

GULF OF MEXICO HYPOXIA, A.K.A. “THE DEAD ZONE”

Nancy N. Rabalais,¹ R. Eugene Turner,² and
William J. Wiseman, Jr.³

¹*Louisiana Universities Marine Consortium, 8124 Hwy. 56, Chauvin,
Louisiana 70344; email: nrabalais@lumcon.edu*

²*Coastal Ecology Institute, and Department of Oceanography & Coastal Sciences,
Louisiana State University, Baton Rouge, Louisiana 70803; email: eturne@lsu.edu*

³*Coastal Studies Institute, and Department of Oceanography & Coastal Sciences,
Louisiana State University, Baton Rouge, Louisiana 70803; email: wwiseman@lsu.edu*

Key Words anoxia, eutrophication, nutrient enrichment, Mississippi River,
coastal, estuary

■ **Abstract** The second largest zone of coastal hypoxia (oxygen-depleted waters) in the world is found on the northern Gulf of Mexico continental shelf adjacent to the outflows of the Mississippi and Atchafalaya Rivers. The combination of high freshwater discharge, wind mixing, regional circulation, and summer warming controls the strength of stratification that goes through a well-defined seasonal cycle. The physical structure of the water column and high nutrient loads that enhance primary production lead to an annual formation of the hypoxic water mass that is dominant from spring through late summer. Paleoindicators in dated sediment cores indicate that hypoxic conditions likely began to appear around the turn of the last century and became more severe since the 1950s as the nitrate flux from the Mississippi River to the Gulf of Mexico tripled. Whereas increased nutrients enhance the production of some organisms, others are eliminated from water masses (they either emigrate from the area or die) where the oxygen level falls below 2 mg l^{-1} or lower for a prolonged period. A hypoxia-stressed benthos is typified by short-lived, smaller surface deposit-feeding polychaetes and the absence of marine invertebrates such as pericaridean crustaceans, bivalves, gastropods, and ophiuroids. The changes in benthic communities, along with the low dissolved oxygen, result in altered sediment structure and sediment biogeochemical cycles. Important fisheries are variably affected by increased or decreased food supplies, mortality, forced migration, reduction in suitable habitat, increased susceptibility to predation, and disruption of life cycles.

INTRODUCTION

Waters with less than full oxygen saturation occur in many parts of the world's oceans (Kamykowski & Zentara 1990). Hypoxic (low oxygen) and anoxic (no oxygen) waters have existed throughout geologic time and presently occur in many

of the ocean's deeper environs, such as oxygen minimum layers, deep basins, and fjords. The occurrence of hypoxia and anoxia in shallow, coastal and estuarine areas, however, appears to be increasing, most likely accelerated by human activities (Diaz & Rosenberg 1995). One of the world's largest zones of estuarine and coastal hypoxia is located in the northern Gulf of Mexico on the Louisiana/Texas continental shelf. Referred to as the "Dead Zone" in the popular press and literature, the areal extent of the severe oxygen deficiency reached a record size of 20,700 km² in mid-summer 2001 (Rabalais et al. 2001). The term dead zone refers to the failure to capture fish, shrimp, and crabs in bottom-dragging trawls when the oxygen concentration falls below a critical level in water near the seabed (Renaud 1986). The numbers of stressed or dying benthic infaunal organisms within the sediments increase substantially when the oxygen levels remain low for prolonged periods, biodiversity is diminished, and community structure and ecosystem functioning are altered (Rabalais et al. 2001a,b). Higher in the water column and in the surface mixed layer, however, there is sufficient oxygen to support sizeable populations of fish and swimming crabs. Also, there are anaerobic or hypoxia-adapted organisms that survive in sediments overlain by hypoxic or anoxic waters, so that the term dead zone is not entirely accurate (Rabalais & Turner 2001a). Still, the area is large enough to garner a high level of public attention, if only because of the lack of catchable demersal fish and shrimp.

There is no universally accepted terminology or concentration limits to describe oxygen-deficient conditions (Tyson & Pearson 1991). Hypoxia is a term long used by physiologists to describe conditions or responses produced by stressful levels of oxygen deficiency. The use of the term to describe oxygen-deficient environments became common in the mid- to late 1970s, and was especially attributed to those working in the Gulf of Mexico by Tyson & Pearson (1991). Based on laboratory or field-observed responses of organisms to oxygen stress, hypoxia has been variously defined as corresponding to a range of 3.0–0.2 ml l⁻¹, with the consensus in favor of 1.4 ml l⁻¹ (= 2 mg l⁻¹ or ppm). Another convenient threshold for effects that was adopted by Breitburg (2002) was dissolved oxygen concentration <50% saturation owing to avoidance behavior, reduced growth, or other signs of physiological stress in sensitive fish. For this review, we define hypoxia for the northern Gulf of Mexico as dissolved oxygen levels below 2 mg l⁻¹. This is the level below which bottom-dragging trawls usually do not capture any shrimp or demersal fish (Renaud 1986). This concentration approximates 20% oxygen saturation in 25°C and salinity of 35 in summertime bottom waters of the Gulf of Mexico (Rabalais et al. 1999); in less saline, cooler Chesapeake Bay waters 2 mg l⁻¹ equals 24% saturation at 20°C and salinity of 15 (Breitburg 2002). The range of organismal responses depends on the severity of the hypoxia, the length of exposure, and the periodicity and frequency of exposure. The hypoxic zone of the northern Gulf of Mexico, one of hundreds globally, will be the focal point of this review with similarities and differences drawn from other coastal and estuarine areas.

The coastal areas of the Baltic Sea, northern Gulf of Mexico, and northwestern shelf of the Black Sea are the largest such coastal hypoxic zones in the world, reaching 84,000 km², 21,000 km², and 40,000 km² (until recently), respectively

(Rosenberg 1985, Rabalais et al. 2002, Mee 2001). Smaller and less frequent zones of hypoxia occur in the northern Adriatic Sea (Justić et al. 1987), the southern bight of the North Sea (Fransz & Verhagen 1985) and in many U.S. coastal and estuarine areas, for example, New York Bight (Garside & Malone 1978, Swanson & Sindermann 1979, Swanson & Parker 1988), Chesapeake Bay (Officer et al. 1984, Malone 1991), Long Island Sound (Welsh & Eller 1991, Welsh et al. 1994, Parker & O'Reilly 1991), Mobile Bay (Turner et al. 1987), and the Neuse River estuary (Paerl et al. 1998). In a review of 47 known anthropogenic hypoxic zones where benthic community effects were documented, Diaz & Rosenberg (1995) noted that no other environmental variable of such ecological importance to estuarine and coastal marine ecosystems around the world as dissolved oxygen has changed so drastically and in such a short period of time. For those zones reviewed, they found that there was a consistent trend of increasing severity (either duration, intensity, or size) where hypoxia occurred historically, or hypoxia existed presently when it did not occur before. The occurrence of hypoxia in estuarine and coastal areas is increasing and the trend is consistent with the increase in human activities that result in nutrient over-enrichment.

Hypoxia is but one of the symptoms of eutrophication, defined by Nixon (1995) as an increase in the rate of production and accumulation of carbon in aquatic systems. Eutrophication may be a natural process, but very often results from an increase in nutrient loading, particularly by forms of nitrogen and phosphorus. Coastal eutrophication, often accompanied by hypoxia, tracks increases in population, a focusing of that populace in coastal regions, agricultural expansion in river basins, and increasing food and energy consumption (Nixon 1995; Howarth et al. 1995, 1996; Vitousek et al. 1997; Caraco & Cole 1999; Bennett et al. 2001). Nutrient over-enrichment from anthropogenic sources is one of the major stressors impacting estuarine and coastal ecosystems (Bricker et al. 1999, Howarth et al. 2000, National Research Council 2000, Cloern 2001). There is increasing concern in many areas around the world that an oversupply of nutrients from multiple sources is having pervasive ecological effects on shallow coastal waters. These effects include reduced light penetration, increased abundance of nuisance macroalgae, loss of aquatic habitat such as seagrass or macroalgal beds, noxious and toxic algal blooms, hypoxia and anoxia, shifts in trophic interactions and food webs, and impacts on living resources (Vitousek et al. 1997, Schramm 1999, Anderson et al. 2002, Rabalais 2002). Whereas many of these primary and secondary responses of ecosystems to nutrient over-enrichment are interrelated, this review will focus on aspects of hypoxia, emphasizing the Gulf of Mexico, in describing causes, temporal and spatial variability, effects on living resources, historical changes, and management challenges.

CAUSES OF HYPOXIA—FRESH WATER AND NUTRIENTS

Two principal factors lead to the development and maintenance of hypoxia. First, the water column must be stratified so that the bottom layer is isolated from the surface layer and the diffusion of oxygen from surface to bottom. The physical

structure is dictated by water masses that differ in temperature or salinity or both. Fresher waters derived from rivers and seasonally-warmed surface waters are less dense than, and reside above, the saltier, cooler and more dense water masses near the bottom. Both salinity and temperature are important in influencing the strength of stratification in the northern Gulf of Mexico (Rabalais et al. 1991), Chesapeake Bay (Officer et al. 1984), and Kiel Bay (Arntz 1981), whereas stratification is controlled primarily by temperature in the Gulf of Trieste (Stachowitsch 1986), New York Bight (Falkowski et al. 1980), and Long Island Sound (Welsh & Eller 1991). Stratification goes through a well-defined seasonal cycle that generally exhibits maximum stratification during summer and weakest stratification during winter months (Figure 1). This cycle is due to the strength and phasing of river discharge, wind mixing, regional circulation and air-sea heat exchange processes.

The second factor is decomposition of organic matter that leads to reduced oxygen levels in the bottom waters. The source of the organic matter settling to the seabed in the northern Gulf of Mexico is mostly from phytoplankton growth stimulated by riverine-delivered nutrients, although some river-borne organic matter is delivered by the Mississippi River (Eadie et al. 1994, Turner & Rabalais 1994a, Committee on Environment and Natural Resources 2000). The concentrations and total loads of nitrogen, phosphorus, and silica to the coastal ocean influence the productivity of the phytoplankton community, the types of phytoplankton that are most likely to grow, and ultimately the flux of phytoplankton-derived organic matter (Turner & Rabalais 1994b, Lohrenz et al. 1997, Dortch et al. 2001). Phytoplankton not incorporated into the food web and fecal material generated by the food web sink into bottom waters where they are decomposed by aerobic bacteria, causing oxygen depletion. The relative influence of the physical features of the system and the progression of biological processes varies spatially and over an annual cycle. Both are inter-related in the northern Gulf of Mexico and directly linked with the dynamics of the Mississippi and Atchafalaya River discharge. (The Atchafalaya River carries up to one-third of diverted Mississippi River discharge to a second delta 180 km west of the birdfoot delta.)

Some coastal areas and estuaries are more susceptible to eutrophication, including the formation of hypoxia, from nutrient enrichment based on two key physical features of the water body—the dilution capacity of the water column and its flushing/retention time (National Research Council 2000). Systems with relatively large volumes and short flushing times are less susceptible to eutrophication; systems with longer flushing times are more susceptible. Superimposed upon this continuum of susceptibility are the nutrient loadings to the water body, the timing of the loads, and the relative proportion of the nutrients. Light availability can play a critical role in determining the response of estuarine systems to nutrient loading (Cloern 1999), and grazing of phytoplankton by benthic filter feeders or water column zooplankton can limit the accumulation of algal biomass (Alpine & Cloern 1992).

SOURCES OF NUTRIENTS

Human activity has dramatically increased the flux of phosphorus and nitrogen to the world's oceans. The fluvial drainage of phosphorus from terrestrial and freshwater ecosystems is currently nearly three times greater than pre-industrial levels (Bennett et al. 2001). The change in nitrogen flux is even more dramatic, for example fourfold in the Mississippi River, eightfold in the rivers of the northeastern United States, and tenfold in the rivers draining to the North Sea (Howarth et al. 1996). The human activities and sources of increased nitrogen and phosphorus vary across watersheds, but their relative proportion and rate of change identify potential foci for eventual attempts at reduction. Nonpoint sources of nutrients are the dominant and least easily controlled inputs into coastal waters from large watersheds, and especially from watersheds with extensive agricultural activity (e.g., Mississippi River system) or atmospheric nitrogen pollution from fossil-fuel combustion (e.g., dominant in the northeastern United States).

