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# Nutrient Changes in the Mississippi River and System Responses on the Adjacent Continental Shelf

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**ABSTRACT:** The Mississippi River system ranks among the world's top 10 rivers in freshwater and sediment inputs to the coastal ocean. The river contributes 90% of the freshwater loading to the Gulf of Mexico, and terminates amidst one of the United States' most productive fisheries regions and the location of the largest zone of hypoxia in the western Atlantic Ocean. Significant increases in riverine nutrient concentrations and loadings of nitrate and phosphorus and decreases in silicate have occurred this century, and have accelerated since 1950. Consequently, major alterations have occurred in the probable nutrient limitation and overall stoichiometric nutrient balance in the adjacent continental shelf system. Changes in the nutrient balances and reduction in riverine silica loading to the continental shelf appear to have led to phytoplankton species shifts offshore and to an increase in primary production. The phytoplankton community response, as indicated by long-term changes in biological uptake of silicate and accumulation of biologically bound silica in sediments, has shown how the system has responded to changes in riverine nutrient loadings. Indeed, the accumulation of biologically bound silica in sediments beneath the Mississippi River plume increased during the past two decades, presumably in response to increased nitrogen loading. The duration, size, and severity of hypoxia has probably increased as a consequence of the increased primary production. Management alternatives directed at water pollution issues within the Mississippi River watershed may have unintended and contrasting impacts on the coastal waters of the northern Gulf of Mexico.

## Introduction

There is a general consensus that the eutrophication of estuaries and enclosed coastal seas has increased over the last several decades. Evidence from the Baltic Sea, Kattegat, Skagerrak, and Dutch Wadden Sea suggests a long-term increase in the frequency of phytoplankton blooms, including noxious forms (Smayda 1990). Also, an increase in the areal extent and/or severity of hypoxia was observed, for example, in Chesapeake Bay (Officer et al. 1984), the northern Adriatic Sea

(Justić et al. 1987), and some areas of the Baltic Sea (e.g., Andersson and Rydberg 1988). The Mississippi and Atchafalaya rivers debouch onto a continental shelf that is relatively open compared to the more enclosed water bodies noted above, but the biological effects of increased riverine nutrient loads appear comparable to those seen of enclosed coasts.

Changes in riverine end-member nutrient concentrations and ratios may affect coastal ecosystems in several ways. One potential effect is to influence phytoplankton production rates. Significant increases in nutrient concentrations and loadings of nitrate and phosphorus and decreases in silicate

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have occurred in the Mississippi River this century, and have accelerated since 1950 (Turner and Rabalais 1991, 1994a). As a result, alterations have occurred in the relative composition of nutrients and in probable nutrient limitation in adjacent continental shelf waters (Justić et al. 1993, 1994, 1995a, b). If, indeed, silica is a nutrient limiting phytoplankton growth, a decrease in diatom abundance on the continental shelf could follow declining riverine silicate supplies. An increase in nitrate-nitrogen concentration, however, may allow for more efficient diatom growth at lower silicate concentrations. On the other hand, while the frequency of probable silica limitation has changed overall annually (Justić et al. 1994) or at certain times of the year (Dortch and Whitedge 1992), the production of diatoms may have remained unchanged or increased during spring, the critical period for carbon production and flux related to the formation of bottom water hypoxia (Qureshi 1995). Even if diatom production remains unchanged, increased nitrogen loading is likely to stimulate non-diatom algal production. A second possible effect involves a shift in phytoplankton community composition. Increased nitrogen and phosphorus concentrations will favor the growth of flagellates (Officer and Ryther 1980). In the case of nitrogen-limited coastal phytoplankton populations, nuisance blooms might develop as the silica:nitrogen atomic ratio approaches 1:1 (the Redfield ratio; Redfield 1958), as is in the case of the lower Mississippi River system (Turner and Rabalais 1991, 1994a). The combination of primary production changes and species shifts could affect subsequent carbon utilization, carbon flux, and the areal extent or severity of hypoxia on the continental shelf. The northern Gulf of Mexico adjacent to the outflows of the Mississippi and Atchafalaya rivers is the location of the largest zone of hypoxia in the western Atlantic Ocean (as great as 9,500 km<sup>2</sup> in summer; Rabalais et al. 1991, 1994a, b).

The effects of changes in riverine nitrogen, phosphorus, and silica fluxes to the continental shelf at the terminus of the Mississippi River is the focus of this synthesis. We provide background information on the Mississippi River discharge, the river's influence on the physical and chemical characteristics of the adjacent coastal waters, and important biological processes of the study area. We document changes in Mississippi River nutrient concentrations, loadings and ratios, and similar changes in nutrient properties of adjacent continental shelf waters. We then address biological responses to these nutrient alterations, including shifts in probable nutrient limitations for phytoplankton growth, shifts in phytoplankton community structure, phytoplankton production, and in-

dicators of eutrophication and increased oxygen stress.

### The Mississippi River System

The Mississippi River watershed, the largest in the United States, encompasses 41% of the area of the conterminous 48 states (Fig. 1). The Mississippi River ranks among the world's top 10 rivers in discharge (580 km<sup>3</sup> yr<sup>-1</sup>) and sediment yields (210 × 10<sup>6</sup> t yr<sup>-1</sup>) to the coastal ocean (Milliman and Meade 1983). Major alterations in the morphology of the main river channel and widespread landscape alterations in the watershed, along with anthropogenic additions of nitrogen and phosphorus, have resulted in dramatic water quality changes this century (Turner and Rabalais 1991).

The Mississippi and Atchafalaya rivers are the primary riverine sources of fresh water to the Louisiana continental shelf (Dinnel and Wiseman 1986) and to the Gulf of Mexico (90% of fresh-water inflow to the Gulf; National Oceanic and Atmospheric Administration 1987). One-third of the flow of the Mississippi River system enters the Gulf via the Atchafalaya River. Of the remaining discharge from the Mississippi River delta proper, approximately 53% flows westward onto the Louisiana shelf (United States Army Corps of Engineers 1974). The long-term peak flow occurs in April. Although flow is reduced in summer, large-scale circulation patterns often retain the fresh water on the shelf. Freshwater inflow from the Mississippi and Atchafalaya is a major feature of the Louisiana shelf, even though it is a fairly open system, and fresh water attributed to these rivers may be traced as far west as Port Aransas on the south Texas coast (Smith 1980) and as far east as the Atlantic seaboard, under combinations of major floods and appropriate oceanographic conditions (Atkinson and Wallace 1975; Tester and Atkinson 1994; Walker et al. 1994).

Within the northern Gulf of Mexico, the influence of the Mississippi and Atchafalaya outflows is evident in plots of surface salinity and Secchi disk values accumulated from numerous hydrographic cruises between 85°W (just east of Cape San Blas, Florida) to 95°W (just west of Galveston Bay, Texas) (Fig. 2). The influence of the freshwater input is more obvious to the west of the Mississippi delta (approximately 89°W) than to the east, with additional inputs near 91°W (the Atchafalaya delta). Plots of nutrient values (example given for silicate in Fig. 2) show a more pronounced decrease in concentration over an equal distance from the deltas when compared to the salinity plot. This indicates a nonconservative mixing due to biological uptake.

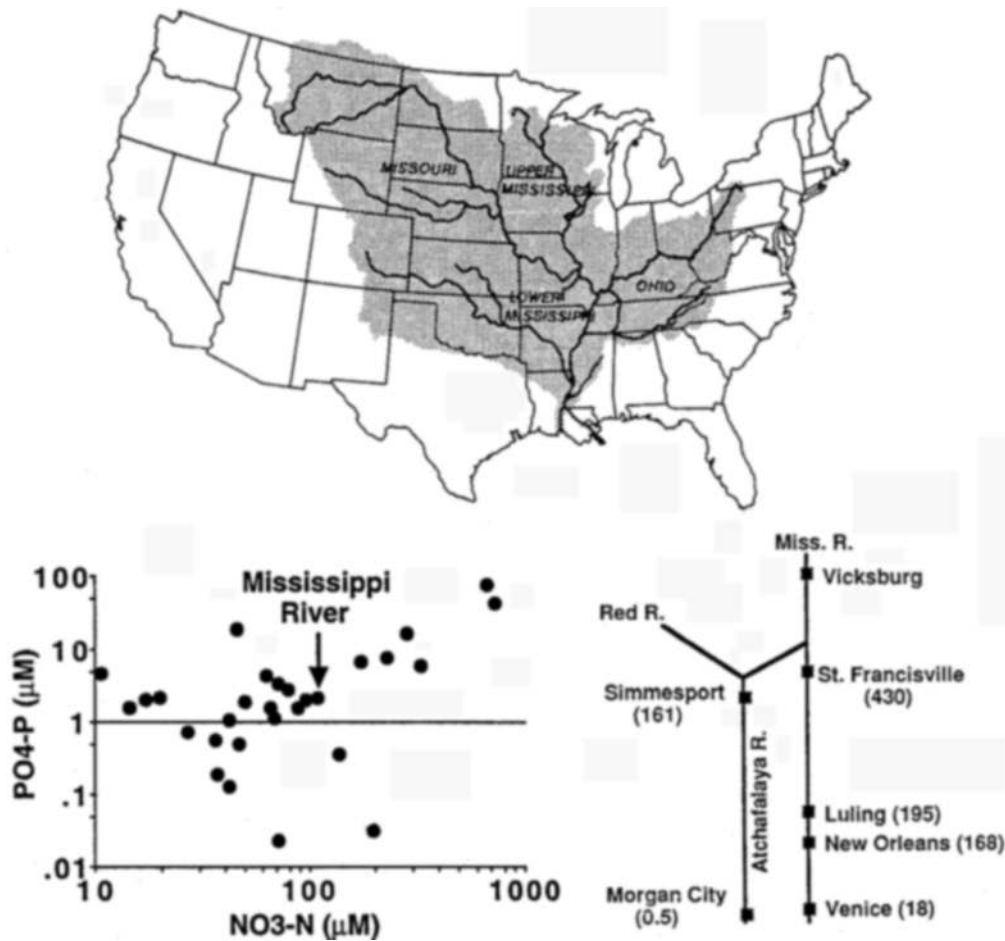


Fig. 1. Drainage of the Mississippi River (from Turner and Rabalais 1991); comparison of annual average N concentration and P concentration of major world rivers with the Mississippi (modified from Turner et al. 1990; Meybeck 1982); and schematic of sampling stations along the lower Mississippi River, with distance from the terminus (km) in parentheses (from Turner and Rabalais 1991).

### Adjacent Continental Shelf Hydrography

Freshwater discharge from the Mississippi and Atchafalaya rivers rapidly forms the Louisiana Coastal Current, a highly stratified coastal current that flows, on average, westward along the Louisiana coast and then southward along the Texas coast. At the beginning of the flood season, coastal winds are from the southeast. As spring progresses, the winds along the south Texas coast become favorable for upwelling and the local flow reverses and turns toward the north and east (Cochrane and Kelly 1986). This reversal has been documented as far east as Cameron, Louisiana ( $93^{\circ}20'W$ ), and inferred as far east as the Isles Dernieres ( $90^{\circ}50'W$ ) (Kimsey and Temple 1963, 1964).

Density stratification in the Louisiana Coastal Current, particularly near the two major freshwater sources, is due primarily to salinity. While the strongest haline stratification is associated with the Louisiana Coastal Current, a secondary pycnocline often

occurs and is best developed during the summer as a result of both the initial spring flood discharge, vernal warming, and return flow along the shelf break from the Texas shelf (Cochrane and Kelly 1986). This secondary, seasonal pycnocline resembles that observed near the Islay front (Hill and Simpson 1989). The summer hypoxia (see below) found in this region is capped by this seasonal pycnocline.

