U.S. GLOBEC

GLOBAL OCEAN ECOSYSTEMS DYNAMICS

A Component of the U.S. Global Change Research Program

GLOBEC in the GULF of MEXICO: LARGE RIVERS AND MARINE POPULATIONS

Report of a U.S. GLOBEC Workshop
January 13-15, 1999

U.S. Global Ecosystems Dynamics

Report Number 19

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This is a report of a workshop on Large Rivers and Marine Populations held at the Louisiana Universities Marine Consortium (LUMCON) on January 13-15, 1999. Michael Dagg, Peter Ortner, and Jose Torres were conveners and editors of the workshop report. The workshop was sponsored by U.S. GLOBEC and by NOAA's Center for Sponsored Ocean Research (CSCOR).

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Executive Summary

The world's most productive fisheries are always associated with large inputs of nutrients from either upwelling or land runoff. Coastal regions dominated by large rivers are important to the biological production of the world's oceans because these rivers generally carry large amounts of "new" nitrogen. In the U.S., the Mississippi River is the major large river, with discharge equal to approximately 2.2 times that of the Columbia River and 2.9 times that of the Yukon River. River waters stimulate high rates of primary production on the shelf, which in turn stimulate and support high rates of zooplankton production and fisheries production. There is a characteristic group of copepod species in the vicinity of the Mississippi River plume which is numerically dominated by *Temora turbinata*, *Eucalanus pileatus*, *Centropages furcatus*, *Paracalanus* spp., and in the lowest salinity waters, *Acartia tonsa*. *Paracalanus* spp. is highly selected as a food for larval and juvenile fish. Egg production rates of these species are closely linked to their food regime, responding dramatically to increases in food concentration associated with river plumes. Population responses in these copepods are especially rapid in summer because of high temperatures (> 30°C). These copepods directly or indirectly support large populations of fish. Approximately 20% of the U.S. commercial fishery landings by dollar value are from the northern Gulf of Mexico and there are major recreational fisheries in this region. Approximately 90% of the commercial fisheries from the Gulf of Mexico comes from what has been referred to as the "fertile crescent," the area affected directly by the Mississippi River. Fisheries data suggest that an ecosystem shift towards a system more dominated by pelagic fish species (the gulf menhaden, *Brevoortia patronus,* vs. the demersal Atlantic croaker, *Migropogonius undulatus*) may have occurred in the northern Gulf of Mexico, possibly associated with increased nutrient input to the region.

Input of dissolved inorganic nitrogen from the Mississippi River to the Gulf of Mexico has increased dramatically during the past several decades. In addition to an overall stimulation of biological production at all trophic levels, the influx of large amounts of new nitrogen preferentially stimulates, for reasons that aren't completely understood, the "classical" food chain (N-P-Z) rather than the microbial web more typical of oligotrophic waters. A fraction of the organic material from the highly productive water column sinks to the bottom and fuels the annual development of an extensive zone of bottom-water hypoxia.

Weather and climate forcings to this system are tractable for study and are linked to broader scale processes. River plumes are positively buoyant and their transport and mixing process are highly sensitive and immediately responsive to changes in local wind fields. Satellite imagery shows buoyant plumes respond, on the scale of hours, to changes in winds. Larger scale forcings such as ENSO events, modify precipitation patterns over the drainage basin and affect the intensity and duration of winter storms. On longer time scales, it has been shown that anomalies in sea-surface temperature in the Gulf of Mexico are significantly correlated with the Pacific Decadal Oscillation.

A workshop was held in January 1999 to discuss relationships between the Mississippi River, the production of marine populations and ecosystem responses in the Gulf of Mexico, and to discuss how these relationships might be affected by changes in weather and climate.

Introduction

Global Ocean Ecosystem Dynamics (U.S. GLOBEC) is a component of the U.S. Global Change Research Program, with the goals of understanding and ultimately predicting how populations of marine animals (holozooplankton, fish and benthic invertebrates) respond to natural and anthropogenic changes in global climate. Although coastal regions dominated by large rivers are exceptionally important to global production of marine animals, no GLOBEC program to date has focused on these issues. As a first step towards establishment of such a program, a workshop supported by NOAA's Center for Sponsored Ocean Research (CSCOR) and U.S. GLOBEC was held at the Louisiana Universities Marine Consortium (LUMCON) in January 1999. The scientific goal of the workshop was to identify and explore the relationships between large rivers and marine populations and how these relationships might be affected by climate changes. Twenty-nine scientists attended (Appendix 1).

Background

Coastal regions dominated by large rivers are important to the biological production of the world's oceans for several reasons, including:

- large rivers are distinctly different from smaller ones because they have "extended estuaries," where estuarine processes extend well out over the continental shelf;
- many of the world's large rivers discharge high nutrient loads into otherwise oligotrophic regions;
- boundaries/fronts associated with large river plumes are important micro- and meso-scale regions for biological production, animal aggregation and fisheries recruitment; and
- new nitrogen associated with riverine discharge generally supports the classic N-P-Z-F food web resulting in high fisheries production.

These systems are good indicators of global change because they quickly respond to variations in weather and climate.

- Climatic or anthropogenically caused changes of small magnitude throughout the drainage basin of a large river can result in a large response in the coastal shelf environment because of the magnifying or concentrating effects associated with drainage; characteristics of discharged river water result from an integration of processes that occur over broader time and space scales. As a result, riverine discharges of freshwater and nutrients are responsive to changes in rainfall in the drainage basins, and riverine discharge of nutrients is responsive to anthropogenic activities in the drainage basin.
- Buoyant plumes are quickly responsive to wind. The processing of plume materials is partially dependent on plume location (over deep vs. shallow water) so a change in the wind regime can significantly alter the ultimate fate of discharged materials.

The Mississippi River and the northern Gulf of Mexico. In the U.S., the Mississippi River is the major large river, with discharge equal to approximately 2.2 times that of the Columbia River and 2.9 times that of the Yukon River. The Mississippi River supports much of the biological production in the northern Gulf of Mexico. There is a direct relationship between the flux of inorganic nitrogen into the northern Gulf of Mexico via the Mississippi River and the primary production observed within a 6900 km^2 area around the delta (Lohrenz et al. 1997).

High rates of primary production stimulate and support high rates of zooplankton production. Concentrations of copepod nauplii are >1000 l^{-1} at some plume edge stations during the summer (Dagg and Whitledge 1991) and even during the less productive winter period are often >100 l^{-1} (Dagg et al. 1987). There is a characteristic group of copepod species in the vicinity of the Mississippi River plume which is numerically dominated by *Temora turbinata*, *Eucalanus pileatus*, *Centropages furcatus*, *Paracalanus* spp., and in the lowest salinity waters, *Acartia tonsa*. *Paracalanus* spp. is often highly selected as a food for larval and juvenile fish (Govoni et al. 1983; 1986). Egg production rates of these species are closely linked to their food regime (Dagg 1988), responding dramatically to increases in food concentration associated with river plumes. Population responses in these copepods are especially rapid in summer because of high temperatures (>30^{o}C). In higher salinity waters directly beneath the river plumes, a more oceanic community dominates, including *Eucalanus attenuatus*, *Calanus tenuicornis, Phaenna spinifera* and two *Candacia* species (Ortner et al. 1989; Dagg 1995).