Some estuaries receive nutrients across their boundary with the ocean along with inputs from land, rivers, and atmospheric deposition (Boynton et al. 1995, Nixon et al. 1995). Offshore waters on continental shelves can similarly receive nutrients from river inputs from land, direct deposition from the atmosphere, and advection of deeper, nutrient-rich oceanic waters. The relative proportion of these inputs varies among coastal waters of the U.S., but can be a dominant nutrient input (Nixon et al. 1996). In the northern Gulf of Mexico, however, the Mississippi River drainage is by far the dominant source of nutrients fueling the hypoxia zone.

Dunn (1996) calculated the nutrient inflows from 37 U.S. streams discharging into the Gulf of Mexico for water years 1972–1993. The combined flows of the Mississippi and Atchafalaya Rivers account for 91% of the estimated total nitrogen load. If only streams between Galveston Bay (Texas) and the Mississippi River delta are considered, i.e., those most likely to influence the zone of hypoxia, the combined flows of the Mississippi and Atchafalaya Rivers account for 96% of the annual freshwater discharge and 98.5% of the total annual nitrogen load. Similar calculations for the annual total phosphorus load are 88% of the total 37 streams and 98% of the streams between Galveston Bay and the Mississippi River delta. The relative contribution of direct atmospheric deposition of nitrogen to the total nitrogen load for an area twice the size of the hypoxic zone is 1% (Goolsby et al. 1999). Groundwater sources to the area affected by hypoxia are unlikely to be important because of the lack of shallow aquifers along the Louisiana coast and the low potential for transfer in a cross-shelf direction to the area where hypoxia develops (Rabalais et al. 1999). The relative contribution of offshore sources of nutrients from upwelled waters of the continental slope is unknown but expected to be minimal considering the alongshore current regime. The Mississippi River system is, by far, the major source of nutrients to the northern Gulf of Mexico where hypoxia is likely to develop, and thereby influences the primary production

on the shelf and eventual flux of organic matter to the lower water column below the pycnocline.

Away from the discharges of the Mississippi and Atchafalaya Rivers, there is a consistent westward and downstream transition from lower to higher salinities, higher to lower nutrients, and higher to lower surface chlorophyll concentrations (Rabalais et al. 1996, 1999). Ultimately nutrients become limiting to phytoplankton productivity. These gradients away from the riverine sources are further reflected in the flux of organic material as seen in surface-to-bottom pigment ratios and accumulation of phaeopigments in the lower water column. Respiration rates are related to chlorophyll *a* concentrations (Turner & Allen 1982a). Therefore, there is a consistent transition away from the river discharges along the coastal plume in flux of organic material, respiration rates and incidence of bottom water hypoxia. The variability in freshwater discharge and related flux of nutrients on seasonal, annual, decadal, and longer scales underlies many important physical and biological processes affecting coastal productivity and food webs.

DIMENSIONS OF GULF HYPOXIA

The shelfwide distribution of hypoxia is determined annually from a five-day mapping cruise in mid-summer, usually between mid-July and mid-August (Rabalais et al. 1999). The hypoxic water mass extends west from the Mississippi River bird-foot delta across the Louisiana shelf and onto the upper Texas coast, from within 1 km of the barrier shoreface to as much as 125 km offshore. Hypoxia is found in water depths up to 60 m, but more typically between 5 and 30 m. Hypoxia is not found just in a thin lens overlying bottom sediments, but occurs well up into the water column depending on the location of the pycnocline(s). Hypoxia may encompass from 10% to over 80% of the lower water column, but normally affects 20–50% (Figure 1).

Mid-summer hypoxic zones, between 1985 and 1992, generally formed in two distinct areas west of the Mississippi and Atchafalaya River deltas (Figure 2), with the total area averaging 8000–9000 km² (Figure 3). The size of the hypoxic zone doubled in response to the Great Mississippi River Flood of 1993, forming a single continuous zone across the Louisiana shelf (Figures 2 and 3). The examples from 1986 and 1993 (Figure 2) illustrate the typical pre- and post-flood distribution and doubling in average size between the two periods (Rabalais et al. 2002). Persistent currents from the west to the east across the Louisiana shelf often force the hypoxic water mass onto the southeastern shelf, which is represented by the 1998 example (Figure 2). Although the extent of hypoxia across the bottom in 1998 was less than 1997 (Figure 3), the volume of the hypoxic water mass was greater because more of the total depth of the water column was hypoxic in 1998 compared to 1997 (N. Rabalais et al. unpublished data). Low river discharge and nutrient flux in 1988 and 2000 resulted in smaller areas of hypoxia. Hypoxia developed in the spring of 1988 when discharge was normal, but was confined to a single station off Terrebonne Bay in July when flow reached a record low. The smaller area of

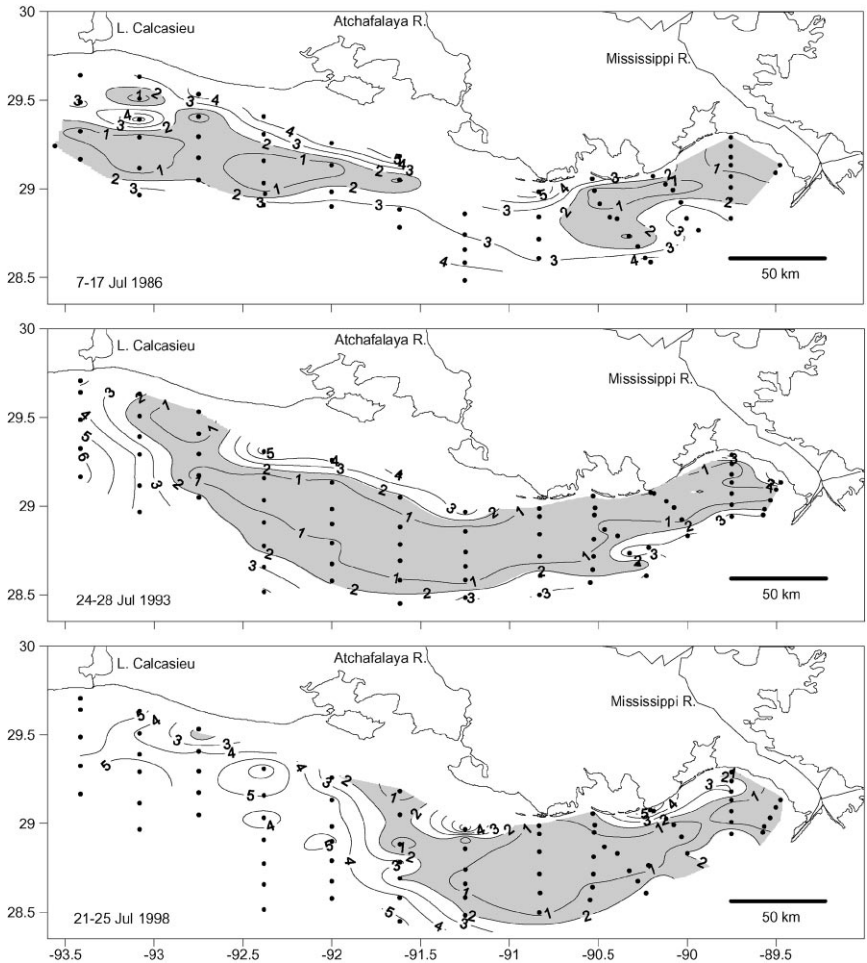


Figure 2 Bottom-water oxygen contours for mid-summer cruises in 1986, 1993, and 1998. The area of dissolved oxygen less than 2 mg l^{-1} is indicated by shading.

hypoxia in 2000 was proportional to the reduced Mississippi River discharge and nutrient flux that spring.

A compilation of sixteen mid-summer shelfwide surveys (1985–2001, Figure 4) shows that the frequency of >50% occurrence of hypoxia is highest down current (west) from the freshwater and nutrient discharges of the Mississippi and Atchafalaya Rivers. There are strong statistical relationships among nitrate flux, primary production, net production, and hypoxia in the area between the Mississippi River and transect C off Terrebonne Bay (Justić et al. 1993, 1997; Lohrenz et al. 1997). Similar statistical relationships exist between Atchafalaya River

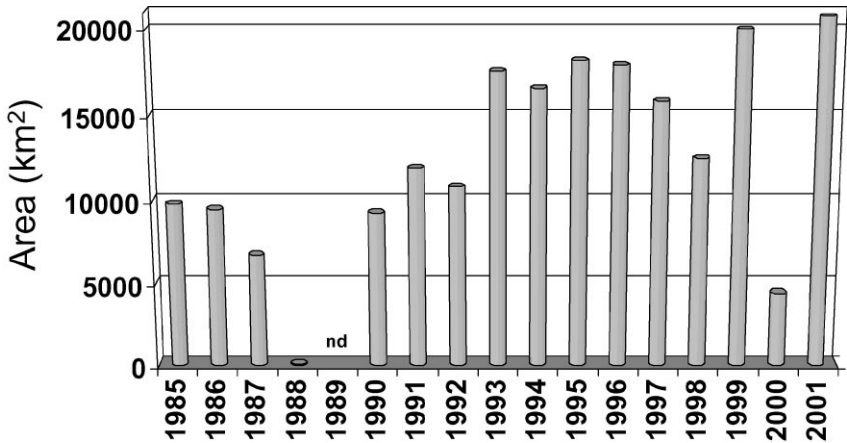


Figure 3 Estimated areal extent of bottom-water hypoxia ($\leq 2 \text{ mg l}^{-1}$) for mid-summer cruises in 1985–2001 (updated from Rabalais et al. 1999, Rabalais & Turner 2001b). nd = no data collected.

discharge and hypoxia on the southwestern Louisiana shelf (Pokryfki & Randall 1987).

More frequent sampling along transect C on the southeastern Louisiana coast (location shown in Figure 4) indicates that critically depressed dissolved oxygen concentrations occur below the pycnocline from as early as late February through early October and nearly continuously from mid-May through mid-September (Rabalais et al. 1999). Data from fisheries' independent trawl surveys in the Mississippi River bight, the area immediately west of the birdfoot delta, indicate that hypoxia occurs in that area in 6- to 10-m water depth as late as November (T. Romaine,

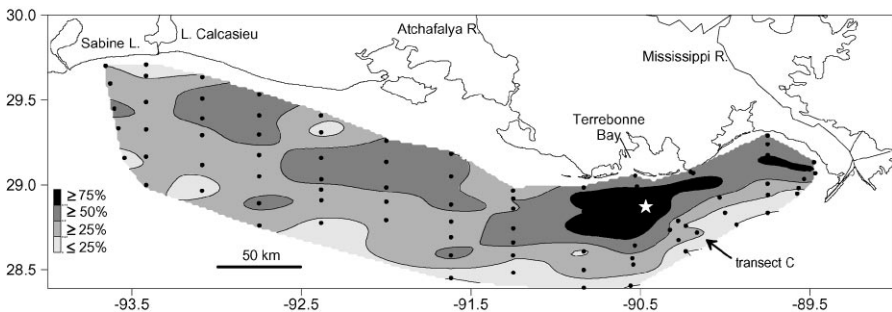


Figure 4 Distribution of frequency of occurrence of mid-summer bottom-water hypoxia over the 60- to 80-station grid from 1985–2001 (updated from Rabalais et al. 1999, Rabalais & Turner 2001b). Star indicates general location of stations C6A and C6B; transect C identified.

personal communication). Hypoxia is rare in late fall and winter. The monthly average value of bottom oxygen for each station along transect C is shown along a depth gradient from onshore to offshore by month (Figure 5), and illustrates the seasonal progression of worsening hypoxia along an increasingly greater portion of the seabed in May through August. The persistence of extensive and severe hypoxia into September and October depends on the timing of the breakdown of vertical stratification by winds from either tropical storms or passage of cold fronts.

Once hypoxia becomes well established in mid-summer, much of the onshore-offshore variability in distribution can be attributed to wind-induced cross-shelf advection (Rabalais et al. 1991) (Figure 6). The low oxygen water mass is displaced into deeper water following winds that produce downwelling-favorable conditions. Upwelling-favorable conditions push the hypoxic water mass closer to the barrier island shore. Similar advection of saline, hypoxic water onto the flanks of Chesapeake Bay and into the lower reaches of the Choptank River, an adjoining tributary estuary, is driven by large-amplitude wind and tidally forced lateral internal oscillations of the pycnocline in the mainstem of the Bay (Breitburg 1990, Sanford et al. 1990). It is the impingement of these hypoxic water masses close to shore that results in "jubilees" along Louisiana barrier islands. Jubilees are events that usually follow a north wind and movement of the hypoxic water mass onto shore where stunned or stressed fish, shrimp and crabs are concentrated in the shallow waters along the beach and can be easily harvested. A jubilee "gone bad" occurs when the water mass is extremely low in oxygen or contains hydrogen sulfide, and the trapped fish cannot escape, resulting in massive fish kills. Similar jubilees occur along the eastern shore of Mobile Bay in response to intrusion of upwelled hypoxic water (Loesch 1960, May 1973).

