

Effects of eutrophication on bottom habitat and prey resources of demersal fishes

Sean P. Powers^{1,*}, Charles H. Peterson², Robert R. Christian³, Elizabeth Sullivan²,
Monica J. Powers², Melanie J. Bishop², Christopher P. Buzzelli²

¹Department of Marine Sciences, University of South Alabama and the Dauphin Island Sea Laboratory, 101 Bienville Boulevard, Dauphin Island, Alabama 36528, USA

²University of North Carolina at Chapel Hill, Institute of Marine Sciences, Morehead City, North Carolina 28557, USA

³Department of Biology, East Carolina University, Greenville, North Carolina 27858, USA

ABSTRACT: Estuarine benthic habitats serve as essential feeding grounds for demersal finfishes and shellfishes and provide a link between the water column and demersal fisheries in coastal foodwebs. We hypothesize that the cascading linkages of water-column conditions to benthic invertebrates and from benthic invertebrates (as prey) to demersal fishes are a primary mechanism by which water-quality degradation affects sustainable production of demersal fisheries in coastal ecosystems. To evaluate these linkages, we related changes in water quality to changes in bottom-habitat quality for fishes (defined by the availability of prey resources) and assessed how changes in habitat quality affect fish diet. We examined the first link (water-column conditions to benthos) by intensively sampling the benthic community in the Neuse River Estuary, North Carolina, during 2 summers (1997 and 1998) in which depletion of bottom-water oxygen occurred. Dramatic decreases in the abundance of benthic macroinvertebrates were evident after hypoxia/anoxia in both years. Abundances of the clam *Macoma balthica*, a key prey item for fishes and crabs and the biomass dominant in the benthos, decreased by over 90% in deep and mid-depth areas (>2 m) throughout the estuary after hypoxia/anoxia in 1997. Although summer decreases in benthic macroinvertebrates were also exhibited in 1998, a year of less frequent and less severe hypoxia, the magnitude of decline was less than that of 1997. To evaluate how these changes in prey abundance may affect demersal fishes, we analyzed the diet of Atlantic croaker *Micropogonias undulatus*, the most abundant demersal fish in the system, prior to and after summer hypoxia of 1998. This analysis demonstrated a shift in croaker diet away from clams, an abundant item before hypoxia, to less nutritional items such as plant and detrital material afterwards. This dietary shift reflects the decreased abundance of clams as a result of hypoxia/anoxia. We conclude from our study of the Neuse River Estuary that hypoxia/anoxia events degrade essential fish habitat and that this degradation has the potential to reduce the capacity of the system to support production of demersal fisheries.

KEY WORDS: Benthic invertebrates · Essential fish habitat · Habitat degradation · Hypoxia · Secondary production · Trophic linkages · Neuse River Estuary

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INTRODUCTION

Nutrient enrichment is a pervasive and growing problem for aquatic ecosystems (Rosenberg 1985, Elmgren 1989, Nixon 1995, Jørgensen & Richardson 1996, Livingston 2001), where increased nutrient loading typically results in elevated rates of phytoplankton

production (Richardson & Heilmann 1995, Paerl et al. 1998, Cloern 2001). In oligotrophic waters, inputs of nutrients and the resultant increased primary productivity typically enhance secondary production (Pearson 1975, Nixon & Buckley 2002) including that of fishes (Caddy 1993, Maceina & Bayne 2001). In eutrophic systems, however, which already have high levels of

primary production, additional nutrients may translate into additional production for pelagic fishes (Breitburg 2002) but not for demersal fishes (Breitburg 2002, Eby & Crowder 2002). For benthic habitats, much of the increased primary production is delivered directly to microbial loops (Baird et al. 2004). Higher rates of microbial decomposition can deplete dissolved oxygen near the sediment–water interface and produce H_2S that enters the water column (Stanley & Nixon 1992, Diaz & Rosenberg 1995). The resultant hypoxia or anoxia can persist for long enough to cause mortality of benthic invertebrates under conditions of strong water-column stratification or stagnation (Falkowski et al. 1980, Rabalais et al. 1994, Gray et al. 2002). Because benthic invertebrates represent an important and easily accessible prey resource for demersal fishes and crabs, factors influencing macroinvertebrate populations can affect production of demersal fishes (Peterson et al. 2000). We hypothesize that these cascading linkages, from water-column conditions to benthic invertebrates and then from benthic invertebrates (prey) to demersal fishes (predators), can lead to degradation of essential fish habitat and thereby represent a primary mechanism by which eutrophication affects sustainability of demersal fish production in aquatic ecosystems.

Low dissolved oxygen (DO) concentrations (hypoxia, $DO < 2.0 \text{ mg l}^{-1}$ or anoxia, $DO = 0 \text{ mg l}^{-1}$) are a symptom of eutrophication in a growing number of estuarine environments worldwide (Rosenberg 1985, Cooper & Brush 1991, Diaz & Rosenberg 1995, Diaz 2001). The direct, short-term effects of hypoxic/anoxic events on benthic macroinvertebrate communities are well-documented; however, the longer-term implications of such events on trophic linkages are not fully understood (Breitburg et al. 1997, Breitburg 2002). Declines in the abundance of benthic macroinvertebrates occur in areas that experience either prolonged (e.g. Josefson & Widbom 1988, Nordberg et al. 2001) or episodic (e.g. Tenore 1972, Harper et al. 1981, Pearson & Rosenberg 1992, Rabalais et al. 2001a, Hansen et al. 2002) hypoxia/anoxia. The magnitude of these decreases in benthos is primarily dependent on the duration, spatial extent, and severity of the low-oxygen event (Diaz & Rosenberg 1995, Rabalais et al. 2001b, Gray et al. 2002). Mobile consumers of benthic macroinvertebrates usually emigrate from areas where dissolved oxygen concentrations reach hypoxic levels (Pihl et al. 1991, Pearson & Rosenberg 1992, Rabalais et al. 2001a). If low-oxygen conditions are relatively mild, some of these demersal consumers may remain in the vicinity and, over the short term, exploit stunned or moribund benthic prey resources not normally available (Pihl et al. 1992, Pihl 1994, Seitz et al. 2003). As dissolved oxygen concentrations rise, mobile demersal

