Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems

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Abstract

In the mid-1800s, the agricultural chemist Justus von Liebig demonstrated strong positive relationships between soil nutrient supplies and the growth yields of terrestrial plants, and it has since been found that freshwater and marine plants are equally responsive to nutrient inputs. Anthropogenic inputs of nutrients to the Earth's surface and atmosphere have increased greatly during the past two centuries. This nutrient enrichment, or eutrophication, can lead to highly undesirable changes in ecosystem structure and function, however. In this paper we briefly review the process, the impacts, and the potential management of cultural eutrophication in freshwater, marine, and terrestrial ecosystems. We present two brief case studies (one freshwater and one marine) demonstrating that nutrient loading restriction is the essential cornerstone of aquatic eutrophication control. In addition, we present results of a preliminary statistical analysis that is consistent with the hypothesis that anthropogenic emissions of oxidized nitrogen could be influencing atmospheric levels of carbon dioxide via nitrogen stimulation of global primary production. © 1999 Elsevier Science Ltd. All rights reserved.

1. Introduction and origins of the problem

During the several centuries since the industrial revolution, humankind's activities have caused strong alterations in the structure and function of their environment. Human population growth has placed ever-increasing demands on both aquatic and terrestrial ecosystems, and between one-third to one-half of the land's surface has been transformed: we have dramatically changed the globe by land clearing, agriculture, forestry, animal husbandry and urbanization, and by altering hydrological cycles (Vitousek et al., 1997a). In addition, we have significantly altered the composition of many natural biological communities by harvesting activities, and by the unintentional and the deliberate introduction of non-native species (Bottsford et al., 1997; Chapin et al., 1997; Dobson et al., 1997; Matson et al., 1997; Noble and Dirzo, 1997). Human activities have also had profound impacts upon the global biogeochemical cycles of carbon (C), nitrogen (N), and phosphorus (P) (Schlesinger, 1991; Vitousek et al., 1997a, b). In this paper we focus on anthropogenic changes in the fluxes of N and P, and examine the impacts of these two essential plant nutrients on aquatic and terrestrial ecosystems.

Human activity has profoundly altered the global biogeochemical cycle of N (Galloway et al., 1995; Vitousek et al., 1997a, b). Humans have approximately doubled the rate of N input into the terrestrial N cycle, and these rates are still increasing (Vitousek et al., 1997a). Overall, anthropogenic inputs currently add at least as much fixed N to terrestrial ecosystems as do all natural sources combined, and humans mobilize more than 50 million metric tonnes of N via land transformations (Vitousek et al., 1997b). The global production of agricultural fertilizers increased from <10 million metric tonnes of N in 1950 to ca. 80 million metric tonnes in 1990, and its production is predicted by some authors to exceed 135 million metric tonnes of N by 2030 (Vitousek et al., 1997b). Substantial additional N

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is applied to croplands in the form of animal manures, for which regulatory standards are generally far less stringent than those applied to human sewage (Carpenter et al., 1998). A small but significant fraction of the total agricultural N applied to land is in excess of plant requirements for growth, and this surplus N may: (1) accumulate in soils; (2) move from the land into surface waters; (3) migrate into groundwaters; or (4) enter the atmosphere via ammonia volatilization and nitrous oxide production (cf. Nolan et al., 1997; Vitousek et al., 1997b; Carpenter et al., 1998). The combustion of fossil fuels causes an additional emission of > 20 million metric tonnes of N into the atmosphere (Vitousek et al., 1997a), a significant fraction of which subsequently returns to the land and ocean surface via wet and dry deposition. This atmospheric deposition of N can have strong effects on the structure and function of both terrestrial and marine ecosystems (Paerl, 1995; Waring and Running, 1998).

Human activities also have strong effects on the fluxes of P to the landscape. Large quantities of P minerals are mined and processed to create P-containing fertilizers, and these fertilizers are heavily applied worldwide even to soils that already contain ample P reserves. As is true of N, substantial quantities of P are also added to the land in the form of animal manures. In many areas, P inputs from fertilizers and manures greatly exceed P outputs in farm produce, and P is thus accumulating yearly in the soil (Foy and Withers, 1995; Carpenter et al., 1998). This trend has important implications for eutrophication control because the total amount of P exported in runoff from the landscape to surface waters increases linearly with the soil P content (Sharpley et al., 1996; see also Smith et al., 1995). In Northern Ireland, for example, soil P reserves have accumulated at a rate of ca. 1000 kg P km^{-2} $year^{-1}$ over the past 50 years, and these increases have been accompanied by increases in the loss rates of inorganic P in runoff of ca. 2 mg m^{-3} $year^{-1}$ (Foy et al., 1995). Although small, this rate of change in runoff P is limnologically and ecologically significant when continued over periods of decades or more (Foy et al., 1995).

In addition to the atmospheric and agricultural sources of N and P mentioned above, humans use flowing waters as convenient wastewater disposal systems. The loading of N and P to the world's rivers, lakes, and oceans is thus very strongly influenced by human population densities, the population densities of livestock, and land use (Omernik, 1977; Reckhow et al., 1980; Jones et al., 1984; Cole et al., 1993; Caraco, 1995; Howarth et al., 1995, 1996; Jaworski et al., 1997; Smith et al., 1997). In the review that follows, we will examine the environmental implications of these fluxes of N and P to the biosphere, and will focus on the impacts of excessive nutrient inputs upon freshwater, marine, and terrestrial ecosystems.

2. Nutrient limitation and the eutrophication concept

It has been known since work of the German agricultural chemist Justus von Liebig that the yield of plants can be limited by the nutrient that is present in the environment in the least quantity relative to plant demands for growth (von Liebig, 1855); this theory has come to be known as Liebig's Law of the Minimum. Of the many mineral resources required for plant growth, inorganic N and P are the two principal nutrients that have been found to limit the growth of terrestrial plants (Schlesinger, 1991; Vitousek and Howarth, 1991). This nutrient limitation of plant biomass is not restricted to terrestrial ecosystems alone, however. The supply rate of N and P also strongly influences the growth of algae and vascular plants in freshwater and marine ecosystems (Vollenweider, 1968; Hecky and Kilham, 1988; Howarth, 1988; Smith, 1998).

Ecosystems can in fact be described using terms referring to their supplies of growth-limiting nutrients (Table 1). For example, the classification scheme developed originally by Weber (1907) for bogs can be used to categorize surface waters by the relative magnitudes of their nutrient inputs (Hutchinson 1969, 1973). Waters having relatively large supplies of nutrients are termed eutrophic (well nourished), and those having poor

Table 1
Average characteristics of lakes (Nürnberg, 1996), streams (Dodds et al., 1998), and coastal marine waters (Håkanson, 1994) of different trophic states[a]

	Trophic state	TN (mg m^{-3})	TP (mg m^{-3})	chl *a* (mg m^{-3})	SD (m)
Lakes	Oligotrophic	< 350	< 10	< 3.5	> 4
	Mesotrophic	$350-650$	$10-30$	$3.5-9$	$2-4$
	Eutrophic	$650-1200$	$30-100$	$9-25$	$1-2$
	Hypertrophic	> 1200	> 100	> 25	< 1
				Suspended chl *a* (mg m^{-3})	Benthic chl *a* (mg m^{-2})
Streams	Oligotrophic	< 700	< 25	< 10	< 20
	Mesotrophic	$700-1500$	$25-75$	$10-30$	$20-70$
	Eutrophic	> 1500	> 75	> 30	> 70
				chl *a* (mg m^{-3})	SD (m)
Marine	Oligotrophic	< 260	< 10	< 1	> 6
	Mesotrophic	$260-350$	$10-30$	$1-3$	$3-6$
	Eutrophic	$350-400$	$30-40$	$3-5$	$1.5-3$
	Hypertrophic	> 400	> 40	> 5	< 1.5

[a] The terms oligotrophic, mesotrophic, and eutrophic correspond to systems receiving low, intermediate, and high inputs of nutrients. Hypertrophic is the term used for systems receiving greatly excessive nutrient inputs. TN, total nitrogen; TP, total phosphorus; TIN, total inorganic nitrogen; chl *a*, chlorophyll *a*; SD, Secchi disk transparency.

nutrient supplies are termed oligotrophic (poorly nourished). Waters having intermediate nutrient supplies are termed mesotrophic. *Eutrophication* is the process by which water bodies are made more eutrophic through an increase in their nutrient supply. Although this term is most commonly applied to freshwater lakes and reservoirs, it can also be applied to flowing waters, estuaries, and coastal marine waters (Edmondson, 1995). In Section 3 we will examine the impacts of eutrophication on freshwater and marine ecosystems, and will present brief reviews of two successful cases of eutrophication control and restoration. In Section 4, we will apply the term eutrophication when examining the effects of anthropogenic N enrichment on terrestrial ecosystems.

The concept of nutrient limitation can be considered the keystone of eutrophication research. In effect, it implies: (1) that one key nutrient should be the primary limiting factor for plant growth in a given ecosystem; (2) that the growth of plants in a given ecosystem should be proportional to the rate of supply of this nutrient; and (3) that the control of eutrophication should be accomplished by restricting the loading of this key nutrient to the ecosystem (Smith, 1998). The practical importance of these three conclusions for eutrophication management will be made evident in the next two sections.

3. Eutrophication of aquatic ecosystems

The external supplies of N and P to aquatic ecosystems are derived from a wide variety of sources, including groundwater, fluvial, and atmospheric inputs. The sum of these three sources can be termed the *external load*. As can be seen in Table 2, the external supplies of nutrients to a water body can originate both as *point sources*, which are localized and more easily monitored and controlled, and as *nonpoint sources*, which are diffuse and much more difficult to monitor and regulate. The relative contributions of these two types of sources can differ substantially from watershed to watershed, depending upon local human population densities and land use.

N and P exports from point and nonpoint sources can have profound effects upon the quality of receiving waters (Carpenter et al., 1998; Correll, 1998). Just as fertilizing an agricultural crop or forest can result in enhanced plant growth, the most common effects of increased N and P supplies on aquatic ecosystems are perceived as increases in the abundance of algae and aquatic plants. However, the environmental consequences of excessive nutrient enrichment are more serious and far-reaching than nuisance increases in plant growth alone. The degradation of water resources by eutrophication can result in losses of their component species, as well as losses of the amenities or services

Table 2
Sources of point and nonpoint chemical inputs recognized by US statutes (from Carpenter et al., 1998, modified from Novotny and Olem, 1994)

Point sources
Wastewater effluent (municipal and industrial)
Runoff and leachate from waste disposal sites
Runoff and infiltration from animal feedlots
Runoff from mines, oil fields, and unsewered industrial sites
Storm sewer outfalls from cities with populations >100,000
Overflows of combined storm and sanitary sewers
Runoff from construction sites with an area >2 ha

Nonpoint sources
Runoff from agriculture (including return flows from irrigated agriculture)
Runoff from pastures and rangelands
Urban runoff from unsewered areas and sewered areas with populations <100,000
Septic tank leachage and runoff from failed septic systems
Runoff from construction sites with an area <2 ha
Runoff from abandoned mines
Atmospheric deposition over a water surface
Activities on land that generate contaminants, such as logging, wetland conversion, construction and development of land or waterways

that these systems provide (cf. Postel and Carpenter, 1996; US EPA 1996a; Carpenter et al., 1998). Impairment of aquatic resources by eutrophication thus can have substantial economic effects (Carpenter et al., 1997), and there are tradeoffs between benefits from polluting activities and the ecosystem services that are foregone due to the consequences of eutrophication (Carpenter et al., 1999).

Eutrophication in fact is the most widespread water quality problem in the US and many other nations (Carpenter et al., 1998). It accounts for almost one-half of the impaired lake area and 60% of impaired river reaches in the US (US EPA 1996a), and is also the most common pollution problem in US estuaries (National Research Council, 1993). The major effects of cultural eutrophication on freshwater and marine ecosystems are reviewed briefly below.

