

Relationship between environmental conditions and zooplankton community structure during summer hypoxia in the northern Gulf of Mexico

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The environmental conditions and mesozooplankton community were monitored during summer cruises in 2003, 2004 and 2006–2008 in the northern Gulf of Mexico. Data were collected on temperature, salinity, dissolved oxygen, chlorophyll-*a* and zooplankton taxonomic abundances. Environmental conditions were largely related to the influence of the Mississippi River plume. The zooplankton community was numerically dominated by copepods, with various meroplankton and other non-copepod zooplankton present in lower abundances. Cluster analysis revealed four distinct groups of co-occurring zooplankton taxa. Two of these were numerically dominant, one characterized by the copepod *Acartia* spp. and a second consisting of several copepod taxa (including larger-bodied genera) and salps. Relative to the group containing *Acartia* spp., this second dominant group was more abundant at higher salinity, lower temperature and greater vertical extent of hypoxic water into the water column above the seafloor. Dissolved oxygen, as vertical extent of hypoxia, was of comparable importance to temperature and salinity in predicting the abundances of zooplankton taxa. Variability of the zooplankton community with environmental conditions, and particularly the greater abundance of larger taxa in association with hypoxia, has implications for the contribution of zooplankton-mediated vertical flux to oxygen drawdown, and for the quality of the food environment for larval and other planktivorous fish.

KEYWORDS: abundance; community ordination; copepods; dead-zone; hypoxia; taxonomic composition

INTRODUCTION

In the last half-century, the occurrence and extent of bottom water hypoxia ($<2 \text{ mg L}^{-1}$ dissolved O_2) has increased in coastal oceans (Diaz and Rosenberg, 2008). This trend is thought to be caused largely by cultural eutrophication; increased nutrient loadings (primarily nitrogen) result in greater primary production, leading

to more sedimentation of organic matter and fueling greater microbial respiration and oxygen consumption (Nixon, 1990; Cloern, 2001; Diaz, 2001). The northern Gulf of Mexico (NGOMEX) is one of the world's largest regions of coastal hypoxia (Rabalais *et al.*, 2002). The relative importance of different processes in controlling the spatial and temporal extent of hypoxia in

the NGOMEX is not fully understood. Although physical and external factors control the atmospheric ventilation of bottom waters, sources of water and nutrient loading from the Mississippi River into the NGOMEX, observed patterns of hypoxia can also be influenced by biological activities within the system, particularly the magnitude of primary production, microbial respiration and the biological mediation of the vertical flux of organic matter (Bianchi *et al.*, 2010).

Low dissolved oxygen concentrations can affect the structure of biological communities, having positive effects on some living marine resources and negative effects on others (Breitburg *et al.*, 1997, 2001). The effects of hypoxia on benthic and demersal marine species are better known than for their pelagic counterparts, with direct mortality or emigration common for the former (Diaz and Rosenberg, 1995; Rabalais *et al.*, 2002). In the plankton, cultural eutrophication and the associated increases in phytoplankton production may positively influence zooplankton growth (Capriulo *et al.*, 2002). However, studies have shown that related increases in the occurrence and severity of hypoxia can have negative effects on zooplankton. Much of this work has involved laboratory experiments on the common coastal copepod *Acartia tonsa*, and has found that exposure to hypoxia can decrease egg production rate and hatching success (Lutz *et al.*, 1994; Sedlacek and Marcus, 2005). Hypoxia can also result in copepod prey being more susceptible to predation by gelatinous zooplankton (Purcell *et al.*, 2001; Decker *et al.*, 2004), and severe hypoxia can directly cause copepod mortality (Roman *et al.*, 1993; Stalder and Marcus, 1997). Such effects have the potential to decrease the population growth rate of zooplankton, as has been demonstrated for the abundant coastal copepod species *A. tonsa* (Marcus *et al.*, 2004; Richmond *et al.*, 2006). *Acartia* spp. is an important constituent of the NGOMEX zooplankton, although a number of other species are also common in this diverse community (Ortner *et al.*, 1989; Kimmel *et al.*, 2010). Similar population level effects could be expected for the other copepods and zooplankton species in the Gulf of Mexico, particularly since the life stages of *A. tonsa* appear to be quite tolerant of low oxygen relative to the co-occurring copepod species *Labidocera aestiva* and *Centropages hamatus* (Stalder and Marcus, 1997).

Because hypoxia has the potential to cause population level effects on copepods and other zooplankton, one might expect to find relationships between the structure of the zooplankton community and the occurrence and severity of hypoxia in the NGOMEX. Gulf of Mexico metazoan zooplankton consists largely of a diverse assemblage of copepods, as well as other species

such as larvaceans and various meroplanktonic larvae (Hopkins, 1982; Ortner *et al.*, 1989; Checkley *et al.*, 1992). A wide range of feeding modes and trophic roles are found among NGOMEX zooplankton (Turner, 1984, 1986; Green and Dagg, 1997), with copepods and other zooplankton able to graze a substantial portion of the region's primary production (Dagg, 1995; Liu and Dagg, 2003). Several studies have examined mesozooplankton abundance and distribution in relation to coastal hypoxia (Qureshi and Rabalais, 2001; Kimmel *et al.*, 2009, 2010; Pierson *et al.*, 2009; Zhang *et al.*, 2009). In general, it appears that hypoxia can drive the size structure of the zooplankton community present and the vertical distribution of zooplankton in the water column. However, little has been done to describe detailed zooplankton taxonomic composition in relation to hypoxia (although see Kimmel *et al.*, 2010).

