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Phytoplankton Ecology of North Carolina Estuaries

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ABSTRACT: Numerous phytoplankton-oriented ecological studies have been conducted since 1965 in the extensive North Carolina estuarine system. Throughout a range of geomorphological estuarine types, a basic underlying pattern of phytoplankton productivity and abundance following water temperature seasonal fluctuations was observed. Overlying this solar-driven pattern was a secondary forcing mechanism consisting of a complex interaction between meteorology and hydrology, resulting in periodic winter or early spring algal blooms and productivity pulses in the lower riverine estuaries. Wet winters caused abundant nitrate to reach the lower estuaries and stimulate the blooms, whereas dry winters resulted in low winter phytoplankton abundance and primary production. Dinoflagellates (*Heterocapsa triquetra, Prorocentrum minimum, Gymnodinium* spp.) and various cryptomonads dominated these cool-weather estuarine blooms. Sounds were less productive than the riverine estuaries, and were dominated by diatoms such as *Skeletonema costatum, Thalassiosira* spp., *Melosira* spp., and *Nitzschia* spp., as were the most saline portions of riverine estuaries. Nutrient-limitation studies found that nitrogen was the principal limiting nutrient in these estuarine systems over a range of trophic states, with phosphorus occasionally co-limiting. Freshwater and oligohaline portions of large coastal plain rivers were often subject to summer blue-green algal blooms. Formation of these blooms on a year-to-year basis was also determined by meteorology and hydrology: wet winters or springs and consequent nutrient loading, coupled with low summer flow conditions and regeneration of nutrients from the sediments. Dry winters or springs resulted in less available nutrients for subsequent summer regeneration, and high flow conditions in summer flushed out the blooms. In recent years, there has been a dramatic increase in reported fish kills attributed to toxic dinoflagellate blooms, particularly in nutrient-enriched estuarine areas. This issue has become a major coastal ecological and economic concern.

Introduction

The estuarine system of coastal North Carolina is vital to the economy of the state, providing a highly productive environment for commercial and sport fishing and an attractive area for both in-state and out-of-state tourism. Over the past 25 yr, deteriorating water quality and other environmental issues have caused considerable concern among researchers, state officials, and the public. These problems include reduction of prime sport fish stocks (particularly striped bass), dinoflagellate bloom-induced fish kills, finfish and shellfish disease outbreaks, areas of oxygen-depleted (dead) water, freshwater intrusion into fish nursery areas, and massive blue-green algal blooms in the lower reaches of large coastal rivers (Copeland and Gray 1989). Many of these concerns are common to coastal waters in other geographic regions of the world, as well. The North Carolina coastline includes all types of coastal plain estuaries (riverine, lagoonal, and sounds). With the broad range of geomorphological estuarine types in this state, and the variety of environmental issues in question, North Carolina is a productive location for estuarine research applicable to coastal plain systems in diverse locales.

Objectives

The objectives of this study were to review the published literature pertaining to phytoplankton of the North Carolina estuarine systems, summarize and synthesize the findings, and draw conclusions that are both generally applicable to this region and are relevant to systems in other geographical locations. The source material included the refereed literature together with a rich body of less widely circulated technical reports. Phytoplankton community structure, abundance, biomass, productivity, and toxicity, and the biotic or abiotic factors affecting or controlling these variables are discussed for the study areas. Major freshwater tributaries having important relationships with the estuaries were also examined.

Field Study Distribution

The coastal region of the state of North Carolina lies approximately between 33°50′N and 36°30′N latitude and 75°W and 78°15′W longitude. The Albemarle-Pamlico Sound system is the second-largest estuarine system in the United States (Fig. 1), but the phytoplankton in the sound proper has received little scrutiny. Estuarine phytoplankton

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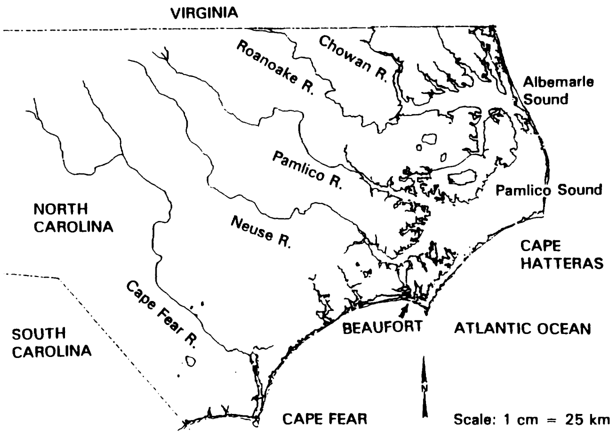

Fig. 1. Major estuaries and coastal rivers of North Carolina.

studies have been concentrated in two subestuaries of this system, the Pamlico and Neuse river estuaries (Fig. 1). A third major focus has been the Beaufort-Morehead City area, where several academic, state, and federal government laboratories are located. This area encompasses Bogue Sound, Core Sound, the Beaufort Channel, the Newport River Estuary, and Calico Creek. Two other systems have been investigated: Gales Creek, a small estuary located 20 km to the south of Beaufort along Bogue Sound, and the Cape Fear River Estuary, located adjacent to the city of Wilmington. Among the freshwater and oligohaline river areas, phytoplankton in the Chowan River, which feeds into Albemarle Sound, and the lower Neuse River have received research attention because of repeated incidences of blue-green algal blooms.

Results

The Beaufort Area

The phytoplankton of the Beaufort-Morehead City estuarine areas has received considerable attention, beginning with primary productivity studies conducted in the 1960s (Williams 1966; Williams and Murdoch 1966). The Beaufort Channel varies from 4 m to 10 m in depth, and has a salinity range from 24‰ to 36‰. Photosynthesis generally followed the temperature cycle through the year, with daily gross photosynthesis ranging between 120 mg C m^{-3} and 720 mg C m^{-3} (Williams and Murdoch 1966). Maximum photosynthesis generally occurred at either the 50% or 100% irradiance level, and on an areal basis mean annual gross photosynthesis was 113 g C m^{-2} yr^{-1}. Chlorophyll *a* concentrations averaged 4.8 μg l^{-1} in December–May and 3.6 μg l^{-1} June–October. Phytoplankton cell counts did not correlate with photosynthesis and ranged from low to moderate in comparison with other regional studies (Table 1). Centric diatoms predominated, especially *Skeletonema costatum,* and flagellates were often subdominant.

