Marine Biology 112, 349–361 (1992)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

# Hypoxia-induced structural changes in the diet of bottom-feeding fish and Crustacea*

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Date of final manuscript acceptance: November 21, 1991. Communicated by T. Fenchel, Helsingør

**Abstract.** Interactive effects of three alternating normoxia-hypoxia cycles on benthic prey exploitation by mobile fish (spot, *Leiostomus xanthurus*; and hogchoker, *Trinectes maculatus*) and a burrowing crustacean (*Squilla empusa*) were investigated in the York River, Chesapeake Bay, Virginia, USA, in 1989. Predators collected in four depth strata (A: 5 to 10 m; B: 10 to 14 m; C: 14 to 20 m; D: > 20 m) variously affected by hypoxia were separated into size classes (three for spot and two each for hogchoker and mantis shrimp) to examine potential ontogenetic influences in prey selection. The most severe effects of hypoxia on the benthos occurred in the two deepest strata (C and D) and decreased in shallower strata (B > A), with Stratum A never affected by low oxygen. Predators investigated exhibited dietary evidence of optimal prey exploitation during or immediately after hypoxic events. In most instances gut contents contained significantly larger, deeper-burrowing prey during periods of low oxygen than during alternating periods of normal oxygen levels. Spot consumed a greater biomass (45 to 73%) of polychaetes than other prey, with crustaceans initially also constituting a main dietary component but decreasing in importance later in the study period. The deep-burrowing anemone, *Edwardsia elegans*, was an important prey species for spot, particularly in the lower depth strata affected by hypoxia. Prey consumed by 10- to 15-cm-long spot increased significantly in size during some hypoxic events, suggesting a sublethal effect of hypoxia on large benthic species. Polychaetes (primarily *Glycera americana*, *Notomastis latericeus* and *Loimia medusa*) were dominant dietary components in hogchoker, making up between 85 and 98% of the diet. Bivalve siphons became important prey for hogchoker in the three deepest strata and were only consumed after the August hypoxia. Stomach contents of mantis shrimp were difficult to identify in most instances due to the near complete mastication of consumed prey. Crustaceans were important prey initially but became less conspicuous in the diet subsequent to the July hypoxia event, when hydroids became more dominant. Overall, predator species exhibited optimal exploitation of moribund or slowly recovering benthos affected by hypoxia. The sublethal effects of hypoxia through increased availability of benthos to resident predators can have important consequences for energy flow in areas such as the York River which experience periodic low-oxygen cycles.

## Introduction

Marine coastal eutrophication is common worldwide and has been implicated as the cause of structural and functional changes in pelagic and benthic ecosystems (Elmgren 1989, Rosenberg et al. 1990, Boesch et al. 1991). Nutrient loading often results in increased primary production, changes in species composition, or altered duration and timing of plankton blooms. Higher production in the shallow pelagic system often results in higher organic material transfer to benthic communities (Cohen et al. 1984, Malone et al. 1986). Organic enrichment increases food for benthic populations but also results in an increased oxygen demand in bottom water during remineralization (Malone et al. 1988). Where water column mixing is limited, for example due to temperature or salinity stratification, hypoxia ($O_2 < 2$ mg $l^{-1}$) or anoxia ($O_2 < 0.2$ mg $l^{-1}$) may occur (Haas 1977). Anoxia generally results in severe reductions in the abundance and biomass of macrobenthic organisms (e.g. Rosenberg 1977, Holland et al. 1987) and limits the distribution of commercially important finfish and shellfish species (e.g. May 1973, Rossignol-Strick 1985). Effects of hypoxia are less well documented, but evidence suggests that benthic species, including fish, exhibit behavioural and physiological responses that may influence community structure and function (Rosenberg and Loo 1988, Pihl 1989, Baden et al. 1990, Pihl et al. 1991).

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Low oxygen levels are characteristic of Chesapeake Bay during summer (Officer et al. 1984, Kuo and Neilson 1987). Many predators and their prey in this estuary are potentially affected by such phenomena. Spot (*Leiostomus xanthurus* Lacépède) and hogchoker (*Trinectes maculatus* Bloch and Schneider) are among the more common bottom-feeding fish species in estuaries along the southeast coast of the United States (Dovel et al. 1969, Stickney et al. 1975, Chao and Musick 1977, Koski 1978). Spot spawn in the Atlantic and juveniles use estuaries as nursery areas for 1 to 2 yr (Chao and Musick 1977, Kobylinski and Sheridan 1979, Beckman and Dean 1984, O'Niel and Weinstein 1987). The hogchoker resides in low-salinity coastal waters, with juveniles (0-group) found upstream in almost fresh water and older year-classes (1- to 4-group) occupying the lower, more saline part of the estuary where spawning occurs (Dovel et al. 1969, Peters and Boyd 1972, Markle 1976). The mantis shrimp (*Squilla empusa* Say) is abundant in Chesapeake Bay (Wass 1972) and ranges in distribution throughout the western Atlantic from Maine (USA) through the Gulf of Mexico to Surinam, South America, where it burrows in soft sediments (Manning 1969). Few details of the ecology, including the diet, of this species are known. The purpose of this investigation was to evaluate interactions between water column hypoxia and structural changes in the diets of two species of demersal bottom-feeding fish and a stomatopod crustacean. The diets of spot, hogchoker and the mantis shrimp were analysed during three alternating cycles of normoxia and hypoxia in the lower York River, a tributary in Chesapeake Bay, USA. The investigation was based on analysis of 649 (28 empty), 1228 (672 empty) and 771 (406 empty) stomachs from spot, hogchoker and mantis shrimp, respectively, collected during the summer of 1989.

## Materials and methods

### Study area

The lower York River, Virginia, is a major tributary of Chesapeake Bay (Fig. 1), and exhibits predictable cycles of hypoxia and normoxia during summer. The lunar neap-spring tidal cycle establishes vertical density stratification-destratification of the water column, and controls the set-up of hypoxia (Haas 1977). Periods of stratification occur during neap tide when tidal currents are reduced (Haas 1977, Hayward et al. 1986). Variation in freshwater input is thought to have little effect on stratification, and thus establishment of hypoxia (Hayward et al. 1986). Strong wind events are able to interrupt the onset of hypoxia and completely mix the river vertically with respect to oxygen (Diaz et al. in press). Seasonal hypoxia may first appear as early as May, but usually starts in June, and is most severe in August. By September hypoxia dissipates with the onset of fall cooling (Kuo and Neilson 1987).