Strong wind events interact with the waters of the coastal current throughout the year. Intense wind mixing due to cold air outbreaks and frontal passages is active from as early as late September to as late as June. Local squalls and thunderstorms, as well as tropical storms and hurricanes, are important during the summer months (DiMego et al. 1976). These wind events often result in the complete homogenization of the water column (Wiseman et al. 1986). At other times, winds are not strong enough to fully break down the local strat-

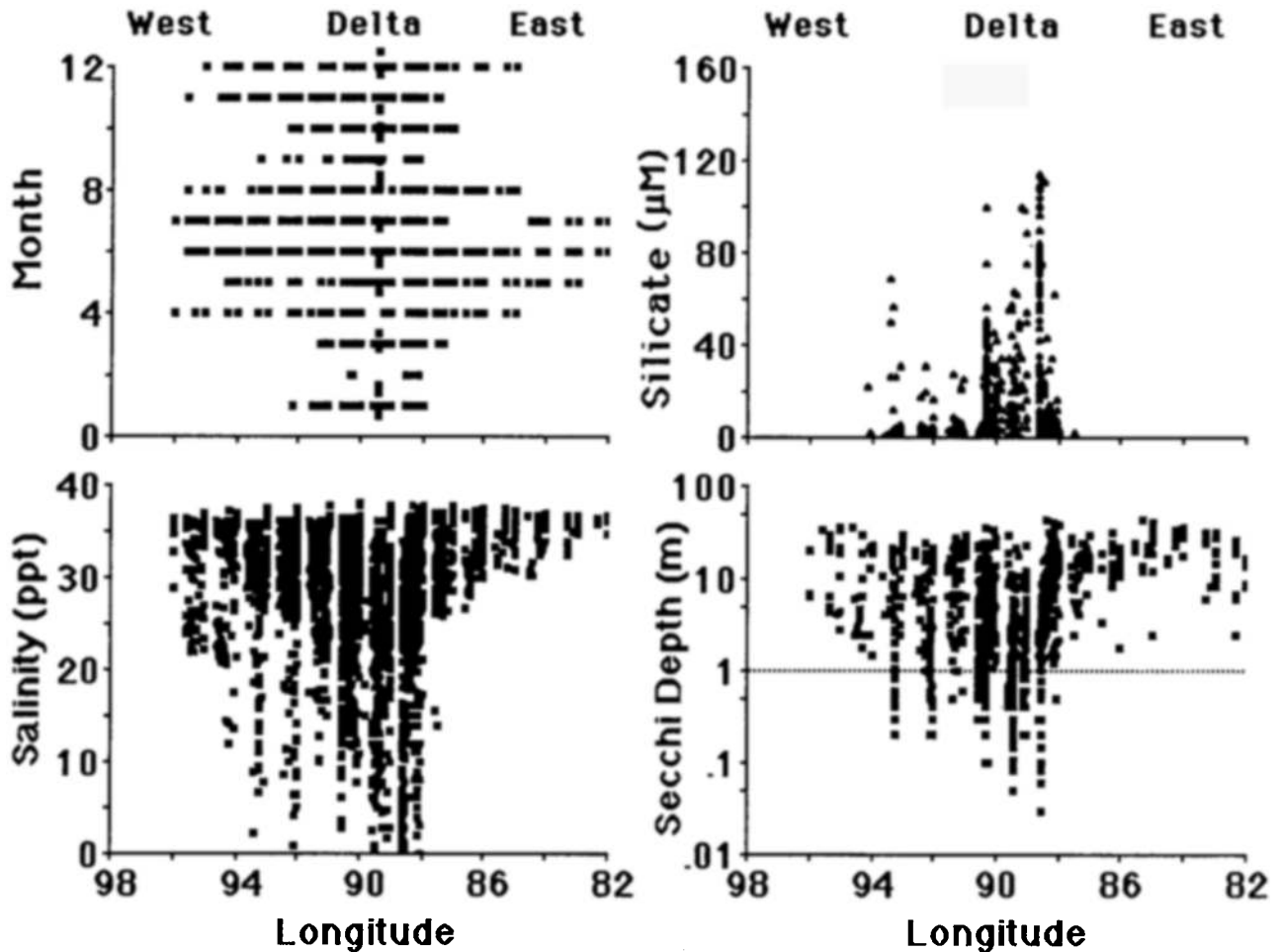


Fig. 2. Plots of surface salinity, Secchi disk depth, and silicate concentration from a series of hydrographic cruises in 10–100 m water depth for 1972–1991, for the months and longitudes indicated (R. E. Turner and N. N. Rabalais unpublished data).

ification, but they result in localized coastal upwelling, which alters the stratification (Dagg 1988).

The development and persistence of bottom water hypoxia is intimately linked to the temporal and spatial variability of the hydrographic properties. The strong persistent summer halocline prevents effective reoxygenation of deep waters from the upper layers. The fall destruction of the halocline by wind mixing and thermal cooling of surface waters heralds the termination of hypoxic conditions. The morphology of the hypoxic region is controlled by the structure of the secondary near-bottom pycnocline (Wiseman et al. unpublished data). The summer halocline associated with the Louisiana Coastal Current isolates near-bottom waters from direct wind forcing. This effect, in conjunction with the pressure gradients driving up-coast flow along the Texas inner shelf, results in slow-moving bottom waters over the Louisiana inner shelf. This allows biological processes,

described below, to deplete the oxygen content of the near-bottom waters.

#### Biological Processes

High biological productivity in the immediate ( $320 \text{ g C m}^{-2} \text{ yr}^{-1}$ , Lohrenz et al. 1990) and extended plume ( $290 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) of the Mississippi River (Sklar and Turner 1981) is mediated by high nutrient inputs and regeneration, and favorable light conditions. Small-scale, short-term variability in productivity is the consequence of various factors, such as nutrient concentrations, temperature, and salinity (Lohrenz et al. 1990, 1994), but on a seasonal time-scale it is most influenced by Mississippi River flow and nutrient flux to the system (Justić et al. 1993). “New” nutrients become depleted along the river-to-ocean mixing gradient through dilution and biological uptake, and regenerated nutrients support primary production for great distances from the river mouth (Dortch et al.

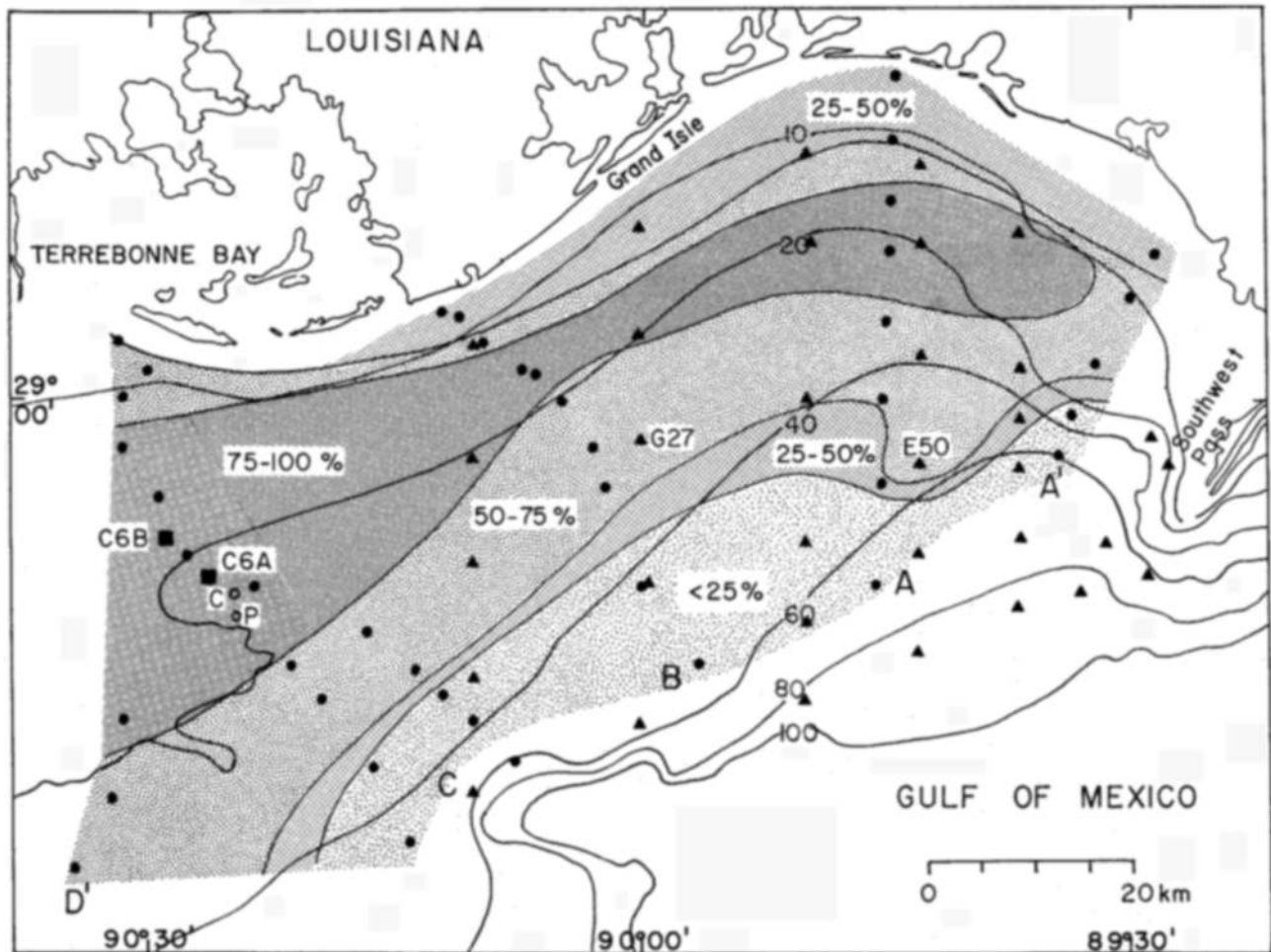


Fig. 3. Station locations within the Mississippi River bight for hypoxia monitoring on transects A'-D' (closed circles), mooring locations (C6A and C6B), LaSER stations (closed triangles, those referred to in text are labeled), and "Platform" and "Control" stations of Fucik (1974) and Ward et al. (1979) (open circles marked with "C" and "P"). Stippled intensity corresponds to frequency of occurrence of mid-summer hypoxia at monitoring stations (1985-1987, 1990-1993, N. N. Rabalais, R. E. Turner, and W. J. Wiseman, Jr. unpublished data).

1992a). Particulate organic carbon flux to the lower water column is high in the extended plume over the inner shelf (approximately  $500\text{--}600\text{ mg C m}^{-2}\text{ d}^{-1}$  in 15 m water depth; Qureshi 1995; see also Redalje et al. 1994). The fraction of production exported from the surface waters is highly variable and ranges from 10% to 200%, with the higher percentages in the spring. A large proportion of the particulate organic carbon flux reaches the bottom incorporated in zooplankton fecal pellets as well as individual cells or in cell aggregates.

There is great daily and weekly variability in current flow and stratification on the shelf and, therefore, no simple description of the couplings between carbon production in surface waters and delivery and recycling in bottom waters at this time scale. However, there is evidence of an ecological "signal" (couplings) amidst the "noise" (the vari-

ability) when more extensive datasets and longer time periods are examined (e.g., marine-origin phytoplankton pigments and biogenic silica in surficial sediments and Pb-210 dated sediment cores; Rabalais et al. 1992a; Turner and Rabalais 1994b). These couplings implicate changes in riverine nutrients and nutrient ratios (discussed below) with the overall effects on productivity, carbon accumulation at the seabed, and low oxygen conditions on this shelf.

