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Consolidated points and issues for discussion on the Hypoxia Advisory Panel Subgroup 1 Teleconference – 11-15-06

Hypoxia Advisory Panel Subgroup 1 - Characterization of the Causes of Hypoxia

Subgroup 1 Charge:

The development, persistence and areal extent of hypoxia is thought to result from interactions in physical, chemical and biological oceanographic processes along the northern Gulf continental shelf; and changes in the Mississippi River Basin that affect nutrient loads and fresh water flow.

A. Address the state-of-the-science and the importance of various processes in the formation of hypoxia in the Gulf of Mexico. These issues include:

> i. increased volume or funneling of fresh water discharges from the Mississippi River;
>
> ii. changes in hydrologic or geomorphic processes in the Gulf of Mexico and the Mississippi River Basin;
>
> iii. increased nutrient loads due to coastal wetlands losses, upwelling or increased loadings from the Mississippi River Basin;
>
> iv. increased stratification, and seasonal changes in magnitude and spatial distribution of stratification and nutrient concentrations in the Gulf;
>
> v. temporal and spatial changes in nutrient limitation or co-limitation, for nitrogen or phosphorus, as significant factors in the development of the hypoxic zone;
>
> vi. the implications of reduction of phosphorus or nitrogen without concomitant reduction of the other.

B. Comment on the state of the science for characterizing the onset, volume, extent and duration of the hypoxic zone.

In developing responses to assignments within the charge the Hypoxia Advisory Panel is considering the following:

Based on understanding of the current science,

- Are there summaries, conclusions, and recommendations presented in the 2000 Integrated Assessment that are not accurate or valid?
- What new findings are most relevant to this review and how do they alter our understanding of the causes of hypoxia?
- What are the strengths and limitations in scientific understanding of the issue?
- What scientific questions should be answered over the next five years?

Material Provided by Alan Blumberg, Denis Gilbert, and Don Wright

This material addresses but is not limited to the following parts of the charge: 1(A)(i) - the importance of increased volume or funneling of fresh water discharge from the Mississippi River, 1(A)(ii) - changes in hydrologic or geomorphic processes in the Gulf of Mexico and Mississippi Basin, and 1(A)(iv) - increased stratification, and seasonal changes in the magnitude and spatial distribution of stratification and nutrient concentrations in the Gulf.

Subgroup 1 – Characterization of the Causes of Hypoxia
Physical Background to Hypoxia: 4th Draft

Oxygen budget: general considerations

In this sub section, we review the physical oceanographic factors involved in hypoxia in the northern Gulf of Mexico. Justic *et al* (2006) point out that estimating the relative importance of physics versus biology in explaining hypoxia in stagnant benthic waters is very difficult owing to the complexity of the system. Rowe and Chapman (2002) have noted that physical factors are probably just as important as nitrate loading in contributing to the hypoxic conditions on the Texas-Louisiana shelf. Boesch (2003), on the other hand has disagreed and makes the argument that it is increased nitrate loading that has brought about the problem. That debate notwithstanding, the fact is that hypoxia cannot be understood or modeled with taking into account the full, complex, suite of physical and biogeochemical processes.

In simple terms, hypoxic conditions arise because the consumption of oxygen exceeds the import or production of "new" oxygenated water. The oxygen balance in the bottom layer can be expressed at lowest order by

$$\frac{\partial O_2}{\partial t} = -u\frac{\partial O_2}{\partial x} - v\frac{\partial O_2}{\partial y} + w\frac{\partial O_2}{\partial z} + K_z\frac{\partial^2 O_2}{\partial z^2} + \vec{F}_{as} - \text{Respiration} + \text{in situ photosynthesis}$$

in which the left hand term represents the change of oxygen concentration with time, the first term on the right represents the horizontal advection by across shelf currents, u, the second term represents the horizontal advection by along-shelf currents, v, the third term on the right represents vertical transport by upwelling, the fourth term represents vertical mixing (K_z is eddy viscosity), the term labeled $\vec{F}_{as}$ is oxygen flux across the air-sea interface, the term labeled "Respiration" is the non-conservative sink (i.e. consumption) and the final term refers to *in situ* production of oxygen by photosynthesis which has been measured near the bed by Dortch et al. (1994) and Rowe et al. (1995). The horizontal advection terms may reflect contributions from tides, wind stress, large-scale eddies or topographically trapped shelf waves. Relatively advanced three dimensional models are required to adequately account for these contributions. The respiration term is

the one that relates most directly to organic matter mineralisation and must be understood in the context of the biogeochemical processes addressed by other sub-teams. In the following, we will first address factors that affect vertical mixing and then review current understandings of the processes controlling horizontal advection (i.e. contributors to u and v).

Factors that control (or suppress) vertical mixing

Here, we focus on the physical oceanographic processes that govern the vertical diffusive terms. Key physical factors that affect oxygen dynamics include buoyancy fluxes (which cause stratification that suppresses mixing), near-bed suspended sediment (which causes benthic stratification that also suppresses mixing), tidal and wind-driven currents (which are the sources of the shear that enhances mixing) and waves (which enhance vertical mixing). The gradient Richardson number, Ri, expresses the ratio of turbulence suppression relative to shear production of turbulence via

$$\mathrm{Ri} = \frac{-\frac{g}{\rho}\frac{d\rho}{dz}}{\left(du/dz\right)^2} = \left(\frac{N}{\left(du/dz\right)}\right)^2 \quad .$$

When Ri > ¼, turbulence is strongly suppressed and vertical transport of oxygen from surface to bottom layers by turbulent mixing is unlikely to occur. At lowest order, scaling allows Ri to be estimated by

$$\mathrm{Ri} \approx \frac{-\frac{g}{\rho}\frac{\Delta\rho}{h}}{\left(U/h\right)^2} = \frac{\Delta\rho}{\rho}\frac{gh}{U^2}$$

where h is the characteristic vertical scale of the pycnocline, or plume thickness, ρ is water density, Δρ is the density difference and U is the speed of the mean current. Thus, high density contrasts and/or weak currents suppress vertical mixing and are favorable to hypoxia.

The mouths of the Mississippi are highly stratified "salt wedge" estuaries during low and normal flows and the effluent issues onto the shelf as a discrete layer of fresh water that is spread westward in the surface layer. Total buoyancy fluxes are, of course, proportional to river discharge. This causes the turbulent-suppressing stratification of the upper water column that is strongly implicated in hypoxia. Over the Louisiana shelf, Δρ in the upper water column is large (order 10 kg m^{-3}) because of the fresh water discharge from the Mississippi River and U is typically small because of the low tide range and weak wind-driven circulation. The characteristic thickness of the pycnocline and/or surface plume is on the order of a meter or two. Therefore, under stratified conditions, Ri is commonly (O) 10, considerably higher than the critical value of ¼.

As Rowe and Chapman (2002, 2003) (among others) point out, the resulting stratified region influenced by the Mississippi plume exerts a strong control on the extent and spatial distribution of hypoxia. Justic *et al.* (2006) maintain that this stable stratification is just as important in causing hypoxia as the nutrient-enhanced primary productivity in the surface layer. The buoyancy fluxes from the river also contribute to regional circulation in the form of baroclinic flows (Garvine 2001; Garcia Berdeal et al. 2002; Hetland 2005; Hetland and Signell 2005). Morey *et al.* (2005) present evidence that upwelling wind stress can cause pooling of low salinity water over the shelf. Numerical modeling approaches to predicting the shelf-wide spreading of the buoyant Mississippi plume are offered by Hetland (2005) and Hetland and DiMarco (in press).

Stratification near the bed is also important on the Louisiana shelf and can also restrict the delivery of oxygen to the bed. In this case, however, $\Delta\rho$ is attributable to resuspended sediment and fluid mud rather than to freshwater input. To the west of the "birds foot", convergence of suspended sediment fluxes can lead to the formation of bottom layers of fluid mud on the order of 1-2 m thick that suppress vertical mixing (Wright et al., 1997; Friedrichs et al., 2000). In this case, the gradient Richardson number is determined by the gradient in suspended sediment concentration instead of salinity, i.e.

$$\mathrm{Ri} = \frac{-\frac{g}{\rho}\frac{\partial\rho}{\partial z}}{\left(\partial u/\partial z\right)^2} \cong gs\frac{(\partial c'/\partial z)}{(\partial u/\partial z)^2} \cong \frac{B}{|u|^2},$$

where c' is sediment volume concentration, s is sediment density relative to water density and B is the buoyancy anomaly within the turbid benthic layer of the thickness h' given by

$$B = gs\int_0^{h'} c'dz\,.$$

During the time of the tripod deployment reported by Wright et al. (1997; 2001), sediment resuspension by moderate waves caused Ri to exceed the critical value of 0.25. For the bottom boundary layer, Friedrichs et al (2000), and Wright et al (2001), found Ri to be between 4.5 and 8 during times low waves when fluid mud layers of < 1 m were present due to flux convergence. When near bed sediment concentrations were attributable primarily to local resuspension (as during moderate to high waves) Ri hovered near the critical value of 1/4.

Buoyancy is only half of vertical mixing problem. The other half involves the flows and the associated shear that produces turbulence. These flows have several forcings, including tides, wind-driven currents, continental shelf waves, internal waves and wind-induced gravity waves. In most inner shelf environments, tidal currents are the major source of mixing. However, tidal currents and tidal mixing over the Louisiana shelf are extremely weak because the tide range is only about 40 cm and the tides are diurnal. So the contribution of tides to the vertical exchange of oxygen is minimal. Wind-driven currents are more important but occur episodically during wind events. These currents, which are described in somewhat more detail in the following subsection, are also weak

for most of the time. High-frequency internal wave with frequencies near N have been observed to cause mixing in the region immediately seaward of the active river mouths (Wright and Coleman, 1971; Wiseman et al, Breaking and white capping waves also contribute to mixing in the upper water column. Non-breaking, long period waves contribute little to water column mixing but can be an important source of shear within the thin wave boundary layer at the bed. The paper by Sheremet and Stone (2003) shows that storm waves are attenuated by propagating over muddy bottom and this would presumably reduce mixing.

