

# The Role of Nutrient Loading and Eutrophication in Estuarine Ecology

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Eutrophication is a process that can be defined as an increase in the rate of supply of organic matter (OM) to an ecosystem. We provide a general overview of the major features driving estuarine eutrophication and outline some of the consequences of that process. The main chemical constituent of OM is carbon (C), and therefore rates of eutrophication are expressed in units of C per area per unit time. OM occurs in both particulate and dissolved forms. Allochthonous OM originates outside the estuary, whereas autochthonous OM is generated within the system, mostly by primary producers or by benthic regeneration of OM. The supply rates of limiting nutrients regulate phytoplankton productivity that contributes to inputs of autochthonous OM. The trophic status of an estuary is often based on eutrophication rates and can be categorized as oligotrophic (<100 g C m<sup>-2</sup> y<sup>-1</sup>), mesotrophic (100–300 g C m<sup>-2</sup> y<sup>-1</sup>), eutrophic (300–500 g C m<sup>-2</sup> y<sup>-1</sup>), or hypertrophic (>500 g C m<sup>-2</sup> y<sup>-1</sup>). Ecosystem responses to eutrophication depend on both export rates (flushing, microbially mediated losses through respiration, and denitrification) and recycling/regeneration rates within the estuary. The mitigation of the effects of eutrophication involves the regulation of inorganic nutrient (primarily N and P) inputs into receiving waters. Appropriately scaled and parameterized nutrient and hydrologic controls are the only realistic options for controlling phytoplankton blooms, algal toxicity, and other symptoms of eutrophication in estuarine ecosystems. *Key words:* biogeochemistry, coastal, estuary, eutrophic, management, microbial, phytoplankton, zooplankton. — *Environ Health Perspect* 109(suppl 5):699–706 (2001). <http://ehpnet1.niehs.nih.gov/docs/2001/suppl-5/699-706pinckney/abstract.html>

In the continental United States, estuaries comprise more than 80% of the coastline along the Atlantic Ocean and Gulf of Mexico and more than 10% of the Pacific coast. These fragile habitats, which are among this nation's most important natural resources, are experiencing declining water quality and eutrophication (1–4). In a recent comprehensive survey of the trophic status of estuaries in the continental United States, Bricker et al. (3) concluded that 84 estuaries, representing 65% of the total estuarine surface area, were presently showing signs of moderate to high eutrophic conditions (Table 1). Rapidly growing and diversifying anthropogenic inputs associated with agriculture, aquaculture, urbanization, coastal development, and industrial expansion are a primary cause of the decline in the quality of natural habitats in these sensitive waters (1,5,6).

Within the past three decades, many of our estuarine and coastal waters have changed from balanced and productive ecosystems to ones experiencing sudden trophic changes, biogeochemical alterations, and a deterioration in habitat quality. Nuisance and sometimes harmful phytoplankton blooms, accompanied by oxygen depletion, toxicity, fish kills, and shellfish mortality, are becoming more common (2,3). The purpose of this general overview is to furnish a working definition for estuarine eutrophication and to outline some key ecological features associated with the underlying processes. Although a comprehensive review of all the facets of

eutrophication are well beyond the scope of this concise overview, we have incorporated many key concepts and have supplied a few selected examples to illustrate different aspects of estuarine eutrophication. Our overall goal is to provide readers with a broad working knowledge of eutrophication processes in the context of environmental health issues.

## A Definition of Eutrophication

The terms eutrophic, mesotrophic, and oligotrophic are adjectives commonly used to describe the overall state of fertility or “trophic status” of aquatic ecosystems. These three broad categories delineate a gradient that ranges from nutrient-poor, low-biomass systems (oligotrophic) to nutrient-rich, high-biomass habitats (eutrophic). The term eutrophication, in contrast, describes a process rather than a trophic state. Nixon (1) proposed that eutrophication be defined as “an increase in the rate of supply of organic matter to an ecosystem.” This definition has gained wide acceptance and may be the most frequently used quantitative measure of eutrophication. Organic matter (OM) is composed of many heterogeneous chemical compounds. The prevailing chemical element in OM is carbon (C), and therefore OM is most easily quantified in terms of units of C. Hence, OM concentrations may be expressed as particulate organic carbon (POC) and dissolved organic carbon (DOC) with units of  $\mu\text{mol CL}^{-1}$ , or alternatively  $\text{g Cm}^{-3}$ . Rates of eutrophication are subsequently expressed in units of C per area (or volume) per unit time.

Although this working definition of eutrophication is simple, the actual quantification of rates is a formidable task and the concentrations of many of the constituents may be unknown for most ecosystems. In estuaries, OM occurs in both particulate (POM; plant debris, detritus, phytoplankton) and dissolved forms (DOM; humics, mucopolysaccharides, peptides, lipids). The distinction between POM and DOM is arbitrary and depends on the methods used to separate the two fractions (e.g., filtration, ultrafiltration, centrifugation, dialysis). Colloids and large proteins, for example, may be included in either fraction depending on the separation methodology. Measuring these components requires specialized analytical techniques such as C–H–N elemental analysis, dissolved organic carbon analysis, and ultrafiltration. In addition, the rates of supply of different forms of OM are highly variable in natural ecosystems and are strongly influenced by the land use characteristics of the watershed (rural, agricultural, urban, etc.), hydrology, and climatology (6–8).