Oxygen-depleted bottom waters are seasonally dominant features of the Louisiana continental shelf adjacent to the deltas of the Mississippi and Atchafalaya rivers (Rabalais et al. 1991, 1992b, 1994a, b). The areal extent of bottom-water hypoxia ( $\leq 2\text{ mg l}^{-1}$  dissolved oxygen) in mid-summer may cover as much as  $9,500\text{ km}^2$ , with the spatial configuration varying interannually (Fig. 3). Sam-

ples from a transect on the southeastern shelf and continuous time series data off Terrebonne Bay document hypoxic bottom waters as early as February and as late as October, with widespread, persistent, and severe hypoxia or anoxia from mid-May to mid-September. Spatial and temporal variability in the distribution of hypoxia exists and is, at least partially, related to the amplitude and phasing of the Mississippi River discharge (Rabalais et al. 1994a; Wiseman et al. unpublished data) and, consequently, to nutrient flux to the coastal waters and subsequent production and flux of carbon from surface waters to the lower water column and seabed.

Seasonal variations in net productivity in the northern Gulf of Mexico (as exemplified by stations C6A and C6B in Fig. 3) are coherent with the dynamics of freshwater discharge (Justić et al. 1993). The surface layer (0 m to 0.5 m) shows an oxygen surplus relative to the saturation values during February–July; the maximum occurs during April and May and coincides with the maximum flow of the Mississippi River. The bottom layer (approximately 20 m), on the contrary, exhibits an oxygen deficit throughout the year; it reaches its greatest deficit value in July. Bottom hypoxia in the northern Gulf is most pronounced during periods of high water-column stability when surface-to-bottom density differences are greatest (Rabalais et al. 1991, Wiseman et al. unpublished data). The correlation between Mississippi River flow and surface oxygen surplus is greatest with a time-lag of 1 mo, and the highest correlation for bottom oxygen deficit is with a time-lag of 2 mo (Justić et al. 1993). These findings suggest the oxygen surplus in the surface layer following high flow depends on nutrients ultimately coming from the river but regenerated many times. Annual mass balance calculations (Turner and Rabalais 1991; Dortch et al. 1992a) and N uptake measurements in the fall suggest every N atom is recycled approximately four times, although recycling may be less important in the spring (Dortch et al. 1992a). This is important because a surplus of oxygen relative to the saturation value is a good indicator of net productivity in the surface waters. An oxygen surplus also means there is an excess of organic matter derived from primary production that can be redistributed within the system; some of this will eventually reach the sediments. The development of summer hypoxia in the northern Gulf of Mexico (as exemplified by stations C6A and C6B, Fig. 3) is associated with the decay of organic matter accumulated during spring phytoplankton blooms (Qureshi 1995). These findings demonstrate a close coupling between riverborne nutrients, net productivity, and hypoxia, as well as implicate the effects of anthro-

pogenic nutrient loads on a coastal marine ecosystem.

### Methods

We present data mostly from published results, which provide the appropriate details of collection and analysis methods. In addition, we present two new syntheses: historical changes in phytoplankton species composition and in benthic foraminiferal communities. More detailed methods are provided for the latter two syntheses.

While the influence of the Mississippi and Atchafalaya rivers can be seen as far as the south Texas coast (Smith 1980), the northeastern Gulf, the south Florida region, and the United States East Coast (Walker et al. 1994 and references therein), we limit our discussion of consequences of riverine nutrient changes to the areas influenced by the immediate and extended plumes of the current birdfoot delta in the Mississippi River bight west to about 90°30'W (the entrance to Terrebonne Bay) (Fig. 3). The oceanographic data include the following: monitoring cruises conducted during the period 1985–1993, across the width of the Louisiana shelf, primarily in mid-summer (transects A' through D' in Fig. 3); data from the southeastern shelf off Terrebonne Bay on a biweekly to monthly basis in 1985–1986 and 1990–1993 (transect C in Fig. 3); more frequent sampling at an instrument mooring (stations C6A and C6B in Fig. 3); six cruises covering 10 m to 80 m water depth within the Mississippi River bight between 1987 and 1990 (i.e., LaSER stations in Fig. 3); and miscellaneous other cruises within the study area.

Standard water column profile data were obtained from a Hydrolab Surveyor II, Hydrolab Surveyor 3, or a SeaBird CTD system. All dissolved oxygen probes were calibrated and quality controlled with Winkler titrations; conductivity was calibrated by discrete measurements analyzed on an AutoSal salinometer. Nutrients were measured on a Technicon Auto Analyzer according to methods described in Parsons et al. (1984).

### Changes in Nutrients

#### LOWER MISSISSIPPI RIVER

Water quality data for the lower Mississippi River, previously elaborated by Turner and Rabalais (1991) and updated, were collected from stations at St. Francisville, Luling, New Orleans, and Venice (Fig. 1). The mean annual concentration of nitrate was approximately the same in 1905–1906 and 1933–1934 as in the 1950s, but it has doubled in the last 35 yr (Fig. 4). The mean annual concentration of silicate was approximately the same in 1905–1906 as in the early 1950s, then it declined by 50%. Concentrations of nitrate and silicate ap-



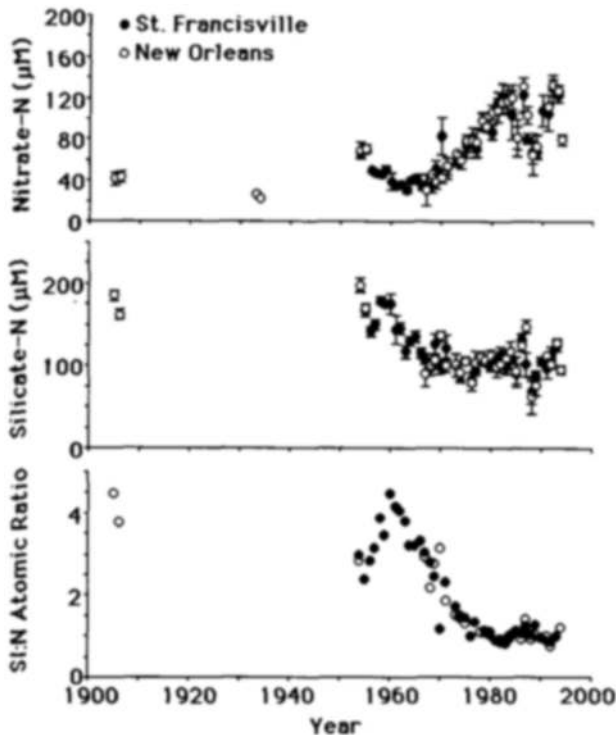


Fig. 4. Average annual concentrations of nitrate and silicate and Si:N ratio from 1905 through 1994 in lower Mississippi River for stations indicated (see Fig. 1) (modified and updated from Turner and Rabalais 1991, 1994a).

pear to have stabilized, but trends are masked by increased variability in the data from the 1980s and early 1990s. We found no substantial records of total phosphorus concentrations in the lower Mississippi River before 1972. Although the concentration of total phosphorus appears to have increased since 1972, variations among years are large.

The rise in nitrate since 1960 was coincidental with an increase in application of nitrogen fertilizer in the watershed sufficient to account for the changes in water quality (Turner and Rabalais 1991). The decrease in silicate since 1960 appears to be a consequence of upstream phosphorus additions that stimulated freshwater diatom production and an eventual burial in freshwater sediments of silica in diatom remains (e.g., Schelske and Stoermer 1971; Schelske et al. 1986), thus reducing the annual supply of riverine silicate to coastal waters.

The silicate:nitrate ratios have changed as the concentrations varied (Figs. 4 and 5). The silicate:nitrate atomic ratio was approximately 4:1 at the beginning of this century, dropped to 3:1 in 1950, and then rose to approximately 4.5:1 during the next 10 yr, before plummeting to 1:1 in the 1980s. The ratio appears stable (little variation) at 1:1 through 1994.

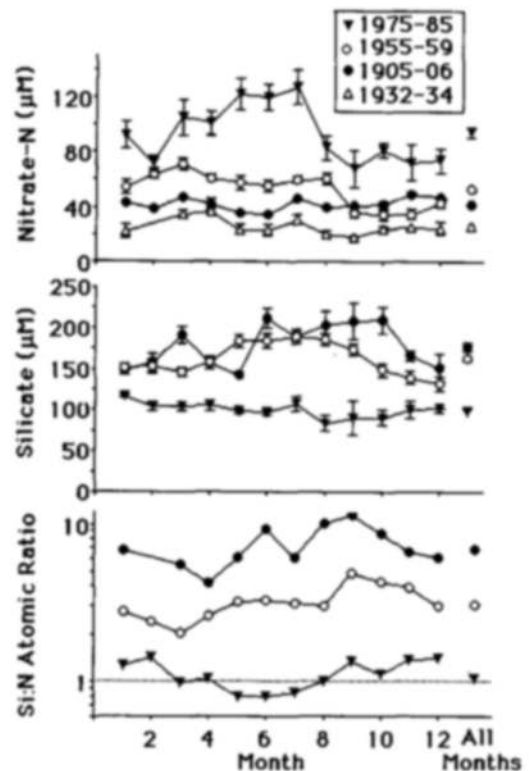


Fig. 5. Monthly average concentrations of nitrate and silicate, and Si:N ratio, in the lower Mississippi River for periods indicated (modified and updated from Turner and Rabalais 1991, 1994a).

The seasonal patterns in nitrate and silicate concentration have also changed during this century (Fig. 5). There was no pronounced peak in nitrate concentration earlier this century, whereas there were spring peaks from 1975 to 1985, presumably related to seasonal agricultural activities, timed with long-term peak river flow. A seasonal summer-fall maximum in silicate concentration, in contrast, is no longer evident (Fig. 5). Consequently the seasonal signal of silica:nitrogen atomic ratio has also changed. The seasonal shifts in nutrient concentrations and ratios become increasingly relevant in light of the close temporal coupling of river flow to surface water net productivity (1-mo lag) and subsequent bottom water oxygen deficiency (2-mo lag) described above.

The proportions of dissolved Si, N, and P in the lower Mississippi River have changed historically such that they now closely approximate the Redfield ratio (Si:N:P = 16:16:1; Fig. 6) (Justić et al. 1995 a, b). We compared the data for two periods: 1960–1962 and 1981–1987 (Table 1; data from Turner and Rabalais 1991). Substantial increases in N (300%) and P (200%) concentrations occurred over several decades, and Si decreased (50%). (No