consumers return. But, because recolonization of bottom areas by macroinvertebrates is largely dependent on larval supply (Santos & Simon 1980, Powers et al. 2001), the recovery of prey resources following an extensive hypoxic/anoxic period requires considerably more time than is necessary for predators to migrate back into the area. Given that recolonization of the benthic community may require months, one critical issue that has yet to be addressed is to what degree and for how long the depletion of prey affects production of demersal fishes and crustaceans after a hypoxic event.

Establishing the linkages between water quality, benthic macroinvertebrate communities and demersal fishes requires that we relate changes in water quality to changes in fish-habitat quality (defined by the availability of appropriate prey resources). We explored this linkage by intensively sampling seasonal changes in water-column DO and in the benthic community in the Neuse River Estuary, North Carolina, over the summer season of hypoxia/anoxia in 2 successive years (1997 and 1998). We then evaluated the consequences of changes in benthic prey abundance on the *in situ* diet of Atlantic croaker *Micropogonias undulatus*, the most common demersal fish in the system.

MATERIALS AND METHODS

Study site. The Neuse River, North Carolina, USA drains a 16 000 km² watershed that is dominated by forestry and row-crop agriculture but has been greatly modified in recent years by growing urbanization, industrialization and animal production (Stow et al. 2001, Cooper et al. 2004). Loading of nitrogen within the river basin has increased by 30% over recent decades (Stow et al. 2001). Symptoms of declining water quality (e.g. nuisance algal blooms, hypoxia, and fish kills, Paerl et al. 1998), have also increased in frequency over this same time period in the estuary fed by the Neuse River. Hydrologically, the Neuse River Estuary (Fig. 1), which flows into Pamlico Sound, has variable salinity, dependent on changing freshwater and saltwater inputs (Pinckney et al. 1997). Depth is relatively shallow (average <5 m), and mixing is strongly wind-driven, with little lunar influence (Robbins & Bales 1995). Hypoxia and anoxia are seasonal events in the Neuse River Estuary, usually occurring in deep waters for at least a short period of time each summer from June to September (Lenihan & Peterson 1998, Paerl et al. 1998, Buzzelli et al. 2002). Persistent areas of bottom-water hypoxia generally encompass the deep and mid-depth areas (>3 m) of the Neuse River Estuary, with the shallower stations experiencing only episodic (lasting 4 to 12 h) hypoxic events (Luettich et al. 2001).

Hydrographic surveys. Hydrographic data were collected from spring 1997 through fall 1998. Sampling was designed to estimate the spatial extent and document the temporal pattern of low-oxygen water masses in the Neuse River Estuary (Luettich et al. 1999). Hydrographic measurements (temperature, salinity, and dissolved oxygen) were taken weekly at mid-channel stations during the spring, summer and fall of 1997 and 1998. More extensive hydrographic surveys of mid-channel and cross-channel stations (transects from one shoreline to the other) were made every 2 wk in the summers of 1997 and 1998 (Luettich et al. 1999, Buzzelli et al. 2002). Continuous hydrographic data were collected at 2 mid-channel stations (T90, T115) where unattended monitoring instruments were placed throughout both years (Fig. 1).

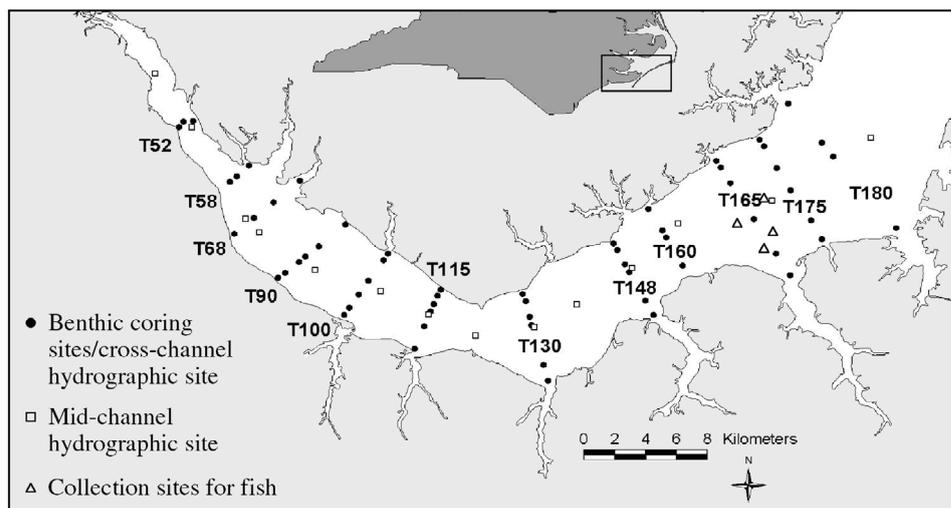
Benthic macroinvertebrates. To assess how low-oxygen events altered the benthic invertebrate prey community on the bottom of the estuary, we sampled benthic macrofauna over a wide expanse of the estuary both before and after the season of hypoxia/anoxia in 1997 and again in 1998. Benthic macrofauna was first sampled on a total of 12 cross-river transects in June 1997 (Fig. 1). We sampled 2 each of shallow (<3 m), deep (>6 m), and mid-depth (3 to 6 m) sites across most transects. A subset of 6 transects (Transects 90, 115, 160, 165, 175, 180: Fig. 1), chosen to cover the whole estuary, was re-sampled in August 1997. All transects were again re-sampled in June 1998, whereas in September 1998 the subset of transects re-sampled was expanded to 8 (the same 6 sampled in the previous August plus Transects 100 and 148: Fig. 1). All benthic samples were collected by SCUBA divers using aluminum cores of 10 cm diameter and 25 cm height (sediment-surface area sampled by 1 core = 78.5 cm²). We took 10 replicate cores, haphazardly located within a 2 m radius at each site on each sampling date. Samples