Sources of OM can come from two major pathways (1,6). Allochthonous OM originates outside the estuary and is transported into the estuary either from watershed runoff and riverine inflow (usually the primary source) or from coastal waters through tidal inlets (usually less important). Autochthonous OM is generated within the system, mostly through photosynthesis by primary producers or by benthic regeneration of OM. In estuarine habitats, the dominant primary producers are phytoplankton, benthic microalgae, epiphytes, seagrasses, and other submerged aquatic vegetation. Primary productivity, measured by

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either  $^{14}\text{CO}_2$  uptake or  $\text{O}_2$  evolution methods for determining photosynthetic rates, is fairly well known for many estuaries. For a few select estuaries, rates of photosynthesis and estimates of primary production have been recorded routinely for several decades and offer useful databases for assessing long-term trends in trophic state. Using the known (or estimated) annual organic C supply (in units of  $\text{g C m}^{-2} \text{y}^{-1}$ ), the trophic status of an estuary can be categorized as oligotrophic (<100), mesotrophic (100–300), eutrophic (300–500), or hypertrophic (>500) (1). By definition, this annual estimate should include both allochthonous and autochthonous OM inputs. However, in practice, most estuaries are classified solely on estimates of the autochthonous primary production of phytoplankton.

## DOC and POC

Dissolved organic carbon, the major component in DOM, is one of the largest organic carbon pools on earth and plays a central role in the biogeochemistry in estuarine, coastal, and oceanic environments (7). This broad class of compounds, although present in high concentrations in most estuaries, is usually not considered in most OM budget calculations; nonetheless, it is a large source of OM for estuaries. In Gulf of Mexico estuaries, for example, DOC fluxes range from 10 to more than 300 kilotons  $\text{C y}^{-1}$  (Table 2) (8). DOC is a mixture of a range of sizes of organic molecules, that are usually characterized by size or weight. A significant fraction of the DOC in estuarine waters is composed of colloidal or macromolecular OM (9–11), which plays an important role in the carbon cycle, trace metal scavenging (12), and biogeochemical processes (13–15). DOM sources in coastal systems include production through phytoplankton exudates (mucopolysaccharides) or phytodetritus (16–18), inefficient zooplankton feeding (19), fecal pellet decomposition, sedimentary inputs through benthic exchange (20), urban/agricultural runoff (16), and sewage inputs. The pool of organic substances is dynamic. Some DOC can be rapidly recycled by bacteria (21), whereas other compounds undergo photochemical degradation into more labile, low molecular weight DOC that can be used directly by some phytoplankton (22).

**Table 1.** Broad characterization of the trophic status of U.S. estuaries and the relative proportion of the total estuarine surface area represented by each category.<sup>a</sup>

Eutrophic condition	Number of estuaries	Total estuarine surface area (%)
High	44	40
Moderate	40	25
Low	38	35
Total	122	100

<sup>a</sup>Data compiled from Bricker et al. (3).

POC suspended in the water column of estuaries is composed mainly of bacteria, phytoplankton, small zooplankton (ciliates, rotifers, and other microheterotrophs), fecal material (feces and pseudofeces), and decaying plant material (detritus) (23–25). Although larger invertebrates and fish are also a form of POC, these animals are excluded either by sample collection or filtration techniques and are usually not considered in estimates of POC. Likewise, surface sediments contain many of the components listed above that are delivered by deposition processes. Phytoplankton POC is a major source of OM in sediments. Under phytoplankton bloom conditions, the growth rate of phytoplankton species and biomass accumulation exceeds the grazing and export rates. Under these conditions, large amounts of phytoplankton C can be deposited onto the sediment (24). Macrophytes, such as the saltmarsh cordgrass *Spartina*, seagrasses, and seaweeds can also contribute large amounts of POC and POM in the form of detritus (23–25). Sharp chemical gradients and redox conditions in the sediments foster high rates of microbial activity and biogeochemical cycling (26). Aerobic decomposition processes consume oxygen at the sediment–water interface. When oxygen consumption exceeds the rate of replenishment (by diffusion or mixing processes), the bottom water may become anoxic. In shallow estuaries, wind-induced waves or tidal currents may resuspend the deposited POC as well as the various dissolved organic and inorganic degradation products. Resuspension events can elevate nutrient concentrations in the water column, reduce the amount of light available for photosynthesis, and decrease the dissolved  $\text{O}_2$  concentrations due to aerobic decomposition of the particulate matter (20). However, strong mixing events can rapidly oxygenate (within hours) the entire water column and effectively remove all traces of anoxia (except for mortalities incurred during the anoxic event).

## Causes of Eutrophication

The ultimate cause of estuarine eutrophication is an increase in organic matter loading. This loading is accomplished by either (or both) an

increase in the inputs of allochthonous C from the watershed or by increased phytoplankton and macrophyte primary production within the estuary. In the strictest sense of the definition, all estuaries undergo eutrophication periodically (27). Chronic and episodic changes in hydrodynamics, geomorphology, and climate—including catastrophic events such as hurricanes, floods, landslides, volcanism, and earthquakes—are all features that influence OM input rates. By their very nature, estuarine ecosystems have evolved over time to buffer themselves, and in some cases capitalize on, these pulsing events (27). However, the ecological context of eutrophication involves time and space scales that transcend ephemeral and seasonal events. Annual to decadal scales often are used to assess the long-term changes in OM loading as well as the ecosystem responses to increased loading rates.

