Seasonal Hypoxia and Models of Benthic Response in a Texas Bay

Christine Ritter[1]

Paul A. Montagna

The University of Texas at Austin
Marine Science Institute
750 Channel View Drive
Port Aransas, Texas 78373

ABSTRACT: Hypoxia occurs during summer in the southeastern region of Corpus Christi Bay, Texas. The objectives of this study were to identify potential causes of recurrent hypoxic events, to determine hypoxic effects on benthic macroinfauna, and to develop models of benthic response. Long-term and short-term hydrographic surveys were performed, and macroinfaunal samples were collected from normoxic and hypoxic regions of the bay. Hypoxia occurred in seven of the nine summers sampled (1988 to 1996). In 1994, the hypoxic event persisted for approximately 3 wk. Hypoxic events were associated with water column stratification where the difference between bottom and surface salinity was as high as 7.2‰ and averaged 4.1‰. The salinity difference is surprising because water column stratification is not expected in shallow (< 4 m), windy (average 18.5 km h^{-1}) bays. Stratification did occur—hypersaline bottom water in a relatively stagnant portion of the bay—in spite of mixing forces (i.e., high winds), giving rise to hypoxia. Benthic biomass decreased 12-fold, and abundance and diversity decreased 5-fold under hypoxic conditions. In addition, dominance patterns shifted as oxygen levels declined from 5 mg O_2 l^{-1} to < 1 mg O_2 l^{-1}. The polychaete *Streblospio benedicti* and oligochaetes tolerated low oxygen better than other infauna. Community response to hypoxic disturbance was fit to a nonparametric categorical model and a parametric logistic model. Biomass, abundance, and diversity exhibited a lag response at < 3 mg l^{-1}, and increased exponentially from 3 mg l^{-1} to 6 mg l^{-1}. Based on both models, 3 mg l^{-1} appears to define the breakpoint between normoxic and hypoxic benthic communities in Corpus Christi Bay. This value is higher than traditional definitions of hypoxia, < 2 mg l^{-1} or < 2 ml l^{-1} (ca. 2.8 mg l^{-1}).

Introduction

Hypoxia is a common estuarine phenomenon and is defined as occurring when dissolved oxygen concentration declines below 2 mg O_2 l^{-1} (Dauer et al. 1992). The onset of hypoxia has been linked with water column stratification, decomposition of organic matter (Officer et al. 1984; Pokryfki and Randall 1987; Rabalais et al. 1991) and sulfide conditions (Gunter 1942; Gamenick et al. 1996; Gamenick et al. 1997). Occurrence of hypoxia is widespread, having been reported in the Chesapeake Bay area (Officer et al. 1984; Sanford et al. 1990; Cooper and Brush 1991; Kuo et al. 1991; Breitburg 1992; Pihl et al. 1992; Dauer et al. 1993), Gullmar Fjord basin, Sweden (Josefson and Widbom 1988), eastern Hiuchi Sound, Japan (Sanukida et al. 1984), Hillsborough Bay, Florida (Santos and Simon 1980), the Gulf of Mexico (McKinney and Harper 1980; Harper et al. 1981; Pavela et al. 1983; Pokryfki and Randall 1987; Rabalais et al. 1991), and many other places (summarized in Diaz and Rosenberg 1995). Hypoxia is considered a disturbance because few animals are able to tolerate the

physiological stress associated with extended exposure to low oxygen conditions.

Hypoxia usually occurs in deep waters coincident with stratification (Gunter 1942; Officer et al. 1984; Rabalais et al. 1991; Livingston 1996). Texas bays are generally shallow, windy, and well mixed. Based on vertical mixing processes, hypoxia would not be expected to occur in Texas bays, although it has been reported in isolated locales (Gunter 1942). We know it occurs during summer in Corpus Christi Bay, Texas (Montagna and Kalke 1992; Martin and Montagna 1995), where the water-residence time is long (ca. 5.5 mo). An estuary with a long water-residence time is more likely to develop hypoxia than an estuary with a similar nutrient load but a shorter water-residence time (Turner and Rabalais 1999). Hypoxia in Corpus Christi Bay was first noted in summer 1988 (Montagna and Kalke 1992) and recurred each summer through 1997 (Montagna personal observation).

The presence of hypoxia in Corpus Christi Bay raised two questions: What effect does hypoxia have on benthic macroinfauna? and What is causing the hypoxia? To answer these questions, we conducted long-term and short-term hydrographic surveys and a broad-scale spatial survey to deter-

---

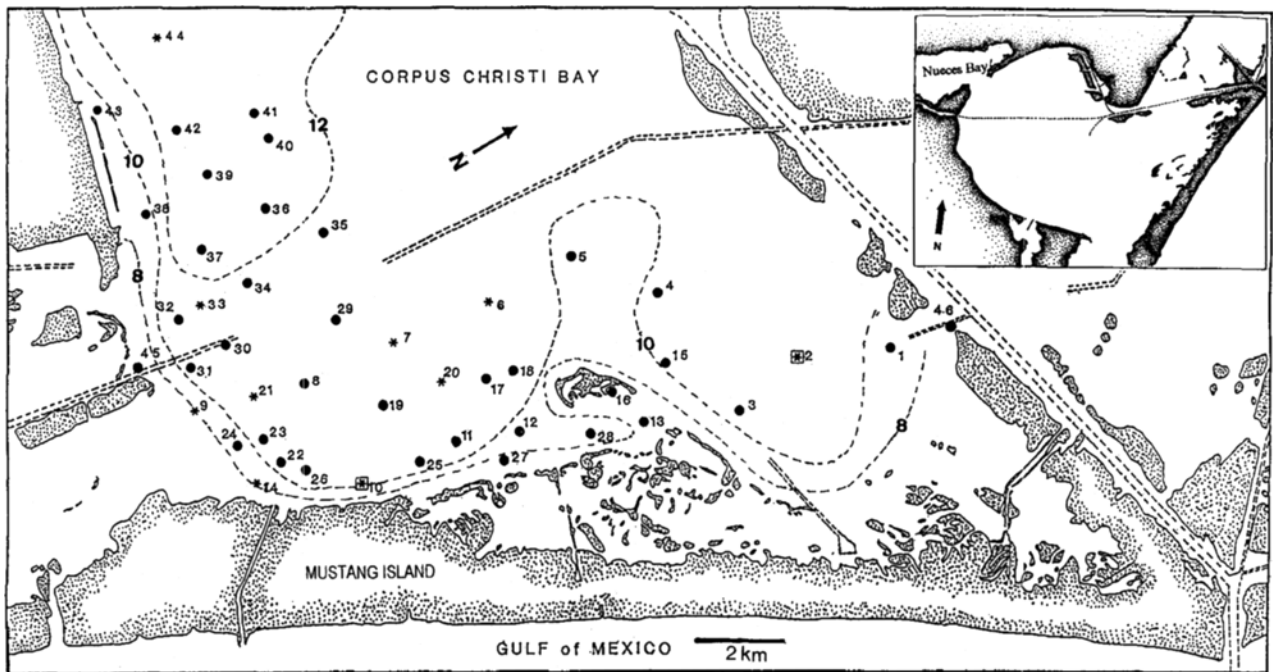[1] Corresponding author; tele: 512/749-6779; fax: 512/749-6777; e-mail: chrisr@utmsi.utexas.edu.

Fig. 1.   Map of the study area and sampling stations. Biological samples were collected at stations denoted by *. Stations denoted by ☐ are part of a long-term program. Depth contours (single dashed lines; ft.) are drawn from a navigation chart (United States Department of Commerce 1986). Double dashed lines indicate dredged navigation channels. Wide double dash is the Corpus Christi Ship Channel. Narrow double dash is the Intracoastal Waterway.

mine the extent of hypoxia. The spatial survey was followed by a study of the benthic macrofaunal community.

Materials and Methods

Study Location

Corpus Christi Bay is a shallow (~3.2 m; Orlando et al. 1991), almost enclosed bay with a level bottom (Fig. 1; other maps of the region can be found in Montagna and Kalke 1992; Martin and Montagna 1995). Corpus Christi Bay is microtidal and is subjected to strong meteorological forcing (Ward 1980). Average monthly wind speeds range from 17 km h⁻¹ to 28 km h⁻¹. Wind direction is consistently from the southeast between April and September (Port of Corpus Christi Authority 1993). It receives an average of 74 cm yr⁻¹ of rainfall and 25 m³ s⁻¹ inflow (Orlando et al. 1991). The average evaporation rate is 151 cm yr⁻¹. South Texas bays are characterized by broad climate variations that alternate between wet and dry cycles (Montagna and Kalke 1995).

Hydrographic Surveys

Two temporal hydrographic surveys were conducted. The long-term survey sampled two stations in Corpus Christi Bay on a quarterly basis from October 1987 to December 1997, with a hiatus be-

tween fall 1988 and spring 1990. These long-term stations were also sampled in the short-term survey. The short-term survey sampled every 3 wk between May 3 and August 26, 1994, at stations 1–12, near the hypoxic region identified by Montagna and Kalke (1992) and Martin and Montagna (1995) (Fig. 1). (The long-term stations D and E in Montagna and Kalke [1992] and Martin and Montagna [1995] are short-term stations 10 and 2, respectively [Fig. 1].)