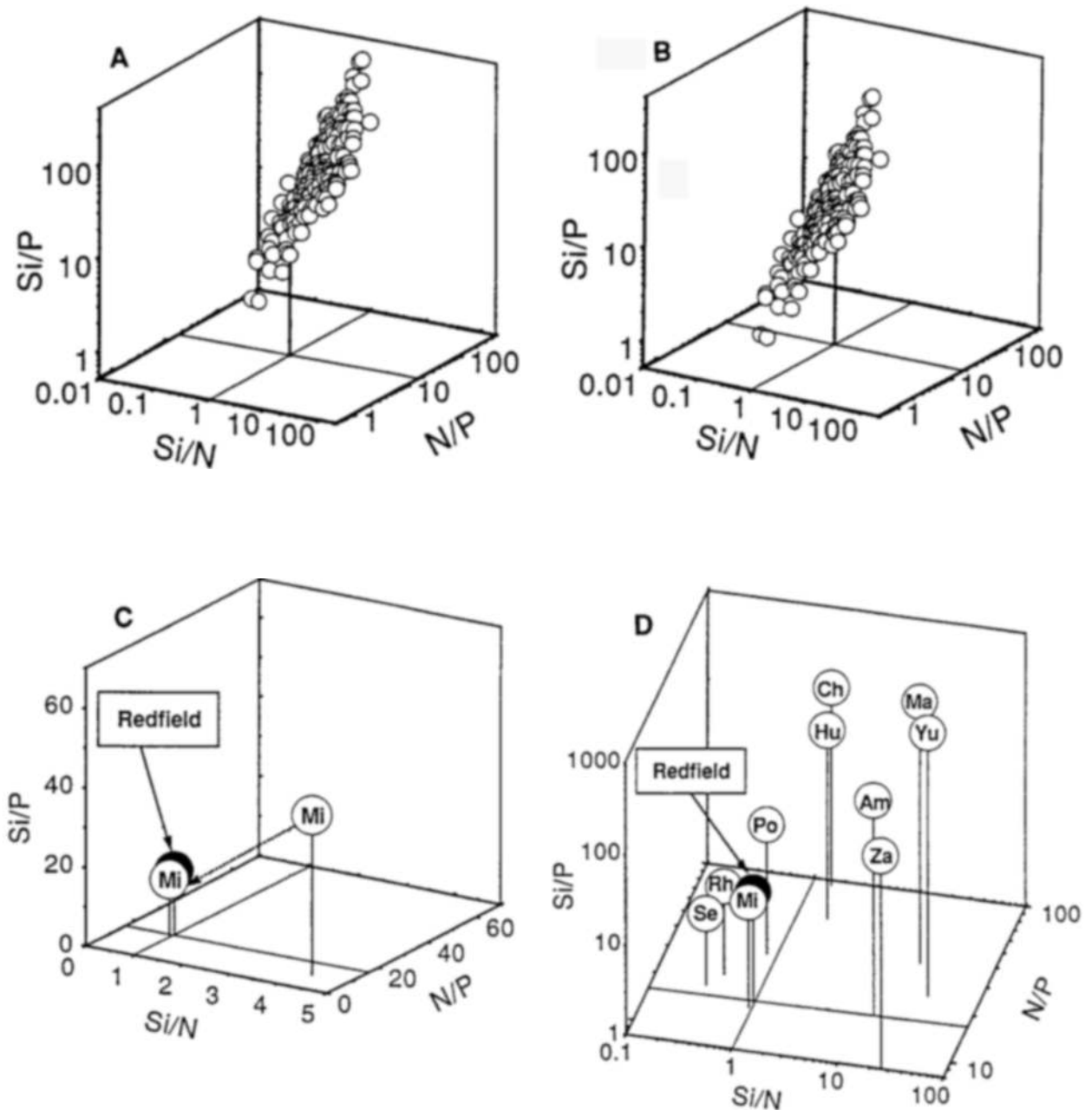


Fig. 6. Scatter diagrams of atomic ratios of dissolved inorganic nitrogen (N), reactive phosphorus (P), and reactive silica (Si) in surface waters of the northern Gulf of Mexico for (A) reconstructed data for 1960 and (B) ambient nutrient ratios during 1985–1991. Vertical bar indicates the Redfield ratio (Si:N:P = 16:16:1). (C) Shift in mean atomic ratio of nitrate-nitrogen (N), total phosphorus (P), and reactive silica (Si) in the Mississippi River (Mi) from 1960–1962 to 1981–1987. (D) Clustering of N, P, and Si in the Amazon (Am), Changjiang (Ch), Huanghe (Hu), Mackenzie (Ma), Mississippi (Mi), Po (Po), Rhine (Rh), Seine (Se), Yukon (Yu), and Zaire (Za) rivers. Data for the Mississippi River is in Table 1. (Modified from Justić et al. 1995a).

data on total P concentration in the Mississippi River were reported prior to 1973; however, total P in the river showed a moderate increase between 1973 and 1987. By applying a linear least-squares regression on the 1973–1987 data, we estimated ( $p < 0.01$ ) that the total P concentration increased

twofold between 1960–1962 and 1981–1987.) Accordingly, the Si:N ratio decreased from 4.2 to 0.9, the Si:P ratio decreased from 39.8 to 14, and the N:P ratio increased from 9 to 15. By applying the Redfield ratio as a criterion for stoichiometric nutrient balance, one can distinguish between P-de-

TABLE 1. Historical changes in concentrations ( $\mu\text{M}$ ) and atomic ratios of nitrogen (N), phosphorus (P) and silica (Si) in the lower Mississippi River and the northern Gulf of Mexico;  $\bar{x}$  = mean value, n = number of data, S = standard error,  $p < 0.001$  = highly significant difference in nutrient concentrations between the two periods, based on a two-sample *t*-test (modified from Justić et al. 1995b).

		Mississippi River		Northern Gulf of Mexico	
		1960–1962	1981–1987	1960 <sup>a</sup>	1985–1991
Nutrient concentration ( $\mu\text{M}$ ):					
N <sup>a</sup>	$\bar{x}$	36.5	114	2.23	8.13
	n	72	200	219	219
	S	2.9	6.0	0.16	0.60
		(p < 0.001)			
P <sup>b</sup>	$\bar{x}$	3.9	7.7	0.14	0.34
	n	—	234	231	231
	S	—	0.4	0.01	0.02
		(p < 0.001)			
Si <sup>c</sup>	$\bar{x}$	155.1	108	8.97	5.34
	n	72	71	235	235
	S	7.5	4.3	0.55	0.33
		(p < 0.001)			
Average atomic ratios:					
	Si:N	4.2	0.9	4.0	0.7
	N:P	9	15	16	24
	Si:P	39.8	14	64	16

<sup>a</sup> N-NO<sub>3</sub> for the Mississippi River, dissolved inorganic nitrogen (DIN = NO<sub>3</sub><sup>-</sup> + NH<sub>4</sub><sup>+</sup> + NO<sub>2</sub>) for the northern Gulf of Mexico.

<sup>b</sup> Total P for the Mississippi River, reactive P for the northern Gulf of Mexico.

<sup>c</sup> Reactive Si.

<sup>d</sup> Reconstructed data.

efficient, N-deficient, and Si-deficient rivers, and those having a well-balanced nutrient composition. The nutrient ratios for the Mississippi River (1981–1987 database) show an almost perfect coincidence with the Redfield ratio (Fig. 6). The proportions of Si, N, and P have changed over time in such a way that they now suggest a balanced nutrient composition.

#### ADJACENT CONTINENTAL SHELF

We analyzed extensive nutrient datasets from the northern Gulf of Mexico to examine how the coastal nutrient structure may reflect long-term changes in the proportions of dissolved Si, N, and P in riverine loads (Justić et al. 1994, 1995a, b). Reliable long-term datasets of the northern Gulf's nutrient composition 30 yr ago were not available, however. We reconstructed, therefore, the past

coastal nutrient composition by assuming that the relative proportion of nutrients in the river-dominated coastal waters reflects the changing composition of riverine nutrients (Table 1). This assumption was made in view of the fact that the Mississippi River is the most important nutrient source to the northern Gulf of Mexico. The detailed reconstruction procedure is given in Justić et al. (1995b). By calculating the specific rates of change for Si:N, Si:P, and N:P ratios in the Mississippi River, we obtained a reasonable estimation of coastal nutrient composition 30 yr ago. Comparison of the reconstructed data with the available historical nutrient data (Thomas and Simmons 1960; Turner and Rabalais 1994a) showed a reasonable agreement between the measured and the reconstructed nutrient ratios. A similar reconstruction technique for the northern Adriatic Sea produced results that closely paralleled the real data (Justić et al. 1995a, b).

Comparison of measured and reconstructed nutrient ratios for the northern Gulf adjacent to the Mississippi River outflow reveals long-term changes in proportions of nutrients in the surface waters (Justić et al. 1995a, b) (Fig. 6). The reconstructed nutrient ratios for 1960, on average, scatter further from the Redfield ratio (Si:N:P = 16:16:1; the center of the grid) than the recent data. By applying the Redfield ratio as a criterion for balanced nutrient composition, it appears that P and N deficiency have decreased while Si deficiency has increased. Equally important, recent nutrient ratios scatter very close to the Redfield ratio, suggesting an almost perfectly balanced nutrient composition.

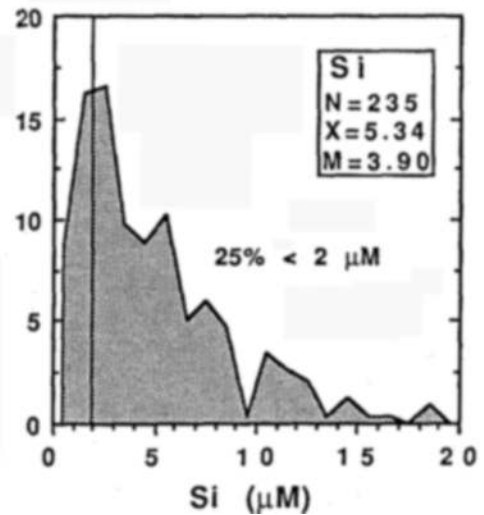
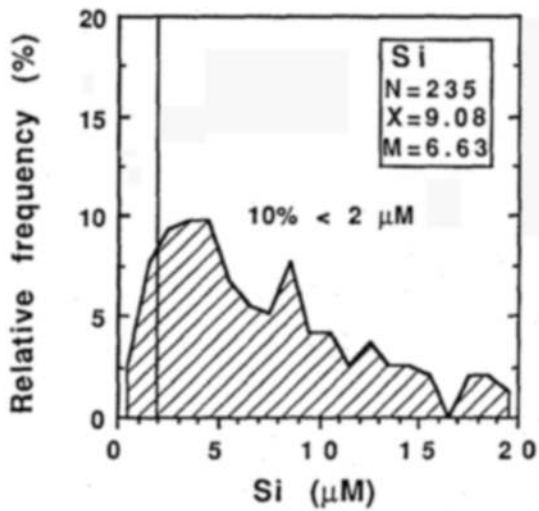
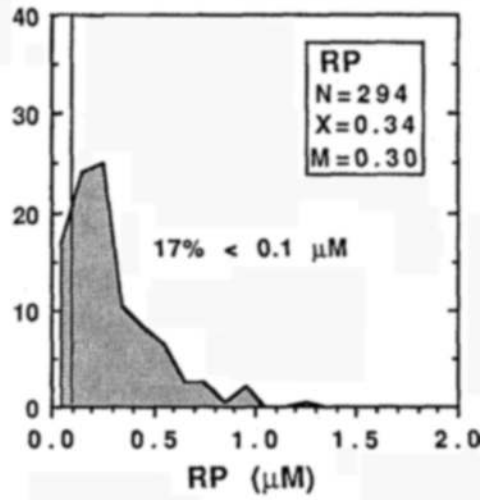
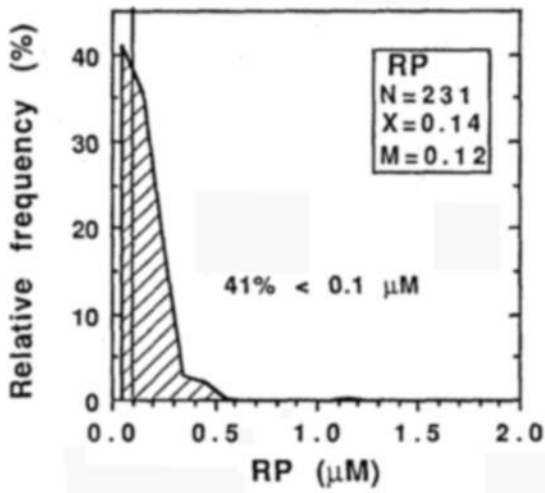
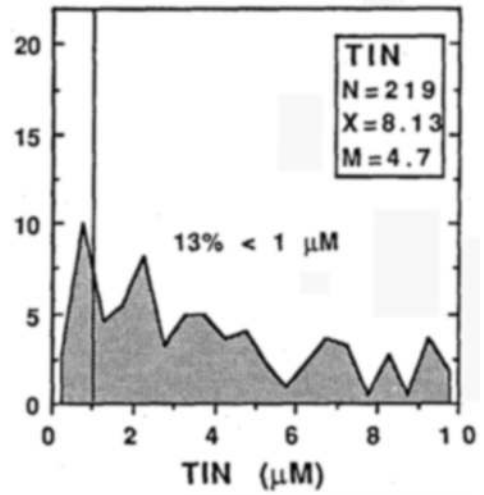
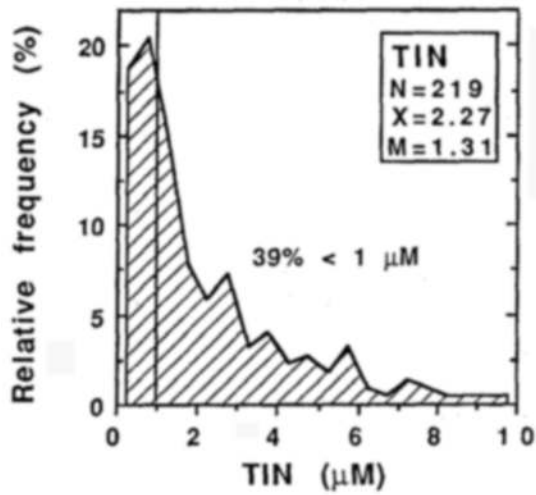
Probable nutrient limitation (Dortch and Whitledge 1992) was also assessed by comparing the ambient nutrient concentrations with the  $k_s$  for nutrient uptake and, in the case of Si, a threshold value for uptake. Plots of relative frequencies (Justić et al. 1994) (Fig. 7) show that dissolved N concentrations in the surface layer of the northern Gulf of Mexico during the period 1985–1992 were lower than 1  $\mu\text{M}$  in about 13% of the cases. Reactive P was below 0.1  $\mu\text{M}$  in 17% of the cases, and reactive Si concentrations lower than 2  $\mu\text{M}$  occurred in 25% of the cases. In contrast, the corresponding frequencies were 39%, 41%, and 10%, respectively, in 1960. These findings are important because studies of nutrient uptake kinetics (i.e.,