Although many factors influence estuarine and coastal primary productivity, the rates of supply of nutrients are fundamentally important in regulating this process. In estuarine ecosystems, nitrogen (N) is commonly the most limiting nutrient for phytoplankton production (1,28). Biologically available N can occur in many dissolved organic (DON) and inorganic (DIN) nitrogen forms. Allochthonous N that enters from outside the estuary is commonly referred to as new N because it represents additional N that can be used for phytoplankton growth and production. In contrast, autochthonous or regenerated N is nitrogen that is captured and then recycled in the estuary.

In N-limited systems, ambient N concentrations govern phytoplankton growth rates and primary productivity (29). Nutrient acquisition is a major factor determining the outcome of competitive interactions and phytoplankton community composition (i.e., the species that make up the community) (30). Nutrient uptake and assimilation by phytoplankton varies between species and N source (31,32). Uptake rates are influenced by the nutritional state and N-starved individuals may take up N at higher rates (33,34). In some species, ammonium inhibits nitrate and/or urea uptake (35–37). An additional source of N available to phytoplankton is in

**Table 2.** Estimates of dissolved organic carbon concentrations and inputs into selected Gulf of Mexico estuaries.<sup>a</sup>

River/Estuary	DOC concentration ( $\mu\text{M C}$ )	Annual DOC input ( $\times 10^{10} \text{ g C/year}$ )
Nueces/Corpus Christi, TX	560–630	0.5–0.6
San Antonio–Guadalupe, TX	330–480	0.1–0.2
Lavaca Bay, TX	830	3
Colorado, TX	650	2
Galveston Bay, TX	420–480	6.7
Sabine–Neches, TX	530	8.7
Lake Pontchartrain, LA	425–485	2.3
Mobile Bay, AL	424 ± 105	31.7 ± 7
Barataria, LA	558	4–28
Mississippi River, LA	270–330	170–209

<sup>a</sup>Data compiled from Guo et al. (8).

the form of low molecular weight DON such as urea and amino acids (38).

Nitrogen formulations can also regulate the cell-size distribution of phytoplankton communities. The larger species may have the capacity for more internal storage of nutrients and become dominant in fluctuating nutrient regimes (39,40). In general, smaller species have a higher preference for  $\text{NH}_4^+$  uptake over  $\text{NO}_3^-$  than larger phytoplankton species (41). The implication is that long-term changes in the sources and concentrations of N compounds in N-limited systems may alter both the species composition of the phytoplankton community and the relative size distribution of phytoplankton cells. Therefore, prolonged eutrophication can have cascading effects on the composition of the phytoplankton community, food web relationships, and biogeochemical cycling of impacted ecosystems.

Although N is the primary limiting nutrient in most estuaries, other nutrients may be important, especially as regulators of phytoplankton community composition. In some estuaries, phosphate ( $\text{PO}_4^{3-}$ ) can also be limiting or colimiting during winter months or when N concentrations are elevated (42,43). Occasionally, silicate (Si), which is an essential nutrient for diatoms, is a limiting nutrient for diatom growth in some systems (43–45). The Redfield ratio is used frequently to infer the potential limiting nutrient. A stoichiometric molar ratio of 16 N:1 P is accepted as the “ideal” ratio for phytoplankton growth. Higher values of the Redfield ratio are interpreted as indicative of P limitation and, conversely, low ratios suggest N limitation. However, direct application of this principle is problematic for estuarine systems. Measurements of nutrient concentrations to infer limiting nutrients neglect the importance of nutrient cycling rates. Rapid regeneration of nutrients and short turnover times, which are a known characteristic of estuaries, can mask the “true” nutrient availability and hence limitation. Furthermore, measures of water column nutrient concentrations represent what is available for use by phytoplankton. Large amounts of N and other nutrients may be sequestered and stored in biomass (i.e., POM) and therefore not considered when budgets are constructed. Nutrient addition and dilution bioassays, in which natural samples are incubated under various nutrient concentrations, allow the phytoplankton to function as bioindicators to signal which nutrient(s) is limiting (46,47). This experimental approach offers a direct and reliable assessment of the identity and relative proportions of limiting nutrients.

## Nutrient Input Sources

Nutrient input sources can be broadly grouped into two categories. Point sources include inputs derived from sewage outfalls,

wastewater treatment plants, industrial wastewater, and stormwater drains. Nonpoint sources of nutrients are primarily watershed runoff (riverine inputs), groundwater, and atmospheric deposition (rainfall and dryfall). Although the nutrient concentrations from localized, identifiable point sources are easily regulated, more diffuse nonpoint sources are difficult to control. In addition, numerous surveys have shown nonpoint source loading to be a dominant source of new N and other nutrient inputs in many estuarine watersheds, especially those dominated by agricultural activities (1,44). Nonpoint nutrient sources are therefore of major concern for most estuaries. Vegetated buffer zones, located along the margin of rivers and estuaries, are frequently employed as effective management practices to control nonpoint source nutrient inputs derived from watershed runoff.