Understanding the interplay between zooplankton and hypoxia is essential to the broader understanding of hypoxia's consequences for aquatic living resources in the NGOMEX. In this study, we hypothesized that zooplankton taxonomic composition would vary in a predictable manner relative to environmental conditions, and that hypoxia would be an important environmental predictor of zooplankton composition, even after accounting for the influence of co-varying environmental variables (e.g. temperature, salinity or chlorophyll-*a*). This hypothesis was tested by analyzing the relationships between the abundance of different metazoan zooplankton taxa and the hydrographic setting in a data set taken during five summertime cruises along the northern Gulf of Mexico continental shelf. We described changes in the zooplankton community associated with different hydrographic conditions during the period of peak seasonal hypoxia in the NGOMEX (July–August). When interpreted with reference to taxon-specific ecology, observed relationships will help to reveal how hypoxia influences the zooplankton community that occurs in the NGOMEX.

METHOD

Samples were taken along the same north–south transects described in Rabalais *et al.* (Rabalais *et al.*, 2002), with cruises during late July through early August of 2003, 2004, 2006, 2007 and 2008. Hydrographic profiles were taken at specific locations along transects (Fig. 1), using a CTD equipped with sensors for *in situ* fluorescence and dissolved oxygen. Fluorescence was converted to chlorophyll-*a* by collecting analogous water samples for chlorophyll-*a* determination and regressing the two variables to create a fluorescence to

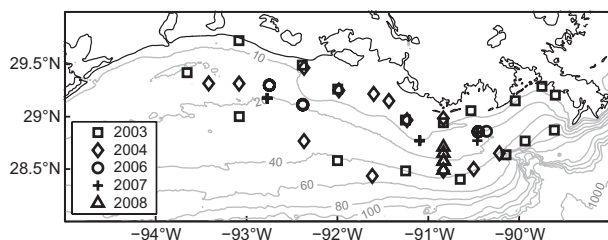


Fig. 1. Map of the sampling region showing locations of discrete samples taken during each cruise.

chlorophyll-*a* conversion factor for each cruise year of the study (Yentsch and Menzel, 1963). In 2003 and 2004, the cruise objectives were to survey a large area to gain an understanding of the spatial variability in zooplankton and fish in relation to hypoxia. In 2006–2008, the cruise objectives were more process oriented, to examine zooplankton and fish response to hypoxia over various spatial and temporal scales. Consequently, the cruise tracks and overall coverage differed between the two early years and each subsequent year. Zooplankton samples were collected during each CTD cast using a pump and hose with the intake attached to the CTD, and filtering water through a 64 μm sieve (Kimmel *et al.*, 2010). The pump used was a high-capacity, diaphragm pump (Ingersoll-Rand), with a 10 cm diameter opening and a flow of $\sim 220 \text{ L min}^{-1}$. The pump was run for 5 min to collect each sample, and final volumes filtered ranged from 0.78 to 1.69 m^3 . Animals collected on the sieve were then back-rinsed into containers and preserved in a 4% formaldehyde solution.

Zooplankton samples were sorted in the laboratory by sub-sampling a known volume with a Folsom plankton splitter and/or Stempel pipette. Individuals in sub-samples were then enumerated under a dissecting microscope, identifying organisms to the lowest taxon possible. When necessary, samples were first size fractionated with 500, 200 and 64 μm sieves to permit sufficient counts of rarer organisms for abundance estimates. In these cases, the size fraction containing the highest count of an individual taxon was used to estimate its abundance. In all cases, >100 individuals or the entire sample was counted.

As an index of stratification, the change in water density ($\Delta\sigma$) from the surface to bottom measurements was calculated for each CTD profile. The proportion of the water column that was hypoxic ($<2 \text{ mg L}^{-1} \text{ O}_2$) was calculated from the continuous oxygen CTD profile, and used as an indication of the vertical extent of hypoxia above the sea floor (P_{hyp}). CTD profiles of hydrographic environmental data were then binned into three depth strata, corresponding with zooplankton

samples taken from surface, middle and bottom layers of the water column. Variations in the environmental data set were then explored using principle components analysis (PCA) with classification of samples according to the year. The primary goals of this analysis were to identify the main environmental gradients occurring during our study, and determine whether any years were anomalous in terms of the environment sampled. PCA works well for these purposes since it organizes samples in multivariate space based on environmental measurements, constructing and identifying axes that represent the greatest ranges of environmental variability (Legendre and Legendre, 1998). Clear separation of samples grouped by year in PCA would indicate that environmental conditions were not comparable among years, whereas intermingling of samples from each year would indicate that samples were taken across a similar range of environmental conditions each year.