It is reasonable to expect a relationship between fisheries production and riverine nutrient inputs into this system (Nixon 1988). This is especially true because other sources of nutrients are less significant than in temperate or higher latitude regions. Fish production is high in the vicinity of Mississippi River plumes and farther afield (e.g. Grimes and Finucane 1991; Ortner and Dagg 1995). Approximately 20% of the U.S. commercial fishery landings by dollar value are from the northern Gulf of Mexico and there are major recreational fisheries in this region. Approximately 90% of the commercial fisheries from the Gulf of Mexico comes from what has been referred to as the "fertile crescent," the area affected directly by the Mississippi River (Anon. 1995). The largest volume fishery in the region is gulf menhaden, *Brevoortia patronus*, a pelagic planktivore. Menhaden recruitment increased in the mid-1970s (Govoni 1997). Inshore fishery-independent surveys for the same time period support this observation (Chesney et al. in press). The inshore fishery-independent data for Louisiana and data from bycatch studies in coastal Louisiana also suggest an increased abundance of pelagics and a decrease in demersal nekton (Adkins 1992; Chesney et al. in press). In both fishery-independent surveys and bycatch studies, relative CPUE for menhaden increased significantly (Gunter 1936; Anonymous 1992; Chesney et al. in press). During the same period, there has been an increase in the CPUE of another small pelagic fish, the bay anchovy *Anchoa mitchilli* (Chesney et al. in press). In contrast, some demersal fish appear to have decreased during the same time period. A dramatic example is the Atlantic croaker, *Micropogonius undulatus* which had its CPUE decrease from 207.4:6.0 in a comparison of bycatch rate between the 1930s and 1990s (Gunter 1936; Anonymous 1992). Another dramatic example is star drum, *Stellifer lanceolatus*, 30.6:0.3. Taken together, these data suggest that an ecosystem shift towards a system with increased abundance of pelagics and a decline in the abundance of demersal fish may have occurred in the northern Gulf of Mexico. Such a shift has been observed in other systems where eutrophication has been combined with heavy exploitation rates of the fisheries but the mechanism for these shifts is not well understood (Caddy 1993).

Input of dissolved inorganic nitrogen from the Mississippi River to the Gulf of Mexico has increased dramatically during the past several decades. The large drainage basin of the Mississippi River encompasses an intensive agricultural region which has a moderate population density. During recent years, the net input of dissolved nitrogen to the land within the drainage basin of the Mississippi River has been 2220 kg N $km^{-2}y^{-1}$ (Howarth et al. 1996). This nitrogen comes from fertilizer application (1840 kg N $km^{-2}y^{-1}$), nitrogen fixation from crops (1060 kg N $km^{-2}y^{-1}$) and atmospheric deposition of anthropogenic nitrogen (620 kg N $km^{-2}y^{-1}$). The net deposition is less than the total input because the region exports 1300 kg N $km^{-2}y^{-1}$ as food and feed. Approximately 25% of the net anthropogenic input to the drainage basin, 565 kg N $km^{-2}y^{-1}$, is eventually delivered via the Mississippi River system to the coastal zone of the Gulf of Mexico (Howarth et al. 1996). This results in the delivery of 1.82 Tg N y^{-1} (130 Gmol y^{-1}) to the northern Gulf of Mexico (Howarth et al. 1996). Riverine concentrations of nitrate at Southwest Pass are commonly >100 µM (Dagg and Whitledge 1991). This nitrogen could support 30 gC m^{-2} yr^{-1} of new production if it were uniformly distributed over the entire Louisiana-Texas shelf west of the Mississippi River (Dagg and Whitledge 1991). In reality, the region of direct stimulation is much smaller and the degree of stimulation within that region is much larger.

In addition to an overall stimulation of biological production at all trophic levels, the influx of large amounts of new nitrogen preferentially stimulates, for reasons that aren’t completely understood, the “classical” food chain (N-P-Z) rather than the microbial web more typical of oligotrophic waters (Legendre and Rassoulzadegan 1995). Thus, not only is the overall production of the northern Gulf stimulated by the riverine nutrient inputs but the type of food web that is stimulated supports a more efficient transfer of fixed carbon from phytoplankton to fish.

Additional stimulation of productivity may be associated with small scale physical structures. There is evidence that riverine fronts and boundaries associated with the Mississippi River provide sites for enhanced feeding and growth of zooplankton and immature fish, and ultimately for enhanced fisheries recruitment (Grimes and Kingsford 1996; Grimes and Finucane 1991). Nevertheless, the evidence for these enhancements in larval fish is not apparent for all species (Govoni 1997) and an increase in predation induced mortality may offset gains in individual growth and feeding.

A fraction of the organic material from this highly productive water column sinks to the bottom and fuels the annual development of an extensive zone of bottom-water hypoxia (Rabalais et al. 1994). A shelf-wide survey of the distribution of oxygen from the Mississippi River to the Louisiana-Texas border has been made each summer since 1985. Hypoxia was observed in bottom water during each summer survey with the exception of 1988, a summer of exceptionally low freshwater input from the Mississippi River. The area of hypoxia has been as large as 18,000 km^2 (Wiseman et al. 1997). Based on this record, hypoxia has existed in this region for more than a decade. These data also indicate significant variability in the extent and distribution of hypoxia. To date, this variability is not completely predictable because the complex of factors, including organic matter input, trophic process in the pelagic environment, the degree of stratification and input of mixing energy, and the strength and direction of prevailing winds which affect the distribution and transport of river water, are not completely understood. Statistical analysis shows a significant correlation between river flow and oxygen deficit in bottom water on the inner shelf, but with a two month lag (Justic et al. 1993).

Prior to these systematic surveys, data are less extensive but direct measurements indicate that some hypoxia existed in bottom waters of Louisiana as early as 1973 (Renaud 1986).

Longer records have been obtained from bottom cores taken on the Louisiana continental shelf. Cores representing the past 100 years of sediment accumulation show increasing concentrations of organic matter over this time. Virtually all of this material is marine in origin (Eadie et al. 1994). Stable isotope signatures and accumulation patterns of organic carbon indicate water column productivity has increased significantly since the 1960s, a period that coincides with a doubling of the nitrate loading from the Mississippi River. Presence of glauconite, a mineral associated with hypoxic conditions, suggests hypoxia existed but was less common before the early 1940s (Nelsen et al. 1994). The foraminifera assemblage from these cores indicates there was a significant shift in species composition at about this same time, with more recent community structure closely resembling that currently found in hypoxic waters (Nelsen et al. 1994).

Current knowledge of the specific consequences of bottom water hypoxia for the ecosystem and economics of the northern Gulf of Mexico are summarized in a separate report (Diaz and Solow 1999).