Estuarine eutrophication is driven generally by nonpoint sources of nutrients (48). A regional-scale analysis of fluxes of N from the North Atlantic coast demonstrated that nonpoint sources of N exceeded sewage inputs (or point sources) for all regions in both Europe and North America (49). Overall sewage contributed only 12% of the flux of N from North America. Non-point sources also dominated P inputs to surface waters of the United States (50,51). Because of the effort to control P pollution, nonpoint sources of P have grown in relative importance since 1980 (52–54). For the Mississippi River, sewage and industrial point sources contribute an estimated 10% (49) to 20% (55) of the total N flux (organic and inorganic) and 40% of the total P flux (55). One quarter of the N and P inputs into the Chesapeake Bay come from wastewater treatment plants and other point sources (56,57). For heavily populated watersheds with relatively small surface areas, wastewater can be a major source of N to an estuary (58). Even in some estuaries fed by larger watersheds, wastewater can be the largest source of N if the watershed is heavily polluted. Wastewater contributes approximately 60% of the N inputs to

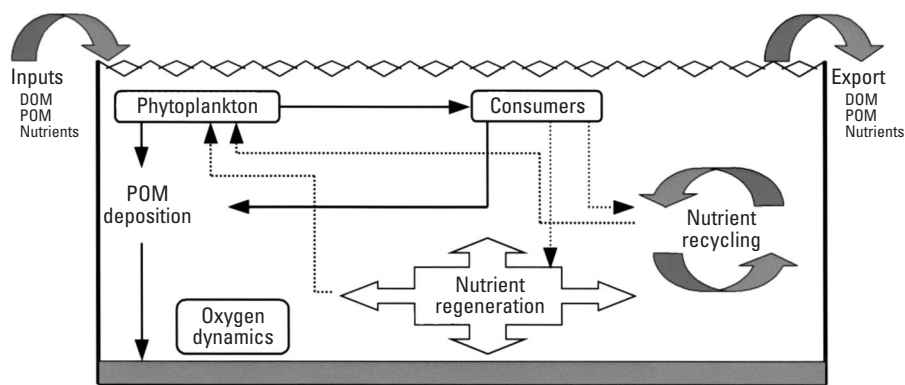
the Long Island Sound, New York, largely due to sewage from New York City (59).

A rapidly emerging source of nutrients to estuarine and coastal waters is atmospheric deposition in the form of rain (wet) and fine particulates (dry) (60,61). This source provides diverse organic and inorganic chemical species in both dissolved and particulate forms. Atmospherically deposited nitrogen (ADN) is a dynamic mixture of biologically available dissolved inorganic ( $\text{NO}_3^-$ ,  $\text{NO}_2^-$ ,  $\text{NH}_4^+$ ; DIN) and organic compounds (amino acids, organonitrates, urea; DON) (62–65). The combustion of fossil fuels and emissions of agricultural and industrial N-containing compounds into the atmosphere (as gases, aerosols, and fine particulates) is a highly significant and growing percentage of total N inputs into estuarine and coastal ecosystems (6,60,61). Current estimates of the percentage of total (i.e., natural + anthropogenic) new N inputs attributed to direct ADN range from 10 to 50%, depending on location and relative sources (6,61,63). For many estuaries, ADN is the single most abundant new N source and warrants scrutiny as a key modulator of eutrophication processes.

Although nutrient concentrations are usually the most common factor limiting primary production in estuaries, physical factors may also play a role. In systems with a high concentration of suspended particulates, light penetration may be a principal limiting or colimiting regulator (66,67) because the rate of photosynthesis is a function of both light quantity (irradiance) and spectral distribution (light quality) (68). Irradiance levels and light exposure of phytoplankton are likewise determined by the vertical mixing rate of the water column (69).

## Nutrient Loading

Eutrophication of most estuaries is linked to the rate at which nutrients (and OM) are added to the system (Figure 1). Nutrient loading is a generic term for which the definition varies depending on the context in which it is used. In a broad sense, loading is the rate of supply of



**Figure 1.** Major estuarine processes related to estuarine eutrophication. DOM and POM refer to dissolved and particulate organic matter, respectively.

a particular entity to receiving waters; it is expressed frequently as a rate (e.g., tons N  $y^{-1}$ ). Ecosystem responses depend on several critical physical–chemical characteristics and processes. Estuary size (surface area), depth, volume, flushing rate, water residence time, tidal exchange, vertical mixing, and stratification are all factors that affect the transport, transformation, retention, and export of nutrients.

Although there are many methods for calculating loading, the simplest approach is to multiply the nutrient concentration (g N  $m^{-3}$ ) by the river discharge rate ( $m^3 s^{-1}$ ), groundwater flow rate ( $m^3 s^{-1}$ ), or rainfall amounts (cm  $m^{-2}$ ). The accuracy of loading rate estimations is therefore related to the accuracy of measurements of two variables: flow rate and entity concentration. Nutrient loading rates, calculated on an annual basis, can be highly variable from year to year (Table 3). The frequency of the measurements becomes especially important during episodic events that add large volumes of water to the system (rainstorms, hurricanes). During these events, nutrient and OM loading over just a few days can exceed the total loading for an entire year (Figures 2, 3). Although concentrations of OM or nutrients may be low because of dilution by large volumes of water, the actual loading rates may be very high because of the total volume of water flowing into the estuary. Unfortunately, during extreme weather events, remote instrumentation (for measuring discharge rates) is frequently damaged and field collections of water samples for chemical analyses are postponed because of personnel safety concerns. Therefore, some of the largest loading events are frequently missed, or approximated with low accuracy, during such periods.

