59–73.
- RHEE, G.-Y. 1978. Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. *Limnol. Oceanogr.* **23**: 10–25.
- RICHARDSON, K., AND B. B. JØRGENSEN. 1996. Eutrophication: Definition, history and effects, p. 1–19. *In* B. B. Jørgensen and K. Richardson [eds.], *Eutrophication in coastal marine ecosystems*. Coastal and Marine Studies 52. American Geophysical Union.
- RILEY, G. A. 1965. A mathematical model of regional variations in plankton. *Limnol. Oceanogr.* (suppl. 2) **10**: R202–R215.
- SAKAMOTO, M. 1966. Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. *Archiv Hydrobiol.* **62**: 1–28.
- SCHINDLER, D. W. 1977. Evolution of phosphorus limitation in lakes. *Science* **195**: 260–262.
- SENF, W. H. 1978. Dependence of light-saturated rates of algal photosynthesis on intracellular concentrations of phosphorus. *Limnol. Oceanogr.* **23**: 709–718.
- SHARP, J. H. 2001. Marine and aquatic communities, stress from eutrophication, p. 1–11. *In* *Encyclopedia of biodiversity*, v. 4. Academic.
- SMITH, S. V. 1984. Phosphorus versus nitrogen limitation in the marine environment. *Limnol. Oceanogr.* **29**: 1149–1160.
- SMITH, V. H. 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: An empirical and theoretical analysis. *Limnol. Oceanogr.* **27**: 1101–1112.
- . 1998. Cultural eutrophication of inland, estuarine, and coastal waters, p. 7–49. *In* M. L. Pace and P. M. Groffman [eds.], *Successes, limitations and frontiers in ecosystem science*. Springer-Verlag.
- , G. D. TILMAN, AND J. C. NEKOLA. 1999. Eutrophication: Effects of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environ. Pollut.* **100**: 179–196.
- STERNER, R. W., AND J. J. ELSER. 2002. *Ecological stoichiometry*. Princeton Univ. Press.
- UNITED NATIONS ENVIRONMENT PROGRAMME. 1995. Global programme of action for the protection of the marine environment from land-based activities. Report UNEP(OCA)/LBA/IG.2/7. United Nations Environment Programme.
- VITOUSEK, P. M., AND R. W. HOWARTH. 1991. Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* **13**: 87–115.
- WALLIN, M. 1991. Nutrient loading models for coastal waters. UNGI report 80. Uppsala Universitet Naturgeografiska Institutionen.

*Received: 16 April 2004*  
*Accepted: 6 August 2004*  
*Amended: 24 August 2004*