3.1. Effects on lakes and reservoirs

A vital key to the management of lake and reservoir eutrophication has been the development of models linking water body nutrient concentrations to aspects of water quality that are considered by the public to be important and worth preserving (Smith, 1998). Perhaps the most commonly identified Quality Variable of Concern in aquatic ecosystems (Reckhow and Chapra, 1983) is the accumulation of nuisance levels of algal biomass, which are easily observed by the public. Moreover, the reduction of algal biomass to levels that are acceptable to the public has been a feature common to all successful eutrophication control efforts (Smith, 1998). As would be expected from Liebig's Law of the

Minimum, there is a remarkable consistency in the response of algal biomass to nutrient enrichment. Strong positive relationships between algal biomass and nutrient loading have been observed in most lakes and reservoirs that have been studied (Dillon and Rigler, 1974; Jones and Bachmann, 1976; OECD, 1982).

Excessive nutrient enrichment also has many additional effects on the biology, chemistry, and human use of lakes and reservoirs, however. These secondary effects are frequently deleterious, and may be of great concern to users of the resource (Table 3). For example, eutrophic lakes are typically characterized by shifts towards dominance of the phytoplankton by blue-green algae (cyanobacteria), some of which produce compounds that are more toxic than cobra venom (Skulberg et al., 1984; Carmichael, 1991).

In order to predict the effects of N and P inputs on receiving waters, it is necessary to be able to predict how water body nutrient concentrations vary as the external N and P inputs are changed. The development of quantitative models that relate external nutrient inputs to the resulting water column concentrations of nutrients in the water body itself was a second key development in eutrophication research. This conceptual advance resulted from the introduction of mass-balance approaches to aquatic ecosystems; the mass-balance approach apparently was not broadly applied to eutrophication modeling until Vollenweider (1968). In the 30 years since the publication of Vollenweider's report, however, a rigorous quantitative framework has developed to predict the responses of freshwater lakes and reservoirs to eutrophication. Essential to this framework are the calculations of mass budgets for both N and P, and the parallel calculation of a hydraulic budget for the water body.

P is the primary limiting nutrient in most lakes and reservoirs (Schindler, 1977; Hecky and Kilham, 1988). Consequently most eutrophication management frameworks focus primarily on the control of P loading (e.g. Dillon and Rigler, 1975; Canfield and Bachmann, 1981; OECD, 1982; Sas, 1989; Salas and Martino, 1991; Foy

Table 3
Effects of eutrophication on lakes and reservoirs (modified from Smith, 1998)

Increased biomass of freshwater phytoplankton and periphyton
Shifts in phytoplankton species composition to taxa that may be toxic or inedible (e.g. bloom-forming cyanobacteria)
Changes in vascular plant production, biomass, and species composition
Reduced water clarity
Decreases in the perceived aesthetic value of the water body
Taste, odor, and water supply filtration problems
Possible health risks in water supplies
Elevated pH and dissolved oxygen depletion in the water column
Increased fish production and harvest
Shifts in fish species composition towards less desirable species
Increased probability of fish kills

et al., 1996). However, analogous input–output models for total N have been developed by Kratzer (1979), Bachmann (1981, 1984), Baker et al. (1981, 1985), Canfield and Bachmann (1981), OECD (1982), and Reckhow (1988), and these models are very relevant to any assessment of the current or future N status of lakes (Smith, 1998). A detailed overview of nutrient loading models for lakes and reservoirs is beyond the scope of this paper, but their derivation and application is comprehensively summarized in Reckhow and Chapra (1983) (see also Reckhow and Chapra, 1999).

3.2. Successful restoration of eutrophic lakes: Lake Maggiore as a case study

Successful eutrophication management and control is based primarily on the restriction of nutrient inputs to the waterbody, and this nutrient loading restriction can be accomplished by a wide variety of external and internal controls (Cooke et al., 1993). For comprehensive treatments of eutrophication and the restoration of eutrophic lakes and reservoirs, see Reckhow and Chapra (1983), Sas (1989), Edmondson (1991), Harper (1992), Sutcliffe and Jones (1992), Welch and Lindell (1992), Cooke et al. (1993), and Smith (1998).

Perhaps the most widely recognized success story in eutrophication is that of Lake Washington (Seattle, USA), where the diversion of wastewater effluents led to a profound improvement of water quality in the lake. However, this example has been discussed in detail elsewhere (e.g. Edmondson, 1991; Laws, 1993; Smith, 1998), and will not be repeated here. Another excellent example of successful lake restoration is that of Lago Maggiore, Italy. Eutrophication is the most widespread water quality problem in lowland Italian lakes, and has been caused by industrial and economic development, the use of P-containing detergents and fertilizers, and the disposal of untreated human sewage into the lakes. Lago Maggiore, is the second largest and best-studied lake in Italy, and it provides an excellent case study of cultural eutrophication and recovery after external nutrient loading controls were implemented in the watershed (Roggiu et al., 1985; de Bernardi et al., 1996).

Lago Maggiore is a large (212.5 km^2), deep (mean depth, 177 m), P-limited lake. It is located in an extensive drainage area belonging to Italy and to Switzerland, although 80% of the lake's total surface area is within Italy (de Bernardi et al., 1996). The population of permanent residents in the watershed is about 670,000 people, but the lake is also an extremely popular recreational site, and the tourist industry can account for more than 12 million tourist-days per year. Nearly half of this tourist use is concentrated along the lake shore region (de Bernardi et al., 1996). In addition, the lake is used extensively for sport commercial fisheries, and boating (de Bernardi et al., 1996).

Until the 1950s Lake Maggiore exhibited the characteristics of oligotrophy, with low epilimnetic concentrations of inorganic N and P, and low levels of primary productivity (Roggiu et al., 1985). However, cultural eutrophication of the lake accelerated rapidly after the late 1950s. Total P concentrations in the lake water increased to 30–35 mg m^{-3} during 1976-77, and concentrations of nitrate-N increased twofold (Roggiu et al., 1985). Over a threefold increase in phytoplankton production was observed by the mid-1970s, and nuisance blooms of cyanobacteria also occurred (de Bernardi et al., 1996). Mosello and Ruggiu (1985) subsequently applied the OECD (1982) modeling framework in order to assess water quality restoration strategies for the lake, and they concluded that a 67% reduction in external P loading would be required to return Lago Maggiore to oligotrophic conditions.

Marked improvements in water quality have occurred in recent years, and the reversal of eutrophication has continued to the present. These improvements can be attributed to the construction of sewage treatment plants that serve 60–70% of the total population in the drainage basin, which has caused dramatic reductions in nutrient loadings to the lake. In addition, further reductions in P loading have occurred as a result of restrictions in the use of P-containing detergents, as well as reduced industrial activity that followed an industrial crisis in the 1980s. Epilimnetic concentrations of total P have subsequently declined threefold to ca. 10 mg m^{-3}, and a parallel decrease has occurred in algal biomass as measured by concentrations of chlorophyll *a* (de Bernardi et al., 1996). Phytoplankton species diversity also is increasing, with major changes in the relative abundance of diatoms and cyanobacteria.

Further reductions in P loading are planned in order to maintain total P concentrations in the lake permanently below 10 mg m^{-3}, including the construction of sewage treatment facilities sufficient to handle waste from ca. 80% of the population in the watershed. It is hoped that these improvements will restore water quality in Lago Maggiore to conditions that are close to its pre-impacted trophic state (de Bernardi et al., 1996).

Current nutrient loading models exhibit a high degree of variance in their predictions, and that restrictions in external nutrient loading alone do not necessarily cause immediate water quality improvements in all systems (Sas, 1989; Moss, 1990; Scheffer et al., 1993; Carvalho et al., 1995). There are two important areas in freshwater eutrophication research that require much further study. First, we require a better knowledge of the factors regulating internal sources of nutrients and within-lake nutrient dynamics before we can predict more precisely the changes in water column concentrations that occur once the external nutrient loading is altered (Nürnberg, 1984). In addition, there are strong interactions between nutrients and food webs that must be considered if we are to understand more completely the ecosystem-level changes that can occur after alterations of external nutrient loadings to any lake or reservoir (Edmondson, 1993; Carpenter et al., 1995).

Food-web structure can profoundly alter the responses of a waterbody to nutrient inputs (Hrbácek et al., 1961; Shapiro, 1979; Mazumder, 1994; Carpenter et al., 1995; Proulx et al., 1996). For example, during the recovery of Lake Washington from eutrophication, the sudden appearance of large populations of herbivorous *Daphnia* had profound effects on algal biomass and transparency (Edmondson and Litt, 1982; Edmondson, 1994). *Daphnia* are efficient grazers capable of clearing the water column of edible algal cells, and their appearance in 1976 led to an unexpectedly sharp increase in transparency that has persisted to the present (Edmondson, 1994). Similarly, major changes in the pelagic community occurred from 1983 to 1995 during the oligotrophication of Lago Maggiore. These changes included not only shifts in phytoplankton species composition, but also changes in communities of planktonic invertebrates and fish (Manca and Ruggiu, 1998). The implications of these changes are still being studied, but Manca and Ruggiu (1998) concluded that changes in phytoplankton abundance and average cell size may have resulted not only from P loading restriction, but also from changes in the structure of the lake's food web.

3.3. Effects of nutrient inputs on rivers and streams

Although the majority of freshwater eutrophication research during the past several decades has focussed on lakes and reservoirs, the nutrient enrichment of flowing waters is also of great concern. In the continental US, for example the mean total phosphorus (TP) concentration of streamwater at 381 riverine sites was found to be 130 mg m^{-3} (Smith et al., 1987). This value greatly exceeds the mesotrophic–eutrophic TP boundary of 75 mg m^{-3} recently proposed by Dodds et al. (1998). Similarly, Smith et al. (1993) concluded that 48% of 410 water quality monitoring stations failed to meet the widely accepted US EPA (1988) standard of 100 mg m^{-3}. In a more recent study, Smith et al. (1997) found that 61% of 2048 cataloging units failed to meet the EPA standard. These data suggest that the water quality in a majority of US streams and rivers is poor from the standpoint of eutrophication. Moss et al. (1989) have similarly reported extensive eutrophication of a major river system in the UK, and Köhler and Gelbrecht (1998) documented significant eutrophication in several major rivers in Germany.

Although many streams and rivers worldwide currently exhibit high nutrient concentrations, a prevailing view for many years held that many rivers are insensitive to nutrient inputs (e.g. Hynes, 1969). This argument

was based upon the assumption that other physical, chemical, and biotic factors potentially restrict the effects of nutrient enrichment on algal growth in rivers and streams. For example, light availability can influence the biomass accumulation of benthic algae (periphyton) in low-order streams shaded by extensive forest canopies (Gregory, 1980; Triska et al., 1983). Restriction of light penetration into the water column by high concentrations of inorganic suspended solids also can potentially limit the growth of both benthic and suspended algae in rivers, just as it can restrict phytoplankton biomass in turbid reservoirs (Hoyer and Jones, 1983). Furthermore, the hydraulic flow regime can greatly alter periphyton standing crops in flowing waters, and herbivore grazing often is noted as an additional biological constraint on periphyton growth and productivity. For many years, flowing waters thus were frequently perceived as nutrient saturated, because factors such as light limitation and short hydraulic residence times should restrict or prevent any potential algal responses to nutrient enrichment.

This opinion no longer appears to be tenable, however. Evidence from studies performed in a wide variety of geographical locations now suggests that flowing waters are indeed sensitive to anthropogenic inputs of N and P. Some of the earliest experimental evidence comes from Huntsman (1948), who fertilized an oligotrophic stream in Nova Scotia, Canada, with bags of agricultural NPK fertilizer. Sites downstream of the fertilizer additions immediately exhibited increased abundances of attached filamentous green algae and fish. Ten years later, Correll (1958) performed an enrichment of a Michigan stream using continuous additions of ammonium phosphate. The TP concentration of the stream water increased from background levels of ca. 8 mg m^{-3} to 70 mg m^{-3} at the enrichment site, and elevated concentrations of total P were observed up to 4 km downstream; periphyton growth on submersed artificial substrates increased threefold in response to these nutrient additions (cf. Correll, 1998).

