ESTUARINE ECOLOGY
Second Edition

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4.1 INTRODUCTION

Phytoplankton means “drifting plant” in Greek. These planktonic microalgae comprise several taxonomic groups (e.g., chlorophytes, chrysophytes, cryptophytes, cyanobacteria, diatoms, and dinoflagellates; Fig. 4.1) that conduct a large share of photosynthesis and primary production and play a central role in carbon, nutrient (i.e., N and P), and oxygen cycling in estuarine and coastal waters (jointly termed coastal waters). In most coastal ecosystems, phytoplankton account for at least half of ecosystem primary production (Cloern, 2001; Harding et al., 2002). Hence, phytoplankton are of fundamental importance in supporting estuarine food webs. They are also key drivers of biogeochemical cycling and play a central role in determining water quality. Phytoplankton have fast growth rates, in the order of one doubling per day, and members of some groups (dinoflagellates, cryptophytes, and cyanobacteria) can proliferate in explosive ways, forming dense “blooms” that can discolor affected waters and cause water quality problems (Paerl, 1988; Hallegraeff, 1993; Richardson, 1997; Anderson et al., 1998). When blooms die or “crash,” they can sink to the seafloor, where they decompose rapidly and fuel high rates of oxygen consumption, leading to oxygen-depleted bottom waters (i.e., hypoxia and anoxia; Officer et al., 1984; Rabalais and Turner, 2001; Diaz and Rosenberg, 2008). Some bloom species also produce foul odors and tastes, which can be problematic from water supply, recreational, and aquaculture perspectives. Lastly, some species produce secondary metabolites that can be toxic to higher fauna (Carmichael, 2001), including zooplankton grazers, fish, and a variety of mammals, including humans.

A bulk of the phytoplankton exists as microscopic solitary cells, although some form multicellular chains and others form aggregates that are visible to the naked eye. They exist in several size classes, including the picoplankton (<2 μm), nanoplankton (2–20 μm), and microplankton (>20 μm). The relative contributions of these size classes to total phytoplankton biomass vary according to nutrient status, physical (temperature, irradiance, and mixing), and hydrologic (freshwater discharge) conditions, as well as climatic regimes. Generally, phytoplankton cells are denser than water, having silica, cellulose, and/or carbonate components, and thus tend to sink. Various mechanisms allow phytoplankton to remain in the illuminated upper water column. Some cells remain easily suspended because of their diminutive size. Others glide or actively swim (i.e., flagella), while some adjust their buoyancy by altering cellular density, or forming cellular vesicles that contain gases or oils. Major phytoplankton groups (e.g., diatoms, dinoflagellates, and cyanobacteria) form cysts and inactive cells as “resting stages” during unfavorable growth periods that sink to the sediments. These cells may be reactivated when favorable conditions reappear (Smetacek, 1985).
4.2 THE PLAYERS: PHYTOPLANKTON COMMUNITY COMPOSITION AND FUNCTION

Coastal phytoplankton communities can be grouped taxonomically and functionally; each approach has specific relevance and application with regard to trophic and biogeochemical roles that these groups play. Taxonomically, the phytoplankton can be divided into prokaryotic and eukaryotic groups.

4.2.1 Cyanobacteria

Cyanobacteria are prokaryotic phytoplankton that have bacteria-like cellular features (i.e., lack of well-defined nucleus and no membrane bound organelles). The cyanobacteria exist in spheroid single or aggregated cells, aggregated or solitary nonheterocystous filamentous, and heterocystous filamentous groups (Stanier and Cohen-Bazire, 1977; Komárek and Anagnostidis, 1986). Heterocysts are thick-walled cells that house oxygen-sensitive nitrogen (N$_2$) fixation (Wolk, 1982), an important physiological process. This enables these taxa to simultaneously photosynthesize and fix atmospheric N$_2$, converting it to biologically available ammonia (NH$_3$, Fogg, 1982, Pael and Zehr, 2000). Nitrogen fixation provides biologically available N during N-limited conditions, which frequently characterize coastal waters. Some spheroid and nonheterocystous filamentous groups can also fix N$_2$, mostly during darkness and in oxygen-deplete microenvironments (aggregates, biofilms, mats, and as endosymbionts). This can restrict their distributions (Pael and Zehr, 2000; Pael and Kuparinen, 2002; Zehr and Pael, 2009).

Interestingly, while N$_2$ fixing cyanobacteria are capable of meeting their N requirements under N-depleted conditions, these diazotrophs (i.e., N-fixing taxa) rarely dominate the phytoplankton communities in N-depleted estuaries. Notable exceptions are brackish, lagoonal, and periodically stratified waters, where water column stability and low salinity appear to favor this group (Pael, 1990; Pael and Zehr, 2000). In the brackish Baltic Sea, extensive blooms of heterocystous filamentous genera (Aphanizomenon, Anabaena, and Nodularia) occur during vertically stratified summer months (Kononen et al., 1996). These blooms are significant sources of “new” N supporting production and eutrophication of the Baltic Sea (Elmgren and Larsson, 2001). Other examples include non- or microtidal lagoonal estuarine systems such as Peel-Harvey Estuary in Australia (Nodularia; Huber, 1986), Lake Ponchartrain, LA (Anabaena; Dortch et al., 1999), and the subestuaries (Chowan, Neuse) of the lagoonal Pamlico Sound system, NC (Pael et al., 1983, 2001). Salinity does not appear to be a barrier to the expansion of diazotrophic cyanobacteria in estuaries (Moisander and Pael, 2000; Moisander et al., 2002a). Grazing pressure, likewise, does not explain the puzzling lack of diazotrophic cyanobacterial dominance (Pael et al., 2001). However, physical
constraints, including excessive turbulence, persistent vertical mixing, and high rates of flushing (i.e., short residence time) that characterize many of the world’s estuarine and coastal ecosystems, prevent dominance by these otherwise opportunistic genera (Paerl and Zehr, 2000; Moisander et al., 2002b). This may help explain why chronic N limitation persists in these systems, (i.e., biological N fixation cannot meet ecosystem N demands).

Blooms of the heterocystous N₂ fixing cyanobacteria can produce a variety of odor and taste compounds (geosmins and 2-methylisoborneol), rendering affected waters unsuitable for consumption, aquaculture, and recreational purposes (Stewart and Falconer, 2008). Lastly, some cyanobacterial bloom species produce alkaloid, peptide, and other compounds that can be toxic on ingestion or contact with affected waters (Carmichael, 1997, 2001; Stewart and Falconer, 2008).

The subtropical-tropical oceanic, nonheterocystous, filamentous N₂ fixing genus *Trichodesmium* can, at times, make excursions into coastal waters when it is carried in major currents (Atlantic and Gulf of Mexico Gulf Stream, Kuroshio current in the South China Sea) that take it close to coastal regions. *Trichodesmium* blooms can be spectacular when concentrated in these current systems, forming yellow-brown slicks of aggregated filaments, referred to as sea sawdust (Fogg, 1982; Paerl, 1999). *Trichodesmium* blooms can provide a major source of “new” N supporting primary production in these waters (Capone et al., 1997). They also produce secondary metabolites that may play a role in deterring grazing by dominant crustacean zooplankton (Hawser et al., 1992), and thereby affect food web dynamics.

The remaining non-N₂ fixing cyanobacterial genera make up an important, and at times dominant, fraction of estuarine phytoplankton biomass. In particular, small (<3 μm) cocoid “picoplanktonic” cyanobacteria (*Synechococcus* spp. and *Prochlorococcus* spp.) can at times constitute more than 50% of estuarine phytoplankton (Marshall and Lacouture, 1986; Ray et al., 1989; Gaulke et al., 2010).

The eukaryotic coastal phytoplankton are partitioned into the following major groups: the chlorophytes—or green algae, the cryptophytes—dominated by cryptomonads, the chrysophytes—dominated by numerous flagellates, the bacillariophytes—or diatoms, the prymnesiophytes, and the dinophytes—or dinoflagellates. Each group plays an important role in primary production, food web dynamics, and biogeochemical cycling. They also differentially (and at times uniquely) respond to nutrient enrichment, hydrologic forcing (freshwater discharge and salinity regimes), irradiance gradients, and grazing pressures.