were sieved through 0.5 mm mesh and all material that did not pass through the mesh was preserved in 10% buffered formalin and stained with Rose Bengal. From the 10 replicate benthic samples at each site, a subset of 5 was randomly selected for analysis. All invertebrates, whole and fragmented, and articulated bivalve shells were picked from the remaining sediment and organic debris. This refined sample was then examined with a dissecting scope (Wild, 6 to 50×) and all organisms were identified to the lowest possible taxon.

Fish diet. Atlantic croaker *Micropogonias undulatus* were collected with 2 min mongoose trawls (50 mm mesh with 35 mm thread bag) at each of 4 sites near Transects 165 and 175 in June and September 1998. The fish were kept on ice in the field and frozen immediately upon return to the laboratory. They were later defrosted and body-index measurements were taken (wet weight, total length and standard length). Stomachs were dissected (anterior of the pyloric sphincter), weighed (wet weight), and preserved in ethanol with Rose Bengal stain. Gut contents were identified to the lowest possible taxonomic level. The numbers (N) of each type of item present in a stomach were recorded, and the percent of total stomach volume (V) made up by each item was estimated. These data were then used to calculate an index of relative importance (IRI) and a modified index (MI) (Hayse 1989): $IRI = (\%N + \%V) \times \%F$ and $MI = \%F \times \%V$, where F = frequency.

Data analyses. Nonmetric multidimensional scaling (nMDS) was performed using PRIMER 5 (PRIMER-E, Plymouth, UK; Warwick & Clarke 1991) to examine patterns in benthic community structure relating to the depth and position of stations along the longitudinal axis of the estuary (distance downstream from the freshwater end of the estuary) for each of the 4 sampling periods. Depth was chosen as a variable for examination because oxygen depletion in bottom-water co-

Fig. 1. Neuse River Estuary showing hydrographic sampling sites (cross-channel [numbered transects], mid-channel and continuous recording stations), benthic coring sites and fish collections



varies with depth such that deep and mid-depth stations experience prolonged episodes of low dissolved oxygen in the summer whereas shallow depths do not. Position along the longitudinal axis of the estuary was chosen because benthic community structure may vary along the salinity gradient of the estuary or with the longitudinal extent of hypoxic bottom-waters. All ordinations were of averages of untransformed data for each station, calculated using the 5 replicates. Bray-Curtis measures of dissimilarity were used in construction of the plots. Visual comparisons of plots generated for each collection period were used to characterize differences in community structure by depth and position in the estuary. In addition, the abundances of the 5 dominant taxa were superimposed onto nMDS plots to show their contribution to the multivariate pattern.

To test whether sampling period (June and August 1997, June and September 1998), distance along the longitudinal axis of the estuary (Transects 90, 115, 165, and 175; Fig. 1), depth stratum (shallow [<3 m], mid [3 to 6 m] and deep [>6 m]), and the interactions of these factors were significant for *Macoma balthica* or *M. mitchelli* abundances, we performed 3-factor analysis

of variance (ANOVA) on transformed ($\log x + 1$) *M. balthica* and *M. mitchelli* abundances. Transformation of the data was necessary after Cochran's C-test detected heterogeneity of variance in the untransformed data. After transformation, Cochran's C-tests confirmed homogeneity of variances at $\alpha = 0.05$. To resolve the significant 2-factor interactions, we performed Scheffé's post hoc contrasts (Day & Quinn 1989) within each level of 1 of the factors (depth stratum within each of the 4 sampling periods). For fish-diet analysis, Student's *t*-tests were performed to identify significant changes in MI values of the major diet groups from June to September 1998.