Continuously recording (15-min interval) oxygen meters have been deployed near the bottom (20-m water depth) at Stations C6A or C6B off Terrebonne Bay during spring-fall since 1990 (Rabalais et al. 1999). There is variability within the year and between years, but the pattern generally depicted is (a) gradual decline of bottom oxygen concentrations through the spring and summer, with periodic reoxygenation from wind-mixing events, (b) persistent hypoxia and often anoxia for extended periods of the record in May-September, (c) isolated intrusion of higher oxygen content waters from deeper water during upwelling-favorable wind conditions, and (d) persistent wind-mixing events in the late summer and fall that mix the water column sufficiently to prevent prolonged instances of bottom-water hypoxia. The illustrated bottom oxygen series from station C6A from mid-June through mid-September 1990 (Figure 7) shows prolonged periods of hypoxia and anoxia, a short period of elevated dissolved oxygen in late August, and persistent reaeration of the water column beginning in late September. For comparison, a recording oxygen meter was deployed during the same period near the bottom in 20-m water depth but 77 km to the east and closer to the Mississippi River delta (Figure 7, Rabalais et al. 1994). At that station, hypoxia occurred for only

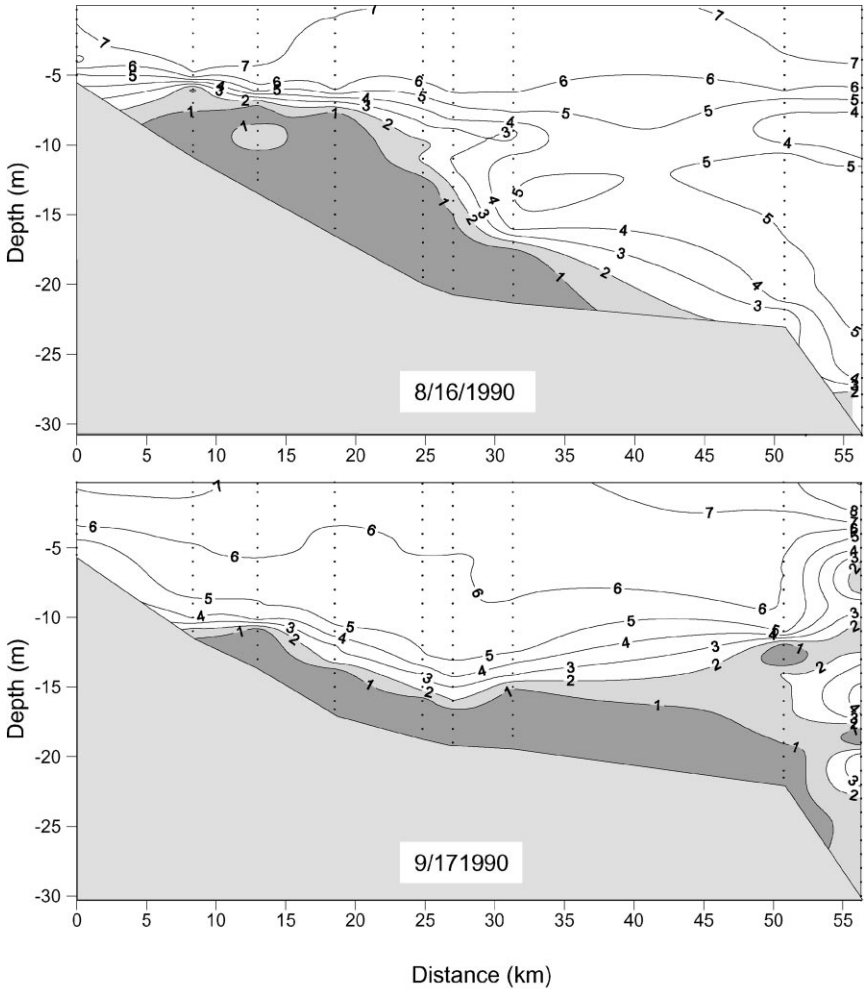


Figure 6 Cross-shelf contours for dissolved oxygen concentration (mg l^{-1}) during an upwelling-favorable wind condition (16 August 1990) and a downwelling-favorable wind condition (17 September 1990).

44% of the record from mid-June through mid-October (compared to 75% at station C6A), and there was a strong diurnal pattern in the oxygen time-series data for the former and not for the latter. The dominant coherence at the diurnal peaks of the oxygen record, from the site in the Mississippi River bight, with the bottom pressure record from a gauge located just offshore of Terrebonne Bay suggests that the dissolved oxygen signal was due principally to advection of the interface between hypoxic and normoxic water by tidal currents. These two bottom

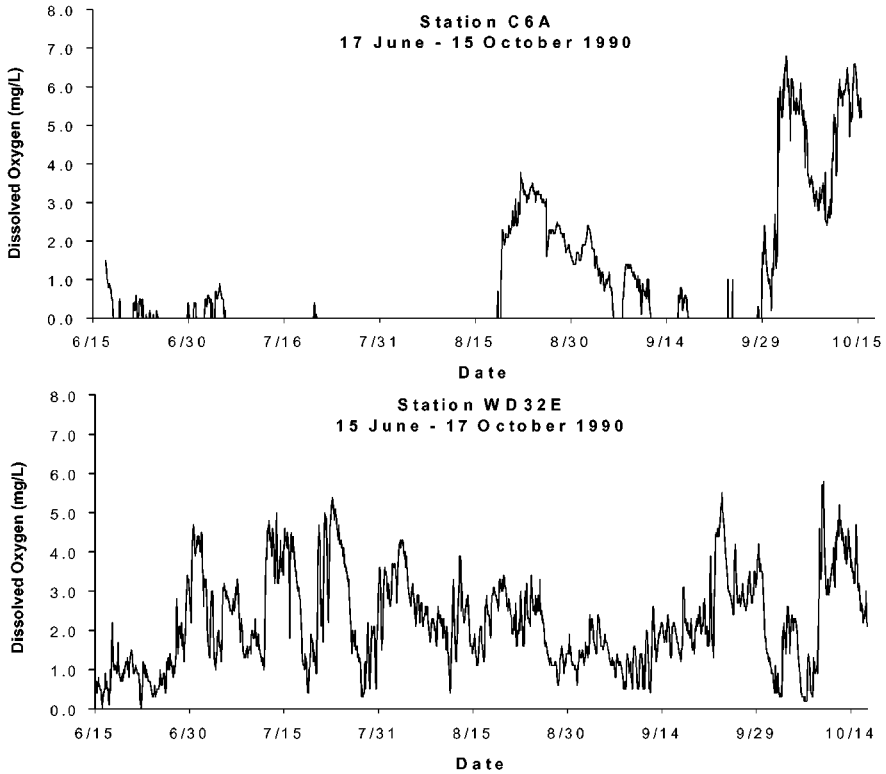


Figure 7 Time-series plots of bottom dissolved oxygen concentration (mg l^{-1} in 1-hr intervals) at stations C6A on transect C and WD32E, 77 km to the east in the Mississippi River bight (from Rabalais et al. 1994; reproduced with permission of the Estuarine Research Federation).

oxygen records illustrate the differences of exposure of benthic and demersal organisms to persistent, severe low oxygen versus intermittent periods of hypoxia and normoxia.

Most instances of hypoxia elsewhere in the northern Gulf of Mexico along the Texas, Mississippi, Alabama, and Florida coasts are infrequent, short-lived, and limited in extent (N.N. Rabalais 1992, unpublished data). Hypoxia on the upper Texas coast is usually an extension of the hypoxic zone off Louisiana (Harper et al. 1991, Pokryfki & Randall 1987), although isolated areas may be found farther south (Gulf States Fisheries Commission 1982–91). Hypoxia east of the Mississippi River is also isolated and ephemeral, but occurs more frequently during high stages of the Mississippi River in flood years or when summer currents move more Mississippi River water to the east of the birdfoot delta. Hypoxia occurs off Mobile Bay in bathymetric low areas (Rabalais 1992). From limited data where both sides of

the delta were surveyed (Turner & Allen 1982b), there was no evidence that the area of low oxygen formed a continuous band around the delta.

HISTORY OF HYPOXIA AND RELATED FACTORS

Whereas Gulf of Mexico coastal hypoxia has been systematically mapped only since 1985, there are data that document its presence since the early 1970s (Rabalais 1992, Rabalais et al. 1999, 2002). [Several references to low oxygen in the Gulf during the mid-1930s are clearly referring to data from the oxygen minimum layer in deeper Gulf waters that are not connected to the continental shelf hypoxia (Rabalais et al. 1999, 2002).] A series of environmental assessments of oil and gas production activities, strategic petroleum reserve sites, and locations for offshore oil lightering operations and groundfish fishery assessments put an increasing number of scientists onto the Louisiana continental shelf with conductivity/temperature/depth/oxygen meters in the period 1972–1984. These studies were usually site-specific and rarely assessed the entire Louisiana continental shelf where hypoxia has been documented since 1985 (Figure 2), but still showed that hypoxia occurred in many locations in waters 5–30 m deep in the spring to fall, with most occurrences in the summer. In 1975–1976, Louisiana shelfwide surveys and surveys between Mobile Bay and Atchafalaya Bay (Ragan et al. 1978, Turner & Allen 1982b, respectively) found hypoxic areas that were less extensive than those mapped since 1985; however, the Turner & Allen (1982b) study area was smaller than the present-day grid. Whereas it appears from this compilation of data that hypoxia may have been increasing in frequency or extent, the history of hypoxia over decadal and century scales remained poorly resolved.

One might expect a propensity for the northern Gulf of Mexico ecosystem to develop hypoxia naturally because of the high volume of fresh water and nutrients delivered by the Mississippi River and the nature of the stratified coastal system. The question is often posed: hasn't hypoxia always been a feature of this system? Because relevant water column data do not exist before 1972, and systematic surveys did not start until 1985, we turned to the sediment record for paleoindicators of long-term transitions related to eutrophication and oxygen conditions beneath the Mississippi River plume. Sediment cores from inside and outside the current hypoxic region contain chemical and biological remains that reflect conditions extant in surface and bottom waters at the time the sediment was deposited and thus provide clues to decadal and century-long changes.

Sediment core indicators clearly document recent eutrophication and increased organic sedimentation in bottom waters, with the changes more apparent in areas of chronic hypoxia and coincident with the increasing nitrogen loads from the Mississippi River system in the 1950s (Eadie et al. 1994, Turner & Rabalais 1994a). This evidence comes as an increased accumulation of diatom remains (biologically bound silica) and marine-origin carbon (stable carbon isotope analysis) accumulation in the sediments. The increases in diatom-based productivity

were also indicated in an analysis of changing dissolved silicate mixing diagrams along the Mississippi River plume (Turner & Rabalais 1994b). There have been no significant increases in either the riverine organic carbon or silica loads (Goolsby et al. 1999). The suspended sediment loads carried by the Mississippi River to the Gulf of Mexico have decreased by one-half since the Mississippi valley was first settled by European colonists (Meade et al. 1990). Alterations occurred as a result of deforestation and agriculture, changes in land management, and construction of dams, diversions, and levees. The decrease in suspended sediments has happened mostly since 1950 when the largest natural sources of sediments in the drainage basin were cut off from the Mississippi River mainstem by the construction of large reservoirs on the Missouri and Arkansas Rivers (Meade & Parker 1995). This large decrease in sediments from the western tributaries was counterbalanced somewhat by a five- to tenfold increase in sediment loads in the Ohio River as a result of deforestation and row-crop farming (Keown et al. 1986). A decrease in sediment load could potentially affect both the particulate and dissolved organic nitrogen flux. Because Mississippi River suspended sediment load has decreased since the 1950s (Meade 1995) and the dissolved inorganic nitrogen pool has increased from anthropogenic influences (Turner & Rabalais 1991), the relative importance of the organic nitrogen associated with the suspended sediment load might be less for the Mississippi River than for other large world rivers (Mayer et al. 1998). It is reasonable to infer that the increases in paleoindicators of phytoplankton productivity in the sediment record since the 1950s are related to in situ production of marine algae stimulated by dissolved inorganic nutrients.