### 4.2.2 Chlorophytes

Chlorophytes or “green algae” are common and at times dominant in the low salinity, upstream segments of estuaries (Tomas, 1997). They exist as free-floating solitary or aggregated cells varying in size and shape, from small cocoid cells (2- to 5-μm diameter) resembling the picoplankton to larger ovoid- and disk-shaped cells (the desmids) that can exist as small groups of stacked cells (e.g., *Scenedesmus*). The chlorophytes also contain flagellated genera (e.g., *Chlamydomonas*) that can accumulate as bright-green blooms. Chlorophytes have relatively fast growth rates and thrive in well-flushed, short residence time, low salinity waters. These waters tend to have elevated nutrient concentrations, favoring fast-growing species. While the chlorophytes can form blooms, there are no known toxic species and hence blooms are not considered to be particularly “harmful.” Large accumulations of ungrazed cells can, however, contribute to bottom water hypoxia by sinking out of the illuminated euphotic zone.

### 4.2.3 Cryptophytes

Cryptophytes, while taxonomically distinct from the chlorophytes, have similar morphological and ecological characteristics. Cryptophytes are similar in size to the chlorophytes and possess flagella, which help them maintain an optimal position, relative to light and nutrient conditions, in the upper water column (cf., Tomas, 1997; Reynolds, 2006). Almost all cryptophytes are unicellular and ovoid in shape (e.g., the genus *Cryptomonas*). They are asymmetric, with two unequal flagella located on one end of the cell. These serve as forward and reverse “thrusters,” propelling them in a distinct (from chlorophytes) and highly effective manner. Most cryptophytes also have an “oral groove,” which helps them capture small prey items, such as bacteria. This provides considerable metabolic flexibility, enabling the cells to function in photosynthetic autotrophic and heterotrophic modes. Some cryptophytes have “lost” their photosynthetic apparatus (e.g., *Gonium monas* spp.); hence, they derive all their nutrition heterotrophically. The photosynthetic cryptophytes contain chlorophylls *a* and *c₂*, xanthophylls, and an either blue or red phycobiliprotein. This imparts a brownish, reddish, or even bluish color to blooms. Their preferred habitat is fresh to brackish nutrient-enriched waters. As a result, blooms are often observed just upstream of strong salinity gradients, in the oligohaline regions of estuaries.
Blooms are not known to be toxic. The most “harmful” aspect of these blooms is that they can contribute significant amounts of organic matter to bottom waters when they die, potentially enhancing hypoxic conditions.

### 4.2.4 Chrysophytes

Chrysophytes contain chlorophyll a and a yellowish-brown carotenoid pigment called fucoxanthin. Blooms typically appear light brown to golden in appearance. Most species are free-swimming (flagellar) and unicellular, but some exist as colonial forms. Chrysophytes have complex life cycles and some may spend part of their life as amoeoboid cells. They also have quite complex morphologies. For example, the freshwater genus *Dinobryon* has individual cells that are surrounded by vase-shaped loricae, composed of chitin fibrils and other polysaccharides. The colonies grow as branched or unbranched chains. A colonial form, *Synura*, has cells that are covered by silica scales. Some species are colorless, but most contain photosynthetic pigments. They exhibit a great deal of metabolic flexibility; for example, they can be facultative heterotrophs in the absence of light or when high concentrations of dissolved organic matter are present.

In recent years, the toxic picoplanktonic chrysophyte *Aureococcus anophagefferens* and related species have proliferated as “brown tides” in estuaries along the US Northeast and mid-Atlantic as well as some of the Texas Gulf of Mexico lagoonal estuaries (Bricelj and Lonsdale, 1997; Gobler et al., 2002). This motile species has bloomed at densities high enough to effectively “shade out” bottom-dwelling higher plant (seagrass) and benthic microalgal communities, leading to increases in hypoxic conditions, and adversely affecting bottom habitat for infauna, including commercially important shellfish species. The recent upsurge of this chrysophyte appears linked to a complex set of biogeochemical changes brought about by droughts, excessive groundwater withdrawal, and nutrient enrichment in nearby coastal regions, which have locally increased salinity, nutrient, and organic matter concentrations. In addition, increased hypoxia and other adverse effects on the infauna in these habitats have reduced grazing on this organism, further increasing its dominance (i.e., positive feedback; Gobler et al., 2002).

### 4.2.5 Diatoms

Diatoms belong to the class Bacillariophyceae of the phylum Bacillariophyta. They are among the most abundant, widespread, and productive phytoplankton in coastal waters and serve a central role in planktonic food webs (Hasle et al., 1996). Diatoms tend to prefer waters with moderate to high nutrient concentrations. They are capable of very fast growth rates, on the order of two doublings per day or even faster, and as such tend to bloom during springtime, when relatively high nutrient loads often coincide with maximum freshwater runoff conditions or when upwelling might take place. In general, diatoms are an excellent source of food for grazers, including zooplankton, benthic filter feeders, larvae, and planktivorous fish (e.g., menhaden). Several diatom genera (*Rhizosolenia* and *Hemiaulus*) have species capable of hosting endosymbiotic *N*₂ fixing cyanobacteria, which facilitate growth under *N*-limited conditions.

Morphologically, diatoms are complex, as their siliceous cell walls or frustules take on many different shapes and sizes. There are two major groups, defined by the general shapes of the frustules, the boat-shaped pennate and round, pill-box-shaped centrates. Pennate diatoms are generally indicative of benthic forms, but they are often resuspended from the bottom to become important in plankton communities. Diatoms occur as either solitary or joined (in chains) planktonic cells or attached to a substratum by means of gelatinous extrusions or long chains. Some species are capable of movement via “jet propulsion” accomplished through mucilaginous excretions, while other species are free floating and are dependent on currents for transport. Diatoms have complex life cycles that involve benthic “resting stages” that tend to occur after an extended pelagic growth phase (Smetacek, 1985). Diatom cells range in size from 2 µm to well over 100 µm. Because they rely on silicon for cell wall formation, growth, and reproduction of diatoms may, at times, be controlled or “limited” by silicon supply. Silicon limitation can be particularly evident when nitrogen and phosphorus supplies are elevated relative to silicon as a result of “cultural eutrophication” (Officer and Ryther, 1980; Turner et al., 1998; Humborg et al., 2008).

Diatoms are considered highly desirable phytoplankton in estuaries, in that they support key planktonic and benthic food webs (Hasle et al., 1996; Tomas, 1997; Reynolds, 2006). However, some species produce toxins that may be harmful to resident grazers and higher level consumers, including man. One toxic genus, *Pseudo-nitzschia*, can be problematic, and it appears to have increased in bloom frequency in response to eutrophication in the Mississippi discharge plume of the northern Gulf of Mexico and other estuaries (Parsons et al., 2002). The causes of *Pseudo-nitzschia* blooms are unclear but may be related
to overall increases in nutrient loading and shifts in ratios of nutrient supply (Parsons et al., 2002).

4.2.6 Prymnesiophytes

Prymnesiophytes, or haptophytes, include about 500 species in 50 genera, with many additional fossil genera and species, most notably the coccolithophorids. This group is primarily unicellular, photosynthetic, and constitutes an important source of food in coastal waters (Tomas, 1997). Prymnesiophytes, while containing chlorophyll, are often a golden-brown color because of the presence of the carotenoid accessory pigments diadinoxanthin and fucoxanthin. Prymnesiophytes may have a complex life cycle, altering between motile and nonmotile morphologies. Many prymnesiophytes are covered with scales, which, such as diatoms, can lead to complex architecture. They also have spines and various species have quite diverse morphologies. They may be calcified (calcium carbonate) and rarely comprise silica plates.