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Fig. 7. Relative frequency polygons showing temporal changes in surface nutrient structure of the northern Gulf of Mexico, assuming that the relative rates of change in nutrient concentrations over the intervening period were the same as in the Mississippi River ( $\Delta N = +8.0\%/yr$ ;  $\Delta P = +4.3\%/yr$ ;  $\Delta Si = -1.4\%/yr$ ); TIN = dissolved inorganic N, RP = reactive P, Si = reactive Si, N = number of data, X = mean value, M = median. Vertical lines indicate threshold values for nutrient uptake based on literature data from studies of phytoplankton uptake kinetics. (From Justić et al. 1994).

1960

1985-1991



Rhee 1973; Harrison et al. 1977; Goldman and Gilbert 1983; Nelson and Brzezinski 1990) indicate that concentrations of 1  $\mu\text{M}$ , 0.1  $\mu\text{M}$ , and 2  $\mu\text{M}$  may be considered as threshold values for N, P, and Si uptake, respectively. Thus, it appears that overall nutrient limitation has decreased.

Changes in riverine nutrient loads and nutrient ratios may affect coastal phytoplankton communities in several ways. The Si:N:P ratio of marine diatoms, which are abundant constituents of coastal phytoplankton communities and comprise most of the biomass, is approximately 16:16:1 when nutrient levels are sufficient. Deviations from this ratio in nutrients available in the water column may be a limiting factor for diatoms, as well as for other phytoplankton groups (Hecky and Kilham 1988; Dortch and Whitledge 1992). Also, a decreasing Si:N ratio may exacerbate eutrophication by reducing the potential for diatom growth in favor of noxious flagellates (Officer and Ryther 1980). Another reasonable hypothesis that follows a more favorable, balanced nutrient composition, as evidenced in the Mississippi River and in the coastal waters as well, is that surface primary productivity has increased under these conditions.

### Consequences of Shifts in Nutrient Composition

#### PHYTOPLANKTON SPECIES COMPOSITION

The changes in riverine and coastal nutrient concentrations and ratios over time suggest that there should be observable changes in phytoplankton species composition. The increasing N availability and decreasing Si:N ratios should lead to increases in dominance of lightly-silicified diatoms and nondiatoms. Published reports of phytoplankton species composition for 1955–1957 near the delta (Simmons and Thomas 1962) and for 1972–1973 approximately 80 km west of the delta (Fucik 1974; Ward et al. 1979) were compared with data for 1990–1993 from near the delta and from stations C6A and C6B in 20 m water depth off Terrebonne Bay (Dortch et al. unpublished data) (Appendices 1–3, Fig. 3). This comparison is qualitative because of differences in locations, seasons sampled, and methodology. The methodology used in earlier reports may have missed common nondiatoms, such as small coccoid cyanobacteria and phytoflagellates, which now often dominate. Consequently, it was not possible to determine whether the dominance of these groups has increased. A conservative approach was taken in this comparative analysis. Data were compiled by matching season and location as closely as possible and including in the recent data only the phytoplankton types that would have been observed in

the earlier studies. In addition, because of uncertainties of taxonomy, differences were only noted where organisms were identified unambiguously.

Demonstrable changes have occurred in the diatom and nondiatom species composition from the 1950s and 1970s to present. Some heavily silicified diatom species are either not observed at all in recent samples (boldface type in the Appendices) or are much less dominant. For example, no *Melosira* species, which appear heavily silicified, were observed in 1990–1993 but were present in both 1955–1957 and 1972–1973. *Asterionella japonica* (= *Asterionellopsis glacialis*, Round et al. 1990) was observed recently at low salinities in the spring but is not a dominant species as it was from 1955–1957.

Similarly, more lightly silicified diatoms are documented for the 1970s and present, especially at higher salinities. *Rhizosolenia fragilissima* and *Ceratulina pelagica*, which are so lightly silicified they are sometimes difficult to see, were not reported for 1955–1957. Two species of *Leptocylindricus* spp. were frequently dominant in 1990–1993 but were a minor constituent in 1955–1957. During 1972–1973, lightly silicified diatoms were reported, including *Rhizosolenia delicatula*, *Leptocylindricus danicus*, and *Ceratulina pelagica*, but a more quantitative analysis would be required to determine if their abundance was less than at present.

The data suggest that the shift in dominant diatom composition, toward more lightly silicified species, occurred between 1955–1957 and 1972–1973, but methodological differences preclude conclusions about changes in nondiatoms. Since Si availability continued to decrease after the early 1970s (Turner and Rabalais 1991), a continued shift in species composition to nondiatoms would be expected. The phytoplankton at stations C6A and C6B in 1990–1993 often were dominated numerically by small flagellates and cyanobacteria (not shown in Appendix 3). They were not considered in this comparison, because it is not clear whether they would have been observed in the 1972–1973 study, even if present in large numbers. It is also tempting to hypothesize that the presence of *Trichodesmium* sp. in 1990–1993, but not in the earlier studies, indicates decreased Si availability. *Trichodesmium* sp., however, is a bloom-forming species that has been reported previously for this region (Eleuterius et al. 1981).

Several species with importance to human health are now present but were either absent before or have increased in dominance. The dominance of *Nitzschia pungens* on the Louisiana shelf appears to have increased dramatically since the 1950s, and concentrations now frequently exceed  $1 \times 10^6$  cells  $\text{l}^{-1}$ . Some forms of this species have been associated with amnesiac shellfish poisoning

(reviewed in Shumway 1990; Hallegraeff 1993). Samples from a recent bloom at station C6B have been identified (G. Fryxell, personal communication) as a sometimes toxic form of *Nitzschia pungens*, now called *Pseudonitzschia pseudodelicatissima* (Martin et al. 1990). Since this species is heavily silicified for a marine diatom (Conley et al. 1989), it is difficult to attribute its increase to decreasing Si:N ratios, although it could be responding to increasing N availability. *Dinophysis caudata*, a dinoflagellate which may be associated with diarrhetic shellfish poisoning (Dickey et al. 1992), was not recorded in the earlier studies. Recently, it was often present at low to moderate concentrations; sometimes it was dominant and reached concentrations as high as  $1 \times 10^5$  cells  $l^{-1}$ .

The indicated shift from heavily to lightly silicified forms may have altered carbon flux via directly sinking phytoplankton cells, if silica has become limiting. Subsequently, organic loading to the seabed and, possibly, oxygen depletion may have been affected. On the other hand, an increase in nondiatom forms that are less preferentially grazed than diatoms may have increased the flux of these cells into the lower water column and altered oxygen consumption in a different manner.

#### SILICATE-BASED PHYTOPLANKTON COMMUNITY RESPONSE

Bien et al. (1958) first documented the dilution and nonconservative uptake of silicate in the Mississippi River plume by sampling from the river mouth seaward in 1953 and 1955. A notable characteristic of the mixing diagram is that the concentration of silicate often falls below the conservative mixing line, thus indicating biological uptake. Uptake can be statistically modeled as a deviation from this mixing line, which we did for 31 adequately sample datasets (Turner and Rabalais 1994a). We found that the concentration of silicate at the 20‰ mixing point declined in the last several decades during the winter-spring (January–April) and summer months (June–August); however, there was no discernible change during the fall-winter months (October–December). We normalized for the effects of varying concentrations in the riverine end-member (e.g., Loder and Reichard 1981) and compared the estimated net silicate uptake at 30‰ as a function of silicate riverine end-member concentration (Fig. 8). Nonconservative uptake of silicate was indicated in all data collections. The net uptake (at 30‰) above dilution ranged from 1% to 19% of the intercept concentration, and the data groups before and after 1979 were remarkably similar. The net silicate uptake appears higher after 1979 than before 1979 (Fig. 8); these differences were apparent in the

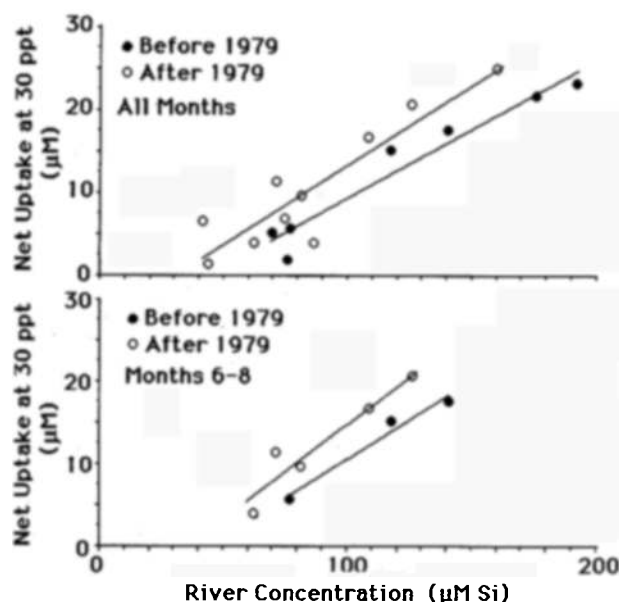


Fig. 8. The estimated net uptake of silicate above dilution losses at 30‰, for all data (top), and for summer data (months 6–8). (From Turner and Rabalais 1994a.)

summer months during peak hypoxia development (June–August) as well. The results from this analysis suggest that net silicate uptake in the dilution gradient from river to sea has remained the same, or even increased, as the concentration decreased. Two causal factors explaining this result are related to the effects of other nutrients and changes in the light regime this century.

The 20–30‰ range of the mixing zone is where light conditions improve rapidly in the seaward direction and where the highest primary production rates are usually observed (Sklar and Turner 1981; Lohrenz et al. 1990). The light conditions in this region may have changed because of dams trapping sediments, especially in the Mississippi River watershed. Phytoplankton production should have increased sooner in the mixing gradient and with greater strength if turbidity decreased during this period of watershed manipulation. Also, Justić et al. (1995a, b) analyzed the nutrient ratios within the Mississippi River and offshore waters. They observed that the ratios of N, P, and Si, although different in the last several decades, were now closer to the Redfield ratio, an indicator of improved nutrient conditions for phytoplankton growth. They suggested that coastal phytoplankton production would be stimulated by the favorable balance of N, P, and Si, rather than an increase in any one particular nutrient.