In addition to directly stimulating marine populations via nutrient inputs, large rivers establish physical structures that enhance biological interactions. For example, yellowfin tuna, a major commercial fishery in the Gulf, spawn near Mississippi River plumes (Lang et al. 1994) and recreational anglers harvest several tunas and tuna-like fishes in the Gulf. There is some evidence that tunas may select oceanic features within which to spawn and, by enhanced feeding in such regions, promote survival and growth of early life stages (Richards et al. 1989). Prominent oceanographic features of the Gulf of Mexico (i.e. the Loop Current and associated fronts, Mississippi River plumes and associated fronts, warm and cold core eddies) are habitats where physical and biological conditions potentially can influence growth and survival of tuna larvae. These features, and the magnitude of phytoplankton production in the Gulf of Mexico, are likely to be affected by climatic changes. In the permanently stratified open Gulf, the mixed layer deepens to the nutricline only with the intrusion of the cold air masses and their accompanying strong winds and evaporative cooling. The consequent nutrient additions to the euphotic zone have appreciable effects upon upper water column biology (Ortner et al. 1984). Offshore spawning by some Gulf fisheries species is associated with the passage of cold fronts. In non-ENSO years, such fronts pass over the Gulf about every 10-14 days in winter. In ENSO years, intensity and frequency increase.

Effects of large rivers are not confined to near-field environments but can be observed over large spatial scales. In coastal systems of the Gulf of Mexico, there is a general pattern of increasing oligotrophy with distance from the Mississippi River, ending with the coral reef systems of south Florida and the Yucatan. This pattern, however, is distinctly non-uniform both temporally and spatially because discharges interact with major oceanographic features. For example, a band of low salinity Mississippi River water, with elevated chlorophyll concentrations, was observed off Miami (Ortner et al. 1995) and off Cape Lookout, NC (Atkinson and Tester 1994) in September 1993. Transport time from the river mouth to NC was approximately one month. During this particular period, winds in the northern Gulf of Mexico had an abnormally strong westerly component. River water, typically transported along the shelf to the west of the Mississippi delta, was instead transported offshore and east, and became entrained in the

Loop Current which then transported it along the west Florida shelf towards and through the Florida Straits. Production processes in the west Florida shelf region are stimulated by local upwelling but interactions with river water provide an additional stimulus on some occasions. In other years, when transport of Mississippi River water is more typically to the west, freshwater signals are commonly observed on the shelf as far away as the Texas-Mexico border. Interaction of river water with spin-off eddies from the Loop Current is common during these years, and rich riverine waters are entrained and transported far out into the Gulf. Clearly, the biological impacts of large rivers can occur over large spatial and temporal scales, and these impacts may be sensitive to climatic changes and changes in nutrient dynamics within the drainage basin.

Weather and climate forcings to this system are tractable for study and are linked to broader scale processes. For example, river plumes are positively buoyant and their transport and mixing processes are highly sensitive and immediately responsive to changes in local wind fields. Satellite imagery clearly shows that buoyant plumes respond, on the scale of hours, to changes in winds. Larger scale forcings, such as ENSO events, can have effects by modifying precipitation patterns over the drainage basin or by affecting the intensity and duration of winter storms. On longer time scales, it has been shown that anomalies in sea-surface temperature in the Gulf of Mexico are significantly correlated with the Pacific Decadal Oscillation (Enfield and Mestas-Nunez 1999).

In summary, new nutrients supplied to coastal waters by large rivers support a disproportionately large amount of zooplankton and fish production. The northern Gulf of Mexico is dominated by the large inputs of freshwater and nutrients from the Mississippi River. There are demonstrated relationships between these inputs and population responses in zooplankton and fish and there are suggestions of an ecosystem shift towards a system more dominated by pelagic fish species.

Mechanisms are being discussed for reducing nitrogen inputs from the drainage basin to the gulf. If reductions are accomplished, the ecosystem responses will undoubtedly include a reduction in productivity and a reduction in the extent and duration of bottom-water hypoxia. Quantitative understanding of these relationships is required. Other responses are unclear. This is an ideal place for examination of biological responses within a river dominated system to weather, climate, and other environmental changes.

A workshop was held in January 1999 to discuss relationships between the Mississippi River, the production of marine populations and ecosystem responses in the Gulf of Mexico, and to discuss how these relationships might be affected by changes in weather and climate.

Workshop Summary

Working group discussions were held under three headings:

- Large scale natural and anthropogenic linkages;
- Trophic interactions and community structure; and
- Frontal processes, plume dynamics and near-field responses.

Separate reports were presented in a plenary session and later synthesized into the summary presented here.

From a human perspective, the Mississippi River has both positive and negative aspects on animal populations in the northern Gulf of Mexico. On one hand, riverine inputs and associated riverine processes result in biological stimulation with associated enhancements to fisheries production. On the other hand, organic materials from this enhanced production fuel development of a large hypoxic zone which has deleterious effects on animal populations. Questions developed by workshop participants considered both perspectives and fell into three broad categories.

I. SCALES OF IMPACTS (TEMPORAL AND SPATIAL)

(a) <u>nutrients</u>. We know that the Mississippi River contributes more than 90% of the riverine fresh water input to the northern Gulf of Mexico but assessing the importance of the associated nutrient input to the ecosystem, and specifically to fisheries, requires information on other nutrient inputs. A more refined N-budget is required.

> What are the nutrient inputs to the shelf from the river, and from atmospheric, lateral, and groundwater sources, and what are the important/dominant scales of these inputs?
>
> What is the contribution of shelf-slope exchanges to the nutrient budgets of the shelf and the open Gulf?

(b) <u>physical and biological properties</u>. We know that dissolved inorganic nitrogen in river plumes is taken up by phytoplankton within 100-200 km from point of discharge and within time scales of days to weeks, but responses in copepod and fish populations occur over significantly broader temporal and spatial scales. It is important to more rigorously define the scales of both primary impacts (distribution of near-field properties) and of secondary impacts (distribution of far-field properties).

> What are the temporal and spatial distributions of the Mississippi River plume and its associated materials (nutrients and suspended sediments)?
>
> What are the spatial and temporal distributions of biological communities stimulated by riverine nutrients?

What contribution does the riverine nutrient input make to support of the biological communities in the far-field (on the shelf to the E and W, in the open Gulf), and what are the temporal and spatial patterns?

(c) hypoxia. We know that bottom-water hypoxia, ultimately fueled by riverine nutrients, develops on the shelf almost every summer and that there are temporal lags and spatial offsets between nutrient inputs and hypoxia.

What is the magnitude and what are the time and space scales of shelf hypoxia?

II. PROCESSES AND MECHANISMS

(a) distribution of plumes and associated materials. Processing and fates of riverine materials are dependent in part on where the river plumes flow. Processes occurring in and beneath plumes over deep water are different from processes occurring in and beneath plumes over shallow coastal water.

What are the physical and meteorological processes affecting the transport, retention and mixing of discharge plumes and their associated suspended sediments and nutrients?

What are the important processes for transport of Mississippi River or shelf water into the central Gulf?

(b) biological responses. We know river discharge is highly variable. Associated with this there is significant variability in nutrient and suspended sediment discharge, both highly but non-linearly correlated with precipitation in the drainage basin. Water column stratification is also affected by patterns of fresh water discharge. Meteorological conditions can significantly affect the transport of discharged water and associated materials. For these and other reasons, biological responses are likely to be highly variable.

