

Sedimentological evidence of an increase in *Pseudo-nitzschia* (Bacillariophyceae) abundance in response to coastal eutrophication

Abstract—*Pseudo-nitzschia* H. Peragallo, a marine planktonic diatom genus containing some species capable of producing the neurotoxin domoic acid, is often documented in extremely high concentrations in the northern Gulf of Mexico in the plume of the Mississippi River, especially when river flow and nutrient inputs are high. Limited historical data suggest that *Pseudo-nitzschia* abundance has increased in the northern Gulf of Mexico since the 1950s. Five sediment cores were collected and analyzed to test whether *Pseudo-nitzschia* increases coincided with increasing nutrient concentrations in the Mississippi River, thereby suggesting a cause–effect relationship. *Pseudo-nitzschia* abundance increased in all five cores, correlating significantly with increasing nitrate fluxes and decreasing silicate to nitrate ratios. A diatom dissolution index, based partly on scanning electron microscopic analysis of the fine structure of *Pseudo-nitzschia* and other lightly silicified diatom valves preserved in the sediment, indicates that the increase in *Pseudo-nitzschia* abundance appears to reflect a response to eutrophication rather than diagenesis. This study provides evidence for a possible link between coastal eutrophication and harmful algal blooms.

Harmful algal blooms appear to be increasing in frequency and intensity on a global scale, adversely affecting ecosystems and societal interests like human health, tourism, and fisheries (Smayda 1990; Hallegraeff 1993). There is debate, however, whether the perceived increase is actual or the product of increased awareness and communication. One way to address the apparent increase in harmful algal blooms would be to study long-term trends in phytoplankton populations. Unfortunately, regular phytoplankton monitoring was not initiated in most coastal areas prior to the last two decades, hence the debate. The sediment record, however, may provide a long-term data set of preservable phytoplankton remains (e.g., diatom frustules and dinoflagellate cysts) to test whether harmful algal blooms are increasing and, if so, if the increase is due to the eutrophication of coastal waters.

Several sedimentological studies have focused on the development of eutrophication in estuarine and coastal waters (e.g., Turner and Rabalais 1994; Cooper 1995; Andr n 1999). Additionally, harmful algal remains preserved in the sediment have been used as a proxy of historical population dynamics and past bloom events (e.g., Dickman and Glenwright 1997; Dale et al. 1999). A direct link between eutrophication and harmful algal blooms, however, has not been established by such studies. Dickman and Glenwright (1997) attempted to find a link between intensifying eutrophication and an increase in *Pseudo-nitzschia* blooms in Hong Kong Harbor, but poor preservation of *Pseudo-nitzschia* valves hindered the study. Dale et al. (1999) demonstrated that dinoflagellate cyst concentrations doubled in four sediment cores taken in the Oslofjord, Norway, since the late 1800s (particularly the cyst of *Lingulodinium polyedra*) and argued

that the increase was due to eutrophication. No noxious or harmful incidences associated with this species, however, have been reported in the vicinity. Although the sediment record appears to be a logical location to find data to test whether harmful algal blooms have increased in response to coastal eutrophication, no study has successfully used this method to establish the link. The prominence of *Pseudo-nitzschia* in the northern Gulf of Mexico may provide an ideal case to establish such a connection.

Pseudo-nitzschia appears to have increased in abundance in the northern Gulf of Mexico since the 1950s (Dortch et al. 1997). Contemporaneously, nitrogen inputs doubled and silica inputs decreased by 50%, probably as a result of increased fertilizer use in the watershed of the Mississippi River and silica sequestering by freshwater diatoms behind upstream dams (Turner and Rabalais 1991). High concentrations of *Pseudo-nitzschia* ($>10^6$ cells L^{-1}) are currently observed, dominated by *P. pseudodelicatissima*, a species recently confirmed to be capable of producing domoic acid in the region (Parsons et al. 1999a; Pan et al. 2001). The increase and current high abundances may be a response to the increasing nitrogen inputs from the Mississippi and Atchafalaya Rivers coupled with induced stresses caused by silica limitation.

Several other studies have indicated that high abundances of *Pseudo-nitzschia* appear to be associated with increased nutrient inputs. In some cases, the increase in nutrients is due to natural phenomena, such as upwelling (Abrantes and Moita 1999; Trainer et al. 2000), but in others, agricultural run-off (Smith et al. 1990) appears to be the cause. Although there is circumstantial evidence that higher nutrient inputs result in higher numbers of *Pseudo-nitzschia*, there is no direct proof establishing this link. The sediment record, however, may provide a means to determine whether *Pseudo-nitzschia* abundances have increased over time, and whether increasing eutrophication is the cause.

Pseudo-nitzschia is considered to be a lightly silicified genus that will not preserve well in sediments (C. Lange pers. comm.). Dissolution processes, which can be significant at the sediment–water interface and in upper sediment horizons (Van Cappellen and Qui 1997; Willey and Spivack 1997), can effectively remove *Pseudo-nitzschia* from the remaining, more resistant diatom assemblage. The long, needle shape of the *Pseudo-nitzschia* valve is more easily fragmented than compactly shaped valves (e.g., centric diatoms). Other researchers (e.g., Dickman and Glenwright 1997; Abrantes and Moita 1999) have searched for *Pseudo-nitzschia* in sediments with little success.