Productivity studies (light–dark bottle oxygen method) were conducted at 33 stations throughout the shallow estuarine systems near Beaufort, covering an area of about 400 km^2 (Williams 1966). This ystem is composed of euhaline sounds, riverine estuaries, tidal creeks and marshlands, with salinities ranging from 3‰ to 31‰. Photosynthesis was greatest near the heads of the North and Newport rivers where freshwater influence was strongest, and minimal at the lower portions of the estuaries farthest from freshwater influence. The areas with greatest photosynthesis received farm-

TABLE 1. Phytoplankton cell density estimates (no. ml^{-1}) from North Carolina estuarine systems.

Estuary	Period	Study Mean	Range
Beaufort Channel			
Williams and Murdoch (1966)	1964–1965	2,000	130–5,400
Beaufort estuaries			
Thayer (1974)	1967–1968	1,700	360–8,200
Calico Creek			
Sanders and Kuenzler (1979)	1974–1975	—[a]	1,000–1,000,000
Pamlico R. Estuary			
Hobbie (1971)	1966–1967	—	1,000–340,000
Stanley and Daniel (1986)	1985	4,200	630–20,600
Neuse River Estuary			
Mallin et al. (1991)	1988–1989	1,600	210–4,200
Mallin (1992)	1990–1991	1,700	560–4,400
Cape Fear River Estuary			
Carpenter (1971[b])	1969–1970	1,700	250–7,300
Birkhead et al. (1979)	1971–1976	1,800	x

[a] = Data not available.

TABLE 2. Annual phytoplankton production estimates of various North Carolina estuarine systems.

Estuarine System	Volumetric g C m^{-3}	Areal g C m^{-2}
Beaufort Channel (Williams and Murdoch 1966)	17.0	68.0
Beaufort area estuaries (Williams 1966)	45.0	52.5
Beaufort area estuaries (Thayer 1971)	56.0	66.6
Calico Creek (Sanders and Kuenzler 1979)	315.0	145.0
Neuse River Estuary (Mallin et al. 1991; Mallin 1992)[a]	75.0	280.0
Neuse River Estuary (Paerl et al. In press)[b]	108.0	370.0
Newport River (Williams and Murdoch 1966)	74.0	74.0
Pamlico River Estuary (Kuenzler et al. 1979)	150.0	500.0
South River (Fisher et al. 1982)	144.0	288.0

[a] Mean of three mesohaline stations, May 1988–October 1990.
[b] Entire estuarine system, May 1988–November 1993.

land drainage and sewage input. Maximal photosynthesis generally occurred at 50% irradiance level. Areal gross photosynthesis ranged from 30 g C m^{-2} yr^{-1} to 321 g C m^{-2} yr^{-1}, and was usually between 80 g C m^{-2} yr^{-1} and 160 g C m^{-2} yr^{-1}. Weighted averages for gross photosynthesis and respiration for the year were 99.6 g C m^{-2} yr^{-1} and 47.1 g C m^{-2} yr^{-1}, respectively.

Thayer (1971) examined phytoplankton productivity (^{14}C-uptake method) and nutrient distribution at the same stations used by Williams (1966). A similar pattern emerged—photosynthesis following seasonal temperature variations, and higher rates in areas with the most freshwater influence. Areal net photosynthesis ranged from 81 mg C m^{-2} d^{-1} to 534 mg C m^{-2} d^{-1}, with a weighted net yearly mean of 66.6 g C m^{-2} yr^{-1}. Despite the methodological differences, this figure compared well with the net photosynthesis determined by Williams (1966) over the same area (Table 2).

The measured primary productivity values from the Beaufort-Morehead City estuarine systems may have been somewhat underestimated. They were obtained using bottles incubated under static irradiance conditions, with areal photosynthesis integrated according to field vertical-light attenuation measurements. This may have overemphasized the effects of photoinhibition and light limitation, in some cases. Because of wind and tidal mixing in these areas the phytoplankton are in motion and receiving constantly varying irradiance, so true productivity may actually have been greater (Mallin and Paerl 1992).

Nitrogen and phosphorus levels were highest in upstream locations, and the generally low N:P ratios suggested that N was the limiting nutrient. Chlorophyll *a* ranged from low to moderate (Table 3) and did not correlate with phytoplankton densities. Cell densities displayed a maximum in December and minima in March and July. Diatoms dominated throughout the year, with dinoflagellates second in importance. In addition to planktonic forms, large benthic diatoms transported

TABLE 3. Mean annual reported chlorophyll *a* concentrations (μg l^{-1}) for various North Carolina estuarine systems.

Area/Study	Period	Study Mean	Range
Beaufort Channel			
Williams and Murdoch (1966)	1964–1965	4.2	2.0–9.3
Beaufort estuaries			
Thayer (1971)	1967–1968	3.8	1.6–9.4
Gales Creek			
Campbell (1973)	1965–1966	4.6	0–18.7
Calico Creek			
Sanders and Kuenzler (1979)	1974–1975	—[a]	6.0–140.0
Pamlico River Estuary			
Hobbie (1971)	1966–1967	10.8	1.0–48.0
Stanley (1987)	1986	17.3	0.8–184.2
Neuse River Estuary			
Christian et al. (1991)	1985–1989	10.5	—
Mallin et al. (1991)	1988–1989	11.8	2.2–23.0
Mallin (1992)	1990–1991	14.3	1.6–64.8

[a] = Data not available.

TABLE 4. Phytoplankton taxa cited as particularly abundant by authors of various North Carolina estuarine studies. Estuary: B = Beaufort-Morehead City area, CC = Calico Creek, CF = Cape Fear Estuary, GC = Gales Creek, N = Neuse River Estuary, P = Pamlico River Estuary, SC = South Creek. Season: F = fall, Sp = spring, Su = summer, W = winter. Salinity: FW = freshwater, O = oligohaline (0.5–5‰), M = mesohaline (6–18‰), P = polyhaline (19–25‰), E = euhaline (26–35‰).