Prymnesiophytes of the genus *Chrysochromulina* form blooms that can cause serious fisheries problems. Large blooms, such as those that have been reported in the Baltic Sea region are problematic because of the mucilage surrounding the algal cells, which may clog fish gills and also render them permeable to dissolved toxins (cf., Richardson, 1997). Another problem with blooms is the production of dimethyl sulfide, a noxious-smelling compound that can alter fish migration routes, adversely affecting the ecology and sustainability of commercial and recreational fish species.

4.2.7 Dinoflagellates

Dinoflagellates are unicellular, highly evolved phytoplankters that are morphologically and functionally diverse. Their cell sizes range from less than 10 μm to over 1000 μm (Hasle et al., 1996; Reynolds, 2006). Dinoflagellate means “whirling flagella.” Each dinoflagellate has two flagella, facilitating rapid forward and lateral movement. Dinoflagellates are surrounded by a complex covering called the amphiesma, which consists of outer and inner continuous membranes, and between which lie a series of flattened vesicles. In armored forms, these vesicles contain cellulose plates called thecae. If this armor is lacking or shed under certain environmental conditions, the cells are “naked.”

Most dinoflagellates are photosynthetic, possessing chlorophyll *a* and accessory pigments, including the diagnostic carotenoid peridinin. Dinoflagellates are important and at times dominant estuarine primary producers, sustaining the grazing component of the food web. Some dinoflagellates are facultative heterotrophs, engulfing and ingesting bacteria and smaller phytoplankton as prey and also consuming dissolved organic carbon compounds. Even though their growth rates are generally slower than chlorophytes, cryptophytes, and diatoms, dinoflagellates can form large, and in some cases harmful, blooms in estuaries. Examples include several red tide species (e.g., *Karenia brevis* and *Noctiluca* spp.) that are toxic to a wide variety of finfish, shellfish, and other fauna, including humans. These organisms are often of oceanic origins but can enter and proliferate in estuaries, especially during summer months (Hasle et al., 1996). These dinoflagellates produce neurotoxins that affect muscle function in susceptible organisms. Humans may also be affected by eating fish or shellfish containing the toxins. The resulting diseases include ciguatera (from eating affected fish) and paralytic shellfish poisoning (from eating affected shellfish, such as clams, mussels, and oysters); they can be serious but are not usually fatal. Other more exclusively estuarine toxic dinoflagellates include *Karlodinium*, *Gymnodinium*, and *Proocentrum* species (Hasle et al., 1996). These species produce toxic substances that have been implicated in fish kills. Their increased presence and proliferation has been linked to eutrophication. Other nontoxic dinoflagellate blooms are linked to seasonal patterns of freshwater runoff, salinity, and light regimes. These blooms are often composed of highly desirable nontoxic genera (e.g., *Heterocapsa*) that are of central importance in supporting estuarine food webs. One of the more interesting biological properties of dinoflagellates is the ability of some species to produce light through bioluminescence, the same mechanism that makes fireflies glow. In addition, there are some dinoflagellates that are parasites on fish or on other protists (Hasle et al., 1996).

4.2.8 Phytoplankton Communities

Phytoplankton communities are dynamic multispecies assemblages that exhibit spatial patchiness (microns to meters) and temporal variability over scales ranging from minutes to days (Dustan and Pinckney, 1989). Because these primary producers play a central role in the regulation of estuarine biogeochemical cycling, detailed characterizations of the community-level processes that structure phytoplankton communities are essential for understanding overall ecosystem dynamics. A critical prerequisite for characterizing these processes is the ability to determine the taxonomic composition of natural phytoplankton assemblages reliably and accurately.
The high degree of inherent spatiotemporal variability at the ecosystem scale requires that analytical approaches for describing phytoplankton taxonomic diversity be applicable for processing large numbers of samples quickly with minimal cost. The most reliable technique for enumerating single species in mixed phytoplankton samples is microscopic counts, but these are tedious, require a high level of expertise, and are costly. In addition, species-level identification and enumeration may not be necessary for examining larger scale phytoplankton impacts on biogeochemical cycling and trophodynamics. Often, examinations at coarser taxonomic levels (i.e., class and group) are effective and make quantification easier. Chemosystematic pigments encoding specific functional phytoplankton groups (i.e., diatoms, chlorophytes, dinoflagellates, cyanobacteria, and cryptomonads, Fig. 4.1) can also be used (Jeffrey et al., 1997, 1999). In particular, carotenoids specific for different algal groups provide diagnostic biomarkers for determining the relative abundance of key phytoplankton groups. Photopigment extracts from natural microalgal samples can be separated and quantified by high performance liquid chromatography (Millie et al., 1993; Wright et al., 1996; Paerl et al., 2003). Photopigments that have been used as markers are shown in Figure 4.1 and detailed in the study by Paerl et al. (2003). When compared to total phytoplankton biomass (based on chlorophyll a) and cell counts, diagnostic photopigments can quantitatively determine the contributions of each phytoplankton group (Tester et al., 1995; Lewitus et al., 2005).

Molecular techniques that are useful for assessing phytoplankton diversity are rooted in organic chemistry and fundamentally rely on obtaining an informative molecule (e.g., nucleic acid) from phytoplankton cells. The following paragraphs outline some of these molecular techniques. References are provided for students who want to acquire more information on this subject. DNA is a commonly targeted molecule used in diversity studies, although RNA may also be used. Both nucleic acid forms are informative molecules because they contain a “code” or series of nucleotides. Stretches of nucleotides can be specifically amplified (using primers and the Polymerase Chain Reaction, PCR) cloned, sequenced, and then these sequences can be compared by various phylogenetic analyses (e.g., phylogenetic tree building). Diversity estimates can be done based on the number of individual sequences obtained per cloning effort (rarefaction curves).

Commonly, rRNA genes are targeted and sequenced to study genus-level phytoplankton diversity. This is primarily due to the vast number of publically available rRNA sequences obtained to originally study the evolution of life (Woese and Fox, 1977; Pace et al., 1985). Because of the conserved nature of rRNA genes, the phylogenetic resolution (i.e., ability to distinguish phytoplankton) is limited to around the genus level. Other genomic regions that evolve more rapidly than rRNA genes, such as the ITS region, the rRNA intergenic spacer region, or other intergenic regions (Urbach et al., 1998; Rocap et al., 2002) can better differentiate populations to a subgenus level. Also, protein encoding genes have been targeted for diversity studies that are focused on the diversity of organisms capable of a particular metabolic activity such as nifH encoding for the nitrogenase enzyme or rbcL encoding for RuBisCO subunit (John et al., 2006; Zehr and Paerl, 2009).

With a sequence database in hand, fingerprinting techniques (e.g., Terminal Restriction Fragment Length Polymorphism, TRFLP, Automated rRNA Intergenic Spacer Analysis, ARISA, or Denaturing Gradient Gel Electrophoresis, DGGE; e.g., Diez et al., 2001) can be used to distinguish differences in phytoplankton communities between samples. RNA is also a useful and targetable molecule for studying phytoplankton diversity. Largely due to the susceptibility of RNA to enzyme degradation, its use first requires reverse transcription to cDNA. Recently, applied approaches utilize an amplification step before cDNA synthesis, so that small quantities of RNA that can be quickly and efficiently sampled can still be used for sequence analysis (Frias-Lopez et al., 2008). Examining the sequence diversity of RNA provides an indication of phytoplankton that are presumably active in the environment (where as DNA is indicative of presence or absence). For example, rbcL transcripts recovered off the coast of FL were indicative of shifts in the major phytoplankton in the Mississippi River plume region (Paul et al., 2000).