Hierarchical agglomerative cluster analysis (R-mode, furthest neighbor method) was performed on zooplankton abundance data to identify groups of taxa that co-occurred in samples. To reveal relationships between abundances of taxa and environmental data, canonical correspondence analysis (CCA) was used. CCA can be thought of as a special case of multiple regression, allowing multiple dependent variables (taxonomic abundances) in addition to independent ones (environmental variables). This method was chosen for its non-linear model of species responses to environmental conditions, which performs well on data sets with heterogeneous environmental and taxonomic compositions (Lepš and Šmilauer, 2003), such as was expected throughout our study in the NGOMEX and in the vicinity of the Mississippi River Plume. The non-linear species response seemed particularly appropriate to apply along an eutrophication gradient, since zooplankton abundance may increase with chlorophyll-*a* (food) concentration up to a point but decrease thereafter due to negative effects of increasing hypoxia with high primary production and chlorophyll levels. Explanatory environmental variables were chosen manually by forward selection in the CCA, selecting only those variables that were significantly related to taxonomic abundances ($P \leq 0.05$) according to Monte Carlo permutation tests. Environmental variables tested were water temperature, salinity, dissolved oxygen and chlorophyll-*a* values in the depth layer specific to each zooplankton sample, and also total water column depth, the density-based stratification index ($\Delta\sigma$) and the proportion of the water column that was hypoxic (P_{hyp}). In addition, the relationships between zooplankton abundances and large-scale forcing were explored using passive environmental variables in the CCA, including the total

Table I: Environmental data

	2003	2004	2006	2007	2008
Temp	29.5 (26.2, 30.7)	31.5 (28.6, 33.4)	29.9 (27.1, 31.2)	29.0 (22.4, 29.8)	27.2 (22.7, 29.7)
sal	28.3 (11.0, 36.0)	22.7 (3.8, 30.8)	32.0 (27.1, 36.0)	32.2 (23.2, 36.5)	32.5 (27.2, 36.3)
DO	5.6 (0.0, 7.8)	6.6 (1.5, 11.4)	5.2 (0.0, 6.7)	4.3 (0.5, 7.4)	4.7 (0.6, 8.5)
chl	2.7 (0.0, 12.1)	1.7 (0.9, 3.7)	1.0 (0.5, 2.7)	1.8 (0.7, 5.1)	1.9 (1.8, 2.0)
$\Delta\sigma$	6.0 (0.3, 17.4)	3.8 (0.0, 14.1)	3.7 (1.3, 5.9)	4.5 (2.0, 5.3)	7.0 (6.1, 8.4)
P_{hyp}	0.04 (0.00, 0.20)	0.05 (0.00, 0.17)	0.13 (0.00, 0.44)	0.15 (0.00, 0.57)	0.23 (0.10, 0.41)
rivf	17.0	23.0	9.0	28.1	22.7
hypa	7000	15 000	17 000	21 000	21 000

Mean (minimum, maximum) of environmental variables measured in samples taken during each cruise in the NGOMEX. temperature ($^{\circ}\text{C}$) = temp; salinity = sal; dissolved oxygen (mg L^{-1}) = DO; chlorophyll-*a* ($\mu\text{g L}^{-1}$) = chl; stratification index = $\Delta\sigma$; proportion of the water column that is hypoxic = P_{hyp} ; 30-day averaged Mississippi and Atchafalaya River flow (rivf, $\text{m}^3 \text{s}^{-1} \times 1000$); total NGOMEX hypoxic area (hypa, km^2).

summer hypoxic area in the NGOMEX (km^2 ; Liu *et al.*, 2010) and the 30-day average (prior to each cruise) of combined flow from the Mississippi River at Tarbert Landing and Atchafalaya River at Simmesport ($\text{m}^3 \text{s}^{-1} \times 1000$; www.usgs.gov). Averaging flow over 30 days was done because this is a comparable time scale to the generation time of temperate to tropical copepods (Mauchline, 1998), which were the dominant forms in our samples. Zooplankton taxa that were observed in less than 5% of all samples were excluded from both cluster analysis and CCA to prevent these rare taxa from having an inordinate influence on the statistical results. Due to the properties of CCA and similar ordination methods, the choice of data transformation should be based more on how the transformation would relate to the hypothesis being addressed, rather than with the sole objective of obtaining normally distributed data (Lepš and Šmilauer, 2003). An environmental variable such as the extent of the hypoxic zone (P_{hyp}) could directly influence abundance without excluding species entirely from a region. Therefore, a data transformation that decreased the range of variability in abundances could result in no perceived relationship between zooplankton and hypoxia in the CCA, even if such relationship existed. Because of this, we chose not to apply any transformation to abundance data prior to analysis, instead exploring the full range of variation in abundances and their relationship directly to measured environmental variables.

RESULTS

Hydrographic environment

Zooplankton samples were collected from water with a broad range of hydrographic characteristics (Table I), including temperature between 22.4 and 33.4 $^{\circ}\text{C}$ and salinity as low as 3.8 in samples close to shore (within 10 m isobath) and as high as 36.5 offshore and in

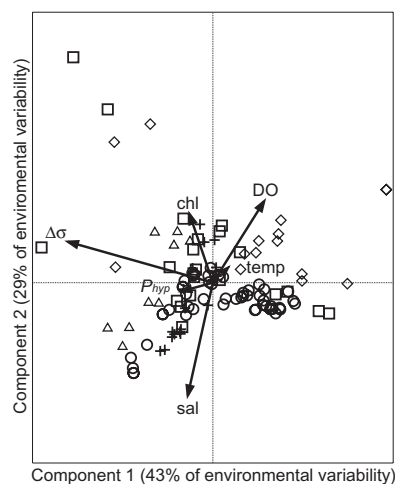


Fig. 2. Biplot showing the first two components (axes) of PCA on measured environmental variables. Environmental variable abbreviations are identical to those in Table I. Symbols for sample year are identical to those in Fig. 1.

bottom water. Dissolved oxygen averaged between 4.3 and 6.6 mg L^{-1} , with hypoxic to anoxic waters occurring in the bottom layer during all years (Table I). Mean chlorophyll-*a* from samples taken on each cruise was between 1.0 and 2.7 $\mu\text{g L}^{-1}$. In general, stratification was present in the sampling region over the entire study, with an average of $>3 \text{ kg m}^{-3}$ density difference between surface and bottom in all years. The proportion of the water column that was hypoxic varied at our sampling stations from near 0.0 to a maximum of 0.57.