Taxa	Estuary	Season	Salinity
Bacillariophyceae			
Asterionella japonica	CF	Sp, W	P, E
Chaetocerus spp.	B, GC	W, Sp, Su, F	E
Cyclotella spp.	N, P, SC	W, Sp	M, P
Melosira spp.	N, GC	Sp	M, P
Navicula spp.	CC, P, SC	W, Sp, Su	O, M, P, E
Nitzschia spp.	B, N	W, Sp, Su, F	M, P, E
Skeletonema costatum	B, CC, CF, GC, N, P	F, Sp	M, P, E
Thalassiosira spp.	CF, N	W, Sp, Su, F	M, P, E
Thalassionema nitzschoides	N	Su	M
Chlorophyceae			
Chlamydomonas spp.	CC, GC, N	Su, F, W	O, M
Nannochloris spp.	CC	Su	M, P
Chrysophyceae			
Calicomonas ovalis	GC, P, SC	W, Sp, Su, F	M, P
Pseudopedinella pyraforme	P, SC	F, W	M
Cryptophyceae			
Chroomonas amphioxiae	CF, N	Sp, Su, F	O, M, P, E
Chroomonas minuta	N, P	W, Sp, Su, F	M
Cryptomonas testaceae	GC, N	Sp, Su	O, M
Cryptomonas ovata	P	Su, F	M
Cyanophyceae			
Phormidium spp.	N	Su	M
Unidentified coccoid	P	W, Sp, Su, F	M
Dinophyceae			
Gymnodinium spp.	B, N, P, SC	W, Su, F	M, P
Heterocapsa triquetra	GC, N, P, SC	W, Sp	M, P
Katodinium rotundatum	B, CF, GC, P, N	W, Sp, F	M, P, E
Prorocentrum minimum	B, GC, N, P, SC	W, Sp	M, P
Pfiesteria piscicida	N, P	Su	O, M, P, E
Prasinophyceae			
Nephroselmis gilva	CC	Su	P
Pyramimonas spp.	GC, N	F, W	O, M, P
Xanthophyceae			
Olisthodiscus carterae	GC	Sp, Su	P, E

into the water column through turbulence were often abundant (Table 4).

Nutrient limitation bioassays were subsequently conducted in waters representing the same areas as in the previous productivity studies (Thayer 1974). Phosphorus was limiting at some stations, nitrogen at all stations, and other nutrients did not limit phytoplankton growth. When glucose or dead *Spartina* material were added as organic substrates, there was less available N and P in the water samples and photosynthesis was reduced. There was apparently little N and P available over much of this estuarine area and the extensive marshes may have depleted the nutrients from the water column through immobilization by bacteria decomposing the organic marsh material. Paerl (1985) utilized in situ cubitainer bioassays to determine that amendments of rainwater stimulated phytoplankton growth in Bogue Sound water, with continentally-derived rain more stimulatory than oceanic-derived rain. Nitrogen, derived from rainfall, was the nutrient stimulating productivity in these studies. Decomposition of organic substrates low in N and P relative to the amount of carbon may be an important process limiting the supply of nutrients to the phytoplankton in this area. However, it is important to note that bioassay results have demonstrated that nitrogen limitation is common in nonmarsh areas of other North Carolina estuaries as well (see later sections of this review). In nutrient-poor coastal sounds, nitrogen limitation is likely important regardless of the amount of nearby marsh vegetation.

A eutrophic part of this estuarine system is Calico Creek, a sewage-impacted system with abundant nutrients, and salinities ranging from 0.5‰ to 34‰ (Sanders and Kuenzler 1979). High annual estimates for net productivity were reported, despite the shallow (0.5 m) mean depth of the estuary (Table 2). Phytoplankton cell counts were about 1,000 ml^{-1} in November–March and 100,000 ml^{-1} in June–August, with a maximum of 1,000,000 ml^{-1} in September. Primary productivity in winter (about 260 mg C m^{-3} d^{-1}) was similar to that found in other estuaries, but summer values in Calico Creek (1,700 mg C m^{-3} d^{-1}) were much higher. The community was dominated by diatoms and green algae (Chlorophyceae), with blue-green algae (Cyanophyceae) and dinoflagellates occasionally in abundance. Although total phytoplankton biomass did not differ appreciably during summer and winter, changes in community composition followed a marked seasonality. Diatoms were dominant during winter, but small green algae became extremely abundant in summer, with *Nannochloris arvensis* and *Nephroselmis gilva* together accounting for >80% of the phytoplankton numbers (Table 4). An interesting phenomenon was that blooms of *N. arvensis* would move up and down the estuary during the summer, staying in a salinity range of 15‰ to 25‰.

Most of the phytoplankton information generated from the Beaufort-Morehead City area estuaries is now 25 yr old. A reassessment of productivity dynamics and nutrient limitation would be very worthwhile. With the extensive background data available, this system could serve as an ideal model of how 25 yr of increasing population pressure and anthropogenic impacts affect the primary producers of geomorphologically diverse estuaries.

The Pamlico River Estuary

The Pamlico River Estuary, draining an area of about 14,000 km^2, is the major tributary of mid-Pamlico Sound (Copeland et al. 1984; Fig. 1). From 1966 to 1968 chlorophyll *a* and phytoplankton densities ranged from moderate to very high (Tables 1 and 3); dinoflagellates predominated, with diatoms becoming more abundant near the mouth of the estuary (Hobbie 1971). From January through March there was a bloom consisting of the dinoflagellate *Heterocapsa triquetra* (reported as *Peridinium triquetra*), along with other dinoflagellates, including *Gyrodinium aureolum, Katodinium rotundatum,* and *Prorocentrum minimum* (Table 4). A subsequent decrease was later followed (August–September) by a peak consisting of various dinoflagellates and the chrysophyte *Calycomonas ovalis.* Low densities prevailed fall through January. Continuing research indicated that the winter dinoflagellate bloom was a common occurrence, and was supported by elevated concentrations of nitrate reaching the middle and lower areas of the estuary because of low temperatures and concomitant low uptake upstream (Hobbie et al. 1972). Nitrate loading to the estuary is typically high during December–February because of high winter rainfall and runoff (Hobbie et al. 1972). Hobbie (1971) considered the Pamlico River to be highly eutrophic, and *Heterocapsa triquetra* an indicator species of nutrient enrichment.

Copeland and Hobbie (1972) suggested that the estuary was nitrogen-limited because of the high water-column phosphate concentrations from incoming river loading and mining waste discharge from Texasgulf Industries, located along the middle of the estuary. Waste release from the mining industry caused intermittent patches of high phosphate concentrations (>90 μM P) to move seaward in the middle estuary (Hobbie 1971). Bioassays conducted in experimental estuaries and pools (mesocosms) indicated that the system was N-limited because additions of mining waste did not increase phytoplankton biomass (Carpenter 1971a). These experiments also showed a significant increase in filamentous blue-green algal abundance over the control mesocosms in most of the mining waste addition treatments.

The phytoplankton and nutrient kinetics of the estuary were later (1975–1977) investigated by Kuenzler et al. (1979). The phytoplankton community was similar to that described by Hobbie (1971), including a winter bloom of *Heterocapsa triquetra*. During blooms, chlorophyll *a* peaks reached 100 μg l^{-1}, and the authors felt that based on increased biomass, phytoplankton had increased in the estuary since the mid-1960s. The estuary was N-limited, and only 5% of the N was supplied by inputs and the rest by regeneration (Kuenzler et al. 1979). Nitrate and ammonia were low in the water and phosphate was high. There was sufficient phosphate for phytoplankton at all times in the water, primarily from the phosphate mining and processing industry effluent.