RESULTS

Hydrographic data

Salinity and temperature stratification of the water column were common during the summers of 1997 and 1998 (Luettich et al. 1999). Severely hypoxic (≤ 2 mg l^{-1}) conditions in bottom waters were detected in the sum-

Table 1. Hypoxia-severity rankings for Neuse River Estuary sampling sites based on twice-weekly hydrographic surveys ($n = 12$) from June to September 1997. Transects ran from N to S through shallow (<3 m), mid (3 to 6 m) and deep (>6 m) waters. Severity rankings were low: only 1 observation with DO levels ≤ 2.0 mg l^{-1} and no observations < 0.5 mg l^{-1} ; moderate: 2 to 3 observations < 2.0 mg l^{-1} , none of these < 0.5 mg l^{-1} ; high: ≥ 4 observations < 2.0 mg l^{-1} or ≥ 1 observations < 0.5 mg l^{-1}

Transect	Depth	DO < 2 mg l^{-1}		DO < 0.5 mg l^{-1}		Hypoxia severity	
		1997	1998	1997	1998	1997	1998
90	Shallow (north shore)	0	1	0	0	Low	Low
	Mid	3	2	0	0	Moderate	Moderate
	Deep	6	5	2	2	High	High
	Deep	6	5	1	2	High	High
	Mid	3	2	1	0	High	Moderate
	Shallow (south shore)	0	1	0	0	Low	Low
115	Shallow (north shore)	0	0	0	0	Low	Low
	Mid	2	3	0	0	Moderate	Moderate
	Deep	4	5	1	0	High	High
	Deep	4	5	1	0	High	High
	Mid	2	2	0	0	Moderate	Moderate
	Shallow (south shore)	0	0	0	0	Low	Low
165	Shallow (north shore)	0	0	0	0	Low	Low
	Mid	1	0	0	0	Low	Low
	Deep	3	0	3	0	High	Low
	Deep	2	1	2	1	High	High
	Mid	1	0	0	0	Low	Low
	Shallow (south shore)	1	0	0	0	Low	Low
175	Shallow (north shore)	1	1	0	0	Low	Low
	Mid	2	1	2	0	High	Low
	Deep	3	1	3	0	High	Low
	Deep	2	1	2	0	High	Low
	Mid	2	0	0	0	Moderate	Low
	Shallow (south shore)	1	0	0	0	Low	Low
Total	Shallow	3	3	0	0	Low	Low
	Mid	16	11	3	0	Moderate-high	Low-moderate
	Deep	30	23	15	5	High	Moderate-high

mers of 1997 and 1998 during periods of water-column stratification. The mid-channel depth of the oxycline, the zone between oxygenated surface waters and severely hypoxic bottom-waters averaged 1.0 to 1.5 m above the bottom at deep sites during hypoxic periods. In the hydrographic data, 2 patterns were evident for low dissolved oxygen: (1) oxygen depletion (hypoxia or anoxia) was more severe at deeper depths (Table 1); (2) the frequency of occurrence and average and seasonal maximum spatial extent of bottom water hypoxia were greater in 1997 than 1998 (Table 2). In summer 1997, the most persistent event of severe hypoxia occurred in bottom waters in July and early August of 1997, with a brief return to oxygenated conditions at deep sites before short-term hypoxia occurred again in early September of 1997 (Luettich et al. 1999). Deep sites on Transects 90, 115, 165, 175 experienced almost continuous (inferred from our weekly mid-channel surveys) exposure to severely hypoxic condition for the entire month of July 1997.

Table 2. Spatial extent of hypoxic (dissolved oxygen <2 mg l⁻¹) bottom water in Neuse River Estuary during summers of 1997 and 1998 based on weekly mid-river hydrographic sampling. % upstream, % downstream: percent of total hypoxic bottom area above Transect 120 (upstream) or below Transect 120 (downstream)

Sampling date	Total hypoxic bottom area (km ²)	% upstream	% downstream
1997			
10 Jun	0		
24 Jun	81	57	43
1 Jul	9	100	0
8 Jul	70	59	41
15 Jul	14	95	5
21 Jul	117	75	25
29 Jul	75	74	26
4 Aug	16	100	0
12 Aug	12	100	0
20 Aug	53	82	18
27 Aug	14	100	0
17 Sep	68	55	45
Average	44	81	19
1998			
2 Jun	85	30	70
8 Jun	0		
15 Jun	0		
30 Jun	0		
6 Jul	0		
13 Jul	0		
21 Jul	45	64	35
30 Jul	68	83	17
4 Aug	0		
10 Aug	69	90	10
17 Aug	50	100	0
25 Aug	18	100	0
9 Sep	0		
Average	26	78	22

In summer 1998, hypoxic conditions were not detected in deep mid-river sites on Transects 165 and 175 after late July or downstream of Transect 90 after late August. Deep and middle-depth sites on or upstream of Transect 115 experienced 2 periods when hypoxic conditions were detected on at least 2 consecutive sampling dates: on May 27 and June 2, 1998, hypoxic conditions were recorded at deep and mid-depth sites on or upstream of Transect 115. On June 6, 1998 hypoxic conditions were not recorded anywhere on these transects. The second period of sustained hypoxia was first detected on July 21, then again on July 30, but ended before August 4, 1998. For Transects 165 and 175, there were no hypoxic events that persisted for 2 consecutive weekly measurements in 1998.

The area of seafloor habitat covered by hypoxic bottom-water averaged 44 km² (range = 0 to 117 km²) in the summer of 1997 and 26 km² (range = 0 to 85 km²) in the summer of 1998 (Table 2). For the period June 10 to September 2, 1997, only 1 (June 10) of a total of 10 sampling dates displayed no hypoxic bottom water. From June 2 to September 9, 1998, 7 out of 13 surveys revealed no hypoxia anywhere in the estuary (Table 2). During both years the majority (>78%) of the hypoxic area was upstream of Transect 120 (Table 2), although this upstream region comprises only half the areal extent of the downstream region. Differences in the frequency of occurrence of hypoxic conditions between 1997 and 1998 were for the most part evident in the area downstream of Transect 120 not in the upstream section (Table 1).