Based on the results of principal components analysis, comparable ranges of environmental conditions were sampled among the years of this study (Fig. 2). The first two principal components in PCA explained 72% of the variability in the environmental data. The PCA revealed a strong gradient (PCA axis 1, 43% of observed environmental variability) related to the degree of water column stratification ($\Delta\sigma$). The extent of hypoxia (P_{hyp}) was positively associated with

stratification along this axis, reflecting the importance of stratification in maintaining bottom water hypoxia. The independent second PCA axis (29% of observed environmental variability) was most strongly associated with salinity. Chlorophyll-*a* and dissolved oxygen concentrations were negatively related to salinity along this axis, likely reflecting high chlorophyll and oxygen concentrations in the region of greatest freshwater influence from the Mississippi and Atchafalaya Rivers. Water temperature was also positively associated with oxygen concentration, reflecting the fact that warmer surface water had higher dissolved oxygen levels than colder deep water. The third PCA axis (not shown, 18% of environmental variability) was most closely related to chlorophyll-*a* concentration.

Zooplankton community

The average zooplankton abundance and taxonomic composition across all cruises is shown in Fig. 3. Copepod nauplii were the most abundant form observed. The numerically dominant calanoid copepods were *Acartia* spp., *Centropages* spp. and *Paracalanus* spp., with *Eucalanus* spp. and other calanoids occurring less frequently and in lower abundance. *Oithona* spp. was the numerically dominant cyclopoid copepod. Meroplankton, including the larvae of large crustaceans, bivalve and gastropod molluscs, and various worms, were present but usually represented a small fraction of total zooplankton abundance. A number of other zooplankton taxa were also present, including harpacticoid and poecilostomatoid copepods, cladocerans, the larvacean *Oikopleura* spp., and gelatinous medusa, chaetognaths and salps. In total, 26 classes or taxa of zooplankton were identified that occurred in

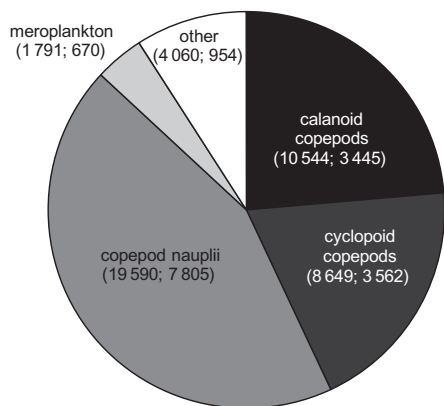


Fig. 3. Relative abundances of different zooplankton taxonomic groups averaged across all cruises. Actual values are shown as (abundance; standard error of abundance), where abundance is in individuals m^{-3} .

$\geq 5\%$ of samples (Fig. 4). These taxa were classified into four groups based on co-occurrence in samples, delineated in the dendrogram results of hierarchical agglomerative cluster analysis (Fig. 4). The most numerically abundant, co-occurrence group 1 had an average of 23 500 individuals m^{-3} in samples, and was characterized by the occurrence of *Acartia* spp., and copepod eggs and nauplii. The second most abundant was co-occurrence group 3, with an average of 15 700 individuals m^{-3} in samples. This group included *Paracalanus* spp., several other large calanoid copepods, the cyclopoid *Oithona* spp., the poecilostomatoid *Corycaeus* spp. and salps. Co-occurrence groups 2 and 4 were much less abundant, with study averages of 1600 and 3600 individuals m^{-3} , respectively. Both included a mixture of copepod taxa and meroplanktonic larvae, and group 4 also contained *Oikopleura* spp. and chaetognaths.

Environment–zooplankton relationships

Zooplankton abundances were significantly related to water temperature, salinity and P_{hyp} in the CCA ($P \leq 0.05$, Monte Carlo permutation tests). The resulting

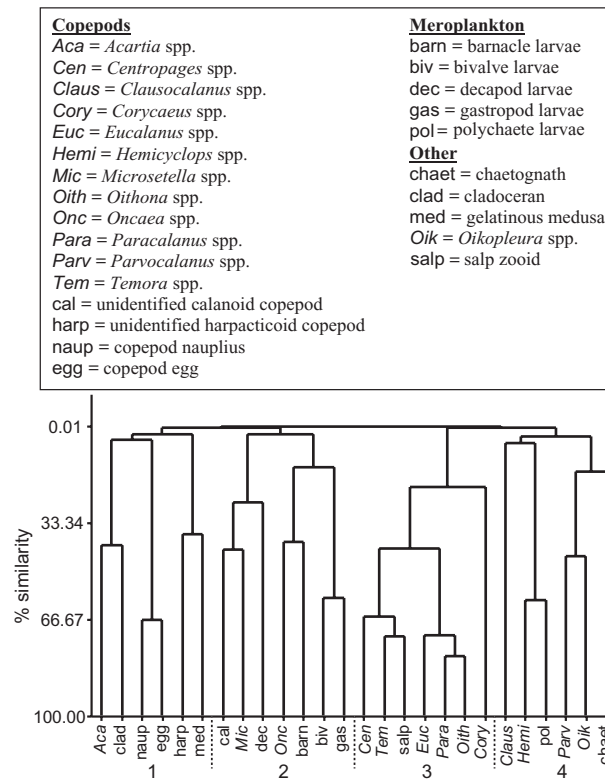


Fig. 4. Dendrogram results of hierarchical agglomerative cluster analysis on taxonomic abundances, denoting groups of co-occurring taxa by the numbers 1 through 4 at the bottom of each branch. Abbreviations for each taxon are defined in the legend.