In spite of these potential downfalls, we hypothesized that a suitable environment conducive to optimal diatom preservation could be found in the coastal sediments of Louisiana. Earlier studies demonstrated that approximately 50% of the *Pseudo-nitzschia* in the water column sink to the bottom

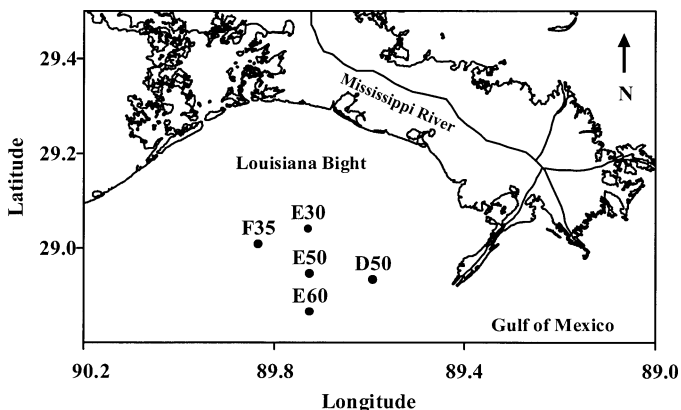


Fig. 1. The locations of the five coring sites in the Louisiana Bight west of the Mississippi River in the northern Gulf of Mexico.

(approximately 20 m water depth, Dortch et al. 1997), where a living, photosynthesizing *Pseudo-nitzschia* population has been observed (Parsons et al. pers. obs.). Terrigenous sedimentation rates in the region vary from 0 to >6 cm yr⁻¹. Areas with high terrigenous sedimentation rates can result in the rapid burial of diatoms and therefore better preservation by quickly burying the diatoms, removing them from the sediment–water interface (Van Cappellen and Qui 1997; Willey and Spivack 1997). Sediment pore water pH measurements indicate neutral to acidic conditions on the Louisiana shelf (Turner, unpubl. data), which are conducive for diatom valve preservation. Hypoxia is prevalent in the bottom waters of the Louisiana shelf (Turner and Rabalais 1991, 1994), reducing benthic activity and bioturbation processes that would otherwise mix near-surface sediments, increase exchange at the sediment–water interface, and hinder diatom valve preservation (Van Cappellen and Qui 1997; Willey and Spivack 1997). Varved sediments have been noted in several sediment cores collected in Louisiana coastal waters, demonstrating the lack of destructive mixing processes (N. Rabalais, pers. obs.). Finally, a large amount of phytoplankton biomass reaches the benthos (Dortch et al. 1997), including diatom valves. Such a high flux of biogenic silica to the sediment might allow dissolved silica to easily saturate in interstitial waters, thereby providing a better opportunity for optimal valve preservation. The purpose of this study was to determine whether *Pseudo-nitzschia* valves were preserved below the sediment–water interface at multiple locations in Louisiana coastal waters, and whether the preserved valves reflected a stimulatory response to the documented development of eutrophication in the vicinity.

Materials and methods—Sediment cores were collected at five sites in the Louisiana Bight (D50, E30, E50, E60, and F35) during an oceanographic cruise in April 1997 (Fig. 1). All box core collections had an undisturbed sediment–water interface and vertical integrity (i.e., lack of sloughing). Three 7.6-cm-diameter plastic core tubes were inserted into the box core sample to create triplicate subsamples. Compaction measurements were made during tube insertion and removal. All cores were stored in a walk-in refrigerator on board the

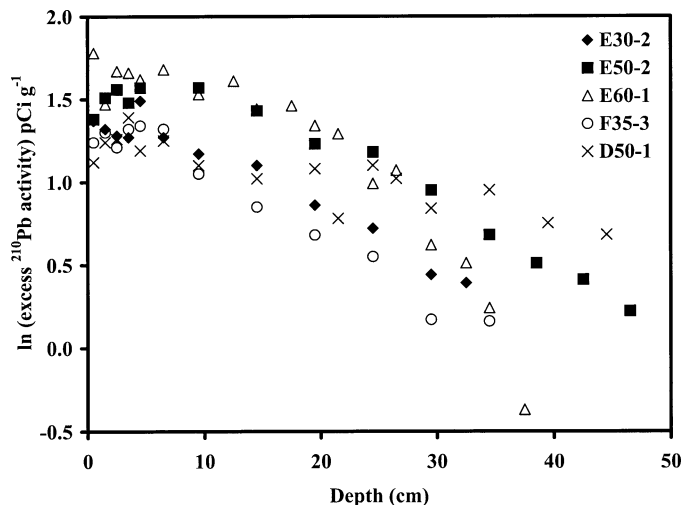


Fig. 2. The $\ln(\text{excess } ^{210}\text{Pb activity (pCi g}^{-1}\text{)})$ versus core depth for each of the five dated sediment cores. The regression lines for each profile (not shown) have the following equations and r^2 values. D50-1: $y = -0.013x + 1.2907$, $r^2 = 0.79$; E30-2: $y = -0.03x + 1.674$, $r^2 = 0.97$; E50-2: $y = -0.036x + 2.217$, $r^2 = 0.99$; E60-1: $y = -0.058x + 2.32$, $r^2 = 0.87$; F35-3: $y = -0.042x + 1.507$, $r^2 = 0.98$. Because of surface sediment mixing, the following samples were not used to calculate the regression line: D50-1 (0.5 cm), E30-2 (4.5 cm), E50-2 (0.5–4.5, 9.5 cm), E60-1 (0.5–4.5 cm), and F35-3 (0.5–3.5 cm).

RV *Pelican* and then at Louisiana Universities Marine Consortium (LUMCON) until processing.