Current regimes and horizontal advective processes

Circulation in the northern Gulf of Mexico can be considered on two scales: Gulf-wide deep sea circulation and shelf circulation near the coast. Among the most prominent features of the large-scale Gulf-wide circulation are the Loop Current and the Loop Current Eddy System (Oey, 2005; Justic *et al.* , 2006). Although these features impinge on and affect the outer shelf and are the focus of large-scale models, Rabalais *et al.* (1999) conclude that local wind forcing and buoyancy are more important to shelf circulation inshore of the 50 meter isobath. Direct ship-board observations by Jarosz and Murray (1998) during five separate cruises led those authors to conclude that the momentum balance on the inner and mid shelf to the west of the active "bird's foot" delta is dominated by wind stress. At times when wind stress was zero, currents were also nil suggesting a minimal role for buoyancy forcing over that part of the shelf.

The coastal physical oceanographic regime of the Louisiana shelf is presently scaled and constrained by the elongate "bird's foot" delta, which creates a barrier to east-west currents (Wiseman and Dinnel, 1988). By blocking along-isobath flow, this active delta lobe causes shelf circulation to be divided into two cells: one to the east and one to the west of the bird's foot (Smith and Jacobs, 2005). The most recent and comprehensive analysis of the shelf circulation in this region is that of Smith and Jacobs (2005) who assimilated extensive sets of current observational data with the governing dynamical shallow water equations. The Smith and Jacobs study assumes the rather simplistic situation of barotropic currents. More sophisticated models (e.g. Morey et al., 2003 and Zavala et al.,2003) take into account the baroclinic effects that typify the Louisiana shelf.

The observations reported by Smith and Jacobs (2005) show that depth averaged flows to the west of the bird's foot during spring and summer are weak and variable but generally set from west to east. Zavala et al. 2003 predict east to west near-coastal currents in all months but July. Stronger and more persistent flows from east to west prevail during autumn and winter.

Hydrodynamic models: present status

Alan Blumberg is working on this; I believe that he has been out of the country.

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Comments from Alan Blumberg

1. You asked what value for the buoyancy anomaly I used in my analysis. In the "Physical Background to Hypoxia: 3rd Draft" it says that delta rho is 10kg/m^3 over the LA-Texas shelf. I used that and 1000kg/m^3 as rho. The Ri of 100 says no mixing of this pycnocline is possible.

2. More information on the tidal mixing fronts we have been discussing. I have been in contact with many of the northern gulf tidal people I know (Lakshmi Kantha, Bob Weisberg, Cheryl Ann Blain, Dong-Shan Ko, Paul Martin, Harvey Seim) to get more info.

Two references for you:

1. Mooers, C. N. K. (editor) "Baroclinic Processes on Continental Shelves", AGU, 1986. has a good paper by Simpson and James - nicely written with nice schematic diagrams, satellite images, and plots.

2. Seim, H. E., B. Kjerfve, and J. E. Sneed, "Tides of the Mississippi Sound and the Adjacent Continental Shelf", Estuar. Coast. Shelf. Sci.25, 143-156,1987.

Ko tells me that he and his group are running a high resolution model for the northern part of Gulf of Mexico (NGOMNFS) which covers the Alabama/MS and Louisiana shelves. He has compared the tidal prediction to the NOAA NOS tide gauge measurement and found that the prediction is very good. He can look into the Simpson-Hunter criterion for us but I don't think it will happen soon.

We should all look at his NGOMNFS predictions on the NRLSSC website: http://www7320.nrlssc.navy.mil/NGOMNFS_WWW/

Comments from Denis Gilbert:

In the present email, I answer some of the questions you raised in the physics Word document and I also touch upon some of the issues raised in other email messages sent by either of you.

1) **Tidal mixing.** I have performed literature searches with SCOPUS and with ASFA, but to no avail. I came across a couple papers that deal with tides on the Florida coast, but saw nothing that would quantify tidal mixing (generated by bottom stress) in the coastal waters of the states of Mississippi, Louisiana or Texas. This clearly appears to be a missing ingredient in the present state of knowledge of local ocean physics.

2) **Richardson number estimates**. The vertical scale (e.g. 10 m, 4m, 1m, etc) over which the buoyancy frequency and vertical shear are estimated must always be mentioned when stating Richardson number estimates. Alan's vertical scale was 10 m, and high Ri values are to be expected on this kind of vertical scale. In general, as we estimate Ri on progressively smaller vertical scales, we obtain lower values of Ri. This is consistent with the fact that overturning events are usually observed on relatively small vertical scales (often less than one meter).

3) **Internal waves, interfacial waves, solitons**. So far, I have not come across a paper that would describe those classes of motions in the area of the Mississippi River plume or nearby coastal waters. Although it would be possible to speak of internal waves in very general terms, I would prefer to discuss "real-world" measurements from a published paper, if any exists. Unfortunately, the search engines I have been using tend to search only the titles and abstracts of papers. I may thus be missing those papers that describe internal waves into the body of the paper without mentioning the keyword "internal waves" in the abstract.

4) **Inclusion of other terms in our oxygen dynamics equation**. I think we should at least add a "w" term to take into account upwelling/downwelling processes. This was considered useful by some of the biogeochemists on the HAP. Also, in the sentence that immediately follows our oxygen balance equation on page 1, I would replace "across-shelf mean currents" by "across-shelf currents" and would also replace "along-shelf mean currents" by "along-shelf currents" to take into account time-varying currents. Perhaps more importantly, we are still missing an oxygen balance equation for the upper layer, where in addition to respiration and photosynthesis, we should have an air-sea gas exchange term. See equation (3) of Justic et al (2002) for an example of how this can be parameterized (PDF attached).

Material Provided by Tom Bianchi

Material addresses but is not limited to part 1(A)(iii) of the charge: increased nutrient loads due to coastal wetlands losses, upwelling or increased loadings from the MississippRiver Basin.

Linkages between Organic Matter Inputs, Sediment Dynamics, and Hypoxia Events on the Louisiana Shelf (USA)

Thomas S. Bianchi

Hypoxia in northern GOM

Hypoxic-to-anoxic conditions (2-0 mg O_2 L^{-1}) occur in the bottom waters of the northern Gulf of Mexico during late spring and summer where the rate of oxygen consumption exceeds its rate of input from physical transport plus photosynthetic generation. Although consumption of oxygen in the water column via primarily oxic respiration is an important process, current data and models indicate that the loss of oxygen at and near the seafloor may be the most important sink leading to hypoxic and anoxic conditions in the overlying water in this region (Morse et al., unpublished). Rowe and Chapman (2002) have a proposed that processes related to hypoxia are different along a gradient stretching west from the delta (brown water), to green water, and finally to blue water. The presumption has been that the cause of hypoxia differs at each site: the brown water region is dominated by flocculating clay, green water is dominated by primary production enhanced by the nutrient load, and the blue water is controlled by stratification. So the driving forces here are: geochemical reactions driving hypoxia near the river mouth, biological production and respiration dominating farther from the mouth, and physical stratification controlling development of hypoxia distal to the river mouth.

The strong pycnocline that develops during the summer months on the Louisiana shelf west of the Mississippi River in the northern Gulf of Mexico (NGOM) inhibits vertical mixing and re-oxygenation of the bottom waters which results in hypoxia of bottom waters. Strong mixing from storms during the winter allows bottom water to be aerated frequently and precludes hypoxia during this time. Although these are the overarching factors driving the development and destruction of hypoxia in the NGOM, much variability in geochemical and physical processes over small temporal and spatial scales that appear to exert strong controls over the timing and location of hypoxia development. Time-series data have shown that the extent of hypoxia can vary over short timescales due to rapid changes (order of hours to days) in the position of the freshwater plume (from changes in local winds) and stratification (from the passage of atmospheric fronts) (DiMarco, et al., 2006, submitted). Modeling results support these quick response times following forcing events (Hetland and DiMarco, 2006, submitted).

Studies in the Gulf of Mexico have shown that aerobic respiration in the sediments is low during hypoxic events (Rowe et al., 2002); this suggests that anaerobic respiration, build up of reduced compounds and subsequent oxidation of these reduced species in the benthic boundary layer (BBL) and sediments may account for a large percentage of the oxygen draw down in this area (Morse and Rowe, 1999). Unfortunately, the role of sediments in controlling hypoxia and currently not well understood.

General Background of Dynamics of RiOMars

River-dominated margins are dynamic regions that receive inputs of organic carbon derived from both terrestrial and marine sources. In these environments, the input of vascular plant-derived organic matter from land is significant (Hedges and Parker, 1976;

Hedges and Ertel, 1982; Hedges, 1992), and marine primary productivity is high due to high nutrient inputs associated with riverine discharge (Turner and Rabalais, 1991; Redalje et al., 1994; Hedges and Keil, 1995). Major rivers (and associated deltaic environments) provide the dominant pathway for the input of terrestrial organic carbon to marine sediments and play a disproportionately important role in transporting terrestrial materials to the ocean. Approximately 60% of the total suspended matter and 66% of the total dissolved solids transported from the conterminous U.S. to the ocean is carried by the Mississippi (Presley et al. 1980), the largest river in North America. The importance of river dominated margins to global organic carbon burial (Hedges and Kiel 1995) is indicative of the tremendous magnitude of material fluxes in these river-dominated regions (see also NSF RiOMar initiative: http://www.tulane.edu/~riomar). It has been estimated that 80% of the total organic carbon preserved in marine sediments occurs in "terrigenous-deltaic" regions near river mouths (Romankevich, 1984; Berner, 1989). Once particulate particulate organic carbon (POC) is introduced by the river or fixed on the shelves, it is carried along the Louisiana shelf, decomposed, buried, or transported to deeper regions in the Gulf of Mexico. Based on coastal primary production estimates, riverine inputs and a limited number of seabed samples, earlier studies estimated that only 20-50% of the organic carbon in coastal waters off the Mississippi is actually buried in Louisiana shelf sediments, and that <40% of the organic carbon buried is of terrestrial origin (Eadie et al., 1994; Trefry et al., 1994). There are two possible explanations for this observation: (1) Large amounts of terrestrial organic carbon and marine organic carbon are being remineralized in shelf waters and sediments or (2) POC is transported off the shelf and buried in slope and Mississippi Canyon sediments. Understanding the transport and burial of organic matter on such a dynamic shelf is critical to in determining the benthic-pelagic linkages in hypoxia events.