In 1985 there was a somewhat different phytoplankton pattern. The normal winter dinoflagellate bloom was flushed out by high flows from winter storms, with densities only reaching 1,000–2,000 ml^{-1} (Stanley and Daniel 1986). Densities were generally dominated by small flagellated chrysophytes (*Calycomonas ovalis* and *Pseudopedinella pyraforme*), dinoflagellates (*H. triquetra, P. minimum,* and *Gymnodinium* spp.), and various diatoms (Table 4). Diatoms reached densities of 200–500 ml^{-1} in late spring and early summer and chrysophyte densities were over 10,000 ml^{-1} in summer and early fall. Biomass, as wet weight, followed the same pattern as densities, peaking in spring and summer. Nannoplankton (cells <20 μm in diameter) made up 60% of the biomass. In 1986 two winter dinoflagellate blooms occurred, in December and March, with chlorophyll *a* exceeding 100 $\mu g\ l^{-1}$ (Stanley 1987). Otherwise chlorophyll *a* ranged between 5–25 $\mu g\ l^{-1}$ in spring and winter and >50 $\mu g\ l^{-1}$ in June and October. Nitrate was assimilated rapidly upon entering the estuary, displaying an inverse areal pattern to that of salinity. Highest mean chlorophyll values occurred at stations where salinity ranged from 4.5‰ to 9‰.

South Creek is a tributary of the Pamlico River Estuary. There were summer abundance peaks in 1983 and 1984 and a winter peak in 1983 (*H. triquetra*) but no winter bloom in 1984 due to excessive storm runoff (Stanley and Daniel 1985). Diatoms composed 25% of the community biomass in winter and <10% the rest of the year, green algae were 42% in spring and <5% the rest of the year, dinoflagellates were 34–46% in winter and 1–2% in summer, and chrysophytes (mainly *C. ovalis*) were 60–90% of the community biomass in summer and fall. Due to the low salinity of the system, the South Creek densities were dominated year-round by various size phytoflagellates rather than alternating with diatoms (Table 4).

The Pamlico Estuary has frequently sustained bottom-water hypoxia events, especially during summer (Hobbie et al. 1972; Davis et al. 1978; Copeland et al. 1984). Additionally, at least one winter (1977) anoxia event has been associated with a bloom of *H. triquetra* during stratified conditions (Davis et al. 1978). Davis et al. (1978) concluded that deoxygenation depends on physical conditions resulting in stratification of the water column, and the high primary productivity and frequency of algal blooms provide the labile organic carbon source for water-column respiration. They suggested that nutrient input reductions may be important for controlling deoxygenation by reducing the available pool of labile organic matter during summer respiration. In contrast, Stanley and Nixon (1992) analyzed long-term datasets (1975–1990) and concluded that the events were "natural features" of the system, caused by summer warm temperatures, vertical stratification, and periods of decreased wind stress. The authors found no significant statistical relationship between chlorophyll levels or algal bloom frequency and hypoxia events. They agreed that respiration rates associated with the planktonic particulate organic carbon load found by Davis et al. (1978) were sufficiently great to result in anoxia events, but they did not address the question of BOD source material in their concluding interpretation that reduction of anthropogenic nutrients may not be effective in reducing summer hypoxia (Stanley and Nixon 1992).

Further trends analyses indicated that nitrate and ammonia concentrations significantly decreased in the upper and middle estuary between 1969 and 1991, but nitrate did not decrease in the lower estuary (Stanley 1993a). During this same period phosphate significantly increased in the middle and lower estuary (due to phosphate mining activities), and showed no trend in the upper estuary. In the upper estuary, chlorophyll *a* concentrations tripled from 1970 to 1991, and bottom-water DO decreased slightly, with no significant trends for these parameters in the middle and lower estuary. Although increases in chlorophyll and phosphate and decreases in DO are common indicators of eutrophication, Stanley (1993a) concluded that eutrophication was not increasing because of the decrease in dissolved inorganic nitrogen concentrations in the system and lack of a phosphate trend in the upper estuary.

Some earlier studies suggested that because the river was already phosphate-rich (1–2 μM P), additional loading from mining waste would not affect the biota of the Pamlico River Estuary (Hobbie 1971; Hobbie et al. 1972). Phosphate loading to the system is high; data from 1986 showed phosphate concentrations in the middle estuary ranged between 0.5 μM P and 68 μM P, with average values of approximately 5 μM P (Stanley 1987, Appendix 1j). Phosphate mining and effluent discharge to the middle estuary (Texasgulf Industries) began in 1964 (Copeland and Hobbie 1972). However, all phytoplankton-related studies concerning the Pamlico River Estuary were initiated in 1966 or afterward. Thus, there are no published "before" data to serve as a baseline for comparison with later studies; hence, any statements regarding eutrophication or the effects of industrial loading must be interpreted with this consideration. Recently (1992) Texasgulf began a wastewater recycling program that has led to 80–90% reductions in effluent TP levels (Stanley 1993b). Considering sediment storage of nutrients, the effect of these loading reductions on this estuary's biotic communities will be interesting to follow. It would be an appropriate opportunity to conduct nutrient limitation bioassays and productivity measurements in the upper, middle, and lower estuary.

To summarize, in the Pamlico River Estuary diatoms were dominant only near the river mouth in the higher salinities. In 5–10‰ salinities, dinoflagellates were most abundant. Small flagellates dominated the Pamlico River and South Creek during the summer blooms. Blue-green algae were not important in the Pamlico River or South Creek. The system is N limited, with abundant phosphorus year-round. A winter dinoflagellate bloom in the middle estuary often is triggered by runoff and nitrate loading, and this bloom can be sometimes flushed out by excessive flow from winter storms. This eutrophic estuary is characterized by high chlorophyll concentrations and primary productivity, summer anoxia events, and blooms of *Calycomonas ovata* and *Heterocapsa triquetra.*

The Neuse River Estuary

The Neuse River Estuary drains an area of approximately 16,000 km^2 (Christian et al. 1991) and is the major tributary of southern Pamlico Sound (Fig. 1). Nutrient loading has increased in recent decades, primarily from agricultural and wastewater effluent point sources (Stanley 1988). Nutrient concentrations in the estuary usually are maximal in the freshwater area upstream of New Bern, and decrease progressively downstream (Christian et al. 1989, 1991). Chlorophyll *a* usually reaches highest ambient concentrations in the oligohaline area approximately 15 km downstream of New Bern (Christian et al. 1991). Phytoplankton in the mesohaline lower estuary near the juncture with Pamlico Sound are dominated by diatoms in summer and early spring, often under more saline conditions. Principal diatom taxa were *Thalassiosira* spp., *Cyclotella meneghiniana, Thalassionema nitzschoides, Nitzschia closterium,* and *Skeletonema costatum* (Table 4). Cryptomonads (*Chroomonas amphioxiae, C. minuta,* and *Cryptomonas testaceae*) were also very abundant, especially during periods of freshwater influence in spring and fall (Mallin et al. 1991; Mallin 1992). Dinoflagellates were usually abundant under all conditions, and principal species found were *Heterocapsa triquetra, Prorocentrum minimum, Katodinium rotundatum,* and *Gymnodinium* spp. (Mallin et al. 1991; Mallin 1992). Abundance of both centric diatoms and dinoflagellates was positively correlated with zooplankton grazing rates over a 2-yr period (Mallin 1992; Mallin and Paerl 1994).