Similar results were found by Elwood et al. (1981), who enriched two reaches of a shaded oligotrophic Tennessee stream for 95 days with inorganic P. Stream water P concentrations were increased by over an order of magnitude, and resulted in significantly increased benthic algal biomass, increased rates of detritus decomposition, and increased abundances of macroinvertebrate consumers. A strong sensitivity to P enrichment was reported by Peterson et al. (1983, 1985), in an Alaskan tundra river. These authors observed strong increases in downstream periphyton biomass following the inorganic P additions, and the stimulation of primary productivity subsequently cascaded into stream consumer populations (Hershey et al., 1988). Krewer and Holm (1986) and Horner et al. (1990) also found that the growth of periphyton in laboratory

stream channels was strongly dependent on the concentration of P in the flowing water.

P is not the sole limiting nutrient in streams and rivers, however. As noted in several of the studies cited above, enrichment with both N and P often produces higher algal yields than additions of N or P alone, and these data suggest that both N and P can be co-limiting to algal communities in streams. In other streams, N alone may be the primary limiting nutrient. For example, both whole-stream N enrichment studies by Gregory (1980) and artificial trough experiments by Triska et al. (1983) suggested potential N limitation, but in both of these studies the responses of periphyton to nutrient enrichment were strongly damped by low light availability. Strong N limitation of benthic algae has also been inferred in streams of Arizona (Grimm and Fisher, 1986), California (Hill and Knight, 1988), Missouri (Lohman et al., 1991), and Montana (Lohman and Priscu, 1992). Although studies of nutrient limitation of suspended riverine algae are much less common, Köhler and Gelbrecht (1998) have recently reported chemical evidence for N and P limitation of suspended algal growth in a large river system in Germany.

The above data suggest that, rather than being rare or uncommon, nutrient limitation of algal growth in flowing waters is both common and widespread. This hypothesis is strongly supported by numerous comparative analyses. The nutrient enrichment of streams and rivers typically is accompanied by increases in the biomass of suspended and/or benthic algae (Smart et al., 1985; Soballe and Kimmel, 1987; Lohmann et al., 1991; Welch et al., 1992; McGarrigle, 1993; Basu and Pick, 1996; Van Nieuwenhuyse and Jones, 1996; Dodds et al., 1997, 1998). The production of algae per unit total P often is significantly lower in rivers than in lakes and reservoirs. However, this difference, in part, may be caused by the higher washout loss rate that the flowing water may impose on suspended algal biomass (Soballe and Kimmel, 1987; Van Nieuwenhuyse and Jones, 1996). For example, Van Nieuwenhuyse and Jones (1996) and Lohman and Jones (1999) detected differences among streams in their response to nutrients (TN and TP) that could be accounted for by including watershed area as an additional explanatory variable. The effect of watershed area on suspended algal biomass in these two studies was attributed to high hydraulic flushing rates in the lower-order streams.

However, effects of hydraulic residence time on suspended algal biomass in rivers are not always strongly apparent. For example, with the exception of three sites (including two sites with exceptionally short residence times of ca. 1 day), a highly significant positive relationship was evident between phytoplankton biomass and stream water TP concentrations in the eutrophic River Bure, UK (Moss et al., 1989). Similarly, in their comparative analysis of streams, Basu and Pick (1996)

did not find a significant effect of hydraulic residence time in streams that were fifth order and larger.

A parallel dependence of phytoplankton biomass on total P has also been observed in other rapidly flushed systems. For example, Hoyer and Jones (1983) observed a strong Chl–TP relationship in 96 reservoirs in Missouri and Iowa that encompassed an extremely wide range of hydraulic residence times (7.6–12,000 days). They found that high concentrations of inorganic suspended solids reduced the algal yield in these turbid reservoirs, but did not observe a significant effect of flushing rate. Similarly, Soballe et al. (1992) observed a strong correlation between Chl *a* and TP in 45 mainstem and tributary reservoirs operated by the Tennessee Valley Authority and the US Army Corps of Engineers. The Chl *a* produced per unit TP tended to be lower in the mainstem systems, but it is difficult to conclude whether this difference in yield resulted from higher concentrations of inorganic suspended solids or shorter hydraulic residence times in the mainstem reservoirs, or from a combination of both factors.

Not surprisingly, nutrient enrichment of flowing waters can cause a variety of water quality problems (Table 4), and efforts to restrict fluxes of N and P from the landscape into streams and rivers will be necessary to improve the eutrophication-related water quality of flowing waters. The degree of nutrient loading control required to maintain satisfactory water quality will likely vary from site to site, and the objective criteria used in judging acceptable versus non-acceptable water quality are not yet as well developed as for lakes and reservoirs. However, two recent studies have provided independent estimates of the target stream water nutrient concentrations that need to be maintained in order to assure acceptable stream water quality. McGarrigle (1993) concluded that maintaining a mean annual dissolved inorganic P concentration < 47 mg m^{-3} was necessary to prevent the nuisance growth of attached algae, and to preserve water quality suitable for salmonid fishes, in Irish rivers. Similarly, Miltner and Rankin

(1998) observed deleterious effects of eutrophication on fish communities in low-order Ohio streams when total inorganic nitrogen (TIN) and dissolved inorganic phosphorus (SRP) concentrations exceeded 610 and 60 mg m^{-3}, respectively.

Additional estimates of critical in-stream nutrient levels have been derived by Dodds et al. (1997) from a large comparative analysis of stream ecosystems. These authors concluded that maintenance of stream water total N concentrations < 350 mg N m^{-3} and total P concentrations < 30 mg P m^{-3} would be necessary to keep benthic algal biomass below nuisance levels of 100 mg m^{-2}. Quantitative tools such as the spreadsheet model used by Dodds et al. (1997), and the more complex SPARROW model of Smith et al. (1997), will hopefully prove to be of practical value in linking target stream water nutrient concentrations to specific watershed nutrient control strategies. Thus, although the knowledge base of eutrophication science for flowing waters is far behind that for lakes and reservoirs, quantitative tools that link stream water nutrient concentrations and in-stream water quality are now being developed.

3.4. Effects on estuarine and coastal marine ecosystems

Streams and rivers serve as rapid conduits for anthropogenic pollutants to estuarine and coastal marine environments. For example, fertilizer inputs dominate net anthropogenic inputs of N in most drainage basins supplying water to the North Atlantic Ocean (Howarth et al., 1996). In addition, the anthopogenic deposition rates of oxidized (NO$_y$) and reduced (NH$_x$) forms of N to these same 13 watersheds are estimated to exceed pre-industrial inputs by several-fold (Howarth et al., 1996). Increased inputs of P eroded from the landscape and carried from human wastewater into the world's rivers have increased global fluxes of P to the oceans almost three-fold from historic levels of ca. 8 million metric tonnes per year to current loadings of ca. 22 million metric tonnes per year (Howarth et al., 1995).

These trends in anthropogenic N inputs are of great concern because nutrient limitation of algal production has been demonstrated or inferred in many estuarine and marine waters (Hecky and Kilham, 1988; Howarth, 1988, 1993; Vitousek and Howarth, 1991; Lapointe and Clark 1992; Downing, 1997). Not surprisingly, wide-ranging effects of this nutrient enrichment are easily visible in coastal ecosystems (Table 5), and the degradation in water quality that accompanies marine eutrophication can have significant socioeconomic impacts (Shumway 1990; Bundy, 1992; Culotta, 1992; McClelland and Valiela, 1998).

The problem of marine eutrophication has been highlighted in recent years by the occurrence of increasingly severe toxic phytoplankton blooms in many

Table 4
Effects of eutrophication on stream ecosystems (modified from Quinn, 1991, as cited in US EPA, 1996b)

Increased biomass and changes in species composition of suspended algae and periphyton
Reduced water clarity
Taste and odor problems
Blockage of intake screens and filters
Fouling of submerged lines and nets
Disruption of flocculation and chlorination processes at water treatment plants
Restriction of swimming and other water-based recreation
Harmful diel fluctuations in pH and in dissolved oxygen concentrations
Dense algal mats reduce habitat quality for macroinvertebrates and fish spawning
Increased probability of fish kills

Table 5
Effects of eutrophication on estuarine and coastal marine ecosystems (modified from Smith, 1998)

Increased biomass of marine phytoplankton and epiphytic algae
Shifts in phytoplankton species composition to taxa that may be toxic or inedible (e.g., bloom-forming dinoflagellates)
Increases in nuisance blooms of gelatinous zooplankton
Changes in macroalgal production, biomass, and species composition
Changes in vascular plant production, biomass, and species composition
Reduced water clarity
Death and losses of coral reef communities
Decreases in the perceived aesthetic value of the water body
Elevated pH and dissolved oxygen depletion in the water column
Shifts in composition towards less desirable animal species
Increased probability of kills of recreationally and commercially important animal species

near-shore waters worldwide. Toxic phytoplankton blooms in the sea are of even greater concern than in freshwater ecosystems. The diversity of toxic species is much larger, and their presence can lead to significant impacts on the edibility and marketability of marine foodstuffs (Shumway, 1990; Smayda and Shimizu, 1993; Anderson and Garrison, 1997). For example, exceptional blooms in May–June 1988 of the toxin-producing prymnesiophycean flagellate *Chrysochromulina polyepsis* in the Baltic sea caused what was termed a "silent spring in the sea" (Rosenberg et al., 1988). The toxins from these algal blooms influenced the entire ecosystem, and caused kills of large numbers of macroalgae, invertebrates, and fish (Rosenberg et al., 1988). In recent years, many estuaries along the Atlantic coast of the USA have similarly experienced extensive fishkills that have been attributed to the newly identified toxic dinoflagellate *Pfisteria piscicida* (Burkholder et al., 1992; Burkholder and Glasgow, 1997).

Toxic phytoplankton blooms are not the only major consequence of marine eutrophication, however. Eutrophication of marine waters has also been accompanied: (1) by macroalgal blooms in shallow estuaries (Valiela et al., 1997); (2) by the development of a region of water column anoxia in the Gulf of Mexico that at times exceeds 6000 square miles in surface area (Tyson, 1997; Malakoff, 1998); and (3) by losses to commercial finfish and shellfish fisheries in many regions (Shumway, 1990; Valiela et al., 1997). Overviews of the diverse problems associated with marine eutrophication and its control can be found in Valiela (1992), Vollenweider et al. (1992a, b), Howarth (1993), Nixon (1995), and Malone et al. (1996).

The possibility of applying an OECD-like approach to the management of marine eutrophication has been considered by Vollenweider (1992), and the development of such a modeling framework was a major recommendation of a recent US national nutrient assessment workshop (US EPA, 1996b). Efforts are

underway to apply the OECD's critical load concept to Norwegian marine waters, and Hessen et al. (1992) have suggested that this could be accomplished by:

1. defining (if possible) site-specific relationships between spring or summer levels of chlorophyll and late winter maximum concentrations of dissolved N;
2. defining the critical load of N (or critical water column N concentration) yielding a critical level of chlorophyll; and
3. defining the degree to which current loadings exceed the critical loading values; this latter calculation would provide an estimate of the minimum required load reduction needed to restore acceptable marine water quality.

This general approach is very likely to be as successful as it has been for freshwater lakes and reservoirs. For example, Nixon (1992) has reported a strong dependence of marine productivity on external N loading, and strong empirical relationships between phytoplankton biomass and nutrient concentrations in the water column have also been found (Ketchum, 1969; Ilus and Keskitalo, 1987; Meuwig, 1997; Smith, 1998). This accumulating body of evidence suggests that a management framework similar to that used successfully in lakes and reservoirs can indeed be applied to the control of eutrophication in estuarine and coastal marine ecosystems.

The results to date are reassuring. Several aspects of the OECD (1982) approach have been applied successfully in a recent study of the Northern Adriatic Sea (cf. Vollenweider et al., 1992b; Giovanardi and Tromellini, 1992). In addition, Wallin et al. (1992) have developed eutrophication models for coastal areas of the Baltic Sea based upon N loading and total N concentrations in the water column. In Norway, efforts are continuing to explore the critical load concept in fjords and marine areas (Hessen et al., 1992, 1997). Because of the more open physical structure and more complex hydrological structure of estuarine and coastal marine systems, the development of such models may be a formidable task, however. Moreover, the high diversity of biotic habitat types that are present in marine systems will almost certainly make it necessary to develop separate but complementary predictive frameworks for coral reef-, seagrass-, macroalgae-, and plankton-dominated ecosystems.