The two subsampled 7.6-cm cores that exhibited the least amount of compaction were split into 1-cm sections using a threaded core extruder. The third core was archived. One of the split cores was used for ²¹⁰Pb dating using the constant rate of supply model as outlined in Parsons et al. (1999b). The 1-cm sections of the second core were divided for various analyses (e.g., biogenic silica, pigments, diatoms, foraminiferans), of which only the diatom analytical results were utilized for this study. Approximately 1 ml of wet sediment was put into preweighed, 15-ml screw-capped, polypropylene centrifuge tubes. Wet weights were determined by subtracting the tube weight from the sediment plus tube weight. Microspheres were added to quantify diatom numbers per gram wet weight sediment (Parsons 1996). Diatom samples were then subjected to a boiling nitric acid digestion and rinsed–centrifuged six times with deionized distilled water (Parsons et al. 1999b). Two drops of cleaned solution were permanently mounted onto No. 1, 22-mm coverslips with Naphrax® for light microscopic analysis, and two drops were mounted onto an aluminum stub for scanning electron microscopic (SEM) analysis (Parsons et al. 1999a). The deepest sample from each sediment core, as well as samples at 10-cm increments, were initially analyzed. Additional samples were selected to provide higher temporal resolution as deemed necessary. The ²¹⁰Pb-derived sedimentation rates obtained from the first replicate core were corrected for compaction and applied to the compaction-corrected depths of the second replicate core to obtain dates for each sediment sample analyzed for diatom analysis. This indirect method of dating was deemed appropriate because both replicate cores were obtained from the same box core.

At least 500 siliceous, phytoplanktonic microfossils (i.e., diatoms, silicoflagellates, chrysophycean statospores) were enumerated for each sample using Nomarski/DIC illumination on an Olympus® BH-2 or a Zeiss® Universal microscope at $\times 1,000$ magnification. In cases where samples contained fewer than 500 microfossils, the whole slide was examined and the reduced number of microfossils was acknowledged in the calculation of the preservation index (see below).

The majority of the microfossils (>98% in all cases) were diatoms. Fragments were quantified using techniques outlined in Schrader and Gersonde (1978) with the following modification. Apical measurements of fragments of long, thin pennate species were taken, summed, and divided by the average length of a complete valve of the respective species (e.g., *Pseudo-nitzschia*, *Thalassiothrix*, *Lioloma*). We were initially concerned about the different counting methods used for such valves (length measurements = higher precision counts = higher resolution) versus the other diatom valves (half valve counts = lower precision counts = lower resolution). The difference in resolution was noted and discounted for the following reasons. The difference in resolution is only problematic for pennates. Centrics and pennates fragment differently and were therefore counted differently (Schrader and Gersonde 1978). Shorter or more robust pennate valves (e.g., *Nitzschia* and *Navicula*) generally fragment into two halves (if at all) and are easily accounted for. Longer, thinner valves (e.g., *Pseudo-nitzschia*, *Thalassiothrix*, *Lioloma*) often fragment into smaller pieces (<50% of the total valve), and in these cases, the difference in resolution is a concern. Therefore, all long, thin valves were counted using the following technique: valve fragments were measured (apical length), fragment lengths were summed, and the total length was divided by the average valve length for each species/genera (as determined from water column phytoplankton counts; 80 μm for *Pseudo-nitzschia*, 120 μm for *Thalassiothrix*, 1,000 μm for *Lioloma*). Ten years of water column phytoplankton counts by Q. Dortch (unpubl.), however, demonstrated that *Pseudo-nitzschia* spp. and *Thalassiothrix* spp. are the only common diatoms with such a valve shape, with others being much rarer (e.g., *Lioloma* and *Nitzschia longissima*). Therefore, potential counting discrepancies will have minor implications, if any.

Pseudo-nitzschia valves and fragments could not be consistently distinguished to species level using differential interference contrast microscopy, so specimens were separated into three groups: the “*pungens*” group—larger, more heavily silicified valves, including *P. pungens* and *P. multiseriata* (Parsons et al. 1998); the “*delicatissima*” group—smaller, more lightly silicified valves, including *P. pseudodelicatissima* and *P. delicatissima* (Parsons et al. 1998); and “*P. other*”—a composite grouping of three species (*P. subfraudulenta*, *Pseudo-nitzschia* sp. c.f. *N. americana*, and *Pseudo-nitzschia* sp. 1; Parsons et al. 1998) that could be distinguished from other *Pseudo-nitzschia* species but were grouped together because of their rarity in examined samples. The relative abundance of *Pseudo-nitzschia* was calculated by dividing the number of *Pseudo-nitzschia* valves counted (total or each group) by the total number of diatom valves enumerated. Selected samples (i.e., those containing *Pseudo-nitzschia* valves) were examined on an ISI WB-6

SEM to confirm the presence of *Pseudo-nitzschia* and to distinguish the species within the *delicatissima* and *pungens* groups. The SEM was also used to document the presence of fragile valves (e.g., *Skeletonema costatum*) and valve fine structure (e.g., cribra) to assess valve preservation in each sample.

A preservation index (PI) was formulated to quantitatively assess diatom valve preservation. The PI ranged from 0 (poor preservation) to 5 (optimal preservation) and was calculated using the following equation.

$$\text{PI} = \text{V} + \text{P} + \text{S} + \text{F} + \text{M} \quad (1)$$

V is the total valves counted times 0.002. This gives a range from 0 (for zero valves counted) to 1 (for 500+ valves counted). P indicates the presence (1) or absence (0) of *Pseudo-nitzschia* spp. Similarly, S indicates the presence (1) or absence (0) of *Skeletonema* spp. *Skeletonema* spp. are one of the dominant phytoplankton groups that sink into sediment traps along the Louisiana shelf (Dortch et al. unpubl.), and their absence in the sediment indicates dissolution (Schuette and Schrader 1979). F is equal to 1 minus the percentage of total valves that are fragmented and has a value of 0 (all fragmented) to 1 (none fragmented). M indicates the presence (1) or absence (0) of valve microstructure (e.g., velum/cribra) on any valve.