The study area was divided into four depth strata that corresponded to the occurrence of hypoxia (Fig. 1), based on the previous work of Haas (1977) and Kuo and Neilson (1987). Stratum A, from 5 to 10 m depth, was above the depth at which hypoxia typically occurs. In the York River, only depths greater than 10 m seem to be affected by hypoxia, so for mobile fauna the shallow areas should represent a refuge from hypoxia. Stratum B, from 10 to 14 m depth, was sometimes affected by hypoxia. Strata C, from 14 to 20 m depth, and D, > 20 m depth, were always affected by seasonal hypoxia when it occurred (Kuo and Neilson 1987). The average silt-clay percentage within each stratum was 36, 80, 93 and 78 for

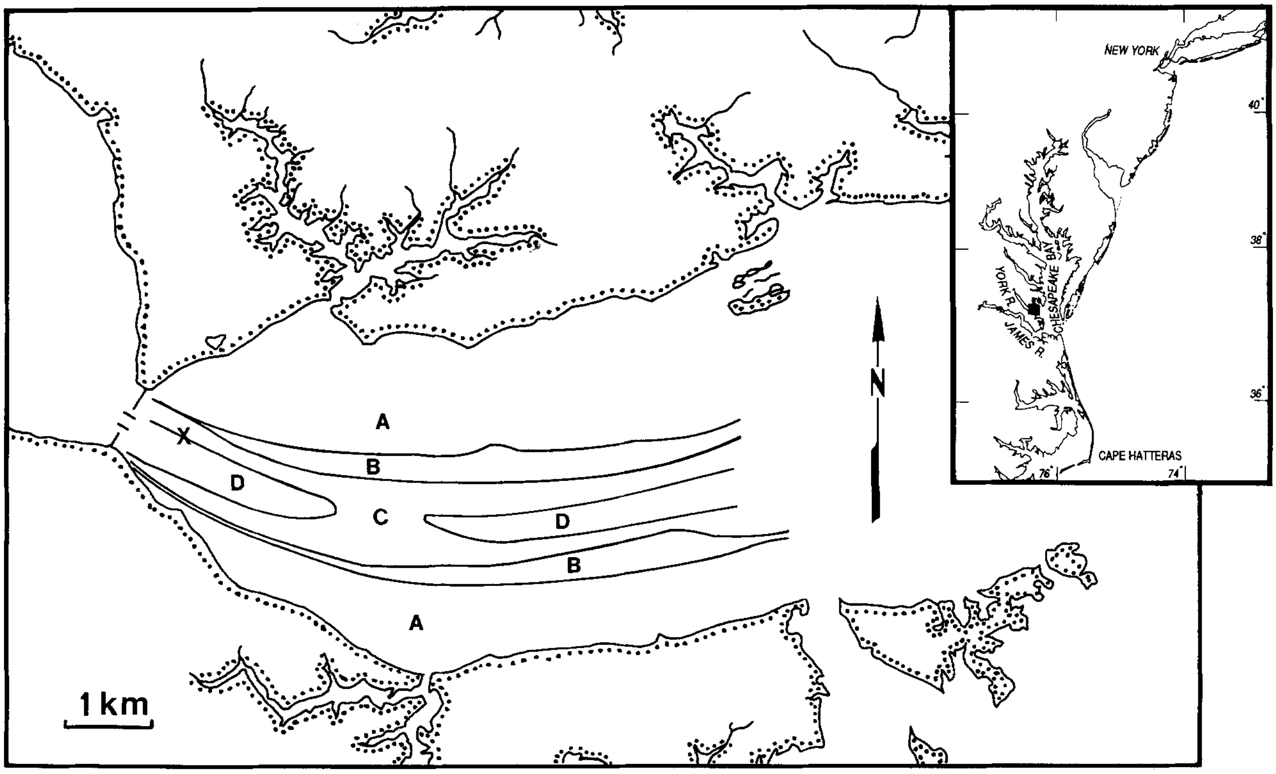

**Fig. 1.** Lower York River study area, USA, with depth boundaries of strata delineated. Stratum A is 5 to 10 m, Stratum B is 10 to 14 m, Stratum C is 14 to 20 m and Stratum D is > 20 m. Radio-telemetering environmental data buoy was located within Stratum C (indicated by X)

A, B, C and D, respectively. During our study bottom temperature ranged between 15 and 26 °C and bottom salinity from 17 to 25 ppt (see Fig. 2; Pihl et al. 1991).

### Sample collection

Species investigated were sampled with a 4.9 m otter trawl fitted with a net having a wing stretch-mesh size of 19 mm and a cod end stretch-mesh size of 6.3 mm. Trawling in four different depth strata (Stratum A = 5 to 10 m; Stratum B = 10 to 14 m; Stratum C = 14 to 20 m; Stratum D > 20 m) was accomplished weekly or biweekly between 26 June and 20 October, 1989 (Fig. 1 and 2). On each occasion two to three trawl samples were taken within each stratum. The length of each trawl sample was 400 to 500 m, covering an area of about 1500 $m^2$. Trawls were made against the current during daytime periods of low tidal flow. Fish and stomatopods were taken to the laboratory and cooled under refrigeration or on ice within 5 min of capture to prevent further digestion of stomach contents. Fish total length was measured and individuals were separated into 5-cm size-classes (spot: 5–10, 10–15 and 15–20 cm; hogchoker: 5–10 and 10–15 cm). In mantis shrimp, the shortest carapace length (posterior orbital margin to posterior mid-dorsal carapace margin) was used to separate individuals into adult and juvenile cohorts based on length-frequency distributions.

If available, stomachs from 5 to 20 individuals of each size-class per species were taken from each depth stratum during sampling. If fewer than five individuals per size class were collected on any sample date they were not included in the analysis. In October all three species were caught in low densities and no stomachs were analysed. After dissection, fish stomach contents were preserved in 4% buffered formalin. Stomach contents from individuals within each size-class and depth stratum were pooled on each sampling occasion and subsequently fractionated by washing through nested sieves (6.3, 3.3, 2.0, 1.0 and 0.5 mm). The wet weight of prey on each sieve fraction was determined to the nearest 1.0 mg. Size distribution of stomach contents from fish collected between strata are reported and analysed herein as biomass retained on the different sieve sizes.

Mantis shrimp were frozen whole and the stomachs were later removed and preserved in 70% ethanol for 1 d. All stomach contents were identified to the lowest practical taxonomic unit under a stereo dissecting microscope. The wet weight of each prey category was determined to the nearest 1 mg. Stomach contents of mantis shrimp were sometimes quantified into gross taxonomic categories (crustaceans, hydroids, molluscs, polychaetes and others) by volumetric analysis due to the high incidence of macerated food in the gut.