Benthic macroinvertebrates

Analysis of cores revealed an infaunal community typical of southeastern US and mid-Atlantic mesohaline estuaries (see Tenore 1972). By biomass, *Macoma balthica* and *M. mitchelli* accounted for the majority (80 to 90%) of the infaunal community of the Neuse River Estuary prior to hypoxic conditions. Spionid and capitellid polychaetes accounted for the majority of the remaining infaunal biomass. The bivalves *Mulinia lateralis* and *Rangia cuneata* were also present near the upper reaches of the estuary. Amphipods and chironomid larvae (insects) were common in many samples, although they accounted for a small proportion of total biomass. Prior to hypoxic conditions in June 1997, nMDS plots showed relatively little separation among stations by depth (Fig. 2). Following the summer of intense hypoxia at deep and some mid-depth stations, separation of shallow and deep stations by depth was evident (Fig. 2). This depth pattern persisted for both sampling dates in 1998. Superimposing the abundances of individual taxa onto the nMDS plots to show

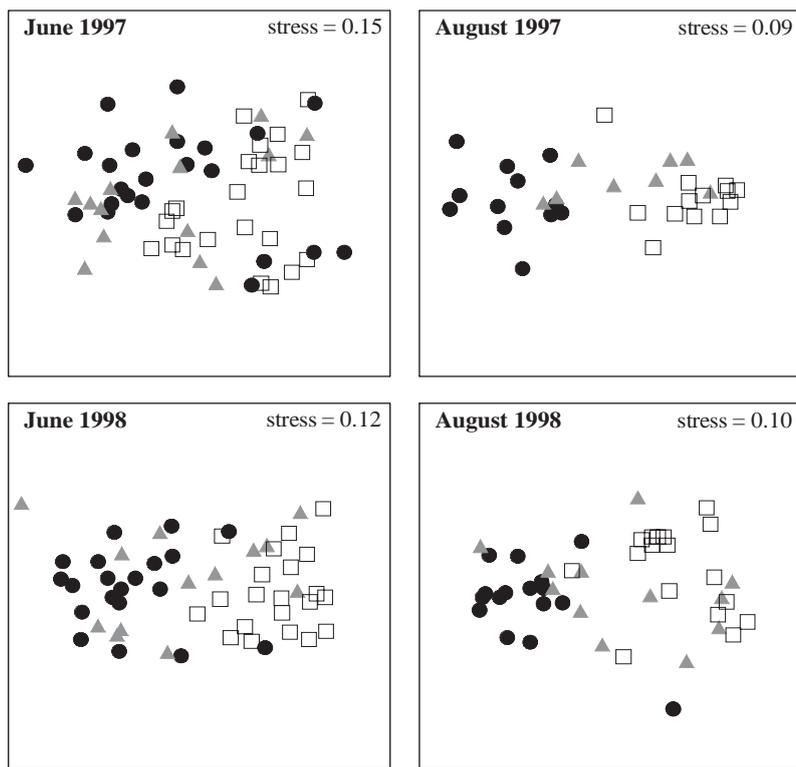


Fig. 2. nMDS ordinations of assemblages of macrofauna in shallow (●), mid (▲) and deep (□) depths of Neuse River in June and August 1997 and June and August 1998. Data points represent averages of untransformed data from each site ($n = 5$). Stress indicates degree to which plot represents data (stresses of < 0.15 are considered good representations, with minimal risk of misinterpretation)

their contribution to the multivariate pattern among depths, revealed that *M. balthica*, *M. mitchelli* and spionid polychaetes each responded in a similar manner to station depth, with highest densities at shallow depths (Fig. 3).

Results of ANOVAs testing whether the abundances of *Macoma balthica* or *M. mitchelli* varied with sampling date, transect location and depth stratum, were consistent with the emergence and persistence of the depth pattern evident in the nMDS plots. For each species, ANOVA showed all 2-way interactions among combinations of sampling period, depth stratum, and transect location to be significant ($p < 0.05$) or marginally significant ($0.05 < p < 0.10$). The 3-way interaction was not significant for either *Macoma* species. To resolve the 'sampling period \times depth' interaction, we examined how abundance varied with depth within each sampling period. Abundance of *M. balthica* differed with depth only for the August 1997 sampling period (Fig. 4). *M. mitchelli* abundances differed with depth in both post-hypoxia samplings (August 1997, September 1998), but did not differ in either of the June sampling periods. In August 1997, *M. balthica*

and *M. mitchelli* abundances were essentially zero at all deep sites, and significantly lower than at the shallow depth ($p < 0.05$ for both *M. balthica* and *M. mitchelli*). Abundances of *M. mitchelli* also differed with depth in September 1998: shallow depths had higher abundances than deep and mid-depth areas ($p < 0.05$ for both comparisons), which did not differ ($p > 0.05$). *M. balthica* displayed an identical pattern of changing abundance with depth in September 1998, but no difference was significant. Consequently, both species of *Macoma* displayed an absence of detectable depth relationships in early summer before the season of oxygen depletion, followed by evolution of a pattern over the course of summer such that deep areas became relatively depleted. This seasonal response was quantitatively stronger in 1997 and even extended the detectable depletion to mid-depths for *M. mitchelli* in summer 1997 (Fig. 4).

Analysis of the interaction of transect location and depth revealed greater depletion of both species of *Macoma* at mid-depth sites on up-river transects (90 and 115) than down-river transects (165 and 175). For *M. balthica* and *M. mitchelli*, deep and mid-depth sites had lower abundances than shallow sites ($p < 0.05$ for all post hoc contrasts) on Transects 90 and 115, whereas mid-depth sites showed higher abundances than deep sites ($p < 0.05$ for post hoc contrasts) and did not differ from shallow sites ($p > 0.05$ for post hoc contrasts) on Transects 165 and 175.

