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Direct and indirect effects of hypoxia on benthos in Corpus Christi Bay, Texas, U.S.A.

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Abstract

Hypoxia (low oxygen conditions) has been found in the southeastern region of Corpus Christi Bay, Texas, U.S.A. every summer since 1988. The objectives of the current study were to determine direct and indirect effects of hypoxia on macrofauna. Direct physiological effects of hypoxia include reduction of benthic abundance, biomass, diversity, species richness and species evenness because of physiological intolerance. Indirect ecological effects of hypoxia include predation of emerging benthic fauna from the sediment. Macrofaunal community characteristics were compared vertically within sediments in caged and uncaged sediment samples in hypoxic and normoxic areas. Cage effects were determined with partial cages, which had reduced flow and no predator exclusion. Dissolved oxygen concentrations during the experiment was monitored in water column profiles and continuous measurement of bottom water in the hypoxic and normoxic areas. Hypoxia in Corpus Christi Bay in 1999 occurred as transient events, many of which were of short duration (less than 1 h) and moderate intensity (around 2 mg l^{-1}). The macrobenthic community characteristics (i.e., abundance, biomass, species richness, diversity, and evenness) were directly affected by hypoxia as indicated by depressed levels and few deeper-dwelling organisms in the hypoxic area. Community structure was also different between the hypoxic and normoxic areas because of loss of species (presumably due to intolerance to low oxygen) in the hypoxic areas. Benthic invertebrates were found primarily in the surface in the hypoxic area, but there was no significant indication of indirect effects, i.e., increased predation pressure in the hypoxic area. The increased exposure to predation risk may be mitigated by predator avoidance of hypoxic areas. In conclusion, hypoxia in Corpus Christi Bay has negative direct effects on benthic organisms, but no indirect effects, such as increased predation pressure. The most significant finding is the interaction between hypoxia and vertical distributions of infauna, which drive hypoxia intolerant organisms to the surface and out of sediments.

Keywords: Caging experiment; Dissolved oxygen; Gulf of Mexico; Infauna; Macrobenthos

1. Introduction

Hypoxia is a common estuarine phenomenon defined as dissolved oxygen (DO) concentrations below 2 mg l^{-1} (Dauer et al., 1992). Hypoxia in Corpus Christi Bay, Texas was first documented in 1988 (Montagna and Kalke, 1992) and later confirmed to reoccur every summer (Martin and Montagna, 1995; Ritter and Montagna, 1999). In Corpus Christi Bay, hypoxia is thought to be a result of salinity stratification due to the high temperatures, evaporation, and rainfall occurring in summer (Ritter and Montagna, 1999).

Hypoxia is a serious disturbance because few animals can tolerate the physiological stress of extended

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exposure to low oxygen concentrations (Diaz and Rosenberg, 1995). Hypoxia in Corpus Christi Bay is correlated to about a 10 fold reduction in benthic standing stock and diversity (Ritter and Montagna, 1999). Direct effects of hypoxia include reduced benthic abundance and biomass (Dauer et al., 1992), avoidance by mobile epifauna, emergence of infauna, physical inactivity and death (Tyson and Pearson, 1991; Diaz et al., 1992). Indirect effects of hypoxia on benthos include predation of emerging benthic fauna from the sediment (Phil et al., 1992). The degree to which it is mainly direct or indirect effects that are responsible for the reduced benthic standing stocks is relatively unknown. For example, could hypoxia cause a change in vertical distributions of infauna relative to normoxic areas? Could this increase predation rates on infauna? For example, community change during hypoxic periods has been observed in Corpus Christi Bay, but it is unknown how much of the change is due to direct or indirect effects.

The goal of the study was to determine the direct and indirect effects of hypoxia on the benthos in Corpus Christi Bay, Texas. This was achieved by testing the following hypotheses: 1) Hypoxia reduces macrobenthic abundance, biomass, and diversity, 2) Predation reduces macrobenthic abundance, biomass, and diversity, 3) Predation and hypoxia together yield a greater reduction of macrobenthic abundance, biomass, and diversity than either alone, and 4) hypoxia causes macrobenthos to move vertically to the surface sediments. Hypotheses were tested by comparing depth distributions of macrofauna in caged and uncaged sediment samples in a hypoxic and normoxic areas. Cage effects were determined with partial cages, which had reduced flow and no predator exclusion. A bay-wide survey of hydrographic parameters, and continuous monitoring at the hypoxic and normoxic areas were also conducted to determine the real-time values and trends of hypoxia during the experiments.

2. Methods

2.1. Study location

Corpus Christi Bay, Texas, U.S.A. is a shallow (~3.2 m; Orlando et al., 1991), almost enclosed bay with a level bottom (Fig. 1). Corpus Christi Bay is microtidal and subject to strong meteorological forcing. Like other south Texas bays, it is characterized by broad climate variations that alternate between wet and dry cycles (Montagna and Kalke, 1995).

2.2. Hypoxia effects study design

An experiment was conducted to determine if direct or indirect effects of hypoxia were responsible for responses of macrofaunal community characteristics, e.g., abundance, biomass, and diversity. A four-way, partially hierarchical, experiment was designed to determine the direct and indirect effects of hypoxia (Fig. 2). The two main treatments of the experimental design were oxygen area and caging main effects. In addition samples were collected three and six weeks

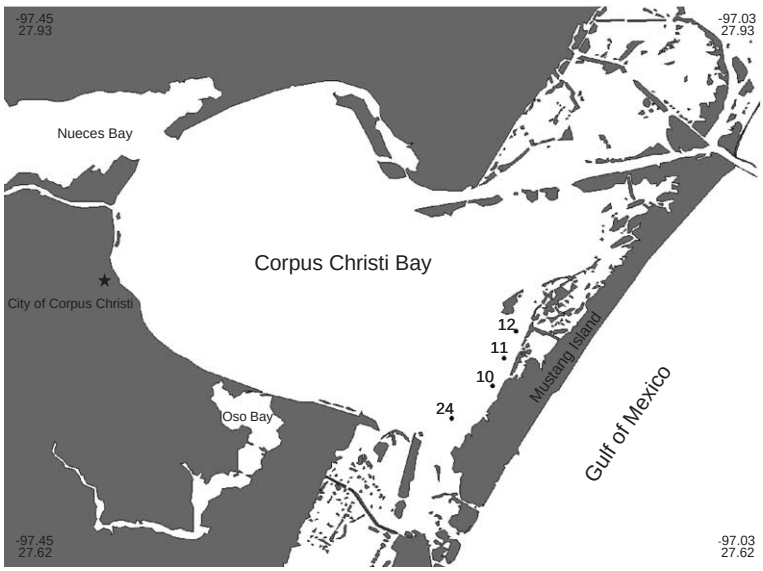

Fig. 1. Map of stations in Corpus Christi Bay, Texas, U.S.A.