Time courses for several surrogates for oxygen conditions are shown in Figure 8. The mineral glauconite forms under reducing conditions in sediments, and its abundance is an indication of low oxygen conditions. (Glauconite also forms in reducing sediments whose overlying waters are $>2 \text{ mg l}^{-1}$ dissolved oxygen.) The average glauconite abundance in the coarse fraction of sediments was $\sim 5.8\%$ from 1900 to a transition period between 1940 and 1950, when it increased to $\sim 13.4\%$ (Figure 8; Nelsen et al. 1994), suggesting that hypoxia may have existed at some level before the 1940–1950 time period, but that it worsened since then. Benthic foraminiferans and ostracods are also useful indicators of reduced oxygen levels because oxygen stress decreases their overall diversity as measured by the Shannon-Wiener Diversity Index (SWDI). Foraminiferal and ostracod diversity decreased since the 1940s and early 1950s, respectively (Figure 8; Nelsen et al. 1994, TA Nelsen, unpublished data). While present-day foraminiferal diversity is generally low in the Mississippi River bight, comparisons among assemblages from areas of different oxygen depletion indicate that the dominance of *Ammonia parkinsoniana* over *Elphidium* spp. (A-E index) was much more pronounced in oxygen-depleted compared to well-oxygenated waters (Rabalais et al. 1996, Sen Gupta et al. 1996). The A-E index has also proven to be a strong, consistent oxygen-stress signal in other coastal areas (Chesapeake Bay, Karlson et al. 2000; Long Island Sound, Thomas et al. 2000). The A-E index from sediment cores increased significantly after the 1950s, suggesting increased oxygen stress

(in intensity or duration) in the last half century (Figure 8). *Buliminella morgani*, a hypoxia-tolerant species, known only from the Gulf of Mexico, dominates the present-day population (>50%) within areas of chronic seasonal hypoxia, and has also increased markedly in recent decades (Sen Gupta et al. 1996). *Quinqueloculina* sp. (a hypoxia-intolerant foraminiferan) was a conspicuous member of the fauna from 1700 to 1900 (not illustrated; Rabalais et al. 1996), indicating that oxygen stress was not a problem prior to 1900. The trend of hypoxia, beginning at some level at the turn of the century with a significant increase after the 1950s when nitrate loads began to increase in the Mississippi River, has been further corroborated by analysis of bacterial chloropigments in dated sediment cores from the Mississippi River bight (Chen et al. 2001).

The long-term changes in hypoxia indicators can be compared with other long-term data sets and conditions in the watershed and Mississippi River to devise a scenario of what factors have changed through time that are most relevant to the changing hypoxia indicated in the sediment cores. The surrogates for oxygen conditions indicate an overall increase in continental shelf oxygen stress (in intensity or duration or both) in the last 100 years that seems especially severe since the 1950s. The indicators of worsening oxygen conditions parallel the increase in indicators of surface water primary production that accumulate in the sediments, i.e., diatom remains and phytoplankton-derived carbon, and the increasing flux of dissolved nitrate in the Mississippi River discharge (Turner & Rabalais 1991, 1994a; Goolsby et al. 1999).

In addition to a steady population increase within the Mississippi basin with related inputs of nitrogen through municipal wastewater systems, human activities have changed the natural functioning of the Mississippi River system. Navigation channelization and flood control through leveeing along the length of the river are clearly important watershed alterations, but most of these activities occurred well before the 1950s. Other significant alterations in landscape (e.g., deforestation, conversion of wetlands to cropland, loss of riparian zones, expansion of artificial agricultural drainage) removed most of the buffer for removing nutrients from runoff into the Mississippi tributaries and main stem. There was an increase in the area of land artificially drained between 1900 and 1920, and another significant burst in drainage during 1945–1960 (Mitsch et al. 2001). There was a dramatic increase in nitrogen input into the Mississippi River drainage basin, primarily from fertilizer application, between the 1950s and 1980s (Goolsby et al. 1999). These important alterations in land use and nitrogen input led to significant increases in riverine nitrate concentrations and flux to the Gulf (Turner & Rabalais 1991, Goolsby et al. 1999).

Because the amount of fresh water delivered to the northern Gulf of Mexico influences both the nitrogen load and the strength of salinity stratification on the shelf, climate-induced variability in river discharge will influence the extent and severity of hypoxia. Annual river discharge since the early 1900s has been highly variable, but total annual discharge increased by only 15% since 1900 and 30% since the 1950s (Bratkovich et al. 1994). This is in contrast to the 300% increase

in nitrate load since the 1950s (Turner & Rabalais 1991, Goolsby et al. 1999). Clearly, the most significant driver in the change in nitrate load is the increase in nitrate river concentration, not freshwater discharge (Justić et al. 2002). In addition, the change in annual freshwater discharge appears to be due mostly to increased discharge in September–December (Bratkovich et al. 1994), a period less important to both the physical and biological processes that lead to hypoxia development and maintenance.

Organic carbon supplied by the Mississippi River was proposed as a cause of the formation of hypoxia in the Gulf (Carey et al. 1999). This view has been largely discounted (Committee on Environment and Natural Resources 2001) because: (a) the suspended sediment load in the river has declined by about half since the 1950s, (b) the particulate organic load that could settle on the Louisiana shelf has also most likely decreased since then, (c) the distances to which particulate organic carbon would need to be transported to affect the large area of hypoxia are too great for the riverine particles to provide a significant load, and (d) stable carbon isotope data for sediment cores from the hypoxic zone indicate that 80% of the carbon accumulated in the sediments is of marine, not terrestrial origin. A similar argument for carbon associated with wetland loss in coastal Louisiana can be applied. Wetland loss rates in coastal Louisiana peaked at 1200 ha yr⁻¹ in the period 1955 to 1978, but the loss rate subsequently declined (Turner 1997), and mass flux calculations clearly indicate that this is a relatively small source of organic carbon to the hypoxic region. In addition, stable carbon isotope analyses indicate that wetland organic carbon accumulation is confined to a narrow band next to shore (Turner & Rabalais 1994a).

Where sufficient long-term data exist, e.g., Chesapeake Bay, the northern Adriatic Sea, the Baltic and the Black Seas, there is clear evidence for increases in nutrient flux, increased primary production, and worsening hypoxia (Cloern 2001). Thorough analyses of multiple indicators in sediment cores from the Chesapeake Bay indicate that sedimentation rates and eutrophication of the waters of the Bay have increased dramatically since the time of European settlement of the watershed (Cooper & Brush 1993, Cooper 1995, Karlson et al. 2000). In addition, results indicate that hypoxia and anoxia may have been more severe and of longer duration in the last 50 years, particularly since the 1970s. The sediment core findings corroborate long-term changes in Chesapeake Bay water column chlorophyll biomass since the 1950s (Harding & Perry 1997). The parallels of the Chesapeake Bay eutrophication and hypoxia to those of the Mississippi River watershed and Gulf of Mexico hypoxia are striking, in particular those of the last half-century.

EFFECTS OF HYPOXIA ON LIVING RESOURCES

Increases in loads of nitrogen and phosphorus, sometimes accompanied by reductions in dissolved silicate, to estuarine and coastal systems can result in enhancement of primary and often secondary production (Nixon 1995, Cloern 2001,

Rabalais & Turner 2001a, Rabalais 2002). The shifts in nutrient ratios may also shift the composition of the phytoplankton base and thus affect trophic interactions, the transfer of energy through marine food webs, and the flux of carbon that causes the development of hypoxia (Officer & Ryther 1980, Turner et al. 1998, Dortch et al. 2001, Turner 2001). Whereas these multiple effects of nutrient enhancement certainly deserve attention (Rabalais 2002), we focus here on the effects of hypoxia, or the reduction in available oxygen, on living resources in the Gulf of Mexico with comparative information from elsewhere, especially where information on Gulf resources is more limited.

As the oxygen concentration falls from saturated or optimal levels toward depletion, a variety of physiological impairments, including survivability, affect animals residing in the lower water column, in the sediments, or attached to hard substrates. The obvious effects of hypoxia/anoxia are displacement of pelagic organisms and selective loss of demersal and benthic organisms (Figure 9) (Rabalais et al. 2001a,b). These impacts may be aperiodic or recurring with some or full

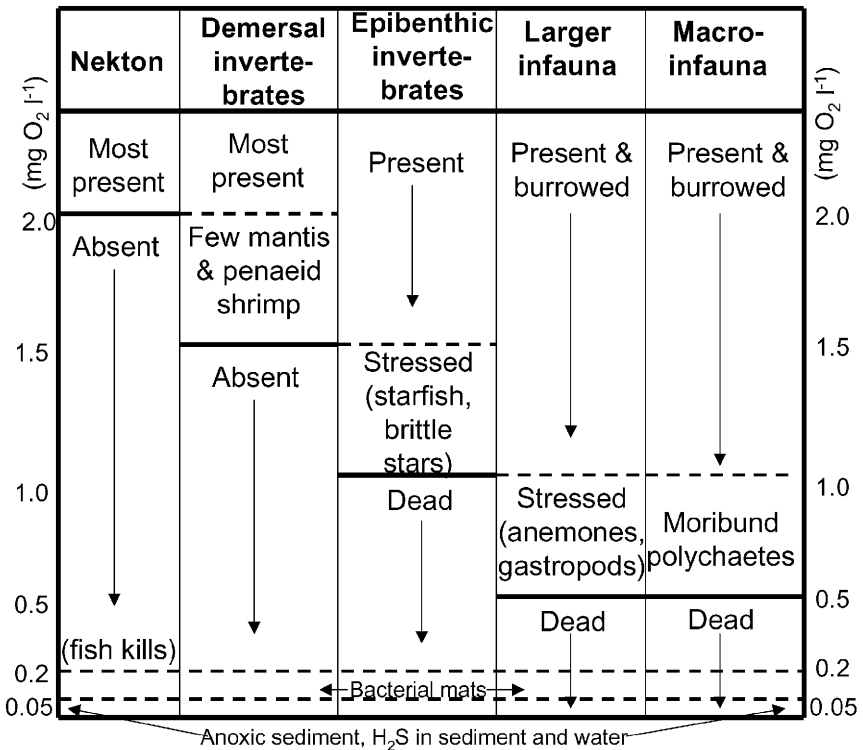


Figure 9 Progressive changes in fish and invertebrate fauna as oxygen concentration decreases from 2 mg l⁻¹ to anoxia (from Rabalais et al. 2001a; reproduced with permission of the Americal Geophysical Union).

recovery, or permanent so that long-term ecosystem structure and function shift. Some organisms are adapted physiologically or behaviorally to persist in or avoid hypoxic environments (Burnett & Stickle 2001, Marcus 2001, Purcell et al. 2001). Behavioral responses include active avoidance, a response only available for swimming organisms versus those attached to substrates or associated with the bottom, and reduced feeding. Physiological adaptations include dormancy, reduction in molting and growth rates, increased ventilation rate, increased circulation of blood past respiratory organs, increased production of hemoglobin or other oxygen binding proteins, and anaerobic metabolism.

The distribution, abundance, and community composition of micro- and macrozooplankton are affected by episodic hypoxic/anoxic conditions in estuarine and coastal areas (Marcus 2001, Qureshi & Rabalais 2001, Purcell et al. 2001, Powers et al. 2001). Stages of the copepods *Acartia tonsa* and *Oithona colcarva* that normally migrated to bottom waters in Chesapeake Bay during daylight hours were not found there when oxygen levels were $<1.0 \text{ mg l}^{-1}$, but were concentrated at the pycnocline (Roman et al. 1993). *A. tonsa* also did not occur in anoxic bottom waters of a stratified lagoon in France, with the depth distribution varying with the location of the oxycline above the bottom (Cervetto et al. 1995). Qureshi & Rabalais (2001) found a similar exclusion of copepod nauplii, copepodites and adults when the oxygen concentration was less than 1 mg l^{-1} in the Gulf of Mexico hypoxic zone, and vertical migration appeared to be disrupted at some stations. They also found a concentration of copepods and copepod nauplii below the pycnocline-oxycline but above the bottom where the oxygen concentration was reduced. Meroplankton (a water column life stage that alternates with a benthic life stage; usually larvae of benthic invertebrates) were also concentrated above oxygen-deficient bottom waters in summer and were either delaying metamorphosis or were unable to recruit to the seabed. Among polychaete larvae, however, only *Paraprionospio pinnata* appeared to be delaying metamorphosis by remaining in the water column above the seabed until the oxygen concentration returned to a level above 2 mg l^{-1} ; other polychaete larvae were distributed throughout the water column regardless of oxygen concentration (Powers et al. 2001). Eventual recruitment of macroinfaunal benthos to mostly defaunated sediments following long periods of hypoxia/anoxia was characterized by the predominance of juvenile *P. pinnata* owing to their delayed metamorphosis in combination with the inability of other recruits to survive conditions at the bottom (low oxygen and possibly hydrogen sulfide).