Fish diets

Gut-content analysis of *Micropogonias undulatus* revealed that food types shifted in importance between June and September 1998 at the 4 sites (all > 5 m deep: see Fig. 1) that were sampled both before and after hypoxia. Although a wide range of items was found in the fish stomachs, both the IRI and MI values show that gut contents predominately consisted of 4 different items: shell, tissue, polychaetes and plant matter ('tissue' is unidentifiable animal tissue that has been digested to an extent that prohibits confident visual differentiation). These 4 items all had MI values approaching or above 1000 for at least 1 of the 2 dates,

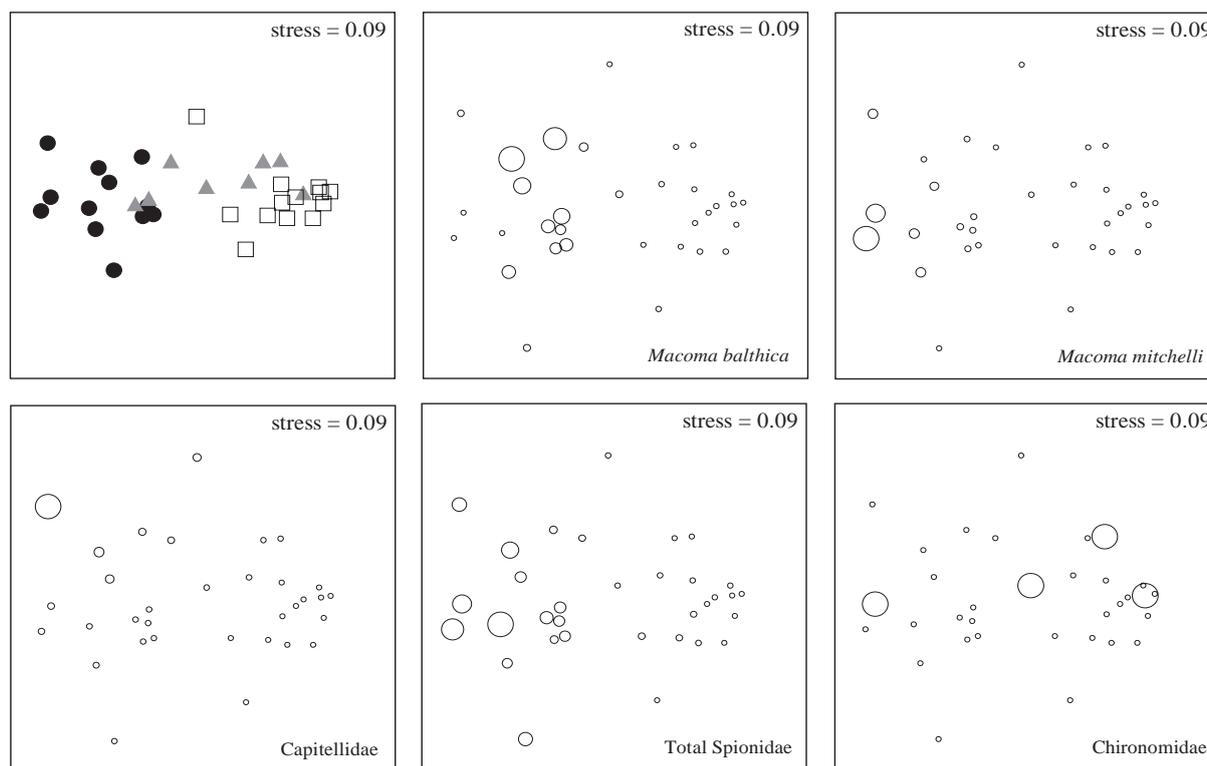


Fig. 3. nMDS ordination of assemblages of macrofauna found at shallow (●), mid (▲) and deep (□) depths of the Neuse River and relative abundances (represented by size of data points) of *Macoma balthica*, *M. mitchelli*, Capitellidae, Spionidae and Chironomidae in August 1997. Data points represent averages of untransformed data from each site ($n = 5$) and stress indicates degree to which plot represents data. Abundance patterns of *M. balthica*, *M. mitchelli* and Spionidae are highly representative of overall multivariate pattern. Similar findings were evident for the 3 other collection periods

while the other food items rarely reached a MI of 500. Analysis of the croaker diets (MI) from the 4 sites indicated that the importance of shell (indicative of feeding on *Macoma* spp. based upon our examination of gut contents from experimental assays) decreased between June and September ($p = 0.02$) while the importance of polychaetes and plants increased ($p < 0.02$). These data indicate that the fish were preying on fewer (or smaller) bivalves after hypoxia, and that they were instead relying more on polychaete and plant material (Fig. 5).

DISCUSSION

Declines in dissolved oxygen that result in large part from eutrophication (Diaz & Rosenberg 1995, Jørgensen & Richardson 1996, Gray et al. 2002) degrade the estuarine bottom habitat essential for rearing of demersal fishes and crustaceans. Significant changes in the quality of bottom habitat occurred over the course of the summer in the Neuse River Estuary. Although an array of physical and biological factors is known to affect benthic

community composition, the data reported here provide strong evidence that the stress of low oxygen caused substantial impacts on macrofaunal community composition between June and September 1997 in the deep and mid-depth habitats of the Neuse River Estuary. Furthermore, our comparison between years in seasonal changes in the benthic community supports the conclusion that the degree of habitat degradation reflects the severity of summer hypoxia. Finally, the fish diet analyses support our contention that hypoxia-induced changes in benthic habitat can be transmitted up the food chain to demersal fishes.