The spatial extent of summer hypoxia was determined in a third hydrographic study conducted in July 1996. This study collected data at 46 stations in the southeastern portion of Corpus Christi Bay (Fig. 1), including the 12 stations of the short-term survey. The hydrographic data were collected on a finer spatial scale than in the long-term and short-term temporal surveys. Stations 1–28 were sampled on July 24, 1996, and stations 6, 10, 23, 29–43 were sampled on July 25, 1996. In conjunction with the biological survey, hydrographic data were collected from stations 2, 6, 7, 9, 10, 14, 20, 21, and 33, and the additional stations 44, 45, and 46. Hydrographic data were collected at the surface and bottom (ca. 15 cm above the sediment surface) at each station using a Hydrolab 4000. The sonde unit measures salinity (‰), temperature (± 0.15°C), dissolved oxygen (± 0.2 mg l⁻¹), oxidation reduc-

tion potential (± 0.05 mV), conductivity (± 0.015–1.5 mmhos cm [1] depending on range), depth (± 1 m), and pH (± 0.1 units). A stratification index, σ, was calculated as the difference between bottom and surface salinity. The greater the σ value, the greater the effective water column stratification.

Depth profiles of dissolved oxygen concentrations and salinity were used to determine the vertical hydrographic differences between normoxic and hypoxic stations. Stations were designated normoxic or hypoxic based on average oxygen concentration obtained during 1996.

BIOLOGICAL EFFECTS STUDY

Biological samples were collected from 10 of the 46 stations (Fig. 1). Benthic samples and hydrographic data were collected from stations 6, 7, 9, 20, 21, and 33 on July 26, 1996, and from stations 2, 10, 14, and 44 on July 30, 1996. As noted previously, stations 2 and 10 are the same as long-term stations D and E in Montagna and Kalke (1992) and Martin and Montagna (1995). Stations with low oxygen, and within the hypoxic region identified by previous studies, were designated as hypoxic. The other stations were designated as normoxic.

Macrofauna were sampled with a 6.7-cm diameter core tube. The core was divided into 0–3 cm and 3–10 cm sections. Three replicates were taken at each station. All replicates were taken remotely within a 2 m radius. Macrofauna samples were preserved in 5% buffered formalin, sorted using 0.5-mm sieves, identified, and counted as described in Montagna and Kalke (1992). To measure biomass, sorted samples were dried for at least 24 h at 55°C and weighed. Mollusks were placed in 2 N HCl for 1–5 min to dissolve carbonate shells, and the sample was washed before drying.

Sediment grain size at each station was determined from one 6.7-cm diameter core sediment sample. Sediment samples were sectioned as for the macrofaunal samples. Percent composition by weight was measured for four sediment components: rubble, sand, silt, and clay, using standard geologic procedures as described in Montagna and Kalke (1992).

Total organic carbon (TOC) of surface sediment was determined using a subsample of the 0–3 cm vertical section from an additional 6.7-cm diameter core. The sediment sample was placed in a petri dish, weighed wet, dried at 55°C, weighed dry for porosity estimates, and stored in the oven. After drying, the sample was ground with mortar and pestle into fine grains and stored in the oven. The day prior to CHN analysis, samples were homogenized, placed in silver boats, and acidified under a vent hood to dissolve any calcium carbonate. CHN

analysis was conducted according to the dynamic flush combustion method using an Elemental Analyzer EA1108 coupled with an autosampler AS200.

STATISTICAL ANALYSIS

An a posteriori linear regression was calculated to determine the significance of the association between hypoxia and water column stratification, as defined by the stratification index, σ. Differences in biomass, abundance, and diversity between normoxic and hypoxic benthic communities were determined with two-way nested ANOVA using SAS software (SAS Institute Inc. 1985). There were two treatments (hypoxic and normoxic), five stations within treatments, and three replicates per station. The residuals of abundance and biomass were normally distributed. Two measures of diversity were used: N0 and N1. The most fundamental measure of diversity is N0, the total number of species present in a sample. N0 does not account for variability among species abundances, which is assessed by Shannon's Index (H') and Hill's Number (N1). The Shannon index (H') measures the probability of predicting the species of an organism drawn randomly from a collection of S species and n organisms (Ludwig and Reynolds 1988). Hill's Number (N1), the exponential form of the Shannon Index, estimates the number of abundant species in a sample (Ludwig and Reynolds 1988). The indices were calculated as follows.

$$H' = \sum (p_i \ln p_i), \qquad \text{where}$$

$$p_i = n_i/n, \qquad \text{where}$$

$$n_i = \text{abundance of species } i, \text{ and}$$

$$n = \text{total abundance}$$

$$N1 = e^{H'}.$$

Principal components analysis (PCA) was performed on benthic species composition to determine community relationships among stations. The PCA was conducted using SAS software (SAS Institute Inc. 1985) on the covariance matrix of data standardized to a normal distribution. Three factors were retained and species loadings were calculated for each of these factors. Differences in percent sand and TOC between hypoxic and normoxic stations were tested using a Student T-test.

BENTHIC RESPONSE MODELS

Macrobenthic response to hypoxia was analyzed using two models; one was nonparametric and the other was parametric. In the nonparametric model, biological effects were analyzed by categories of hypoxic intensity. We assumed that disturbance intensity is defined as increasing as the concentra-

tion of dissolved oxygen decreases. We defined six intensity levels, one for each integer unit of dissolved oxygen between 0 mg l^{-1} and 6 mg l^{-1}. Community and environmental data were averaged for each category. No data were available for the categories of 3–4 mg l^{-1} and 0–1 mg l^{-1}.

A parametric logistic model was used to describe how estuarine benthic communities respond to declining oxygen concentrations. The logistic model was chosen because it produces a facultative response curve. The use of the logistic model assumes a lag period of little or no benthic response, an exponential recovery phase where the community is responding to changes in dissolved oxygen concentrations, and a maximum phase where the community characteristics modeled have reached a carrying capacity.

The logistic model, used to describe population growth, is appropriate for the prediction of community recovery. In this application, the lag phase is the range where there is no community response to increasing oxygen concentrations. The exponential growth phase is a function of organismal and population growth, recruitment, and immigration. The maximum phase represents population or community carrying capacity as in logistic growth.

The logistic model was used only in the forward direction to predict population growth. It is not certain that the logistic model can be used to predict macrobenthic change due to declining oxygen concentrations, which is in the backward direction. We propose its use to determine a lethal effect range represented by the lag phase. The lethal effect range is a function of organism mortality arising from asphyxiation and predation. The logistic model is

$$Y = \frac{M}{(1 + ce^{(-a \cdot X)})}$$

where X is the concentration of dissolved oxygen and Y is the value of a benthic community characteristic (i.e., biomass, abundance, or one of the diversity indices); M is the maximum value for the benthic characteristic; c is a parameter for the lag phase of response to increasing oxygen conditions; and a represents the exponential recovery rate. The parameter M was constrained to a maximum of 15 for biomass, 40,000 for abundance, 25 for N0 (number of species), and 15 for Hill's N1.

Results

TEMPORAL HYDROGRAPHIC SURVEYS

Hypoxia occurred during the long-term survey at station 10 every summer between 1988 and 1997 with the exception of 1992 and 1996 (Fig. 2), but
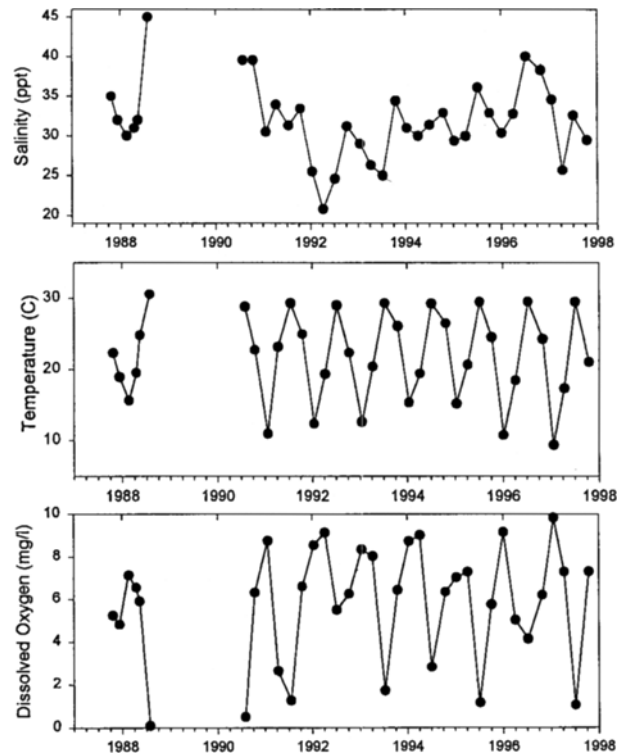

Fig. 2. Long-term bottom hydrographic variations in Corpus Christi Bay station 10, which is station D in Montagna and Kalke (1992) and Martin and Montagna (1995).

it never occurred at station 2. Dissolved oxygen concentrations at the bottom were low when bottom salinity was high. Hypoxia occurred only during summer when water temperature was highest.

During the short-term survey in 1994, the hypoxia lasted 3 wk. Hypoxia was present during the period between June 14 and July 5, 1994. The hypoxic area extended about 3 km south from station 10 but in no other direction. Again, an association was found between hypoxia and high salinity bottom water.