3.5. Successful restoration of eutrophic marine ecosystems: Hillsborough Bay, Florida, as a case study

If the general principles applied successfully to freshwater eutrophication control can be extended to estuarine and coastal marine ecosystems, then the restriction of

external nutrient inputs should be a keystone in water quality restoration. Deliberate nutrient loading reductions indeed have led to dramatic improvements in Hillsborough Bay, a subdivision of Tampa Bay, Florida (Johansson and Lewis, 1992). Restrictions of N and P loading to Hillsborough Bay were accomplished by implementing advanced wastewater treatment in the watershed, and by reducing the nutrient inputs from fertilizer industries. These loading reductions were followed almost immediately by significant reductions in phytoplankton biomass, and by increases in water transparency and dissolved O_2 concentrations in the bay. In addition, seagrasses and macroalgae have revegetated the shallow areas around the bay that had been barren for decades (Johansson and Lewis, 1992). A similar success story, involving the reversal of eutrophication in Kaneohe Bay (Hawaii, USA), is summarized by Laws (1993). Other marine eutrophication case studies of interest include: the Chesapeake Bay and Northern Adriatic Sea (Malone et al., 1996); Dutch Wadden Sea (de Jonge, 1990; Kennish, 1998); the Harvey-Peel Estuary, Australia (McComb, 1995); the Florida Keys, USA (Lapointe and Clark, 1992); and the Neuse River Estuary, NC, USA (Paerl et al., 1990, 1995).

4. Eutrophication of terrestrial ecosystems

Numerous nutrient addition experiments and observational studies have shown that N is the key limiting element that determines the productivity, diversity, dynamics and species composition of terrestrial ecosystems (e.g. Tilman, 1982; Tamm, 1991; Vitousek and Howarth, 1991). The reasons for N limitation of terrestrial ecosystems are many. First, plants have high requirements for N. Second, the parent materials from which soils have formed did not contain N because the most stable form of N is the gas, N_2. The N content of soils, thus, is mainly of biological origin, formed via microbial N fixation. Although both N and P can be growth-limiting nutrients in both aquatic and terrestrial ecosystems, the primary productivity of freshwater ecosystems more often is limited by P than by N, whereas the opposite occurs in terrestrial ecosystems. This difference is explained qualitatively, not by differences in the N and P requirements of terrestrial versus freshwater plants, but by a simple physical process. Nitrate is readily leached from soils, whereas phosphate has a movement rate through soil that is orders of magnitude slower. As a crude first approximation, freshwaters exhibit a chemistry that reflects inputs that erode or leach from surrounding terrestrial habitats, whereas terrestrial soils have a chemistry reflecting the compounds that remain in the soil; soils thus are typically relatively nitrate poor and phosphate rich.

This important difference in the retention of N and P by soils is very important because humans are now having a major impact on the N budget of the Earth. Before human alterations to the global N cycle, the terrestrial N cycle had an annual rate of N fixation from natural sources of 90 to 140 Tg year^{-1} (Soderlund and Rosswall, 1982; Paul and Clark, 1989; Schlesinger, 1991; note: 1 Tg $= 10^{12}$ g). Three human-controlled processes now release similar amounts of additional N, doubling the rate of N input to terrestrial ecosystems. The industrial production of nitrogenous fertilizers used in agriculture now results in the release of about 80 Tg year^{-1} (Vitousek et al., 1997b). Combustion of fossil fuels results in the fixation of about an additional 20 Tg year^{-1}, and the farming of legume crops such as peas, alfalfa, soybeans, and vetch, fixes about an additional 40 Tg year^{-1} (Vitousek et al., 1997b). Because of its mobility via atmospheric transport (as ammonium or nitrous oxide), and via water (as nitrate), this added N is redistributed around the Earth. The pre-industrial rates of N deposition in terrestrial habitats are not well known, but these inputs likely were less than 1 or 2 kg N ha^{-1} year^{-1}. Human impacts on the terrestrial N cycle have dramatically increased rates of N deposition in some ecosystems, such as those of the Netherlands, to rates as high as 40–90 kg ha^{-1} year^{-1}. This represents a massive increase in the effective N supply rates to these ecosystems because the annual rate of N mineralization in most native forest soils ranges only from 10 to 60 kg ha^{-1} year^{-1}.

4.1. Impacts of N loading on terrestrial ecosystems

Because N is the major nutrient limiting plant growth in most terrestrial ecosystems, it is not surprising that anthropogenic N addition increases primary productivity. It is just this effect that has led to the high rate of N fertilization in agriculture which, as discussed in Section 3 is the major cause of inadvertent N addition to other ecosystems. The shifts in primary production that result from increasing N additions can have many impacts on the dynamics, structure and functioning of terrestrial ecosystems. First, each plant species has morphological and physiological characteristics that constrain it to being a superior competitor only at a particular point or region along a primary productivity gradient (Tilman, 1988). It is this inherent constraint that explains the shifts in plant composition that occur along major natural environmental gradients, such as gradients from rich to poor soils that occur along slopes, or elevational or latitudinal gradients in productivity. The traits that allow a given plant species to perform well in more productive ecosystems (e.g. greater height, lower allocation to roots, higher tissue N levels, greater maximal rates of photosynthesis, larger seed size, etc.) are not the traits that allow it to do well in less productive ecosystems

(e.g. high allocation to roots, low allocation to stem, nutrient-conservation via low tissue N, long-lived leaves, etc.). Thus, one of the impacts of N addition to an ecosystem is a shifts in the species composition of the ecosystem (e.g. Tilman, 1982, 1988). In the Netherlands, high rates of anthropogenic N deposition have caused the loss of formerly species-rich heathlands and their conversion to depauperate grasslands and forest (Aerts and Berendse, 1988). Similarly, experimental N addition to Minnesota grasslands has caused a marked loss of plant diversity, and led to the displacement of native warm-season prairie forbs by one or two non-native grass species. Long-term N addition to a British grassland led to more than a five-fold loss of plant diversity (Thurston, 1969). Comparable effects of N addition on plant diversity have occurred in other European grasslands (Bobbink et al., 1988) and in a California grassland (Huenneke et al., 1990).

As would be expected, such shifts in plant diversity and plant species composition, and thus in the traits of the primary producers, have impacts that ramify throughout the entire food chain (Hurd et al., 1971; Hurd and Wolf, 1974; Kirchner, 1977; Vince et al., 1981; Sedlacek et al., 1988; Siemann, 1998). For instance, the species diversity and composition of both herbivorous and predatory/parasitic insects changed significantly in response to experimental N additions to a Minnesota grassland (Haddad et al., 1999). Thus, the responses of terrestrial ecosystems to N eutrophication are qualitatively similar to the responses of aquatic ecosystems to N or P addition (Mundie et al., 1991; Lathrop and Carpenter, 1992; Peterson et al., 1993; Perrin and Richardson, 1997; Carpenter et al., 1998).

N additions to terrestrial ecosystems also can have major effects on soil chemistry. Long-term studies at the Rothamsted Experiment Station in the UK, for example, have shown that addition of ammonium results in a dramatic acidification of soils (Powlson, 1994). N addition also greatly increases the leaching rates of nitrate (Dise and Wright, 1995), and of many base cations, including calcium (Waring and Running, 1998). The impacts of N addition on soil C stores are less clear, however. In agricultural soils, long-term (150 year) addition of NPK fertilizer did not lead to significant changes in soil C compared to unfertilized plots (Jenkinson et al., 1994). However, N addition in Minnesota grasslands did lead to net C storage in soils at certain rates. For rates of N addition less than about 5 g m^{-2} year^{-1}, up to about 20 g of C was stored in soil for every gram of N added as fertilizer to habitats that were dominated by native warm-season bunchgrasses, which are efficient users of N (Wedin and Tilman, 1996). However, at higher rates of N addition, these communities shifted in species composition toward cool-season grasses that are inefficient N users and that produce readily decomposed litter. Despite high rates of N

addition, such communities did not exhibit any net storage of carbon in their soils. In these communities, the added N was leached from the ecosystem and soil C did not accumulate (Wedin and Tilman, 1996). Strong deleterious effects of excess N loading on forest ecosystems also have been observed (Aber et al., 1989; Waring and Running, 1998).

N additions also can modify the year-to-year stability of ecosystem productivity. A long-term study of grassland dynamics in Minnesota has show that grasslands that received higher rates of N addition had primary production that was less resistant to drought. This response to drought was caused by the effects of N addition on plant species diversity and species composition (Tilman and Downing 1994). Additional analyses revealed a similar pattern of plant response to the more usual year-to-year climatic variations that occur among non-drought years. In particular, the more diverse plots exhibited lower year-to-year variability in their productivity than did low-diversity plots, and much of the difference in diversity was caused by the rate of experimental N addition to these 207 plots (Tilman 1996).

Additional effects of excess N loading on terrestrial ecosystems are shown in Table 6. For a more extensive list of N loading effects on soil–plant–animal interactions, and a valuable summary of the major environmental impacts of this "embarrassment of riches", see Jefferies and Maron (1995). Other overviews can be found in Boring et al. (1988), Hornung and Williams (1994) and Galloway et al. (1995).

In total, human domination of the N cycle is greatly increasing the rate of N addition to terrestrial ecosystems. Because N is the major limiting nutrient, terrestrial ecosystems are in turn very sensitive to these changes in the external supply of N. N eutrophication of the biosphere thus may well have dramatic long-term effects upon the structure and dynamics of many terrestrial ecosystems. Many terrestrial ecosystems are likely

Table 6
Effects of nitrogen enrichment on terrestrial ecosystems (modified from Tamm, 1981)

Increased total production of vascular plants
Increased susceptibility of some plant species to herbivory, disease, and cold stress
Changes in soil chemistry
Nitrate leaching and accumulation in groundwater
Changes in plant and microbial community structure
Decreased dominance by legumes
Increased dominance by grasses
Decreases in asymbiotic N-fixing bacteria
Changes in animal community structure
Increases in deer, wild boar, wintering geese and swans, wood pigeons, and ducks
Decreases in quail, partridge, rabbit, hare, and open-vegetation birds

to lose plant, herbivore, and predator species diversity. They are also likely to exhibit pronounced shifts in species composition to favor once-rare species, which are often non-native weeds. Because of leaching, the soils will tend to become increasingly impoverished in elements other than N. Although the N-enhanced rate of terrestrial primary productivity may be higher for a period of time, it also may be more variable and less stable.

If the observed short-term effects of high experimental rates of N addition described above are indicative of the long-term effects of chronic, lower rates of N deposition, we conclude that most of the terrestrial ecosystems of the world are likely to be dramatically transformed over the next century by anthropogenic N eutrophication. As is true of aquatic ecosystems, the successful management and control of eutrophication in terrestrial ecosystems will be based upon objective estimates of critical N loading (e.g. Wilson et al., 1995). These critical loads are indices of ecosystem susceptibility, defined as a quantitative estimate of exposure to ammonium or nitrate, below which detectable changes in ecosystem structure and function do not appear to occur; essentially a critical load is the amount of N deposition that an ecosystem can tolerate without damage (Jefferies and Maron, 1997). A complete management framework will also require the identification and delineation of the source areas that contribute to N deposition, and the development of models that relate N source strengths to actual N deposition rates (for a parallel example concerning S source strengths, S deposition, and critical S loads in acidification control, see Figs. 33 and 34 in Likens and Bormann, 1995).

5. Possible effects of altered nutrient fluxes on atmospheric carbon dioxide concentrations

As we have seen in the above discussions of eutrophication, nutrient limitation of primary production is very common in the biosphere. Moreover, primary production by terrestrial and aquatic ecosystems contributes to the sequestration of atmospheric CO_2, and thus serves as an important sink in the global C cycle. Widespread evidence for N limitation of terrestrial and aquatic primary productivity thus implies that recent increases in anthropogenic loadings of inorganic N to the biosphere potentially could contribute to an enhancement of C uptake and storage by the world's biota (cf. Peterson and Melillo, 1985; Paerl, 1993, 1995; Schindler and Bayley, 1993; Schimel, 1995). We address this important secondary effect of eutrophication briefly in the next section.