#### BIOLOGICALLY BOUND SILICA AND CARBON ACCUMULATION

As noted earlier, nearly coincidental trends in silicate (decreasing) and nitrogen (increasing)

concentrations in the Mississippi River caused the average annual dissolved silicate:nitrate-N atomic ratio (Si:N) to decline from about 4:1 earlier this century to 1:1 this decade. The present Si:N ratio (1:1, Fig. 4) is thought to be a significant limiting threshold for diatom growth, intraspecific competition, and production (Officer and Ryther 1980; Smayda 1990; Dortch and Whitley 1992; Turner and Rabalais 1994a). Thus, two contrasting hypotheses predict changes in phytoplankton on this coast since the 1950s. The first is that the coastal phytoplankton are nitrogen, not silica, limited, and higher nitrogen loading will result in proportionally higher phytoplankton production rates. A competing hypothesis is that the combination of lower silica fluxes and a Si:N ratio near 1:1 will result in lower phytoplankton production rates through limits on diatom production along with species composition shifts. This is a nontrivial issue for managers, because diatoms are an ecologically important constituent of phytoplankton and contribute significantly to the organic loading of bottom waters and sediments and the subsequent oxygen depletion.

We documented that surficial sediments, directly downstream and beneath the surface riverine-estuarine dilution plume, reflected the in situ primary production and subsequent transport of organic carbon from surface to bottom waters within the Mississippi River bight (Rabalais et al. 1992a; Turner and Rabalais 1994b) (Fig. 9). We further quantified the silica in the skeletal remains of diatoms sequestered as biologically bound silica (BSi) in dated sediment cores from the same region. The highest concentrations of BSi were in sediments deposited in 25–50 m water depth in the middle of the sampling area. The % BSi in sediments from deeper waters (110 m and 200 m) were generally stable through time but rose in the shallower stations (10 m and 20 m) around the beginning of this century. At the intermediate depths (27 m to 50 m), where both the % BSi concentration and accumulation rates were highest, coincidental changes in the % BSi with time were evident, especially in the 1955 to 1965 period (a rise and fall) and a post 1975 (1980?) rise that was sustained to the sampling date (1989) (Turner and Rabalais 1994b) (Fig. 10). The general pattern that emerges is an equilibrium accumulation of BSi from 1800 to 1900, then a slow rise, followed by a more dramatic rise in the past two decades. Diagenesis of the BSi undoubtedly occurs in these cores, but will be a relatively low because the sedimentation rate is high ( $>0.5 \text{ cm yr}^{-1}$ ). Furthermore, others have found the record of BSi to be a good indicator of in situ production. Conley et al. (1993) summarized for freshwater lakes that, in

general, accumulation of BSi in sediments mimics overlying water column productivity, and that, the more diatoms that are produced by nutrient-enhanced growth, the more BSi will be deposited. Additional information is in Turner and Rabalais (1994b).

If the assumption is made that the BSi:C ratio at the time of deposition remained constant this century, then the increased BSi deposition represents a significant change in carbon deposition rates (up to 43% higher in cores dated after 1980 than those dated between 1900 to 1960). The pattern in % BSi changes parallels the documented increases in nitrogen loading in the lower Mississippi River, over the same period during which the silicate concentrations have been decreasing (Fig. 10). We conclude from our analyses that the flux of diatoms from surface to bottom waters, beneath the Mississippi River plume, increased this century. These changes were coincidental with changes in riverine nitrogen loadings and resulted in higher organic sedimentation to bottom water layers. The depletion of bottom water oxygen, its persistence and areal coverage on this shelf, is thus indicated to have been altered this century.

Conley et al. (1993) predicted that coastal marine systems would not see long-term depletion of dissolved silicate with eutrophication as in enclosed lakes, because regeneration within the system would maintain sufficient dissolved silicate levels to prevent silica limitation. Our results which show continued accumulation of biologically bound Si in sediments beneath the plume and similar or higher net silicate uptake by phytoplankton in the plume surface waters, in spite of lower concentrations of Si delivered by the Mississippi River, support this hypothesis.

#### CONSEQUENCES TO HYPOXIC BOTTOM WATER FORMATION AND SEVERITY

Long-term changes in the severity and extent of hypoxia cannot be assessed directly, because systematic sampling of dissolved oxygen concentrations in bottom water did not begin until 1985. Prior records of hypoxia, dating to 1973, were obtained sporadically as components of other studies; previous events were drawn from anecdotal relationships with shrimp trawl yields. Therefore, biological, mineral, or chemical indicators of eutrophication and/or hypoxia preserved in sediments, where accumulation rates record historical changes, provide clues to prior hydrographic and biological conditions.

We used dominance trends of benthic foraminifera to determine their use as indicators of reduced oxygen levels and/or carbon-enriched sediments (Sen Gupta et al. 1981; Sen Gupta and Ma-

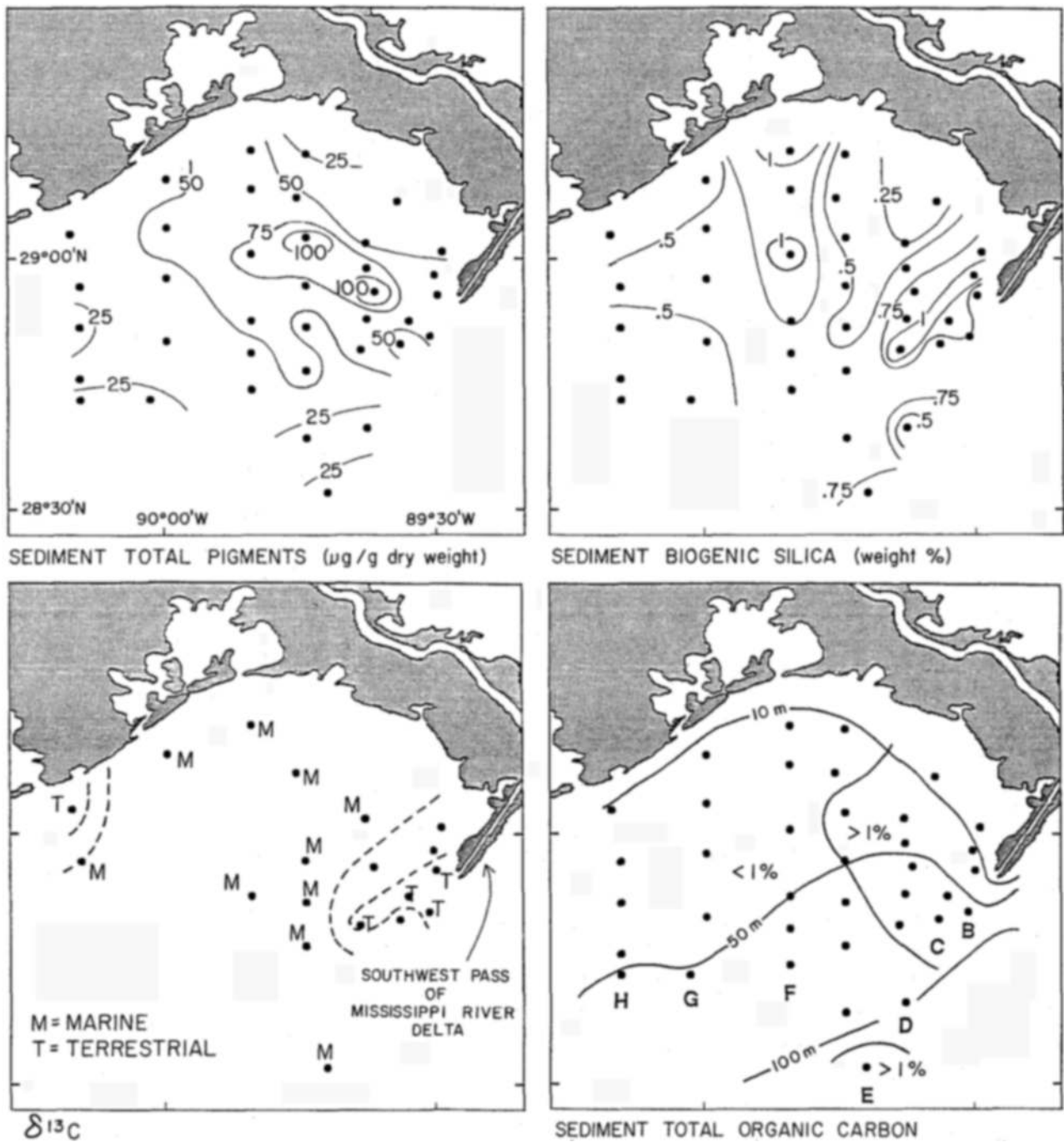


Fig. 9. The spatial distribution in April 1989 of phytoplankton pigments ( $\mu\text{g g}^{-1}$  dry weight sediment), biogenic silica (% BSi by weight),  $\delta^{13}\text{C}$  signature, and total organic carbon (% by dry weight of sediments), in sediments beneath the Mississippi River plume (from Turner and Rabalais 1994b).

chain-Castillo 1993). The same series of Pb-210 dated sediment cores used for BSi analyses (Turner and Rabalais 1994b; Fig. 3) were used for determination of benthic foraminifera. Some down-core shifts in species abundances at station G27 (Fig. 3) in the Mississippi River bight were inter-

preted as foraminiferal responses to increasing oxygen stress (Sen Gupta et al. 1996). Benthic foraminiferal density and diversity are generally low in this environment, but a comparison of assemblages in surficial sediments from areas differentially affected by oxygen depletion indicates that the dom-



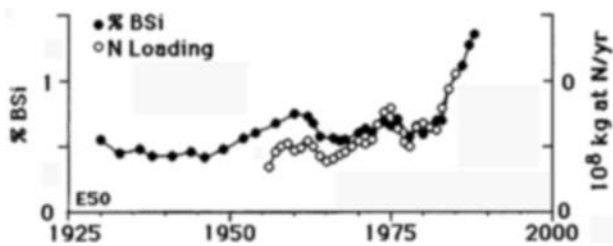


Fig. 10. Average % BSi concentration of sediments in each section of Pb-210 dated sediment cores from station E50. A 3-yr running average for each sampling date is shown. The % BSi data are superimposed with a 3-yr running average of the nitrogen loading from the Mississippi River through the delta passes (from Turner and Rabalais 1994b).

inance of *Ammonia parkinsoniana* over *Elphidium* spp. is much more pronounced under hypoxia than in well-oxygenated waters. The abundance of *A. parkinsoniana* is also correlated with phytoplankton biomass in surface waters and % BSi (food source indicator) in sediments. In the context of modern hypoxia, species distribution in dated sediment cores reveals stratigraphic trends in the *Ammonia:Elphidium* ratio that indicate an overall increase in oxygen stress (in intensity or duration) in the last 100 yr (Fig. 11). In particular, the stress seems especially severe since the 1950s. For this time period, both *Ammonia* and *Elphidium* become less important components of the assemblage, while *Fursenkoina* (known to be hypoxia tolerant elsewhere) shows an unusual dominance. *Quinqueloculina* (a significant component of the modern assemblage only in well-oxygenated waters) has been absent from the record of this core since the 1870s but was a conspicuous element of the fauna in the previous 100 yr. Thus, there are indications that oxygen deficiency stress increased as nutrient loads and carbon flux to the seabed increased.