Date	23 July 1999																							
Area	Hypoxic												Normoxic											
Station	24						10						24						10					
Plot	1			2			3			4			5			6			7			8		
Cage	C	U	P	C	U	P	C	U	P	C	U	P	C	U	P	C	U	P	C	U	P	C	U	P
Section	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10

Fig. 2. Experimental design of hypoxia effects study begun on 30 June 1999. The design is a four-way, partially hierarchical analysis of variance. Main effects are sampling dates (1 = 25 July 1999, 2 = 17 August 1999), oxygen area (Hypoxic or Normoxic), cage treatment (C = caged, U = Uncaged, P = partial cage), and core sections (0–3, 3–10 cm). The nested, hierarchical replicates are stations within areas and plots within area-station cells. Two replicate core samples were taken in each cell. Just one sampling date is shown, the same box would be repeated for the second date.

after experiment initiation, so sampling date is the third main fixed effect. All sediment samples were split into two vertical (surface and bottom) sections, so section depth is the fourth main effect. The oxygen treatment area consisted of stations inside (hypoxic) and outside (normoxic) the region of seasonal hypoxia. The hypoxic and normoxic regions are large and many previously sampled stations are known to represent the region.

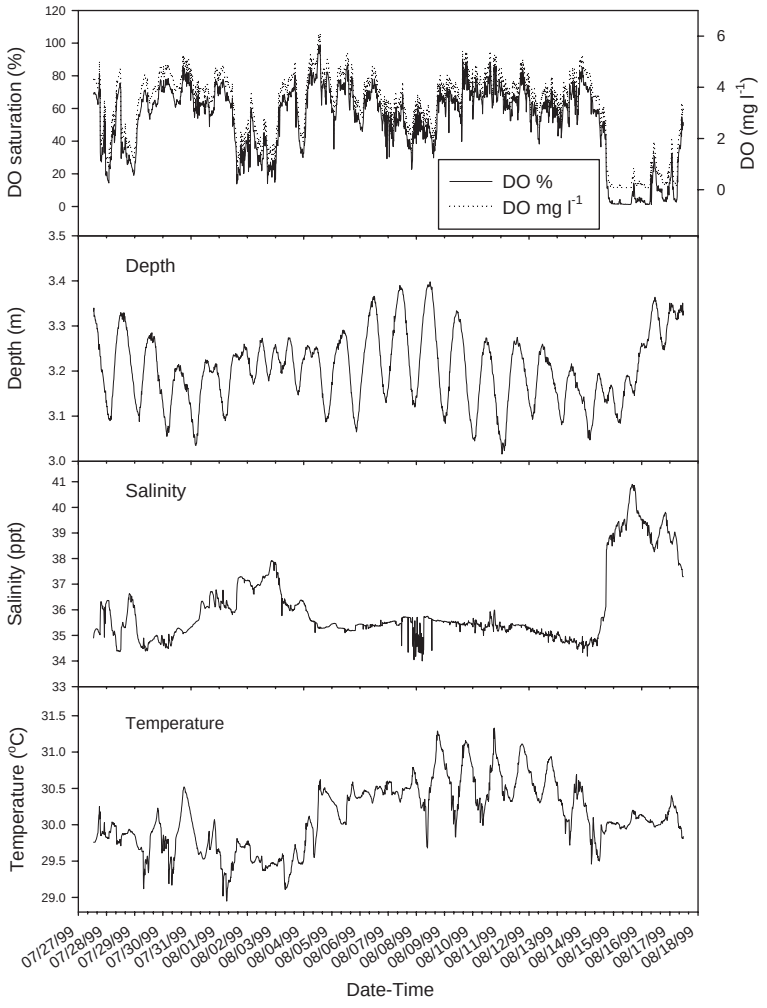

Fig. 3. Continuous hydrographic data recorded at station 10 from 27 July through 18 August 1999.

Because just two replicate stations were chosen, this is a random nested variable within each oxygen treatment area. The historically hypoxic stations chosen were 10 and 24 (2.99 km apart), and the historically normoxic stations chosen were 11 and 12 (1.79 km apart). The second treatment consisted of three cage types: uncaged (ambient), caged (predator exclusion), and partially caged (hydrodynamic control) sediments. Two plots were created within each station and a full suite of cage types was emplaced within each plot, thus cage treatments were replicated within stations. The replicate plots were arranged at equidistant intervals around the circumference of a 5 m circle. Cage treatments were randomly assigned to one of six positions. Cages were 1 m H 1 m M 0.5 m high. The partial cage was the same as the whole cage with half of each side cut out. This cage reduces flow, but does not affect the distribution of mobile predatory fish and hence is a suitable cage control. The experiment was set up on 30 June 1999 and samples were taken on two dates (23 July 1999 and 17 August 1999) during the period when hypoxia occurs in Corpus Christi Bay (Ritter and Montagna, 1999). On each sampling date, two samples were taken from each of the cage treatments. Every sample was split into two vertical sections for a total of 192 samples (=2 dates H 2 areas H 2 stations H 2 plots H 3 cages H 2 replicates H 2 sections). The statistical model describing the experiment consists of four treatments (date, oxygen area, cage, and section), two fully nested forms of replication (stations and plots), and samples within cage-plots. Thus, there are four replicates for each cell: the two samples from a cage, which are pseudoreplicates, from each of the two plots, which are the true replicates. The experimental design is represented as a four-way analysis of variance (ANOVA), two-plot partially hierarchical model (Fig. 2).