Bottom-water dissolved oxygen was continuously monitored throughout the study at a depth of 18 m (1 m above the sediment) with a radio-telemetering data buoy equipped with a Seabird Seacat CTD and SB 13 oxygen probe (Mountford et al. 1989, Diaz et al. in press). Water-column dissolved oxygen was also profiled from the surface to the bottom at 1 m intervals with a Yellow Spring Instruments meter (model YSI-58) during the three periods of hypoxia. The oxygen probe was repeatedly calibrated by means of Winkler titration.

### Statistical analysis

The assumption made in comparing fish and crustacean feeding was that predator species did not differ through time and between strata in their selectivity of prey species and size categories. Thus, the null hypothesis tested in all comparisons was that of no difference in feeding selectivity across strata or time. Data were standardized as the percent composition of stomach contents to adjust the marginal structures of the tables and allow comparisons of the conditional probabilities across strata and time (Agresti 1990). The odds ratio Chi-square statistic was used to test the null hypothesis (Fleiss 1981).

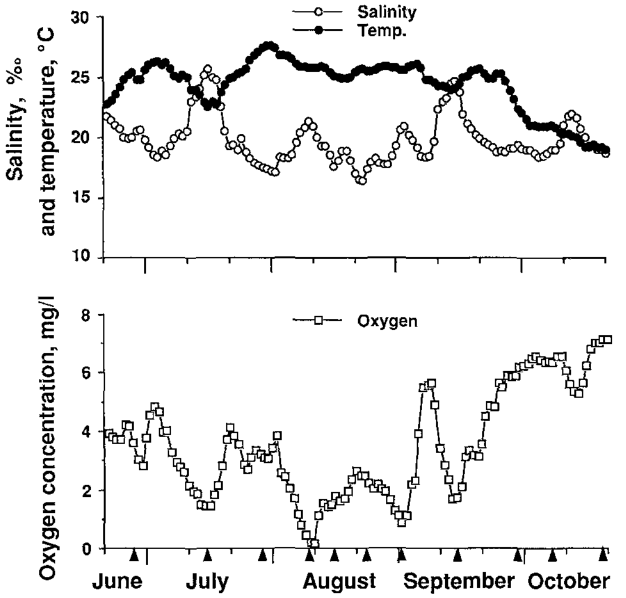

**Fig. 2.** Daily mean salinity, temperature, and oxygen concentration in the bottom water (18 m depth) in the York River (26 June to 20 October 1989). Means are calculated from measurements recorded continuously every 20 min by an automated radio-telemetering data buoy. Filled triangles indicate the times trawl collections were made

## Results

### Oxygen concentrations and species collections

Three major hypoxic periods were observed during the investigation (Fig. 2). Low concentrations of dissolved oxygen in the water column coincided with water-mass stratification during neap tide in mid-July, early August and early September. Daily mean ($n = 72$) oxygen concentration of 2 mg $l^{-1}$ or less occurred for 6 d (11 to 16 July) during the first period, 14 d during the second period (5 to 18 August, with oxygen concentrations below 1 mg $l^{-1}$ for 4 d) and 6 d (28 August to 2 September) during the third period (Fig. 2). During the last hypoxia, a storm disrupted the oxygen stratification, reducing the severity of this low-oxygen period. A few days after the storm, mean oxygen concentration again declined and dropped below 2 mg $l^{-1}$ for an additional 2 d, 13 and 14 September. The percentage of time that oxygen was 2 mg $l^{-1}$ or less during the investigated hypoxic events was 89, 78 and 91 respectively. During normoxic periods oxygen concentrations displayed a strong semidiurnal tidal cycle. Oxygen concentrations typically changed by 1 to 3 mg $l^{-1}$ above or below the oxygen mean during each tidal cycle. With the onset of each of the hypoxic events there was a dampening in the range of oxygen concentration to less than ± 1 mg $l^{-1}$ per tidal cycle. At the end of the hypoxic event the range again increased.

Vertical distribution of oxygen was measured in the four depth strata on all sampling occasions and is shown for the three hypoxic events in Fig. 3. In Stratum A hypoxia was never observed. Strata B and C had oxygen concentration below 2 mg $l^{-1}$ in the bottom water during the July and August hypoxia, whereas in Stratum D hypoxia also occurred in September. In Stratum D low oxy-

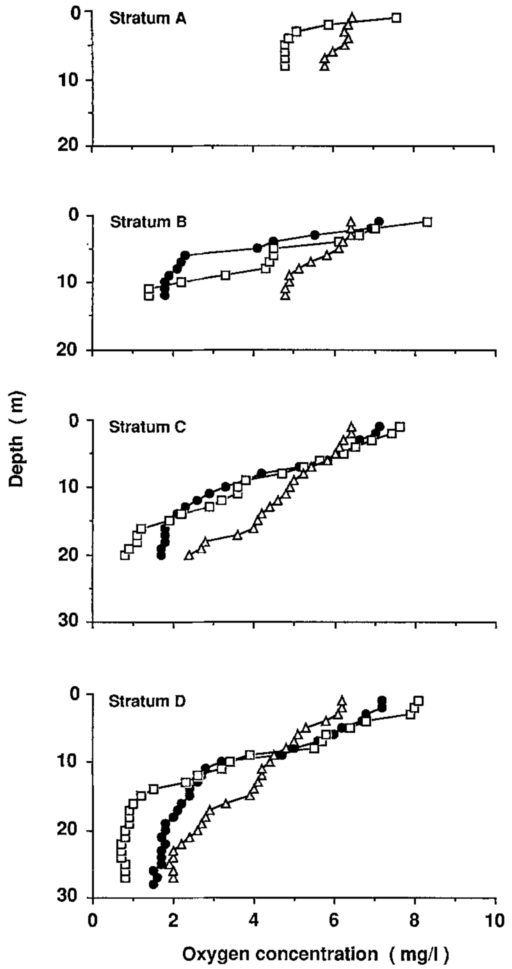

**Fig. 3.** Vertical distribution of oxygen concentration in the four depth strata in York River during the periods of hypoxia, 14 July (●), 9 August (□) and 1 September (△), in 1989. Oxygen was measured with an air- and Winkler-calibrated YSI oxygen meter at every meter from surface to bottom

gen concentration was measured in the water column from between 15 to 20 m depth down to the bottom.

Species were sampled before, during and after the hypoxic periods as shown in Fig. 2, and stomachs were analysed. Hogchoker were almost absent from all depth strata during the most severe hypoxia in early August, and only stomachs from spot and mantis shrimp were analysed.

## Food selection

### *Spot*

Three size-classes of spot were sampled during the study (Fig. 4). The smallest fish (5 to 10 cm) were mainly caught in Stratum A during the beginning of the study, mid-size (10 to 15 cm) individuals were found within most depth strata during all sampling periods, and the largest fish (15 to 20 cm) were mainly sampled in depth Strata B and C.