Several potential estimates for N-stimulated C uptake by plants have appeared in the literature, ranging in magnitude from ca. 0.2 to 1.2 Gt C year^{-1} (Peterson and Melillo, 1985; Schlesinger, 1993; Hudson et al.,

1994; Townshend et al., 1994). However, there are very large uncertainties associated with not only with these values, but also for current estimates of the C pool sizes and flux strengths used to develop global C budgets. Given such uncertainties, and the impacts of other environmental phenomena such as the El Niño-Southern Oscillation (ENSO) (Keeling and Revelle, 1991; Williams, 1997), the question immediately arises as to how we could detect such an effect of eutrophication on a global scale. In this section, we report very preliminary evidence suggesting that anthropogenic NO_x emissions associated with fossil fuel combustion may be correlated with the rate of CO_2 loss from the atmosphere to the biosphere, as estimated from atmospheric CO_2 measurements at Mauna Loa during 1960–80.

We (V.H.S. and J.C.N.) have used empirical statistical methods as a preliminary inspection tool in our attempt to look for possible effects of N eutrophication on the global carbon cycle. We first compiled estimates of annual total C emissions from the combustion of natural gas, liquid and solid fuels, and from global cement production (Marland et al., 1988). We also digitized data from one report of estimated CO_2 release from terrestrial biota and soils due to changes in land use (Houghton, 1986). Although there is disagreement about the accuracy of estimates of biotic release (Detwiler and Hall, 1988; Houghton 1988), these data nonetheless provided a consistent index of trends in net biotic C flux during the period 1958–80. The sum of these sources provided an estimate of total annual C inputs to the atmosphere. As in Enting and Pearman (1986), we used annual mean CO_2 concentrations measured at Mauna Loa (Keeling, 1988) as an index of trends in atmospheric CO_2. Sea-surface temperature anomalies reported by Barber (1988) were used as an index of potential effects of the ENSO (Keeling and Revelle, 1985).

The net removal rate of C from the atmosphere by all sinks in this initial analysis was estimated as the difference between the annual growth rate of CO_2 at Mauna Loa (ppm year^{-1}) and the estimated total annual input from all of the above C sources to the atmosphere (Gt C year^{-1}). A multiple regression analysis of these data suggested that a significant portion of the variability in net C removal was associated with the ENSO, but also suggested that the net removal rate during 1958–80 increased at a rate of ca. 0.054 Gt C year^{-1} (Table 7). Both of these effects can also be seen in a graphical analysis of the atmospheric CO_2 data and fossil fuel emissions made by Keeling (1983).

The apparent increase in net annual C removal rate suggested by Table 7 is generally consistent with the hypothesis that global rates of net primary production may have increased during the past several decades. One potential explanation for this trend is a recent stimulation of plant growth in the biosphere due to increased

Table 7
Results of a multiple regression analysis of net carbon removal rates (Gt C year^{-1}) on year and on sea-surface temperature anomalies (°C) observed at Chicama, Peru[a]

Source	Estimate	SE	T	p
Constant	102.004	46.38	2.20	0.040
Sea-surface temperature anomaly	−0.678	0.22	−3.13	0.006
Year	0.054	0.02	2.29	0.034

Source	ANOVA[b]					
	Df	SS	MS	F	p	R^2
Regression	2	8.09	4.05	8.33	0.003	0.467
Error	19	9.23	0.49			

[a] The sea-surface temperature data were digitized from Fig. 9.2 in Barber (1988).

Table 8
Results of a multiple regression analysis of net carbon removal rates (Gt C year^{-1}) on oxidized nitrogen emissions to the atmosphere (NO_y, Mt N year^{-1}) and on sea-surface temperature anomalies (°C) observed at Chicama, Peru[a]

Source	Estimate	SE	T	p
Constant	2.545	0.704	3.62	0.002
Sea-surface temperature anomaly	−0.706	0.224	−3.15	0.005
NO_y emissions	0.087	0.037	2.36	0.030

Source	ANOVA[b]					
	Df	SS	MS	F	p	R^2
Regression	2	8.021	4.011	8.03	0.003	0.472
Error	18	8.987	0.499			

[a] The data for global NO_y emissions were digitized from Fig. 1 in Hameed and Dignon (1988); values for 1961–65 and 1975 were interpolated.
[b] ANOVA, analysis of variance.

anthropogenic fluxes of N to the atmosphere. We performed a preliminary statistical test of this hypothesis using estimates of global NO_x emissions from fossil fuel combustion, which increased steadily during the period 1960–80 (Hameed and Dignon, 1988). When these data were included in a subsequent multiple regression analysis, we found a significant positive effect of NO_x emissions on net C removal (Table 8).

This provisional analysis suggests that N enrichment from fossil fuel combustion could have significantly enhanced global primary production during the past several decades. However, the processes that affect the N cycle, and its effects on the biological pump, are very complex (Falkowski, 1997). In this very provisional modeling effort we have considered only the possible effects of anthropogenic oxidized N emissions to the atmosphere. We have not yet been able to perform a larger test that includes global estimates of anthropogenic NH_x emissions (Schlesinger and Hartley, 1992); similarly, we did not consider the possible effects of atmospheric dissolved organic N deposition, which also may be biologically available for plant growth (e.g. Chapin et al., 1993; Paerl, 1997; Peierls and Paerl, 1997). Moreover, we have not been able to include in our very simple model structure the additional stimulatory effects that direct fluvial N inputs to the world's oceans potentially may have upon CO_2 fixation and sequestration by coastal marine ecosystems; neither have we been able consider the potential moderating effects that food web structure may have upon marine CO_2 fixation and sequestration (cf. Huntley et al., 1991; Ingrid et al., 1996; Schindler et al., 1997). We also note that many other factors have covaried with anthropogenic NO_x emissions during this time period, and we recognize that alternative hypotheses could be proposed which do not rely upon the N enrichment of primary production. The above statistical analyses thus constitute far from a complete analysis of the potential

sensitivity of the global C budget to anthropogenic N emissions, and we note that future changes in land use alone could result in either the net addition or the net storage of hundreds of Gt C during the next several centuries (Schimel, 1995).

Human alterations of the N cycle may have effects that are visible at the scale of the global atmosphere (Schimel, 1995), and that the provisional analyses presented here provide very preliminary evidence that is generally consistent with the hypothesis that anthropogenic NO_x emissions to the atmosphere may influence atmospheric CO_2 concentrations. We also stress that we cannot evaluate the extent to which this potential consequence of cultural eutrophication (if it is actually present) will continue in the future, because of the important issue of N saturation in terrestrial ecosystems. As stressed by Schimel et al. (1995), the uptake of atmospheric CO_2 due to long-term increases in N deposition could increase as human N pollution increases; however, this increase may occur only up to a critical threshold loading value, beyond which any additional N input will cause significant ecosystem degradation (cf. Aber et al., 1989; Schultze, 1989; Waring and Running, 1998). More detailed studies are needed in order to accept or reject the tentative conclusions that we have drawn here, and we urge further additional research and modeling efforts to expand our understanding of the links between anthropogenic N inputs and the global C cycle.

References

Aber, J.D., Nadelhoffer, K.J., Steudler, P., Melillo, J., 1989. Nitrogen saturation in northern forest ecosystems. BioScience 39, 378–386.

Aerts, R., Berendse, F., 1988. The effect of increased nutrient availability on vegetation dynamics in wet heathlands. Vegetatio 76, 63–69.

Anderson, D.M., Garrison, D.J., 1997. The ecology and oceanography of harmful algal blooms. Limnology and Oceanography 42, 1009–1305.

Bachmann, R.W., 1981. Prediction of total nitrogen in lakes and reservoirs. In: Restoration of Lakes and Inland Waters (US EPA 440/5-81-010). US Environmental Protection Agency, Washington, D.C, pp. 320–324.

Bachmann, R.W., 1984. Calculation of phosphorus and nitrogen loadings to natural and artificial lakes. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 22, 239–243.

Baker, L.A., Brezonik, P.L., Kratzer, C.R., 1981. Nutrient Loading–Trophic State Relationships in Florida Lakes (Publication No. 56). Florida Water Resources Research Center, University of Florida, Gainesville, FL.

Baker, L.A., Brezonik, P.L., Kratzer, C.R., 1985. Nutrient loading models for Florida lakes. Lake and Reservoir Management: Practical Implications. North American Lake Management Society, Merrifield, VA, pp. 253–258.

Barber, R.T., 1988. Ocean basin ecosystems. In: Pomeroy, L.R., Alberts, J.J. (Eds.), Concepts of Ecosystem Ecology. Springer, New York, pp. 171–193.

Basu, B.K., Pick, F.R., 1996. Factors regulating phytoplankton and zooplankton biomass in temperate rivers. Limnology and Oceanography 41, 1572–1577.

Bobbink, R., Bik, L., Willems, J.H., 1988. Effects of nitrogen fertilization on vegetation structure and dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grassland. Acta Botanica Neerlandica 37, 231–242.

Boring, L.R., Swank, W.T., Waide, J.B., Henderson, G.S., 1988. Sources, fates, and impacts of nitrogen inputs to terrestrial ecosystems: review and synthesis. Biogeochemistry 6, 119–159.

Bottsford, L.W., Castilla, J.C., Peterson, C.H., 1997. The management of fisheries and marine ecosystems. Science 277, 509–515.

Bundy, M.M., 1992. Estuarine management from a global economic perspective. Water Science and Technology 26, 2735–2739.

Burkholder, J.M., Glasgow, H.B. Jr., 1997. *Pfiesteria piscicida* and other *Pfiesteria*-like dinoflagellates: behavior, impacts, and environmental controls. Limnology and Oceanography 42, 1052–1075.

Burkholder, J.M., Noga, E.J., Hobbs, C.W., Glasgow, H.B. Jr., Smith, S.A., 1992. New "phantom" dinoflagellate is the causative agent of major estuarine fish kills. Nature 358, 407–410.

Canfield, D.E. Jr., Bachmann, R.W., 1981. Prediction of total phosphorus concentrations, chlorophyll *a*, and Secchi depths in natural and artificial lakes. Canadian Journal of Fisheries and Aquatic Sciences 38, 414–423.

Caraco, N.F., 1995. Influence of human populations on P transfers to aquatic ecosystems: a regional scale study using large rivers. In: Tiessen, H. (Ed.), Phosphorus in the Global Environment. John Wiley, New York, pp. 235–244.

Carmichael, W.W., 1991. Toxic freshwater blue-green algae (cyanobacteria): an overlooked health threat. Health Environ. Digest 5, 1–4.

Carpenter, S.R., Bolgrien, D., Lathrop, R.C., Stowe, C.A., Reed, T., Wilson, M.A., 1997. Ecological and economic analysis of lake eutrophication by nonpoint pollution. Australian Journal of Ecology 23, 68–79.

Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N., Smith, V.H., 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecological Applications 8, 559–568.

Carpenter, S.R., Christensen, D.L., Cole, J.J., Cottingham, K.L., He, X., Hodgson, J.R., Kitchell, J.F., Knight, S.E., Pace, M.L., Post, D.M., Schindler, D.E., Voichick, N., 1995. Biological control of eutrophication. Environmental Science and Technology 29, 784–786.

Carpenter, S.R., Ludwig, D., Brock, W.A., 1999. Management of eutrophication for lakes subject to potentially irreversible change. Ecological Applications 9, (in press).

Carvalho, L., Beklioglu, M., Moss, B., 1995. Changes in a deep lake following sewage diversion—a challenge to the orthodoxy of external phosphorus control as a restoration strategy? Freshwater Biology 34, 399–410.

Chapin, F.S. III, Moilanen, L., Kielland, K., 1993. Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. Nature 361, 150–153.

Chapin, F.S. III, Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., Tilman, D., 1997. Biotic control over the functioning of ecosystems. Science 277, 500–504.

Cole, J.J., Peierls, B.L., Caraco, N.F., Pace, M.L., 1993. Nitrogen loading of rivers as a human-driven process. In: McDonnell, M.J., Pickett, S.T.A. (Eds.), Humans as components of ecosystems. Springer, New York, pp. 141–157.