In order to conclude that hypoxia was the most likely cause of the observed changes in benthic communities between June and August 1997, dissolved oxygen concentrations over that time period must have been sufficient to cause infaunal mortality. The dissolved oxygen dynamics at all deep sites on all transects included at least 1 to 2 wk under 0.5 mgDO l^{-1} (Tables 1 & 2), a concentration known to cause mass mortality of benthic infauna (see Diaz & Rosenberg 1995 for review). Resolution of DO data does not allow more precise temporal estimates, but these events were of sufficient

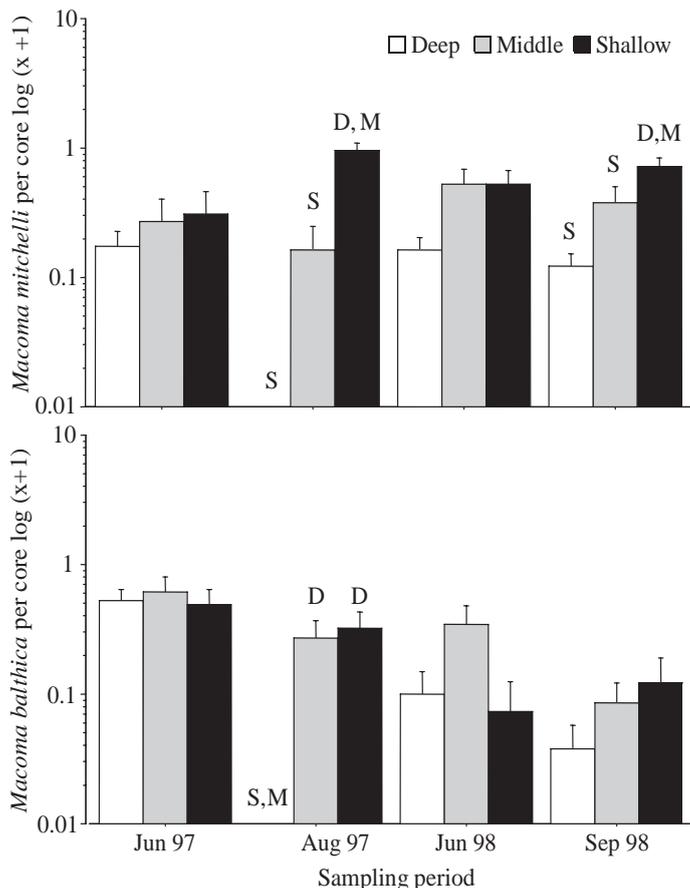


Fig. 4. *Macoma mitchelli* and *M. balthica*. Mean abundance (+1 SE) of 76.3 cm⁻² core within in each depth stratum for the 4 sampling periods. Data were log (x + 1)-transformed. Letters above bars denote significant post hoc differences (p < 0.05), where S = mean values differed from shallow sites, M = mean values differed from mid-depth sites, D = mean values differed from deep sites within the relevant sampling period

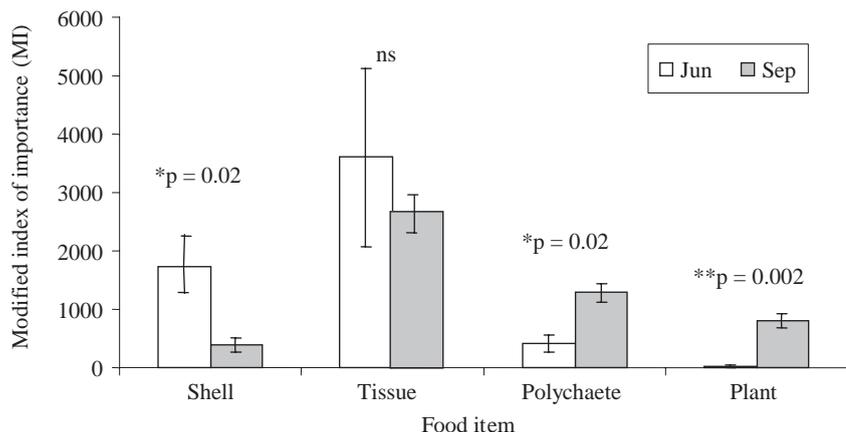


Fig. 5. *Micropogonias undulatus*. Mean (+1 SE) values of modified index of importance (MI) for 4 diet groupings for Atlantic croaker before and after hypoxia. Statistical significance based on Student's *t*-test results for June 1998 versus September 1998 fish collections

intensity to have caused the mortality observed in *Macoma balthica* (Modig & Ólafsson 2001, Borsuk et al. 2002). The weaker response of the benthic community to the less intense hypoxia of summer 1998 also supports the conclusion that the stress of persistent low DO was indeed the cause of the declines in *Macoma* spp. in summer 1997.