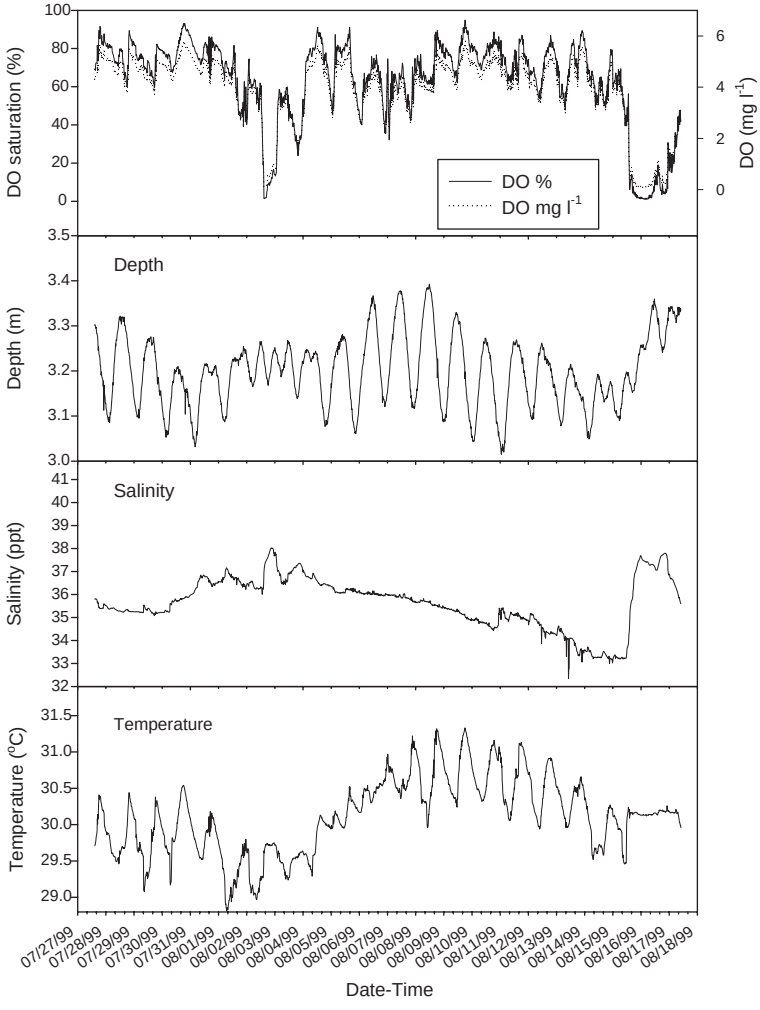

Fig. 4. Continuous hydrographic data recorded at station 11 from 27 July through 18 August 1999.

2.3. Macrobenthos sampling and analysis

Macrofauna were sampled with a 6.7-cm diameter core and sectioned at 0–3 and 3–10 cm depth intervals. All samples were taken by scuba diver. 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, samples were dried for at least 24 h at 55 EC and weighed. Before drying, mollusks were placed in 2 N HCl for 1 to 5 min to dissolve the carbonate shells, and then washed.

Prior to statistical analysis, abundance and biomass data were transformed with natural logarithm transformations $\ln(n\ m^{-2}+1)$ and $\ln(g\ m^{-2}+1)$. The species data from both replicates and both sections were pooled by plot (i.e., each replicate cage) prior to calculating diversity so that sample sizes were larger than just one partial sediment core. Diversity and evenness indices were calculated using the following formulas (Ludwig and Reynolds 1988): Species richness (S) is a raw measure of diversity and is the total number of species for each pool. Shannon's diversity index (HN) is a measure of both diversity and evenness and is calculated as $HN=E\ (p_i \ln p_i)$, where $p_i=n_i/n$ (n_i=abundance of species i, and n=total abundance). Pielou's evenness index was calculated as $J'=H'/\ln(S)$.

Statistical analysis was conducted with ANOVA, using SAS 8.01 (SAS Institute, Inc., 1989). Using the RANDOM statement in the general linear model (GLM) procedure forces SAS to calculate expected mean squares and correct F-values for mixed models with fixed and random effects. Post hoc differences among sample means were calculated using the Tukey test. The distribution of the residuals from the GLM was analyzed using the UNIVARIATE procedure to check for normality. The log transformed data fit a normal distribution better than the untransformed data. Community characteristics analyzed were abundance, biomass, species richness (S), Shannon diversity to the base e (H'), and Pielou's evenness (J'). Macrofauna data reported in the Results Section are detransformed from the natural logarithm mean values. Power of the ANOVA to detect change was calculated using formulas given in Kirk (1982).

Community structure of macrofauna species was analyzed by multivariate methods. Species data were pooled by date-area-cage treatment and log transformed prior to analysis. Ordination of samples was performed using the non-metric multidimensional scaling (MDS) procedure described by Clarke and Warwick (2001) and implemented in Primer software (Clarke and Gorley, 2001). The software was used to create a Bray–Curtis similarity matrix among all samples and then a non-

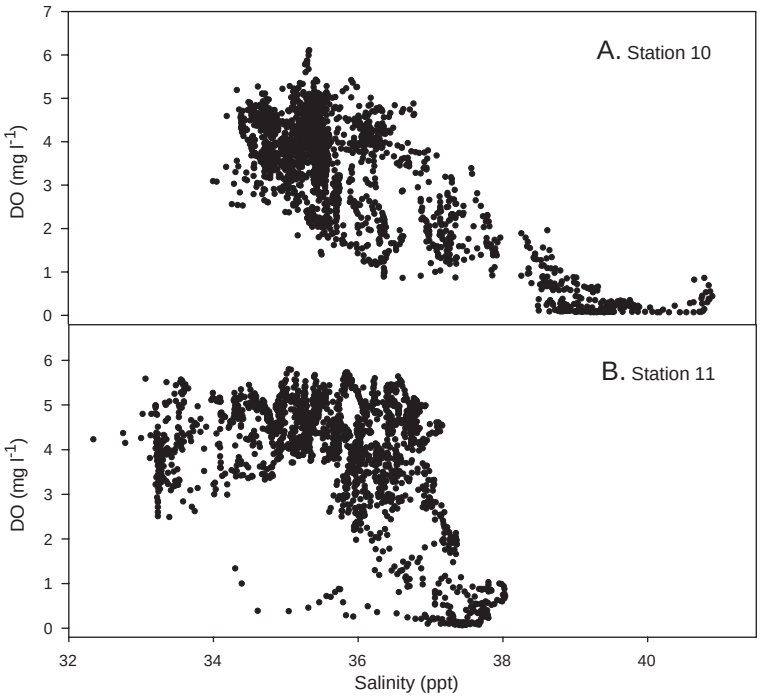

Fig. 5. Relationship between salinity and dissolved oxygen based on all continuos data taken between 27 July and 18 August 1999 at hypoxic station 10, and normoxic station 11.

parametric multivariate plot of the spatial relationship among the samples. A hierarchical cluster analysis was preformed on the similarity matrix using the group average technique. A cluster analysis determines and ranks the similarities of community structures.