Crustaceans and polychaetes constituted the dominant biomass of prey items eaten by spot (Table 1). Polychaetes dominated in all depth strata and in all size-classes of fish, contributing between 45 and 73% of the biomass consumed. The polychaete *Paraprinospio pinnata* was consumed at all depths and represented the greatest biomass in spot stomachs, followed by *Glycinde solitaria*, *Eteone heteropoda*, *Nereis succinea*, *Pectinaria gouldii* and *Clymenella torquata*. Among the crustaceans, mysids, cumaceans, harpacticoid copepods and the shrimp *Ogyrides alphaerostris* dominated in biomass at most depths and in most size-classes of spot. Other food items taken were the burrowing sea anemone *Edwardsia elegans*, gobiid fish and tunicates.

Crustaceans were generally more important prey early in the study than later in the season (Fig. 4). A relative increase in the proportion of crustaceans in the diet of spot was observed during the first two hypoxic periods (July, August). This increase was significant at depth Strata B and C ($P<0.01$), but was not seen during the third (September) hypoxic event. During the August hypoxia, *Crangon septemspinosa* and *Ogyrides alphaerostris* made up most of the food taken by mid-sized spot in Strata B and C, and polychaetes were of little importance. Subsequently, the proportion of polychaetes increased significantly in the diet of spot from Stratum B ($P<0.01$) but not in those from Stratum C. Large species such as *Clymenella torquata*, *Glycera americana* and *Nephtys* sp. were consumed in the three deepest strata, especially by 10- to 15-cm spot. Among other prey eaten, *Edwardsia elegans* contributed the greatest biomass. This species was mainly found in fish from Strata B, C and D, and occurred only after the second hypoxic period.

The size distribution of prey consumed by 10- to 15-cm spot varied by depth and sample date (Fig. 5). In late June prey from fish collected in the four depth strata were all retained on the three smallest (2.0 to 0.5 mm) sieves. During and after the first hypoxia in July a significant increase ($P<0.01$) in size of prey consumed was observed in fish from Strata B and C as evidenced by the retention of most prey on the 3.3 mm sieve. During the severe hypoxia in early August, prey size consumed by spot increased further within these two depth strata ($P<0.01$). Most stomach contents were retained on the 3.3 mm sieve, and some were also retained on the largest (6.3 mm) sieve. At the same time, stomach contents of spot from Stratum A were retained mainly on the 2.0 mm sieve. Subsequent to the August hypoxia, food size decreased significantly in Strata B and C ($P<0.01$) but not in Stratum A or D. The third hypoxic period (early September) had little apparent effect on the prey size consumed and patterns resembled pre-hypoxia data observed in late June, with most prey retained on the three smallest sieves. Similar analyses for spot in the smallest and largest size categories were not possible because of the low numbers of fish collected.

### *Hogchoker*

Polychaetes were the dominant prey for both size-classes of hogchoker, contributing between 85 and 98% of the

**Table 1.** *Leiostomus xanthurus*. Mean percent biomass of food items in the diet of three size-classes (5–10, 10–15, 15–20 cm) of spot from the four depth strata (A, B, C, D) during the period 26 June to 28 September 1989 in the lower York River, Virginia, USA