With a core sequence library, several approaches can then be taken to examine diversity further. For example, quantitative PCR (qPCR) may be used to enumerate portions of phytoplankton diversity across samples. More and more researchers are turning to high throughput methods to obtain sequence data. Recent approaches have aimed to bypass the necessity of PCR amplification (which may have influential biases) for diversity studies by collecting large amounts of biomass from the environment and directly sequencing molecules from this biomass. Despite impressive bioinformatic and high yield sequencing advances, the diversity of phytoplankton (and heterotrophic plankton) in the environment is still too high for random sampling to be useful for assessing diversity (Venter et al., 2004).
Targeted high throughput sequencing in this manner (e.g., targeting variable regions of the 16S rRNA gene) appears to carry some value for assessing diversity (Huse et al., 2008).

4.3 SPATIAL AND TEMPORAL PATTERNS OF PHYTOPLANKTON BIOMASS AND PRODUCTIVITY

Phytoplankton often account for at least half of ecosystem primary production in coastal waters. Their rates of primary production are remarkably variable and range from near undetectable to several gC/m²/day. Phytoplankton also have fast growth rates. Hence, they can rapidly respond to diverse chemical (nutrients and toxicants), physical (light, temperature, and turbulence), and biotic (grazing) impacts over a wide range of concentrations and intensities. Changes in phytoplankton communities often precede changes in ecosystem function, including shifts in material flux, oxygen balance, food webs and fisheries, and potentially, permanent losses of higher plant and animal assemblages.

Coastal phytoplankton communities typically show strong seasonal and spatial distributions. This is illustrated for Pamlico Sound and Chesapeake Bay, two of the largest estuarine systems in the United States (Figs. 4.2 and 4.3). In both systems, the distribution of phytoplankton biomass, as chlorophyll a, is strongly influenced by the delivery of freshwater (i.e., discharge), which also delivers watershed-based nutrients to support new primary productivity and the development of phytoplankton biomass. In addition to being a source of new nutrients, freshwater discharge also determines flow rates, flushing, and resultant residence time of estuarine waters, that is, the amount of time it takes for fresh water and nutrients delivered to the estuary to move through the system before exiting to the coastal ocean. Flushing rates and residence times are strong determinants of where the maximum amount of phytoplankton biomass can develop and build up in response to nutrient inputs. For example, during high flow periods, nutrient delivery to the system will be high. Simultaneously, high flow will create short residence time conditions, restricting phytoplankton growth and biomass buildup to the most downstream, widest and longest residence time segments of the estuary, a phenomenon that is illustrated in Figures 4.2 and 4.3. In the Pamlico Sound system, high flow conditions typically lead to maximum phytoplankton biomass (as Chl a) in the downstream segments of the estuaries and open waters of the Sound itself (Fig. 4.2), while under low flow, long residence time conditions, phytoplankton biomass maxima are typically in the upper estuarine regions.

Most phytoplankton are phototrophs; hence, photosynthetic activities and growth rates are strongly controlled by the availability and quality of light (Cloern, 1999; Reynolds, 2006). Photosynthetic as well as carbon and nutrient assimilatory processes, respiration, energy metabolism, and growth are mediated by enzymes that are temperature sensitive. As such, seasonality plays an important role in the control of photosynthetic production (primary production), biomass, and composition (cf., Harrison and Turpin, 1982; Marshall and Lacouture, 1986; Malone et al., 1996; Pinckney et al., 1999; Valdes-Weaver et al., 2006). Typically, maximum rates of primary production and growth occur during springtime when light and/or nutrient availability are both high, leading to spring bloom conditions. If nutrient availability remains high during summertime through input and/or recycling, blooms may persist throughout this period. These are also periods of maximum temperatures, favoring relatively high growth rates. Not all phytoplankton groups and individual species respond similarly to shifting light, temperature, and nutrient gradients; this is largely due to the individual energetic, nutrient, and other requirements (e.g., water column stability, salinity, trace metals, pH, and dissolved inorganic carbon) for supporting and sustaining optimal growth. Differential grazing on these groups and species may exert selective "top-down" control.

Some dinoflagellate species show sudden, strong positive responses to increases in light levels and day length that occur in late winter. This, combined with increased nutrient-enriched runoff and a lack of intense grazing create ideal conditions for large blooms (e.g., Heterocapsa spp.) that can occur as early as late January in temperate waters (Paerl et al., 1998; Litaker et al., 2002).

Other phytoplankton groups dominate during spring and summer. Typically, diatoms tend to bloom in early spring, because they exhibit relatively fast growth rates, even at fairly low temperatures and hence can take advantage of early spring freshwater runoff (Harding, 1994; Harding et al., 2002; Valdes-Weaver et al., 2006; Harding and Miller, 2009). If runoff is extremely high such as during spring floods, large segments of estuaries can turn fresh; these conditions typically favor chlorophytes and a variety of flagellates (cryptomonads and chrysophytes), which prefer low salinity, high nutrient supply conditions (Paerl et al., 2006a,b; Valdes-Weaver et al., 2006). Motile taxa such
FIGURE 4.2 Spatial relationships of phytoplankton biomass, as chlorophyll $a$ (Chl $a$), and freshwater discharge to the Pamlico Sound System, NC. Surface water Chl $a$ concentrations were estimated using aircraft-based SeaWiFS remote sensing (Courtesy L. Harding, University of Maryland), calibrated by field-based Chl $a$ data. Under relatively low flow, long residence time conditions, phytoplankton biomass is concentrated in the upper reaches of the Neuse and Pamlico R. Estuaries. Under moderate flow, phytoplankton biomass maxima extend further downstream. Under high flow (short residence time), phytoplankton biomass maxima are shifted further downstream into Pamlico Sound. Source: Figure adapted from Paerl et al., 2007.
4.4 FACTORS CONTROLLING PHYTOPLANKTON PRODUCTIVITY AND COMMUNITY COMPOSITION

4.4.1 Light

Light is of fundamental importance in controlling the activity, biomass, distribution, and composition of phytoplankton. Phytoplankton use light in the 400–700 nm part of the visible light spectrum. This part of the spectrum is termed photosynthetically active radiation or PAR. Both the instantaneous flux of light, or irradiance, and the total amount of light available during daylight tend to be excellent predictors of photosynthetic performance and primary production (Jassby and Platt, 1976). Light availability is controlled by the concentration of key light attenuating substances, turbidity, color, and photopigments (dominated by Chl a). Estuarine turbidity may be due to suspended sediments, chlorophyll and other algal photopigments, and colored dissolved organic matter content (Gallegos et al., 1990). Together with surface irradiance, these components determine the attenuation or extinction coefficient $K_d$. Vertical mixing rates and phytoplankton vertical migration capabilities also strongly affect photosynthetic rates (Mallin and Paerl, 1992). Phytoplankton photosynthetic response to light can be described with photosynthesis–irradiance curves.
experienced in well-mixed surface waters (Marra, 1978; Mallin and Paerl, 1992), with maximum rates often occurring under well-mixed conditions. Presumably, mixed conditions ensure that exposure to optimal nutrient and nutrient regimes can be achieved near-simultaneously, enabling cells to maintain high rates of photosynthetic production. Falkowski (1980) showed that under vertically mixed conditions, algal cells can rapidly adapt to changing light and maximize photosynthesis by varying their photosynthetic pigment composition and enzyme concentrations, with response times of 1 h or less. Marra (1978) and Mallin and Paerl (1992) showed that algal cells rotated through a vertical series of depths often had significantly greater photosynthetic production, even though the total light available was the same in both cases. Platt and Gallegos (1980) developed a model simulating phytoplankton photoadaptation to demonstrate that a mixed-water column generated about 20% more photosynthesis than a static system. However, excessive vertical mixing, especially in deeper turbid waters, can be detrimental since it can force phytoplankton into completely dark, aphotic waters, where photosynthesis ceases.

Under vertically stratified conditions, phytoplankton taxa that are able to adjust their position in the water column are frequently at an advantage. They can migrate to and maintain their position at light levels supporting optimal photosynthetic production and growth, while periodically migrating into deeper, nutrient-rich waters to access essential nutrients supplies (Ralston et al., 2007). In particular, near-surface dwelling bloom taxa (some dinoflagellate, cryptophyte, and some cyanobacterial species) use such a strategy to maintain dominance when other factors conducive to bloom formation (elevated temperatures, lack of grazing, optimal flow, and residence time conditions) prevail.