SPATIAL HYDROGRAPHIC SURVEY

Surprisingly, station 10 was not hypoxic during the 1996 spatial hydrographic survey; however, hypoxia was found south of station 10 in a triangular region in southeast Corpus Christi Bay. Bottom dissolved oxygen concentrations below 3 mg l^{-1} were found at 14 stations, seven of which were below 2 mg l^{-1}. Dissolved oxygen concentrations varied daily for those stations (n = 11) resampled during the spatial hydrographic and biological sampling in 1996. Changes in dissolved oxygen ranged from 0.01 mg l^{-1} to 3.06 mg l^{-1} over periods ranging from 2 d to 6 d. For example, dissolved oxygen at station 21 was 2.03 mg l^{-1} on July
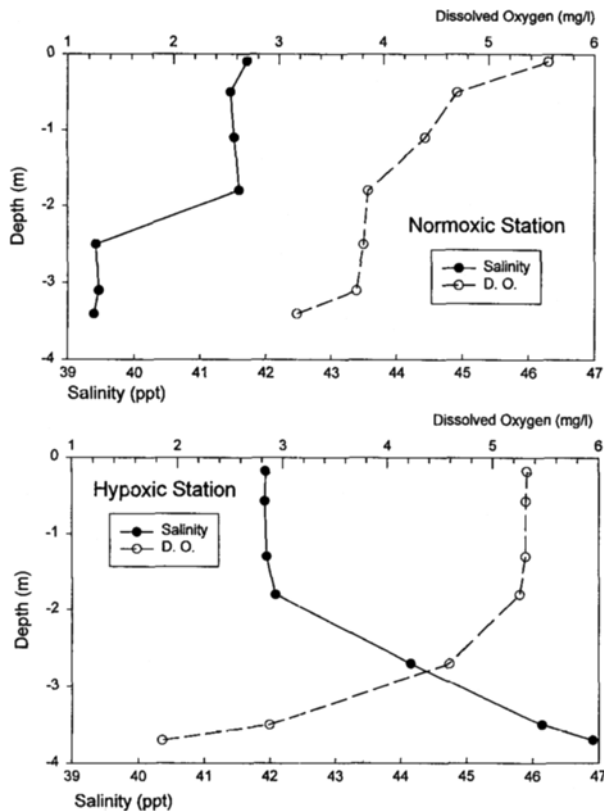
Fig. 3. Representative vertical profiles of stratification at the normoxic station 6 and the hypoxic station 22 in Fig. 1.
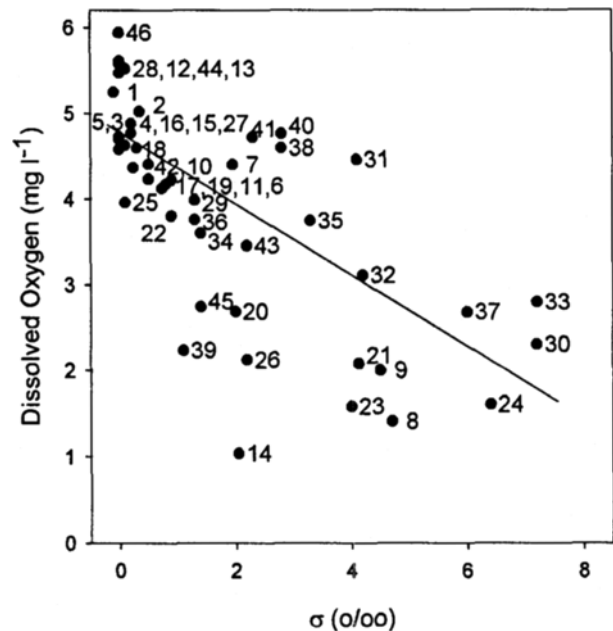

Fig. 4. Correlation between dissolved oxygen and water column stratification during 1996 spatial hydrographic survey as indexed by σ ($R^2 = 0.49$ and $\alpha = 0.0001$). Symbols as in Fig. 1.

24, 1996, 3.75 mg l $^{-1}$ on July 26, 1996, and 0.44 on July 30, 1996.

The presence of hypoxia was associated with high bottom salinity and water column stratification (Figs. 3 and 4). Temperature was constant throughout the water column ($29.6–29.7°C$ for normoxic; $29.8–30.0°C$ for hypoxic), indicating water mass differences were being influenced by salinity differences (Fig. 3). Salinity differences are probably due to the influx of saline water of the same temperature. The halocline for both profiles was at a depth of ca. 2 m. Salinity of surface waters at both stations was similar; however, differences were found with regard to the bottom water mass. The stratification index, σ, at the normoxic station was ca. $-2‰$, indicating bottom water less saline than the surface, which could occur due to evaporation, the lack of vertical mixing forces, and/or transport of less saline (ca. $34‰$) oceanic water from the navigation channels. This pattern is reversed at the hypoxic station, where σ was ca. $5‰$. The net difference between normoxic and hypoxic bottom salinities was $8‰$ (Fig. 3).

A significant ($\alpha = 0.0001$) inverse correlation was found between dissolved oxygen and σ for all stations in the 1996 spatial hydrographic survey

(Fig. 4). The relationship between σ and dissolved oxygen concentration (DO) is described by the regression DO $= 4.69 \times \sigma - 0.44$ ($R^2 = 0.49$). Station σ values ranged from $-0.1‰$ to $7.2‰$. A distinct region traversing the Corpus Christi Ship Channel exhibited the greatest stratification (Fig. 5). Stations 24, 30, 33, and 37 had $\sigma > 6$. The σ value of surrounding stations (8, 9, 21, 23, 31, and 32) ranged between 4 and 6. Based on all hydrographic data, three regions of Corpus Christi Bay were identified with summer hypoxia (Fig. 6). The southernmost corner of the bay is chronically hypoxic during the summer.

BENTHIC RESPONSES

Community characteristics were different between hypoxic and normoxic stations, indicating benthic effects due to hypoxia (Table 1). Diversity, measured by N0 and N1, was significantly lower ($\alpha = 0.0001$) for hypoxic stations than normoxic stations. Abundance and biomass were also significantly lower ($\alpha = 0.007$ and $\alpha = 0.0001$, respectively) at hypoxic than normoxic stations. It is unlikely that treatment differences were due to substrate heterogeneity, because sand content was the same at hypoxic and normoxic stations ($\alpha = 0.05$). Treatment differences may be related to significant differences of TOC concentration ($\alpha = 0.004$).

On average, normoxic stations had twice as much dissolved oxygen as hypoxic stations (Table 1). The absence of normal oxygen levels at hypoxic
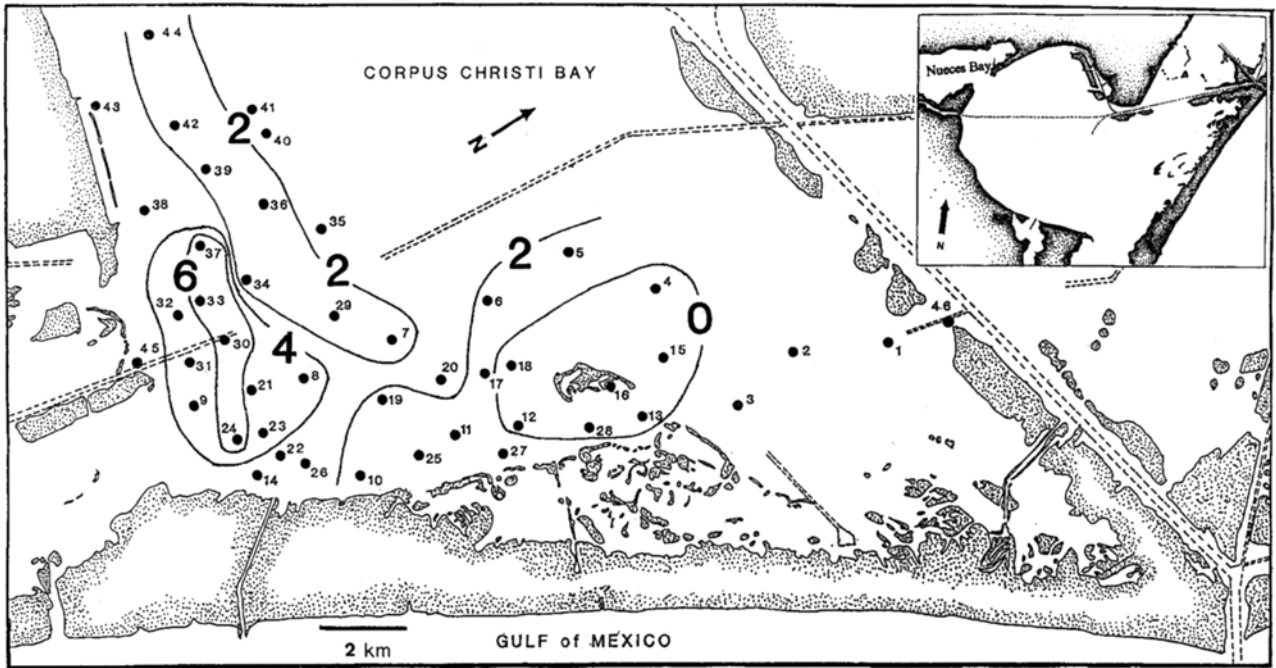
Fig. 5. Map of study area depicting water column stratification in 1996 indicated by σ isopleths. $\sigma = S_{bottom} - S_{surface}$. Symbols as in Fig. 1.

stations influenced sediment productivity, as indicated by a biomass standing stock twelvefold less than normoxic stations. Benthic effects at hypoxic stations are further evidenced by the fivefold decrease in abundance and diversity as compared with normoxic stations.