Table II: CCA statistics

Correlation coefficients of environmental variables with CCA axes	Axis 1	Axis 2	Axis 3
Temp	0.45	-0.53	-0.14
sal	-0.71	0.21	-0.20
P_{hyp}	-0.56	-0.22	0.32
rivf (supplementary)	0.52	0.32	0.31
hypa (supplementary)	-0.61	0.11	0.07
Ordination summary statistics			
Species–environment correlations	0.82	0.67	0.49
Cumulative percentage variance of species data explained by axes	11.1	14.7	16.3

Results of CCA relating taxonomic abundances to measured environmental variables. Environmental variable abbreviations are identical to those used in Table I.

three environmental ordination axes explained 16.3% of the variation in the zooplankton data (Table II). This percent variation explained should be viewed in reference to the CCA method used. For ecological data analyzed using CCA, this value is usually low (often <10%). This is not reflective of the quality of the CCA model, which should be judged more heavily based on the statistical significance of the zooplankton–environment relationships (from Monte Carlo permutation tests), and perhaps most importantly, the ecological interpretability of the results (ter Braak and Verdonschot, 1995). The first ordination axis accounted for 11.1% of this variability, and was most strongly related to the gradient in salinity and P_{hyp} . The second ordination axis explained an additional 3.6% of taxonomic variability, and was closely related to the water temperature gradient. Regarding the distribution of zooplankton, the taxa from co-occurrence group 3 were clearly separated from others (Fig. 5), with greater abundances associated with high salinity, intermediate water temperature and high vertical extent of hypoxia (P_{hyp}). Abundances of zooplankton from co-occurrence group 3 were also generally higher in samples taken during years when the hypoxic area was larger. The zooplankton from co-occurrence group 1 were most abundant at low to intermediate values of salinity and P_{hyp} and intermediate to high temperature. Co-occurrence groups 2 and 4 were poorly separated in the CCA, both containing taxa that occurred in greatest abundance at intermediate to high salinity, and low to intermediate values of temperature and P_{hyp} . For many of the taxa in groups 1, 2 and 4, abundances were generally higher in samples taken during years with relatively high average river flow for the 30 days prior to cruise.

To explore the responses of the zooplankton to environmental conditions in greater detail, we looked at the abundances of zooplankton from each co-occurrence group in relation to both temperature and salinity

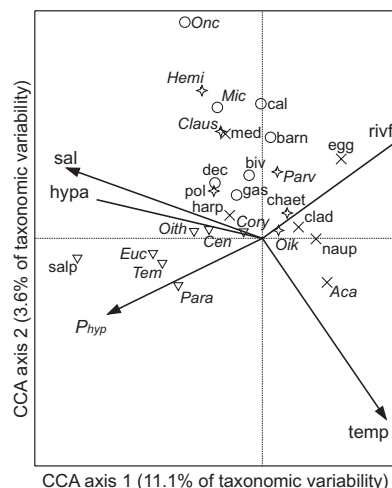


Fig. 5. Biplot of the first two canonical axes of CCA on the environment–zooplankton abundance data set. Supplementary environmental variables including total NGOMEX hypoxic area (hypa) and Mississippi and Atchafalaya River flows (rivf) are passively projected onto the diagram. Environmental variable abbreviations are identical to those in Table I. Taxonomic abbreviations are identical to those in Fig. 4. Symbols for each taxon are coded to indicate co-occurrence group membership. Group 1, multi; Group 2, open circle; Group 3, inverted triangle; Group 4, star.

(Fig. 6) and to P_{hyp} values (Fig. 7a–e), as well as at total zooplankton abundance in relation to dissolved oxygen concentration (Fig. 7f). The results corroborate those of the CCA, with abundances of zooplankton from group 1 clearly highest in samples with higher temperatures (29–32°C), low to intermediate salinities (12–33) and low to intermediate P_{hyp} (<0.3). Abundances of zooplankton from group 3 were highest at higher salinities (>27), intermediate water temperatures (28–31°C) and higher P_{hyp} values than for the other taxa (maximum at 0.4). Zooplankton from groups 2 and 4 were generally much less abundant than from groups 1 and 3, and were found in highest abundance at intermediate to high salinities (>23), lower temperatures ($\leq 31^\circ\text{C}$) and low to intermediate P_{hyp} (≤ 0.3). Although zooplankton were quite abundant even in locations with high values of P_{hyp} (Fig. 7e), total abundances were consistently low directly within the hypoxic waters (Fig. 7f).