Most pelagic cnidarians and ctenophores (commonly grouped as jellyfish) do not live in hypoxic waters, although some species occur in high densities at very low oxygen concentrations or concentrate at the pycnocline/oxycline above severely hypoxic waters like the other zooplankton described above (Purcell et al. 2001). Experimental work with the schyphomedusan *Chrysaura quinquecirrha* and the ctenophore *Mnemiopsis leidyi* from Chesapeake Bay shows that the two jellyfish have prolonged survival at dissolved oxygen concentrations less than 2 mg l^{-1} . They also prey on fish larvae that are less tolerant of low oxygen

conditions, giving these jellyfish a competitive advantage over fish in hypoxic waters such as Chesapeake Bay, the Black Sea, and potentially the Gulf of Mexico. The abundance of *C. quinquecirrha* has increased over the Louisiana-Texas continental shelf from 5% of all SEAMAP (Southeast Area Mapping and Assessment Program for fisheries-independent groundfish surveys) stations sampled between 1987 and 1991 to 13–18% since 1992. At the same time, the mean oxygen concentration in the bottom water of stations where this jellyfish was collected dropped from 6.3 mg l⁻¹ in 1987 to 3.4 mg l⁻¹ in 1997 (Purcell et al. 2001). Summertime *C. quinquecirrha* medusa populations increased numerically and expanded away from shore across the portion of the Louisiana shelf where hypoxia is most frequent in summer, and there was a significant overlap between summer *C. quinquecirrha* abundance and lower water column hypoxia (Graham 2001). Changes in abundance of these jellyfish, however, as noted by Graham (2001), could also be related to overfishing of predators such as menhaden, expansion of hard substrates available for benthic polyp stages, and long-term climate variations, although eutrophication and increasing hypoxia appear to be a more credible explanation.

The responses of the fauna associated with the lower water column or seabed vary, depending on the concentration of dissolved oxygen, but there is a fairly consistent pattern of progressive stress and mortality as the oxygen concentration decreases from 2 mg l⁻¹ to anoxia (Rabalais et al. 2001a,b). Motile organisms (fish, portunid crabs, stomatopods, penaeid shrimp, and squid) are seldom found in bottom waters with oxygen concentrations less than 2 mg l⁻¹. Below 1.5 to 1 mg l⁻¹ oxygen concentration, less motile and burrowing invertebrates exhibit stress behavior, such as emergence from the sediments. They eventually die if the oxygen remains low for an extended period. As oxygen levels fall from 0.5 mg l⁻¹ toward 0 mg l⁻¹, there is a fairly linear decrease in benthic infaunal diversity, abundance, and biomass. The sediments are never completely azoic, however. Some macroinfauna, such as the polychaetes *Ampharete* and *Magelona* and the sipunculan *Aspidosiphon*, are capable of surviving extremely low dissolved oxygen concentrations and/or high hydrogen sulfide concentrations. At minimal concentrations just above anoxia, sulfur-oxidizing bacteria form white mats on the sediment surface, and at 0 mg l⁻¹, there is no sign of aerobic life, just black anoxic sediments.

The severely stressed seasonal hypoxic/anoxic zone of the Louisiana inner shelf in the northern Gulf of Mexico loses many higher taxa during the peak of hypoxia (Rabalais et al. 2001b). Larger, longer-lived burrowing infauna are replaced by short-lived, smaller surface deposit-feeding polychaetes. Certain typical marine invertebrates are absent from the fauna, for example, pericaridean crustaceans, bivalves, gastropods, and ophiuroids. The hypoxia-affected fauna in Chesapeake Bay is characterized by a lower proportion of deeper-burrowing equilibrium species such as long-lived bivalves and a greater dominance of short-lived surface-dwelling forms (Dauer et al. 1992). Long-term trends for the Skagerrak coast of western Sweden in semi-enclosed fjordic areas experiencing increased

oxygen stress (Rosenberg 1990) show declines in the total abundance and biomass of macroinfauna, abundance and biomass of mollusks, and abundance of suspension feeders and carnivores. These changes in benthic communities result in an impoverished diet for bottom-feeding fish and crustaceans and contribute, along with low dissolved oxygen, to altered sediment structure and sediment biogeochemical cycles.

Although there is a consistent decline in the macroinfauna as the oxygen concentration approaches 0 mg l^{-1} , many of the meiofaunal populations maintain similar numbers to those found under normoxic conditions. Other populations, however, go through a definite decline. Within a given habitat, certain species of foraminiferans and nematodes are typically most tolerant to hypoxia and anoxia while crustacean meiofauna, primarily the harpacticoid copepods, are least tolerant (Murrell & Fleeger 1989, Wetzel et al. 2001). Even apparent declines in the number of nematodes might as easily be explained by their apparent ability to emigrate into the water column in high numbers where they survive hypoxic conditions until normoxic conditions are re-established (Wetzel et al. 2001). While the numbers of macroinfauna become sufficiently depleted to no longer serve as a suitable food resource for demersal feeders such as shrimp, nematode numbers remain surprisingly high. Nematodes, although reduced in abundance at more severely affected stations (15-m depth) than inshore stations (8-m depth) on the southeastern Louisiana shelf, average about 1200 individuals per 10 cm^2 over an annual cycle (Murrell & Fleeger 1989). The insensitivity of nematode densities to oxygen deficiency or their occasional increase under severe hypoxia (Josefson & Widbom 1988, Cook et al. 2000) may make these remaining meiofaunal organisms potential food for foraging fish. The relative suitability of this potential nematode food to demersal feeders on the shelf compared to harpacticoid copepods and macroinfauna is not known. Fish and shrimp would not be potential predators during mid-summer severe hypoxia, but nematodes may be suitable prey for some foragers during the fall after hypoxia dissipates.

Important fishery resources are variably affected by direct mortality, forced migration, reduction in suitable habitat, increased susceptibility to predation, changes in food resources, and disruption of life cycles (Rabalais et al. 2001a). The effects of eutrophication, including hypoxia, are well known for some systems and include the increase in production of some species with a loss of others, including commercially important fisheries. The multi-level impacts of increased nutrient inputs and worsening hypoxia are not known for many components of productivity in the Gulf of Mexico, including pelagic and benthic, primary and secondary, food web linkages, and ultimately, fisheries yield. Comparisons of ecosystems along a gradient of increasing nutrient enrichment and eutrophication, or changes of a specific ecosystem over time through a gradient toward increasing eutrophication, provide information on how nutrient enrichment affects coastal communities. Caddy (1993) suggested a unimodal distribution of fishery yield in semi-enclosed seas in response to increasing eutrophication. The fishery yield is low in waters with low nutrients, but the yield increases as the nutrients increase, up to a point. As the

ecosystem becomes increasingly eutrophied, there is a drop in fishery yield, but the decreases vary by habitat and feeding mode. The benthos are the first resources to be reduced by increasing frequency of seasonal hypoxia and eventually anoxia; bottom-feeding fishes then decline. The 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 gradient of increasing eutrophication is not known. It is well documented, however, that there is a negative relationship between the catch of brown shrimp (the largest economic fishery in the northern Gulf of Mexico) and the relative size of the mid-summer hypoxic zone (Zimmerman & Nance 2001). The catch per unit effort of brown shrimp has also declined significantly during the recent interval in which hypoxia was known to expand. As noted above for alternative hypotheses for increasing jellyfish abundances in areas of hypoxia off Louisiana, there may be additional or alternative reasons for shrimp decline in fisheries-dependent data, such as a trend of decreasing salinity in the coastal marshes, loss of habitat, or changes in fishing pressure.

Documenting the loss of fisheries related to the secondary effects of eutrophication, such as the loss of seabed vegetation and extensive bottom-water oxygen depletion, is complicated by poor fisheries data, inadequate economic indicators, increased fishing effort during the period of habitat degradation, natural variability of fish populations, shifts in harvestable populations, and climatic variability (Caddy 2000, Jackson et al. 2001, Boesch et al. 2001). Eutrophication of surface waters accompanied by oxygen deficient bottom waters can shift dominant fish stocks from demersal to pelagic. In the Baltic Sea and Kattegatt, where eutrophication-related ecological changes occurred mainly after World War II (reviewed by Elmgren & Larsson 2001a), some fish stocks increased because of increased food supply (e.g., pike perch in Baltic archipelagos) while others decreased (e.g., from oxygen deficiency that reduced Baltic cod recruitment and eventual harvest). Similar shifts are suggested by limited data on the Mississippi River-influenced shelf, with the increase in selected pelagic species in bycatch from trawls and a decrease in certain demersal species (Chesney & Baltz 2001). Still another analysis, however, indicated that the pelagic fishery yield may be impacted by extensive hypoxia on the northern Gulf of Mexico continental shelf (Smith 2001; J. Smith, unpublished data). In the case of commercial fisheries in the Black Sea, it is difficult to distinguish the impacts of eutrophication (e.g., the loss of macroalgal habitat and oxygen deficiency or a shift from benthic to pelagic production), from the possibility of overfishing. After the mid-1970s, benthic fish populations (e.g., turbot) collapsed, and pelagic fish populations (e.g., anchovy and sprat) started to increase. The commercial fisheries diversity declined from some 25 fished species to about 5 in 20 years (1960s to 1980s), while anchovy stocks and fisheries increased rapidly (Mee 2001). The point remains unclear on the gradient of increasing nutrients as to where benefits of higher overall yields become subsumed by environmental problems that lead to decreased landings quantity or quality.

NUTRIENT MANAGEMENT AND RECOVERY

The accelerated time course of coastal eutrophication in the northern Gulf of Mexico since the 1950s was typical for most temperate coastal regions at the terminus of modified rivers flowing through developed countries. In the northern Gulf of Mexico, the time course of eutrophication and hypoxia followed most closely the exponential growth of fertilizer use beginning in the 1950s. Elsewhere in the world, the relative proportion of agriculture-source nutrients may not be as high as in the Mississippi River basin, but other sources of nutrients, such as municipal and industrial wastewater and atmospheric deposition, also increased substantially since the 1950s. The consumption of fertilizers has plateaued in many developed countries, but continues to increase in developing countries (Seitzinger et al. 2002). There is no indication that fertilizer use will decrease, and controlling the non-point sources of nutrient pollution has proven much more difficult than controls emplaced for point sources (Boesch 2002). Without the curtailing of nutrient loads, the trajectory of coastal water quality degradation in the northern Gulf of Mexico will likely continue, or perhaps worsen under scenarios of increased precipitation in climate change models (Justić et al. 1996). Elsewhere in the world, eutrophication, with sometimes accompanying hypoxia, will continue without a reduction in nutrient loads and will certainly accelerate in areas where nutrient loads are on the rise. There are, however, several good examples of nutrient management schemes that have resulted in reversal of symptoms of eutrophication and economically driven experiments where similar results have occurred. However, many attempts to curtail nutrient export to estuarine and coastal waters have met with limited success in meeting reduction goals or environmental goals.

Hypoxia and anoxia have existed in the open waters of the Black Sea for millennia, but hypoxia on the northwestern Black Sea shelf became more frequent and widespread in the 1970s and 1980s (Tolmazin 1985, Zaitsev 1992, Mee 2001), affecting up to 40,000 km² in depths of 8 to 40 m. There is also evidence that the suboxic zone of the open Black Sea enlarged toward the surface by about 10 m since 1970. As a result of the economic collapse of the former Soviet Union and declines in subsidies for fertilizers, the decade of the 1990s witnessed a substantially decreased input of nutrients via the Danube River, which was accompanied by signs of recovery in the pelagic and benthic ecosystems of the Black Sea (Mee 2001). There is a recovery in zoobenthos species diversity, phytoplankton biomass has declined by about 30% from the 1990 maxima, there is some recovery of the diatoms, the phytoplankton are more diverse, the incidence of intense blooms has declined, and there is a limited recovery of some zooplankton stocks and diversity in limited geographic areas. There has been no recovery of benthic macroalgal beds. For the first time in several decades, oxygen deficiency was absent from the northwestern shelf of the Black Sea in 1996, and receded to an area less than 1000 km² in 1999. Most fish stocks in the northwestern Black Sea are still depleted (Mee 2001), however. There should be little doubt of the strong relationships among human activities, Danube River nutrient loads, Black Sea eutrophication, and the

demise of pelagic and benthic coastal ecosystems, as well as similar linkages in the partial recovery of those systems following reduced nutrient loading.