Community structure of hypoxic stations was significantly different from that of normoxic stations
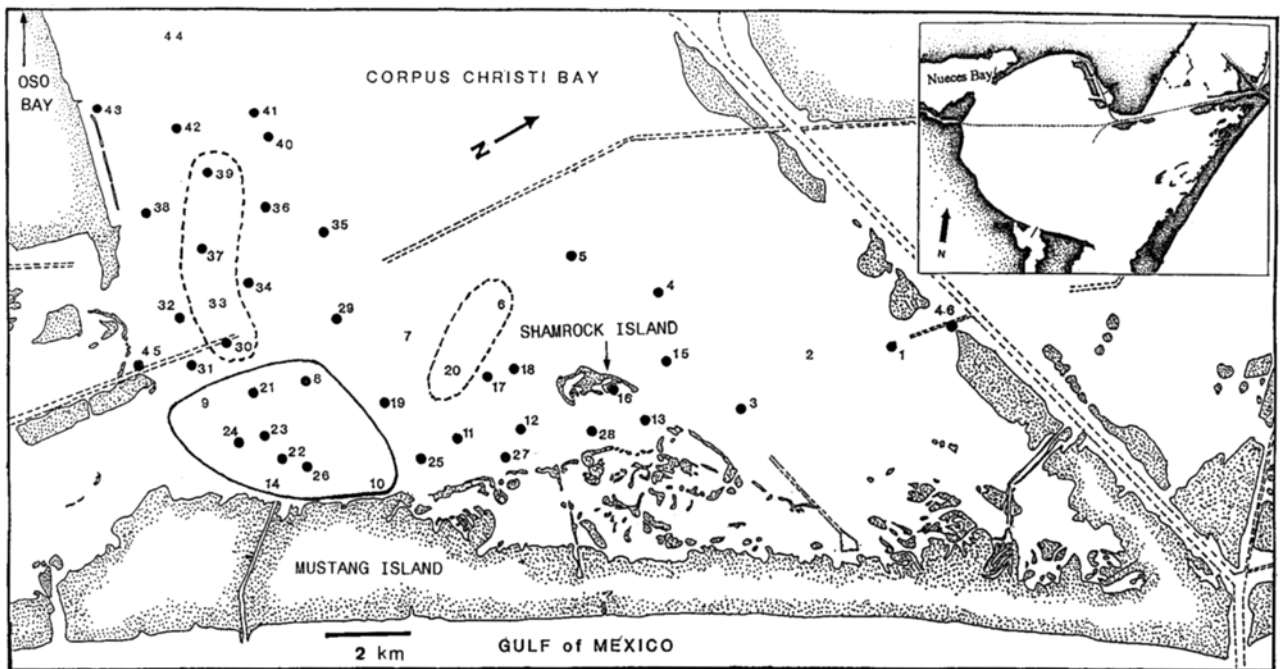

Fig. 6. Map of study area illustrating summer hypoxic regions based on all hydrographic surveys. The region enclosed by a solid line is generally < 2 mg l⁻¹. The regions enclosed by dashed lines are generally < 3 mg l⁻¹.

TABLE 1. Community and bottom environmental characteristics of each station. Salinity and dissolved oxygen (DO) values represent averages over a 6-d period in July 1996. Biomass, density, and diversity are averages of three replicates taken on one day.

Station	Biomass (g m⁻²)	Density (no. m⁻²)	No. Species (0.01 m⁻²)	No. Dominant Species (N1)	DO (mg l⁻¹)	TOC (wt. %)	Salinity (‰)	Sediment (% sand)
			Diversity					
2	6.151	21,651	20	8.4	5.03	0.96	39.4	72.8
6	6.504	13,047	20	12.1	4.12	0.70	40.7	4.6
7	0.096	1,324	4	3.2	4.41	0.56	41.9	2.6
10	0.006	662	1	1.0	4.37	0.60	41.3	69.3
44	9.125	22,691	20	10.5	5.52	0.84	38.1	71.5
Normoxic average	4.376	11,875	13	7.0	4.69	0.73	40.3	44.2
9	0.343	3,782	4	2.2	2.00	1.16	45.9	84.7
14	0.006	189	1	1.0	1.04	1.19	44.2	82.0
20	0.674	3,498	4	1.7	2.69	0.88	42.0	1.5
21	0.144	4,538	2	1.1	2.07	1.25	45.7	40.2
33	0.512	756	2	1.5	2.79	1.17	48.8	11.2
Hypoxic average	0.343	2,553	2.6	1.5	2.12	1.13	45.3	43.9

as indicated by PCA. Three factors were required to differentiate between normoxic and hypoxic stations (Fig. 7). One normoxic station (10) was grouped with hypoxic stations because it was known to have been hypoxic 2 wk prior to the study, as well as having a history of hypoxia (Fig. 2). Stations 10, 20, 21, and 33 were closely associated and shared negative PCA factor 3 values with stations 9 and 14 (Fig. 7). The normoxic stations appeared to be less closely associated but were distinctly separated along the positive axis for PCA factor 3.

Different species were responsible for the trends in each of the factors (Fig. 8). Factor 1 represented the presence of *Streblospio benedicti* (SB) as a dominant organism at most stations. Factor 2 represented the presence of oligochaetes (OL), *Mediomastus ambiseta* (MA), *Paleanotus heteroseta* (PH), and *Polydora caulleryi* (PC) and the absence of *Streblospio benedicti* (SB). Factor 3 represented the absence of oligochaetes (OL) and the presence of *Polydora caulleryi* (PC), *Tharyx setigera* (TS), and *Mediomastus ambiseta* (MA), and was the principal axis that separated hypoxic from normoxic stations. Negative values of factor 3 were due to the presence of *Streblospio benedicti* (SB), oligochaetes (OL), and *Haploscoloplos fragilis* (HF) that dominated hypoxic stations.

Most stations were dominated by deposit feeders (Tables 2 and 3). The only exceptions were stations 9 and 14, which were dominated by oligochaetes (omnivorous scavengers). *Streblospio benedicti* dominated three hypoxic stations (20, 21, and 33) and station 10. *Mediomastus ambiseta* dominated two normoxic stations (6 and 7).

Biological responses appeared to be a function of oxygen concentration categories (Table 4). Dissolved oxygen concentrations were divided into six declining categories at 1 mg l⁻¹ intervals to represent hypoxia intensity increases. Based on this

categorical model, biomass, density and diversity declined, and shifts in community dominance occurred with increasing hypoxic intensity (Table 4). Biomass declined 2.3-fold between intensity levels 1 and 2, 18.2-fold between levels 1 and 4, and 764-fold between levels 1 and 5. Animal abundance declined 3.1-fold between levels 1 and 2, 7.1-fold between levels 1 and 4, and 117.3-fold between levels 1 and 5. The number of species present declined 1.7-fold from level 1 to 2, 6.7-fold from level 1 to 4, and 20-fold from level 1 to 5. Dominance patterns shifted as dissolved oxygen levels declined from 5 mg l⁻¹ (Table 4). At intensity level 1, *Polydora caulleryi* and *Tharyx setigera* were codominant. Level 2 was dominated by *Mediomastus ambiseta* and level 4 was dominated by *Streblospio benedicti*, both of which are considered opportunistic species (Ranaisinghe et al. 1994). Level 5 was dominated by oligochaetes. Patterns of shifting dominance may indicate sequential success of species more tolerant of lower oxygen concentration ranges or opportunistically taking advantage of increased sediment TOC.