DISCUSSION

Environmental conditions in the northern Gulf of Mexico were comparable among years, but more variable in space (Table I), as would be expected near the Mississippi River Plume and an open shelf system. The average proportion of the water column that was hypoxic in our samples (P_{hyp}) agreed in magnitude with

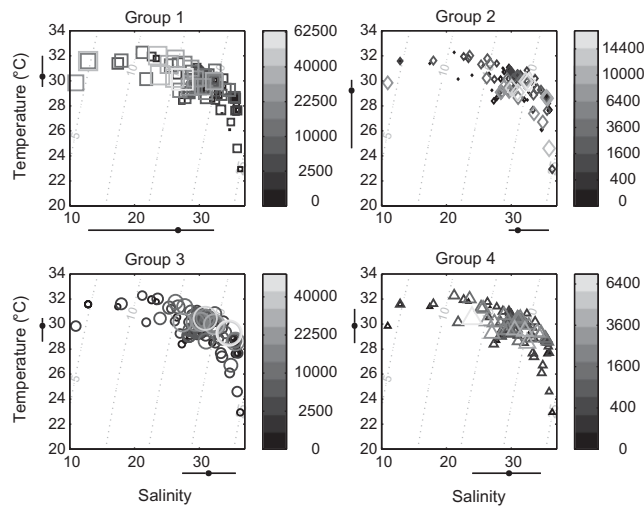


Fig. 6. Measured abundances of zooplankton (magnitude indicated by symbol shading and size) in each co-occurrence group plotted against their associated temperature and salinity. The solid black circles plotted next to each axis indicate the average temperature and salinity at which an individual from each group was found (mean temperature and salinity of samples weighted by animal abundance). The error bars around each solid black circle indicate the temperature and salinity ranges within which 50% of all the zooplankton in a given group were observed.

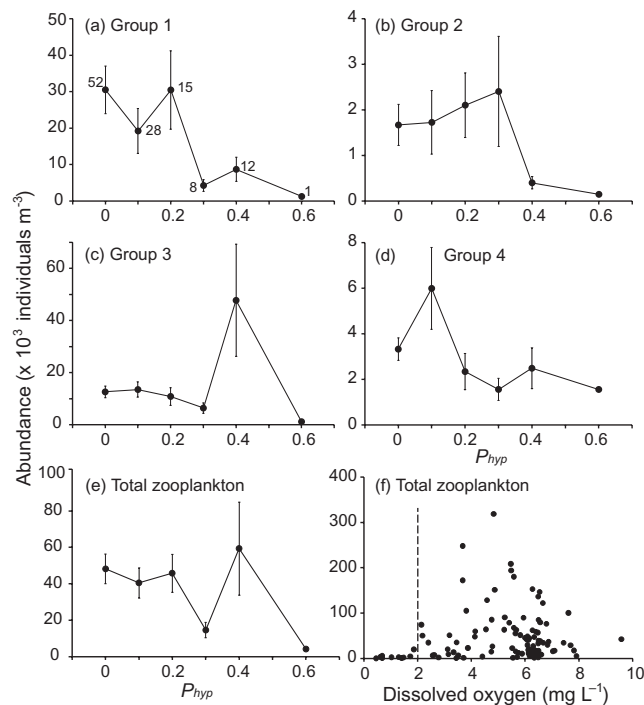


Fig. 7. Mean abundances of each co-occurrence group (a–d) and total zooplankton (e) at 10% intervals of P_{hyp} . Error bars are \pm standard error of the mean. Number of samples for each P_{hyp} interval are shown adjacent to corresponding symbols in (a). Total zooplankton abundances are also shown in relation to the absolute dissolved oxygen concentration from which they were collected (f), where the dashed vertical line represents the normoxic–hypoxic transition.

measured hypoxic area in the NGOMEX, both having lowest values in 2003 and increasing sequentially in 2004 and 2006–2008 (Table I; Liu *et al.*, 2010). However, spatial coverage of the NGOMEX area

varied among cruises, and comparisons among years in our data set should therefore be made with caution. For example, spatial coverage in 2008 was along a single transect between the Mississippi and Atchafalaya River

Deltas, whereas other years covered a broader spatial region in the East to West direction (Fig. 1). Thus, inter-annual differences in the means and ranges of environmental conditions (Table I) indicate different conditions sampled among years, but do not necessarily reflect differences in the mean conditions region-wide. Still, our observations are generally consistent with previous reports. The zooplankton community in our study was dominated by a diverse assemblage of copepods, typical of the Mississippi River outflow region (Ortner *et al.*, 1989; Qureshi and Rabalais, 2001). The copepod *Acartia* spp. and copepod nauplii (group 1) were abundant in low to intermediate salinity waters (≤ 33), and a more diverse assemblage including copepods and other zooplankton (groups 2–4) were more abundant at intermediate to high salinity (>23), both similar to previous observations (Ortner *et al.*, 1989; Kimmel *et al.*, 2009).

The influence of salinity on NGOMEX zooplankton taxonomic composition is the likely explanation for the high abundance *Acartia* spp. and co-occurring taxa (group 1) across a broad range of salinities. Copepods of the genus *Acartia* are well known to be most successful in nearshore and estuarine habitats (Paffenhöfer and Stearns, 1988; Tester and Turner, 1991). By comparison, most of the other common taxa observed in the NGOMEX were most abundant at salinity >23 (Fig. 6). The effect of temperature on zooplankton is that of greater growth at higher temperatures, at least within a species thermal range (Heinle, 1969; Huntley and Lopez, 1992). The range of temperatures encountered in our study was rather narrow with a maximum value near 33°C and relatively few samples below 28°C (Table I). Apart from the taxa of co-occurrence group 2, highest zooplankton abundances consistently occurred in samples of $\geq 28^{\circ}\text{C}$ (Fig. 6).