How does the short-term, seasonal, annual and decadal variability in discharge of fresh water, suspended sediments and nutrients affect production of animal populations? How do these inputs and patterns control the structure of the food web (diversity, number of trophic levels, species composition or functional groupings) and the spatial structure of biomass and production?

How will changes in the amounts and rates of nutrient delivery impact community structure and animal production, especially fisheries community structure and production?

(c) pelagic–benthic coupling, vertical flux and hypoxia. The shelf of the northern Gulf of Mexico is broad and shallow implying important linkages between the pelagic and benthic environments. Increased nutrient inputs to the northern Gulf of Mexico have resulted in increased biological productivity (eutrophy), and some fraction of this water column production sinks to the bottom, supporting benthic production and creating an oxygen demand. In other systems, nutrient increases beyond a certain level lead to radical shifts in ecosystem structure (dystrophy).

> What are the linkages between riverine inputs, physical processes on the shelf, the productivity and structure of the pelagic community, vertical flux, and hypoxia? How does the development of hypoxic areas on the shelf affect overall system production, the ratio of benthic to pelagic production, and the volume and quality of available fish habitat?
>
> Where along the continuum between eutrophy and dystrophy does the "fertile crescent" fall and what are the controlling processes?

(d) <u>small scale frontal processes</u>. We know that frontal boundaries are regions of enhanced biological processes.

> What significance are the high gradient environments between river plumes and receiving waters to the overall enhancement of biological production, especially fisheries production, in the northern Gulf of Mexico?

(e) <u>transport and fisheries recruitment</u>. Understanding recruitment processes requires knowledge of physical transport. In the northern Gulf of Mexico, transport refers to at least four distinguishable processes: transport within the plume itself; cross-shelf transport; alongshore transport within the Louisiana Coastal Current including quasi-persistent features such as the mesoscale gyre that occurs northwest of the Southwest Pass; and transport from the inner shelf into estuarine juvenile habitats. Depending upon the life history of the particular species of interest, one or more of these processes must be quantitatively understood to predict recruitment.

> How do transport and retention processes interact with growth and survival of the target zooplankton and fish species to affect recruitment?

III. LINKS TO CLIMATE AND GLOBAL CHANGE

(a) <u>climate shifts</u>. We know that river plumes, coastal transport processes, and shelf-slope exchanges are all sensitive to local wind regimes which could change with climate shifts. There is evidence that precipitation within the drainage basin has increased over the past two decades and global models indicate this pattern will continue. There is also evidence that climate change can directly affect processes in the open gulf.

> How will climate change modulate the characteristics of river forcing and influence the physical–biological couplings of the shelf environment?
>
> Do the large scale climatic processes, through their effects on the timing and/or scale of the Mississippi River input, affect food web structure/fishery yield?

(b) anthropogenic adjustments. Changes to characteristics of the river discharge can be anthropogenically induced. Dissolved inorganic nitrogen has increased dramatically in recent decades because of the application of nitrogenous fertilizers within the drainage basin. Patterns of river discharge have been altered by the construction of a river levee system that effectively (with rare and highly visible exceptions) prevents river flooding. There is consideration being given to mechanisms for reducing nitrogen inputs as a means of reducing hypoxia in the northern Gulf of Mexico.

> What effects will changing agricultural practices have on nutrient loading, on food web structure and on hypoxia in the northern Gulf of Mexico?
>
> How will the large-scale climatic processes identified as affecting the Mississippi River drainage basin and the northern Gulf of Mexico affect the production and species composition of animal populations?

IV. TARGET TAXA

Gulf menhaden *(Brevoortia patronus*) and Atlantic croaker (*Micropogonius undulatus*) can serve as target fish species to address these questions in the northern Gulf of Mexico. Both species of fish mature rapidly, reaching sexual maturity within two years, making them highly responsive to processes affecting physical-biological coupling. Recruitment of gulf menhaden, a planktivorous fish throughout its entire life, has apparently increased significantly with increasing nutrient input to the northern Gulf. In contrast, populations of croaker, a planktivore during larval stages but a demersal carnivore as an adult, have declined dramatically over the same time. This suggests a shift in community structure has occurred, a shift involving a decline in demersal production and an increase in pelagic production. Gulf menhaden live approximately three years, whereas Atlantic croaker live longer, five-to-six years.

Larvae and postlarvae of both fish feed on copepod nauplii in surface waters. Both are dependent on the copepod community of mid-salinity waters associated with river plumes – *Temora turbinata*, *Centropages furcatus*, *Eucalanus pileatus*, *Paracalanus* spp. and *Acartia tonsa*. These copepods will serve as target zooplankton species. Juveniles and adult menhaden are planktivores, juvenile croaker consume benthic invertebrates and adults consume benthic invertebrates and small fish.

V. CONCLUSIONS and RECOMMENDATIONS

The workshop attendees were in agreement that U.S. GLOBEC and NOAA should be encouraged to develop a full science or implementation plan on the themes discussed in this workshop.

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Appendix II: Abstracts of presentations

Nutrient Inputs and Fish Production

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It has been recognized for most of the past century that there is a causal link between nutrient supply, the level of primary production, and the yield of fish and shellfish from freshwater and marine ecosystems. Quantifying this relationship in the sea has proven difficult for many reasons, not the least of which is that a variety of factors in addition to nutrient supply also influence primary production and fisheries yields. Nevertheless, it has recently proven possible to use field and mesocosm experimental data to establish an empirical relationship between the input of dissolved inorganic nitrogen and primary production by the phytoplankton in a range of coastal, shelf, and open ocean areas. Similarly, there is a good correlation between reported levels of primary production (^{14}C uptake) and commercial fisheries yields across a wide range of marine systems. Both empirical relationships are non-linear and they can be combined into one computed relationship between nitrogen loading and fisheries yield that is roughly hyperbolic in form. Such a positive result does not, of course, imply that increased nitrogen input will necessarily result in increased fish production in all systems. For example, in areas with strong vertical stratification, nitrogen fertilization may lead to hypoxia or anoxia in the deeper waters with consequent loss of fishery habitat and yield.

Nutrient Supply And Structure Of Pelagic Food Webs In Marine Systems

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The present discussion concentrates on the role of nutrients in the bottom-up control of pelagic food webs, and it considers the grazing of phytoplankton by zooplankton as the primary top-down control. Three aspects are examined: quantity of the limiting nutrient, chemical composition of nutrients, i.e. ratios of certain elements, and frequency or steadiness of nutrient inputs.

The *quantity of the limiting nutrient*, together with irradiance and water temperature, controls the rate of photosynthesis, i.e. phytoplankton production per unit biomass; when production is low, phytoplankton are generally small (<5 µm; picoplanktonic cyanobacteria, µ-flagellates), so that there is generally low transfer of biogenic carbon (BC) to large pelagic animals (except when there is package of small particles into large ones by large microphagous zooplankton, i.e. salps, doliolids, appendicularians, pteropods; Fortier et al. 1994); when production is high, there is either potentially high BC transfer to large animals, or massive sinking to depth of ungrazed cells.