The severe degradation of water quality in Tampa Bay and loss of valuable habitat, particularly seagrass beds, was followed by nutrient management schemes that reduced the nitrogen and phosphorus inputs to the bay (Johansson & Lewis 1992). Four years after improved sewage treatment, ambient chlorophyll *a* concentrations decreased in Hillsborough Bay, and the noxious filamentous cyanobacteria *Schizothrix calcicola* also decreased. Modest seagrass recovery followed. An aggressive nutrient management program with broad-scale public, institutional, and private participation continues under the Tampa Bay Estuary Program (National Research Council 2000), with the current goal to hold gains made in nutrient load reductions by making additional reductions in point and diffuse sources to offset the effects of anticipated high rate of population growth in the region.

On a larger scale, with the causes of hypoxia more clearly defined and the sources of nutrients fairly well understood, a Task Force forwarded to Congress in 2001 an Action Plan for Reducing, Mitigating, and Controlling Hypoxia in the Northern Gulf of Mexico (Mississippi River/Gulf of Mexico Watershed Nutrient Task Force 2001, Rabalais et al. 2002). Reaching this step of nutrient policy development required a scientific consensus that the increase in nitrogen loading was the primary factor in the worsening of hypoxia in the northern Gulf of Mexico. Finding common ground on the hypoxia assessment and a general action plan that calls for reducing hypoxia in the northern Gulf of Mexico by two-thirds was not reached without debate or controversy (Rabalais et al. 2002). The next step, development of a detailed resource management plan that will probably require the reduction of nitrogen inputs by 30% for a watershed covering 41% of the contiguous United States, remains a daunting task.

Within estuaries and coastal systems, a decrease in external nutrient loads does not produce an immediate shift in the eutrophic condition of the system, in part because of the continued remineralization of labile carbon and releases of regenerated nutrients. The response of the Black Sea coastal ecosystem to lower nutrient loading took almost a decade. Seagrass recovery in Tampa Bay lagged nutrient load reductions by about 8 years. Boynton & Kemp (2000) suggested a nutrient memory over timescales of a year rather than seasonal periods as suggested by Chesapeake Bay water residence times. Assessing the recovery of Chesapeake Bay in response to the nutrient load reductions achieved so far is complicated by numerous factors. One indicator that could be attributed to reduced nutrients is a return of sea grasses to some regions, although the present coverage is only a small portion of the habitat occupied in the 1950s (Boesch 2001). Justić et al. (1997) suggested that at least a year of continued carbon respiration following high deposition of carbon in a flood year contributed to oxygen demand on the Louisiana continental shelf in the following summer. Researchers within the narrow, coastal inlets of the Bodden are less optimistic about system recovery where nutrients to that sector of the Baltic were reduced greatly during the last decade of the twentieth century, but the expected improvement of water quality has not been demonstrated

(Meyer-Reil & Köster 2000). In addition, there is an inertia in terrestrial systems and rivers and streams with regard to losses from land to sea following nutrient reductions actually achieved or planned (Grimvall et al. 2000). On the timescale of a few years, changes in the anthropogenic impact on water quality may easily be overshadowed by natural fluctuations in climate. These facts are relevant to management strategies to mitigate nutrient loads to estuaries and coastal waters, and the perceived projection for recovery.

For many environmental problems, including excess nutrients, scientists, political institutions, and society must often agree on policy and intervention measures in the face of scientific uncertainty. Fortunately, around the globe, measures to decrease excess nutrient loads proceeded without complete scientific consensus on which nutrients to reduce, how much, and by what methods. Knowledge gaps will remain and new ones will surface, but most action plans for reducing and mitigating the effects of nutrients are conceived within a long-term adaptive management strategy that links management actions with monitoring, research, modeling, and a commitment to reassess conditions periodically (Elmgren 2001, Elmgren & Larsson 2001b, Rabalais et al. 2002). This can only improve the long-term prognosis for improved water quality resulting from robust actions while improving the science.

ACKNOWLEDGMENTS

The data presented were collected beginning in 1985 with support from the National Oceanic and Atmospheric Administration (NOAA), National Ocean Service, and subsequently from the Louisiana Board of Regents Support Fund, NOAA Nutrient Enhanced Coastal Ocean Productivity program, the Louisiana-Texas Physical Oceanography Program sponsored by Minerals Management Service (MMS), the Louisiana Sea Grant College Program, the NOAA National Undersea Research Program, the MMS University Research Initiative, the Gulf of Mexico Program, and the NOAA Coastal Ocean Program. We thank these organizations for their support. We also thank Ben Cole for maintaining our data in a manner helpful to analysis of long-term trends and for assistance with the preparation of figures.

**The Annual Review of Ecology and Systematics is online at
<http://ecolsys.annualreviews.org>**

LITERATURE CITED

- Alpine AE, Cloern JE. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnol. Oceanogr.* 37:946–55
- Anderson DM, Glibert PM, Burkholder JM. 2002. Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. *Estuaries*. 25: In press
- Arntz WE. 1981. Zonation and dynamics of macrobenthos in an area stressed by oxygen deficiency. In *Stress Effects on Natural*

- Ecosystems*, ed. GW Barrett, R Rosenberg, pp. 215–25. New York: Wiley
- Bennett EM, Carpenter SR, Caraco NF. 2001. Human impact on erodable phosphorus and eutrophication: a global perspective. *Bio-Science* 51:227–34
- Boesch DF. 2001. Science and integrated drainage basin coastal management. Chesapeake Bay and Mississippi Delta. See von Bodungen & Turner 2001, pp. 37–50
- Boesch DF. 2002. Challenges and opportunities for science in reducing nutrient over-enrichment of coastal ecosystems. *Estuaries* 25: In press
- Boesch DF, Burreson E, Dennison W, Houde E, Kemp M, et al. 2001. Factors in the decline of coastal ecosystems. *Science* 293:1589–90
- Boynton WR, Garber JH, Summers R, Kemp WM. 1995. Inputs, transformations, and transport of nitrogen and phosphorus in Chesapeake Bay and selected tributaries. *Estuaries* 18:285–314
- Boynton WR, Kemp WM. 2000. Influence of river flow and nutrient loads on selected ecosystem processes. A synthesis of Chesapeake Bay data. In *Estuarine Science: A Synthetic Approach to Research and Practice*, ed. JE Hobbie, pp. 269–98. Washington, DC: Island
- Bratkovich A, Dinnel SP, Goolsby DA. 1994. Variability and prediction of freshwater and nitrate fluxes for the Louisiana-Texas shelf: Mississippi and Atchafalaya River source functions. *Estuaries* 17:766–78
- Breitburg DL. 1990. Near-shore hypoxia in the Chesapeake Bay: patterns and relationships among physical factors. *Estuar. Coast. Shelf Sci.* 30:593–609
- Breitburg DL. 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. *Estuaries* 25: In press
- Bricker SB, Clement CG, Pirhalla DE, Orlando SP, Farrow DRG. 1999. *National estuarine Eutrophication Assessment: Effects of Nutrient Enrichment in the Nation's Estuaries*. Silver Spring, MD: NOAA 71 pp.
- Burnett LE, Stickle WB. 2001. Physiological responses to hypoxia. See Rabalais & Turner 2001a, pp. 101–14
- Caddy JF. 1993. Toward a comparative evaluation of human impacts on fishery ecosystems of enclosed and semi-enclosed seas. *Rev. Fish. Sci.* 1:57–95
- Caddy JF. 2000. Marine catchment basin effects versus impacts of fisheries on semi-enclosed seas. *ICES J. Mar. Sci.* 57:628–40
- Caraco NF, Cole JJ. 1999. Human impact on nitrate export: an analysis using major world rivers. *Ambio* 28:167–70
- Carey AC, Pennock JR, Hehrter JC, Lyons WB, Schroeder WW, et al. 1999. The role of the Mississippi River in Gulf of Mexico hypoxia. *Rep. Fertilizer Inst., Environ. Inst. Publ. No. 70*. Univ. Ala., Tuscaloosa 79 pp.
- Cervetto G, Pagano M, Gaudy R. 1995. Feeding behavior and migrations in a natural population of the copepod *Acartia tonsa*. *Hydrobiologia* 300/301:237–48
- Chen N, Bianchi TS, McKee BA, Bland JM. 2001. Historical trends of hypoxia on the Louisiana shelf: application of pigments as biomarkers. *Org. Geochem.* 32:543–61
- Chesney EJ, Baltz DM. 2001. The effects of hypoxia on the northern Gulf of Mexico coastal ecosystem: a fisheries perspective. See Rabalais & Turner 2001a, pp. 321–54
- Cloern JE. 1999. The relative importance of light and nutrient limitation of phytoplankton growth: a simple index of coastal ecosystems sensitivity to nutrient enrichment. *Aquat. Ecol.* 33:3–16
- Cloern JE. 2001. Review. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.* 210:223–53
- Comm. Environ. Nat. Resour. (CENR). 2000. *Integrated Assessment of Hypoxia in the Northern Gulf of Mexico*. Washington, DC: Nat. Sci. Tech. Council. 58 pp.
- Cook AA, Lambshead PJD, Hawkins LE, Mitchell N, Levin LA. 2000. Nematode abundance at the oxygen minimum zone in the Arabian Sea. *Deep-Sea Res. II* 47:75–85
- Cooper SR. 1995. Chesapeake Bay watershed

- historical land use: impact on water quality and diatom communities. *Ecol. Appl.* 5:703–23
- Cooper SR, Brush GS. 1993. A 2500-year history of anoxia and eutrophication in Chesapeake Bay. *Estuaries* 16:617–26
- Dauer DM, Rodi AJ Jr, Ranasinghe JA. 1992. Effects of low dissolved oxygen events on the macrobenthos of the lower Chesapeake Bay. *Estuaries* 15:384–91
- Diaz RJ, Rosenberg R. 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanogr. Mar. Biol. Ann. Rev.* 33:245–303
- Dortch Q, Rabalais NN, Turner RE, Qureshi NA. 2001. Impacts of changing Si/N ratios and phytoplankton species composition. See Rabalais & Turner 2001a, pp. 37–48
- Dunn DD. 1996. Trends in nutrient inflows to the Gulf of Mexico from streams draining the conterminous United States 1972–1993. *US Geol. Surv., Water-Res. Invest. Rep.* 96–4113. Austin, TX: US Geol. Surv. 60 pp.
- Dyer KR, Orth RJ, eds. 1994. *Changes in Fluxes in Estuaries: Implications from Science to Management, Proc. ECSA22/ERF Symp., Int. Symp. Ser.* Fredensborg, Denmark: Olsen & Olsen. 483 pp.
- Eadie BJ, McKee BA, Lansing MB, Robbins JA, Metz S, et al. 1994. Records of nutrient-enhanced coastal ocean productivity in sediments from the Louisiana continental shelf. *Estuaries* 17:754–65
- Elmgren R. 2001. Understanding human impact on the Baltic ecosystem: changing views in recent decades. *Ambio* 30:222–31
- Elmgren R, Larsson U. 2001a. Eutrophication in the Baltic Sea area. Integrated coastal management issues. See von Bodungen & Turner 2001, pp. 15–35
- Elmgren R, Larsson U. 2001b. Nitrogen and the Baltic Sea: managing nitrogen in relation to phosphorus. In *Optimizing Nitrogen Management in Food And Energy Production and Environmental Protection: Proc. 2nd Int. Nitrogen Conf. Sci. Pol. Sci. World* 1(S2):371–77
- Falkowski PG, Hopkins TS, Walsh JJ. 1980. An analysis of factors affecting oxygen depletion in the New York bight. *J. Mar. Res.* 38:479–506
- Fransz HG, Verhagen JHG. 1985. Modeling research on the production cycle of phytoplankton in the southern bight of the North Sea in relation to riverborne nutrient loads. *Netherlands J. Sea Res.* 19:241–50
- Garside C, Malone TC. 1978. Monthly oxygen and carbon budgets of the New York bight apex. *Estuar. Coast. Shelf Sci.* 6:93–104
- Goolsby DA, Battaglin WA, Lawrence GB, Artz RS, Aulenbach BT, et al. 1999. Flux and sources of nutrients in the Mississippi-Atchafalaya River Basin, Topic 3 Rep. Integrated Assessment of Hypoxia in the Gulf of Mexico. *NOAA Coast. Ocean Prog. Dec. Anal. Ser.* 17. Silver Spring, MD: NOAA. 130 pp.
- Graham WM. 2001. Numerical increases and distributional shifts of *Chrysaora quinquecirrha* (Desor) and *Aurelia aurita* (Linné) (Cnidaria: Scyphozoa) in the northern Gulf of Mexico. *Hydrobiologia* 451:97–111
- Grimvall A, Stålnacke P, Tonderski A. 2000. Time scales of nutrient losses from land to sea—a European perspective. *Ecol. Eng.* 14:363–71
- Gulf States Mar. Fish. Comm. 1982–91. *SEAMAP Environmental and Biological Atlas of the Gulf of Mexico, 1982*. Ocean Springs, MS: Gulf States Mar. Fish. Comm.
- Harding LW Jr, Perry ES. 1997. Long-term increase of phytoplankton biomass in Chesapeake Bay, 1950–1994. *Mar. Ecol. Prog. Ser.* 157:39–52
- Harper DE Jr, McKinney LD, Nance JM, Salzer RR. 1991. Recovery responses of two benthic assemblages following an acute hypoxic event on the Texas continental shelf, northwestern Gulf of Mexico. See Tyson & Pearson 1991a, pp. 49–64
- Howarth R, Anderson D, Cloern J, Elfring C, Hopkinson C, et al. 2000. Nutrient pollution of coastal rivers, bays, and seas. *Issues Ecol.* 7:1–15