2.4. Oxygen monitoring

Water column hydrographic profiles at all four stations were determined seven times over the course of the study period. A Hydrolab 4000 multiparameter sonde was used to measure salinity, temperature, dissolved oxygen, and depth from surface to bottom at 0.5 m intervals.

Continuous measurements of dissolved oxygen, salinity, and temperature were collected at two stations: one hypoxic station 10 and one normoxic station 11, which were 1.80 km apart. These two stations are adjacent and were thought to represent the boundary conditions between the normoxic and hypoxic areas. The continuous data were collected via YSI 600 XLM monitors that were attached to semi-permanent, low-relief moorings. Monitors were located using differential GPS (global positioning system) equipment, deployed and retrieved by divers. Data was collected between 27 July 1999 and 18 August 1999.

3. Results

3.1. Dissolved oxygen conditions

During the summer of 1999, continuous hydrographic monitoring of bottom conditions at hypoxic station 10 (Fig. 3) and normoxic station 11 (Fig. 4) revealed hydrographic similarities. Between 1 August 1999 and 3 August 1999, salinity increased roughly 2 ppt at both stations, and then decreased. On 14 August 1999, salinity at station 10 increased 4 ppt over approximately half a day, and ultimately increased a total of 6 ppt before declining again. At station 11, salinity increased approximately 4 ppt over the same time frame. Both periods of increased salinity were accompanied by hypoxia at both stations, although it was more intense at station 10.

Table 1
Observed hypoxia events from continuous recordings during summer 1999 at stations 10 and 11

Begin		End		Duration of hypoxia (h)	
Date	Time	Date	Time	≤ 2 mg/l	≤ 1 mg/l
A) Hypoxic station 10					
27 July	19:01	27 July	20:01	1	0
27 July	20:46	27 July	20:46	<0.25	0
27 July	23:16	28 July	04:01	4.75	0.75
28 July	12:31	28 July	12:31	<0.25	0
28 July	16:46	29 July	01:01	8	0
01 August	14:46	01 August	19:01	4	0.25
01 August	19:31	01 August	22:16	2.25	0
02 August	01:01	02 August	02:16	0.75	0
02 August	08:46	02 August	13:31	4.5	0
02 August	17:01	03 August	00:31	7.5	0.25
03 August	23:01	03 August	23:31	0.5	0
06 August	23:01	06 August	23:01	<0.25	0
07 August	01:01	07 August	01:01	<0.25	0
07 August	20:01	07 August	20:46	0.75	0
08 August	14:01	08 August	14:01	<0.25	0
08 August	14:46	08 August	14:46	<0.25	0
14 August	17:46	17 August	17:16	61.5	54.5
Hypoxic Total				97	55.75
B) Normoxic station 11					
02 August	13:46	03 August	02:01	12.25	10.25
03 August	17:31	03 August	18:01	0.5	0
03 August	18:31	03 August	21:16	2.75	0
07 August	01:31	07 August	01:31	<0.25	0
15 August	13:46	17 August	04:46	39.0	32.0
17 August	05:31	17 August	05:31	<0.25	0
17 August	06:16	17 August	06:31	0.25	0
Normoxic Total				55.25	42.25

Dissolved oxygen and temperature follow a diel cycle over the course of a day (Figs. 3 and 4) and may fluctuate with the tide. Salinity does not exhibit such a cycle, but when the tidal signature broke down between 1 August 1999 and 5 August 1999, bottom salinity increased. Dissolved oxygen does not appear to be directly related to temperature or water depth at either station. Dissolved oxygen concentration appears to be directly related to bottom salinity over the ranges 34–41 ppt at station 10 (Fig. 5A), and 35–38 ppt at station 11 (Fig. 5B).

Seventeen separate instances of hypoxia were observed at station 10, and seven at station 11 (Table 1). The duration of 10 instances at station 10 were an hour or less; the duration of four instances at station 11 were an hour or less. At station 10, hypoxia was recorded for a total of 97 h, 55.75 of which D.O. ≤ 1 mg l^{-1}. At station 11, hypoxia was recorded for a total of 55.25 h, 42.25 of which D.O. ≤ 1 mg l^{-1}. The net effect of the oxygen conditions was that station 10 was hypoxic as expected, but station 11 was simply less hypoxic rather than normoxic. Although station 11 is referred to normoxic below, this designation is based on historical sampling because it was actually, just less hypoxic during the course of the current study.

Both sampling areas exhibited water column stratification over the study period (Fig. 6). The stratification was more intense at the hypoxic area than the normoxic area as indicated by steeper slopes of the gradients in salinity and dissolved oxygen. The average change in salinity from top to bottom was only 0.5 ppt in the normoxic area, but 1.5 ppt in the hypoxic area. Dissolved oxygen declined more rapidly with depth at the hypoxic area relative to the normoxic area. The bottom water dissolved oxygen average concentration was only 0.4 mg l^{-1} lower in the hypoxic area than in the normoxic area during the current sampling.