Cooke, G.D., Welch, E.B., Peterson, S.A., Newroth, P.R., 1993. Restoration and manangement of lakes and reservoirs, Lewis Publishers, Boca Raton, FL.

Correll, D.L., 1958. Alteration of the Productivity of a Trout Stream by the Addition of Phosphate. M.S. thesis, Michigan State University, East Lansing, MI.

Correll, D.L., 1998. The role of phosphorus in the eutrophication of receiving waters: a review. Journal of Environmental Quality 27, 261–266.

Culotta, E., 1992. Red menace in the world's oceans. Science 257, 1476–1477.

de Bernardi, R., Calderoni, A., Mosello, R., 1996. Environmental problems in Italian lakes, and lakes Maggiore and Orta as successful examples of correct management leading to restoration. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 26, 123–138.

de Jonge, V.N., 1990. Response of the Dutch Wadden Sea ecosystem to phosphorus discharges from the River Rhine. Hydrobiologia 195, 49–62.

Detwiler, R.P., Hall, C.A.S., 1988. Tropical forests and the global carbon cycle. Science 239, 42–47.

Dillon, P.J., Rigler, F.H., 1974. The phosphorus–chlorophyll relationship in lakes. Limnology and Oceanography 19, 767–773.

Dillon, P.J., Rigler, F.H., 1975. A simple method for predicting the capacity of a lake for development based on lake trophic state. Journal of the Fisheries Research Board of Canada 31, 1518–1531.

Dise, N.B., Wright, R.F., 1995. Leaching from European forests in relation to N deposition. Forest Ecology and Management 71, 153–161.

Dobson, A.P., Bradshaw, A.D., Baker, A.J.M., 1997. Hopes for the future: restoration ecology and conservation biology. Science 277, 515–522.

Dodds, W.K., Smith, V.H., Zander, B., 1997. Developing nutrient targets to control benthic chlorophyll levels in streams: a case study of the Clark Fork River. Water Research 31, 1738–1750.

Dodds, W.K., Jones, J.R., Welch, E.B., 1998. Suggested classification of stream trophic state: distributions of temperate stream types by chlorophyll, total nitrogen, and phosphorus. Water Research 32, 1455–1462.

Downing, J.A., 1997. Marine nitrogen:phosphorus stoichiometry and the global N:P cycle. Biogeochemistry 37, 237–252.

Edmondson, W.T., 1991. The uses of ecology: Lake Washington and beyond. University of Washington Press, Seattle, WA.

Edmondson, W.T., 1993. Eutrophication effects on the food chains of lakes: long-term studies. Memoire dell'Istituto Italiano di Idrobiologia 52, 113–132.

Edmondson, W.T., 1994. Sixty years of Lake Washington: a curriculum vitae. Lake Reservoir Management 10, 75–84.

Edmondson, W.T., 1995. Eutrophication. Encyclopedia of Environmental Biology, vol. 1. Academic Press, New York, pp.697–703.

Edmondson, W.T., Litt, A.N., 1982. *Daphnia* in Lake Washington. Limnology and Oceanography 27, 272–293.

Elwood, J.W., Newbold, J.D., Trimble, A.F., Stark, R.W., 1981. The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and primary producers. Ecology 62, 146–158.

Enting, I.G., Pearman, G.I., 1986. The use of observations in calibrating and validating carbon cycle models. In: Trabalka, J.R., Reichle, D.E. (Eds.), The Changing Carbon Cycle: a Global Analysis. Springer, New York, pp. 425–458.

Falkowski, P., 1997. Evolution of the nitrogen cycle and its influence on the biological sequestration of CO_2 in the ocean. Nature 387, 272–275.

Foy, R.H., Withers, P.J.A., 1995. The contribution of agricultural phosphorus to eutrophication. In: Proceedings No. 365. The Fertiliser Society, Greenhill House, Thorpewood, Peterborough, UK.

Foy, R.H., Smith, R.V., Jordan, C., Lennox, S.D., 1995. Upward trend in soluble phosphorus loadings to Lough Neagh despite phosphorus reduction at sewage treatment works. Water Research 29, 1051–1063.

Foy, R.H., Gibson, C.E., Champ, T., 1996. The effectiveness of restricting phosphorus loading from sewage treatment works as a means of controlling eutrophication in Irish lakes. In: Giller, P.S., Miller, A.A. (Eds.), Disturbance and Recovery of Ecological Systems. Royal Irish Academy, Dublin, Ireland, pp. 134–152.

Galloway, J.N., Schlesinger, W.H., Levy, H. II, Michaels, A, Schnoor, J.L., 1995. Nitrogen fixation: anthropogenic enhancement-environmental response. Global Biogeochemical Cycles 9, 235–252.

Giovanardi, F., Tromellini, E., 1992. Statistical assessment of trophic conditions. Application of the OECD methodology to the marine environment. In: Vollenweider, R.A., Marchetti, R., Viviani, R. (Eds.), Marine Coastal Eutrophication. The Response of Marine Transitional Systems to Human Impact: Problems and Perspectives for Restoration. Science of the Total Environment Supplement 1992. Elsevier Science Amsterdam, The Netherlands, pp. 211–233.

Gregory, S.V., 1980. Effects of Light, Nutrients and Grazing on Periphyton Communities in Streams. Ph.D. thesis, Oregon State University, Corvallis, OR.

Grimm, N.B., Fisher, S.G., 1986. Nitrogen limitation in a Sonoran Desert stream. Journal of the North American Benthological Society 5, 2–15.

Haddad, N.M., Haarstad, J., Tilman, D., 1999. The effects of long-term nitrogen loading on grassland insect communities. Ecology (submitted).

Håkanson, L., 1994. A review of effect–dose-sensitivity models for aquatic ecosystems. Internationale Revue der Gesamten Hydrobiologie 79, 621–667.

Hameed, S., Dignon, J., 1988. Changes in the geographical distributions of global emissions of NO_x and SO_x from fossil-fuel combustion between 1966 and 1980. Atmospheric Environment 22, 441–449.

Harper, D., 1992. Eutrophication of Freshwaters: Principles, Problems, Restoration, Chapman and Hall, New York.

Hecky, R.E., Kilham, P., 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. Limnology and Oceanography 33, 796–822.

Hershey, A.E., Hiltner, A.L., Hullar, M.A.J., Miller, M.C., Vestal, J.R., Lock, M.A., Rundle, S., 1988. Nutrient influence on a stream grazer: *Orthocladius* microcommunities respond to nutrient input. Ecology 69, 1383–1392.

Hessen, D.O., Vadstein, O., Magnusson, J., 1992. Nitrogen to Marine Areas: on the Application of a Critical Load Concept. Background document to the workshop "Critical Loads for Nitrogen" in Lökeberg, Sweden, 6–10 April 1992. Environment Canada and Nordic Council of Ministers, NORD, 41.

Hessen, D.O., Hindar, A., Holtan, G., 1997. The significance of nitrogen runoff for eutrophication of freshwater and marine recipients. Ambio 26.

Hill, W.R., Knight, A.W., 1988. Nutrient and light limitation of algae in two northern California streams. Journal of Phycology 24, 125–132.

Houghton, R.A., 1986. Estimating changes in the carbon content of terrestrial ecosystems from historical data. In: Trabalka, J.R., Reichle, D.E. (Eds.), The Changing Carbon Cycle: a Global Analysis. Springer, New York, pp. 175–193.

Houghton, R.A., 1988. The global carbon cycle. Science 241, 1736.

Horner, R.R., Welch, E.B., Seeley, M.R., Jacoby, J.M., 1990. Reponses of periphyton to changes in current velocity, suspended sediment and phosphorus concentration. Freshwater Biology 24, 215–232.

Hornung, M., Williams, M.L., 1994. Impacts of Nitrogen Deposition in Terrestrial Ecosystems, UK Group on Impacts of Atmospheric Nitrogen, London.

Howarth, R.W., 1988. Nutrient limitation of net primary production in marine ecosystems. Annual Review of Ecology and Systematics 19, 898–910.

Howarth, R.W., 1993. The role of nutrients in coastal waters. In: Managing Wastewater in Coastal Urban Areas. Report from the National Research Council Committee on Wastewater Management for Coastal Urban Areas. National Academy Press, Washington, D.C, pp. 77–202.

Howarth, R.W., Jensen, H., Marino, R., Postma, H., 1995. Transport to and processing of P in near-shore and oceanic waters. In: Tiessen, H. (Ed.), Phosphorus in the Global Environment: Transfers, Cycles and Management. SCOPE54. Wiley, Chichester, UK, pp. 323–345.

Howarth, R.W., Billen, G., Swaney, D., Townsend, A., Jaworski, N., Lajtha, K., Downing, J.A., Elmgren, R., Caraco, N., Jordan, T., Berendse, F., Freney, J., Kudeyarov, V., Murdoch, P., Zhao-Liang, Z., 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to the North Atlantic Ocean: natural and human influences. Biogeochemistry 35, 75–139.

Hoyer, M.V., Jones, J.R., 1983. Factors affecting the relation between phosphorus and chlorophyll *a* in midwestern reservoirs. Canadian Journal of Fisheries and Aquatic Sciences 40, 192–199.

Hrbácek, J., Dvoráková, M., Korínek, M., Procházková, L., 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of metabolism of the whole plankton association. Verhandlunger der Internationale Vereinigung für Theoretische und Angewandte Limnologie 14, 192–195.

Hudson, R.J.M., Gherini, S.A., Goldstein, R.A., 1994. Modeling the global carbon cycle: nitrogen fertilization of the terrestrial biosphere and the 'missing' CO_2 sink. Global Biogeochemical Cycles 8, 307–333.

Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A., Vitousek, P.M., 1990. Effects of soil resources on plant invasion and community structure in California serpentine grassland. Ecology 71, 478–491.

Huntley, M.E., Lopez, M.D.G., Karl, D.M., 1991. Top predators in the Southern Ocean: a major leak in the biological carbon pump. Science 253, 64–66.

Huntsman, A.G., 1948. Fertility and fertilisation of streams. Journal of the Fisheries Research Board of Canada 7, 248–253.

Hurd, L.E., Mellinger, M.V., Wolf, L.L., McNaughton, S.J., 1971. Stability and diversity at three trophic levels in terrestrial successional ecosystems. Science 173, 1134–1136.

Hurd, L.E., Wolf, L.L., 1974. Stability in relation to nutrient enrichment in arthropod consumers of old-field successional ecosystems. Ecological Monographs 44, 465–482.

Hutchinson, G.E., 1969. Eutrophication, past and present. Eutrophication: Causes, Consequences, Correctives. National Academy of Sciences, Washington, D.C, pp. 17–26.

Hutchinson, G.E., 1973. Eutrophication. The scientific background of a contemporary practical problem. American Scientist 61, 269–279.

Hynes, H.B.N., 1969. The enrichment of streams. Eutrophication: Causes, Consequences, Correctives. National Academy of Sciences, Washington, D.C, pp. 188–196.

Ilus, E., Keskitalo, J., 1987. Phytoplankton in the sea around the Loviisa nuclear power station, south coast of Finland. Annales Botanica Fennici 24, 35–61.

Ingrid, G., Andersen, T., Vadstein, O., 1996. Pelagic food webs and eutrophication of coastal waters: impact of grazers on algal communities. Marine Pollution Bulletin 33, 22–35.

Jaworski, N.A., Howarth, R.W., Hetling, L.J., 1997. Atmospheric deposition of nitrogen oxides onto the landscape contributes to coastal eutrophication in the northeast United States. Environmental Science and Technology 31, 1995–2004.

Jefferies, R.L, Maron, J.L., 1997. The embarrassment of riches: atmospheric deposition of nitrogen and community and ecosystem processes. Trends in Ecology and Evolution 12, 74–78.

Jenkinson, D.S., Bradbury, N.J., Coleman, K., 1994. How the Rothamsted classical experiments have been used to develop and test models for the turnover of carbon and nitrogen in soil. In: Leigh, R.A., Johnston, A.E. (Eds.), Long-term Experiments in Agricultural and Ecological Sciences. CAB International, Wallingford, UK, pp. 117–138.