The impact of nutrient loading will depend on how quickly the inputs are transferred through the estuary. The accumulation of OM and nutrients in the system can be viewed conceptually as the difference between inputs and outputs (export) (Figure 1). Nutrients and OM can be exported from the estuary by tidal flushing or through microbial processes that convert the combined form into an elemental form (regeneration). The combined forms of N can be exported from the estuary by tidal flushing or through microbial processes that convert the combined form into an elemental form (regeneration). The combined forms of N can be converted to  $N_2$  through coupled nitrification–denitrification (a microbially mediated process). Ammonium, a primary decomposition product from OM, is first transformed by microbes to nitrite ( $NO_2^-$ ) and then nitrate ( $NO_3^-$ ) under oxic conditions (nitrification). Under anoxic conditions,  $NO_3^-$  and  $NO_2^-$  can be further transformed to nitrogen gas ( $N_2$ ) by denitrification. A recent survey of 14 coastal marine systems showed that denitrification rates were highly variable but may remove from 3 to 100% of the total dissolved inorganic N loading (70). Denitrification is one of the primary pathways by which excess N can be removed from an estuary.

The export rate of OM is also a function of the residence time of water in the estuary. The hydraulic residence time of an estuary—which is the time required to replace the equivalent amount of freshwater in the estuary by freshwater inputs—varies depending on many factors, including freshwater input, circulation, and bathymetry. Mathematically, this phenomenon is treated as a mass-balance calculation in which input volume is assumed to equal output volume. A variety of methods have been used to calculate residence times (in units of time) and flushing rates (in units of volume per unit of time) (71,72). One of the simplest, but also among the least accurate, is the freshwater fraction method, based on the ratio of freshwater content of the estuary and the freshwater inflow rate (73). Another common approach, the tidal prism method (74), is based on the volume of water that enters the estuary over a tidal cycle and the volume of freshwater entering over the same period. Residence times for Gulf of

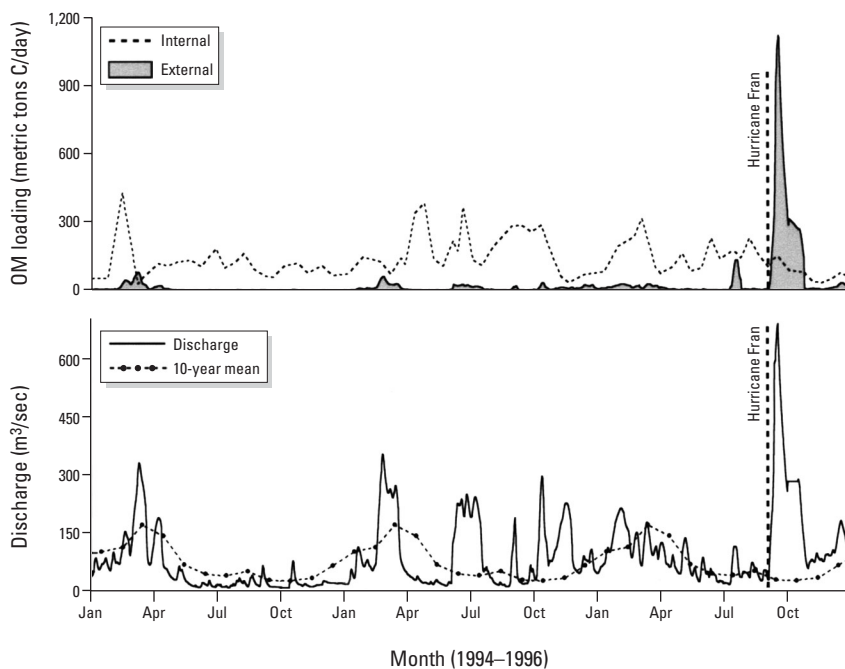
Mexico estuaries range from 1 to 350 days, depending on the estuary (73).

Regeneration and recycling processes within the estuary are important determinants of system responses and recovery from increased OM and nutrient loading. The increase in primary production associated with eutrophication will increase the concentrations of OM by two main mechanisms: secretion of mucopolysaccharides by phytoplankton, especially under conditions of stress, and bacterial degradation of phytoplankton-derived DOM and subsequent release of DOM and nutrients. DOM (e.g., glucose, urea, amino acids) may contain many of the inorganic nutrients required for the growth and metabolism of heterotrophic bacteria in aquatic systems (75–77). The uptake of  $NH_4^+$ , in particular, by heterotrophic bacteria is often significant (78). The bacterial community may compete with the phytoplankton for available inorganic nutrients and, in the presence of mixotrophic

**Table 3.** Estimated total annual inputs from riverine sources to the Neuse River Estuary, North Carolina (1994–1998).<sup>a</sup>

Constituent	Year					Average
	1994	1995	1996	1997	1998	
Particulate carbon (metric tons C)	2,492	4,137	5,228	1,842	2,564	3,253
Particulate nitrogen (metric tons N)	336	425	571	257	270	372
Nitrate ( $NO_3^-$ ) (metric tons N)	575	1,515	1,946	1,363	1,940	1,468
Ammonium (metric tons N)	94	159	389	87	133	172
Total DIN (metric tons N)	669	1,674	2,335	1,450	2,073	1,640
Phosphate ( $PO_4^{3-}$ )	126	155	169	58	132	128

<sup>a</sup>Data compiled from Paerl et al. (63).