The occurrence of hypoxia could influence zooplankton abundance through increased mortality (Roman *et al.*, 1993; Stalder and Marcus, 1997; Decker *et al.*, 2004) and decreased growth (Lutz *et al.*, 1994; Marcus *et al.*, 2004; Sedlacek and Marcus, 2005; Richmond *et al.*, 2006). While our data do not directly demonstrate these effects, they do indicate active avoidance of hypoxic bottom waters by many zooplankton taxa. Although abundances were low within hypoxic bottom waters (Fig. 7f), zooplankton were abundant in the upper oxygenated layers even when hypoxia was present throughout the lower portion of the lower water column (Fig. 7a–e). The higher abundance of *Acartia* spp. at low P_{hyp} and of *Centropages* spp. at higher P_{hyp} (Fig. 5) is contradictory to experimental evidence that *Acartia tonsa* is more tolerant of low oxygen concentrations than co-occurring *Centropages hamatus* in the Gulf of Mexico (Stalder and Marcus, 1997). Also, both

Centropages spp. and *Paracalanus* spp. appear to avoid hypoxic waters in the NGOMEX (Kimmel *et al.*, 2010), but were more abundant in sample from regions with higher P_{hyp} values (Fig. 5). These observations also suggest active avoidance of hypoxic waters, with taxa associated with higher P_{hyp} primarily residing in the oxygenated water overlying extensive hypoxia. Copepod eggs passively sink and are therefore unable to avoid bottom hypoxia. This potential source of mortality could give sac-spawning copepods that carry their eggs a selective advantage over broadcast spawners in avoiding exposure of eggs to hypoxia (Uye, 1994). However, of the sac-spawning copepods that we observed (*Corycaeus* spp., *Microsetella* spp., *Oithona* spp. and *Oncaea* spp.), only *Oithona* spp. showed a slight tendency for higher abundance with increasing P_{hyp} (Fig. 5).

Ultimately, P_{hyp} was a better predictor of zooplankton taxonomic abundances than either chlorophyll-*a* concentration or absolute oxygen concentration. Many of the larger bodied zooplankton (group 3) were more abundant in association with greater vertical extent of hypoxia, consistent with the results of Kimmel *et al.* (Kimmel *et al.*, 2010). This zooplankton– P_{hyp} relationship may reflect several mechanisms. Greater abundances of these taxa with high P_{hyp} suggests the possibility that hypoxic bottom waters serve as a refuge for large zooplankton from fish predation, as suggested by other studies (Ludsin *et al.*, 2009; Kimmel *et al.*, 2010; Larsson and Lampert, 2011). Thus, lower abundances of large copepod species in association with lower P_{hyp} could reflect reductions in their numbers due to size selective predation, with larger taxa being more susceptible to visual predators. The relationship between zooplankton abundances and P_{hyp} could also be partly due to the effect of zooplankton on hypoxia, with larger taxa potentially contributing to greater fecal pellet vertical flux and oxygen drawdown in bottom waters. Sedimentation of zooplankton fecal pellets can be important to the vertical flux of organic matter (Frangoulis *et al.*, 2005) and bacterial respiration of this organic matter is potentially significant to the development and maintenance of hypoxia in coastal regions (Dagg *et al.*, 2007, 2008; Shek and Liu, 2010). Studies using sediment traps in the NGOMEX have suggested a vertical flux of $180\text{--}600\text{ mg C m}^{-2}\text{ day}^{-1}$ for the region immediately offshore of the Mississippi River plume (Redalje *et al.*, 1994; Qureshi, 1995), and zooplankton fecal pellets comprised around 50% of the carbon in these traps (Qureshi, 1995; Turner *et al.*, 1998; Rabalais *et al.*, 2001).

For those zooplankton taxa that produce rapidly sinking fecal pellets, we estimated potential fecal pellet carbon production over the study area, assuming a

Table III: Literature reviewed fecal pellet properties

Group	Grp FCP	Group mean PSV	Taxon	PSV	Abund	PPR	PCC	Ind FCP	Pop FCP
1	100	30	<i>Aca</i>	30	2887	87	20	1.7	100
2	132	53	<i>Eur</i>	30	38	20	25	0.5	0
			<i>Cal</i>	100 ^a	660	100 ^a	100 ^a	10	132
			barn	30 ^b	56	4	20 ^b	0.1	0
3	738	94	<i>Cen</i>	90	498	30	130 ^c	3.9	39
			<i>Tem</i>	100	467	90	150	13.5	126
			salp	100	72			240	345
			<i>Euc</i>	130	235	75	211 ^c	15.8	74
			<i>Para</i>	50	5334	80	20 ^b	1.6	154
			<i>Claus</i>	70	142	35	20 ^b	0.7	2
4	205	77	<i>Oik</i>	60	1996	504	10 ^d	5.0	201
			chaet	100	64	2	900	1.8	2

^aEstimated for a mixed assemblage of calanoid copepods based on Mauchline (1998) and Frangoulis et al. (2005).

^bAssumed identical to *Acartia* based on similar body or pellet size ranges.