The taxonomic composition of the phytoplankton assemblage is a major factor that determines the structure and functioning of pelagic food webs. It largely (but not solely) depends on the *chemical composition of nutrients*, i.e. the ratios of some elements. When there is low Si vs. N and P, diatoms are often replaced by non-Si taxa, e.g. dinoflagellates, prymnesiophytes, and picoplanktonic cyanobacteria; when there is low Si and high N vs. P, dinoflagellates and prymnesiophytes are often favored; when there is low Si and high P vs. N, there may be blooms of N_2-fixing filamentous, heterocystous cyanobacteria, which are then not limited by either N or P. It follows that: the chemical composition of nutrients may determine the sizes and edibility of phytoplankton; because small phytoplankton are grazed by microzooplankton, whose generation times are similar to those of small cells, there is tight coupling between primary production and grazing (no blooms), but generally low transfer of biogenic carbon to large pelagic animals; inedible large phytoplankton sink to depth as aggregated ungrazed cells; edible large phytoplankton potentially lead to high BC transfer to large animals.

The level of phytoplankton production and the taxonomic composition of phytoplankton (previous two paragraphs) are necessary but not sufficient conditions to ensure high BC transfer to large pelagic animals: because phytoplankton assemblages are generally not long-lasting, they influence food webs only if their time scales match those of the zooplankton grazers; ephemeral blooms of large phytoplankton may be either grazed or sink to depth, according to their taxonomic composition (edible taxa or not) and the presence or not of opportunistic grazers, but they generally have no lasting effects on the heterotrophic components of food webs. Because the generation times of microzooplankton are similar to those of small phytoplankton, the present paragraph mostly concerns large phytoplankton and their mesozooplankton grazers. Concerning the *frequency or steadiness of nutrient inputs*, when these are steady or high-frequency, the production characteristics of large phytoplankton match the generation times of large grazers (i.e. from weeks to months); when the inputs are low-frequency, the production characteristics of large phytoplankton may match the seasonal or annual patterns of grazers; when the inputs are irregular and/or short-lived, there is low matching, so that ungrazed blooms of large phytoplankton are often followed by massive sinking to depth of ungrazed cells.

Legendre & Rassoulzadegan (1995) proposed that the various trophic pathways in the pelagic environment are part of a continuum. They divided the continuum into four pathways: the *microbial loop* is an almost closed system of heterotrophic bacteria and zooflagellate grazers, in which the grazers release dissolved organic matter used as substrate by bacteria; the *microbial food web* has the same components as the microbial loop, plus small phytoplankton, so that there is possible

BC export toward large metazoans (the expressions “microbial loop” and “microbial food web” are often confounded in the literature); in the *multivorous food web*, the herbivorous and microbial trophic modes both play significant roles; the *herbivorous food web* is dominated by large phytoplankton and herbivorous grazing.

The three aspects of nutrients discussed above are involved in the control of food webs, an alternative BC pathway being the sinking to depth of ungrazed phytoplankton. The information concerning these effects is summarized here in an “identification key”:

1. *Quantity of nutrients*
    - low: small phytoplankton, leading to the *microbial food web* or the *microbial loop*
    - intermediate and high: large phytoplankton, see 2
2. Large phytoplankton: effects of the *chemical composition of nutrients*
    - high Si:N and Si:P: diatoms, see 3
    - low Si:N and high N:P: dinoflagellates
        - edible taxa, see 3
        - inedible taxa: blooms, followed by *sinking to depth* of ungrazed phytoplankton
    - low Si:N and high P:N: sometimes blooms of inedible N_2-fixing filamentous cyanobacteria, leading to the *sinking to depth* of ungrazed cells
3. Large edible phytoplankton: effects of the *frequency of nutrient inputs*
    - match the characteristics of zooplankton grazers
        - high nutrient flux, high Si:N and Si:P: diatom-based *herbivorous food web*
        - high nutrient flux, low Si:N and Si:P: dinoflagellate-based *herbivorous food web*
        - intermediate nutrient flux: diatom- or dinoflagellate-based *multivorous food web*
    - mismatch: blooms, followed by *sinking to depth* of ungrazed phytoplankton

The anthropogenic inputs of nutrient in coastal waters may affect the three aspects of nutrients discussed above, resulting in harmful algal blooms (HABs; several ideas below are from Paerl 1997). Increases in the overall *quantity of nutrients* enhance phytoplankton production, which may be transferred or not to large pelagic animals; in vertically stratified shallow waters, the massive sinking to the bottom of ungrazed phytoplankton increases the biological oxygen demand, leading to hypoxia (reduction of oxygen concentrations) and sometimes anoxia (depletion of oxygen). Changes in the *chemical composition of nutrients* may have different effects: low Si:N and Si:P generally promote the growth of taxa other than diatoms, some of these not leading to food webs that support large pelagic animals; P loading is presently low, but there is episodic release in the water column of P accumulated in sediments, causing HABs of toxic N_2-fixing filamentous, heterocystous cyanobacteria; high anthropogenic N inputs in coastal and continentally bound seas in the Northern Hemisphere generally correspond to the main HAB areas. Concerning changes in the *frequency of inputs*, continuous inputs may favor the establishment of new, stable food webs if the phytoplankton taxa are edible, whereas irregular and/or short-lived inputs increase the likelihood of massive sinking to the bottom of ungrazed phytoplankton.

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Physical and Biological Processes in the Northern Gulf of Mexico Determined from Remote Sensing

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The Mississippi River is the largest river in North America draining 40% of the continental U.S. and discharging 18,400 m^3 s^{-1} and 210 million tons of sediment annually to the northern Gulf of Mexico. Approximately 70% of the flow enters the Gulf through the bird-foot delta and the remaining 30% is carried down the Atchafalaya River. These river discharges have a large impact on physical and biological processes in the northern Gulf of Mexico. Available discharge data show that at least 70% of the combined Mississippi/Atchafalaya River flow is discharged onto the Louisiana shelf west of the bird-foot delta.

The river discharges entering the Gulf of Mexico can be readily detected in satellite imagery by their high reflectance, due to backscattering from suspended sediments, and their low temperatures. Satellite measurements from the NOAA AVHRR have been used extensively to investigate circulation processes and the fate of river waters in the northern Gulf of Mexico. Studies have shown that the buoyant plume of the Mississippi and Atchafalaya Rivers respond within hours to changes in wind forcing. The surface geometry of the Mississippi sediment plume is predictable from measurements of wind speed, direction and river discharge. East winds prevail with a frequency of about 62% throughout the year, forcing a westward flow of river water along the Louisiana coast and further downstream. Circulation is complex around the bird-foot delta as a result of the protrusion of land 70 km or so into the Gulf. During northeast wind conditions, most of the river discharge east of the bird-foot delta flow southward and then westward to join the flows from South Pass and Southwest Pass. West of the delta, these combined effluents turn northward where the flow splits, with a portion of the flow forming a clockwise gyre within the Louisiana Bight and a separate portion of the flow continuing westward along the Louisiana coast. During east wind periods, it is estimated that 60-80% of the discharge from the bird-foot delta moves westward. During west winds, the flow of river water around the bird-foot delta reverses and most of the freshwater moves eastward and southward. From October to March, strong west winds interrupt the prevailing east winds every 5-7 days with the passage of winter storms. During summer, relatively weak southwest winds can occur for several weeks to months reversing the direction of river waters for an extended period of time.