The distribution of mobile muds, which are thicker near the Southwest pass, varies greatly on a seasonal basis (Corbett et al., 2004). Like the Amazon delta, the seafloor along the LA shelf west of the Mississippi outlet is characterized by significant physical mixing (resuspension) producing a fluidized layer of sediments (mobile muds) that may have penetrated as deep as 8-9 cm in the winter season. Organic carbon of both terrestrial and marine origin, trapped within the surface mixed layer, will undergo significant biogeochemical decomposition mediated by microbial activity and fueled by additions of fresh planktonic material (Blair and Aller, 1995) prior to burial in the accumulation layer. Thus, the mixed layer works as a very efficient biogeochemical reactor and may lead to significant breakdown of organic carbon. It is estimated that about 50% of the sediments delivered to this region are temporarily stored near the delta – with a large fraction transported along/across the shelf in the BBL (Corbett et al., 2004, 2006a). Winter fronts are most likely responsible for the resuspension and transport of sediments along- and off-shore the Louisiana coast (Allison et al., 2000; Corbett et al., 2004). Recent hurricanes (Katrina and Rita) were responsible for the cross-shelf transport of as much as 6 to 19 years of typical decadal sediment accumulation to regions beyond 50 m (Corbett et al., 2006b). Similarly, other work has shown that labile sedimentary organic matter, produced by *in situ* diatom production in the Mississippi River plume, is rapidly (day to weeks) shunted to Mississippi Canyon, via the same

mechanisms of transport (Bianchi et al., 2006). The supply rate of this labile phytodetritus is temporally consistent enough to support macrobenthic polychaete populations that do not exist in nearshore waters off the Louisiana coast. The removal of labile organic matter that normally can feed into the hypoxic zone by these winter season and hurricane events may act as a cleansing mechanism, not commonly found in traditional estuarine systems (Bianchi, 2007). More work is clearly needed to better understand the interactions between sediment transport, residence time of organic matter in surface sediments, and hypoxia events.

Linkages with Hydrologic Alterations and Source Inputs of Organic Carbon to the Hypoxic Zone

The composition of modern organic carbon inputs to the Louisiana margin is likely to be considerably different than that recorded in buried sediments over the last 100 years. In addition to climatic trends in the catchment, the subaerial deltaic plain has experienced major changes in riverine discharge in the last ~100 years with Atchafalaya capture of Mississippi discharge (Roberts, 1998). Lobe switching along the delta front, in addition to affecting the magnitude of sedimentary organic carbon supply to a point on the margin, may also affect composition due to the input of eroded marsh sediments associated with the transgressive shorelines of inactive lobe areas (Penland et al., 1988). An acceleration in Mississippi delta wetland loss rates in the 20th century (peaking at 11,000 ha yr^{-1} in the 1960's; Dunbar et al., 1990) has been attributed to a host of natural and man-made causes including subsidence and channel dredging. Sediment loads have declined more than 70% in the Mississippi River system since 1850, which has been attributed to a network of water impoundments and the institution of federal/state/local soil conservation practices since the 1930's (Mossa, 1996). Artificial levees, which began being built early in the 1700's, were made continuous and raised following the 1927 flood. By limiting meander belt migration of the river channel, these structures have likely decreased input of soil organic carbon from bank erosion. Since 1927 the river channel below New Orleans has deepened considerably, presumably through bed incision into pre-Plaquemine sediments, which has remobilized "old" carbon in transgressional facies to the margin (Galler et al., 2003).

High rates of primary production and organic matter remineralization along river-dominated coastal margins are largely a result of terrestrial inputs of dissolved and particulate materials carried by rivers (Dagg et al., 2004, and references therein). The Mississippi and Atchafalaya rivers deliver 60% of the nitrogen on the Louisiana shelf and provide the major pathway for the input of terrigenous organic materials to the Gulf of Mexico (Trefry et al., 1994, Turner and Rabalais, 1994, Bianchi et al., 2002). Lohrenz et al. (1997) observed a direct relationship between riverine nutrient fluxes and primary production in Louisiana continental shelf waters. Primary production across the Louisiana shelf is highly dynamic, with rates ranging from as low as 0.5 g C m^{-2} day^{-1} in winter months up to 10 g C m^{-2} day^{-1} during the summer (Lohrenz et al., 1990, Redalje et al., 1994, Lohrenz et al., 1999). According to a recent model by Dagg and Breed (2003),

nitrogen availability in the Mississippi River Plume (MRP) should alter the structure of the phytoplankton community and interactions between different size classes of both phytoplankton and zooplankton. These nutrient-controlled trophic changes in MRP plankton should also result in significant spatial changes in phytoplankton composition across MRP. While the Mississippi River is also major source of dissolved organic carbon (DOC) to the Louisiana shelf, contributing an estimated 3.1 x 10^{-3} Pg DOC annually to the shelf (Bianchi et al., 2004), contributions of DOC from *in-situ* processes such as primary production, zooplankton grazing, and resuspension may also be significant, particularly during periods of high productivity (Benner and Opsahl, 2001). Substantial amounts of DOC can be produced *in-situ* by phytoplankton exudation (Norrman et al., 1995, Fry et al., 1996) and by leaching and bacterially-mediated decay of marine and terrestrially-derived POC (Biddanda and Benner, 1997). Unfortunately, a mechanistic understanding of foodweb processes in the Mississippi River plume are not well understood and may indicate that river nutrients are insufficient to support development and maintenance of the observed vast area of hypoxia (Breed et al. 2004; Green et al. 2006). A recent carbon model for the Mississippi River turbidity plume estimated that sedimentation of autochthonous organic carbon from the immediate plume contributed only 23% of the O_2 demand required for the formation of hypoxia in the region, not including and contributions from the Atchafalaya River (Green et al., 2006)

Terrestrial inputs of organic carbon to continental margin waters of the northern Gulf of Mexico (GOM) are high compared with other coastal margins of the U.S. because of significant discharge from one of the world's largest river systems-the combined inputs of the Mississippi and Atchafalaya Rivers (Hedges and Parker, 1976; Bianchi et al., 1997). Recent work has suggested that much of the terrestrially-derived organic carbon delivered to the shelf is from C_3 and C_4 plants and materials from eroded soils in the northwestern grasslands of the Mississippi River drainage basin. These investigators also concluded that C_4 plant material (^{13}C-enriched values similar to marine organic carbon was transported greater distances offshore because of its characteristically smaller grain size (Goni et al., 1997, 1998; Onstad et al., 2000; Gordon and Goni, 2003). Based on earlier work, Goni et al. (1997) concluded that the C_3 (^{13}C-depleted) terrestrial samples were being deposited on the shelf. However, recent analyses suggested that woody angiosperm material (^{13}C-depleted) preferentially settles within the lower Mississippi and in the proximal portion of the dispersal system on the shelf (Bianchi et al., 2002). More recently, it has been demonstrated that erosion of relict peats in transgressional facies of the lower Mississippi River can provide another source of "old" vascular plant detritus to the Louisiana coastal margin (Galler et al., 2003). Inputs of *Spartina* spp. (C_4 plants) from eroding marshes are also sources also contribute to the C_4 signal found in Louisiana shelf sediments. Recent work indicates C_3 plant material represents, on average, about 30 to 40 % of the total terrestrial signal in surface sediments within the Mississippi Plume region (Wysocki et al. unpublished). This suggests that the remaining terrestrial material (ca. 60-70%) is comprised of C_4 material, derived from distant riverine sources (e.g., mid-western grasslands) and local sources (e.g., *Spartina*

spp.). A key question here, is whether this terrestrially-derived carbon is bioavailable for supporting hypoxia in this region.

Remineralization efficiency in river-dominated margins has been shown to be dependent upon a variety of processes in different sedimentary regimes such as redox (Aller, 1998), mixing dynamics (Canfield et al., 1993), surface area of sediments (Keil et al., 1994), and the chemical composition of river-derived POC (Alexander, 1994). Co-metabolism, a process whereby mixing of fresh labile organic carbon (algal sources) may enhance remineralization (via higher microbial turnover rates) of natural recalcitrant material (i.e., terrestrial carbon) (Lohnis 1926; Canfield et al., 1993; Canfield, 1994; Aller 1998) may also be a major controlling variable on remineralization. Co-metabolism processes in mobile mud belts and in sandy environments in rivers may be high due to significant mixing of both labile phytodetritus and terrestrial carbon. Recent modeling work by has suggested, carbon sources that support hypoxia in the western region of the Louisiana shelf may be supported by resuspension events (Hetland, submitted). Thus, the lateral transport of fluid and mobile muds may provide a mechanism for the utilization of terrestrially-derived organic carbon, which upon immediate delivery to the coast may not usable, but over time via resuspension in fluid and mobile becomes a more viable resource for supporting hypoxia. Further work is needed on this as this remains only speculative at this time.