**Figure 2.** Discharge and organic matter loadings for the Neuse River Estuary, North Carolina (1994–1996). Internal: autochthonous OM loading (primarily phytoplankton productivity); external: allochthonous sources of OM (riverine inputs). Note the large increase in external OM loading and concurrent high discharge after Hurricane Fran. Following that event, the major source of OM loading switches from internal sources to external sources. Graph redrawn from Paerl et al. (63).

algae and/or heterotrophic flagellates (79), for the available DOM.

Another important process in nutrient regeneration and recycling involves trophic pathways. In contrast to the “bottom-up” regulation of phytoplankton biomass and productivity by nutrients and physical features described above, herbivores and omnivores can exert “top-down” controls on phytoplankton and other primary producers. Inorganic N (mostly as  $\text{NH}_4^+$ ) is a product of grazing by microzooplankton such as heterotrophic flagellates (nanoflagellates and ciliates) (80,81) as well as by larger zooplankton and benthic invertebrates. Grazing of bacteria

by protozoa may be responsible for a significant fraction of the regeneration of  $\text{NH}_4^+$  in marine systems (78). Goldman et al. (82) estimate that the amount of N regenerated by heterotrophic grazing of bacteria (i.e., the microbial loop) is about 10–50% of the bacterial N ingested. Therefore the microbial loop can play an integral role in mediating ecosystem responses to eutrophication.

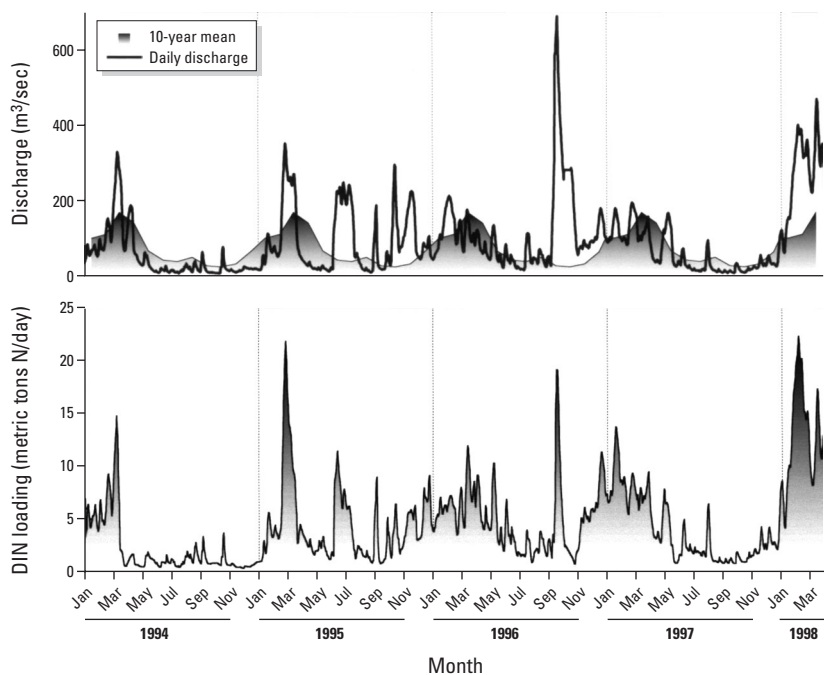
Zooplankton grazers and benthic filter feeders may consume significant amounts of phytoplankton biomass and primary productivity in some estuaries. For example, Li and Smayda (83) reported that, over long time periods (1973–1990), the phytoplankton

biomass in Narragansett Bay, Rhode Island, was controlled by zooplankton grazing. Similarly, Lewitus et al. (84) found that microzooplankton grazing during the summer months in the North Inlet Estuary, South Carolina, was an important regulator of phytoplankton biomass. In Fourleague Bay, Louisiana, Dagg (85) estimated zooplankton grazing rates that were nearly equal to the phytoplankton standing stock in this estuary. Therefore, the standing stock of phytoplankton in the estuary can be conceptualized as the product of a dynamic balance between bottom-up and top-down control mechanisms.