Satellite imagery of surface temperature variability have shown that offshelf flows, i.e. squirts and jets, are advected off the continental shelf in association with warm core eddies and warm core/cold core eddy pairs, resident on the continental slope. Research has shown that the initial impetus for the offshelf flow is wind forcing. These injections of shelf water from the Louisiana and Texas shelves into the deeper Gulf vary greatly in spatial structure (100-350 km long, 10-100 km wide), surface area (300-39,000 km^2), and longevity (1-8 weeks). Surface velocities of 30-100 cm/s have been measured within these features. Research using ocean color sensors has shown that the shelf waters enhance the chlorophyll *a* concentrations of the deeper Gulf. With the launch of the SeaWiFS ocean color sensor in mid-1997, we have gained the ability to detect river waters at greater distances from their source regions. Normalized water leaving radiances from the six visible-band channels of SeaWiFS provide the potential to detect suspended sediments, yellow substances and phytoplankton blooms (resulting from the nutrient enrichment of shelf waters). Efforts are underway by several research groups to obtain "sea-truth" measurements that will enable a more quantitative assessment of in-water biological constituents using SeaWiFS image data and the physical-biological interactions associated with Mississippi River effluents in the northern Gulf of Mexico.

The Structure of Small Scale Fronts in River Plumes

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River plumes occur at the mouths of many rivers. O'Donnell (1993) provides a recent review. Examples include the Connecticut (Garvine, 1974), Frazer (Stronach,1977) and Mississippi Rivers (Wright and Coleman, 1971). Large estuaries also produce outflow plumes. The Delaware Bay (Munchow, 1992) and the Chesapeake Bay (Boicourt et al. 1987) are examples. These plumes are often found to be bounded by fronts, narrow zones of strong horizontal gradients in density and velocity. Garvine and Monk (1974) first documented the structure of the frontal zone in the plume of the Connecticut River. Subsequently, Luketina and Imberger (1987 and 1989) documented a similar phenomenon in the plume of Koombana Bay. In both studies the spatial resolution of the current and density fields were inadequate to properly resolve the structure of the front.

Recently, the combination of the instrument packages developed by O'Donnell (1997), termed SCUD and Trump et al. (1995), termed TOAD have been employed to resolve the structure of the front in the Connecticut River plume. In essence, SCUD is a rigid 3m long array of four electro-magnetic current meters and five conductivity-temperature sensors mounted vertically over the bow of a small boat. Ship speed and position was estimated using a differential GPS system and ship motion was measured by a flux gate compass and a tilt and roll sensor. TOAD is a 600 kHz broadband acoustic Doppler current profiler and conductivity-temperature sensor towed just below a surface float. Together, these instruments observe the water velocity in the interval 0.6 m below the surface and 1.5 m above the bottom in 10 m of water with a vertical resolution of 0.5 m. The density field in the top 3 m is measured. Typical ship speeds and sampling rates resulted in a horizontal resolution of between 2 and 5 m for SCUD and 10 and 25 m for TOAD. O'Donnell et al. (1998) provides details of the observations.

When the front was moving to the west at approximately 0.3 ms^{-1}, two across-front transects revealed a horizontal convergence in the across-front velocity components at 0.6 m of 0.05-0.1 s^{-1}. This was associated with a salt induced horizontal density gradient of 10^{-2} kg/m^4. These patterns are consistent with existing gravity current theories and laboratory observations. An along-front transect with the towed instruments in the zone of maximum surface convergence showed that a downwelling of 0.2 ms^{-1} occurred at the front. Vertical velocities of this magnitude are consistent with a simple argument based on continuity and slow along-front variations.

Structures similar to those summarized have been reported in the outflow plume of the Mississippi River. Theoretical models that explicitly parameterize fronts (see O'Donnell, 1993) for a summary) suggest that they can influence the location and timing of mixing between the plume and the ambient fluid. These structures could, therefore, be important to the distribution of buoyancy on the Gulf of Mexico shelf.

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Shelf-Slope Exchanges in the Northern Gulf of Mexico

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Current measurements have and are currently been made from an extensive array of moorings deployed by the Minerals Management Service (MMS) funded LATEX A and ongoing De Soto Canyon studies. These measurements at the shelf break, both east and west of the Mississippi delta, have shown that: 1) flows are energetic with speeds of 60 to 75 cm/s being fairly common; 2) events have a variety of time scales ranging from a few days to a month or longer; 3) across isobath components of the current are nearly as energetic as the along isobath components; 4) current fluctuations are not generally coherent over along isobath mooring spacing of 70 km or more; 5) there is not a strong relationship of the flow events to the wind fluctuations; and 6) there is little or no apparent seasonal variation in the event characteristics, especially west of the delta. East of the delta there is some evidence that the winter of 1997-1998 was more energetic with predominantly shorter period (< 10 day) fluctuations than in the previous summer.

The LATEX C and Gulfcet I programs (MMS) made extensive aircraft and ship based surveys, respectively, of the northern Gulf of Mexico slope between the 200 and 2000 m isobaths over a three year period. These surveys showed that slope was dominated by cyclonic and anticyclonic eddies of diameters between ~ 40 and 150 km. On the lower slope large anticyclones (~ 200 to 300 km in diameter) that had been shed from the Loop Current occasionally intruded over the 2000 m isobath. However, except near the delta, Loop Current eddies rarely influence directly currents over the shelf break. Consequences of this eddy field on the slope is that shelf-slope exchanges often occur as offshore or onshore jets between eddies rotating in opposite directions. These jets have limited spatial alongshore scales, and can occur at any position on the northern slope. The eddies generally occupy the upper layer which in the case of cyclones can be 800 m or deeper. Therefore, the offshore jets usually occupy the whole of the water column at the shelf break. These eddy generated jets seem to be the prime mechanism for shelf-slope exchange and these events can be quite long lasting (~ months). The existence of a complex eddy field over the slope also creates pathways between the deep Gulf basin and the shelf and vice-versa. Many drifter tracks have shown the effectiveness of the eddy field in transporting water parcels to and from the shelf and deep Gulf basin waters. The SCULP-I (MMS) program deployed a total of 370 drifters on the Louisiana shelf between October 1993 and October 1994. Of these 370 drifters, 107 left the shelf sometime during their 100 to 120 day lifetimes. The drifters that left the shelf were usually entrained by shelf break eddies and transported to the offshore regions in a relatively random manner with only the narrow, northeast Mexican shelf, being favored as an export site. This is because of the prevalence of offshore, oppositely rotating paired eddies adjacent to this slope that arise from the topographic interaction of old Loop Current eddies with the north-south directed Mexican slope.

The region east of the delta had some different characteristics but was still dominated by small scale warm and cold eddies. The upper slope region was dominated by a two layer flow with eastward and westward components above and below about 150 to 200 m depth, respectively. This jet appears to be driven by lower slope anticyclonic eddies. Eddy-driven upwelling in the De Soto canyon is quite common, particularly in the energetic winter months. The dynamics of this process are not yet understood. The eddy field between an extended Loop Current and the Northeast Gulf shelf is often effective in moving filaments of warm Loop Current derived water towards the shelf break.