The dominant patterns of change in the benthic infaunal community between June and August 1997 agree with our predictions of community responses to seasonal hypoxic disturbance. Shallow sites exhibited declines in *Macoma* spp. abundances, but they did not exhibit defaunation to the same degree as all the deep sites. *Macoma* spp. is a very important food species for the dominant demersal consumers in this system, blue crabs (Hines et al. 1990, Seitz et al. 2003), spot (which consume primarily clam siphons: Hines et al. 1990, Skilleter & Peterson 1994), and Atlantic croaker (Eby et al. 2005, this study). By September 1997, mortality of adult *M. balthica* at deep sites was 100%, and recruitment was extremely low (only 2 individuals pooled over all sites), while in middle and shallow sites both adult and juvenile clams were present. This corresponds with observations by Holland et al. (1987), who noted that more than 1 yr-class of *M. balthica* was rarely found at deep sites in the Chesapeake Bay, which experiences seasonal anoxia.

The pattern of smaller declines in benthic infaunal densities at shallower sites is not consistent with an alternative explanation that predation may have been the cause of the summer decline. Although predation by demersal consumers on *Macoma* spp. can contribute to declining prey populations, the spatial and temporal patterns of summertime depletion of *Macoma* spp. that we documented are inconsistent with predation. Under normoxic conditions, demersal predators feed in both shallow and deep waters of the Neuse River Estuary with bias against deep-water locations (Lenihan et al. 2001), whereas the seasonal imposition of hypoxia in deeper waters actually drives demersal predators into shallow areas and enhances their feeding in shallow, not deep, zones (Lenihan et al. 2001, Eby et al. 2005). Consequently, depth-related patterns produced by predators would exhibit a pattern opposite to that observed, namely greater summertime declines in benthic macroinvertebrate densities in shallow sites. Similarly, the interannual difference in the magnitude of summertime decline in macrobenthic densities cannot be explained by differences in predator abundance between 1997 and

1998: the abundances of both spot and croaker, the dominant demersal consumers, were at least 2 times higher in 1998 than in 1997 (Baird et al. 2004).

Our 4 samplings of benthic invertebrate densities provide some insight into the recovery of the benthic community during the fall, winter and spring following severe hypoxia in summer 1997. *Macoma balthica* at deep sites had not regained their June 1997 abundance levels by the following June. Based upon a detailed analysis of *Macoma* spp. collections made in both June and August of 1968, 1969, 1970, and 1971 (years that also experienced severe summer hypoxia), the failed recovery that we report in this study is not representative of most years (H. Porter unpubl. data). A likely explanation for the recovery failure from late summer 1997 to June 1998 is that unusually intense spring rainfall over the Neuse River basin (Luettich et al. 1999) inhibited successful recovery of benthic invertebrates. Luettich et al. (1999) showed that a large portion of the estuary had uncharacteristically low salinities (<2) from March through April as a result of the high freshwater inputs. This interpretation gains support from the observation that *M. mitchelli*, the more estuarine species, showed full recovery, while *M. balthica*, the more stenohaline species, failed to recover its June 1997 density.

Establishing the final, cascading linkage, the impact of degraded bottom habitat on demersal fishes, depends on assessing how declines in benthic prey resources affect demersal predators. Our analysis of gut contents of croaker in the Neuse River Estuary demonstrates a shift in the importance of different dietary items over the course of summer 1998 (Fig. 5). Croaker modified their diets from a large amounts of bivalves (denoted by 'shell') in June to dominance by polychaetes and plant material in September. Croaker are known as opportunistic feeders that modify their diet depending on prey availability (Currin et al. 1984, Hines et al. 1990). Thus, the switch from bivalve prey in June to polychaetes and plant matter in September reflects the large summertime decline in *Macoma* spp. densities in deep and mid-depth areas of the estuary, consistent with the loss of an important and perhaps preferred prey type.

The results of 2 collaborative studies (Baird et al. 2004, Eby et al. 2005) indicate that the summertime declines in availability of benthic invertebrate prey have serious population consequences for demersal fishes as well as impacts on ecosystem processes. Eby et al. (2005) demonstrated that the physiological condition, individual growth rate and population growth of croaker and spot in the Neuse River Estuary were lower in the year of severe hypoxia (1997) than in 2 yr of less intense summertime oxygen depletion (1998, 1999). Combining these results with ours implies that

switching from bivalves to alternative prey resources including plant matter did not suffice to sustain high production of demersal fishes throughout the Neuse River Estuary. This conclusion is also supported by the results of trophic mass-balance modeling by Baird et al. (2004), who demonstrated that production of the benthic infauna in the Neuse River Estuary was sufficient to support energy demands by demersal fishes and blue crabs before but not after the large-scale hypoxic event in July 1997.

Modification of benthic communities has the potential to affect a wide range of important processes in an estuarine system. Of primary interest to humans is fisheries production, which is 1 issue addressed in our study of the Neuse River Estuary. Seasonal hypoxia has resulted in the reduction of lobster catches in the Kattegat (Rosenberg & Loo 1988, Rosenberg et al. 1992), and other extensive hypoxic/anoxic events are responsible for reducing commercial catches of finfishes and crustaceans, both by starvation after loss of the benthic prey community and by direct stress from depleted oxygen (Diaz & Rosenberg 1995). Hypoxia-driven changes in fishery production are not necessarily all negative. When high biomass of opportunists becomes established after hypoxia, then some demersal feeders may benefit as a result of the enhanced prey. For example, shrimps and other demersal consumers of meiofaunal and small macrofaunal invertebrates may experience higher densities of prey following summer hypoxic events because of colonization by numerous small opportunists (Alongi 1985, Pihl 1994, Diaz & Rosenberg 1995, Peterson et al. 2000). Further studies connecting hypoxia to tangible changes in fish habitat and ultimately productivity of fisheries, either positive or negative, are needed given the complex nature of coastal foodwebs and the increase in eutrophication-induced hypoxia events around the world.

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