Phytoplankton primary productivity in the lower Neuse was limited during all seasons by nitrogen, and co-limited during the spring freshet by phosphorus (Paerl et al. 1990b; Rudek et al. 1991). Natural amounts of rainwater added to estuary water proved stimulatory to phytoplankton growth in bioassays, with rainwater nitrate concentration inversely related to pH (Paerl et al. 1990a; Paerl et al. in press).

Longitudinally, the Neuse Estuary showed a progressive decrease in phytoplankton productivity from the New Bern area downstream to the estuary mouth (Boyer et al. 1993; Paerl et al. in press). Primary productivity in general was moderate to high in the lower Neuse Estuary (Table 2). Both primary productivity and ambient surface nitrate concentrations were significantly correlated with river flow upstream at Kinston, which in turn was strongly correlated (after a 2-wk lag period) with rainfall in the headwaters region near Raleigh, thus emphasizing the strong effect meteorology has on estuarine primary production (Mallin et al. 1993). During periods of heavy rainfall, usually in winter or early spring, the normal nutrient-filtering capability of the Neuse Estuary is overloaded and elevated concentrations of nitrate reach the lower estuary. These excess nutrients support algal blooms, particularly the dinoflagellate *Heterocapsa triquetra* in winter, and cryptomonads and the dinoflagellate *Prorocentrum minimum* in spring (Mallin et al. 1991; Mallin et al. 1993). The winter blooms occur less frequently in this system than in the Pamlico River Estuary but still can be expected on average once every 2 yr. Thus, this estuary can be either mesotrophic or eutrophic, with annual volumetric primary production ranging between 60 g C m^{-3} yr^{-1} and 120 g C m^{-3} yr^{-1}, depending on annual meteorological and hydrological conditions.

The Cape Fear River Estuary

The Cape Fear River Estuary is the outlet for the largest and most heavily industrialized river basin in North Carolina (drainage area 23,300 km^2). This estuary differs from the Neuse and Pamlico systems in that it is open to the sea rather than to a more protected sound (Fig. 1). It is also more heavily colored by humic materials than the other two large riverine estuaries. Carpenter (1971b) studied phytoplankton community structure and densities monthly for a year (1969–1970) at three stations over an 8 km stretch near the estuary mouth (just offshore, estuary mouth, and upstream in mesohaline waters). Diatoms dominated species richness with 134 taxa, green algae were second with 25 taxa, and dinoflagellates third with 15. The river mouth station yielded the greatest number of taxa, with diatoms increasing downriver and chlorophytes increasing upriver. Total cell densities increased downriver with yearly mean densities of 2,100 ml^{-1} at the ocean, 1,990 ml^{-1} at the river mouth, and 1,500 ml^{-1} upriver. The overall estuarine yearly mean abundance was similar to that of the Neuse (Table 1). There was a late spring bloom from May through June that was dominated by the diatom *Skeletonema costatum* (5,500 ml^{-1} in June at the ocean station). This was the most important species throughout the study, also blooming in fall and contributing 28.7% of the phytoplankton cells over the study. Other common diatoms were *Asterionella japonica* and *Thalassiosira nana,* which were abundant in late winter and spring. Diatom densities were greatest in the ocean and at the river mouth. The dinoflagellate *Katodinium rotundatum* was abundant May–June with about 250 cell ml^{-1}, and the cryptomonad *Rhodomonas (Chroomonas) amphioxiae* was important all year and peaked April–July with about 270 ml^{-1}. Another phytoplankton survey performed between 1971 and 1976 was related to the start-up of a nuclear power plant drawing cooling water from the estuary (Birkhead et al. 1979). This study concluded that start-up operations did not significantly alter cell densities in the estuary.

Nitrate levels in the oligohaline part of the Cape Fear Estuary are similar to or greater than those in the Neuse and Pamlico estuaries, but phosphate levels are lower (Stanley 1987; Christian et al. 1991; EA Engineering 1991). The Cape Fear has not been visibly afflicted by blue-green algal surface-bloom formation. A study of phytoplankton ecology in these heavily stained waters could provide valuable ecological insights in the study of eutrophication. With its open connection to the sea, this large estuary could be a productive area for the study of river-shelf interactions.

Gales Creek

Gales Creek is a small (<1 km^2) estuary that flows into Bogue Sound about 20 km southwest of Beaufort. The salinities range is 0–35‰ and there is often pronounced salinity stratification in the upper reaches. Campbell (1973) described the phytoplankton community of this estuary, along with a detailed taxonomic key of the phytoflagellates, including 32 newly described species. Chlorophyll *a* ranged from undetectable to 18.7 $\mu g\ l^{-1}$, with a low in December, a small peak in February, a rise to the major peak in August, and then a decrease through the rest of the year. The diatom community exhibited spring and fall peaks, with *Skeletonema costatum* the most important taxa numerically. Important spring species were *S. costatum, Chaetocerus lorenzianus, C. teres,* and *Melosira* spp., in summer *Coscinodiscus granii,* and in fall *Chaetocerus curvicetus* (Table 4). The phytoflagellates (from nine classes) were dominant in terms of cell density in all seasons except for brief spring and fall periods (diatoms). There was a moderate summer pulse, a late summer peak, and an autumn pulse. Dinoflagellates contributed the most species (76), followed by the cryptomonads (12). The middle of the estuary, or mixing basin, contained the most species overall as well as the highest cell densities. The most important phytoflagellate was *Olisthodiscus carterae* (spring–summer), which reached a peak of 8,000 ml^{-1}. Other important phytoflagellates were *Prorocentrum minimum* (spring), *Katodinium rotundatum* and *Calycomonas ovalis* (summer–fall), and *Heterocapsa triquetra* (winter). The estuary was described as having low densities overall because of a high flushing rate and low nitrogen input (Campbell 1973).