^cBased on volume:volume conversion between taxon and *Temora* spp. fecal pellets from Paffenhöfer and Knowles (1979), and assuming same volume-specific C content for both taxa.

^dBased on volume-specific C content from González and Smetacek (1994), and assuming pellet volume of $3 \times 10^{-4} \text{ mm}^3$ estimated from Uye and Kaname (1994).

Shown are: (i) study mean abundances (Abund, individuals m^{-3}); (ii) literature values for fecal pellet settling velocities (PSV, m day^{-1}), production rates (PPR, pellets individual $^{-1} \text{ day}^{-1}$) and carbon contents (PCC, ng C pellet^{-1}), and (iii) estimates of individual fecal carbon production (Ind FCP, $\mu\text{g C individual}^{-1} \text{ day}^{-1}$), as well as abundance and depth integrated fecal C production for each taxon (Pop FCP, $\text{mg C m}^{-2} \text{ day}^{-1}$) and co-occurrence group (Grp FCP, $\text{mg C m}^{-2} \text{ day}^{-1}$), both assuming a water column depth of 20 m. Taxonomic abbreviations are as in Fig. 4.

In addition to footnotes a–d, literature used to estimate taxon-specific parameters includes:

Butler and Dam (1994); Saba et al. (2011): *Acartia* spp.

Frangoulis et al. (2005): *Acartia* and *Temora* spp.

Kwint et al. (1996); Lehtiniemi et al. (2002); Sapanen et al. (2008): *Eurytemora* spp.

Gaonkar and Anil (2010): barnacle nauplii

Gaudy (1974); Bonnet and Carlotti (2001): *Centropages* spp.

Paffenhöfer and Knowles (1979): *Temora*, *Eucalanus*, *Paracalanus* and *Clausocalanus* spp.

Shek and Liu (2010): *Paracalanus* spp.

Ayukai (1990): *Clausocalanus* spp.

Dagg and Brown (2005); Dagg et al. (2008): *Oikopleura* spp.

Yoon et al. (2001); Madin (1982): salps.

Dilling and Alldredge (1993): chaetognatha.

20 m deep water column and using taxonomic abundances and literature reported values of fecal pellet production rates, settling velocities and carbon contents (Table III). Using this approach, we estimated a fecal pellet carbon production rate of $201 \text{ mg C m}^{-2} \text{ day}^{-1}$ by *Oikopleura* spp., comparable to more comprehensive estimates for the same region in August 2004 (average $212 \text{ mg C m}^{-2} \text{ day}^{-1}$, range $17\text{--}526 \text{ mg C m}^{-2} \text{ day}^{-1}$; Dagg et al., 2008). Potential fecal pellet carbon production by group 3, which was most strongly associated with hypoxia as larger P_{hyp} (Fig. 5), was by far the highest of all groups, and the average settling velocity of pellets from this group was also highest (Table III). Thus, of the fecal pellet carbon produced by zooplankton in the NGOMEX, a large fraction is likely derived from co-occurrence group 3, and the pellets from this group have the highest probability of sinking to the bottom-waters and contributing to hypoxia. How important could such fecal pellet production be to oxygen consumption? Using an oxygen-to-carbon ratio of $3.47 \text{ g O}_2 \text{ g}^{-1} \text{ C}$ (Scavia et al., 2003), the respiration of estimated carbon from group 3 pellets (738 mg C

$\text{m}^{-2} \text{ day}^{-1}$, Table III) would consume $0.13 \text{ mg O}_2 \text{ L}^{-1} \text{ day}^{-1}$ throughout a 20 m water column, and higher still if the majority of pellet's carbon were respired in deeper water due to sinking.

Numerous factors could contribute to the observed zooplankton taxonomic composition in the NGOMEX in any given year or location. The approach we used in the current study was to treat each sample as a snapshot of the zooplankton community found in association with a specific set of hydrographic conditions, and look for consistent underlying relationships across the entire data set. The result was a small subset of environmental variables (temperature, salinity and P_{hyp}) that had statistically significant relationships with observed variability in zooplankton taxonomic abundances. Our results suggest that a non-linear model, such as the one assumed by CCA, can be appropriate for describing the abundance of different zooplankton taxa across environmental gradients in seasonally hypoxic coastal regions like the NGOMEX, with highest abundances of many taxa associated with intermediate values of environmental variables (Figs 5–7). It is also noteworthy that, in

addition to water temperature and salinity, the extent of hypoxia (P_{hyp}) was of primary importance in describing zooplankton taxonomic composition; several large copepod taxa and salps were found in higher abundance when vertical extent of hypoxia was relatively high. This relationship could reflect a combined result of the use of hypoxic waters as a refuge from selective predation and contribution of large rapidly sinking fecal pellets to bottom water hypoxia. These observations have important implications for the nutritional environment and recruitment success of larval and planktivorous fishes. Zooplankton and particularly copepods and nauplii are an important component of the diets of fish larvae in the NGOMEX (Ortner *et al.*, 1989), and the copepods classified into co-occurrence group 3 were the major component of the diets of most planktivorous fish taxa in the NGOMEX during 2006–2008 (Ludsin *et al.*, unpublished data). Thus, observed shifts in the abundance of different zooplankton taxa in association with gradients in temperature, salinity and also vertical extent of hypoxia could result in an alteration of the quantity and quality of forage available to larval and planktivorous fish.

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