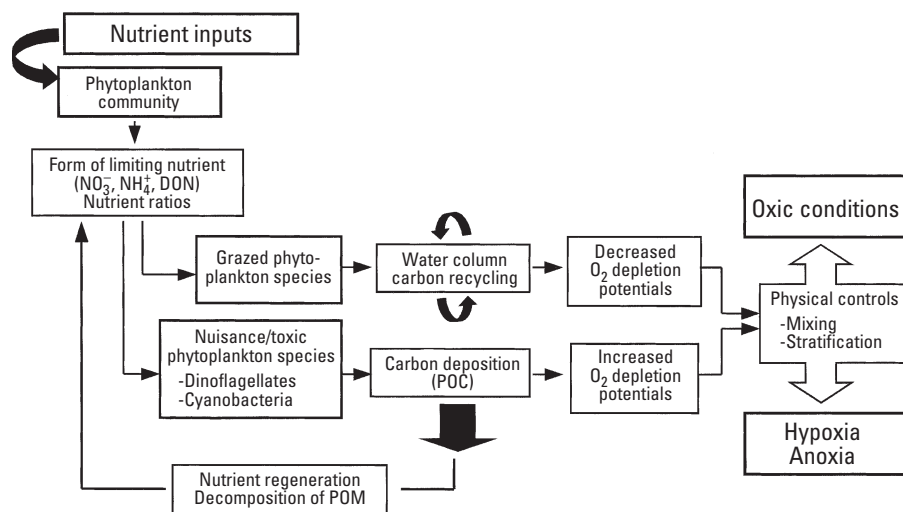
## Consequences of Eutrophication

The cascading effects of anthropogenic new N inputs on estuarine surface waters are conceptualized and summarized in Figure 4. Nitrogen inputs, as well as P, Fe, Si, and other potential rate-limiting nutrients, stimulate phytoplankton growth and modulate community composition. Although primary consumers recycle a portion of phytoplankton C and N, bloom events triggered by new N loading may result in the delivery (deposition) of phytoplankton C to the benthos. Microbial degradation promotes bottom water anoxia, which in turn facilitates sediment nutrient release. Sediment nutrient release events may further stimulate algal blooms, leading to a positive feedback loop that perpetuates blooms and eutrophication. This scenario is particularly relevant in estuaries that have relatively long residence times (months to years), where feedback reactions can be important for sustaining phytoplankton blooms throughout the optimal growth season in the spring and summer. Relatively long residence time and nutrient-sensitive estuaries such as the Chesapeake Bay in Virginia and Maryland, the Pamlico Sound in North Carolina, Florida Bay, and Texas lagoonal systems are susceptible to the detrimental effects of high OM loading and nutrient input. The continued addition of new N and OM, especially over periods of years to decades, sustains and intensifies the eutrophication cycle in estuaries. As long as OM and nutrient inputs exceed losses, the estuary will experience eutrophication.

In some estuaries, phytoplankton C loading, especially following blooms, can produce large-scale bottom water hypoxia ( $<2 \text{ mg O}_2 \text{ L}^{-1}$ ) and anoxia (no detectable dissolved  $\text{O}_2$ ). This phenomenon has been well documented in many estuaries including the Neuse River in North Carolina (63,86) and Chesapeake Bay (87,88). Bottom-water hypoxia/anoxia results from the interaction of excessive C loading with several nonbiological variables, including freshwater discharge, vertical stratification, establishment of a salt wedge, and meteorological conditions (primarily wind) (74,89).



**Figure 3.** River discharge and dissolved inorganic nitrogen (DIN; nitrite, nitrate, ammonium) for the Neuse River Estuary (1994–1998). Note that loading rates exhibit a regular seasonal pattern with large DIN loadings that occur during high river discharge. Graph redrawn from Pearl et al. (63).



**Figure 4.** Relationships among nutrient inputs, phytoplankton responses, and oxygen dynamics.

Hypoxic and anoxic conditions can persist for weeks and cover large areas in estuaries that have relatively long water residence (weeks to months), low flushing rates, and persistent vertical stratification (63). High  $\text{NH}_4^+$  concentrations usually arise from anoxic conditions (90). The anoxic conditions inhibit nitrification and the  $\text{NH}_4^+$  released from the sediments cannot be nitrified to  $\text{NO}_3^-$ . Benthic release of  $\text{PO}_4^{3-}$  is also enhanced under low dissolved oxygen concentrations (90). Thus, persistent anoxic conditions may result in elevated ammonium concentrations which are used by phytoplankton that capitalize on the readily available  $\text{NH}_4^+$ . If these conditions continue, phytoplankton blooms may develop. The tight coupling between anoxia and phytoplankton blooms makes it difficult to assign cause and effect relationships without careful consideration of the hydrological, chemical, and biological conditions initiating and controlling these events. Assessments of conditions during and following bloom events often provide little insight into causative factors (91,92).

Phytoplankton C loading can have a direct impact on the oxygen dynamics of estuaries. However, nutrient and OM inputs can also play a role in determining the predominant species within phytoplankton communities. The alteration of nutrient concentrations and ratios may change the phytoplankton community composition significantly, with subsequent cascading impacts at higher trophic levels of the food web (Figure 4) (93). In estuarine and coastal waters, phytoplankton are exposed to a range of N compounds in varying ratios and supply rates, depending on location relative to N inputs. Previous work has shown that phytoplankton species exhibit different growth responses to N sources (94). In particular, nitrate ( $\text{NO}_3^-$ ) and ammonium ( $\text{NH}_4^+$ ) uptake rates vary spatially and seasonally, suggesting differential community responses to the N sources (95). These species-specific responses may play an important role in structuring natural phytoplankton communities (41) and subsequent biogeochemical alterations (e.g., C and N cycles).

Phytoplankton-mediated assimilation and fate of inorganic nutrients and organic matter (both POM and DOM) are significant components of nutrient transformations in estuarine systems (90,96,97). Microalgal species composition and abundance are intimately linked to higher trophic levels through preferential grazing by herbivores (zooplankton, suspension feeders, deposit feeders) (98–101). The implication for food webs is that some phytoplankton blooms may be ungrazed and deposited in surficial sediments, providing labile carbon substrates for benthic respiration, hypoxia, and anoxia following large blooms. Changes in the phytoplankton species that support primary consumers and

predators may result in the loss of available food for these consumers. The loss of the type (phytoplankton species) and abundance of food resources could result in the displacement of motile species such as fish and crabs to other, more suitable habitats. Species that cannot search for food in other areas (e.g., oysters, clams, benthic infauna, zooplankton, etc.) may suffer reduced reproductive fitness and significant mortalities due to starvation. Many important commercial and recreational fisheries are among groups that may be negatively impacted (1,2,48).