Campbell (1973) emphasized the abundance of the more delicate phytoflagellates, which are destroyed by preservatives but are visible in live samples. It is important to note that almost all of the taxonomic analyses discussed in this estuarine phytoplankton review (including the author's) were done using preserved and/or membrane-filtered samples. As suggested, this treatment may have distorted or destroyed delicate flagellates, possibly leading to underestimates of their abundance. Recent research by Burkholder (1992) indicated that many cryptic dinoflagellates have been overlooked in turbid freshwater systems. Whereas time constraints usually require that samples be preserved for later analysis, a cursory examination of live material is strongly recommended to determine which organisms were originally present.

The Chowan River

The lower reaches of the Chowan River have experienced algal bloom problems in recent years. The upper reaches of the river are characterized by motile unicells and colonies, while the lower river is characterized primarily by summer scum-forming blue-green algae (*Anabaena circinalis, A. aequalis, A. wisconsinense, Microcystis firma,* and *Aphanizomenon flos-aquae*). Subsurface blooms are also formed in summer by *Peridinium* sp. and in winter by *Melosira* sp. (Witherspoon et al. 1979). In 1980 chlorophyll *a* ranged from undetectable to 67 $\mu g\ l^{-1}$, with 67 $\mu g\ l^{-1}$ occurring during the summer blue-green bloom (Kuenzler et al. 1982). In 1981 there was no summer bloom and chlorophyll *a* reached 32 $\mu g\ l^{-1}$.

Nutrient limitation studies were conducted using both the alga *Selenastrum capricornutum* and natural river populations as test organisms (Sauer and Kuenzler 1981). Phosphorus (as orthophosphate) and nitrogen (as nitrate) both limited growth in most experiments; other nutrients did not. However phosphate alone limited growth of nitrogen-fixing blue-greens; therefore P was thought to be more critical to bloom formation. Natural populations provided better information than *S. capricornutum* alone in these experiments. Nitrate, phosphate, and ammonium concentrations were higher in the water column in winter and early spring when discharged in pulp-mill effluent, but concentrations decreased in the warmer seasons due to uptake when algal growth was rapid (Kuenzler et al. 1982). Kuenzler et al. (1982) suggested that although N and P were abundant in the sediments the ultimate cause of the eutrophic conditions was watershed input of nutrients. However, nutrient cycling in the river is important to maintaining algal blooms in the following manner: the high algal productivity during summer is dependent upon release and regeneration of nutrients from organic matter and from the sediments where they were stored during high inflow during the winter (Stanley and Hobbie 1981). In winter, dissolved inorganic nitrogen inflow exceeds uptake by a factor of 12, and in summer uptake of DIN exceeds inflow by a factor of 75. The amount of nutrient input in winter determines the size of the spring bloom. This bloom then decays and sinks to the bottom, adding to the organic content at the sediments and increasing BOD. During summer this causes near anoxic conditions at the sediments which release phosphate into the overlying waters to feed the summer blue-green bloom (Paerl 1982).

Pulp mill effluents also possibly contribute to blue-green algal blooms by restricting growth of other algae such as greens and diatoms (Paerl 1982). Chelation of trace metals by humic substances in the water may affect blue-green algae less than other groups, and light attenuation by the colored water will give a competitive advantage to surface scum-forming blue-greens. Physical factors such as sluggish water (increasing residence time) and stratification (leading to hypolimnetic anoxia) are important factors contributing to bloom formation. The downstream extent of these blooms is limited by salinity of approximately 1‰ (Paerl 1982). Blooms of *Aphanizomenon flos-aquae* are apparently more salinity-tolerant in the Baltic Sea, where they occur in waters up to 20‰ (Graneli et al. 1990).

In the summer of 1981, drought conditions forced saline water from Albemarle Sound upriver, which was an important factor limiting bloom formation during that year. Thus nutrient input, internal cycling, and hydrological conditions are all important factors in the formation and maintenance of algal bloom formation in the lower Chowan River. As of summer–fall 1993, the blooms (dominated by *Anabaena* spp.) were still occurring in this large coastal river.

The Lower Neuse River

The Neuse River, feeding southern Pamlico Sound, has also experienced severe algal bloom problems at times. The main nuisance alga has been the colonial blue-green alga *Microcystis aeruginosa* (Paerl 1983; Christian et al. 1986). The lower river is nutrient-rich, but blooms have only occurred in certain years. Excessive nitrogen and phosphorus loading combined with low summer flow caused bloom formation in 1981. In 1982 high river flow velocities stopped bloom formation despite high nutrient loading (Paerl 1983). During 1982 cell densities downstream in the lower river ranged from 200 ml^{-1} to 50,000 ml^{-1}, with highest densities in early fall. The flora was diverse and dominated by diatoms, green algae, and dinoflagellates. Chlorophyll *a* ranged from 1 $\mu g\ l^{-1}$ 24 $\mu g\ l^{-1}$, with an outlying October peak of 60 $\mu g\ l^{-1}$. Stanley (1983) detected high ammonification rates and stated that recycling of DIN was more than adequate to supply the needs of the phytoplankton during 1982.

In 1983 blue-green algae again bloomed, with chlorophyll *a* (mainly *M. aeruginosa*) peaking at 1,700 $\mu g\ l^{-1}$ at Kinston and then declining upstream of New Bern (Stanley 1983). Below New Bern high biomass (30–50 $\mu g\ l^{-1}$) of other algae occurred, perhaps from nutrient remineralization from the decaying blue-green algal bloom.

A modeling effort (May 1979–July 1985) concluded that river flow was the factor controlling bloom formation, and flows greater than 500 cfs impeded bloom establishment (Christian et al. 1986). High flow increases the flow-through of nutrients downstream, increases turbulence, and decreases water clarity, none of which favor blue-green bloom development (Stanley and Christian 1984). Paerl (1987), who reviewed several years worth of algal bloom data on the lower Neuse, agreed that optimal bloom conditions required low summer flow. However, in 1985 and 1986 there were low summer flows but blooms did not develop. Paerl suggested that drought conditions in spring caused less nutrient loading, and bloom formation did not occur because less nitrogen was available for summer recycling and bloom maintenance. Bioassays demonstrated that nitrate availability controlled the magnitude of primary productivity and blue-green bloom formation, but controlling N input alone without P controls could lead to bloom formation of nitrogen-fixing algae, as in the Chowan. Therefore Paerl (1987) recommended a 30% reduction in N inputs coupled with a 50% P reduction to control bloom formation. In summary, nutrient loading, timing of drought conditions, and flow rates all have affected the formation and magnitude of *Microcystis aeruginosa* blooms in the lower Neuse River. The *Microcystis* blooms have been ultimately constrained by salinity (about 1‰) to the area upstream of New Bern (Paerl et al. 1984), similar to the salinity range limiting *M. aeruginosa* blooms in the Potomac River (Sellner et al. 1988). As of the late 1980s and early 1990s, reported nuisance blue-green blooms in the upper Neuse River may have decreased (North Carolina Department of Environment, Health and Natural Resources unpublished data). There have been no in-depth studies in the bloom area since Paerl (1987), so the reason for the decline is unknown. A reservoir was filled in the headwaters in the mid-1980s (Falls of the Neuse Reservoir), so nutrient trapping may be a factor. However, nutrient pulses and winter–spring blooms continue to be a common occurrence in the estuary (Mallin et al. 1993).