Data on the concentration of nitrate and silicate in the Mississippi River at St. Francisville and New Orleans are from the U.S. Geological Survey (USGS 1955–1995) Water Quality or Water Survey Paper series. Nitrate flux estimates (mol s^{-1}) from the Mississippi River were determined by multiplying the average concentration of nitrate in river water samples (M) by the average river flow (L s^{-1}) for each calendar year in which data were available (1955–1995). River discharge data were obtained for Tarbert Landing from the U.S. Army Corps of Engineers. Historical silicate to nitrate ratios were calculated for Mississippi River inputs by dividing the concentration of silicate (M) by the concentration of nitrate (M) as determined from the available USGS data.

Sediment samples were dated by applying ^{210}Pb -derived sedimentation rate estimates to sample depths. The ^{210}Pb -dated *Pseudo-nitzschia* data were then statistically compared to nitrate flux values and the silicate to nitrate ratio in all cases where nutrient and sediment samples corresponded by date using regression analysis tools in the Minitab® 12.1 computer program.

Results—Five sets of sediment cores were successfully collected and analyzed, giving a fourfold range of sedimentation rates (Table 1, Fig. 2, ranging from 0.56 cm yr^{-1} [E60-2] up to 2.4 cm yr^{-1} [D50-1]). ^{210}Pb results indicated that sediment mixing was evident to some degree in all of the sediment cores (Fig. 2). A regression analysis of excess ^{210}Pb activity below the mixing depth versus core depth resulted in high r^2 values, however, indicating that sediment mixing did not hinder sedimentation rate estimates appreciably (Table 1, Fig. 2). Compaction rates were typical of the region, although the compaction of core D50-1 was noticeably high (30.3%, Table 1), possibly reflecting high sedimentation rates (and therefore high pore water content).

The examination of thirty samples among the five sediment cores demonstrates that *Pseudo-nitzschia* increased in

Table 1. Core dating results and sedimentation rate determination. The ^{210}Pb -dated core refers to one of the triplicate cores taken from the box core that was subjected to ^{210}Pb analysis to determine sedimentation rates (via the constant rate of supply model). The slope refers to the slope of the regression line of core depth versus $\ln(\text{excess } ^{210}\text{Pb activity})$. The r^2 is the goodness of fit of this regression line. The sedimentation rate is calculated by dividing the slope of the regression line by -0.03108 , the decay constant of ^{210}Pb . Percent compaction refers to the degree to which each sediment core was compressed during collection and splitting. The diatom core refers to which triplicate core was used for diatom analysis. Note that samples from D50-1 were used for ^{210}Pb and diatom analysis. The diatom core sedimentation rate was then determined by multiplying the ^{210}Pb -dated core sedimentation rate by the difference in compaction between the two replicate cores (^{210}Pb core % compaction/diatom core % compaction).

^{210}Pb -dated core	Slope	r^2	Sedimentation rate (cm yr $^{-1}$)	^{210}Pb core % compaction	Diatom core	Diatom core % compaction	Sedimentation rate (cm yr $^{-1}$)
D50-1	-0.013	0.79	2.4	30.3	D50-1	30.3	2.4
E30-2	-0.030	0.97	1.00	12.9	E30-1	16.8	0.94
E50-2	-0.036	0.99	0.86	11.9	E50-1	10.9	0.86
E60-1	-0.058	0.87	0.54	9.1	E60-2	5.5	0.56
F35-3	-0.042	0.98	0.74	13.3	F35-2	15.5	0.71

abundance (relative and absolute) upcore in all cases, and, therefore, over time (Fig. 3). Although *Pseudo-nitzschia* abundance varied with core depth (Figs. 3a,c), the cores were in good agreement once ^{210}Pb -derived dates were applied to the sample depths (Figs. 3b,d), despite the fourfold variation in sedimentation rates among the five cores (0.56 cm yr $^{-1}$ [E60] to 2.4 cm yr $^{-1}$ [D50]).

Although total *Pseudo-nitzschia* abundance increased in all five sediment cores (Fig. 3b), the various *Pseudo-nitzschia* groups displayed differences. The more lightly silici-

fied *delicatissima* group, composed primarily of *P. pseudo-delicatissima* according to SEM results (data not shown; <20 valves examined by SEM), increased most dramatically, especially since the 1980s (Fig. 4a, $P = 0.035$). The more heavily silicified *pungens* group, composed primarily of *P. pungens* according to SEM results (data not shown; <20 valves examined by SEM), increased significantly ($P = 0.022$) and steadily since the 1960s (Fig. 4a). The *P.* other group did not increase significantly over time, possibly because of generally low abundance (Fig. 4a). Overall, the ab-