| Prey | 5–10 cm | | | | 10–15 cm | | | | 15–20 cm[a] | | | Overall average |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | A | B | C | D | A | B | C | D | B | C | D | |
| No. of stomachs analysed (empty) | 45 (0) | 55 (4) | 73 (4) | 21 (0) | 82 (2) | 117 (5) | 114 (3) | 54 (2) | 28 (1) | 38 (1) | 22 (1) | |
| Crustacea | 24.2 | 43.0 | 34.0 | 33.0 | 23.8 | 28.6 | 39.3 | 15.4 | 21.2 | 30.3 | 18.5 | 28.3 |
| *Ampelisca* sp. | 0.3 | 0.3 | | | 2.2 | | 0.1 | 1.4 | | | 1.0 | 0.5 |
| Amphipoda | 0.1 | | | | 4.0 | 0.4 | | | 0.2 | 0.8 | | 0.7 |
| *Caprella* sp. | | 0.2 | 0.5 | 2.0 | 3.2 | 1.8 | 1.9 | 1.0 | 1.2 | 0.2 | 1.0 | 1.2 |
| *Corophium* sp. | 0.2 | | 1.5 | 1.0 | | | 5.2 | 0.2 | 0.2 | 1.9 | 2.5 | 1.2 |
| *Crangon septemspinosa* | | | | | 2.8 | 2.3 | 6.2 | | | | | 1.0 |
| Cumacea | 4.3 | 0.2 | 0.5 | 2.0 | 0.8 | 1.5 | 5.1 | 1.2 | 1.2 | 7.1 | 1.5 | 2.3 |
| *Elasmopus levis* | | | | | | <0.1 | | | 1.4 | | | 0.1 |
| *Erictonius* sp. | | | | 1.0 | 1.8 | | | 0.2 | | 8.5 | 0.5 | 1.1 |
| *Gammarus mucronatus* | | | 1.0 | | <0.1 | 0.3 | | 0.2 | | 0.4 | | 0.2 |
| Copepoda, harpacticoid | | 11.3 | 1.0 | | 2.3 | 0.9 | 1.6 | 0.8 | 10.0 | 3.2 | | 2.8 |
| *Hexapanopeus angustiforas* | 6.0 | <0.1 | | | | | | | | | 9.0 | 1.4 |
| *Melita nitida* | | | | | | 0.1 | | | 2.2 | | | 0.2 |
| Mysidae | 10.6 | 15.0 | 10.5 | 26.0 | 5.7 | 7.3 | 12.9 | 4.4 | 3.8 | 8.2 | 1.0 | 9.6 |
| *Ogyrides alphaerostris* | 0.6 | 16.0 | 19.5 | 1.0 | 1.3 | 14.4 | 7.3 | | 0.4 | 0.2 | 2.5 | 5.7 |
| Ostracoda | | | 0.5 | | 0.1 | | 0.3 | | 0.8 | | | 0.1 |
| Mollusca | 0.2 | <0.1 | <0.1 | 1.0 | 0.5 | 1.3 | 4.8 | 1.4 | 0.6 | 1.7 | 2.5 | 1.3 |
| *Acteon punctostriatus* | | | | | 0.2 | | | | | | | <0.1 |
| *Acteocina canaliculata* | | | | | 0.2 | | | | | | | <0.1 |
| *Anadara transversa* | 0.2 | | | | | | | | | 0.5 | | 0.1 |
| *Odostomia engonia* | | | | 1.0 | 0.2 | 0.9 | 1.8 | 1.2 | | 0.2 | | 0.5 |
| *Macoma* sp. | | | | | | 0.1 | 1.3 | | | 0.2 | 1.5 | 0.3 |
| Siphons | | | | | | 0.3 | | 0.2 | 0.4 | | | 0.1 |
| Polychaeta | 52.0 | 55.3 | 62.0 | 62.0 | 63.7 | 57.5 | 44.5 | 73.0 | 60.6 | 60.7 | 72.5 | 60.3 |
| *Asabellides oculata* | | | | | 1.3 | <0.1 | 0.1 | 0.2 | | 0.1 | 1.0 | 0.3 |
| *Chaetopterus variopedatus* | | | | | | 0.1 | | | | | | <0.1 |
| *Clymenella torquata* | 4.4 | 0.3 | | | | | | 5.8 | 4.2 | | | 3.5 |
| *Diopatra cuprea* | | | | | 17.8 | 6.0 | | | | | | <0.1 |
| *Eteone heteropoda* | | 4.7 | 4.8 | 7.0 | 10.7 | 4.9 | 8.8 | 5.8 | 2.9 | 5.5 | 2.5 | 5.2 |
| *Glycera americana* | | | | | 1.0 | 4.4 | 0.9 | 6.2 | | 4.5 | | 1.5 |
| *Glycinde solitaria* | 10.6 | 10.7 | 8.0 | | 3.5 | 8.6 | 5.5 | 0.6 | 6.7 | 4.6 | 3.0 | 5.6 |
| *Lepidametria commensialis* | | | | | | 0.3 | | | | 0.8 | 1.5 | 0.2 |
| *Loimia medusa* | | | | | | 2.9 | | 0.1 | 7.6 | 3.0 | 8.0 | 2.0 |
| *Nephtys* sp. | 2.4 | | | | | 3.0 | | 3.8 | | | | 0.8 |
| *Nereis succinea* | 1.6 | 1.0 | 0.3 | 14.0 | 6.7 | 5.8 | 2.6 | 1.0 | 3.4 | 2.8 | 12.5 | 4.7 |
| *Notomastus latericeus* | | | | 9.0 | 3.0 | | 1.0 | | | 0.5 | 3.5 | 1.5 |
| *Paraprinospio pinnata* | 29.4 | 35.0 | 28.0 | 18.0 | 13.3 | 11.0 | 17.4 | 26.4 | 28.4 | 30.7 | 17.0 | 23.1 |
| *Pectinaria gouldii* | | | | | | 0.3 | | 8.0 | 2.8 | | 22.0 | 3.0 |
| *Pseudeurythoe paucibranchiata* | | | | | | | | 1.4 | | 0.5 | | 0.2 |
| *Marenzellaria viridis* | | | | | | <0.1 | | 0.6 | | | | 0.1 |
| *Scoloplos* sp. | | | | | | 0.8 | | | | 3.0 | | 0.3 |
| *Sigambra tentaculata* | | | | | 0.3 | | | | | 0.3 | | 0.1 |
| *Streblospio benedicti* | | | | | | <0.1 | | | | | | <0.1 |
| Others | 23.2 | 1.7 | 4.0 | 4.0 | 7.2 | 12.9 | 10.6 | 10.3 | 17.4 | 7.1 | 6.0 | 9.5 |
| *Edwardsia elegans* | 4.0 | | | | 1.2 | 4.0 | 6.9 | 5.4 | 3.6 | 5.3 | | 2.8 |
| Egg | | 0.3 | 0.5 | 3.0 | 0.2 | 0.4 | 0.3 | 1.0 | 0.3 | | 1.0 | 0.6 |
| Gobiidae | 19.2 | | | | 2.2 | 1.5 | | | | | | 2.1 |
| Nematoda | | | | | 0.8 | 0.3 | 0.3 | | 0.3 | 0.1 | | 0.2 |
| Nemertina | | 1.0 | | | | | | | | | | 0.1 |
| Nudibranc | | | | | 1.2 | 4.8 | 3.0 | | | 1.2 | | 0.9 |
| Oligochaeta | | 0.3 | 3.5 | 1.0 | | 0.2 | 1.0 | 3.9 | | | | 0.9 |
| *Saccoglossus kowalevskii* | | | | | 1.7 | | | | | | | 0.2 |
| Tunicata | | | | | | 1.1 | | | 13.2 | | | 1.3 |
| Total food weight (mg) | 2369 | 2596 | 3463 | 1416 | 3826 | 7462 | 5161 | 4873 | 4169 | 5576 | 3426 | |