The trend in the categorical model is roughly an exponential decline in biomass, density, and diversity with increasing hypoxic disturbance intensity. A quantitative model, however, requires additional parameters to explain lags or delays in recovery or mortality, and maximum values of benthic characteristics. These parameters are typical of a logistic model. Hence, a logistic model was fit to each community characteristic to quantify the functional response of benthic communities to oxygen concentration changes (Table 5 and Fig. 9). For each community characteristic, a lag period was present at dissolved oxygen levels less than 3 mg l⁻¹ (was represented by the parameter a in the parametric regression model) (Table 5). The lag period was followed by an exponential population growth or recruitment phase. The growth parameter (c) for
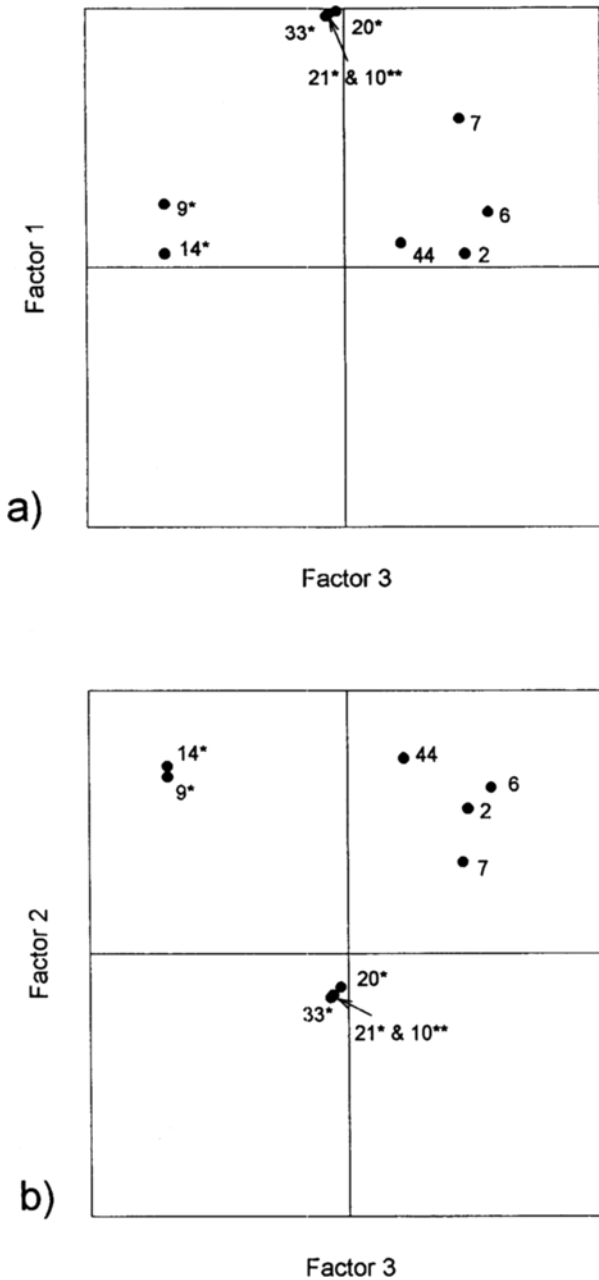
Fig. 7. Principal components analysis of benthic species at stations in the study area based on a) Factors 1 and 3, and b) Factors 2 and 3. The identifier numbers for each point correspond to the station in Fig. 1. * indicates a hypoxic station. ** indicates a normoxic station known to have been hypoxic previously.
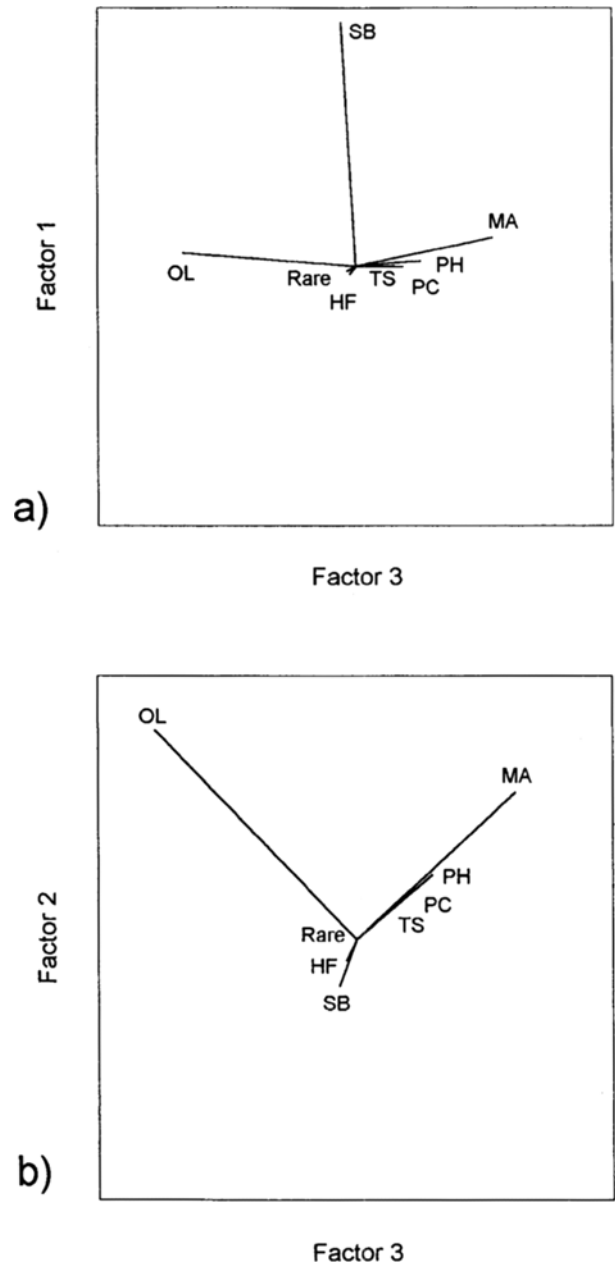
Fig. 8. Principal components analysis of species within the study area based on a) Factors 1 and 3, and b) Factors 2 and 3. The following codes are used in the figure: Oligochaeta (OI.), *Streblospio benedicti* (SB), *Mediomastus ambiseta* (MA), *Paleanotus heteroseta* (PH), *Polydora caulleryi* (PC), *Tharyx setigera* (TS), *Haploscoloplos fragilis* (HF), and 14 rare species (RARE).

each model was of different duration and slope. The final parameter of the logistic model was the carrying capacity (M). Biomass and density models did not reach their maximum carrying capacity over the range of data available. The two diversity indices either reached capacity or approached capacity.

Discussion

Hypoxia has traditionally been defined as dissolved oxygen concentrations < 2 mg l^{-1} (Rosenberg 1980). In the present study, 3 mg l^{-1} is a more appropriate definition of hypoxia for Corpus Christi Bay (Table 4 and Fig. 9). Hypoxia occurs annually in Corpus Christi Bay during the summer

TABLE 2. Feeding mode, tropic group, and stations present for key species identified in principal component analysis. C = Carnivore, D = Deposit, F = Filter, H = Herbivore, O = Omnivore, SV = Scavenger, S = Suspension Feeder, SD = Surface Deposit, SSD = Subsurface Deposit (* = hypothetical assignment).

Species Name	Feeding Mode	Trophic Group	Source of Trophic Information	Stations Present
Streblospio benedicti	S/SD	F	Mannino 1994	6, 7, 9, 10, 20, 21, 33, 44
Oligochaetes	SV	O	Mannino 1994	2, 6, 9, 14, 44
Paleanotus heteroseta	C*	O*	Fauchald and Jumars 1979	2, 6, 44
Polydora caulleryi	S/SD	F	Mannino 1994	2, 6, 44
Tharyx setigera	SD	D	Mannino 1994	2, 6, 9, 44
Mediomastus ambiseta	SSD	D	Mannino 1994	2, 6, 7, 20, 44
Haploscoloplos fragilis	S/SD.	D	Fauchald and Jumars 1979	20, 33
Sigambra tentaculata	C*	O*	Fauchald and Jumars 1979	2
Branchioasychis americana	SSD	D	Fauchald and Jumars 1979	2, 44
Phascolion strombi	C	O	Stephen and Edmonds 1972	2, 44
Turbellaria	C	O	Ruppert and Barnes 1994	2
Ceratonereis irritabilis	C	O	Kalke personal communication	44
Pista palmata	SD	D	Fauchald and Jumars 1979	44
Ampelisca verrilli	SV	O	Kalke personal communication	44
Ancistrosyllis groenlandica	C*	O*	Fauchald and Jumars 1979	44
Pilargidae (unidentified)	C*	O*	Fauchald and Jumars 1979	44
Schistomeringos sp. A	C	O	Fauchald and Jumars 1979	44
Sphaerosyllis sp. A	SD	D	Mannino 1994	44
Caecum johnsoni	SD	D	Kalke personal communication	44
Naineris sp. A	SSD	D	Fauchald and Jumars 1979	44
Malmgreniella taylori	C*	O*	Kalke personal communication	44
Aricidea cf. *fragilis*	SSD	D	Kalke personal communication	6

months of July and August. The recurrence of hypoxia in summer is probably related to high salinity, which promotes water column stratification that isolates bottom water from the surface. During summer, respiration is at maximal rates due to high temperatures, promoting the consumption of a greater amount of oxygen than in other seasons. In addition, the greater sediment TOC found at

hypoxic stations may increase microbial respiration, thereby hastening depletion of oxygen.

The hypoxic area can shift over a period of a few days. For example, station 10 was hypoxic 2 wk prior to the spatial hydrographic survey in 1996 and in previous summers (Fig. 2); however, station 10 was normoxic at the time of the spatial and biological studies. Another example of a shift is station

TABLE 3. Species dominant at each station. Abundance (no. m^{-2}) and percent total abundance are in parentheses.

Stations	1st Dominant	2nd Dominant	3rd Dominant
2	*Polydora caulleryi* (6,429, 30%)	*Mediomastus ambiseta* (3,876, 18%)	*Tharyx setigera* (2,742, 13%)
6	*Mediomastus ambiseta* (3,025, 23%)	*Paleanotus heteroseta* (2,742, 21%)	*Polydora caulleryi* (1,324, 10%)
7	*Mediomastus ambiseta* (662, 50%)	*Streblospio benedicti* (378, 29%)	*Glycinde solitaria* (189, 14%)
10	*Streblospio benedicti* (662, 100%)	NA	NA
44	*Tharyx setigera* (4,066, 18%)	*Mediomastus ambiseta* (3,687, 16%)	Oligochaetes (2,742, 12%)
9	Oligochaeta (2,836, 75%)	*Streblospio benedicti* (567, 15%)	*Laeonereis culveri* (284, 8%)
14	Oligochaeta (189, 100%)	NA	NA
20	*Streblospio benedicti* (3,025, 86%)	*Mediomastus ambiseta* (189, 5%)	Megalops (189, 5%)
21	*Streblospio benedicti* (4,444, 98%)	Nemertea (95, 2%)	NA
33	*Streblospio benedicti* (662, 88%)	*Haploscoloplos fragilis* (95, 12%)	NA

TABLE 4. Community response to different hypoxia intensity categories. Hypoxic categories are based on the average environmental and community characteristics of stations falling within each category. DO = dissolved oxygen.

Hypoxia Intensity Category	DO (mg l⁻¹)	Biomass (g m⁻²)	Density (no. m⁻²)	No. Species (0.01 m⁻²)	No. Dominant Species (N1)	Dominant Species
1	>5	7.64	22,171	20	9.45	Codominance
2	4–5	3.30	7186	12	7.65	*Mediomastus ambiseta*
3	3–4	—	—	—	—	—
4	2–3	0.42	3144	3	1.63	*Streblospio benedicti*
5	1–2	0.01	189	1	1	Oligochaeta
6	0–1	—	—	—	—	—

TABLE 5. Estimated parameters for parametric logistic models of community response to dissolved oxygen concentrations.