The loss of wetlands along coastal Louisiana has been estimated to be about 70 $km^2\ y^{-1}$ (Dunbar et al., 1992), and is generally the result of subsidence, decreased sediment availability, and construction of canals (Webb and Mendelssohn, 1996; Turner, 1997). While there are many critical concerns about the stability of the delta regarding this issue, the fate of this organic matter has never really been addressed as it relates to source inputs to the hypoxic zone. Wetlands could be a possible source of both POC and DOC. The concept of coastal marsh systems as importance food resources for offshore heterotrophs, at both lower and higher trophic levels, is certainly not a new. For example, the "*outwelling hypothesis*" purported that salt marshes transport biologically available organic matter into near-shore waters, thereby enhancing secondary production on the shelf (Odum, 1968). While this phenomenon was generally not supported by many of the earlier studies (Teal, 1962; Odum and de la Cruz, 1967; Haines, 1977), more recent work (e.g., Moran et al., 1991) has shown that 6 to 36% of near-shore DOC off the coast of Georgia originates from coastal salt marshes, thereby enhancing secondary production on the shelf. A study by Bianchi et al. (1997) along with other recent studies have demonstrated (with the use of more efficient biomarkers) that a significantly higher fraction of vascular plant materials is being transported as POC further out to the continental shelf and slope (Moran et al., 1991; Moran and Hodson, 1994; Trefry et al., 1994). If significant outwelling effects of marsh detritus on shelf communities were to documented, the Louisiana coast would likely be the best place to look for it, this region has the highest land loss in the lower 48 states (Baumann and Turner, 1990). Recent estimates, based simply on land loss rates from Louisiana marshes, the mean content of total organic carbon in marsh sediments, and the assumption that a depth of 1 m of marsh is lost when marsh is converted to open water, indicates that there is a yield of 70×10^{11} g C y^{-1}, equivalent to 1.28 g C d^{-1} for each m^2 of an assumed hypoxic zone of 15,000 m^{-2}

(Dagg et al., submitted). If correct, this input is quite large when considering that phytoplankton production on the Louisiana shelf is ca. 0.44 g C m^{-2} d^{-1} (Chen et al., 2000). However, in another recent paper, the annual amount of organic carbon released from Louisiana wetlands was estimated to be considerably lower than the Dagg et al., , **I need to resolve these differences in how these estimates were made, not being partial here, I simply provided more for the Dagg et al., paper because it had more detailed information on how they arrived at their numbers.**

Redox Indices as They Relate to Anoxia/ Hypoxia in Sediments

Studies in the Gulf of Mexico have shown that aerobic respiration in the sediments is low during hypoxic events (Rowe et al., 2002); this suggests that anaerobic respiration, build up of reduced compounds and subsequent oxidation of these reduced species in the BBL and sediments may account for a large percentage of the oxygen draw down in this area (Morse and Rowe, 1999). Other work found that the balance between the frequency of seabed disturbance, rate of geochemical reactions, and reactant concentrations work together to promote efficient remineralization in highly mobile muds near large river mouths (through redox cycling (McKee et al., 2004; Aller et al. ,2004; Chen et al., 2004, 2005). This frequent cycling of reduced and oxidized compounds is likely to have a profound effect on short-term oxygen consumption in the BBL, which could influence development of bottom hypoxia.

Approximately, 81% of the all the pyrite burial in the entire Gulf of Mexico occurs in the Texas-Louisiana region, which is highly influenced by inputs from the Mississippi-Atchafalaya deltaic complex (Lin and Morse, 1991). Nevertheless, dissolved sulfide concentrations are usually low to non-detectible near the sediment-water interface in Louisiana shelf sediments under oxic conditions (e.g., Lin and Morse, 1992; Morse and Rowe, 1999). In fact, while sulfate reduction was shown to be active process in this region (14 to 16 mmol m^{-2} d^{-1}), resulting in the accumulation of substantial concentrations of total reduced inorganic sulfur (TRS), dissolved sulfide was not detectable (~ 1 μM) in porewaters (Morse and Rowe, 1999). This was likely the result of the high dissolved Fe^{2+} concentrations in the porewaters that limited dissolved sulfide via iron sulfide mineral formation. There is clearly no limitation of dissolved Fe in porewaters (ca. 50 to 100 μm) for iron sulfide formation in these sediments. Low sulfide concentrations may also be related to large patches of *Beggiatoa* spp. in this region (Larkin and Strohl, 1990). Filaments of the bacteria *Beggiatoa* spp. and other unidentified filamentous bacteria form on the surface of the sediments at oxygen levels as high as 1 mg l^{-1} but not higher (L. Duet, Q. Dortch, N. Rabalais, unpublished data). In fact, other work, which has detected H_2S in bottom waters, reports that the occurrence of anoxia and production of H_2S in bottom waters on this shelf are limited even though the continental shelf is seasonally hypoxic over a large area and oxygen concentrations are often below 0.5 mg l^{-1} (Rabalais and Turner 2006) – **unfortunately the method used for H_2S detection is not provided in this work.**

Most of the inorganic nitrogen in hypoxic bottom waters is present as nitrate, but there are sometimes significant amounts of ammonium. Denitrification rates in sediments from stations within the hypoxic zone ranged between 150 and 410 µmol N m^{-2} hr^{-1} (Childs et al. 2002, 2003). The highest rates were observed when bottom water oxygen concentrations were between 1 and 3 mg l^{-1}. Denitrification activity was significantly lower at stations where dissolved oxygen was lower than 1 mg l^{-1} or greater than 3 mg l^{-1}. Associated nutrient data indicated that the dominant form of nitrogen shifts from nitrate to ammonium as anoxia is approached (Rabalais and Turner 2006). Earlier field studies on the Louisiana shelf west of the Mississippi River (Lin and Morse, 1991; Morse and Berner, 1995; Rowe et al., 1995, 2002; Morse and Rowe, 1999; Morse unpublished data) have been used to construct a diagenetic model for the response of sediment biogeochemistry to seasonal changes in the redox conditions of the overlying waters (e.g., Rabalais et al., 1994, 2002). The approach was to apply the diagenetic model of Eldridge and Morse (2000) largely derived from the earlier diagenetic models of Van Cappellen and Wang (1996) and Boudreau (1996). These models can be used to make better predictions of how the sediments over time will interface with hypoxia

Just an addition of some macrofaunal response info. here, I do have information on meiofaunal as well. The fish really show now well defined response at all. Despite the anoxic appearance of sediments and detection of hydrogen sulfide in overlying waters, there usually remain some surviving fauna, typically polychaetes of the genera *Magelona, Paraprionospio* or *Sigambra* or sipunculans (Rabalais et al. 2001), so that the sediments are not completely azoic. The hypoxia-affected infauna on the northern Gulf of Mexico is characterized by small, high abundance opportunistic species. *Paraprionospio pinnata* is common at all locations. *P. pinnata* is a highly fecund, multiple-spawning, ubiquitous member of the benthic macroinfauna of the northwestern Gulf of Mexico shelf (Mayfield, 1988).

<u>Material Provided by Hans Paerl</u>

Material addresses nutrient dynamics including nutrient limitation in various parts of the Gulf, temporal and spatial shifts between phosphorus and nitrogen limitation, and perhaps silicon, and the linkage between the period of maximum production and hypoxia. Material addresses relevant parts of the charge: 1(A)(iii) - increased nutrient loads due to coastal wetlands losses, upwelling, or increased loads from the Mississippi River Basin, and 1(A)(v) - temporal and spatial changes in nutrient limitation or co-limitation, for nitrogen or phosphorus, as significant factors in the development of the hypoxic zone

Relevant questions

1. Spatially, what are the patterns of nutrient (N, P, Si) limitation in the N. GOM region affected by riverine discharge and hypoxia? Where and what is the evidence?

2. Temporally, what are the patterns of nutrient (N, P, Si) limitation in the N. GOM region affected by riverine discharge and hypoxia? Where and what is the evidence?

3. Are there seasonal shifts in these patterns, and are there documentable changes in these patterns on the multi-annual and decadal scale?

4. How does bioassay-determined nutrient limitation compare to nutrient limitation inferred from stoichiometric ratio relationships?

5. How do patterns of nutrient limitation determined by bioassays and inferred from stoichiometric relationships change in relation to riverine/wetland nutrient discharge?

6. How do episodic events (i.e. floods and droughts) impact 1-5 relative to more gradual multiannual trends?

7. How do the patterns in 1-6 relate to spatiotemporal patterns in primary production in the N. GOM?

8. Are there documentable linkages (in time and space) between trends in wetland loss, nutrient loading and limitation patterns?

9. What are the roles of upwelling compared to riverine and wetland nutrient inputs?

10. What are the impacts of nutrient limitation (and changes therein) on the composition and function of phytoplankton comprising the base of the food web?

11. What might the biogeochemical consequences of these changes be?

12. What are the potential relationships between these consequences and hypoxia dynamics in the N GOM?

GOM Nutrient-productivity-hypoxia issues: What do we know and what are the uncertainties?

Hans W. Paerl

Introduction

Excessive nutrient loading, dominated by discharge from the Mississippi and Atchafalaya river systems, enhances planktonic primary production in the shallow near-shore receiving waters of the Northern Gulf of Mexico (NGOM) shelf (Lohrenz et al. 1990,

1992; Turner and Rabalais 1994; Rabalais et al.1999a. The nutrients of concern are nitrogen (N), phosphorus (P), and silicon (Si). Both primary productivity and phytoplankton biomass are stimulated by these nutrient sources (Lohrenz et al. 1990, 1992; Ammerman et al. 2004; Sylvan et al. in press). The spatial and temporal extent and magnitudes of this stimulation vary significantly, and this appears related to; 1) amounts of freshwater discharge and their nutrient loads, 2) the nature and frequencies of discharge (i.e. acute, storm- and flood-based vs. more gradual, chronic, seasonal discharge), and 3) the direction and spatial patterns of discharge plumes as they enter and disperse in the NGOM (Justic et al. 1993; Lohrenz et al. 1994; Rabalais et al 1999b). A proportion (range of percentages?) of the freshwater discharge transits via freshwater and coastal wetlands and coastal groundwater aquifers, which, by biogeochemically-processing nutrient loads modify both the concentrations and total loads of nutrients as they make their way to the NGOM (Day et al. 2003; Turner 2005); the extent to which wetlands alter nutrient loads is the subject of considerable debate (Mitch et al. 2001; Day et al. 2003, Turner 2005). Nutrients can also enter this region from deeper offshore sources, via advective transport over the shelf, a modified form of "upwelling" (Chen et al. 2000; Cai et al. 2005). Lastly, nutrients can be deposited directly on the nutrient-sensitive NGOM waters from atmospheric sources such as rain- and dryfall (Goolsby et al. 2000, Paerl et al. 2002).