Light is fundamentally important in regulating phytoplankton productivity and nutrient uptake in turbid coastal ecosystems. Cole and Cloern (1984) showed that phytoplankton net production is directly proportional to the ratio of photic zone depth to water column depth for the weakly stratified San Francisco Bay. Mallin and Paerl (1992) and Harding et al. (1985) have shown similar relationships for the Neuse River Estuary, NC, and the Chesapeake Bay. These relationships demonstrate the important interactive roles that clarity and vertical mixing play in regulating primary production and phytoplankton growth, even in very shallow and turbid estuarine ecosystems (cf., Cloern, 1999, 2001). In Long Island Sound and Narragansett Bay, the initiation of the winter–spring diatom blooms is closely related to increasing light

**FIGURE 4.4** (a) Relationships between dissolved inorganic N input and primary production in a North American and European estuarine and coastal ecosystems. (b) Relationship between dissolved inorganic N input and phytoplankton biomass, as mean annual chlorophyll a content of several Western Australian estuarine systems. Source: From Paerl, 2004, Twomey and Thompson, 2001; Nixon, 1980; 1996.

Under natural conditions (e.g., *in situ* bottle incubations), phytoplankton exhibit vertical photosynthetic rate patterns that closely follow the vertical distribution of ambient light. In clear waters and/or under conditions of high surface irradiance, phytoplankton incubated at the water surface frequently experience light inhibition, while maximum rates of photosynthesis usually occur at subsurface depths experiencing from approximately 30% to 70% of surface irradiance. In highly turbid waters, near-surface light inhibition is less common. The depth of maximum photosynthesis depends not only on optimal light but also on adequate nutrient availability and lack of appreciable grazing, which at times can effectively remove phytoplankton at rates exceeding the rate of primary production. Phytoplankton assemblages are adapted to the fluctuating light regimes
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intensities (Riley, 1967; Hitchcock and Smayda, 1977). In North Carolina’s Newport River and Neuse River Estuaries, late winter dinoflagellate blooms (Heterocapsa triquetra) closely track the increase in light intensities and duration during the winter–spring transition (Paerl et al., 1995; Litaker et al., 2002). Light plays a strong regulatory role with regard to nutrient (specifically nitrogen) uptake and assimilation (Flores et al., 2005), which are energy-dependent processes (cf., Huppe and Turpin, 1994).

4.4.2 Nutrients

Phytoplankton production requires a variety of inorganic and organic nutrients, including carbon (C), nitrogen (N), phosphorus (P), silicon (Si), metals (most importantly iron), and trace elements, as well as vitamins such as B12. The most important are the so-called macronutrients (carbon, nitrogen, phosphorus, and silicon), and among these, nitrogen and phosphorus are most significant, largely because they are usually in shortest supply relative to demand. As a result, availability of these elements controls or “limits” the rates of phytoplankton-mediated primary production (Ryther and Dunstan, 1971; Nixon, 1995, 1996). Furthermore, because different algal species require these nutrients in different fixed proportions, the supply ratios of these and other elements (e.g., N/Si and N/Fe) modulate the growth and competitive interactions among phytoplankton taxonomic groups (PTGs; Syrett, 1981; Dortch and Whitledge, 1992; Stolle et al., 1994; Riegman, 1995; Justić et al., 1995; Turner et al., 1998).

Redfield and Daniel (1934) examined the amounts and relative proportions of nutrients in seawater and related these to cellular nutrient content and ratios of the phytoplankton. They found a remarkable consistency in elemental composition of seawater and marine phytoplankton. The “Redfield ratios” of atomic weights of the elements C:N:Si:P are in the order of 106:16:15:1. In time and space, however, this balance is not constant. It can be altered by episodic nutrient inputs or depletions from a variety of human and natural sources, which are modulated by and delivered to coastal waters by rainfall and runoff, groundwater, and oceanic inputs. Nutrient delivery to coastal waters generally occurs in a nonsteady, pulsed manner, with several nutrients simultaneously being close to limiting, creating “colimited” conditions. Although in estuaries N has been identified as the most limiting nutrient (Ryther and Dunstan, 1971; Nixon, 1995; Granéli et al., 1996; Paerl et al., 1995; Elmegren and Larsson, 2001; Figs. 4.4 and 4.5), N and P colimitation is also commonly observed (Boynston and Kemp, 1985; Malone et al., 1996), especially in the low salinity, upstream segments of estuaries (Fig. 4.6; Fisher et al., 1988; Paerl et al., 1995) and in brackish water deltaic regions where large rivers (e.g., Mississippi) discharge to the coastal ocean (Sylvan et al., 2006). N and P colimitation as well as more exclusive P limitation are most evident during periods of elevated freshwater runoff, which tend to be N enriched (Fisher et al., 1988; Sylvan et al., 2006). Under these conditions, the molar “Redfield ratio” of N:P (16:1) can be greatly exceeded, sometimes reaching 200:1, leading to strong P limitation.

Certain phytoplankton groups have highly specific nutrient requirements. The most notable are diatoms, which have siliceous cell walls or frustules. While this provides for strong, morphologically diverse cell walls, it also makes this group reliant on adequate silicon (Si) supplies. Silicon is a product of weathering of upstream siliceous soils. If these soils are absent or sparse, Si supply may be limited. In addition, the supply ratio of Si to other potentially limiting nutrients (N and P) may dictate the relative availability of one or several nutrients in order to maintain (nutrient) balanced or “Redfield” growth (Redfield, 1958). Hence, if elevated N and/or P loadings occur as a result of human or climatic perturbations, the supply rate of Si may become limiting, leading to changes in the phytoplankton community composition. This appears to be the case in the northern Gulf of Mexico region where Mississippi River discharge supplies excess N and P relative to Si (Justić et al., 1995; Turner, 2001). Sedimentological evidence indicates that the abundance of the lightly silicified (and hence relatively low Si-requiring) diatom Pseudonitzschia has increased since the 1950s, coincidentally with increasing riverine N flux and increasing N:Si ratios (Parsons et al., 2002). Some Pseudonitzschia species produce toxins, so Si deficiency could lead to more frequent toxic diatom blooms (Dortch et al., 2001). In addition, because the abundance of copepods decreases when Si:N ratio falls below 1, the diatom-copepod-fish food web may be disrupted under these conditions (Turner et al., 1998; Turner, 2001).

4.4.3 Temperature

The effects of temperature on phytoplankton were provided in an excellent review by Eppley (1972). He noted that temperature–response curves for phytoplankton growth and photosynthesis were similar for most algal species studied, with relatively rapid declines in production at temperatures in excess of their optima. Goldman (1979) showed that temperature optima for five coastal phytoplankton species fell in the range of 20–25°C. Moreover, it appears that cellular nitrogen content is inversely related
FIGURE 4.5 Results from nutrient addition bioassays conducted at three locations in the Neuse River Estuary, NC. Phytoplankton growth response was measured as accumulation of chlorophyll a after 3-day incubation under natural light and temperature conditions. "C" indicates controls, in which no nutrients were added. Nitrogen was added as either ammonium (NH₄⁺) or nitrate (NO₃⁻) at 10 μM N concentrations. Phosphorus was added as phosphate (PO₄³⁻) at 3 μM P. These summertime bioassays indicate N limitation, which is most profound at more saline downstream locations. Note that per amount of N, ammonium was more stimulatory than nitrate. Source: Reprinted from Paerl and Pfehler, 2008, with permission from Elsevier.

to the temperature-regulated growth of these algal populations, possibly indicating relatively greater effects of temperature on carbon versus nitrogen metabolism. Temperature evidently exerts a selective force for populations whose temperature optima coincide indirectly with environmental conditions, including vertical stratification, nutrient availability, regeneration, and solubility.