- Howarth RW, Billen G, Swaney D, Townsend A, Jaworski N, et al. 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to the North Atlantic Ocean: natural and human influences. *Biogeochemistry* 35:75–79
- Howarth RW, Jensen H, Marino R, Postma H. 1995. Transport to and processing of P in near-shore and oceanic waters. In *Phosphorus in the Global Environment: Transfers, Cycles and Management*, ed. H Tiessen, pp. 323–45. Chichester, UK: Wiley
- Jackson JBC, Kirby MX, Berger WH, Bjorn-dal KA, Botsford LW, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–38
- Johansson JOR, Lewis RR III. 1992. Recent improvements of water quality and biological indicators in Hillsborough Bay, a highly impacted subdivision of Tampa Bay, Florida, USA. In *Marine Coastal Eutrophication. The Response of Marine Transitional Systems to Human Impact: Problems and Perspectives for Restoration. Proc. Int. Conf., Bologna, Italy, March 1990*, ed. RA Vollenweider, R Marchetti, R Viviani, pp. 1199–1215. Amsterdam: Elsevier
- Josefson AB, Widbom B. 1988. Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin. *Mar. Biol.* 100:31–40
- Justić D, Legovic T, Rottini-Sandrini L. 1987. Trends in oxygen content 1911–1984 and occurrence of benthic mortality in the northern Adriatic Sea. *Estuar. Coast. Shelf Sci.* 25:435–45
- Justić D, Rabalais NN, Turner RE. 1996. Effects of climate change on hypoxia in coastal waters: a doubled CO₂ scenario for the northern Gulf of Mexico. *Limnol. Oceanogr.* 41:992–1003
- Justić D, Rabalais NN, Turner RE. 1997. Impacts of climate change on net productivity of coastal waters: implications for carbon budget and hypoxia. *Clim. Res.* 8:225–37
- Justić D, Rabalais NN, Turner RE. 2002. Modeling the impacts of decadal changes in riverine nutrient fluxes on coastal eutrophication near the Mississippi River Delta. *Ecol. Model.* 152:33–46
- Justić D, Rabalais NN, Turner RE, Wiseman WJ Jr. 1993. Seasonal coupling between riverborne nutrients, net productivity and hypoxia. *Mar. Pollut. Bull.* 26:184–89
- Kamykowski D, Zentara S-J. 1990. Hypoxia in the world ocean as recorded in the historical data set. *Deep-Sea Res.* 37:1861–74
- Karlsen AW, Cronin TM, Ishman SE, Willard DA, Kerhin R, et al. 2000. Historical trends in Chesapeake Bay dissolved oxygen based on benthic Foraminifera from sediment cores. *Estuaries* 23:488–508
- Keown MP, Dardeau EA Jr, Causey EM. 1986. Historic trends in the sediment flow regime of the Mississippi River. *Water Resour. Res.* 22:1555–64
- Loesch H. 1960. Sporadic mass shoreward migrations of demersal fish and crustaceans in Mobile Bay, Alabama. *Ecology* 41:292–98
- Lohrenz SE, Fahnenstiel GL, Redalje DG, Lang GA, Chen X, et al. 1997. Variations in primary production of northern Gulf of Mexico continental shelf waters linked to nutrient inputs from the Mississippi River. *Mar. Ecol. Prog. Ser.* 155:45–54
- Malone TC. 1991. River flow, phytoplankton production and oxygen depletion in Chesapeake Bay. See Tyson & Pearson 1991a, pp. 83–93
- Marcus NH. 2001. Zooplankton: responses to and consequences of hypoxia. See Rabalais & Turner 2001a, pp. 49–60
- May EB. 1973. Extensive oxygen depletion in Mobile Bay, Alabama. *Limnol. Oceanogr.* 18:353–66
- Mayer LM, Keil RG, Macko SA, Joye SB, Ruttenberg KC, et al. 1998. Importance of suspended particulates in riverine delivery of bioavailable nitrogen to coastal zones. *Glob. Biogeochem. Cycles* 12(4):573–79
- Meade RH, ed. 1995. Contaminants in the Mississippi River, 1987–1992. *US Geol. Surv. Circ. 1133*. Denver, CO: US Dep. Int. 140 pp.

- Meade RH, Parker R. 1985. Sediment in rivers of the United States. *US Geol. Surv. Water Supply Pap.* 2275, pp. 49–60. Washington, DC: GPO
- Meade RH, Yuzyk TR, Day TJ. 1990. Movement and storage of sediment in rivers of the United States and Canada. In *The Geology of North America, Vol. O-1*, ed. MG Wolman, HC Riggs, pp. 255–80. Boulder, CO: Geol. Soc. Am.
- Mee LD. 2001. Eutrophication in the Black Sea and a basin-wide approach to its control. See von Bodungen & Turner 2001, pp. 71–91
- Meyer-Reil L-A, Köster M. 2000. Eutrophication of marine waters: effects on benthic microbial communities. *Mar. Pollut. Bull.* 41:255–63
- Mississippi River/Gulf of Mexico Watershed Nutrient Task Force. 2001. *Action Plan for Reducing, Mitigating, and Controlling Hypoxia in the Northern Gulf of Mexico*. Washington, DC: EPA
- Mitsch WJ, Day JW Jr, Gilliam JW, Groffman PM, Hey DL, et al. 2001. Reducing nitrogen loading to the Gulf of Mexico from the Mississippi River basin: strategies to counter a persistent ecological problem. *BioScience* 15:373–88
- Murrell MC, Fleeger JW. 1989. Meiofauna abundance on the Gulf of Mexico continental shelf affected by hypoxia. *Cont. Shelf Res.* 9:1049–62
- Natl. Res. Council. 2000. *Clean Coastal Waters—Understanding and Reducing the Effects of Nutrient Pollution*. Washington, DC: Natl. Acad. Press
- Nelsen TA, Blackwelder P, Hood T, McKee B, Romer N, et al. 1994. Time-based correlation of biogenic, lithogenic and authigenic sediment components with anthropogenic inputs in the Gulf of Mexico NECOP study area. *Estuaries* 17:873–85
- Nixon SW. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41:199–219
- Nixon SW, Ammerman JW, Atkinson LP, Berounsky VM, Billen G, et al. 1996. The fate of nitrogen and phosphorus at the land-sea margin of the North Atlantic Ocean. *Biogeochemistry* 35:141–80
- Nixon SW, Granger SL, Nowicki BL. 1995. An assessment of the annual mass balance of carbon, nitrogen, and phosphorus in Narragansett Bay. *Biogeochemistry* 31:15–61
- Officer CB, Biggs RB, Taft JL, Cronin LE, Tyler MA, et al. 1984. Chesapeake Bay anoxia: origin, development and significance. *Science* 223:22–27
- Officer CB, Ryther JH. 1980. The possible importance of silicon in marine eutrophication. *Mar. Ecol. Prog. Ser.* 3:83–91
- Paerl H, Pinckney J, Fear J, Peierls B. 1998. Ecosystem responses to internal and watershed organic matter loading: consequences for hypoxia in the eutrophying Neuse River Estuary, NC, USA. *Mar. Ecol. Prog. Ser.* 166:17–25
- Parker CA, O'Reilly JE. 1991. Oxygen depletion in Long Island Sound: a historical perspective. *Estuaries* 14:248–64
- Pokryfki L, Randall RE. 1987. Nearshore hypoxia in the bottom water of the northwestern Gulf of Mexico from 1981 to 1984. *Mar. Environ. Res.* 22:75–90
- Powers SP, Harper DE Jr, Rabalais NN. 2001. Effect of hypoxia/anoxia on the supply and settlement of benthic invertebrate larvae. See Rabalais & Turner 2001a, pp. 185–210
- Purcell JE, Breitburg DL, Decker MB, Graham WM, Youngbluth MJ, et al. 2001. Pelagic cnidarians and ctenophores in low dissolved oxygen environments: a review. See Rabalais & Turner 2001a, pp. 77–100
- Qureshi NA, Rabalais NN. 2001. Distribution of zooplankton on a seasonally hypoxic continental shelf. See Rabalais & Turner 2001a, pp. 61–76
- Rabalais NN. 1992. *An updated summary of status and trends in indicators of nutrient enrichment in the Gulf of Mexico*. EPA Publ. EPA/800-R-92-004. Stennis Space Cent., MS: Gulf Mexico Program. 421 pp.
- Rabalais NN. 2002. Nitrogen in aquatic ecosystems. *Ambio*. 31:102–12
- Rabalais NN, Harper DE Jr, Turner RE. 2001a. Responses of nekton and demersal and

- benthic fauna to decreasing oxygen concentrations. See Rabalais & Turner 2001a, pp. 115–28
- Rabalais NN, Smith LE, Harper DE Jr, Justić D. 2001b. Effects of seasonal hypoxia on continental shelf benthos. See Rabalais & Turner 2001a, pp. 211–40
- Rabalais NN, Turner RE, eds. 2001a. *Coastal Hypoxia: Consequences for Living Resources and Ecosystems. Coastal and Estuarine Stud.* 58. Washington, DC: Am. Geophys. Union
- Rabalais NN, Turner RE. 2001b. Hypoxia in the Northern Gulf of Mexico: description, causes and change. See Rabalais & Turner 2001a, pp. 1–36
- Rabalais NN, Turner RE, Justić D, Dortch Q, Wiseman WJ Jr. 1999. Characterization of hypoxia: topic 1 report for the integrated assessment of hypoxia in the Gulf of Mexico. *NOAA Coast. Ocean Prog. Decis. Anal. Ser.* 15. Silver Spring, MD: NOAA. 167 pp.
- Rabalais NN, Turner RE, Justić D, Dortch Q, Wiseman WJ Jr, et al. 1996. Nutrient changes in the Mississippi River and system responses on the adjacent continental shelf. *Estuaries* 19:386–407
- Rabalais NN, Turner RE, Scavia D. 2002. Beyond science into policy: Gulf of Mexico hypoxia and the Mississippi River. *BioScience* 52:129–42
- Rabalais NN, Turner RE, Wiseman WJ Jr, Boesch DF. 1991. A brief summary of hypoxia on the northern Gulf of Mexico continental shelf: 1985–1988. See Tyson & Pearson 1991a, pp. 35–46
- Rabalais NN, Wiseman WJ Jr, Turner RE. 1994. Comparison of continuous records of near-bottom dissolved oxygen from the hypoxia zone along the Louisiana coast. *Estuaries* 17:850–61
- Ragan JG, Harris AH, Green JH. 1978. Temperature, salinity and oxygen measurements of surface and bottom waters on the continental shelf off Louisiana during portions of 1975 and 1976. *Prof. Pap. Ser. Biol.* 3:1–29. Thibodaux, LA: Nicholls State Univ.
- Renaud M. 1986. Hypoxia in Louisiana coastal waters during 1983: implications for fisheries. *Fish. Bull.* 84:19–26
- Roman MR, Gauzens AL, Rhinehart WK, White JR. 1993. Effects of low oxygen waters on Chesapeake Bay zooplankton. *Limnol. Oceanogr.* 38:1603–14
- Rosenberg R. 1985. Eutrophication—the future marine coastal nuisance? *Mar. Pollut. Bull.* 16:227–31
- Rosenberg R. 1990. Negative oxygen trends in Swedish coastal bottom waters. *Mar. Pollut. Bull.* 21:335–39
- Sanford LP, Sellner KG, Breitbart DL. 1990. Covariability of dissolved oxygen with physical processes in the summertime Chesapeake Bay. *J. Mar. Res.* 48:567–90
- Schramm W. 1999. Factors influencing seaweed responses to eutrophication: some results from EU-project EUMAC. *J. Appl. Phycol.* 11:69–78
- Seitzinger SP, Koreze C, Bouwman AF, Caraco N, Dentener F, et al. 2002. Global patterns of dissolved inorganic and particulate nitrogen inputs to coastal systems: recent conditions and future projections. *Estuaries*. 25: In press
- Sen Gupta BK, Turner RE, Rabalais NN. 1996. Seasonal oxygen depletion in continental-shelf waters of Louisiana: historical record of benthic foraminifers. *Geology* 24:227–30
- Smith JW. 2001. Distribution of catch in the Gulf menhaden, *Brevoortia patronus*, purse seine fishery in the northern Gulf of Mexico from logbook information: Are there relationships to the hypoxic zone? See Rabalais & Turner 2001a, pp. 311–20
- Stachowitsch M. 1986. The Gulf of Trieste: a sensitive ecosystem. *Nova Thalass.* 8(Suppl. 3):221–35
- Swanson RL, Parker CA. 1988. Physical environmental factors contributing to recurring hypoxia in the New York bight. *Trans. Am. Fish. Soc.* 117:37–47
- Swanson RL, Sindermann CJ, eds. 1979. Oxygen depletion and associated benthic mortalities in New York bight, 1976. *Natl. Ocean. Atmos. Admin. Prof. Pap. 11*. Rockville, MD: Natl. Ocean. Atmos. Admin.
- Thomas E, Gapotchenko T, Varekamp JC,