Community Characteristic	M	a	c	R²	SE
Biomass	15	1.76	11,754.73	0.69	2.27
Abundance	29,291	2.49	183,418.45	0.76	5,573.86
Number of species	25	1.09	150.55	0.55	6.53
Hill's number	15	0.83	56.70	0.51	3.45

20, where dissolved oxygen concentration decreased from 4.01 mg l⁻¹ to 1.36 mg l⁻¹ in 2 d.

Several factors may be related to shifting of the areal extent of the hypoxic area. Horizontal advection and movement of water masses may account

for changing dissolved oxygen concentrations. Changes in respiration rates and oxygen utilization or photosynthesis that produces dissolved oxygen can also alter the equilibrium between ambient air and water oxygen concentrations.

The areal extent of the hypoxic zone was larger and more pervasive than previously thought (Fig. 6). During study design, hypoxia was thought to occur only at station 10 (Montagna and Kalke 1992) but was discovered to extend ~6.7 km westward during the 1996 spatial study. Chronic hypoxia was found in the southeast corner of Corpus
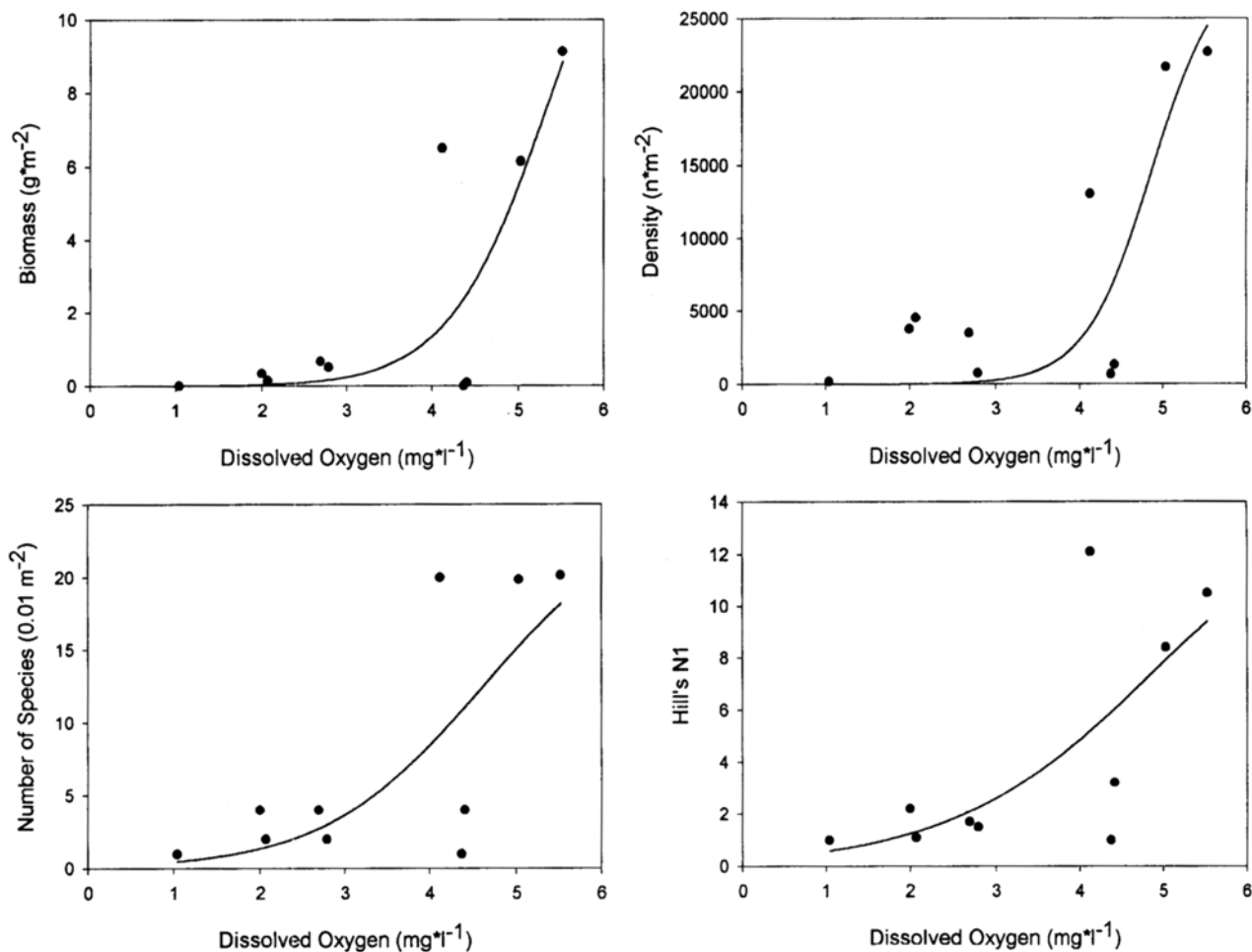
Fig. 9. Mathematical logistic models describing how dissolved oxygen concentrations influence characteristics of benthic communities: biomass, density, number of species, and Hill's Number. Model parameters as in Table 5.

Christi Bay (Fig. 6). In addition, two regions were identified as being intermittently hypoxic (Fig. 6): one extending west and the other north from the chronically hypoxic region.

The contribution of water column stratification and the decomposition of organic matter to the onset and persistence of hypoxia is well established (Boesch and Rabalais 1991; Rabalais et al. 1991; Justić et al. 1995; Wiseman et al. 1997; Rabalais et al. 1998). In the present study, southeast Corpus Christi Bay is stratified (Fig. 5), a relationship exists between low dissolved oxygen concentrations and water column stratification (Fig. 4), and the region stratified is also the hypoxic region (Fig. 6).

Water column stratification is unexpected in Corpus Christi Bay. The shallowness of the bay and lack of bottom depressions lead one to expect that it is well mixed (Armstrong 1987). Nevertheless, stratification has been demonstrated in the hypoxic region of Corpus Christi Bay, where average σ is 4.1‰ and can be as high as 7.2‰. The evidence of water column stratification in Corpus Christi Bay raises two questions: 1) Why isn't the water column mixed? and 2) Where is the high salinity bottom water coming from?

The general distribution of the high salinity bottom water mass indicates that it may be derived from hypersaline Laguna Madre water that is either pumped as cooling water by a power plant into Oso Bay to the west, or enters via the Intracoastal Waterway from the south. Surface evaporation, however, probably contributes to bottom hypersalinity and stratification to a greater extent than intrusion of Laguna Madre water (G. Ward personal communication). Evaporation is indicated by the inverse salinity profiles at normoxic stations (Fig. 3). The southeast corner of Corpus Christi Bay exhibits the least water movement of the entire bay (G. Ward personal communication) and is relatively stagnant (Powell et al. 1997). This part of the bay is in the lee of a barrier island, which inhibits wind forcing during the summer, and is, thus, subject to stagnation. Low circulation may also be related to low tidal forcing (G. Ward personal communication). In addition, the Corpus Christi Ship Channel has altered circulation such that flow vectors in the hypoxic region are the lowest in the entire bay system (Powell et al. 1997). The lack of mixing in conjunction with high evaporation leads to higher bottom-water salinity and stratification. This observation is supported by Livingston's (1996) study linking hypoxia in Apalachicola Bay with salinity and circulation alterations associated with the presence of artificial channels.

Although the hypoxic region is remote from potential nutrient sources (e.g., river inflow, sewage outfalls, or agriculture), organic matter enrich-

ment may also play a role in hypoxia. The long water-residence time (ca. 5.5 mo) and microbial activity may promote the onset and persistence of hypoxia. Stagnation in the hypoxic area (Powell et al. 1997) may lead to higher organic matter deposition rates than the normoxic area. Sediment TOC values at hypoxic stations are on average 54.8% higher than at normoxic stations. Biomass at hypoxic stations is 96% less than normoxic biomass, so TOC increases cannot be accounted for by increased benthic biomass. The average 54.8% increase in TOC at hypoxic stations is concordant with an average 54.8% decrease in dissolved oxygen concentrations and an average 52.2% decrease in percent saturation of oxygen at hypoxic stations. The difference between TOC averages at hypoxic and normoxic stations is only 0.4 wt %, and may be accounted for by instrument error ($\pm$ 10% of TOC value, or ca. 0.1 wt % in this case; E. Ingall, personal communication), differential rates of inorganic sedimentation, and/or natural variation in sediment composition. Greater TOC values in hypoxic stations indicate greater heterotrophic potential, but the amount of labile TOC is not known, so the relative role of organic matter in the onset and persistence of hypoxia is hypothetical.

Reduced macrobenthic community diversity and biomass as a result of hypoxia is consistent with findings by Dauer et al. (1992, 1993) in Chesapeake Bay. In the present study, macroinfaunal biomass was reduced by more than an order of magnitude under hypoxic conditions ($<$ 3 mg l^{-1}). Species abundance was also significantly lowered under hypoxic conditions. The loss of diversity appeared to be related to the loss of carnivorous omnivores that were present at normoxic stations (Table 2).