3.2. Macrobenthos community effects

Standing Stocks (abundance and biomass) did not differ significantly between replicate stations or plots, nor were there triple or quadruple interactions (Table 2). Therefore, this complex ANOVA is relatively easy to interpret. The ANOVA is also powerful to detect change. Power was calculated for the four main effects dates, areas, cages, and sections at the alpha level of 0.05. The power for biomass of the sampling dates test was low at 0.40, but the other three were high at 0.99. For abundance the power was low for dates and cages at 0.3, but high for areas and sections at 0.99. Both abundance and biomass were higher in the normoxic

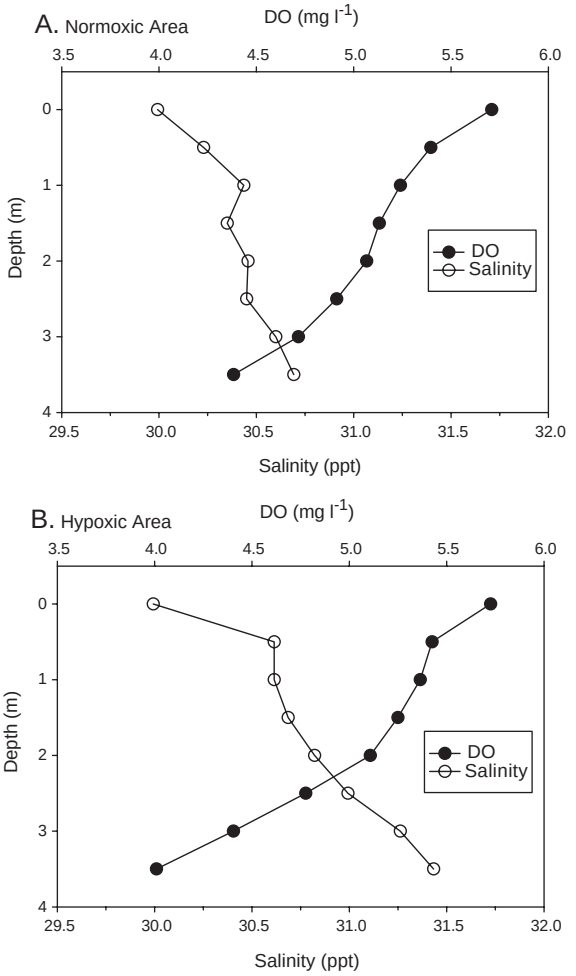

Fig. 6. Profiles of average salinity and dissolved oxygen in two areas over seven sampling periods.

areas than hypoxic areas (Table 3), but only biomass was significant (Table 2). The biomass in cages was significantly different, but abundance was not different. The average detransformed biomass to a depth of 10 cm in cages was 2.70 g m^{-2}, increased 19% to 3.21 g m^{-2} in partial cages, and increased 72% in uncaged plots to 4.64 g m^{-2}, but only caged and uncaged biomass were significantly different (Tukey test). The most significant difference is between section depths (Table 2). The average detransformed abundance in surface sediments (0–3 cm depth) was 6477 n m^{-2}, and it increased 172% to 17,606 n m^{-2} in the bottom section (3–10 cm depth). The average detransformed biomass in surface sediments (0–3 cm depth) was 0.48 g m^{-2}, and it increased 8 fold to 4.31 g m^{-2} in the bottom section (3–10 cm depth).

The most interesting tests are the double interactions between area and cage and area and sections because if

Table 2
Significance of experimental effects on macrobenthic abundance and biomass

ID	Source	*df*	EMS	Abundance		Biomass	
				F value	*P*	*F* value	*P*
1	Date	1	1/18	3.5	0.0631	0.46	0.4984
2	Area	1	2/16	7.39	0.1128	81.94	0.0120
3	Date*area	1	3/18	0.13	0.7147	0.12	0.7343
4	Cage	2	4/18	0.46	0.6349	3.27	0.0405
5	Date*cage	2	5/18	2.03	0.1342	1.70	0.1868
6	Area*cage	2	6/18	1.95	0.1457	2.65	0.0739
7	Date*area*cage	2	7/18	0.06	0.9452	0.08	0.9262
8	Section	1	8/18	44.48	<0.0001	170.48	<0.0001
9	Date*section	1	9/18	3.04	0.0830	6.59	0.0112
10	Area*section	1	10/18	7.94	0.0054	14.88	0.0002
11	Date*area*section	1	11/18	0.12	0.7314	2.27	0.1335
12	Cage*section	2	12/18	0.28	0.7574	4.26	0.0158
13	Date*cage*section	2	13/18	1.15	0.3180	2.17	0.1180
14	Area*cage*section	2	14/18	0.15	0.8588	1.00	0.3698
15	Date*area*cage*section	2	15/18	0.21	0.8080	0.05	0.9495
16	Station (area)	2	16/17	0.88	0.4818	0.24	0.7993
17	Plot (area station)	4	17/18	1.81	0.1288	0.78	0.5408
18	Error	162					

Abbreviations: ID=identification row number for source, *df*=degrees freedom, EMS=expected mean square sources with *F*-test ID quotient, (*P*)=*p*-value.

significant they represent differences in ecological processes between the normoxic and hypoxic areas. There were significant differences for abundance and biomass for the area*section interactions, but not for the area*cage interaction (Table 2). The lack of significance for the area*cage interaction means there are no differences between the two sites in ecological processes affected by the cages. In contrast, the significant area*section interaction indicates that there are many more deeper dwelling organisms in the normoxic area than the hypoxic area (Fig. 7). In the normoxic area, abundance increased 277% from 6039 to 22,792 n m^{-2} and in the deeper section relative to the surface section, and biomass increased 1110% from 0.48 to 5.81 g m^{-2}.

Table 3
Mean community characteristics for area and caging main effects to a depth of 10 cm

Treatment	Abundance	Biomass	*S*	H′	J′
Hypoxic	15,384	2.40*	14.0	1.69*	0.65
Normoxic	25,472	4.82*	16.8	1.88*	0.67
Caged	20,025	2.70*	15.2	1.78	0.66
Partial cage	19,324	3.21	15.4	1.81	0.67
Uncaged	20,047	4.64*	15.4	1.77	0.65

Abundance (n m^{-2}) and biomass (g m^{-2}) values are detransformed from log values. Abbreviations and units: *S*=species richness (n 70 cm^{-2} to a depth of 10 cm), H′=Shannon's diversity index, and J′=Pielou's evenness index, asterisk (*)=significant Tukey difference.