Historic analyses indicate a great deal of variability in seasonal, interannual and decadal-scale patterns and amounts of freshwater and nutrient discharge to the NGOM (Turner and Rabalais 1991; Rabalais et al. 2002). As a result, primary productivity and phytoplankton biomass response can vary dramatically on similar time scales. This has proven to be a significant challenge to interpreting trends in nutrient-driven eutrophication (Harding 1994; Boynton and Kemp 2000; Paerl et al 2006). Furthermore, in the turbid and highly colored (CDOM) waters of the river plumes entering the NGOM nutrient and light availability strongly interact as controls of primary production and biomass. These interactive controls modulate the relationships between nutrient inputs and phytoplankton growth responses in this region (Justic et al. 2003; Lohrenz et al. 1994). Ultimately this affects the formation and fate of autochthonously-produced organic carbon that provides an important source of the "fuel" for bottom water hypoxia in this region.

As nutrients transit the riverine, wetland, nearshore and coastal environments that constitute the NGOM hydrologic continuum, they are actively processed and transformed by microbes, higher fauna and flora as well as geochemical processes in both the water column and sediments (Gardner et al. 1994; Pakulski et al. 1995, 2000; Bode and Dortch 1996; Childs et al. 2002; Liu and Dagg 2003; Wawrick et al. 2004; Jochem et al. 2004; Bianchi ????; Others). The extent to which nutrients are discharged to, cycled and transformed within the receiving waters ultimately determines their availability, persistence and fate. Specifically, the inputs and availability of externally-supplied and internally recycled nutrients strongly influence the amounts and fate of "new" production that provides the "fuel" for hypoxia.

Who are the Primary Producers in the NGOM?

With regard to nutrient primary production interactions, it is important to know who the dominant primary producers are, where they reside, what their contributions to new production are, and what their fate is. In NGOM waters downstream of the rivers, wetlands and intertidal regions, microalgae are by far the dominant primary producers (Lohrenz et al. 1992, 1997; Redalje et al. 1992; Rabalais et al. 1999a). The microalgal communities are dominated by the phytoplankton (Redalje et al. 1994, 1994; Chen et al. 2000), athough benthic microalgal communities are also important sites of primary production and nutrient cycling, especially in near-shore regions (Jochem et al. 2004). As nutrient loads and limitations change over time and space, the proportions of planktonic vs. benthic microalgae may change; i.e. as nutrient inputs are reduced and planktonic primary production is reduced, the microalgal community may shift to a more benthic dominated one. This could yield significant implications for biogeochemical (nutrients, carbon and oxygen) cycling and trophodynamics (Rizzo et al. 1992; Darrow et al. 2003).

What, When and Where are the Limiting Nutrients?

Physically, chemically and biologically, the NGOM region is highly complex and nutrient limitation reflects this complexity. Along the freshwater to full-salinity hydrologic continuum representing the NGOM, ratios of nutrient loads and concentrations vary significantly, both in time and space. For example, depending on the season, specific hydrologic events and conditions (storms, floods, droughts), molar ratios of total N to P (N:P) supplied to these waters can vary from over 300 to less than 5 (Turner et al. 1999; US EPA 2004; Ammerman et al. 2004; Sylvan et al. in press). Furthermore, additional environmental factors, such as flushing rate (residence time), turbidity and water color (light limitation), internal nutrient recycling, and vertical mixing strongly interact to determine which nutrient(s) may be controlling primary production (Lohrenz et al. 1999). Compounding this is the frequent spatial separation between high nutrient loads, the zones of maximum productivity and hypoxia (Lohrenz et al. 1990, 1994; Rowe and Chapman 2002). Conceivably, primary production and algal biomass accumulation limited by a specific nutrient inshore may constitute the “fuel” for hypoxia further offshore, where productivity in the overlying water column may be limited by another nutrient. This scenario appears to be the case during the spring to summer transitional period, when inshore primary production is P limited (Lohrenz et al. 1992, 1997; Ammerman et al. 2004 Sylvan et al. in press), but offshore productivity is largely N limited (Lohrenz 1992, 1997; Dortch and Whitledge 1992). The relevant questions are; which total productivity is greater and what roles do these different sources of productivity play in fueling and driving hypoxia?

Early work on NGOM nutrient limitation tended to focus on the waters overlying the hypoxic zone; typically, these waters are over the shelf, but further offshore than the river plume waters. Stoichiometric N:P ratios indicated that, during summer months when hypoxia was most pronounced, that N should be the most limiting nutrient (Justic et al. 1995; Rabalais et al. 2002). This work has led to the general conclusion that N is most

limiting and that reductions in N loading would be most effective in reducing "new" C fixation and resultant phytoplankton biomass supporting hypoxia (Rabalais et al 2002, 2004). This, coupled with the nutrient loading trend data over the past 40-50 years, which showed N loading increasing more rapidly than P loading, has formed the basis for arguing that N input reductions would be most effective in reducing the eutrophication potential and hence formation of "new" C supporting hypoxic conditions.

While it is likely that N limitation characterizes offshore waters, more recent nutrient addition bioassays (Ammerman et al. 2004; Sylvan et al. in press) and nutrient stoichiometric ratios have shown that inshore productivity appears to be more P limited, especially during periods of highest productivity and phytoplankton biomass formation (Feb-May), when freshwater discharge and total nutrient loading are also highest (Lohrenz et al. 1999; EPA 2004; Sylvan et al. in press).
The strong P limitation during this period appears to be a result of the very high rates of N loading that have increased more rapidly than P loading over recent history (the past 50 years) (Turner et al. 1991, 1999); this is exacerbated during periods of high freshwater runoff, which typically contain very high N:P ratios. Inshore primary productivity tends to shift into more of an N limited mode once freshwater discharge decreases during the drier summer-fall period (June-October). However, total primary production and phytoplankton biomass accumulation are far lower during this more N-limited period than during the earlier P-limited period. Overall, maximum "new" organic C formation tends to coincide with periods of highest N:P, which are P limited (Lohrenz et al. 1992, 1997, 1999; Ammerman et al. 2004; Sylvan et al. in press).

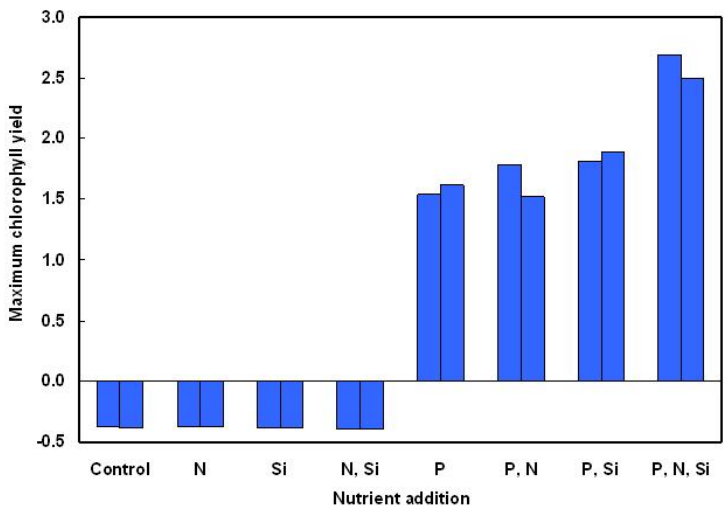
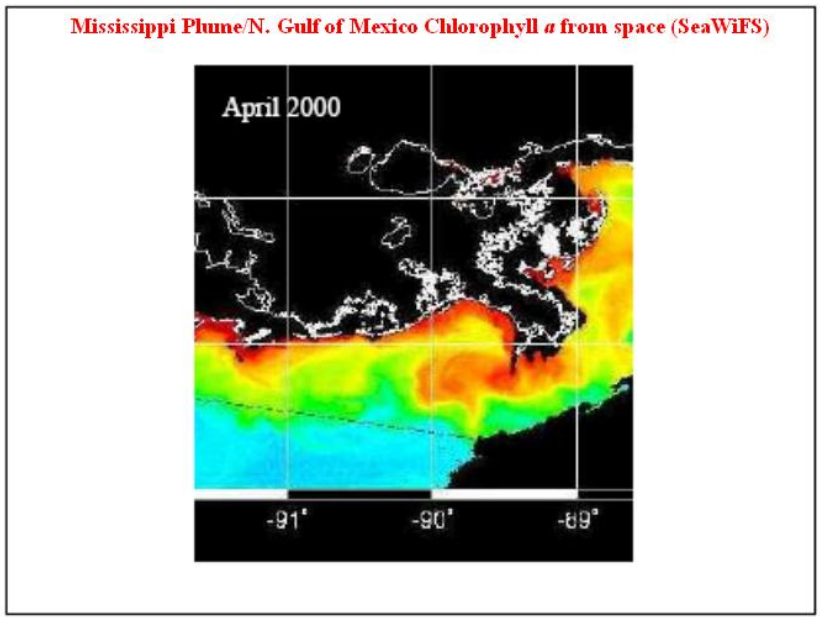


Figure 1: Results of a nutrient addition bioassay in the inshore Mississippi plume region during May 2001. Data courtesy of J. Ammerman (Ammerman et al. 2004).

Field data and remote sensing imagery indicate that *in situ* phytoplankton biomass (as chlorophyll *a*) concentrations can be high in inshore waters that have been shown to be P limited (Fig. 1). Therefore, the following question emerges; what is the spatio-temporal linkage of this P-limited high primary production and phytoplankton biomass accumulation to hypoxic bottom waters located further offshore? Furthermore, what are the relationships between N limited production later in the summer and hypoxic conditions, which typically are most extensive during this period. These potential "relationships" are complicated by the fact that there are strong, co-occurring physical drivers of hypoxia, including vertical density stratification and respiration rates, which tend to be maximal during periods of maximum development of hypoxia (c.f. Rowe and Chapman 2002; Wiseman, others???).