Johansson, J.O.R., Lewis, R.R., III., 1992. Recent improvements in water quality and biological indicators in Hillsborough Bay, a highly impacted subdivision of Tampa Bay, Florida, USA. In: Vollenweider, R.A., Marchetti, R., Viviani, R. (Eds.), Marine Coastal Eutrophication. The Response of Marine Transitional Systems to Human Impact: Problems and Perspectives for Restoration. Science of the Total Environment Supplement 1992. Elsevier Science, Amsterdam, The Netherlands, pp. 1199–1216.

Johnson, G., Volent, Z., Tangen, K., Sakshaug, E., 1997. Time series of harmful and benign phytoplankton blooms in Northwest European waters using the Seawatch buoy system. In: Kahru, M., Brown, C.W. (Eds.), Monitoring Algal Blooms: New Techniques for Detecting Large-Scale Environmental Change, pp. 113–141. Springer-Verlag, New York.

Jones, J.R., Bachmann, R.W., 1976. Prediction of phosphorus and chlorophyll levels in lakes. Journal of the Water Pollution Control Federation 48, 2176–2182.

Jones, J.R., Smart, M.M., Burroughs, J.N., 1984. Factors related to algal biomass in Missouri Ozark streams. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 22, 1867–1875.

Keeling, C.D., 1983. The global carbon cycle: what we know and what we could know from atmospheric, biospheric, and oceanic observations. In Proceedings: Carbon Dioxide Research Conference: Carbon Dioxide, Science and Consensus, CONF-820970. US Department of Energy, Washington, D.C, pp. II.3–II.62.

Keeling, C.D., 1988. Atmospheric CO_2 Concentrations—Mauna Loa, Observatory, Hawaii, 1958–1987. Carbon Dioxide Information Analysis Center Numerical Data Package NDP-001/R1, Oak Ridge National Laboratory, Oak Ridge, TN.

Keeling, C.D., Revelle, R., 1985. Effects of El Niño/Southern Oscillation on the atmospheric content of carbon dioxide. Meteoritics 20, 437–450.

Kennish, M., 1998. Pollution Impacts on Marine Biotic Communities, CRC Press, Boca Raton, FL.

Ketchum, B., 1969. Eutrophication of estuaries. Eutrophication: Causes, Consequences, Correctives. National Academy of Sciences, Washington, D.C, pp. 197–209.

Kirchner, T, 1977. The effects of resource enrichment on the diversity of plants and arthropods in a shortgrass prairie. Ecology 58, 1334–1344.

Köhler, J., Gelbrecht, J., 1998. Interactions between phytoplankton dynamics and nutrient supply along the lowland river Spree, Germany. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 26, 1045–1049.

Kratzer, C.R., 1979. Application of Input–Output Models to Florida Lakes. M.S. thesis, University of Florida, Gainesville, FL.

Krewer, J.A., Holm, H.W., 1982. The phosphorus–chlorophyll a relationship in periphytic communities in a controlled ecosystem. Hydrobiologia 94, 173–176.

Lapointe, B.E., Clark, M.W., 1992. Nutrient inputs from the watershed and coastal eutrophication in the Florida Keys. Estuaries 15, 465–476.

Lathrop, R.C., Carpenter, S.R., 1992. Zooplankton and their relationship to phytoplankton. In: Kitchell, J.F. (Ed.), Food web management: a case study of Lake Mendota. Springer, New York, pp. 127–150.

Laws, E.A., 1993. Aquatic pollution, 3rdWiley, New York.

Likens, G.E., Bormann, F.H., 1995. Biogeochemistry of a Forested Ecosystem, 2nd ed., Springer, New York.

Lohman, K., Jones, J.R., 1999. Nutrient-sestonic chlorophyll relations in northern Ozark streams. Canadian Journal of Fisheries and Aquatic Sciences (in press).

Lohman, K., Jones, J.R., Baysinger-Daniel, C., 1991. Experimental evidence for nitrogen limitation in a northern Ozark stream. Journal of the North American Benthological Society 10, 14–23.

Lohman, K., Priscu, J.C., 1992. Physiological indicators of nutrient deficiency in Cladophora (Chlorophyta) in the Clark Fork of the Columbia River, Montana. Journal of Phycology 28, 443–448.

Malakoff, D., 1998. Death by suffocation in the Gulf of Mexico. Science 281, 190–192.

Malone, T.C., Màlej, A., Smodlaka, N., 1996. Trends in land-use, water quality and fisheries: a comparison of the Northern Adriatic Sea and the Chesapeake Bay. Periodicum Biologorum 98, 137–148.

Marland, G., Boden, T., Griffin, R.C., Huang, S.F., Kanciruk, P., Nelson, T.R. 1988. Estimates of CO_2 Emissions from Fossil Fuel Burning and Cement Manufacturing Based on the United Nations Energy Statistics and the U.S. Bureau of Mines Cement Manufacturing Data. Carbon Dioxide Information Analysis Center Numerical Data Package NDP-030, Oak Ridge National Laboratory, Oak Ridge, TN.

Manca, M., Ruggiu, D., 1998. Consequences of pelagic food-web changes during a long-term lake oligotrophication process. Limnology and Oceanography 43, 1368–1373.

Matson, P.A., Parton, W.J., Power, A.G., Swift, M.J., 1997. Agricultural intensification and ecosystem properties. Science 277, 504–509.

Mazumder, A., 1994. Phosphorus–chlorophyll relationships under contrasting herbivory and thermal stratification: predictions and patterns. Canadian Journal of Fisheries and Aquatic Sciences 51, 401–407.

McClelland, J.W., Valiela, I., 1998. Linking nitrogen in estuarine producers to land-derived sources. Limnology and Oceanography 43, 577–583.

McComb, A.J., 1995. Eutrophic Shallow Estuaries and Lagoons, CRC Press, Boca Raton, FL.

McGarrigle, M.L., 1993. Aspects of river eutrophication in Ireland. Annals of Limnology 29, 355–364.

Meeuwig, J., Peters, R.H., Rasmussen, J., 1997. Patterns in the fog: a cross-system comparison of chlorophyll *a*:nutrient relations in estuaries and lakes. Abstracts of the 1997 Annual Meeting, American Society of Limnology and Oceanography, p.237.

Miltner, R.J., Rankin, E.T., 1998. Primary nutrients and the biotic integrity of rivers and streams. Freshwater Biology 40, 145–158.

Mosello, R., Ruggiu, D., 1985. Nutrient load, trophic conditions and restoration prospects of Lake Maggiore. Internationale Revue der Gesamten Hydrobiologie 70, 63–75.

Moss, B., 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200/201, 367–377.

Moss, B., Hooker, I., Balls, H., Manson, K., 1989. Phytoplankton distribution in a temperate floodplain lake and river system. I. Hydrology, nutrient sources and phytoplankton biomass. Journal of Plankton Research 11, 813–838.

Mundie, J.H., Simpson, K.S., Perrin, C.J., 1991. Responses of stream periphyton and benthic insects to increase in dissolved inorganic phosphorus in a mesocosm. Canadian Journal of Fisheries and Aquatic Sciences 68, 2061–2072.

National Research Council, 1993. Managing wastewater in coastal urban areas, National Academy Press, Washington, D.C.

Nixon, S.W, 1992. Quantifying the relationship between nitrogen input and productivity of marine ecosystems. Adv. Mar. Technol. Conf. 5, 57–83.

Nixon, S.W., 1995. Coastal eutrophication: a definition, social causes, and future concerns. Ophelia 41, 199–220.

Noble, I.R., Dirzo, R., 1997. Forests as human-dominated ecosystems. Science 277, 522–525.

Nolan, B.T., Ruddy, B.C., Hitt, K.J., Helsel, D.R., 1997. Risk of nitrate in groundwaters of the U.S.—A national perspective. Environmental Science and Technology 31, 2229–2236.

Nürnberg, G.K., 1996. Trophic state of clear and colored, soft- and hard-water lakes with special consideration of nutrients, anoxia, phytoplankton and fish. Lakes and Reservoir Management 12, 432–447.

Novotny, V., Olem, H., 1994. Water quality: Prevention, Identification and Management of Diffuse Pollution, Van Nostrand Reinhold, New York.

OECD, 1982. Eutrophication of Waters: Monitoring, Assessment and Control. Organisation for Economic and Cooperative Development, Paris, France.

Omernik, J., 1977. Nonpoint Source–Stream Nutrient Level Relationships: a Nationwide Study (US EPA-600/3-77-105). Special Studies Branch, Corvallis Environmental Research Laboratory, Office of Research and Development, US Environmental Protection Agency, Washington D.C.

Paerl, H.W., 1993. Emerging role of atmospheric nitrogen deposition in coastal eutrophication: biogeochemical and trophic perspectives. Canadian Journal of Fisheries and Aquatic Sciences 50, 2254–2269.

Paerl, H.W., 1995. Coastal eutrophication in relation to atmospheric nitrogen deposition: current perspectives. Ophelia 41, 237–259.

Paerl, H.W., 1997. Coastal eutrophication and harmful algal blooms: importance of atmospheric deposition and groundwater as "new" nitrogen and other nutrient sources. Limnology and Oceanography 42, 1154–1165.

Paerl, H.W., Mallin, M., Rudek, J., Bates, P., 1990. The potential for eutrophication and nuisance algal blooms in the lower Neuse River, NC (Albemarle-Pamlico Estuarine Study Report No. 90-15). North Carolina Natural Resources and Community Development, Raleigh, NC.

Paerl, H.W., Mallin, M., Donahue, C., Go, M., Peierls, B., 1995.

Nitrogen Loading Sources and Eutrophication of the Neuse River Estuary, NC: Direct and Indirect Roles of Atmospheric Deposition (Report No. 291). University of North Carolina Water Resources Research Institute, Raleigh, NC.

Peierls, B.L., Paerl, H.W., 1997. Bioavailability of atmospheric organic nitrogen deposition to coastal phytoplankton. Limnology and Oceanography 42, 1819–1823.

Peterson, B., Melillo, J.M., 1985. The potential storage of carbon caused by eutrophication of the biosphere. Tellus Series B 37, 117–127.

Peterson, B., Hobbie, J.E., Corliss, T.L., Kriet, K., 1983. A continuous-flow periphyton bioassay: tests of nutrient limitation in a tundra stream. Limnology and Oceanography 28, 583–591.

Peterson, B., Hobbie, J.E., Hershey, A.E., Lock, M.A., Ford, T.E., Vestal, J.R., McKinley, V.L., Hullar, M.A.J., Miller, M.C., Ventullo, R.M., Volk, G.S., 1985. Transformation of a tundra river from heterotrophy to autotrophy by addition of phosphorus. Science 229, 1383–1386.

Peterson, B.J., Deegan, L., Helfrich, J., Hobbie, J.E., Hullar, M., Moller, B., Ford, T.E., Hershey, A., Hiltner, A., Kipphut, G., Lock, M.A., Fiebig, D.M., McKinley, V., Miller, M.C., Vestal, J.R., Ventullo, R., Volk, G., 1993. Biological responses of a tundra river to fertilization. Ecology 74, 653–672.

Postel, S.L., Carpenter, S.R., 1997. Freshwater ecosystem services. In: Daily, G.C. (Ed.), Nature's Services. Island Press, Washington, D.C, pp. 195–214.

Paul, E.A., Clark, F.E., 1989. Soil Microbiology and Biochemistry, Academic Press, San Diego.

Perrin, C.J., Richardson, J.S., 1997. N and P limitation of benthos abundance in the Nechako River, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 54, 2574–2583.

Powlson, D.S., 1994. Quantification of nutrient cycles using long-term experiments. In: Leigh, R.A., Johnston, A.E. (Eds.), Long-term Experiments in Agricultural and Ecological Sciences. CAB International, Wallingford, UK, pp. 97–115.

Proulx, M., Pick, F.R., Mazumder, A., Hamilton, P.B., Lean, D.R.S., 1996. Effects of nutrients and planktivorous fish on the phytoplankton of shallow and deep aquatic ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 77, 1556–1572.

Quinn, J.M. 1991. Guidelines for the Control of Undesireable Biological Growths in Water (Consultancy Report No.6213/2). Water Quality Centre, Hamilton, New Zealand.