In contrast, at the hypoxic site, there was only an 80% increase in abundance from 6915 to 12,421 n m^{-2} and 483% increase in biomass from 0.48 to 2.80 g m^{-2} in the deeper section relative to the surface section.

The only other significant interaction of interest is between areas and sections (Table 2). This interaction was only significant for biomass, but it indicates that there is more biomass in deeper dwelling sediments in uncaged plots relative to cages and partial cages than expected (Fig. 8). The interaction is mainly due to change in the caged sample. The caged sample had only 5.7 times more biomass in the deeper section than in the surface. In contrast, the deeper sediments of partial cage samples had 10 times more biomass and the uncaged samples had 12 times more biomass than surface samples.

For species analysis, the sections and replicates within cage-plots were pooled to increase sample size and avoid artifacts due to small sample sizes. Thus, there are no section or plot effects for the species analyses (Table 4). There were no significant differences between replicate stations for richness (*S*), diversity (H′) or evenness (J′). There were no significant differences between any main effects and evenness. There was significantly more richness (16.1) in July than in August (14.6) and more diversity (1.9) in July than August (1.7). There were significant differences between areas for diversity, but richness was barely non-significant. The normoxic area had higher diversity (1.9) than the hypoxic area (1.7).

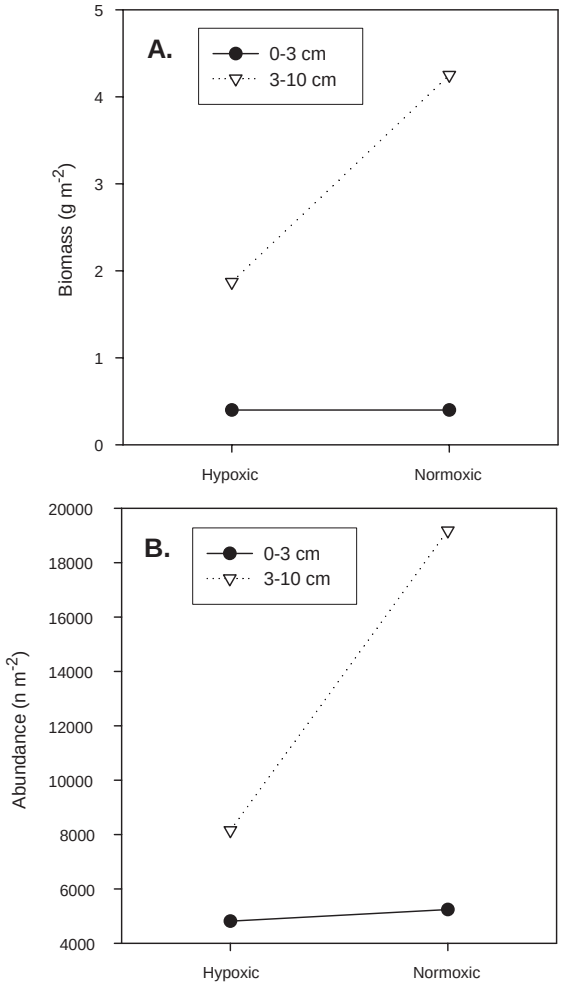

Fig. 7. Interaction between areas and core section depths for A) macrofauna abundance and B) macrofauna biomass.

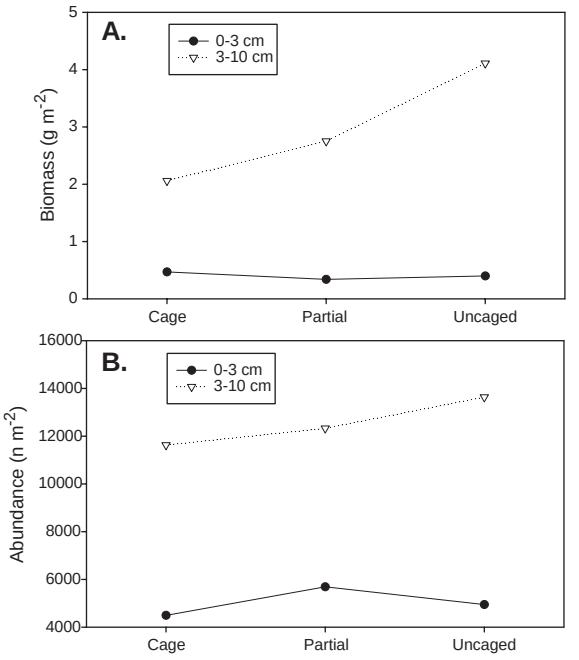

Fig. 8. Interaction between cage treatments and core section depths for A) macrofauna abundance and B) macrofauna biomass.

There was a significant interaction for diversity between area and cage treatments (Table 4). The interaction was mainly due to differences in the cage samples (Fig. 9). Diversity was much lower in the caged samples of the hypoxic zone (1.5) than in the caged normoxic zone (2.0). In contrast, uncaged and partial caged samples had similar diversity in both areas, averaging (1.8).

Multivariate analysis by MDS reveals slightly different community structures for hypoxic and normoxic stations (Fig. 10). There was only a little overlap between two samples from the hypoxic area and all samples from normoxic area. There was also greater variability, or dispersion, among hypoxic stations normoxic stations. Community structure was not different on the basis of sampling dates, stations within an oxygen area, or caging treatments.

A total of 59 species were found (Table 5). Community structure of the normoxic stations was characterized by many individuals of *Polydora caulleryi* and *Mediomastus ambiseta*, and fewer of *Streblospio benedicti*. The community structure of the hypoxic stations was characterized dominance of *S. benedicti*. Although not a dominant species, *Phoronis architecta* was 10 times more prevalent in the hypoxic area than normoxic area. Eleven species were unique to the hypoxic area, and 10 species were unique to the

Table 4
Significance of experimental effects on macrobenthic community diversity based on pooled replicates and core sections within a plot

ID	Source	*df*	EMS	*S* (*P*)	H′ (*P*)	J′ (*P*)
1	Date	1	1/9	0.0339	0.0441	0.2310
2	Area	1	2/3	0.0595	0.0109	0.4125
3	Station (area)	2	3/9	0.3626	0.9395	0.6345
4	Cage	2	4/9	0.9446	0.8914	0.8382
5	Date*area	1	5/9	0.3171	0.1895	0.3770
6	Area*cage	2	6/9	0.1654	0.0354	0.0944
7	Date*cage	2	7/9	0.9052	0.3162	0.4160
8	Date*area*cage	2	8/9	0.9858	0.8023	0.7924
9	Error	34				

Abbreviations: ID = identification row number for source, *df* = degrees freedom, EMS = expected mean square sources with *F*-test quotient, (*P*) = *p*-value, *S* = species richness, H′ = Shannon's diversity index, and J′ = Pielou's evenness index.