There are likely to be periods of P and N co-limitation, which would typically occur between spring and summer months. This condition is similar to large estuarine systems with a history of eutrophication, such as Chesapeake Bay (Fisher el al. 1992). In Chesapeake Bay, N and P co-limitation tends to occur during the spring runoff period when maximum rates of N loading take place. Once the spring runoff peak subsides, N limitation tends to be more prevalent (Malone et al. 1996, Fisher et al. 1992; D'Elia et al 1996). Spatially, the most upstream, freshwater segments of Chesapeake Bay tend to be most P limited, especially during spring runoff conditions, while the more saline down-estuarine waters tend to be most N limited. In Chesapeake Bay, the more turbid upstream freshwater component tends to exhibit interactive light and P limitation or N+P co-limitation (Fisher et al. 1988, Harding et al. 2002). Further downstream, light limitation plays a less important role. This scenario could prove similar to the riverine-coastal continuum in the NGOM, where the most turbid upstream river plume waters are likely to exhibit the highest probability for light-nutrient interactive limitation of primary production (Lohrenz et al. 1999a,b).

While bioassay data tend to indicate P limitation during springtime in the freshwater portions of this continuum and N&P co-limitation and N limitation in the more saline offshore waters during summer months, the bioassays do not account for sediment-water column exchange, because they are excluded during the course of incubation. It is possible, although unlikely because short incubation times, that sediment-water column P cycling in the shallow NGOM water column may minimize P limitation *in situ*. In order for this scenario to be operative, parallel N recycling would have to be far less efficient, which, based on numerous studies does not appear to be the case (Gardner et al. 1994; Bode and Dortch 1996; Pakulski et al. 2000; Wawrick et al. 2004; Jochem and Gardner 2004; Cai and Lohrenz 2005). Bioassay-based N limitation results might also be influenced by the elimination of "internal" sediment-water column N recycling, although this seems unlikely as well, especially if denitrification is operative (Childs et al. 2002). Sediment-based denitrification would lead to N "losses" from the system, thereby exacerbating N limitation. This would not be captured in bioassays, which isolate the sediments form water column during incubation. The relatively short incubation times of bioassays probably preclude these potential artifacts. They offer a "snapshot" of nutrient limitation to complement longer-term, ecosystem-scale assessments.

Interestingly, N and P limitation inferred from stoichiometric ratios of soluble (and hence biologically-available) inorganic or total N or P concentrations and inputs (loads) tend to confirm bioassay-based conclusions concerning specific nutrient limitations. For example, inshore, river influenced waters exhibit quite high molar N:P ratios, often exceeding 50 (c.f. NECOP Reports; US EPA 2004). Nutrient addition bioassays initially conducted in these waters by Lohrenz et al. (1999) and more recently by Sylvan et al. (2006) consistently revealed P limitation, especially during spring periods of maximum primary production and phytoplankton biomass accumulation. These same studies also indicated a tendency towards N and P co-limitation and exclusive N limitation during later summer months, when soluble and total N:P values dipped below 15. It should also be noted however that rates of primary production and phytoplankton biomass during this more N limited period are at least 5 fold lower than spring values, according the GOM NECOP data; c.f. Lohrenz et al. 1999; US EPA 2004; Ammerman et al. 2004). The EPA (2004) report and Sylvan et al. (2006) point out that P-limited spring production of "new" C may play a proportionately greater role than N-limited summer production as a source of "fuel" supporting hypoxia in the NGOM. Transport-wise, the degree and extent to which this elevated spring production accounts for summer hypoxia needs to be quantified. Process-wise, linking zones and periods of high primary production and phytoplankton biomass to those exhibiting bottom water hypoxia is a fundamentally-important and challenging question that underlies the linkage of nutrient-enhanced production with bottom water hypoxia in the NGOM. Extrapolation of C production to hypoxia data along the entire riverine-coastal shelf continuum, where zones and periods of maximum productivity and bottom water hypoxia do not necessarily coincide or overlap, depends on knowing C transport and storage (including burial), internal nutrient and C cycling and C consumption (heterotrophic metabolism and respiration) processes along this continuum (c.f. Redalje et al. 1992; Cai and Lohrenz 2005). These links

between locations and periods of specific nutrient limitation (or stimulation) of production and the fate of this production relative to hypoxia must be clearly-established and quantified in order to formulate long-term, effective nutrient management strategies for this region.

N and P loading in relation to other potentially-limiting nutrients

While excessive N and P loading are implicated in eutrophication of the NGOM, these nutrients also plays a role in the balance, availability and ecological manifestations of other potentially-limiting nutrients, most notably Si and Fe. In the Mississippi plume region, N is supplied in excess of the stoichiometric nutrient ratios needed to support phytoplankton and higher plant growth (i.e. Redfield ratio, Redfield, 1958). If N over-enrichment persists for days to weeks, other nutrient limitations may, at times, dominate; one result is P limitation, which has recently been demonstrated in bioassays (Ammerman et al. 2004 Sylvan et al. in press). In addition to P limitation, N and P co-limitation and Si limitation (of diatom growth) have been observed in the fresh and brackish water components of riverine plumes that can extend more than 100 km into the receiving waters (c.f. Dortch and Whitledge 1992; Lohrenz et al., 1999; Dortch et al. 2001). A similar scenario is evident in the Chesapeake Bay, where elevated N loading accompanying the spring maximal freshwater runoff period increases the potential for P limitation (Fisher and Gustafson, 2004). The biogeochemical and trophic ramifications of such shifts are discussed below.

The roles of chemical forms and amounts of nutrients in phytoplankton community dynamics and eutrophication

Nitrogen and phosphorus are supplied to the NGOM in inorganic and organic forms. In terms of mass loading, both organic and inorganic fractions are significant (Turner and Rabalais 1991; Toon and Dagg 1992a, b, Turner et al. 1999; Cai and Lohrenz 2005). Because they are readily available to phytoplankton and higher plants, dissolved inorganic forms have been the focus of eutrophication studies in the NGOM and elsewhere (c.f. Bode and Dortch 1996; Paerl 1997; Bricker et a. 1999; Lohrenz et al. 1999; Turner and Rabalais 1999; Dortch et al. 2001). However, recent work has shown that dissolved organic forms N and P can be utilized and metabolized by a wide range of microorganisms, including heterotrophic bacteria and microalgae (c.f. Antia et al. 1991, Paerl 1991; Seitzinger and Sanders 1999). The ability of some microalgal groups to utilize dissolved organic N (DON), which often is the most plentiful new N source in estuarine and coastal waters (Cornell et al. 1995, Peierls and Paerl 1997, Seitzinger as Sanders 1999), can provide a competitive advantage (Paerl 1988). For example, some heterotrophic dinoflagellates, cyanobacteria and diatoms can assimilate diverse organic compounds over a range of naturally-occurring concentrations (Molloy and Syrett 1988; Antia et al. 1991; Mulholland et al. 2000; Gobler and Sañudo-Wilhemy 2003). Some phytoplankton groups are capable of photoheterotrophy (i.e. light-stimulated assimilation organic compounds), which could be advantageous in illuminated surface waters where bloom species often thrive (Paerl 1991). This metabolic flexibility enhances the ability of

heterotropic and photoherotrophic microalgal taxa to utilize and exchange a variety of N-containing compounds. This is particularly relevant for planktonic and benthic marine cyanobacterial and dinoflagellate nuisance bloom genera which can utlize diverse inorganic and organic new N inputs, and in the case of some cyanobacteria can also resort to nitrogen (N_2) fixation as a N source when external N sources are depleted (Paerl 1988). Some phytoplankton groups, including HABs use dissolved organic P as a possible source of "new" P to sustain and enhance production (Riegman et al. 1998; Lomas et al. 2001, Oh et al. 2002). Using this "switch hitting" capability, these taxa are able to exploit intermittent or pulse organic nutrient loading events such as periods of riverine runoff following storm events, periodic upwelling and deepening of the mixed layer, atmospheric (rainfall and dryfall) and groundwater discharge (Paerl 1997; Seitzinger and Sanders 1999). This metabolic flexibility is thought to help initiate and sustain massive blooms of cyanobacteria in the eutrophied Baltic Sea, nutrient enriched coastal lagoons, and some estuaries (Paerl 1988; Panosso and Graneli 2000).

Some organic compounds may also have chemotactic and allelopathic functions (c.f. Lewis 1986; Sole et al. 2005). In these capacities, specific compounds that are excreted by some phytoplankton taxa may attract or repel other phytoplankton or bacterial taxa, and serve as cues for establishing specific associations between consortial and symbiotic partners. Specifically, organic N compounds (e.g. amino acids, peptides) may play a central and crucial role in determining microbial community composition, including establishment and proliferation of bloom species.

Historic and contemporaneous evidence supports the contention that anthropogenically and climatically-induced changes in N and P loading have increased NGOM primary productivity, phytoplankton biomass and altered phytoplankton community composition. There are several reasons why phytoplankton community composition may have been altered by changes in nutrient loading: 1) Competitive interactions among phytoplankton taxa based on varying nutrient supply rates based on differing affinities for nutrient uptake and assimilation (i.e. varying nutrient uptake affinities and kinetics), 2) Competitive interactions based on the relationships between nutrient supply rates and photosynthetically available light (i.e. low vs. high light adapted taxa), 3) Competitive interactions based on changes in N vs P supply rates (e.g. differential N vs. P uptake capabilities and selection for nitrogen fixing cyanobacteria), 4) Competition based on the ratios of N and P vs. Si (silicious vs. non-silicious taxa), 5) Differential grazing on phytoplankton taxa (top-down controls), and 6) nutrient-salinity controls (interactive effects of changes in freshwater discharge on NGOM salinity and nutrient regimes due to climatic and watershed hydrologic control changes). Each set of controls can influence the amounts and composition of primary producers. These controls can also interact in time and space, greatly compounding and confounding the interpretation of their combined effects.