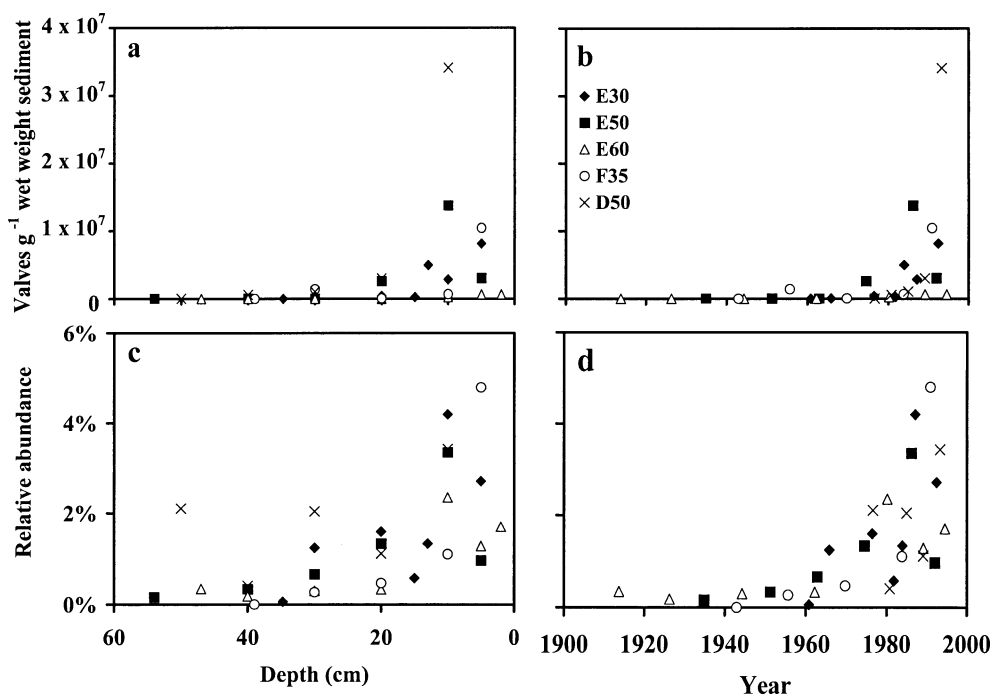


Fig. 3. (a, b) Absolute (valves g $^{-1}$ wet weight sediment) and (c, d) relative (% vs. total diatoms) abundance of total *Pseudo-nitzschia* from samples analyzed from the five sediment cores versus (a, c) core depth and (b, d) ^{210}Pb -derived core dates.

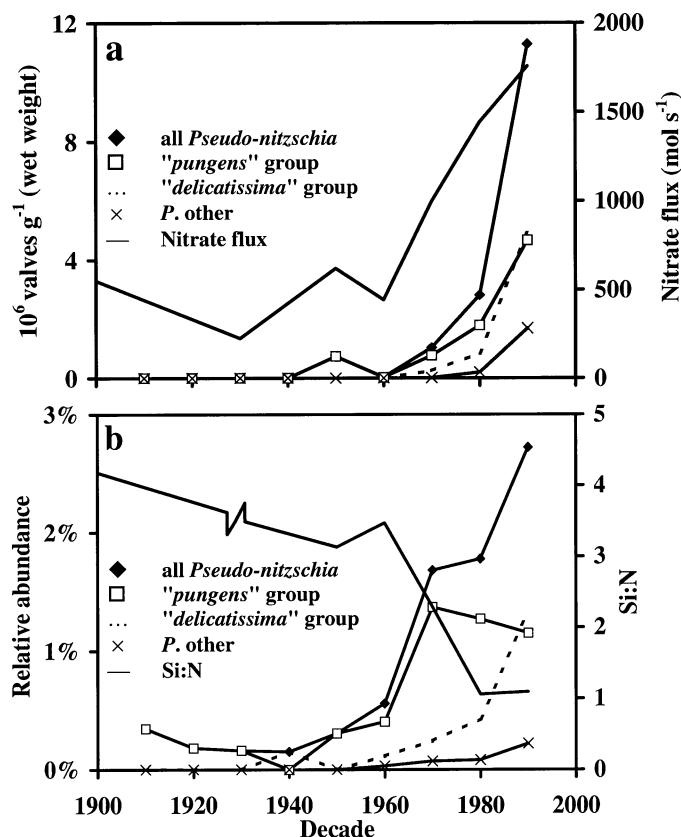


Fig. 4. Comparison of 10-yr averaged (a) absolute and (b) relative *Pseudo-nitzschia* group abundance with (a) nitrate flux ($mol\ s^{-1}$) from the Mississippi River and (b) the silicate to nitrate (Si:N) ratio from the lower Mississippi River. Note gap in Si:N ratio because of lack of silicate data from 1930s.

solute abundance of total *Pseudo-nitzschia* increased significantly over time ($P = 0.032$). The absolute abundance of total *Pseudo-nitzschia*, the *pungens* group, the *delicatissima* group, and *P. other* group were positively correlated with nitrate flux estimates from the Mississippi River ($P = 0.004$, 0.006, 0.003, and 0.012, respectively).

Pseudo-nitzschia also exhibited similar increases in relative abundance (relative to other diatoms, Figs. 3d, 4b), indicating that *Pseudo-nitzschia* increased in abundance up-core at a faster rate than the total number of diatoms (Fig. 5). Overall, the relative abundance of total *Pseudo-nitzschia*, the *pungens* group, the *delicatissima* group, and the *P. other* group were positively correlated with nitrate flux estimates from the Mississippi River ($P = 0.003$, 0.025, 0.029, and 0.005, respectively). Additionally, the relative abundance of total *Pseudo-nitzschia* and the *pungens* group were negatively correlated with the silicate to nitrate ratio ($P = 0.013$ and 0.006, respectively) from the Mississippi River.