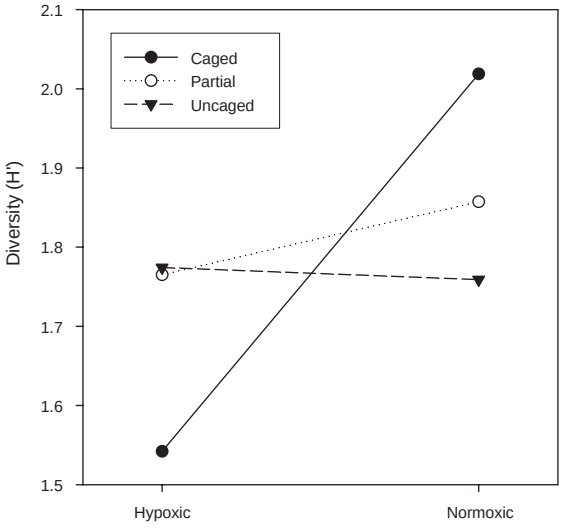

Fig. 9. Interaction between cage treatments and area for macrofauna diversity.

normoxic area, but only one or two individuals of these rare species were found. *Tharyx setigera* and *Gyptis vittata* were found in equal abundance in both areas. The predatory nermertines were more than twice as abundant in the normoxic area than the hypoxic area.

Most species, except *S. benedicti*, were more abundant in deeper sediments of the normoxic area (Table 5). This was especially true of the dominant species *P. caulleryi* and also *T. setigera*. Where as the surface 3 cm had similar numbers of individuals, there was nearly twice as many individuals in the deeper sediments of the normoxic area than in the hypoxic area. The surface 3 cm of the normoxic area had less species (32) than the deeper 3–10 cm sediment (38 species), but the opposite trend occurred in the hypoxic area where there were 38 species in the surface and 34 species in the deeper sediments. The deeper sections of the normoxic and hypoxic areas were most similar, sharing 78% of the species in common. The surface samples shared only 71% of species in common.

4. Discussion

4.1. Scales of hypoxia

Overnight or early morning is usually the most common time period for hypoxia, because dissolved oxygen production by photosynthesis stops at night and biological oxygen demand by aerobic respiration continues at night. Overnight hypoxia was not the norm during 1999. Night onset (i.e., after 9 p.m.) of hypoxia was noted only 3 times in 1999 at station 10. In addition, hypoxia was generally of very short duration, with the majority (14 of 24) of observed hypoxic events lasting for 1 h or less. The longest duration observed in the present study was 61.5 h at station 10, and the event probably continued past removal of the continuous hydrographic monitoring sonde on 17 August 1999. This event at station 10 was severe, and was accompanied by hypoxia at station 11 that lasted for 39 h. The duration of these events are much shorter than those described in Diaz and Rosenberg (1995). To avoid confusion, hypoxic events on the order of days are referred to as "intermittent" after Diaz et al. (1992), and those on the order of hours will be referred to as "brief." It is possible that a short duration event is not sufficient to induce the physiological stress required to induce macrobenthic community response. However, benthos, which are relatively immobile, will respond to length and severity of individual events and to the cumulative impacts of all events.

In the present study, the intensity of disturbance was categorized as hypoxic (D.O. ≤ 2 mg l^{-1}) and severely hypoxic (D.O. ≤ 1 mg l^{-1}). The summer of 1999 was the fourth most severe year for hypoxia between 1994 and 2004 (Applebaum et al., 2005). Prior to the onset of the "brief" hypoxic events on 14 August 1999, dissolved oxygen concentrations were ≤ 1 mg l^{-1} only 4% of the time that station 10 was hypoxic, indicating brief hypoxia may only rarely be intense. However, under brief hypoxic conditions, D.O. was # 1 mg l^{-1} 87% of the time hypoxic at station 10 (14 August 1999–17 August 1999) and D.O. ≤ 1 mg l^{-1} 82% of the time hypoxic at station 11 (15 August 1999–17 August 1999). Dissolved oxygen concentrations may not have been low enough to breech the tolerance levels of many

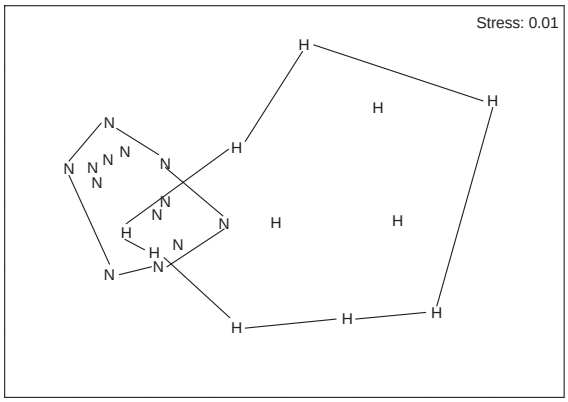

Fig. 10. Multidimensional scaling plot for community structure of species abundance for two areas (H=hypoxic area and N=normoxic area).