Fulton and Paerl (1987a, b) investigated the effect of Neuse River *M. aeruginosa* bloom formation on associated zooplankton species. Strains of *M. aeruginosa* were either toxic or poorly nutritious, and inhibitory to the feeding of several of zooplankton taxa. There were a variety of strategies permitting zooplankton to coexist with *M. aeruginosa* in the blooms. Copepods avoid consumption of *M. aeruginosa,* perhaps by chemosensory means. A group of obligate herbivores (represented by *Diaphanosoma brachyurum*) consume little *M. aeruginosa* in colonial morphology, thereby ingesting little toxin. Their clearance rates on other more nutritious algae are unaffected by the blue-green algae. Another group (represented by *Brachionus calyciflorus* and *Bosmina longirostris*) do consume substantial amounts of colonial *M. aeruginosa* but must be able to better utilize this alga as a nutrition source or have greater tolerance to its toxic effects to succeed during blooms.

Toxic Phytoplankton

Until recently, no documented fish kills in North Carolina estuarine waters were directly attributed to toxic phytoplankton blooms. In November 1987, however, a filament of the Gulf Stream entered North Carolina coastal waters in Onslow Bay, bringing with it elevated numbers of the toxic dinoflagellate *Gymnodinium breve* (formerly *Ptychodiscus brevis*). The bloom had evidently originated off the Gulf Coast in August and was carried in the warm waters of the Gulf Stream around Florida and up the east coast into North Carolina waters (Tester et al. 1991). The unseasonably warm water and stable water-column conditions allowed the bloom to proliferate in coastal and estuarine waters in salinities as low as 25‰. The economic impacts—losses to the commercial fisheries of approximately $26 million (Tester and Fowler 1990)—resulted in the North Carolina coast being designated a national disaster area. While generally the principal problem with *G. breve* is bioaccumulation in shellfish and subsequent sickness in humans, it apparently also caused direct toxicity to and reproductive failure of the bay scallop (Summerson and Peterson 1990). In grazing experiments, it was noted that copepods would ingest *G. breve* without physiological harm, but given a choice, they preferentially ingested the nontoxic *Skeletonema costatum* and avoided ingesting *G. breve* (Turner and Tester 1989). The *G. breve* bloom dissipated from North Carolina waters by March 1988.

In 1988 a new toxic dinoflagellate was discovered, which is believed to be responsible for a large percentage of the heretofore unexplained estuarine fish kills in North Carolina (Burkholder et al. 1992). The organism, *Pfiesteria piscicida* (gen. & sp. nov.; Steidinger et al. unpublished data) was accidentaly introduced along with estuarine water into fish tanks at the North Carolina State University Veterinary School, causing kills in cultures. It was isolated and used in controlled experiments where it caused fish kills. Samples taken at approximately 30% of the estuarine fish kills contained abundant toxic stages of *P. piscicida* (gen. & sp. nov.). In laboratory bioassays this alga proved toxic to a wide variety of fish species, with strongest toxicity in warm water (>25°C) and salinity of 15‰ (Burkholder et al. 1992).

Recent experiments point toward a positive relationship between *P. piscicida* (gen. & sp. nov.) abundance and water-column phosphate concentration (Burkholder et al. 1993). The area suffering most frequently from fish kills is the mesohaline section of the Pamlico River Estuary, adjacent to a large phosphate mining industry that has discharged high phosphate concentrations into the estuary for many years (Copeland et al. 1984; Kuenzler et al. 1984). The presence of this organism has also been confirmed in other east coast locations, including the Chesapeake and Delaware bays and South Carolina (Burkholder et al. 1993). Investigation of the nutritional ecology, behavior, and food-web interactions of *P. piscicida* (gen. & sp. nov.) will be essential to help control the devastating estuarine fish and shellfish kills in North Carolina and other areas. Because of cultural eutrophication and the ease of dispersal of toxic dinoflagellates in recent years (Smayda 1990; Hallegraeff 1993), research concerning *P. piscicida* (gen. & sp. nov.) is likely to have broad geographical implications.

A third species reportedly caused a kill of baitfish in the Currituck, Albemarle Sound area in September 1992 (P. Tester personal communication). The dinoflagellate *Cochlodinium heterolobatum* displayed a minor bloom in Chesapeake Bay, and was subsequently carried south by currents into North Carolina coastal waters, where it reached densities of 67,000 cells ml^{-1}.

The recent increase in fish kills attributed to toxic phytoplankton in North Carolina may be a result of improved reporting and investigative methods. Alternatively, it may be a result of a general increase in anthropogenic nutrient loading from terrestrial and atmospheric sources. Long-term nutrient loading has been suggested as a cause for a general worldwide increase in toxic algal bloom events (Paerl et al. 1990b; Smayda 1990).

Summary and Synthesis

Meteorology, Hydrology, and Algal Blooms

Patterns of estuarine phytoplankton productivity and algal biomass in temperate estuaries have often been noted to rise and fall with water temperature and day length (Williams 1972; Day et al. 1989). In North Carolina the various estuaries generally displayed this basic response. However, in some of these systems an even more pronounced response was controlled by meteorology and hydrology. The riverine estuaries studied often displayed the largest blooms and productivity peaks in winter or spring, depending on magnitude of winter rainfall and the subsequent flushing of nutrients into the lower estuary. The importance of runoff to estuarine biotic response has also been recognized elsewhere recently (Malone et al. 1988; Jordan et al. 1991; Gallegos et al. 1992). Collectively these data indicate that primary productivity studies in temperate estuaries need to include regular assessments in winter as well as during the typical growing season because meteorologically forced, cold-weather algal blooms can account for a considerable portion of a system's annual primary production.

Thus, while there is a consistent, temperature-driven seasonal effect, meteorology and hydrology control ultimate annual production and biomass in riverine estuaries. Winters of elevated watershed rainfall and subsequent runoff are important to both the formation and maintenance of summer blue-green algal blooms in the large coastal plain rivers, as well as formation of winter–spring flagellate blooms downstream in the mesohaline lower estuaries. Elevated watershed rainfall in winter causes nutrient loading, which, after a lag time, stimulates the estuarine winter blooms (Mallin et al. 1993). The magnitude of winter and spring nutrient loading is also crucial to blue-green algal bloom formation and maintenance in North Carolina rivers by providing a nutrient reservoir in the sediments for summer recycling. Summer blue-green algal blooms are additionally dependent upon meteorology in that low flow is essential to their formation, whereas summers of high flow restrict bloom formation. In future studies, the considerable impact that watershed rainfall and runoff have on riverine and estuarine phytoplankton dynamics should be viewed from an ecosystems or river-continuum perspective.