[a] Spot in this size-class were not caught in Stratum A

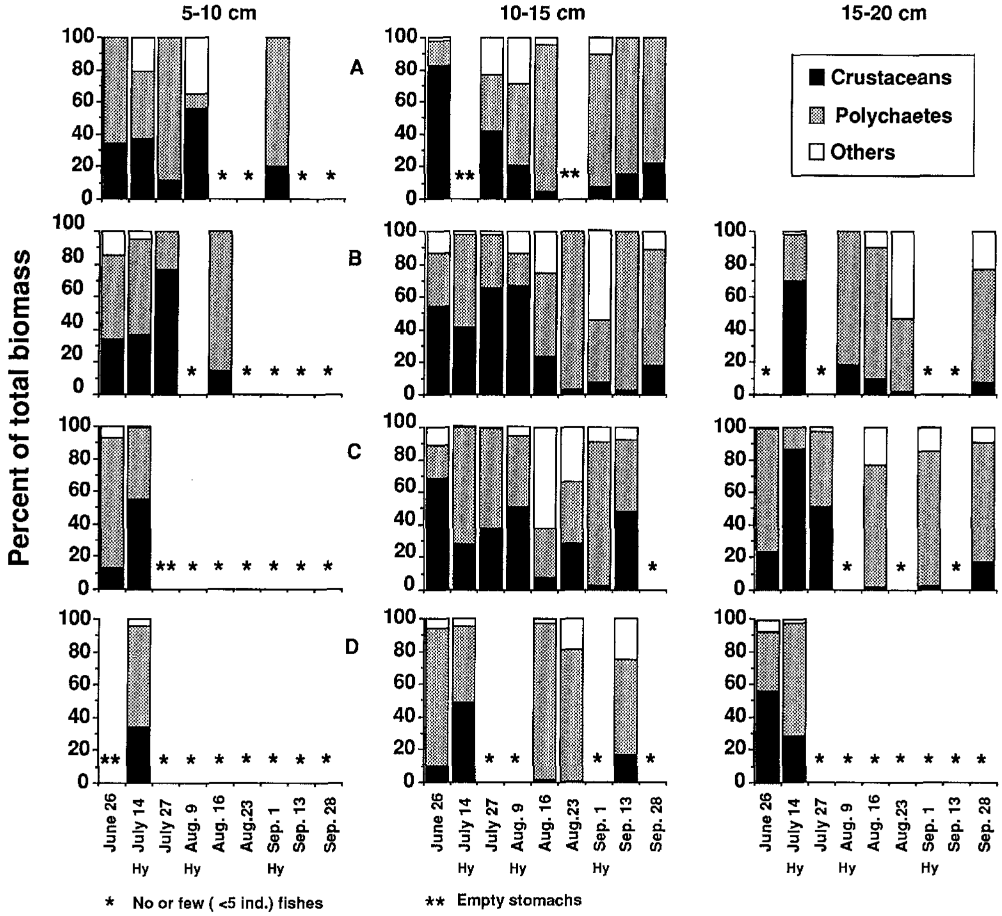

**Fig. 4.** *Leiostomus xanthurus*. Percent of total biomass for crustaceans, polychaetes and other prey items in the diet of three length-classes (5–10, 10–15, 15–20 cm) of spot in the four depth strata (A, B, C, D) in the lower York River (26 June to 28 September 1989). Hy indicates period with hypoxia

diet biomass in the four depth strata (Table 2). *Glycera americana* was the preferred polychaete at all depths, followed by *Notomastus latericeus*, *Loimia medusa* and *Nereis succinea*. Normally, ingested polychaetes found in the stomachs were intact or nearly intact. *Clymenella torquata* was an exception, with mainly posterior ends found. Large prey items dominated the diet and often one or two individuals filled the stomach. Individual wet weight of partly digested *G. americana* sometimes amounted to 2 g. On most occasions when *L. medusa* was eaten a portion of its tube was also found in the stomach. Other prey consumed included nemerteans and bivalves (siphons only). Crustaceans were of little importance in the diet of hogchoker.

Biomass (as percent of total food intake) of the three dominant polychaetes in the diet of hogchoker varied temporally between strata (Fig. 6). For Strata A, C and D *Glycera americana* constituted most of the food taken by 5- to 10-cm fish after the July hypoxia. During September *G. americana* was mainly eaten in the two deepest strata, and *Notomastus latericeus* was the preferred food item in Stratum A. In Stratum B the diet was more variable, with no clear temporal trend for these two species. Larger (10 to 15 cm) hogchoker consumed *G. americana* on most sampling dates; however, during the second half of September, the dominant species taken in depth Strata A, B and C were *Loimia medusa* and *N. latericeus*. Siphons from bivalves were eaten mainly by fish caught within Strata B, C and D, and were only found in stomachs from mid-August through September.

In late June, prey from 5- to 10-cm fish were retained on the three smallest sieves, whereas larger (10 to 15 cm) fish consumed prey distributed over the four largest sieve sizes (Fig. 7). During and after the first hypoxia in July, a significant increase in size of prey consumed in all depth strata was observed for both hogchoker size-classes ($P < 0.01$). The majority of prey consumed were retained on the largest (6.3 mm) sieve at most depths at this time. During the second hypoxic event (early August), hogchoker emigrated from the area, but returned when oxygen conditions improved. Prey consumed in August and thereafter by small (5 to 10 cm) hogchoker were distributed over all sieve sizes. Prey eaten by larger (10 to 15 cm) hogchoker in Strata B, C and D were still mainly retained on the largest sieve and were significantly larger than prey consumed during normoxia in June ($P < 0.01$). The third period of low oxygen in early September had no detectable impact on the size distribution of prey consumed by

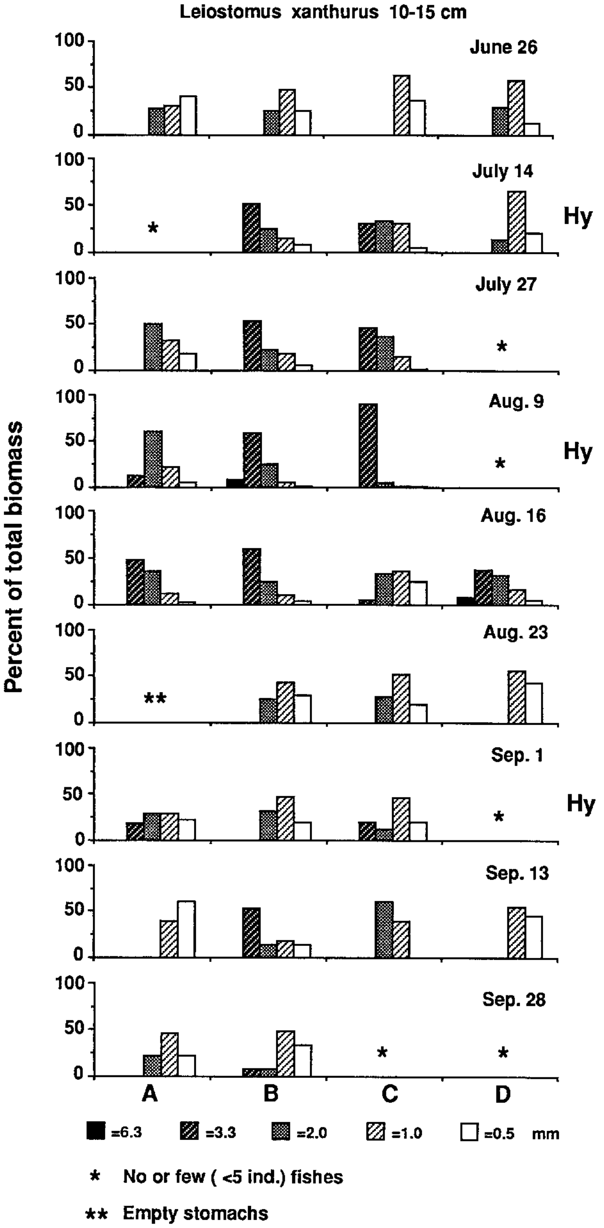

**Fig. 5.** *Leiostomus xanthurus.* Size distribution (percent of total biomass) of prey taken by 10- to 15-cm spot in the four depth strata (A, B, C, D) in the lower York River (26 June to 28 September 1989). All stomach contents were sieved on nested 6.3, 3.3, 2.0, 1.0 and 0.5 mm sieves. Hy indicates period with hypoxia

small or large fish at any depth. Later in September a general decrease in prey size was observed for 10- to 15-cm hogchoker from Strata B and C.

### *Mantis shrimp*

Stomach contents of the mantis shrimp were generally masticated and difficult to identify. Only a small proportion of the ingested prey items could be identified to species, and therefore the stomach contents were separated into major taxonomic groups: crustaceans, hydroids, molluscs, polychaetes, "other" (including algae, fish and tunicates) and "unidentified". On average, about 60% of the prey could be assigned to these major groups and the remaining 40% was categorized as unidentified. The hydroid identified from the guts was *Sertularia cupressina*, a dominant species in Chesapeake Bay (Calder 1971, 1990).