Some phytoplankton taxa are more strongly regulated by temperatures than others. For example, cyanobacterial growth typically exhibits temperature optima in the range of 25–30°C, which is substantially higher than other phytoplankton groups. The fact that cyanobacteria “like it hot” has been linked to an upsurge in cyanobacterial blooms and geographic expansion of such blooms (relative to other
phytoplankton blooms) accompanying regional and global warming (Paerl and Huisman, 2008, 2009).

4.4.4 "Top-Down" Control: Herbivory

Zooplankton, benthic filter feeders, larval and certain juvenile, and adult fish are the primary consumers of coastal phytoplankton. The zooplankton are commonly divided into several size classes, that is, microzooplankton (<200 μm), mesozooplankton (0.2–2 mm), macrozooplankton (2–20 mm), and megazooplankton (>20 mm). The relative contributions of these size classes to total phytoplankton biomass can vary substantially. In terms of numbers, the most abundant zooplankters in coastal ecosystems are microzooplankton. This category includes all heterotrophic protists and protozoans. The mesozooplankton includes calanoid copepods, cladocerans, and thaliacean tunicates.

Zooplankton grazing represents an important control of phytoplankton biomass and community composition; however, its impact varies with factors such as seasonality, vertical mixing, freshwater flushing, and residence time. Phytoplankton generally have faster growth rates than zooplankton, which can result in phytoplankton blooms that accumulate more quickly than the zooplankton that graze them. As a result, some rapidly growing bloom taxa can proliferate in a seemingly unshaken manner. These blooms are primarily limited by the nutrient supply. This is especially true for phytoplankton species that are capable of blooming during winter and early spring, when water temperatures are too low to support rapid growth of zooplankton grazers. During these periods, phytoplankton biomass and composition are largely controlled by physical–chemical factors such as light and nutrient availability. This type of control is termed bottom up. As water temperatures warm up in spring and summer, zooplankton growth rates are enhanced and biomass can accumulate at faster rates. Also, nutrient supplies to phytoplankton may decrease, largely because the main source of nutrients to the estuary, freshwater runoff, decreases during these drier periods. A result of these combined effects is that herbivorous grazing plays a relatively greater role as a control on phytoplankton biomass. This type of control is termed top down. Owing to variable discharge and flow rates as well as other physical factors such as wind-induced mixing, storms, and droughts, there are transitions between periods of low and high grazing control.

Because it is very dynamic and dependent on interacting physical, chemical, and biotic factors, the importance of zooplankton grazing as a control on phytoplankton stocks is a topic that carries a great deal of uncertainty and continues to be hotly debated. Steemann-Nielsen (1958) argued that the commonly observed seasonal patterns of more or less coincidental peaks in phytoplankton and zooplankton abundance supported the hypothesis that grazing maintained algal populations in a steady state, the level of which was determined by the limitations of other environmental conditions (i.e., light, nutrients, and temperature). In contrast, Cushing (1959) used a simple predator–prey model to conclude that
grazing did, indeed, affect the magnitude and timing of phytoplankton stocks and that a lag between peak abundances of phytoplankton and zooplankton populations was readily observable. High rates of grazer-induced mortality have been observed in coastal environments (e.g., Dagg and Turner, 1982; Welschmeyer and Lorenzen, 1985) and in some river plumes (e.g., Malone and Chervin, 1979). For example, in the northern Gulf of Mexico, the copepod community ingested 4–62% of the daily phytoplankton production (Dagg, 1995a). In a productive subtropical estuary (Fourleague Bay, Louisiana), ingestion rates of phytoplankton by the microzooplankton community averaged 43–165% of the daily phytoplankton production (Dagg, 1995b). In contrast, the grazing contribution from the mesozooplankton, composed primarily of the copepod *Acartia tonsa*, was negligible, presumably because of high advective losses and predation by zooplanktivorous fish (Dagg, 1995b).

While zooplankton herbivory may be an important control on coastal phytoplankton production during certain seasons under certain environmental conditions (Martin, 1970), it is not likely to be a severe limitation overall (e.g., Oviatt et al., 1979). Often, grazing is insufficient to balance phytoplankton growth, which can lead to the development of phytoplankton blooms. In Chesapeake and Narragansett Bays, high rates of suspension-feeding rates by ctenophores and medusae on zooplankton may serve to keep zooplankton grazing in balance (Heinle, 1974; Kremer, 1979). Other studies show inverse relationships between abundances of herbivorous crustacean and gelatinous zooplankton from field observations and direct relationships between ctenophore abundance and phytoplankton chlorophyll *a* (Lindahl and Hennon, 1983; Feigenbaum and Kelly, 1984).

In some estuaries, suspension-feeding benthic macrofauna can reduce phytoplankton abundance significantly (Cloern, 1982; Officer et al., 1982). For several estuarine systems, it has been shown that a single dominant suspension-feeding bivalve population was capable of filtering the entire overlying water column in 1–4 days (Cohen et al., 1984; Nichols, 1985; Doering et al., 1986). Such grazing rates can reduce phytoplankton standing stocks significantly. For example, the invasion of zebra mussels (*Dreissena polymorpha*) caused a massive decline in phytoplankton biomass in the Hudson River Estuary (Caraco et al., 1997). Zebra mussels invaded this estuary in 1992 and became well established in 1993 and 1994. During these 2 years, the grazing pressure on phytoplankton increased 10-fold, leading to an 85% decline in phytoplankton biomass (Caraco et al., 1997).

4.5 HUMAN AND CLIMATIC IMPACTS ON COASTAL PHYTOPLANKTON DYNAMICS

4.5.1 Effects of Nutrient Overenrichment on Estuarine Phytoplankton

Coastal primary production and phytoplankton biomass are strongly controlled by the availability and supply rates of nutrients, especially N (Nixon, 1995; Boesch et al., 2001; Paerl and Pipher, 2008) and to a lesser extent P (Sylvan et al., 2006). There is a delicate balance between beneficial nutrient enrichment to sustain a productive and healthy food web, and overfertilization, which can greatly accelerate primary production and promote excessive organic matter production (i.e., eutrophication; Nixon, 1995). If not effectively utilized by the food web, excess organic matter can accumulate, leading to water quality problems and habitat degradation (Fig. 4.7).

Symptoms of eutrophication include phytoplankton blooms, loss of submerged aquatic vegetation, severe oxygen depletion (hypoxia), and fish kills (Paerl, 1988, 2004). Sudden changes in temperature, nutrient depletion, and light availability constraints can cause blooms to die (Paerl, 1988). When blooms die, they sink into deeper waters, where they decompose (Fig. 4.7). This process consumes vast amounts of oxygen, and if deep waters are not mixed with oxygen-rich surface waters, they eventually run out of oxygen, creating hypoxia, which can suffocate finfish and shellfish. Nutrient-stimulated hypoxia is a major cause of habitat loss and finfish and shellfish kills (Diaz and Rosenberg, 2008).

Rapidly expanding urban, agricultural, and industrial activities in coastal watersheds have greatly accelerated the production and delivery of nutrients to nutrient-sensitive estuarine and coastal waters. Anthropogenic and natural sources of N and P are delivered by (i) surface water discharge delivered via creeks and rivers, (ii) subsurface discharge (groundwater), and (iii) atmospheric deposition (rainfall or dry fall, mainly as N). The proportions of these nutrient sources vary geographically and demographically. In rural, agriculturally dominated regions, 50% to over 75% of N and P input originates from diffuse, nonpoint sources such as surface runoff, rainfall, and groundwater (Paerl, 1997; Howarth, 1998; Boesch et al., 2001; Moore, 1999). Point sources, including wastewater, industrial, and municipal discharges, account for the rest. In contrast, N and P loading in urban watersheds (e.g., Narragansett Bay and Puget Sound) are dominated (>50%) by point sources,
while watersheds encompassing both urban centers and intensive agriculture (e.g., Chesapeake Bay and San Francisco Bay regions) exhibit a more even distribution of these source types (Castro et al., 2003).