Diatom valve preservation varied with depth among the five cores (Fig. 6a) but has been optimal since the 1950s (Fig. 6b). *Pseudo-nitzschia* valves were documented at depths of at least 50 cm (in sediment cores D50 and E60, Figs. 3a, 3c, 7a) in sediments ^{210}Pb -dated back to 1913 (E60). Other fragile diatom valves (*Pseudosolenia calcar-*

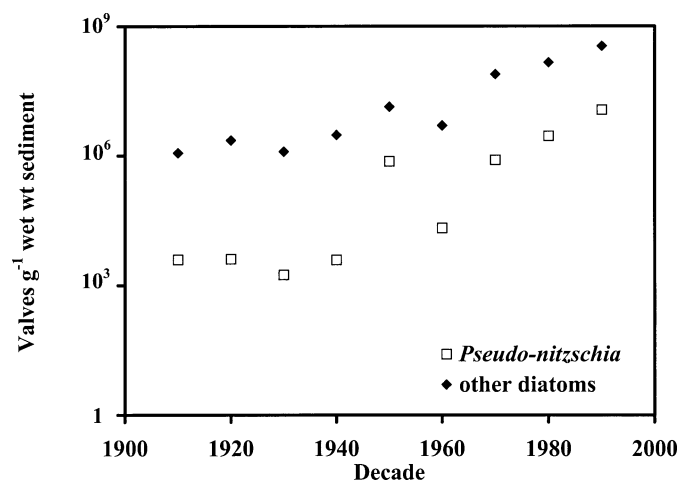


Fig. 5. Ten-year averaged absolute abundance (valves g^{-1} wet weight sediment) of all *Pseudo-nitzschia* and all other diatoms enumerated in the five sediment cores.

avis and *Skeletonema costatum*) were also documented this deep (Fig. 7b,c).

Discussion—*Pseudo-nitzschia* appears to have increased in abundance in the northern Gulf of Mexico (Figs. 3, 4), pos-

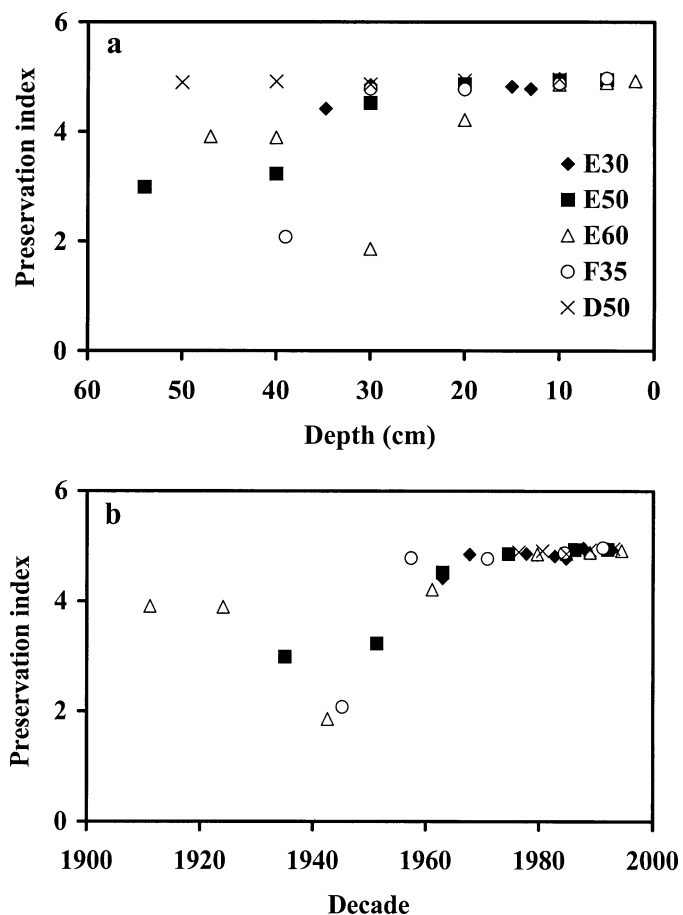


Fig. 6. Diatom valve preservation index versus (a) core depth and (b) ^{210}Pb -derived core dates.