The generation and life histories of slope eddies have not yet been described because of the lack of high resolution databases. It is clear that they can be long lasting and can be moved around by larger scale eddies such as Loop Current anticyclones. The ultimate source of eddy vorticity is the Loop Current and its periodic shedding of large anticyclones.

Biological–Physical Coupling in the Chesapeake Bay Plume

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A major focus in understanding plankton dynamics has been the relative roles of physical and biological controls in structuring the spatial and temporal patterns of biomass and production. Bounded or semi-bounded ocean features such as eddies, rings and buoyant plumes are attractive areas to study these controls on plankton dynamics because the distance hydrography and persistence of these structures allow the investigator to study populations/communities over time and to quantify growth rates, mortality rates, physical inputs and losses. Coastal plumes are characterized by a distinct salinity structure and high biological production relative to ambient shelf waters. Low salinity water discharged from Chesapeake Bay usually makes a broad, anticyclonic turn as it flows onto the continental shelf, subsequently narrowing into a coastal jet as it flows south along the coast (Chao and Boicourt 1986). The spatial and temporal scales of the Chesapeake Bay plume are effected by the discharge rate of water from Chesapeake Bay as well as wind speed and direction. Under downwelling (Northerly) winds, the plume forms a narrow coastal jet which can propagate along the coast at speeds reaching 7 km d^{-1} which can result in low salinity Chesapeake Bay water traveling over 100 km S or the Bay mouth (Boicourt et al. 1987). In contrast, upwelling (Southerly) winds oppose the anticlyclonic turn of the plume and, because of Ekman circulation, result in a seaward spreading and rapid thinning and dilution of plume waters, Thus the coastal plume of Chesapeake Bay can have a horizontal scale of 10 to 100 km, a vertical scale of 5 to 20 m and a time scale of 1 to 20 days (Boicourt et al. 1987). These temporal scales overlap with the scales of growth and patch structure of plankton (bacteria, phytoplankton, protozoa and copepods). Therefore the physics of the plume can influence the growth and trophic interactions among plankton populations of the plume and their mixing rates with surrounding shelf waters.

Drifter experiments conducted in the Chesapeake Bay plume showed that, in general, there was a shift from an autotrophic- to a heterotrophic plankton community with time in the plume waters. Chlorophyll decreased (lost to both sinking and grazing) as bacteria, flagellates and copepods increased in the plume waters (Boicourt et al. 1987; Roman et al. 1988; Malone and Ducklow 1990; McManus and Fuhrman 1990; Glibert et al. 1991). Heterotrophic processes such as bacterial production, ammonium regeneration and copepod grazing usually increased over time as the plume traversed the continental shelf (Boicourt et al. 1987; Roman et al. 1988; Malone and Ducklow 1990; Glibert et al. 1991). The convergence areas associated with frontal processes of the plume usually had high concentrations of copepods.

A convenient biological tracer of plume waters are the larvae of benthic invertebrates which spawn in estuaries. Although many invertebrate larvae have adopted strategies such as vertical migration which help retain them in estuaries with two-layer flow patterns, a number of estuarine invertebrate species have pelagic larvae which are transported to shelf waters where they develop and then return to the estuary. Because these latter invertebrate species have a fairly unambiguous source, they can be used along with more conservative tracers such as salt to trace the flow pattern of plume water on the shelf. However, unlike the salinity of plume water which rapidly (hours to days) increases because of mixing with shelf waters, patches of crab larvae often actively aggregate in surface waters, thus their distribution can provide a signature of past flow events.

As part of the MECCAS (Microbial Exchanges and Coupling in Coastal Atlantic Systems) Project, crab larvae were collected in the shelf waters off Chesapeake Bay in April, June and August (Roman and Boicourt 1999). We conducted both hydrographic (temperature, salinity, nutrients) and biological (chlorophyll, copepods) mapping surveys in conjunction with Eulerian and Lagrangian time studies of the vertical distribution of crab larvae in the Chesapeake Bay plume. These abundance estimates are used with both current meter records and drifter trajectories to infer mechanisms of larval crab dispersion to the shelf waters and recruitment back into Chesapeake Bay. The highest numbers of crab larvae were usually associated with the Chesapeake Bay plume, suggesting that the dominant source of crab larvae to shelf waters was Chesapeake Bay. However, patches of crab larvae also were found in the higher salinity shelf waters, as possible remnants of previous plume discharge events. The distribution of crab larvae in the shelf waters changed on 1-2 day time-scales as a consequence of both variations in the discharge rate of the Chesapeake Bay plume and local wind-driven currents. Downwelling-favorable winds (NW) intensified the coastal jet and confined the plume and crab larvae along the coast. For example in April when NW winds predominated, crab zoeae were transported southward along the coast at speeds that at times exceeded 168 km d^{-1} during a downwelling wind event. In contrast, during June and August upwelling-favorable winds (S,SW) opposed the anticyclonic turn of the plume and, via Ekman circulation, forced the plume and crab larvae to spread seaward. Plume velocities during these conditions generally were less than 48 km d^{-1}. The recruitment of crab larvae to Chesapeake Bay is facilitated in late summer by the dominance of S winds which can reverse the southward flow of shelf waters. Periodic downwelling favorable winds can result in the flow of surface waters and crab larvae towards the entrance of Chesapeake Bay. In addition, approximately 27% of the larval crabs spend at least part of the day in bottom waters which have a residual drift towards the Bay mouth. Thus there appears to be a variety of physical transport mechanisms which can enhance the recruitment of crab larvae into Chesapeake Bay.

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Small and Mesoscale Processes of the Mississippi River Plume.

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The Mississippi River is the single largest source of freshwater and dissolved inorganic nutrients discharged onto the continent shelf of the United States. During the annual discharge peak in spring the concentrations of inorganic nutrients can exceed 100 µMN O_3-N and SiO_3-Si in Louisiana shelf waters west of the Mississippi River delta. Although it is clear that the Mississippi River waters originating at the delta are the primary source of 'new', or allochthonous, nutrients on the western Louisiana shelf, ship-based surveys have generally failed to discern a clear relationship between surface salinity, surface nutrient concentrations, and phytoplankton pigment concentrations in this region. In spring 1993 we (W. Wiseman, Jr., W. Boicourt, and G. Hitchcock) described the surface properties of the river plume originating at Southwest Pass by following surface drifters deployed in the feature. This Lagrangian view of the plume provided a description of the temporal evolution of water parcels as they transit the Louisiana Shelf.