Percent biomass of the five prey groups in the diet of mantis shrimp varied with sampling date and depth (Fig. 8). In late June, mantis shrimp were only found in depth Strata C and D and prey consisted primarily of polychaetes, although molluscs and hydroids were also consumed. During the first period of hypoxia in mid-July, hydroids constituted the dominant prey in mantis shrimp from Stratum D, whereas hydroids and crustaceans were the most important prey in Stratum B. All stomatopods ($n=14$) from Stratum C had empty stomachs at this time. Later in July, when oxygen levels increased, crustaceans became important prey in Strata A, B and C. The proportions of crustaceans, molluscs and polychaetes consumed by mantis shrimp from Stratum D were similar. During the early August hypoxia, crustaceans became important prey for mantis shrimp in Strata A, B and D, but only hydroids were consumed in Stratum C. Later in August, hydroids again became the dominant prey in Stratum C. During the third hypoxic event in early September, polychaetes and crustaceans were the most important prey within all depth strata. Crustaceans remained important components of the diet later in September, especially in Stratum C, and hydroids were also consumed in Strata A and B. Crustaceans and hydroids remained important in the diet of mantis shrimp for the duration of the study.

Crustacean prey in July and August were mainly amphipods, shrimps and xanthid crabs. In September, however, most crustaceans in the diet were juvenile blue crabs (*Callinectes sapidus*), found mainly in mantis shrimp from Strata A and C. *Nereis succinea* was the most common polychaete species found in the stomachs and it occurred throughout the sampling period. *Pectinaria gouldii* also occasionally occurred in gut contents.

## Discussion

Burrowing within the sediment may provide a significant refuge from predation for benthic organisms and many macrobenthic infauna exhibit increased burrowing depths with increasing age (Reading and McGrorty 1978, Blundon and Kennedy 1982, Roberts et al. 1989, Zwarts and Esselink 1989). However, reduced vertical distribution of the macrobenthos in response to hypoxia is known to occur over short time scales (Diaz et al. in press). The interactive effect of improving oxygen conditions in the bottom water after periods of hypoxia, slow improvement of oxygen conditions in the sediment and slow recovery of the lethargic and emerged infauna (Llanso 1990) can potentially be exploited by mobile predators, causing a dramatic effect on energy flow in benthic habitats. During hypoxia, large polychaetes are distributed on or nearer the sediment surface (Baden et al. 1990), thereby rendering them more susceptible to

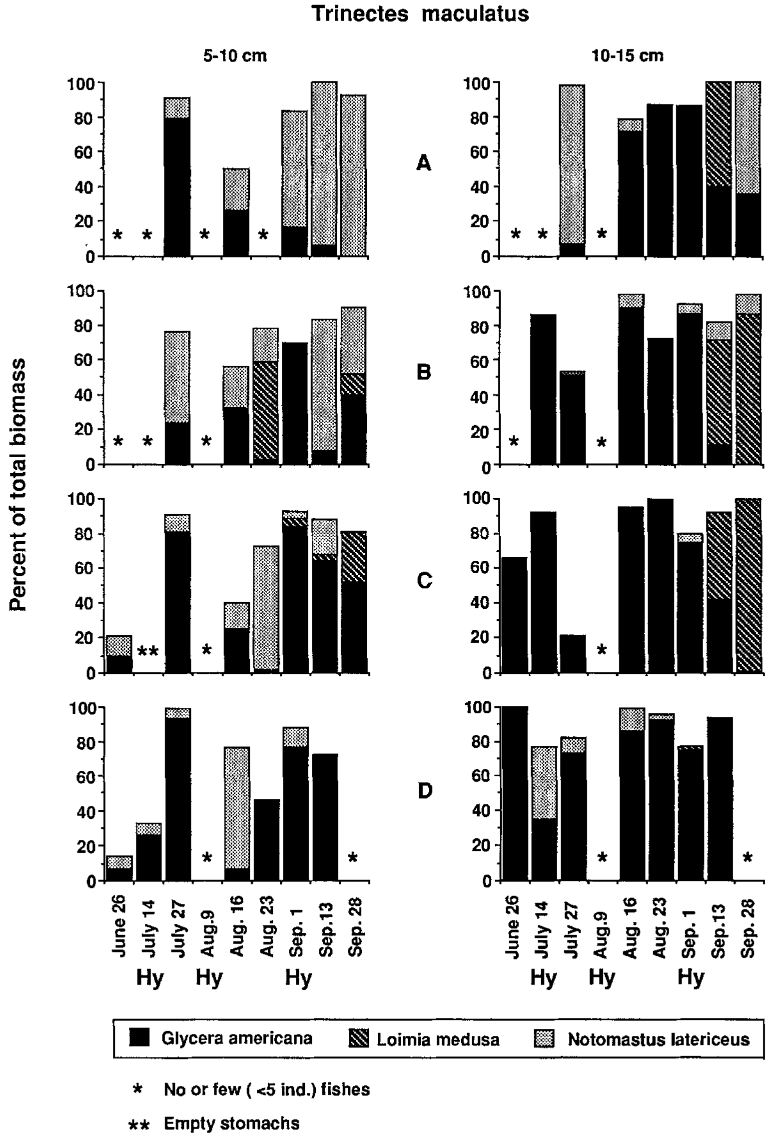

**Fig. 6.** *Trinectes maculatus*. Percent of total biomass for *Glycera americana*, *Loimia medusa* and *Notomastus latericeus* taken by two length-classes (5–10 and 10–15 cm) of hogchoker in the four depth strata (A, B, C, D) in the lower York River (26 June to 28 September 1989). Hy indicates period with hypoxia

predation. Similarly, the bivalves *Macoma baltica* and *Mya arenaria*, both of which are common in the study area, extend their siphons into the water column considerably above the sediment-water interface during hypoxia (Schaffner personal communication) and are therefore more likely to suffer increased risk of partial predation. Previously, studies from a variety of estuarine and coastal areas demonstrated that many infaunal species emerge from the sediments during anoxia (Steimle and Radosh 1979, Jørgensen 1980, Stachowitsch 1984) but few have demonstrated the exploitation of the benthos during less severe hypoxia by resident predators.

It seems clear that the predators investigated in the present study were able to exploit hypoxia-induced prey availability. The diet of all three species studied (spot, hogchoker, mantis shrimp) changed in response to hypoxic events. For example, a significant increase in the size of the prey consumed by the two fish species occurred only during hypoxia. In addition, prey species normally distributed deep in the sediment were eaten only during the low-oxygen events. Although all three species fed on infaunal or epibenthic organisms, each exhibited different feeding strategies.