- Mecray EL, ter Brink MRB. 2000. Benthic Foraminifera and environmental changes in Long Island Sound. *J. Coast. Res.* 16:641–45
- Tolmazin R. 1985. Changing coastal oceanography of the Black Sea. I. Northwestern shelf. *Prog. Oceanogr.* 15:217–76
- Turner RE. 1997. Wetland loss in the northern Gulf of Mexico: multiple working hypotheses. *Estuaries* 20:1–13
- Turner RE. 2001. Some effects of eutrophication on pelagic and demersal marine food webs. See Rabalais & Turner 2001a, pp. 371–98
- Turner RE, Allen RL. 1982a. Plankton respiration rates in the bottom waters of the Mississippi River Delta bight. *Contr. Mar. Sci.* 25:173–79
- Turner RE, Allen RL. 1982b. Bottom water oxygen concentration in the Mississippi River Delta bight. *Contr. Mar. Sci.* 25:161–72
- Turner RE, Qureshi N, Rabalais NN, Dortch Q, Justić D, et al. 1998. Fluctuating silicate:nitrate ratios and coastal plankton food webs. *Proc. Natl. Acad. Sci. USA* 95:13048–51
- Turner RE, Rabalais NN. 1991. Changes in Mississippi River water quality this century: implications for coastal food webs. *BioScience* 41: 140–48
- Turner RE, Rabalais NN. 1994a. Coastal eutrophication near the Mississippi river delta. *Nature* 368:619–21
- Turner RE, Rabalais NN. 1994b. Changes in the Mississippi River nutrient supply and offshore silicate-based phytoplankton community responses. See Dyer & Orth 1994, pp. 147–50
- Turner RE, Schroeder WW, Wiseman WJ Jr. 1987. The role of stratification in the deoxygenation of Mobile Bay and adjacent shelf bottom waters. *Estuaries* 10:13–19
- Tyson RV, Pearson TH, eds. 1991a. *Modern and Ancient Continental Shelf Anoxia*. *Geol. Soc. Spec. Publ.* 58. London: Geol. Soc. 460 pp.
- Tyson RV, Pearson TH. 1991b. Modern and ancient continental shelf anoxia: an overview. See Tyson & Pearson 1991a, pp. 1–24
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, et al. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecol. Appl.* 7:737–50
- von Bodungen B, Turner RK, eds. 2001. *Science and Integrated Coastal Management*. Berlin: Dahlem Univ. Press 364 pp.
- Welsh BL, Eller FC. 1991. Mechanisms controlling summertime oxygen depletion in western Long Island Sound. *Estuaries* 14:265–78
- Welsh BL, Welsh RI, DiGiacomo-Cohen ML. 1994. Quantifying hypoxia and anoxia in Long Island Sound. See Dyer & Orth 1994, pp. 131–37
- Wetzel MA, Fleeger JW, Powers SP. 2001. Effects of hypoxia and anoxia on meiofauna: a review with new data from the Gulf of Mexico. See Rabalais & Turner 2001a, pp. 165–84
- Zaitsev YP. 1992. Recent changes in the trophic structure of the Black Sea. *Fish. Oceanogr.* 1:180–89
- Zimmerman RJ, Nance JM. 2001. Effects of hypoxia on the shrimp fishery of Louisiana and Texas. See Rabalais & Turner 2001a, pp. 293–310

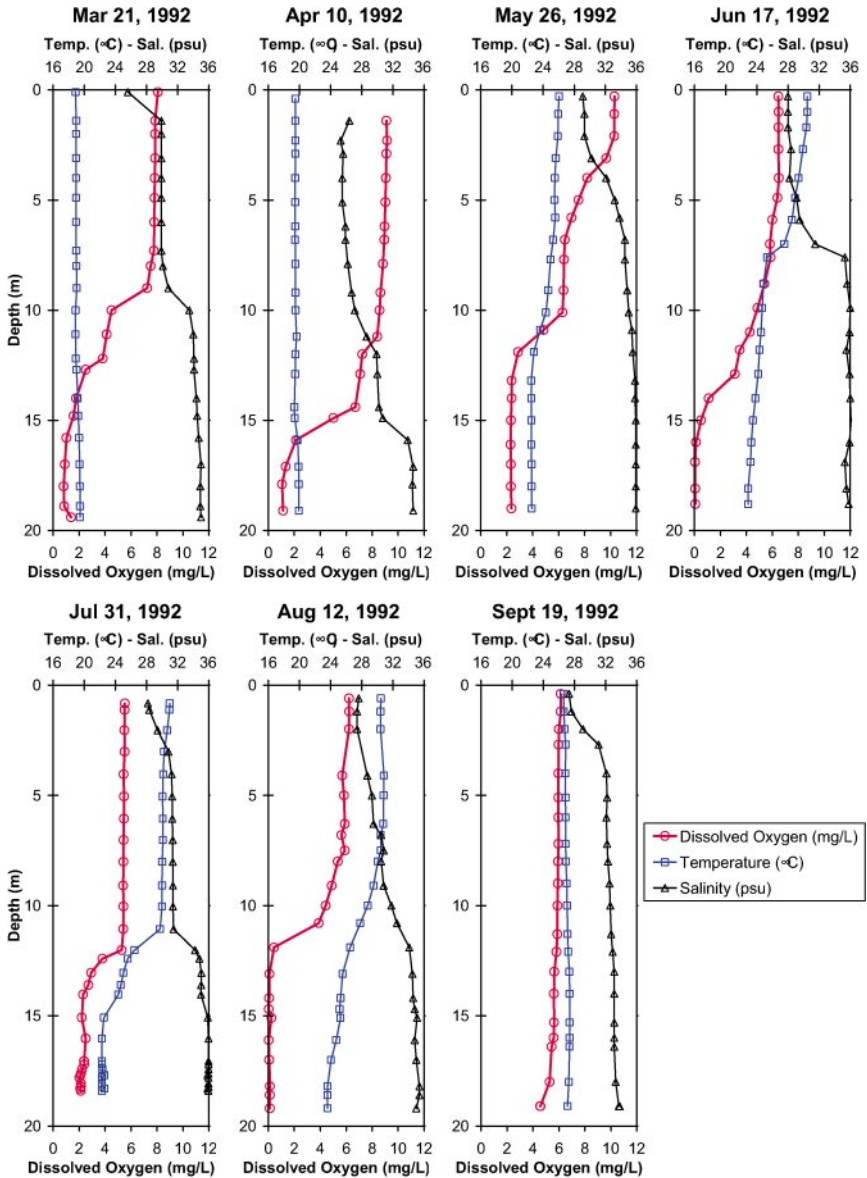


Figure 1 Water column profiles for temperature ($^{\circ}\text{C}$), salinity (psu) and dissolved oxygen (mg L^{-1}) for representative dates of monthly sampling at station C6B off Terrebonne Bay on the southeastern Louisiana shelf in 1992 (modified from Rabalais & Turner 2001b, reprinted with permission of the American Geophysical Union). The station location is identified in Figure 4.

Average Monthly Bottom Dissolved Oxygen (mg/L) 1985 - 2001

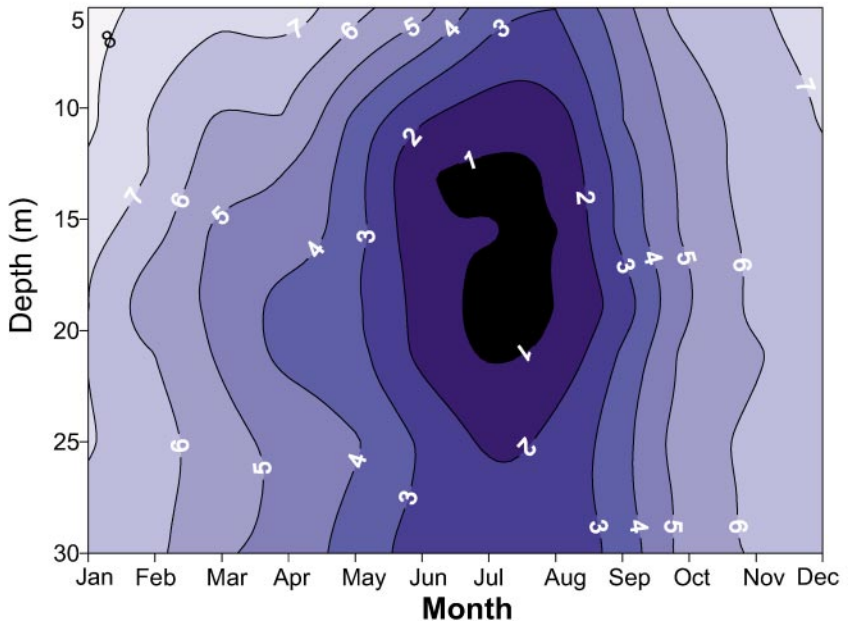


Figure 5 Contours of average values of bottom-water dissolved oxygen (mg l^{-1}) by month for the eight stations along transect C (see Figure 4) by depth across the continental shelf from inshore to offshore and from January through December for the period 1985–2001. [Note, the number of values for each month varies, with fewer data in the winter than in spring-fall.]

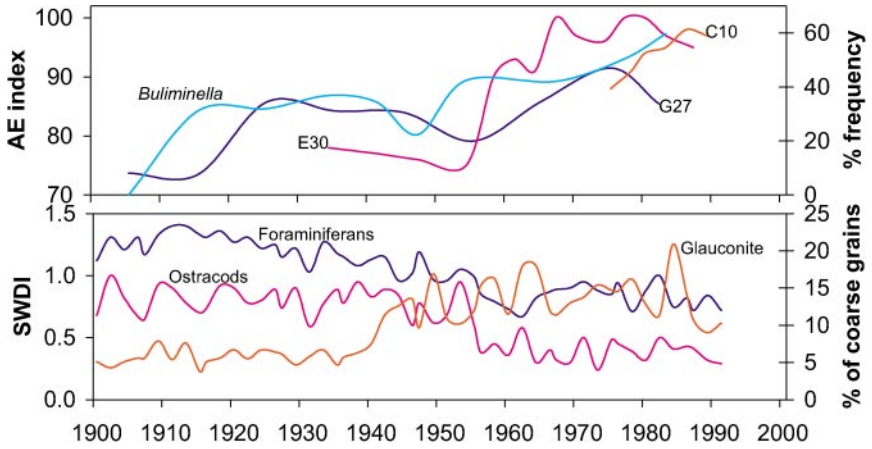


Figure 8 (Top) A-E index for cores C10 (3-yr running average), E30, G27 (Sen Gupta et al. 1996); % frequency of *Buliminella* in core G27 (Rabalais et al. 1996), % frequency of *Quenquiloculina* in core G27 (Rabalais et al. 1996). (Bottom) SWDI (Shannon-Wiener Diversity Index) for foraminiferans and ostracods (Nelsen et al. 1994, TA Nelson unpublished data); % glauconite of coarse grains (Nelsen et al. 1994).