### 4.5.2 The Roles of Climatic Variability in Eutrophication Dynamics

Nutrient, sediment, and other contaminants in coastal waters are strongly influenced by climatic forcing features, especially freshwater discharge, the main delivery mechanism. Climatic shifts, including increasing tropical storm and hurricane frequencies (Goldenberg et al., 2001; Webster et al., 2005) and changing drought conditions, accelerate these inputs. It is therefore useful to develop ecological indicators that could help distinguish human impacts from natural perturbations. This goal is compounded by the fact that human and natural perturbations may be identical, overlap, or act synergistically, potentially blurring this distinction.

Data from the mid-1990s to present show that many coastal systems have experienced the combined stresses of anthropogenic nutrient enrichment, droughts (reduced flushing combined with minimal nutrient inputs), and elevated tropical cyclone activity (high flushing accompanied by elevated nutrient inputs). These distinct perturbations have proved useful for examining impacts of anthropogenic and natural stressors on phytoplankton community structure. Seasonal and storm-induced variations in river discharge, which affect flushing and residence times, strongly affect competition and relative dominance among different PTOs, as a function of their contrasting growth rates and doubling times. For example, the relative contribution of chlorophytes, cryptophytes, and diatoms to the total Chl a pool appeared strongly controlled by periods of elevated river flow in North Carolina’s Neuse River Estuary and downstream Pamlico Sound (Fig. 4.8; Valdes-Weaver et al., 2006; Paerl and Huisman, 2009).

These effects are most likely due to differential nutrient uptake and growth rates among PTOs (Pinckney et al., 1999). Cyanobacteria, which generally have slower growth rates, were more abundant when flushing was minimal (i.e., longer residence times) during summer (Fig. 4.8). Historic trends in dinoflagellate and chlorophyte abundance provide
additional evidence that hydrologic changes have altered phytoplankton community structure in the Neuse River estuary. Both decreases in the occurrence of winter–spring dinoflagellate blooms and increases in the abundance of chlorophytes coincided with the increased frequency and magnitude of hurricanes since 1996 (Fig. 4.8; Pael et al., 2006a,b; Valdes-Weaver et al., 2006). The relatively slow growth rates of dinoflagellates account for their reduced abundance during the ensuing high river discharge events. Overall, phytoplankton composition has been altered since 1994 following major hydrologic changes, specifically flooding from large hurricanes such as Fran and Floyd (Pael et al., 2005, 2006b). These phytoplankton community changes signal potential trophic and biogeochemical alterations.

There is a scientific consensus that the buildup of greenhouse gases in the atmosphere is warming the earth (Houghton et al., 2001, see also Chapter 20). The past decade was the warmest since temperature records began in 1850, and paleo-records indicate that recent warming has no counterpart in the past 1000 years (Crowley, 2000). The global Earth’s temperatures increased by almost 1°C during the past 150 years (Jones et al., 1999), and general circulation models have projected further temperature increases of 1–6°C over the next 100 years (Houghton et al., 2001). A global circulation model-based study that examined the impacts of global warming on the annual runoff of the world’s 33 largest rivers (Miller and Russell, 1992) suggested that runoff increases are likely for 25 of the 33 studied rivers. Under this scenario, the average annual Mississippi River discharge would increase 20% if the concentration of atmospheric CO₂ doubles. Other studies have shown that runoff estimates for the Mississippi River Basin differed greatly between the Canadian model and the Hadley model (Wolock and McCabe, 1999). Both models predict an increase in future extreme rainfall and runoff events, but they disagree in terms of both the magnitude and direction of changes in average annual runoff. The average annual runoff of the Mississippi River Basin, for example, was projected to decrease 30% for the Canadian model but increase 40% for the Hadley model by the year 2099. Estimated changes into major US estuaries projected by the Hadley model by the year 2099 range from -40%
that many coastal and estuarine ecosystems will experience changes in freshwater inflow, although it is unclear in what manner these changes will occur. It is also likely that extreme precipitation events will become more common, as may droughts and floods (Easterling et al., 2000).

Increased global temperatures, combined with an enhanced hydrologic cycle, may influence estuarine and coastal eutrophication in three major ways (Fig. 4.9). First, the magnitude and seasonal patterns of freshwater and nutrient inputs would be affected, which could affect nutrient-enhanced coastal productivity. Second, altered flushing and residence times would affect phytoplankton competitive interactions and hence dominance among major taxonomic groups. Third, increases in air and hence water temperatures will have a direct effect on phytoplankton physiology and growth. For example, cyanobacteria generally prefer much higher temperatures for optimizing growth than other taxonomic groups (e.g., diatoms, cryptophytes, and chlorophytes; Fig. 4.10). Thus, in a warmer world, cyanobacterial growth and possibly bloom formation would be enhanced relative to other competitive taxonomic groups. Such taxonomic shifts would have ramifications for food web and nutrient cycling dynamics (Paerl and Huisman, 2008, 2009).

FIGURE 4.9 Coupling between climate variability, coastal eutrophication, and hypoxia. Source: Reprinted from Jusčić et al, 2005, with permission from Elsevier.

FIGURE 4.10 Temperature dependence of the specific growth rates of two bloom-forming cyanobacteria Microcystis aeruginosa (Reynolds, 2006) and Planktothrix agardhii (Foy et al., 1976), the diatom Asterionella formosa (Butterwick et al., 2005), and the cryptophyte Cryptomonas marssonii (Butterwick et al., 2005). The data are from controlled laboratory experiments using light-saturated and nutrient-saturated conditions. Solid lines are least-squares fits of the data to the temperature-response curve of Chen and Millero (1986).
4.6 HARMFUL ALGAL BLOOMS

Phytoplankton blooms are a rapid and perceptible increase in phytoplankton biomass in an aquatic ecosystem (Fig. 4.11). As discussed above, bloom initiation and persistence is a complex environmental issue that involves specific circulation and current patterns, nutrients, light, herbivory, and other factors. Blooms may produce biotoxins, cause hypoxia, and alter food webs; in each case, they can constitute an environmental health hazard, degrade water quality and habitat, and are therefore deemed “harmful algal blooms” (HABs; Table 4.1). Species in diverse phytoplankton groups can be HABs, including cyanobacteria, dinoflagellates, prasinophytes, and diatoms. During blooms, fish and shellfish may consume these algae, then accumulate and concentrate the biotoxins without apparent harm. This renders the fish and shellfish extremely toxic to whomever consumes them, including marine mammals, sea birds, and humans. In places where HAB monitoring and surveillance programs do not exist, these blooms may go unnoticed until they cause illnesses and/or death in humans who consume products from the sea.

4.7 NUTRIENT MANAGEMENT OF PHYTOPLANKTON PRODUCTION AND COMPOSITION

When controlling and managing the effects of excessive nutrient loading on estuarine and coastal
TABLE 4.1 Economic and public health problems related to coastal harmful algae in the United States