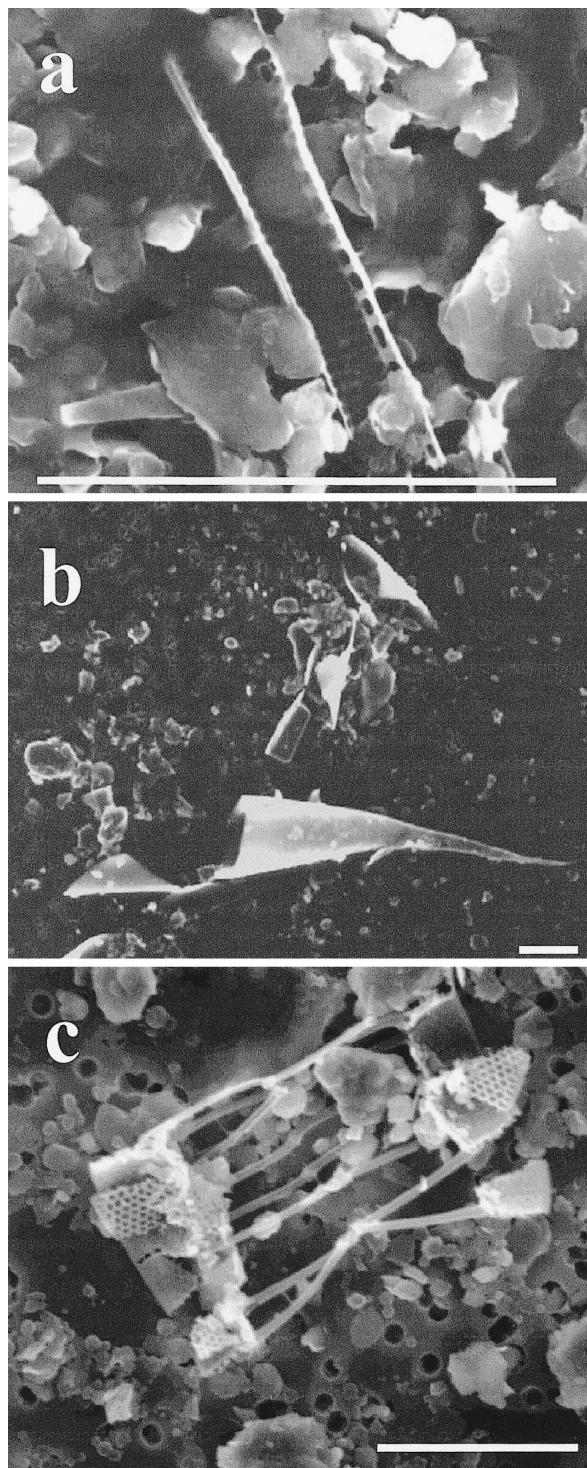


Fig. 7. SEM photomicrographs of (a) *Pseudo-nitzschia pseudodelicatissima*, (b) *Pseudosolenia calcar-avis*, and (c) *Skeletonema costatum* from core sample D50-50 cm. The scale bar for each image represents 10 μm .

sibly because of the increased flux of nitrate from the Mississippi River. Additionally, there is evidence of apparent advantageous growth of some *Pseudo-nitzschia*, such as species in the lightly silicified *delicatissima* group, under high-

nitrate, silica-limited conditions (Figs. 4, 5). The increase in the relative abundance of *Pseudo-nitzschia* (Figs. 3d, 4b) versus other diatom species suggests that not only has *Pseudo-nitzschia* been stimulated by increased nitrate inputs and silica-limited conditions, but possibly disproportionately more than other diatoms.

The hypothesized increase in *Pseudo-nitzschia* abundance in response to eutrophication is consistent with the historical data (Dortch et al. 1997). Earlier studies have demonstrated that diatom productivity was stimulated by increased nutrient loading, as indicated by strong correlations between biogenic silica in dated sediments and regional fertilizer use (Turner and Rabalais 1991; Parsons 1996). Estuarine diatom assemblages have shifted over time from oligotrophic to eutrophic species (Parsons 1996). Studies conducted in other regions have also indicated that high abundances of *Pseudo-nitzschia* appear to be associated with increased nutrient inputs (Smith et al. 1990), although eutrophication has not always been implicated (e.g., upwelling, Abrantes and Moita 1999; Trainor et al. 2000).

The increase in *Pseudo-nitzschia* abundance does not appear to be the product of dissolution processes. The presence of *Pseudo-nitzschia* valves below the sediment–water interface alone suggests adequate valve preservation. Girdle bands were seen on a specimen of *Pseudosolenia calcar-avis* from a depth of 50 cm as well (Fig. 7b). Valves of *Skeletonema costatum*, another species considered to be fragile and poorly preservable (Schuette and Schrader 1979), were also found to preserve at depth (Fig. 7c).

Although fragile diatom valves did preserve with depth in several of the sediment cores, diatom valve preservation was variable among the five cores, especially with regard to core depth (Fig. 6a). When sedimentation rates were factored in, however, it was clear that valve preservation was optimal since the 1950s (Fig. 6b). This observation may reflect regional conditions conducive for preservation (i.e., increased diatom flux, decreased bioturbation, lower interstitial pH) caused by the onset of eutrophication and subsequent hypoxia in the region (Turner and Rabalais 1991, 1994). Therefore, although *Pseudo-nitzschia* valves were documented in sediments dated to the 1910s (suggesting adequate preservation), the documented increase in *Pseudo-nitzschia* abundance during optimal preservation conditions (since the 1950s) appears to reflect actual population dynamics rather than dissolution processes.

A comparison with real-time data substantiates these conclusions. The relative abundance of total *Pseudo-nitzschia* in the 1990s (this study: 2.7% average, Fig. 4b; 1–5% range, Fig. 3d) are lower than those observed at the sediment surface reported in Dortch et al. (1997) for 1990 (17% average, 0–38% range) and 1991 (4.8% average, 0–10% range). The differences between the two studies may reflect spatial differences (station C6A/B used in Dortch et al. [1997] was approximately 60 nautical miles west of the coring sites in a region where *Pseudo-nitzschia* blooms are large and frequent), variability in *Pseudo-nitzschia* flux to the sediment surface (i.e., a bloom event), or variable diagenesis at the sediment–water interface. If the lower core numbers reflect diagenesis, then we can estimate that as few as 16% (based on 1990 data) to as many as 56% (based on 1991 data) of

the *Pseudo-nitzschia* valves at the sediment surface will be preserved to a depth of 5 cm. If we apply these diagenetic rates (16–56%) to 1970s data from Fucik and El Sayed (1979), who sampled near station C6B from 1972–1974, we obtain the following results. Fucik and El Sayed (1979) reported *Pseudo-nitzschia* relative abundance ranging from 0–17% (most <1%). Dortch et al. (1997) reported that approximately the same proportion of *Pseudo-nitzschia* in the water column reached the sediment surface, so that 0–17% of the diatoms reaching the sediment surface should be *Pseudo-nitzschia* as well. If 56% of the diatoms preserve below the sediment surface (the high value calculated above), then 0–9.5% of the diatoms preserved in 1970s sediment should be *Pseudo-nitzschia*. If 16% of the diatoms preserve below the sediment surface (the low value calculated above), then 0–2.7% of the diatoms preserved in 1970s sediment should be *Pseudo-nitzschia*. Figure 4b indicates that *Pseudo-nitzschia* constitutes approximately 1.7% of the diatom assemblage in the 1970s according to this study. Therefore, the sediment core estimates appear to be consistent with available water column data (Fucik and El Sayed 1979; Dortch et al. 1997) and sediment surface data (Dortch et al. 1997).