One important effect of differential nutrient loading is the well-documented increases in N and P relative to Si loading. While N and P loads tend to reflect human activities in and alterations of the watershed, Si loads tend to reflect the mineral (bedrock and soil) composition of the watershed; a geochemical aspect that is less influenced by human watershed perturbations. Agricultural, urban and industrial development and hydrologic alterations in the Mississippi and Achafalaya basins have led to dramatic increases in N and P relative to Si loading. In addition, the construction of reservoirs on tributaries of these river systems has further exacerbated this situation, by trapping Si relative to N and P (Daniel, need reference for this). The overall result has been an increase in N:Si and P:Si ratios (or a decrease in Si:N and Si:P ratios) that can influence both the amounts and composition of phytoplankton; including potential shifts from diatoms to flagellates and dinoflagellates (Turner et al., 1998; Rabalais et al., 2001; Justic et al., 1995). Diatoms are a highly desired food item for a variety of planktonic and benthic grazers, including key zooplankton species serving an intermediate role in the NGOM food web (Dagg 1995). The dinoflagellates and cyanobacteria, while serving roles in the food web, also contain species that may be toxic and/or inedible (Anderson and Garrison 1997). Some of these species can rapidly proliferate under nutrient sufficient and enriched conditions, and thus constitute harmful algal bloom (HAB) species. Toxicity may directly and negatively impact consumers of phytoplankton as well as higher-ranked consumers, including finfish, shellfish and mammals, including humans. If non-toxic but inedible (due to size, shape, coloniality) phytoplankton taxa increase in dominance, trophic transfer may be impaired. Planktonic invertebrates, shellfish and finfish consumers whose diets are highly dependent on the composition and abundance of specific phytoplankton food species and groups may then be affected (Turner et al., 1998). This could have consequences for C flux, with a relatively higher fraction of C being processed via microbial pathways (i.e. the "microbial loop"), or sedimented to the bottom. In either case, a greater fraction of the primary production would remain in the system, as opposed to being exported out of the system via transfer to higher trophic level and fisheries. The net result would be more C metabolized within the system, leading to enhanced oxygen consumption and increased hypoxia potentials.

Sediment paleoecological evidence from Chesapeake Bay, where long-term (at least two centuries) N and P enrichment (and parallel lack of Si enrichment) accompanying human development has been documented, showed a decline in diatom dominance, while total phytoplankton production and C sedimentation increased (Cooper 1995). In the NGOM, this trend appears to have been accompanied by an increase in the relative proportion of less desirable phytoplankton taxa i.e. cyanobacteria (Chen et al. 2001).

In estuarine systems, biogeochemical and trophic responses to altered nutrient loading stoichiometry are linked (Conley, 2000). For example, when phytoplankton composition and biomass are altered in response to relatively high N:P and N:Si loads, the trophic fate of this new production changes. In the case of diatoms, which are readily grazed and packaged as fecal pellets by zooplankton, changes (decreases) in their availability and abundance may affect the downward flux and accumulation of such nutrient-rich pellets

(Dagg et al. 2005). This, in turn, may result in changes in biogenic Si cycling in sediments and availability to future diatom populations. Poorly grazed phytoplankton species, especially bloom-formers, that accumulate in the water column may increase the downward flux of carbon and other nutrients, since they will be less effectively cycled in the water column. This, in turn may exacerbate hypoxia and anoxia potentials and nutrient regeneration in vertically stratified waters, like those of the NGOM during summertime.

Timing, modality, and composition of N sources (ammonium vs. nitrite/nitrate, DON) sources play roles in determining phytoplankton growth responses (Dugdale and Goering 1967, Harrison et al., 1987, Collos 1989, Antia et al., 1991; Riegman 1995, 1998), with possible ramifications for hypoxia (Paerl 2004). Natural phytoplankton communities are exposed to a range of inorganic and organic N compounds at varying ratios and supply rates. Uptake rates of N and other nutrient compounds vary spatially and temporally among phytoplankton communities in the NGOM, with possible differential responses. These taxa-specific responses play a key role in structuring natural phytoplankton communities, and determining bloom dynamics (Collos 1989, Stolte et al. 1994; Paerl 2005). The biogeochemical and trophic effects of changing proportions of N compounds discharged to the NGOM (including when N loads are reduced in response to management actions) should be examined.

In summary, potential biogeochemical and trophic impacts of shifting compositions and quantities of new N and P compounds implicated in marine eutrophication play important roles in determining the magnitude and composition of primary producers. Structural and functional modifications of the primary producer community strongly influence biogeochemical cycling and trophic (heterotrophs, grazers, herbivores and carnivores) responses to nutrient over-enrichment, resultant eutrophication and hypoxia dynamics of estuarine and coastal regions of the NGOM.

It should also be noted that there are strong *in situ* interactions between the complex array of nutrient *and* physical and biotic factors that determine phytoplankton community structure and function (conceptual figure showing the interactive environmental factors controlling phytoplankton community structure and function) (Harrison and Turpin 1982, Malone 1992, Reynolds 1987, Paerl 1988, Cloern 2001). Key physical factors include irradiance (light intensity, quality and flux), temperature, and freshwater discharge (water residence time), vertical mixing and horizontal transport, all of which are being altered by man-induced and climatic changes in the watershed and receiving waters. Finally, there are biotically-induced changes operating contemporaneously and contiguously with physical-chemical stressors. These include changes in the relative abundances of consumers, ranging from zooplankton to benthic invertebrates, shellfish and finfish which are known to strongly impact "top down" control of the quality and quantity of primary and secondary producers. An increasingly significant fraction of these changes are influenced by human activities, including fishing, habitat alteration and pollution

(Jackson et al. 2001). In effect, there are complex man-induced positive and negative feedback reactions taking place that affect our interpretation and predictability of nutrient effects on primary production, phytoplankton and benthic microalgal community structure, and resultant biogeochemical and trophic changes that could ultimately impact hypoxia dynamics. These interactions should be examined in an integrative fashion along with changing nutrient loads and proportions resulting from nutrient input management strategies.

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Material Provided by Daniel Conley and Bob Howarth

Material addresses processes that might lead to nitrogen or phosphorus limitation in the northern Gulf of Mexico.

Processes that might lead to nitrogen or phosphorus limitation in the northern Gulf of Mexico (10/30/06 rough draft with material added by Daniel Conley on 11/8/06):

Whether nitrogen (N) or phosphorus (P) is more limiting to net primary productivity in an aquatic ecosystem depends upon the relative availabilities of these elements to phytoplankton. Although there is some plasticity in the relative needs by phytoplankton for N and P, on average they require N and P in a molar ratio of approximately 16:1 (the "Redfield" ratio). Thus, when the N:P ratio of available N is well above 16:1, P is more limiting to productivity; when the ratio is well below 16:1, N is more limiting. To some extent the availabilities of N and P can be inferred from their inorganic concentrations in solution. However, the inorganic N:P ratio (DIN:DIP) can sometimes be misleading, particularly at low concentrations, due to rapid recycling of nutrients between organic and inorganic pools, to inclusion of some organic N and P in the assay for inorganic nutrients, and to rapid exchange of adsorbed inorganic P and ammonium (NRC 2000; Dodds 2003; Howarth and Marino 2003). The National Academy of Sciences' Committee on Causes and Management of Coastal Eutrophication (NRC 2000) specifically addressed the use of the DIN:DIP ratio to infer nutrient limitation and concluded that when the ratio is well below the Redfield ratio of 16:1, it probably does indeed indicate nitrogen limitation. On the other hand, ratios above the Redfield ratio may or may reflect phosphorus limitation: organic phosphorus recycles far

faster than does organic nitrogen, which can allow nitrogen limitation even at DIN:DIP ratios well above the Redfield ratio (NRC 2000). During the 1980s and 1990s, the DIN:DIP ratio in an area of 5,400 km2 to the west of the Mississippi River on the Lousiana shelf averaged ~ 13:1 (Twilley et al. 1999). This is probably too close to the Redfield ratio to allow an inference on the relative limitation by N or P, although perhaps N limitation is more likely.

The availability of N and P in an ecosystem is controlled both by the external loadings and by internal biogeochemical processes. Ideally, when considering the influence of external loads, one would want information on the load of biologically available nutrients, which is not necessarily well reflected by either the load of dissolved inorganic nutrients or the load of total nutrients. That is, some but not all of the dissolved organic nutrients and particle-bound nutrients delivered to coastal waters become biologically available on ecologically meaningful time scales (days to months to years). For the loading from the Mississippi River, the fate of the particle-bound P is of particular interest, since this is the largest form of P in the River (Sutula et al. 2004). The biovailability of this P is probably very low within the freshwater portions of the Mississippi River, but as the particles encounter the increasingly more saline waters of the Gulf of Mexico, the high ion abundances of seawater causes much of the adsorbed inorganic P to desorb, instantly converting it into highly bioavailable dissolved inorganic P (Fox et al. 1985; Froelich 1988; Howarth et al. 1995; Sutula et al. 2004). As is discussed below, diagenetic processes in the sediments of the Gulf of Mexico also further increase the biologically availability of particle-bound P delivered to the Gulf, and most of this delivered P is believed to become biologically available (Sutula et al. 2004).

Biogeochemical processes within and ecosystem can further alter the availability of nutrients, which potentially can alter the N:P ratio of available nutrients. For many coastal marine systems, the tendency is for benthic processes to make N limitation more prevalent since the N sink through denitrification is relatively larger than is the loss of P through permanent sediment burial (NRC 2000; Blomquist et al. 2004; Howarth and Marino 2006). This is by no means universally true, though, and both N and P dynamics can be quite variable across ecosystems. In a classic study, Nixon et al. (1980) demonstrated that virtually all of the organic P remineralized in sediments in Narragansett Bay escaped back to the overlying water column. On the other hand, the P release from sediments in other systems is frequently less than the rate of P remineralization, due to P adsorption and storage in surface sediments (NRC 2000; Howarth and Marino 2006). The causes of such variability across systems are not fully understood, but are probably due to differences in the amount and forms of iron in the sediments, the extent of sulfate reduction, and mixing by the benthic fauna, particularly as this affects micro-scale variation in pH (Howarth et al. 1995). The complexity of P-sediment exchanges in the Louisiana shelf region are sufficiently complex that in a soon-to-be published model of sediment diagenesis (Morse and Eldridge, in press), P processes were deliberately not considered (John Morse, pers. comm., 10/27/06).