- Paralytic shellfish poisoning (PSP), which occurs in all coastal New England states as well as New York and along much of the west coast from Alaska to California. This problem has also extended to offshore areas in the northeast (causative species—the dinoflagellates *Alexandrium tamarense*, *Alexandrium fundyense*, and *Alexandrium catenella*).
- Neurotoxic shellfish poisoning (NSP) and fish mortalities in the Gulf of Mexico and, more recently, extending along the Atlantic Coast from Florida to the Carolinas (causative species—the dinoflagellate *Karenia brevis*).
- Mortalities of farmed salmonids in the Pacific Northwest (causative species—the diatoms *Chaetoceros convolutus* and *Chaetoceros concavicornis* and the raphidophyte *Heterosigma akashiwo*).
- Recurrent brown tides causing mass mortalities of mussel populations in Rhode Island, massive recruitment failure of scallops, and reduction in eelgrass beds around Long Island (causative species—the previously unknown chrysophyte, *Aureococcus anophagefferens*).
- Ciguatera fish poisoning (CFP), a malady associated with dinoflagellate toxins accumulated in tropical fish flesh, occurring in virtually all subtropical to tropical US waters (Florida, Hawaii, Guam, US Virgin Islands, Puerto Rico, Guam, and other Pacific Territories; major causative species *Gambierdiscus toxicus*, *Prorocentrum* spp., *Ostreopsis* spp., *Coolia monotis*, *Thecadinium* spp., and *Amphidinium carterae*).
- Amnesiac shellfish poisoning (ASP), which occurred first in southeastern Canada in 1987, but has been a problem for the US Pacific coast states over the past 2 years (causative species—the diatoms *Pseudonitzschia pungens* forma *multiseries* and *Pseudonitzschia australis*). This sometimes fatal illness is so named because one of its most severe symptoms is permanent loss of short-term memory. The ASP toxin, domoic acid, has been detected in shellfish from both the West and East Coasts of the United States, and toxic *P. pungens* f. *multiseries* cells have been isolated from Gulf of Mexico waters, although a toxin has yet to be detected in the field. The threat to US shellfish consumers from this alga covers a broad geographic area. The name “ASP” understates the severity of the problem, since domoic acid also accumulates in fish and in crab viscera along the west coast of the United States, where the impact of this toxin on nonmolluscan fisheries may well exceed the loss to molluscan fisheries (e.g., razor clam).
- Diarrhetic shellfish poisoning (DSP), which some consider the most serious and globally widespread phytoplankton-related seafood illness. Major causative species are dinoflagellates *Dinophysis* and *Prorocentrum*. The first confirmed incidence of DSP in North America occurred in 1990 when these toxins were detected in shellfish from the southern coast of Nova Scotia following numerous human illnesses. Another DSP outbreak in Canada occurred in 1992. DSP-producing phytoplankton species occur throughout all temperate coastal waters of the United States, and thus present a potential problem for the future, although no outbreaks of DSP have yet been confirmed.
- Cyanobacteria blooms are becoming more numerous, widespread, and persistent in nutrient-enriched estuarine and coastal waters worldwide. Blooms have multiple negative impacts, such as toxicity, overgrowing, and smothering seagrasses, coral reefs and shellfish habitats, and food web shifts. Some species produce toxins and other bioactive metabolites. Of concern are blooms of toxic heterocystous *N*₂ fixing genera *Nodularia* (full salinity) and *Cylindrospermopsis* (oligohaline). The filamentous, nonheterocystous *N*₂ fixing species *Lyngbya majuscula* produces both dermatotoxins and neurotoxins. Blooms of this subtropical/tropical species have fouled large segments of both Hawaii and Florida’s estuaries and bays. Some tropical harmful cyanobacterial species are speaking into more temperate regions in parts due to global warming, which has expanded their habitat (Paerl and Huisman, 2008).

*Source: In part adapted from Anderson et al. (2000).*

eutrophication and HAB development, anthropogenic point and nonpoint sources are the most significant targets for nutrient reduction. The amounts, forms, and relative proportions of nutrients vary according to human activities, locations, and distributions of population centers and routes of nutrient discharge (i.e., surface, subsurface, and atmospheric). Magnitudes and proportions of *N* and *P* input have been shown to control both phytoplankton community productivity and compositional responses in receiving waters (Smith, 1990), and as such both aspects require careful assessment and management. In point source-dominated watersheds, the emphasis has been on improved wastewater (from sewage and industrial effluent) treatment and removal of both *N* and *P*. In nonpoint source-dominated watersheds, surface runoff, especially that originating from agricultural operations and urban stormwater, are the prime focus of *N* reduction strategies. These strategies include best management practices, including prudent and timely applications of fertilizers, soil conservation, establishment of
riparian vegetative buffer zones, and use of wetlands to enhance “stripping” of runoff-based N (Mitsch et al., 2001).

Both N and P point sources are under intense local, state, and federal scrutiny. Recent agency (e.g., US-Environmental Protection Agency- EPA, 1998, 1999, European Parliament: European Economic Union-EEU-Water Framework, 2003) and legislative action has led to strict N and P discharge limits from wastewater treatment plants, and those plants not able to meet these standards are under considerable and continuing pressure to upgrade. In addition, a phosphate detergent ban was enacted in the mid-1980s in North America, Europe, and parts of Australasia. This has led to marked decreases in P loading in many watersheds. Current strategies aimed at reducing nonpoint N discharge, including riparian buffers, wetland construction, and soil conservation, also retard the movement of P to nutrient-sensitive waters. Therefore, the primary strategies and targets for pursuing N input constraints will yield significant parallel reductions in P.

In addition to surface runoff, atmospheric deposition and groundwater should also be recognized as significant sources of new N potentially stimulating primary production in estuarine and coastal waters (Paerl, 1985, 1997). Local and regional studies have shown atmospheric deposition and groundwater inputs of N to be large, increasing, and of widespread importance in estuarine and coastal environments (Jaworski et al., 1997; Paerl and Whitall, 1999; Valigura, 2001; Paerl et al., 2002). For example, along the US Eastern seaboard, atmospheric deposition accounts for 10% to over 30% of externally supplied N sources (Paerl et al., 2002; Castro et al., 2003). Atmospheric deposition plays an increasingly important role in coastal waters, since surface runoff N is often effectively “filtered” in N-limited estuarine systems as it transits to the ocean (Paerl and Whitall, 1999). Atmospheric deposition as well as groundwater can be directly discharged to coastal waters and bypass this estuarine N filter (Paerl et al., 2002; Moore, 1999; Fig 4.12). It has been suggested that these N inputs may be key drivers of a reported recent increase in HABs in coastal waters (Paerl, 1997; Richardson, 1997). This, combined with observations that N and P loading to these waters has increased steadily in comparison to silicon (Si), may also help explain observed shifts in phytoplankton community away from Si-requiring diatoms to flagellates, dinoflagellates, and cyanobacteria (Dorich and Whitlege, 1992; Riegleman, 1995).

Certain forms of N may be preferred by phytoplankton, including bloom-forming species. For example, in highly turbid estuarine waters where light availability may be limited, N sources that require the least amount of energy for uptake and assimilation may be preferred. This means that under these conditions, the most readily assimilated and least energy-requiring form of N, ammonium, may be
preferred over the oxidized forms nitrite and nitrate (Harrison and Turpin, 1982). Experimental work has confirmed this for nutrient-enriched estuarine and coastal waters (Syrett, 1981; Collos, 1989; Stolte et al., 1994; Rieger, 1995). In addition, some phytoplankton groups and species are more capable than others at utilizing organic forms of N and other nutrients (Paerl, 1988; Antia et al., 1991). These findings stress the need for considering both the qualitative and quantitative influences of N (and other nutrient) loadings on phytoplankton biomass and compositional responses.

An additional challenge for managing estuarine primary production and phytoplankton community composition is the influence of climate change. Some symptoms of climate change, such as increased tropical storm activity, larger oscillations between extremely wet and drought conditions, and hence the more pulsed, episodic manner in which nutrients are supplied to coastal ecosystems, can confound management strategies that are based on average or "normal" hydrologic and nutrient discharge patterns. Since entering the recent period of elevated hurricane activity (Goldenberg et al., 2001), it seems that episodicity is now the norm rather than the exception. This calls for highly adaptive nutrient management strategies that take pulsed instead of more gradual patterns of nutrient and other pollutant input in consideration.

Much work lies ahead to further identify, characterize, and manage nutrient inputs controlling phytoplankton production and composition in estuarine and coastal waters. Research and monitoring are providing information essential for formulating long-term nutrient management strategies aimed at protecting and preserving the high standards of water quality and resourcefulness that we expect. With respect to phytoplankton production and composition needed to sustain desirable estuarine and coastal food webs, this means managing for enough, but not excessive production, and avoiding the promotion of harmful taxa. As we enter the new millennium, fostering a process-based understanding of nutrient–water quality interactions and utilizing this for effective management are key social, economic, and political responsibilities as we ensure long-term conservation and sustainability of coastal waters.

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