#### Summary of Historical Trends

Mississippi River nutrient concentrations and loadings to the adjacent continental shelf have changed dramatically this century, with an acceleration of these changes since the 1950s. The concentrations of dissolved N and P doubled and Si decreased by half, the dissolved Si:N ratio dropped from 4:1 to 1:1, and seasonal trends have changed. The resulting nutrient composition in the receiving Gulf waters shifted toward stoichiometric nutrient ratios closer to the Redfield ratio and more balanced than previously. N and P are indicated to be less limiting now for phytoplankton growth, while some increase in Si limitation is probable. In spite of a probable decrease in Si availability, the overall productivity of the ecosystem appears to have increased. This is evidenced by equal or greater net uptake of silica by the silicate-based phyto-

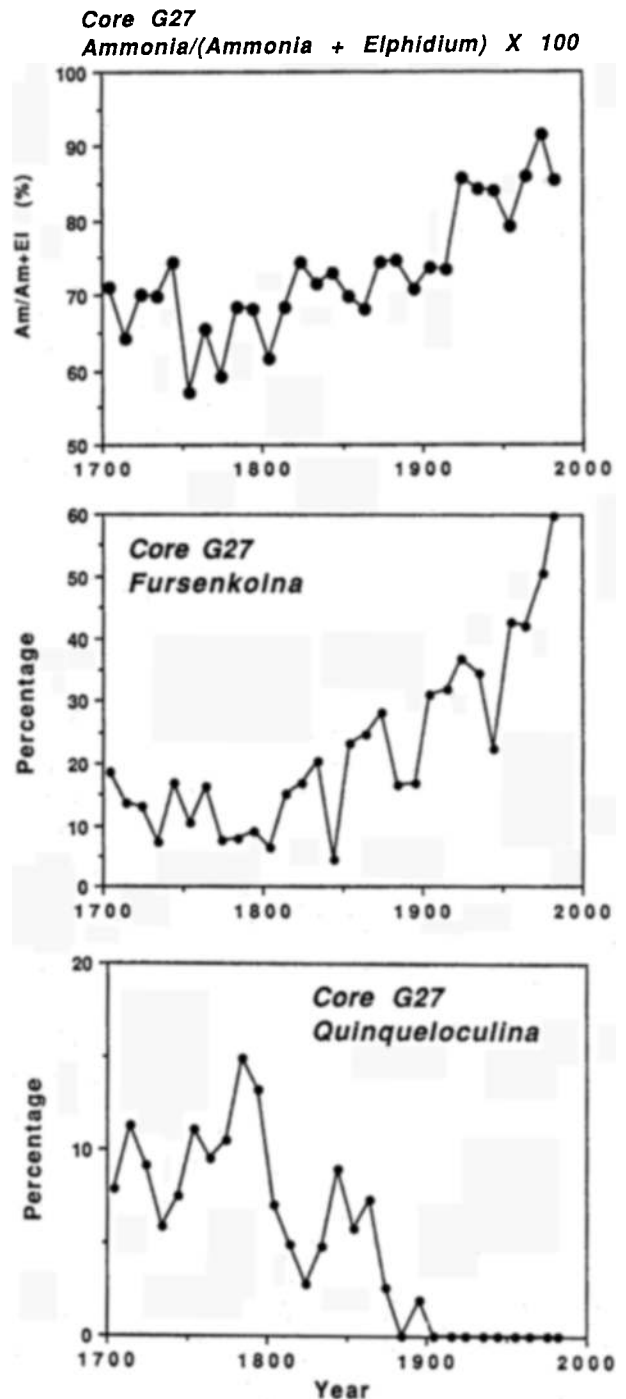


Fig. 11. Changes in benthic foraminifera species with stratigraphic depth in Pb-210 dated sediment core from station G27 in the Mississippi River bight.

plankton community in the mixing zone compared to the 1950s, and greater accumulation rates of BSi in sediments beneath the plume, but not further away, which is in agreement with results found in freshwater systems. The increased % BSi in Missis-

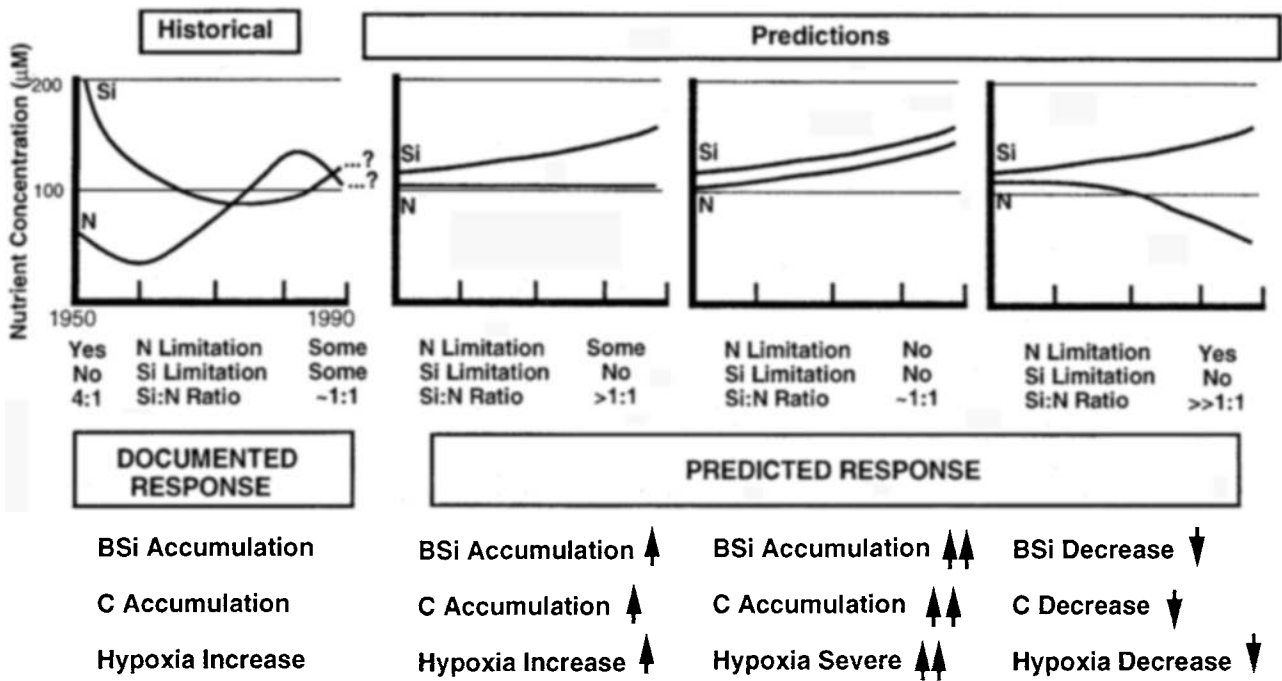


Fig. 12. A schematic of documented historical changes in riverine nutrient concentrations, nutrient ratios, and biological responses, and a series of predicted responses depending on a constant increase of silica and varying changes in nitrogen loadings. A stronger response is indicated by double arrows. (See text for discussion.)

Mississippi River bight sediments that parallels increased N loading to the system is direct evidence for the effects of eutrophication on the shelf adjacent to the Mississippi River. Individual phytoplankton species composition shifts (heavily silicified diatoms to lightly silicified diatoms; diatom to nondiatom) would indicate some population-level responses to reduced Si supplies and/or changes in nutrient ratios. Finally, analysis of benthic foraminifera indicates an increase in oxygen deficiency stress this century, with a dramatic increase since the 1950s. Increased bottom-water hypoxia could result from increased organic loading to the seabed and/or shifts in material flux (quantity and quality) to the lower water column.

The importance of the water column physical structure to the development and persistence of hypoxia is clear, and the discharge of the Mississippi River (i.e., amount of flow) since the 1950s has been relatively constant aside from normal decadal scale variations in runoff. The allocation of flow between the Mississippi River proper and the Atchafalaya River has been maintained by the United States Army Corps of Engineers according to Congressional mandate. Thus, the observed changes in biological responses are probably not due to changes in amount or distribution of freshwater runoff and resultant stratification.

### Predictions

Nutrient levels in the Mississippi River may be influenced by a variety of management and economic decisions, with consequences to the Mississippi River delta coastal ecosystem. Agricultural practices, economic incentives and disincentives, water quality regulations, water treatment practices, and consumer preferences may all contribute to the amount of dissolved N, P, and Si in the Mississippi River. If freshwater phosphorus loading is reduced, we predict that the rate of BSi burial in freshwater sediments will decrease because freshwater diatom production will be lower (similar to the decreased % BSi in more recent Lake Michigan sediments; shown in Conley et al. 1993). The release of dissolved Si from the sediments in the watershed will exceed the uptake of dissolved Si in the water column. The result will be an increase in dissolved Si within the Mississippi River and in the adjacent coastal waters (a return to the 1950s and turn-of-the-century levels). At the same time, controls on N use and loadings within the watershed may or may not be affected.

Based on the biological consequences of documented historical riverine changes, we could suggest three possible scenarios for future system responses (Fig. 12). First, if N concentration remains the same and Si concentration increases, overall N

limitations to phytoplankton productivity will be similar to present, but Si will no longer be limiting. The result would be increased BSi and carbon accumulation in the sediments, and an increase in the extent and severity of hypoxia. Second, if both N and Si concentrations increase, there will be no N or Si limitations and the Si:N ratio will be balanced. The result would be greatly increased BSi and carbon accumulations and substantial increase in the severity of hypoxia. Third, if N concentrations are reduced (e.g., to 1950s values) while Si concentrations increase, then N would again return to the limiting nutrient status, and although Si would be in abundant supply, the system would be restricted by N supplies, and hypoxia would decrease.

Because of the close coupling between riverine nutrient loading and phytoplankton production, reversal of the current effects of nutrient increases and nutrient ratio changes is possible to the degree that water quality trends are altered. However, the management of one nutrient (Si or N) may not be sufficient to reduce eutrophication to an acceptable level if the compensatory qualitative adaptations of species lead to new phytoplankton communities, including those with noxious or toxic species.

The preceding discussion has been based on the assumption that river discharge will remain statistically similar to past conditions. This may not be the case. Possible diversions of fresh water (and associated sediments and nutrients) through Louisiana marshes as a means of reducing coastal land loss and or assisting navigation are being discussed. It is also not clear how much longer the United States Army Corps of Engineers will be able to prevent the Atchafalaya River from capturing the major part of the Mississippi River discharge. Either scenario could severely alter the spatial distribution of fresh water and nutrients onto the shelf.

#### ACKNOWLEDGMENTS

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## APPENDICES

Data from Simmons and Thomas (1962) included four areas east of the Mississippi River delta (two with salinity below 18‰ combined under "River" in Appendix 1, and two with salinity of 18–32‰ combined under "Plume" in Appendix 2). Most of the 1990–1992 data are from west of the delta but are matched for salinity and distance from the river (no stations west of 89°55'W). The July 1990 data included stations east of the delta, but there were no substantial differences in species composition from Simmons and Thomas (1962), and the data were excluded. Methods used by Simmons and Thomas (1962) were reliable for diatoms >0.6 μm, thus Appendices 1 and 2 include only diatoms.

The data of Fucik (1974) and Ward et al. (1979) were obtained from a study of petroleum operations approximately 80 km west of the Mississippi delta. Their data ("Control" and "Platform") are comparable to monthly data in 1990–1993 from nearby stations C6A and C6B (Appendix 3 and Fig. 3). High river flow in spring 1973 and spring–summer 1990 and 1993 makes these periods most comparable. Neither Fucik (1974) nor Ward et al. (1979) cited enumeration methodologies, but their species lists indicate they used the standard Utermohl method. Their listings do not mention any other groups, besides diatoms and dinoflagellates, which should have been observed by this method if they were present. For example, cryptomonads are now often dominant, especially in the fall through early spring, but were not listed by Fucik (1974) or Ward et al. (1979). Consequently, Appendix 3 includes only diatoms, dinoflagellates, and large filamentous cyanobacteria, which they would surely have observed if they had been present.