All of the rivers estuaries examined in this review are anthropogenically impacted to a considerable degree. The hydrology–productivity relationship in unimpacted or oligotrophic systems may not be as robust, if present.

The riverine estuaries, with the most freshwater (and associated nutrient) input, were generally much more productive than the coastal sound areas. In the Beaufort area, highest phytoplankton productivity was found in the upper estuaries most influenced by freshwater, and least in the most marine-influenced sound areas. Regular tidal flushing in the sounds likely contributes to reduced nutrient concentrations and primary productivity relative to the riverine estuaries, where nutrient levels and productivity are more dependent upon meteorological and hydrological forcing. Phytoplankton dynamics in the euhaline sounds are thus controlled mainly by seasonal, temperature-driven patterns. Calico Creek, although a tidal system, receives a considerable volume of wastewater plant effluent and maintains cell densities and volumetric primary productivity rates far exceeding those of the surrounding area. Finally, it should be reiterated that very little is known about the phytoplankton dynamics of the largest North Carolina sounds (Albemarle, Currituck, and Pamlico). Much of the area encompassed by these sounds is remote and far from laboratory facilities and comprehensive studies would likely require major research efforts.

Limiting Factors for Primary Productivity

Light is believed to be limiting to phytoplankton growth in some estuaries due to their often turbid nature (Cloern 1987; Randall and Day 1987). In North Carolina, this may occur at times in upstream fresh to oligohaline sections of riverine estuaries, where both nutrients and turbidity are high. Under the moderately turbid conditions found in meso-to-euhaline estuaries in North Carolina, water-column mixing is likely sufficient to overcome light limitation (Mallin and Paerl 1992).

Bioassays indicated that the riverine estuaries studied (the Neuse and the Pamlico) were both primarily limited by nitrogen. Internal cycling of this nutrient was considered to be important in the riverine systems. The Pamlico is phosphate-rich year-round due to phosphate mining activities, but the Neuse is co-limited by phosphorus in spring when the freshet brings nitrate-rich water from farm fertilization into the system. In the Beaufort-Morehead City area estuaries, nitrogen was always limiting and phosphorus was occasionally co-limiting. Many estuarine systems throughout the world are likewise nitrogen-limited, either seasonally or year-round (D'Elia et al. 1986; Howarth 1988; Graneli et al. 1990; Fisher et al. 1992). In North Carolina, nitrogen limitation was prevalent across a trophic gradient of highly productive (Pamlico), moderately productive (Neuse), and much less productive systems (Beaufort, Morehead City area).

Taxonomic Considerations

Salinity, season, and nutrient loading are all essential elements in the establishment of dominant phytoplankton taxa. On a regional basis, diatoms dominated more saline areas, and *Skeletonema cos-*

tatum was particularly abundant in the most saline-influenced areas (25–35‰), such as the Beaufort-Morehead City area sounds and the lower Cape Fear Estuary. This diatom was mainly present during spring and fall. Other abundant and widespread diatoms included *Thalassiosira* spp., *Chaetocerus* spp., *Melosira* spp., and *Nitzschia* spp., but these taxa displayed less clear-cut seasonal signals. These diatoms were also less predictable because they often displayed community dominance regardless of ambient nutrient concentrations. Flagellates dominated under mesohaline conditions, and cryptomonads (including *Cryptomonas testaceae, Chroomonas amphioxiae,* and *C. minuta*) were present during most of the year. However, blooms of these taxa were stimulated by freshwater inflow, particularly during spring and fall.

Statewide, the most abundant dinoflagellates were the bloom-formers *Heterocapsa triquetra, Prorocentrum minimum, Katodinium rotundatum,* and *Gymnodinium* spp. Blooms of these species are also common in the Chesapeake Bay system (Sellner 1987). These species form a distinct winter–spring group encountered in several of the North Carolina estuaries, primarily in mesohaline riverine areas. While normally present in low numbers during this period of the year, their abundance is generally indicative of a nutrient (nitrate) pulse into the estuary. They appear to follow a strict seasonality and are rarely abundant outside of the cooler months. For example, in the Neuse Estuary during January and February 1990, high nitrate loading caused an *H. triquetra* bloom. In March, this bloom was replaced by a *Thalassiosira–Cyclotella* bloom of similar cell densities, possibly responding to a seasonal signal or decreased nitrate loading (Mallin 1992).

Thus, episodes of nitrate loading are likely to produce mesohaline blooms, dinoflagellate-dominated in winter and cryptophyte-dominated in spring or fall. Centric diatoms also form blooms during periods other than winter, but the appropriate salinity and nutrient status required by these blooms is unclear.

Regarding other taxa, the chrysophyte *Calycomonas ovalis,* a small flagellate, was abundant in the Pamlico Estuary, South Creek, and Gales Creek, and blooms were noted primarily during summer and fall. Summer is normally a period of low flow, high salinity, and the most severe nitrogen limitation (Christian et al. 1991; Rudek et al. 1991). Green algae were encountered more frequently upstream in the fresh-to-oligohaline areas, and flagellated forms were abundant in mesohaline regions mainly during late fall and winter. Yearly mean phytoplankton cell densities were surprisingly similar among the Neuse, Cape Fear, and Beaufort area estuaries, given that primary productivity and chlorophyll levels in the Neuse were considerably higher than in the Beaufort-Morehead City systems.

The foodweb contributions of these phytoplankton assemblages should be a valuable area of research concerning trophic interactions. However, little experimental work concerning zooplankton grazing and phytoplankton communities has been done in this region. The blue-green algae in the lower Neuse River are grazed rather poorly, and only by selected zooplankton taxa (Fulton and Paerl 1987a, b). In the lower estuary, the abundant phytoplankton taxa (centric diatoms and dinoflagellates) are generally consumed efficiently by the resident zooplankton. On average, approximately 43% of the daily phytoplankton primary production is grazed, mainly during warmer seasons (Mallin 1992; Mallin and Paerl 1994). In the Chesapeake Bay system, the winter–spring dominant calanoid copepod *Eurytemora affinis* grazes a portion of the dinoflagellate bloom (Sellner and Olsen 1985). In North Carolina, however, zooplankton abundance and grazing pressure is lowest during winter (Mallin 1992) and the contributions of the dinoflagellate blooms to benthic animal nutrition, system respiration, and bottom-water anoxia events are largely unknown.

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