The dominant *Pseudo-nitzschia* species present (especially during the annual spring bloom) in the northern Gulf of Mexico is *P. pseudodelicatissima* (Dortch et al. 1997; Parsons et al. 1998), a species capable of producing domoic acid in the region (Parsons et al. 1999a, Pan et al. 2001). SEM analysis indicated that *P. pseudodelicatissima* dominated the *delicatissima* group, which exhibited the largest increase in abundance of all the *Pseudo-nitzschia* groups since the 1980s (Figs. 4a,b). This observation suggests that *P. pseudodelicatissima* may be more abundant now than in the past and may therefore pose a domoic acid poisoning threat in the region.

We conclude that the increase in *Pseudo-nitzschia* seen since the 1950s does not appear to be a diagenetic artifact, but rather a response to nutrient stimulation. Therefore, the sediment record substantiates earlier hypotheses that *Pseudo-nitzschia* abundance is stimulated by nutrient loading and indicates that some species may proliferate despite subsequent silica limitation. The sediment record may provide similar time series data for other harmful algal species as well. This study demonstrates that the increase in the abundance of some harmful algae can be documented and may be caused by excessive nutrient loading.

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Primary production, respiration, and calcification of a coral reef mesocosm under increased CO₂ partial pressure

Abstract—The effect of increased CO₂ partial pressure (pCO₂) on the community metabolism (primary production, respiration, and calcification) of a coral community was investigated over periods ranging from 9 to 30 d. The community was set up in an open-top mesocosm within which pCO₂ was manipulated (411, 647, and 918 μatm). The effect of increased pCO₂ on the rate of calcification of the sand area of the mesocosm was also investigated. The net community primary production (NCP) did not change significantly with respect to pCO₂ and was 5.1 ± 0.9 mmol O₂ m⁻² h⁻¹. Dark respiration (*R*) increased slightly during the experiment at high pCO₂, but this did not affect significantly the NCP:*R* ratio (1.0 ± 0.2). The rate of calcification exhibited the trend previously reported; it decreased as a function of increasing pCO₂ and decreasing aragonite saturation state. This re-emphasizes the predictions that reef calcification is likely to decrease during the next century. The dissolution process of calcareous sand does not seem to be affected by open seawater carbonate chemistry; rather, it seems to be controlled by the biogeochemistry of sediment pore water.

The metabolism of organic (photosynthesis and respiration) and inorganic (precipitation and dissolution of CaCO₃) carbon are the two major biological processes affecting the biogeochemical carbon cycle of marine ecosystems. Coral reefs are of particular interest because calcification and photosynthesis are physiologically linked: scleractinian corals, calcifying algae, and coral reef communities exhibit an increased rate of calcium carbonate deposition during the daylight period (i.e., when photosynthesis occurs). Both processes consume dissolved inorganic carbon (DIC) and respond simultaneously to changes in environmental parameters such as light and temperature. It has been suggested (Smith and Buddemeier 1992), and recently demonstrated (Gattuso et al. 1999; Kleypas et al. 1999; Langdon et al. 2000; Leclercq et al. 2000), that an increase in the CO₂ partial pressure (pCO₂) has a negative effect on coral and reef community calcification as a result of a decrease of the ara-

gonite saturation state (Ω_{arag}). The increase in atmospheric pCO₂ forecast for the next century led these authors to predict a significant decrease of marine calcification. This response is now well documented, but previous investigations of the response of reef community calcification to increased pCO₂ did not provide any data on the response of primary production and respiration of corals and coral reef communities (Langdon et al. 2000; Leclercq et al. 2000). Also, in some instances, the seawater DIC system was not manipulated by controlling pCO₂ but by modifying the concentrations of bicarbonate (HCO₃⁻) and carbonate (CO₃²⁻) ions (Langdon et al. 2000). It is important to have a good understanding of the response of primary production and respiration to increased pCO₂ because both processes are tightly coupled to calcification at the organism and community levels (Gattuso et al. 1999). An increase in photosynthetic CO₂ fixation under high pCO₂ could indeed counteract the decrease in calcification (Gattuso et al. 1999). Furthermore, this increase could have two consequences, depending on whether the response times of photosynthesis and calcification are similar or not. If they are similar, the increase in photosynthesis might partly balance the direct effect of increased pCO₂ on net calcification that would be more dramatic than the observed decrease; that is, what we see is an underestimate of the actual decrease of the calcification rate. Alternatively, if the response time of photosynthesis is longer than that of calcification, a delayed acclimation process could occur, and the decrease in calcification reported recently could be an acute response that could significantly diminish as photosynthesis increases; that is, what we see is a short-term decrease of the calcification rate that cannot be extrapolated over years. This issue could be investigated only by doing long-term experiments under varying pCO₂.

Physiological studies have provided valuable information on the metabolic response of marine autotrophs to changes in the DIC system. Several authors have suggested that a carbon-concentrating mechanism (CCM) operates in some