Streblospio benedicti and oligochaetes may be more tolerant of oxygen stress than other organisms and thus indicators of hypoxia. *Streblospio benedicti* was present at all stations except 2 and 14, but it dominated only in hypoxic stations 20, 21, and 33, as well as the previously hypoxic station 10. The other two hypoxic stations (stations 9 and 14) had the lowest average dissolved oxygen concentrations and were dominated by oligochaetes. *Streblospio benedicti* and oligochaetes are considered opportunistic species because they have r-selected life history traits (e.g., rapidly colonize recently disturbed niche space) (Dauer et al. 1992). As opportunists, they may be more capable than other species of taking advantage of the greater concentrations of TOC found at hypoxic stations. It is unlikely they are pioneering into newly defaunated territory because hypoxic disturbance is still occurring and abundance is low. It is more likely they are the remainder of the macrobenthic community better

adapted to tolerate low oxygen conditions. Even the normoxic community appears to be a stressed community. This may be due to hypersalinity or to previous hypoxic disturbance.

Benthic animals vary in ability to tolerate low oxygen levels. For example, certain bivalves and echinoderms can tolerate dissolved oxygen levels ranging from 0.5 mg l^{-1} to 1.0 mg l^{-1} for a period of a few days to weeks (Rosenberg et al. 1991). *Streblospio benedicti* tolerates hypoxic conditions for a period of 2 wk without mortality but dies within 55 h under anoxic conditions in the laboratory (Llansó 1991). The crustaceans *Crangon crangon* and *Carcinus maenas* can tolerate oxygen depletion for only 0.2–2 d whereas the lamellibranchs *Cardium edule* and *Mya arenaria* can persist for 2–7 d (Jørgensen 1980). The ability to withstand hypoxic conditions is related to a species' physiological response to changing environmental conditions. For example, *Capitella* species 1 responds to hypoxia by reducing growth rates (Forbes et al. 1994).

Some macroinfaunal organisms exhibit a behavioral response to hypoxic conditions. For example, the ophiuroid *Amphiura filiformis* leaves the protection of sediment when oxygen levels decline to 0.85 mg l^{-1} (Rosenberg et al. 1991). The threshold for behavioral response varies for different animals (Rosenberg et al. 1991). Many infauna move toward the sediment surface with onset of hypoxic conditions (Rosenberg et al. 1991). For example, ophiuroids emerged from the sediment as oxygen levels dropped below 1 mg l^{-1} (Rosenberg et al. 1991). Emergence of infauna during hypoxia can have serious consequences for the community. Under hypoxic conditions, guts of predator species contain a greater proportion of deep burrowing prey than during normoxic conditions (Pihl et al. 1992). Thus, sublethal effects of hypoxia may temporarily alter the energy flow of the ecosystem (Pihl et al. 1992).

Benthic effects of hypersalinity and hypoxia are potentially confounded. It is difficult to partition benthic effects arising from multiple stressors (e.g., pollution, hypoxia, and salinity variations). Bottom water at each station sampled was hypersaline (between 35‰ and 50‰). Average bottom salinity at hypoxic stations was 44.8‰, only 4.4‰ greater than the 40.4‰ average salinity of normoxic stations. Macrobenthic response to > 2 mg l^{-1} dissolved oxygen may be related to hypersalinity, and hypoxia and hypersalinity may have synergistic benthic effects.

DEFINING HYPOXIA

The most common definition for hypoxia is < 2 mg l^{-1} (Pavela et al. 1983; Pokryfki and Randall 1987; Llansó 1991; Dauer et al. 1992; Pihl et al.

1992; Rabalais et al. 1994; National Oceanic and Atmospheric Administration 1997). Other common definitions are < 2 ppm O_2 (Harper et al. 1981; Sanukida et al. 1984; Dauer et al. 1993) and < 2 ml O_2 l^{-1} (Josephson and Widbom 1988; Rosenberg et al. 1991; Tyson and Pearson 1991; Diaz and Rosenberg 1995). At 20‰ salinity, 25°C, and 1 atmosphere pressure, a dissolved oxygen concentration of 1 ppm = 0.7 ml l^{-1} = 1 mg l^{-1} = 32 μM = 62.5 μg at l^{-1} = 3% O_2 by volume = 14% saturation (Diaz et al. 1992). The trend produced in the quantitative community models (Fig. 9) indicates that macrobenthic response may begin at oxygen levels as high as 4–5 mg l^{-1} and is consistent with the National Oceanic and Atmospheric Administration (1997) definition of oxygen-related biological stress conditions (2–5 mg l^{-1}). The rate of community response to declining oxygen begins to approach zero at oxygen concentrations of roughly 3 mg l^{-1}, indicating this value may be a more appropriate definition of hypoxia for an estuarine hypersaline macrobenthic community than 2 mg l^{-1}. A definition of hypoxia as < 3 mg l^{-1} is roughly consistent with the < 2 ml l^{-1} hypoxia definition. The use of oxygen concentrations expressed in mg l^{-1} (mass volume) is encouraged for comparing study results, because the mass of a gas is not temperature or pressure sensitive as is the volume of a gas.

The parametric and nonparametric models (Fig. 9 and Table 4, respectively) are specific for the southern region of Corpus Christi Bay during summer and may reflect physiological and behavioral responses, community recovery (succession), or a combination of these processes. Movement of hypoxic bottom water could temporarily disturb the macrobenthic community, with the communities in varying stages of decline or recovery. The movement of hypoxic water mass could also lead to benthic communities receiving different frequencies of disturbance and result in variable responses of the benthic community. Hypersalinity could lead to an osmotically stressed community more susceptible to low oxygen conditions.

The nonparametric and parametric models are hypotheses requiring further testing. It would be interesting to conduct a study to detect differences between intensity levels and increasing hypoxic disturbance intensity. Such a study would provide general insight into the influence of disturbance intensity on communities while at the same time defining the influence dissolved oxygen plays in benthic community succession. Frequency of hypoxic disturbance may influence the relative importance of predation and asphyxiation, which results in declines of biomass, abundance, and diversity.

In Corpus Christi Bay, hypoxic events were as-

sociated with water column stratification in summer. Though stratification was not expected in shallow, wind-mixed bays, such as Corpus Christi Bay, it was observed where hypersaline bottom water was present in stagnant, warm conditions. The hypersaline bottom water is probably due to high surface evaporation coupled with low circulation in the southeast region of the bay. Another possible source of high salinity bottom water is the Laguna Madre, which may intrude into the bay via the Intracoastal Waterway or by pumping of hypersaline cooling water by a local power plant. Hypoxia had a significant effect on the macroinfaunal community. Community biomass was reduced by 1200%, and abundance and diversity were reduced by 500%. Community dominance shifted, such that *Streblospio benedicti* was dominant at dissolved oxygen levels of 2–3 mg l^{-1}, and oligochaetes were dominant at oxygen levels of 1–2 mg l^{-1}. Disturbance intensity can be nonparametrically and parametrically modeled using declining oxygen levels as a surrogate for hypoxia intensity. In the intensity model, biomass, density, and diversity dramatically declined with oxygen levels, beginning at 5 mg l^{-1}. At this oxygen level, community dominance began to shift as well. The rate of community response declined with declining oxygen concentrations indicating hypoxia should be defined as dissolved oxygen concentrations, < 3 mg l^{-1} rather than 2 mg l^{-1}, the traditional definition of hypoxia. A single national water quality standard for dissolved oxygen may not be appropriate for all estuarine areas, especially where climatic boundaries are crossed.

ACKNOWLEDGMENTS

LITERATURE CITED

ARMSTRONG, N. E. 1987. The ecology of open-bay bottoms of Texas: A community profile. United States Fish and Wildlife Report 85(7.12).

BREITBURG, D. L. 1992. Episodic hypoxia in Chesapeake Bay: Interacting effects of recruitment, behavior, and physical disturbance. *Ecological Monographs* 62(4):525–546.

BOESCH, D. F. AND N. N. RABALAIS. 1991. Effects of hypoxia on continental shelf benthos: comparisons between the New York Bight and Northern Gulf of Mexico, p. 27–34. *In* R. V.

Tyson and T. H. Pearson (eds.), Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publication No. 58. Geological Society Publishing House, Bath, United Kindgom.

COOPER, S. R. AND G. S. BRUSH. 1991. Long-term history of Chesapeake Bay anoxia. *Science* 254:992–996.

DAUER, D. M., M. W. LUCKENBACH, AND A. J. RODI, JR. 1993. Abundance biomass comparison (ABC method): Effects of an estuarine gradient, anoxic/hypoxic events and contaminated sediments. *Marine Biology* 88:507–518.

DAUER, D. M., A. J. RODI JR., AND J. A. RANASINGHE. 1992. Effects of low dissolved oxygen events on the macrobenthos of the lower Chesapeake Bay. *Estuaries* 15(3):384–391.

DIAZ, R. J., R. J. NEUBAUER, L. C. SCHAFFNER, L. PIHL, AND S. P. BADEN. 1992. Continuous monitoring of dissolved oxygen in an estuary experiencing periodic hypoxia and the effect of hypoxia on macrobenthos and fish. *Science of the Total Environment* Supplement 1992:1055–1068.

DIAZ, R. J. AND R. ROSENBERG. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology Annual Review* 33:245–303.

FAUCHALD, K. AND P. A. JUMARS. 1979. The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review* 17:193–284.

FORBES, T. L., V. E. FORBES, AND M. H. DEPLEDGE. 1994. Individual physiological responses to environmental hypoxia and organic enrichment: Implications for early soft-bottom community succession. *Journal of Marine Research* 52:1081–1100.

GAMENICK, I., A. JAHN, K. VOPEL, AND O. GIERE. 1996. Hypoxia and sulfide as structuring factors in a macrobenthic community on the Baltic Sea shore: Colonization studies and tolerance experiments. *Marine Ecology Progress Series* 144:73–85.