Sulfate reduction is particularly important in affecting the P cycle of coastal marine sediments, since it can transform highly adsorptive forms of iron (III) oxides and hydroxides into non-sorptive iron (II) sulfides (Krom and Berner 1985; Caraco et al. 1989, 1990; Blomqvist et al. 2004). Sulfate reduction may also release P from covalently bound minerals as diagenesis proceeds (Sutula et al. 2004). Sulfate reduction dominates the metabolism of the sediments to the west of the Missippi River on the Lousiana shelf away from the immediate plume of the river (Rowe et al. 2002), as is true for many coastal marine sediments (Howarth 1984), Sutula et al. (2004) have demonstrated that the P content of these sediments is only half of that of the riverine sediments in the Mississippi from which they are derived due to losses during diagenesis. Sulfate reduction and the concomitant changes in sediment iron chemistry may not be the only factor involved, as Sutula et al. (2004) note that significant sediment P is lost in the immediate plume area of the Mississippi River, a high-energy environment subject to physical mixing and sediment reworking which may make sulfate reduction unlikely (the "sub-oxic fluidized bed reactor" processes that Aller 1998 described for other riverine plumes).

Dan: ADD MATERIAL ON DENITRIFICATION IN THE GULF OF MEXICO?

Added by Daniel Conley:

Denitrification is one of the major losses of fixed nitrogen in the oceans (Seitzinger and Giblin 1996), however, its measurement is difficult (Groffman et al. 2006). Denitrification is the reductive respiration of nitrate or nitrite to N_2 or N_2O and includes the recently discovered ANNAMOX process (Dalsgaard et al., 2003). The rates of denitrification are dependent on a variety of factors but the availability of starting products, e.g. nitrate (Kemp et al. 1990) and carbon (Smith and Hollibaugh 1989; Sloth et al. 1995) are major controlling factors. Given that large-scale increases in nitrate concentrations and in productivity that have occurred on the Mississippi River shelf, then certainly the rates of denitrification has probably increased through time as well.

An open question is how much does hypoxia effect the annual rates of denitrification? Lower rates of denitrification have been observed in the Gulf of Mexico zone of hypoxia when low oxygen concentrations were encountered (Childs et al. 2002, 2003), although the observed rates were at the low end of rates reported for other systems (Herbert 1999). Denitrification can be limited by the availability of nitrate, however, nitrate concentrations in the hypoxic area were high enough in the Childs et al. (2002) study not to be limiting. In addition, sulfide which is commonly found in anoxic environments acts to inhibit nitrification (the oxidation of ammonium to nitrate) (Joye and Hollibaugh 1995), thus reducing the availability of nitrate. In Danish coastal waters, rates of denitrification are highest during winter when nitrate concentrations are at their annual maximum (Nielsen et al. 1995) and low rates are observed during the summer. There are no seasonal measurements of denitrification available for the northern Gulf of

Mexico to estimate the overall effect of hypoxia. In general, the overall rates of denitrification are believed to be lower with hypoxia (Sørensen et al. 1987; Graco et al. 2001), although further investigations are needed.

Measurement of the fluxes of N and P from sediments provides a direct means to assess the role of sediment processes on the relative balance of N and P in the overlying water column. There appear to be relatively few studies in the northern Gulf of Mexico where both N and P fluxes from sediments have been determined simultaneously. A compilation of these studies shows a DIN:DIP flux ratio that varies from approximately 1:1 to 25:1, with a mean of ~10:1 (Twilley et al. 1999).

THE ABOVE PARAGRAPH NEEDS MORE DISCUSSION.

ADD SOMETHING ABOUT FEEDBACKS DURING EUTROPHICATION, AND HYSTERESIS (Conley paper in press, etc.).

Added by Daniel Conley:

Hypoxia can act as a positive feedback to enhance the effects of eutrophication. It has long been known in lakes (reference) that the internal P loading from sediments can sustain eutrophication long after reductions in nutrient loading have occurred. In the Baltic Sea, which is one of the largest areas in the world to suffer from eutrophication induced hypoxia, also has large internal P loading from sediments. Release of DIP under anoxic conditions causes massive amounts of DIP to be released from sediments, which are an order of magnitude larger than external inputs from rivers (Conley et al. 2002). Excess of DIP remaining after the spring bloom stimulates the growth of large nuisance blooms of nitrogen fixing cyanobacteria during the summer further enhancing hypoxic conditions in the Baltic Sea (Vahtera et al. 2006). In addition, lower overall rates of denitrification may occur with hypoxia in the Gulf of Mexico acting as a mechanism to increase the residence time of nitrogen in the system, which therefore could act as a positive feedback to enhance hypoxia.

Recent studies suggest that repeated hypoxic events can help to sustain hypoxic conditions (Hagy et al. 2004; Conley et al. 2006). In addition to the changes in nutrient cycling with hypoxia outlined above, large-scale changes in benthic communities occur reducing the abundance of large, slow growing, deeper dwelling animals changing to smaller, fast growing that can colonize rapidly following hypoxia (Diaz and Rosenberg 1995), ultimately changing the rates and processing of organic matter. Although nutrient reductions have occurred in Danish coastal waters, hypoxia continues to worsen with loss of the benthic communities and it appears that a regime shift has occurred sustaining the detrimental effects of eutrophication (Conley et al. 2006). The loss of benthic communities and the inability of the communities to recover with repeated hypoxic

events (Karlson et al. 2002), may make ecosystems more vulnerable to the development of hypoxia as seen in Chesapeake Bay (Hagy et al. 2004).

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Material Provided by Daniel Conley

Material addresses historical changes in hypoxia and productivity in the Gulf of Mexico.

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Contributed by Daniel Conley

Historical changes in hypoxia and productivity in the Gulf of Mexico

There have been relatively few studies of historical changes in hypoxia and productivity in the northern Gulf of Mexico. However, all studies from dated sediment cores show consistent changes in proxies with time, although the timing and response varies depending upon the proxy studied. The pattern of change is concomitant with increased nutrient loading from the Mississippi River causing increasingly severe hypoxia on the shelf. The published data are not sufficient to determine whether increases in the spatial extent of hypoxia has occurred with time.

Briefly, bacterial pigments characteristic of anoxygenic phototrophic sulfur bacteria have their highest concentrations between 1960 and the present (Chen et al. 2001). These bacteriopigments were not present prior to 1900. Further evidence is provided by algal pigments which show increases in the 1960s and their enhanced preservation probably also reflects enhanced preservation with hypoxia as well as nutrient-driven increases in production (Chen et al. 2001). In addition, Rabalais et al. (2004) report increases in algal pigment concentrations over time, with gradual changes

from 1955 to 1970, followed by a steady increase to the late 1990s. Increases in pigment concentrations from one sediment core from west of the Atchafalya River outflow suggests that nutrient driven increases in production occurred later than in the Mississippi River Bight (Rabalais et al. 2004). There has been an increased accumulation of total organic carbon and biogenic silica in recent sediments near the mouth of the Mississippi River (Turner and Rabalais 1994; Turner et al. 2004), although the spatial and temporal variations observed between dated sediment cores are large.

Several studies have examined changes in the benthic foraminiferal community in dated sediment cores (Platon and Sen Gupta 2001; Osterman et al. 2005; Platon et al. 2005). Significant changes in the composition of the benthic foraminiferal community have occurred in the past century and several indicators, e.g. the PEB index (Osterman et al. 2005) and the A/P ratio – agglutinated to porcelaneous orders (Platon et al. 2005), indicate that increases in the intensity of hypoxic events have occurred over the past 50 years. Osterman et al. (2005) also show that several probable low oxygen events occurred in the past 180 years that are associated with high Mississippi River discharge rates, although the recent changes are more extreme than any that occurred in the past.

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Material Provided by Jim Sanders

This material addresses the following part of the charge: 1.(A)(vi) - Implications of reduction of phosphorus or nitrogen without concomitant reduction of the other)

1. Background aspects that will likely be covered by others, but need to be considered here:
   - Evidence for limitation by N, P, or Si—temporal, spatial attributes to limiting factors
   - How increases in nutrient inputs over time have affected limitation patterns
   - How changing nutrient ratios (particularly Si with N or P) affect primary production and producers

2. Other topics:
   - Discussion of the 2004 white paper, and work since that time
   - Implications of N reduction alone
   - Implications of P reduction alone
   - Feasibility of reduction plans that incorporate both
   - Science questions that remain to be answered

Possible questions for invited experts attending Hypoxia Advisory Panel meeting on December 6-8, 2006:

Questions for Dr. James Ammerman:

1. What is the spatial extent of P limitation during the period of maximum productivity. How does this compare to the spatial extent of N limitation?
2. In terms of total amount of volumetric primary production, how does P-limited production compare with N limited primary production?

3. Are the results of your work (Ammerman et al. 2004; Sylvan et al. 2006) compatible with the "Scavia model" relating nutrient enrichment to hypoxia potentials in the NGOM.
4. Based on your knowledge of primary production dynamics, how are periods of P and N limited primary production linked to hypoxia potentials in time and space.
5. Based on your research results as well as the results of others, are we "on target" with the current recommended nutrient reductions aimed at reducing hypoxia in the NGOM? If not, suggest modifications for more effective nutrient reduction strategies and provide rationales.
6. Based on our current knowledge of nutrient limitation and productivity dynamics in the NGOM, what are your recommendations for a long-term nutrient reduction strategy aimed at reversing eutrophication and reducing hypoxia.
7. What additional research and monitoring are needed to address any of the above questions?
8. How does the bioassay approach complement (and agree with) estimates of nutrient limitation? Also, how does the absence of sediment-water column nutrient exchange in bioassays affect results and their implications?