Reckhow, K.H., 1988. Empirical models for trophic state in southeastern U.S. lakes and reservoirs. Water Resources Bulletin 24, 723–734.

Reckhow, K.H., Chapra, S.C., 1983. Engineering Approaches for Lake Management, Vol. 1: Data Analysis and Empirical Modeling, Butterworth, Boston, MA.

Reckhow, K.H., Beaulac, M.N., Simpson, J.T. 1980. Modeling Phosphorus Loading and Lake Response Under Uncertainty: a Manual and Compilation of Export Coefficients (US EPA 440/5-80-011). US Environmental Protection Agency, Washington, D.C.

Reckhow, K.H., Chapra, S.C., 1999. Persistent Organic Pollutants (POPs): State of the Science. Environmental Pollution 100, 209–221.

Roggiu, D., Mosello, R., Pizzolon, L., 1985. Evaluation of nutrient inputs and of the trophic state of Lago Maggiore in recent decades. In: Vismarra, R., Marforio, R., Mezzanotte, V., Cernuschi, S. (Eds.), Lake Pollution and Recovery. Proceedings of the International Congress, European Water Pollution Control Association, Associazione Nazionale di Ingegneria Sanitaria, Italy, pp. 145–153.

Rosenberg, R., Lindahl, O., Blanck, H., 1988. Silent spring in the sea. Ambio 17, 289–290.

Salas, H.J., Martino, P., 1991. A simplified phosphorus trophic state model for warm-water tropical lakes. Water Research 25, 341–350.

Sas, H., 1989. Lake Restoration by Reduction of Nutrient Loading: Expectations, Experiences, Extrapolations, Academia, Richarz, St. Augustin.

Scheffer, M., Hosper, S.H., Meijer, M.-L., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. Trends in Ecology and Evolution 8, 275–279.

Schindler, D.W, 1977. Evolution of phosphorus limitation in lakes. Science 195, 260–262.

Schindler, D.W., Bayley, S., 1993. The biosphere as an increasing sink for atmospheric carbon: estimates from increased nitrogen deposition. Global Biogeochemical Cycles 7, 717–733.

Schindler, D.E., Carpenter, S.E., Cole, J.J., Kitchell, J.F., Pace, M.L., 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. Science 277, 248–251.

Schlesinger, W.H., 1991. Biogeochemistry: An Analysis of Global Change, Academic Press, San Diego.

Schlesinger, W.H., 1993. Response of the terrestrial biosphere to global climate change and human perturbation. Vegetatio 104/105, 295–305.

Schlesinger, W.H., Hartley, A.E., 1992. A global budget for atmospheric NH_3. Biogeochemistry 15, 191–211.

Schimel, D.S., 1995. Terrestrial ecosystems and the carbon cycle. Global Change Biology 1, 77–91.

Schultze, E.-D., 1989. Air pollution and forest decline in a spruce (*Picea abies*) forest. Science 244, 776–783.

Sedlacek, J.D., Barrett, G.W., Shaw, D.R., 1988. Effects of nutrient enrichment on the Auchenorrhyncha (Homoptera) in contrasting grassland communities. Journal of Applied Ecology 25, 537–550.

Shapiro, J., 1979. The need for more biology in lake restoration. In: Lake Restoration (US EPA 440/5-79-001). US Environmental Protection Agency, Washington, D.C, pp. 161–167.

Sharpley, A.N., Daniel, T.C., Sims, J.T., Pote, D.H., 1996. Determining environmentally sound phosphorus levels. Journal of Soil and Water Conservation 51, 160–166.

Shumway, S.E., 1990. A review of the effects of algal blooms on shellfish and aquaculture. Journal of the World Aquacultural Society 21, 65–104.

Siemann, E., 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. Ecology 779, 2057–2070.

Skulberg, O.M., Codd, G.A., Carmichael, W.W., 1984. Toxic blue-green algal blooms in Europe: a growing problem. Ambio 13, 244–247.

Smart, M.M., Jones, J.R., Sebaugh, J.L., 1985. Stream-watershed relations in the Missouri Ozark Plateau Province. Journal of Environmental Quality 14, 77–82.

Smayda, T.J., Shimizu, Y., 1993. Toxic Phytoplankton Blooms in the Sea. Developments in Marine Biology, Vol. 3, Elsevier, New York.

Smith, V.H., 1998. Cultural eutrophication of inland, estuarine, and coastal waters. In: Pace, M.L, Groffman, P.M. (Eds.), Successes, Limitations and Frontiers in Ecosystem Science. Springer, New York, pp. 7–49.

Smith, R.A., Alexander, R.B., Wolman, M.G., 1987. Water-quality trends in the nation's rivers. Science 235, 1507–1615.

Smith, R.A., Alexander, R.B., Lanfear, K.J., 1993. Stream Water Quality in the Conterminous United States — Status and Trends of Selected Indicators during the 1980s (Water Supply Paper 2400.). US Geological Survey.

Smith, R.V., Lennox, S.D., Jordan, C., Foy, R.H., McHale, E., 1995. Increase in soluble phosphorus transported in drainflow from a grassland catchment in response to soil phosphorus accumulation. Soil Use and Management 11, 204–209.

Smith, R.A., Schwarz, G.E., Alexander, R.B., 1997. Regional interpretation of water-quality monitoring data. Water Resources Research 33, 2781–2798.

Soballe, D.M., Kimmel, B.L., 1987. A large-scale comparison of factors influencing phytoplankton abundance in rivers, lakes, and impoundments. Ecology 68, 1943–1954.

Soballe, D.M., Kimmel, B.L., Kennedy, R.H., Gaugish, R.F., 1992. Reservoirs. Biodiversity of the Southeastern United States: Aquatic Communities. John Wiley, New York, pp.421–474.

Soderlund, R., Rosswall, T.H., 1982. The nitrogen cycles. In: Hutzinger, O. (Ed.), Handbook of Environmental Chemistry. Springer, Berlin, pp. 62–81.

Sutcliffe, D.W., Jones, J.G., 1992. Eutrophication: Research and Application to Water Supply, Freshwater Biological Association, Ambleside, UK.

Tamm, C.O., 1991. Nitrogen in terrestrial ecosystems, Springer, Berlin.

Thurston, J., 1969. The effect of liming and fertilizers on the botanical composition of permanent grassland, and on the yield of hay. In: Rorison, I. (Ed.), Ecological Aspects of the Mineral Nutrition of Plants. Blackwell Scientific, Oxford, pp. 3–10.

Tilman, D., 1982. Resource Competition and Community Structure. Monographs in Population Biology, Princeton University Press, Princeton, NJ.

Tilman, D., 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, NJ.

Tilman, D., 1996. Biodiversity: population versus ecosystem stability. Ecology 77, 350–363.

Tilman, D., Downing, J.A., 1994. Biodiversity and stability in grasslands. Nature 367, 363–365.

Townshend, A.R., Braswell, B.H., Holland, E.A., Penner, J.A., 1994. Nitrogen deposition and terrestrial carbon storage: how big is the sink and how long will it last? American Geophysical Society Abstracts, Fall Meeting, December 5–9, San Francisco, CA, p. 55.

Triska, F.J., Kennedy, V.C., Avanzino, R.J., Reilly, B.N., 1983. Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages. In: Fontaine, T.D. III, Bartell, S.M. (Eds.), Dynamics of Lotic Ecosystems. Ann Arbor Science, Ann Arbor, MI, pp. 129–159.

Tyson, R., 1997. "Dead zone" in Gulf of Mexico draws federal-state attention. Environmental Science and Technology 31, 454A–455A.

US EPA, 1988. Quality Criteria for Water (US EPA 440/5-86-001) Office of Water Regulations and Standards, US Government Printing Office (PB81-226759), Washington, D.C.

US EPA, 1996a. Environmental Indicators of Water Quality in the United States (US EPA 841-R-96-02). Office of Water (4503F), US Government Printing Office, Washington, D.C.

US EPA, 1996b. National Nutrient Assessment Workshop. Proceedings, December 4–6, 1995. (US EPA 822-R-96-004) Office of Water, US Government Printing Office, Washington, D.C.

Valiela, I., 1992. Coupling of watersheds and coastal waters: an introduction to the dedicated issue. Estuaries 15, 429–430.

Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D., Foreman, K., 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnology and Oceanography 42, 1105–1118.

Van Nieuwenhuyse, E.E., Jones, J.R., 1996. Phosphorus–chlorophyll relationship in temperate streams and its variation with stream catchment area. Canadian Journal of Fisheries and Aquatic Sciences 53, 99–105.

Vince, S.W., Valiela, I., Teal, J.M., 1981. An experimental study of the structure of herbivorous insect communities in a salt marsh. Ecology 62, 1662–1678.

Vitousek, P.M., Howarth, R.W., 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13, 87–115.

Vitousek, P.M., Mooney, H.A., Lubchenko, J., Melillo, J.M., 1997a. Human domination of Earth's ecosystems. Science 277, 494–499.

Vitousek, P.M., Aber, J., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H., Tilman, G.D., 1997b. Human alteration of the global nitrogen cycle: causes and consequences. Ecological Applications 7, 737–750.

Vollenweider, R.A., 1968. Scientific Fundamentals of Lake and Stream Eutrophication, With Particular Reference to Phosphorus and Nitrogen as Eutrophication Factors. (Technical Report DAS/DSI/68.27). OECD, Paris, France.

Vollenweider, R.A., 1992. Coastal marine eutrophication: principles and control. In: Vollenweider, R.A., Marchetti, R., Viviani, R. (Eds.), Marine Coastal Eutrophication. The Response of Marine Transitional Systems to Human Impact: Problems and Perspectives for Restoration. Science of the Total Environment Supplement 1992. Elsevier Science, Amsterdam, The Netherlands, pp. 1–20.

Vollenweider, R.A., Marchetti, R., Viviani, R. (Eds.), 1992a. Marine Coastal Eutrophication. The Response of Marine Transitional Systems to Human Impact: Problems and Perspectives for Restoration. Science of the Total Environment Supplement 1992. Elsevier Science, Amsterdam, The Netherlands.

Vollenweider, R.A., Rinaldi, A., Montanari, G., 1992b. Eutrophication, structure and dynamics of a marine coastal system: results of a ten-year monitoring along the Emilia-Romagna coast (Northwest Adriatic Sea). In Vollenweider, R.A., Marchetti, R., Viviani, R. (Eds.), Marine Coastal Eutrophication. The Response of Marine Transitional Systems to Human Impact: Problems and Perspectives for Restoration. Science of the Total Environment Supplement 1992. Elsevier Science, Amsterdam, The Netherlands, pp. 63–105.

von Liebig, J., 1855. Principles of agricultural chemistry with special reference to the late researches made in England. In: Pomeroy, L.R. (Ed.), Cycles of Essential Elements. Benchmark Papers in Ecology, Vol. 1. Dowden, Hutchinson, and Ross, UK, pp. 11–28.

Wallin, M., Håkanson, L., Persson, J., 1992. Load models for nutrients in coastal areas, especially from fish farms (in Swedish with English summary). Nordiska ministerrådet, 502.

Waring, R.H., Running, S.W., 1998. Forest Ecosystems: Analysis at Multiple Scales, 2nd ed., academic Press, San Diego, CA.

Weber, C.A., 1907. Aufbau und vegetation der Moore Norddeutschlands. Botanische Jahrbuch 40. Beiblatt zo den botanischen Jahrbuchern 90, 19–34.

Wedin, D.A., Tilman, D., 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. Science 274, 1720–1723.

Welch, E.B., Lindell, T., Ecological Effects of Wastewater: Applied Limnology and Pollutant Effects, 2nd ed., Chapman and Hall, New York.

Welch, E.B., Quinn, J.M., Hickey, C.W., 1992. Periphyton biomass related to point-source nutrient enrichment in seven New Zealand streams. Water Research 26, 669–675.

Williams, N., 1997. El Niño slows greenhouse gas buildup? Science 278, 802.

Wilson, E.J., Wells, T.C.E., Sparks, T.H., 1995. Are calcareous grasslands in the UK under threat from nitrogen deposition An experimental determination of a critical load? Journal of Ecology 83, 823–832.