Table 5
Abundance (n m^{-2}) and depth distribution (cm) of dominant species accounting for at least 0.5% of all found in both areas during the study period

Species	Hypoxic		Normoxic		Number m^{-2}	
	0–3 cm	3–10 cm	0–3 cm	3–10 cm	Mean	Percent
Polydora caulleryi	650	5017	597	11,092	8678	36.1
Mediomastus ambiseta	1341	1194	250	3090	4438	18.4
Streblospio benedicti	3758	1194	892	201	3023	12.6
Tharyx setigera	35	2476	59	2659	2615	10.9
Oligochaetes (unidentified)	219	313	331	1442	1153	4.8
Gyptis vittata	219	685	183	916	1002	4.2
Notomastus latericeus	12	160	53	792	509	2.1
Schizocardium sp.	24	254	59	585	461	1.9
Cossura delta	18	266	53	325	331	1.4
Paleanotus heteroseta	6	160	6	425	299	1.2
Nermertinea (unidentified)	47	59	112	219	219	0.9
Paraprionospio pinnata	53	130	100	124	204	0.9
Phoronis architecta	118	195	0	35	174	0.7
Schistomeringos rudolphi	30	53	35	165	142	0.6
Glycinde solitaria	41	24	77	95	119	0.5
44 other species	357	246	233	629	733	2.9
Total	6928	12,426	6040	22,794	24,094	100.0

species, especially given the brief nature of typical observed events during 1999.

Hypoxia appears to be frequent daily occurrence during summer in Corpus Christi Bay, Texas, U.S.A. In 1999, hypoxia occurred on 13 out of 23 days monitored at station 10, and 6 of 23 days monitored at station 11. Hypoxia occurred as frequently as 3 events in a day at both stations 10 and 11.

4.2. Hypoxia effects

As was the case in a previous study, (Ritter and Montagna, 1999), biomass, abundance, and species richness were reduced in the hypoxic area, compared with the normoxic area. However, levels of benthic characteristics were higher in the present study and the differences between normoxic and hypoxic regions were smaller. For example, in 1996, normoxic species richness was 13 and hypoxic richness 2.6 (Ritter and Montagna, 1999), and in the present study, average richness was 16.8 in the normoxic treatment and 14.0 in the hypoxic treatment. One possible explanation for this discrepancy is that hypoxia only occurred late in the summer (mid-August 1999) as opposed to mid- to late-July as was the case in 1996 (Ritter and Montagna, 1999). Continuous monitoring revealed hypoxia at station 10 as early as 27 July 1999, but low oxygen conditions were brief until 14 August 1999. Hence, the benthic community was only briefly exposed to hypoxia at the end of the experiment. Hypoxia also occurred at station 11, which was designated as a normoxic station based on data collected by Ritter and Montagna (1999). This wider occurrence of hypoxic is another indication that summer of 1999 had moderately severe hypoxia conditions. Hypoxic conditions at station 11, in conjunction with the late onset of hypoxia, may be the cause of the smaller differences found between normoxic and hypoxic community characteristics found in 1999 compared to the summer of 1996.

In spite of the less severe hypoxia conditions earlier in the summer 1999, there were no differences between the first and second sampling dates for abundance, biomass, or evenness (Table 1). Species richness and diversity declined only slightly from the first to second sampling dates.

There is no strong evidence that disturbance by predation is different in the hypoxic and normoxic areas. There were no significant differences among cage treatments for abundance, species richness, diversity, or evenness, indicating that there were no predation effects. Biomass in uncaged treatments was significantly less than biomass in caged treatments (Table 3). If predation were the driver for change, lower biomass would be expected in the uncaged treatment. The lower biomass in the caged treatment could be due to cage effects if the reduced current flow caused oxygen to be even lower within cages than the ambient conditions. The most important test for predation or cages effects differences in the two areas is the area*cage interaction, which was not significant for abundance or biomass (Table 2), or richness or evenness (Table 4). This indicates that the caging effects were the same regardless of the ambient oxygen

concentrations. There was a significant area*cage effect on diversity (Fig. 9). The enclosed sediment had stimulated diversity in the normoxic area, but depressed diversity in the hypoxic area. The diversity change is more likely a cage effect because the reduced current flow in cages could have exacerbated hypoxia within cages. Although, the results indicate there were no strong predation effects, the potential for increased hypoxia in the caging treatment indicates that the effects of predation were not tested as clearly as anticipated. Future studies would be improved by measuring the dissolved oxygen concentrations within cage treatments.

Indirect effects were expected during hypoxic conditions, because infaunal species move to the sediment surface (Jørgensen, 1980) where they are more exposed to predation (Diaz et al., 1992). This appears to have happened during the current study. Infauna were much more prevalent in deeper sediments in the normoxic area than in the hypoxic area (Table 2, Fig. 7), thus a relatively greater percent of the community was at the surface during hypoxia than during normoxia. This strong interaction is a good example of ecological processes being driven directly by hypoxic conditions. Also, the interaction between the area and caging treatments where cages had very low abundance and diversity (Fig. 9) indicate that the cages might have suffered even greater hypoxia than the ambient conditions. Overall, the generally lower abundance and diversity in the hypoxia area, loss of deeper-dwelling species, and effects of the experimental treatments indicate that direct effects or physiological responses are the main drivers of community response patterns in Corpus Christi Bay, Texas.

Other supporting evidence that predation was not important is that fish or other epibenthic predators may have avoided the hypoxic area. Epibenthic predators can tolerate and thrive in hypoxic conditions (Segasti et al., 2000), and migrate higher into the water column so that feeding and predation on benthos is reduced (Segasti et al., 2001). In Corpus Christi Bay, there were nearly half the number of infaunal predatory nemertines in the hypoxic area. The lack of predators in the hypoxic area indicates predation pressure should have been lower and abundance and biomass should have been higher than the normoxic area if predation alone were the contributing cause of observed patterns. A final explanation is that predatory cropping of the community during the frequent, but short, hypoxic events may have stimulated production as predicted by Connell's (1978) intermediate disturbance hypothesis.

In summary, hypoxia drives the benthic community to the surface, and reduces community standing stock and diversity. The new, important finding is there is a direct interaction effect between hypoxia and vertical depth distributions of benthic infauna. In the current study, there could have been hypoxia cage effects, and the two areas were likely hypoxic and less hypoxic. However, the hypoxia effects appear to be a direct physiological response to low oxygen conditions, because there is no evidence that hypoxia enhances predation pressure on macrobenthos in Corpus Christi Bay. Hypoxia as a direct disturbance is also indicated by the more variable response of the community structure observed in the region with greater hypoxia (Fig. 10). The results of the current study support the idea that hypoxia diverts energy transfer to microbial and benthic pathways and causes a reduction in energy transfer to higher trophic levels (Barid et al., 2004).

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