Water samples for 1990–1993 were preserved with glutaraldehyde, and filtered onto 0.2-μm, 3-μm, and 8-μm polycarbonate filters (Dortch et al. 1992b). Organisms on the 3-μm and 8-μm filters were stained with proflavin. The 0.2-μm and 3-μm filters were counted immediately by epifluorescence microscopy, and the 8-μm filters were frozen and counted later. Dominant species for each area and time were picked by ranking the phytoplankton by concentration, summing the ranks, and picking the top-ranked groups.

APPENDIX 1. Comparison of dominant diatoms near the river mouth between 1955–1957 (Simmons and Thomas 1962) and 1990–1992.

Year	February	March	May	June	July	September	October	November
1955				<i>Cyclotella</i> spp. <i>Melosira</i> spp. <i>Skeletonema costatum</i> <i>Chaetoceros affinis</i>			<i>Cyclotella</i> spp. <i>Melosira</i> spp. <i>Skeletonema costatum</i>	
1956	<i>Melosira granulata</i> <i>Coscinodiscus</i> sp. <i>Melosira</i> spp. <i>Cyclotella</i> spp. <i>Skeletonema costatum</i>					<i>Cyclotella comta</i> <i>Melosira</i> spp. <i>Melosira distans</i> <i>Coscinodiscus</i> spp.		<i>Asterionella formosa</i>
1957	<i>Melosira</i> spp. <i>Melosira granulata</i> <i>Melosira distans</i> <i>Cyclotella</i> spp. <i>Cyclotella comta</i>		<i>Melosira</i> sp. <i>Melosira distans</i> <i>Cyclotella</i> sp. <i>Cyclotella meneghiniana</i> <i>Asterionella japonica</i> <i>Chaetoceros</i> spp.					
1990	<i>Plagiogramma vanheurckii</i> <i>Thalassionema nitzschoides</i>						<i>Skeletonema costatum</i> <i>Cyclotella</i> sp. < &gt; 8 $\mu$ m <i>Thalassiosira</i> spp. <i>Thalassiosira/Cyclotella</i> Unident. centric > 8 $\mu$ m <i>Thalassionema nitzschoides</i>	Unident. centric > 8 $\mu$ m <i>Cyclotella</i> spp. < 8 $\mu$ m Unident. pennate < 8 $\mu$ m
1991		<i>Cyclotella</i> spp. < 8 $\mu$ m Unident. centric > 8 $\mu$ m				<i>Chaetoceros</i> spp. <sup>1</sup> <i>Skeletonema costatum</i> <sup>1</sup>		
1992			<i>Cyclotella</i> spp. < 8 $\mu$ m <i>Extubocellulus spinifer</i> ? <i>Thalassiosira/Cyclotella</i>		<i>Thalassiosira/Cyclotella</i> <i>Skeletonema costatum</i> <i>Cyclotella</i> spp. < 8 $\mu$ m Unident. pennate < 8 $\mu$ m <i>Rhizolenia fragilisima</i>			

<sup>1</sup> No counts for diatoms < 8  $\mu$ m.

APPENDIX 2. Comparison of dominant diatoms in the plume between 1955–1957 (Simmons and Thomas 1962) and 1990–1992.

Year	February	March	May	June	July	September	October	November
1955				<i>Cyclotella</i> spp. <i>Skeletonema costatum</i> <i>Chaetoceros affinis</i>		<i>Cyclotella capsia</i> <i>Coscinodiscus</i> spp. <i>Thalassionema nitzschoides</i>	<i>Thalassionema nitzschoides</i> <i>Nitzschia closterium</i> <i>Thalassiothrix frauenfeldii</i>	
1956	<i>Skeletonema costatum</i> <i>Coscinodiscus</i> spp. <i>Rhizosolenia stollterfothii</i> <i>Chaetoceros</i> spp. <i>Asterionella japonica</i> <i>Nitzschia</i> spp.							<i>Asterionella japonica</i> <i>Melostra sulcata</i>
1957			<i>Chaetoceros</i> sp. <i>Chaetoceros vanhoeffenii</i> <i>Chaetoceros affinis</i> <i>Thalassiosira nitzschoides</i> <i>Asterionella japonica</i> <i>Nitzschia</i> sp. <i>Skeletonema costatum</i> <i>Eunotia</i> sp.					
1990					<i>Skeletonema costatum</i> <i>Cyclotella</i> spp. < & > 8 $\mu$ m <i>Rhizosolenia fragilissima</i> <i>Ceratulina pelagica</i> <i>Thalassiosira/Cyclotella</i> <i>Thalassionema nitzschoides</i> <i>Cyclotella</i> spp. > 8 $\mu$ m <i>Chaetoceros</i> spp. <i>Ceratulina</i> sp. (not pelagica) <i>Rhizosolenia fragilissima</i> <i>Chaetoceros curviseptus</i> <sup>1</sup>		<i>Cyclotella</i> spp. < 8 $\mu$ m <i>Nitzschia pungens</i> Unidentified pennate < 8 $\mu$ m	
1991		<i>Skeletonema costatum</i> <i>Leptocylindricus</i> sp. <i>Thalassiosira/Cyclotella</i> <i>Cyclotella</i> sp. < 8 $\mu$ m <i>Nitzschia pungens</i>						
1992			<i>Rhizosolenia fragilissima</i> <i>Nitzschia pungens</i> <i>Leptocylindricus</i> sp.					

<sup>1</sup> No counts for diatoms < 8  $\mu$ m.

APPENDIX 3. Comparison of dominant phytoplankton species mid-shelf along the Louisiana coast between 1972-1973 (Fucik 1974; Ward et al. 1979) and 1990-1993.

Year	Location	September	October	November	April	July	August	October
1972/1973	Platform	<i>Skeletonema costatum</i>	<i>Nitzschia closterium</i> <i>Rhizosolenia shrubsolei</i>	<i>Synedra acus</i> <i>Nitzschia subfraudulenta</i>	<i>Skeletonema costatum</i> <i>Nitzschia pungens</i>	<i>Cyclotella striata</i> <i>Thalassiosira nitzschoides</i>	<i>Cerataulina pelagica</i> <i>Thalassiosira nitzschoides</i>	<i>Skeletonema costatum</i> <i>Rhizosolenia delicatula</i>
1972/1973	Control	<i>Rhizosolenia delicatula</i>	<i>Rhizosolenia shrubsolei</i>	<i>Thalassiosira nitzschoides</i>	<i>Skeletonema costatum</i>	<i>Cyclotella striata</i>		
1990	C6A	<i>Gonyaulax monilata</i> <i>Gonyaulax turbynei</i> <i>Chaetoceros pelagicus</i>	<i>Denticula elegans</i> <i>Skeletonema costatum</i> <i>Thalassiosira nitzschoides</i>	<i>Melosira sp.</i> <i>Asterionella japonica</i>	<i>Nitzschia subfraudulenta</i> <i>Nitzschia pungens</i> <i>Chaetoceros spp.</i>	<b>Melosira sp.</b> <i>Coscinodiscus radiatus</i> <i>Pleurosigma naviculaceum</i>	<i>Cerataulina pelagica</i> <b>Melosira sp.</b> <i>Thalassiosira sp.</i> <i>Rhizosolenia stollerfothii</i>	<i>Nitzschia closterium</i> <i>Rhizosolenia calcar-avoids</i> <i>Nitzschia subfraudulenta</i>
1990	C6A	<i>Skeletonema costatum</i> <i>Nitzschia pungens</i>	<i>Melosira sp.</i> <i>Nitzschia pungens</i>	<i>Exuviella compressa</i> <i>Cyclotella spp.</i> <8 µm	<i>Leptocylindricus danicus</i> <i>Skeletonema costatum</i>	<i>Rhizosolenia shrubsolei</i> <i>Rhizosolenia fragilissima</i>	<i>Rhizosolenia fragilissima</i>	<i>Nitzschia pungens</i>
1991	C6B	<i>Rhizosolenia delicatula</i>	<i>Chaetoceros spp.</i>		<i>Chaetoceros spp.</i>	<i>Leptocylindricus sp.</i>	Unident. naked auto. dino. >8 µm	<i>Chaetoceros spp.</i>
1991	C6B	<i>Ceratulina pelagica</i> <i>Rhizosolenia fragilissima</i> <i>Chaetoceros spp.</i> <i>Nitzschia pungens</i>	<i>Rhizosolenia fragilissima</i>		<i>Nitzschia pungens</i> <i>Thalassiosira sp.</i> <i>Cyclotella spp.</i> <8 µm <i>Nitzschia pungens</i>	<i>Nitzschia pungens</i> <i>Cylindrotheca</i> <i>Cyclotella spp.</i> <8 µm	<b>Hemiaulus sp.</b>	<i>Rhizosolenia fragilissima</i>
1992	C6B	<i>Cyclotella spp.</i> <8 µm <i>Chaetoceros spp.</i>	<i>Nitzschioid-sigmoid pennate</i> <8 µm <i>Chaetoceros spp.</i>		<i>Chaetoceros spp.</i>	<i>Cyclotella sp.</i> >8 µm	<i>Cyclotella sp.</i> >8 µm	<i>Cyclotella spp.</i> <8 µm <i>Nitzschioid-sigmoid pennate</i> <8 µm <i>Chaetoceros spp.</i>
1992	C6B	Unident. pennate <8 µm <i>Nitzschioid-linear pennate</i> <8 µm <i>Chaetoceros curvisetus</i> <i>Chaetoceros socialis</i> <i>Chaetoceros spp.</i>	<i>Cylindrotheca</i>		<i>Rhizosolenia fragilissima</i> Unident. auto. dino. >8 µm <i>Ceratulina spp.</i>	Unident. auto. dino. >8 µm <i>Thalassiosira/Cyclotella</i>	<i>Thalassiosira/Cyclotella</i>	<i>Cylindrotheca</i> <i>Nitzschioid-pennate</i> "boat" >8 µm <i>Cyclotella spp.</i> <8 µm <i>Skeletonema costatum</i> <i>Chaetoceros spp.</i>
1993	C6B	<i>Cyclotella spp.</i> <8 µm <i>Ceratulina pelagica</i>	<i>Chaetoceros curvisetus</i>		<i>Leptocylindricus sp.</i> Unident. pennate <8 µm <i>Leptocylindricus sp.</i>	<i>Chaetoceros spp.</i>	<i>Chaetoceros spp.</i> <i>Nitzschioid-sigmoid pennate</i> >8 µm <i>Chaetoceros spp.</i> <i>Nitzschioid-sigmoid pennate</i> >8 µm <i>Rhizosolenia fragilissima</i>	<i>Chaetoceros curvisetus</i> <i>Nitzschioid-sigmoid pennate</i> >8 µm <i>Rhizosolenia fragilissima</i>
1993	C6B	<i>Nitzschia pungens</i> <i>Chaetoceros spp.</i>	Unident. centric >8 µm <i>Cyclotella spp.</i> <8 µm		<i>Nitzschia pungens</i>	<i>Chaetoceros spp.</i>	<i>Chaetoceros spp.</i> <i>Thalassiosira nitzschoides</i>	Unident. centric >8 µm <i>Cyclotella spp.</i> <8 µm
		<i>Skeletonema costatum</i> Unident. centric >8 µm <i>Rhizosolenia fragilissima</i>	<i>Nitzschia pungens</i>		<i>Rhizosolenia delicatula</i> <i>Skeletonema costatum</i> <i>Ceratulina pelagica</i>	<b>Dinophysis caudata</b> <i>Thalassiosira/Cyclotella</i> <i>Ceratium furca</i>	<i>Thalassiosira sp.</i> <i>Thalassiosira/Cyclotella</i> Unident. centric >8 µm	<i>Nitzschia pungens</i>