In May 1993, the path of the plume was to the northwest in response to wind and the Coriolis force. The trajectories of drifters show the plume rapidly expands seaward of the mouth of the delta. Near the mouth of Southwest Pass the plume surface properties are dominated by a salinity minimum that corresponds to the turbidity maximum. As the plume thins and expands, the surface property fields (temperature, salinity, chlorophyll *a* fluorescence, and transmittance) become increasingly variable. Surface salinity, chlorophyll *a* fluorescence, and transmissivity distributions in transects crossing the plume axis show that surface fields become increasingly patchy as the plume waters mix with adjacent shelf waters. The cross-plume gradients in salinity were strong, with minimum salinity at the shoreward edge of the feature. The increasingly patchy nature of the surface property distributions down the axis of the plume reflects mixing processes that facilitate entrainment of shelf waters across the strong pycnocline at the base of the feature. Inorganic nutrient (NO_3-N, PO_4-P,SiO_3-Si) concentrations in plume surface waters decreased linearly with increasing salinity, indicating conservative mixing within the plume. Maximum phytoplankton concentrations in the plume (< 20 µg chl *a* 1^{-1}) were much less than those predicted from available nutrient levels. Thus small-scale mixing processes are a major determinant of ambient nutrient concentrations in the plume following the discharge of Mississippi River water from the delta.

The Effects of Hypoxia on Animal Distributions

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The largest zone of oxygen-depleted coastal waters in the United States is in the northern Gulf of Mexico on the Louisiana-Texas continental shelf. From 1993 to 1997, the size of the hypoxic zone was greater than 16,000 km^2 in mid-summer. Hypoxic waters (< 2 mg l^{-1}) occur near the bottom and extend to as much as 20 m from the bottom over extensive areas. Oxygen depletion begins in the spring, reaches a maximum in mid-summer and disappears in the fall and winter. The operational definition for hypoxia is based upon the lack of fish and shrimp in trawls when oxygen levels fall below the 2 mg l^{-1} level.

Hypoxia affects the behavior and distribution of zooplankton similar to results from the Chesapeake Bay. The dominant zooplankton in the northern Gulf of Mexico, copepods, are normally in low abundance or absent from oxygen depleted waters < 1 mg l^{-1}. Copepod nauplii are more affected than adult copepods. Anoxia disrupts the diel migratory behavior.

A fairly predictable pattern in responses of components of the benthic and demersal communities follows a decrease in oxygen concentrations from 2 mg l^{-1} to anoxia. Motile fish and crustaceans (e.g., crabs, shrimp and mantis shrimp) are generally absent from bottom habitats when the oxygen falls below 1.5-2 mg l^{-1}. Less motile invertebrates die at oxygen levels below 1.5 mg l^{-1}. The organisms that live in the sediments display stress behavior below 1.0 mg l^{-1}. In the community that typically lives in the sediments, the smaller worms, snails, bivalves and crustaceans, there is a fairly linear decrease in benthic diversity and abundance as oxygen concentrations fall from 0.5 mg l^{-1} to anoxia. Oxygen stressed macroinfaunal communities are characterized by limited taxa (none with direct development, e.g., amphipods), characteristic resistant fauna (e.g., a few polychaetes and sipunculans), a reduced species richness, severely reduced abundances (but never azoic), low biomass, and limited recovery following the abatement of oxygen stress. Meiofaunal communities become reduced in abundance and diversity as the oxygen levels approach zero, but selected nematodes maintain populations. The long-term secondary productivity of the benthos is not known. Differences in benthic foraminiferans demonstrate historic and extant conditons of oxygen stress on the shelf

Penaeid shrimp avoid hypoxic bottom waters and are concentrated on the inshore and western and eastern margins of the zone. Analysis of long-term data from the northern Gulf of Mexico associated with the by-catch of shrimp trawls indicate that there has been a shift in dominance of the some abundant fishes from those that are associated with the bottom (habitat and food resources) to those that are planktivorous in the upper water column. A bell-shaped curve models a continuum of fishery yield in response to increasing nutrients as ecosystems become eutrophic then dystrophic. In waters with low nutrients, the fishery yield is low. As the quantity of nutrients increases, the fishery yield increases. As the ecosystem becomes increasingly eutrophied, there is a drop in fishery yield but the decreases are variable. The benthos are the first resources to be reduced by increasing frequency of seasonal hypoxia and eventually anoxia; bottom-feeding fishes then decline. Loss of a planktivorous fishery follows as eutrophication increases, with eventually a change in the zooplankton community composition. Where the current Gulf of Mexico fisheries lie along the this model of increasing eutrophication is not known.

Potential Climatic-Induced Changes in the Gulf of Mexico

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Introduction

Global and regional climatic signals as well as their effects in the Gulf of Mexico are discussed using Sea Surface Temperature (SST) as an indicator for climatic changes. Our main source of data are SST anomalies with respect to the long term seasonal cycle from the Kaplan reconstructed SST dataset for the period 1856-1991. First, we review the known global and regional climatic signals present in the SST dataset and discuss (qualitatively) their influence on the climate of the Gulf of Mexico. Second, we focus on the Gulf itself and estimate which are the dominant effects there. Amongthe global and regional signals we have the El Nino-Southern Oscillation (ENSO) mode, the global warming, and the non-ENSO modes such as the Pacific Decadal Oscillation (PDO) related modes in the Pacific and the North Atlantic Oscillation (NAO) related multidecadal mode in the Atlantic.

Global ENSO Mode

By far the most dominant signal in the global climate system is the ENSO mode. The ENSO signal is well captured by the first complex Empirical Orthogonal Function of the global SST anomalies, which shows how the amplitude and phase of ENSO vary in space around the globe (Enfield and Mestas-Nunez, 1999a). We note, for example, that the warming in the Atlantic lags the warming in the NINO3 region by 1-3 seasons (3-9 months). We also note that the amplitude of the ENSO signal is very small in the Gulf of Mexico.

Global Warming

Global averages of the SST anomalies show that the oceans are warming and that the rate of warming is not uniform in space. The spatial distribution of the global warming signal can be estimated by differencing the temporally averaged SST anomaly time series for the second and first half of the record or alternatively by calculating the slope of a least-squares line at every grid point (Enfield and Mestas-Nunez 1999a). Both of these show that the global warming signal in the Gulf of Mexico is small.

Decadal to Multidecadal Variability

To look at the decadal to multidecadal variability we first removed the ENSO and the global warming signals from the SST anomaly records. Our analysis of the non-ENSO variability has revealed several modes of variability that correspond to known climatic signal described in the literature (Enfield and Mestas-Nunez 1999a, Mestas-Nunez and Enfield 1999c, Enfield and Mestas-Nunez 1999b). In the North Atlantic, the dominant signal is a multidecadal mode that seems to be related to the NAO. In the Pacific, two modes of variability were found that seem to be related to the PDO. To investigate the importance of these modes in the Gulf of Mexico, we averaged the SST anomalies in the gulf and correlated it with the non-ENSO modes of variability. This analysis shows that the Gulf of Mexico SST anomalies are significantly correlated with the North Pacific multidecadal mode.

Conclusions

It is important to note that the fact that the ENSO and global warming signals are small in the average Gulf of Mexico SST anomalies does not mean that these components do not have an effect on the gulf's climate. ENSO and global warming can affect other variables in the global ocean-atmosphere system (e.g. precipitation, tropical storm activity) and those in turn affect the climate of the gulf. We conclude that further research of the oceanic and atmospheric variables is required to describe the climatic effects in the Gulf of Mexico. The apparent teleconnection with the PDO requires a closer look as well as its potential climatic impacts on the gulf's chemistry and biology.

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