GAMENICK, I., J. RETHMEIER, A. RABENSTEIN, U. FISCHER, AND O. GIERE. 1997. Effects of anoxic and sulfidic conditions on cyanobacteria and macrozoobenthos in shallow coastal sediments of the Southern Baltic Sea. *Archiv für Hydrobiologie* 140(4):465–490.

GUNTER, G. 1942. Offatts Bayou, a locality with recurrent summer mortality of marine organisms. *The American Midland Naturalist* 28(3):631–633.

HARPER, D. E., JR., L. D. McKINNEY, R. R. SALZAR, AND R. J. CASE. 1981. The occurrence of hypoxic bottom water off the upper Texas coast and its effects on the benthic biota. *Contributions in Marine Science* 24:53–79.

JØRGENSEN, B. B. 1980. Seasonal oxygen depletion in the bottom waters of a Danish fjord and its effect on the benthic community. *Oikos* 34:68–76.

JOSEFSON, A. B. AND B. WIDBOM. 1988. Differential response of benthic macrofauna and meiofauna to hypoxia in the Gullmar Fjord basin. *Marine Biology* 100:31–40.

JUSTIĆ, D., N. N. RABALAIS, R. E. TURNER, AND Q. DORTCH. 1995. Changes in the nutrient structure of river-dominated coastal waters: Stoichiometric nutrient balance and its consequences. *Estuarine, Coastal and Shelf Science* 40:339–356.

KUO, A. Y., K. PARK, AND M. Z. MOUSTAFA. 1991. Spatial and temporal variabilities of hypoxia in the Rappahannock River, Virginia. *Estuaries* 14(2):113–121.

LIVINGSTON, R. J. 1996. Eutrophication in estuaries and coastal systems: Relationships of physical alterations, salinity, stratification, and hypoxia, p. 285–318. *In* F. J. Vernberg, W. B. Vernberg, and T. S. Siewicki (eds.), Sustainable Development in the Southeastern Coastal Zone. University of South Carolina Press, Columbia, South Carolina.

LLANSÓ, R. J. 1991. Tolerance of low dissolved oxygen and hydrogen sulfide by the polychaete *Streblospio benedicti* (Webster). *Journal of Marine Biology and Ecology* 153:165–178.

LUDWIG, J. A. AND J. F. REYNOLDS. 1988. Statistical Ecology. John Wiley and Sons, Inc., New York.

MANNINO, A. 1994. Effects of freshwater inflow and small scale spatial variation of macrobenthic community structure in Nueces Bay. M.s. Thesis, University of Texas, Austin, Texas.

MARTIN, C. M. AND P. A. MONTAGNA. 1995. Environmental assessment of LaQuinta Channel, Corpus Christi Bay, Texas. *Texas Journal of Science* 47(3):203–222.

McKINNEY, L. D. AND D. E. HARPER. 1980. The effects of hypoxia on the structure of benthic marine communities in the western Gulf of Mexico. *American Zoologist* 20(4):742 (abstract).

MONTAGNA, P. A. AND R. D. KALKE. 1992. The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces estuaries, Texas. *Estuaries* 15(3): 307–326.

MONTAGNA, P. A. AND R. D. KALKE. 1995. Ecology of infaunal Mollusca in South Texas estuaries. *American Malacological Bulletin* 11(2):163–175.

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (NOAA). 1997. NOAA's Estuarine Eutrophication Survey, Volume 4: Gulf of Mexico Region. Office of Ocean Resources Conservation Assessment, National Ocean Service, Silver Spring, Maryland.

OFFICER, C. B., R. B. BIGGS, J. L. TAFT, L. E. CRONIN, M. A. TYLER, AND W. R. BOYNTON. 1984. Chesapeake Bay anoxia: Origin, development, and significance. *Science* 223:22–27.

ORLANDO, S. P. JR., L. P. ROZAS, G. H. WARD, AND C. J. KLEIN. 1991. Analysis of Salinity Structure and Stability for Texas Estuaries. Strategic Assessment Branch, National Oceanic and Atmospheric Association, National Ocean Service, Rockville, Maryland.

PAVELA, J. S., J. L. ROSS, AND M. E. CHITTENDEN, JR. 1983. Sharp reductions in abundance of fishes and benthic macroinvertebrates in the Gulf of Mexico off Texas associated with hypoxia. *Northeast Gulf Science* 6(2):167–173.

PIHL, L., S. P. BADEN, R. J. DIAZ, AND L. C. SCHAFFNER. 1992. Hypoxia-induced structural changes in the diet of bottomfeeding fish and Crustacea. *Marine Biology* 112:349–361.

POKRYFKI, L. AND R. E. RANDALL. 1987. Nearshore hypoxia in the bottom water of the northwestern Gulf of Mexico from 1981 to 1984. *Marine Environmental Research* 22:75–90.

PORT OF CORPUS CHRISTI AUTHORITY. 1993. Phase II. Safeharbor Environmental Impact Statement. Port of Corpus Christi Authority, Corpus Christi, Texas.

POWELL, G., J. MATSUMOTO, AND W. L. LONGLEY. 1997. Effects of structures and practices on the circulation and salinity patterns of the Corpus Christi Bay National Estuary Program Study Area. CCBNEP-19. Texas Natural Resources Conservation Commission, Austin, Texas.

RABALAIS, N. N., R. E. TURNER, W. J. WISEMAN, JR., AND D. F. BOESCH. 1991. A brief summary of hypoxia on the northern Gulf of Mexico continental shelf: 1985–1988, p. 35–47. In R. V. Tyson and T. H. Pearson (eds.), Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publication No. 58. Geological Society Publishing House, Bath, United Kingdom.

RABALAIS, N. N., R. E. TURNER, W. J. WISEMAN, JR., AND Q. DORTCH. 1998. Consequences of the 1993 Mississippi River Flood in the Gulf of Mexico. *Regulated Rivers: Research & Management* 14:161–177.

RABALAIS, N. N., W. J. WISEMAN, JR., AND R. E. TURNER. 1994. Comparison of continuous records of near-bottom dissolved oxygen from the hypoxia zone along the Louisiana coast. *Estuaries* 17(4):850–861.

RANAISINGHE, J. A., S. B. WEISBERG, D. M. DAUER, L. C. SCHAFFNER, R. J. DIAZ, AND J. B. FRITHSEN. 1994. Chesapeake Bay Benthic Community Restoration Goals. United States Environmental Protection Agency, Chesapeake Bay Program, Annapolis, Maryland. CBP/TRS 107/94.

ROSENBERG, R. 1980. Effects of oxygen deficiency on benthic macrofauna in fjords, p. 499–514. In H. J. Freeland, D. M. Farmer, and C. D. Levings (eds.), Fjord Oceanography. Plenum Publishing Company, New York.

ROSENBERG, R., B. HELLMAN, AND B. JOHANSSON. 1991. Hypoxic tolerance of marine benthic fauna. *Marine Ecology Progress Series* 79:127–131.

RUPPERT, E. E. AND R. D. BARNES. 1994. Invertebrate Zoology, 6th edition. Saunders College Publishing, Fort Worth, Texas.

SANFORD, L. P., K. G. SELLNER, AND D. L. BREITBURG. 1990. Covariability of dissolved oxygen with physical processes in the summertime Chesapeake Bay. *Journal of Marine Research* 48: 567–590.

SANTOS, S. L. AND J. L. SIMON. 1980. Response of soft-bottom benthos to annual catastrophic disturbance in a south Florida estuary. *Marine Ecology Progress Series* 3:347–355.

SANUKIDA, S., H. OKAMOTO, AND M. HITOMI. 1984. Alternation of pollution indicator species of macrobenthos during stagnant period in Eastern Hiuchi Sound. *Bulletin of the Japanese Society of Scientific Fisheries* 50(4):727–728.

SAS INSTITUTE INC. 1985. SAS* Procedures Guide for Personal Computers, Version 6 Edition. SAS Institute Inc., Cary, North Carolina.

STEPHEN, A. C. AND S. J. EDMONDS. 1972. The Phyla Sipuncula and Echiura. Trustees of the British Museum, London.

TURNER, R. E. AND N. N. RABALAIS. 1999. Suspended particulate and dissolved nutrient loadings to Gulf of Mexico estuaries. In T. Bianchi, J. Pennock and R. Twilley (eds.), Biogeochemistry of Gulf of Mexico Estuaries. John Wiley & Sons, New York.

TYSON, R. V. AND T. H. PEARSON. 1991. Modern and ancient continental shelf anoxia: an overview, p. 1–24. In R. V. Tyson and T. H. Pearson (eds.), Modern and Ancient Continental Shelf Anoxia. Geological Society Special Publication No. 58. Geographical Society Publishing House, Bath, United Kingdom.

WARD, G. H., JR. 1980. Hydrography and circulation processes of Gulf estuaries, p. 183–215. In P. Hamilton and K. B. MacDonald (eds.), Estuarine and Wetland Processes. Plenum Publishing Company, New York.

WISEMAN, W. J., N. N. RABALAIS, R. E. TURNER, S. P. DINNEL, AND A. MACNAUGHTON. 1997. Seasonal and interannual variability within the Louisiana coastal current: Stratification and hypoxia. *Journal of Marine Systems* 12:237–248.

UNITED STATES DEPARTMENT OF COMMERCE, NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION, NATIONAL OCEAN SERVICE. 1986. Corpus Christi Bay, Chart 11309, 29th edition, November 15, 1986.

SOURCES OF UNPUBLISHED MATERIALS

INGALL, E. University of Texas, Marine Science Institute, Port Aransas, Texas, personal communication.

WARD, G. University of Texas, Center for Research in Water Resources, Austin, Texas, personal communication.