The development of harmful algal blooms (HABs) is a possible consequence of eutrophication (2). Limiting nutrients, such as N, P, and Si, foster the growth of most photosynthetic phytoplankton species, and therefore high nutrient concentrations may produce algal blooms (28,42,45,48). Some of these blooms may be composed of toxic species (2). Perhaps a more interesting aspect of eutrophication is that DOM, in addition to dissolved inorganic nutrients, may foster the growth of HAB species. Several studies have shown that OM can stimulate the growth of marine dinoflagellates (81,102–104). Inputs of terrestrially derived DOM, particularly humic substances, have been implicated as important factors in blooms of *Gymnodinium breve* off Florida (105) and *Alexandrium tamarense* in the St. Lawrence Estuary in Canada (106). Blooms of toxin-producing *Gymnodinium catenatum* in southeast Tasmanian waters appear to be preceded by a rainfall “trigger” (107) with an associated influx of DOM from land runoff. Dublin et al. (108) showed that both the growth rate and biomass of *G. catenatum* increased when cultures were supplemented with a combination of humic acid and naturally collected DOM. They concluded the effect was manifested as a result of an indirect effect of DOM on micronutrient availability (Se) and/or N and P. Rates of uptake of DON compounds by the brown tide organism *Aureococcus anophagefferens* off Long Island exceed rates of  $\text{NH}_4^+$  uptake (109). Blooms of a similar species (*Aureoumbra lagunensis*) are prevalent in some Texas estuaries (110). Dinoflagellates (*G. breve* and *G. sanguineum*) are among the major HAB formers in the Gulf of Mexico (111). The heterotrophic dinoflagellate *Pfiesteria piscicida* Steidinger & Burkholder and related *Pfiesteria*-like dinoflagellates reportedly use organic compounds (112,113), but the primary mode of nutrition for the nontoxic flagellated zoospore stage seems to be other phytoplankton species (113,114). Even if shifts in phytoplankton community composition do not result in HABs, they can still have cascading effects that ultimately result in major changes in the trophodynamics and food webs in essential nursery habitats. Economically important

resources such as fisheries, recreation, and tourism could be impacted negatively and irreparably by these ecosystem alterations (1,2,48).

Another major group of toxic/nuisance phytoplankton that occurs in estuaries is cyanobacteria. Growing frequencies and geographic expansion of toxic cyanobacterial blooms appears to be a worldwide phenomenon (4,115). The combined effect of increased water residence time and growing pollutant inputs has led to longer exposure periods of opportunistic microorganisms to growth-promoting conditions. Bloom-forming cyanobacteria are often superior competitors under these conditions and frequently thrive in nutrient-enriched waters (116). For non- $\text{N}_2$ -fixing genera such as *Microcystis*, *Oscillatoria*, or *Lyngbya*, both N and P are important. Phosphate alone can stimulate the growth of  $\text{N}_2$ -fixing genera such as *Anabaena*, *Anabaenopsis*, *Aphanizomenon*, *Cylindrospermopsis* (117–119). Riverine and estuarine waters in the southeastern United States tend to exhibit nutrient-enriched, N-limited (low N:P ratios) conditions, favoring cyanobacterial (especially  $\text{N}_2$ -fixing genera) dominance (120). Many cyanobacterial bloom formers also prefer OM-enriched conditions (117), including OM originating from urban wastewater, agricultural runoff, forest humics, and soil erosion products (118). Substantial individuality exists among cyanobacterial nuisance taxa in terms of their abilities to exploit these environmental variables.

## Eutrophication Management

Although OM is the currency used to measure eutrophication, the mitigation of the effects of eutrophication involves the regulation of inorganic nutrient (primarily N and P) inputs into receiving waters. These nutrients may be delivered to the estuary as dissolved inorganic ions or bound to OM and later released as the OM is decomposed by microbial processes. Without question, excessive nutrient inputs lead to estuarine eutrophication. There is little doubt that increases in supply rates and changes in chemical forms and ratios of growth limiting nutrients play roles in regional and global expansion of blooms. While nutrient enrichment can be invoked for at least partially driving HAB expansion, extrapolating specific local examples to other estuaries, as well as regional coastal scales is often confounded by the complicated interplay of physical, chemical, and biotic controls on bloom dynamics. Invariably, even nearby estuaries do not exhibit identical physical (residence time, stratification, advection), chemical (specific nutrient supply and cycling rates), and biological (community composition, microbial associations, grazing) characteristics. Therefore ecosystem sensitivity and response

to enhanced nutrient loading may manifest itself quite differently in such systems, often leading to contrasting trophic states, degrees of ecosystem resiliency to change, desirability of habitats, and resources.

From a water quality management perspective, understanding the mechanistic linkages in space and time between man-made alterations of hydrologic and nutrient regimes in the watershed is of critical importance for identifying growth- and bloom-regulating factors that may be used for developing short- and long-term control strategies to slow eutrophication (121,122). The first step involves the identification of relevant phytoplankton taxa, characterizing environmental controls on their growth and toxin-producing characteristics, and incorporating this information in hydrodynamic and nutrient loading budgets depicting ecosystem physical chemical variability and extremes (88,89,123,124). When these features are known, we can begin to develop realistic and effective management alternatives aimed at controlling algal bloom development and expansion. Arguably, appropriately scaled and parameterized nutrient and hydrologic controls are the only realistic options for controlling bloom, toxicity problems, and eutrophication in estuarine ecosystems.

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