Spot is a generalist and forages opportunistically in the upper sediment layers (O'Niel and Weinstein 1987). The species has a small mouth and the size of prey for juvenile fish does not change dramatically with increasing body size (Stickney et al. 1975, O'Niel and Weinstein 1987). Food items are obtained by random sediment ingestion and subsequent sorting of prey from detritus. Thus, the composition and size distribution of prey in spot diets generally reflects food availability in the upper sediment layers and is not due to active prey selection. During normoxia spot generally preyed upon species typically associated with near-surface sediments (Table 3). However, following the first two hypoxic events an increase in the biomass of larger, deep-burrowing species such as the polychaetes *Clymenella torquata*, *Glycera americana* and *Nephtys* sp. and particularly the infaunal anemone *Edwardsia elegans* was observed, indicating slow recovery and presence in surface sediments and their exploitation by predatory spot.

**Table 2.** *Trinectes maculatus.* Mean percent biomass of food items in the diet of two size-classes (5–10, 10–15 cm) of hogchoker from the four depth strata (A, B, C, D) during the period 26 June to 28 September 1989 in the lower York River, Virginia, USA

| Prey | 5–10 cm | | | | 10–15 cm | | | | Overall average |
|---|---|---|---|---|---|---|---|---|---|
| | A | B | C | D | A | B | C | D | |
| No. of stomachs analysed (empty) | 54 (29) | 83 (44) | 224 (125) | 208 (113) | 82 (45) | 102 (57) | 248 (148) | 227 (111) | |
| Crustacea | 0.8 | 1.7 | 0.2 | 0.7 | 0.2 | <0.1 | 0.6 | 0.1 | 0.5 |
| *Ampelisca* sp. | | | | | | | | 0.1 | <0.1 |
| *Corophium* sp. | | | | | <0.1 | | | | <0.1 |
| *Crangon septemspinosa* | | | | | 0.2 | | | | <0.1 |
| Cumacea | | <0.1 | | | <0.1 | <0.1 | | | <0.1 |
| Mysidae | | 1.7 | | | | | | <0.1 | 0.2 |
| *Ogyrides alphaerostris* | 0.8 | | | 0.5 | | | <0.1 | | 0.2 |
| Mollusca | <0.1 | 5.3 | <0.1 | 4.3 | 2.2 | 4.3 | 3.8 | 2.1 | 2.8 |
| Bivalve siphon | | 5.3 | | 4.3 | 2.2 | 4.3 | 3.8 | 2.1 | 2.8 |
| Polychaeta | 97.6 | 93.0 | 97.5 | 93.0 | 97.7 | 85.4 | 85.5 | 94.6 | 93.0 |
| *Asabellides oculata* | | | | 2.0 | | | | | 0.3 |
| *Clymenella torquata* | 1.6 | | 3.7 | 3.0 | 2.8 | | | 0.4 | 1.4 |
| *Diopatra cuprea* | | | | | | | | 0.1 | <0.1 |
| *Eteone heteropoda* | 1.6 | 1.3 | 8.0 | 2.8 | 0.2 | 0.9 | 0.8 | 0.2 | 2.0 |
| *Glycera americana* | 20.4 | 30.7 | 50.7 | 53.7 | 54.5 | 56.7 | 61.5 | 79.1 | 50.9 |
| *Glycinde solitaria* | | 2.3 | 3.7 | 2.8 | | 1.2 | | | 1.2 |
| *Loimia medusa* | | 10.2 | 6.3 | | 10.0 | 21.3 | 18.6 | 0.4 | 8.3 |
| *Nephtys* sp. | | 2.7 | | | | | 0.8 | | 0.4 |
| *Nereis succinea* | 20.2 | 6.5 | 0.3 | 4.0 | 3.0 | | | 2.0 | 4.5 |
| *Notomastus latericeus* | 52.8 | 34.7 | 20.0 | 15.3 | 27.0 | 5.0 | 0.6 | 9.9 | 20.7 |
| *Paraprinospio pinnata* | 0.4 | 4.5 | 1.5 | 8.0 | | 0.6 | 0.6 | 1.1 | 2.1 |
| *Pectinaria gouldii* | | | | | | | 2.8 | 0.1 | 0.4 |
| *Scoloplos* sp. | | | 3.2 | | | | | <0.1 | 0.4 |
| *Sigambra tentaculata* | 0.4 | | <0.1 | | | | | | 0.1 |
| Others | 1.6 | <0.1 | 2.3 | 2.0 | <0.1 | 10.3 | 10.1 | 3.1 | 3.7 |
| Nemertina | 1.6 | | 2.3 | | | 10.3 | 10.1 | | 3.0 |
| *Saccoglossus kowalevskii* | | | | 2.0 | | | | 1.9 | 0.5 |
| Egg | | | | | | | | 1.3 | 0.2 |
| Total food weight (mg) | 3558 | 5609 | 9788 | 11521 | 16534 | 42401 | 54395 | 47196 | |

**Table 3.** *Leiostomus xanthurus* and *Trinectes maculatus.* Depth distribution patterns of preferred prey items; juv.: juvenile

| Predator<br>Food item | Likely depth distribution (in cm) | Source |
|---|---|---|
| Spot | | |
| *Crangon septemspinosa* | Surface | L. Schaffner personal observation |
| *Ogyrides alphaerostris* | Surface and burrowing | Ruppert and Fox (1988) |
| Mysids | Surface or above | L. Schaffner personal observation |
| Cumaceans | Surface or above | L. Schaffner personal observation |
| Harpacticoid copepods | 0–0.5 | Palmer and Molloy (1986) |
| *Clymenella torquata* | Tails at surface; head 10–15 | Schaffner (1990) |
| *Eteone heteropoda* | 0–5 | Hines and Contois (1984) |
| *Glycinde solitaria* | 0–2 | Schaffner (1990) |
| *Nereis succinea* | 0–2 (juv.); 10–15 (adult) | Hines and Contois (1984) |
| *Paraprinospio pinnata* | 0–2 | Schaffner (1990) |
| *Pectinaria gouldii* | 0–2 | Schaffner (1990) |
| *Edwardsia elegans* | 0–10 | Ruppert and Fox (1988) |
| Tunicates | Surface or above | Schaffner (1990) |
| Hogchoker | | |
| *Glycera americana* | 0–2 (juv.); 5–10 (adult) | Schaffner (1990) |
| *Loimia medusa* | Tentacles at surface, 2–15 | Schaffner (1990) |
| *Nereis succinea* | 0–2 (juv.); 10–15 (adult) | Hines and Contois (1984) |
| *Notomastus latericeus* | 2–5 (juv.); 5–10 (adult) | Schaffner (1990) |

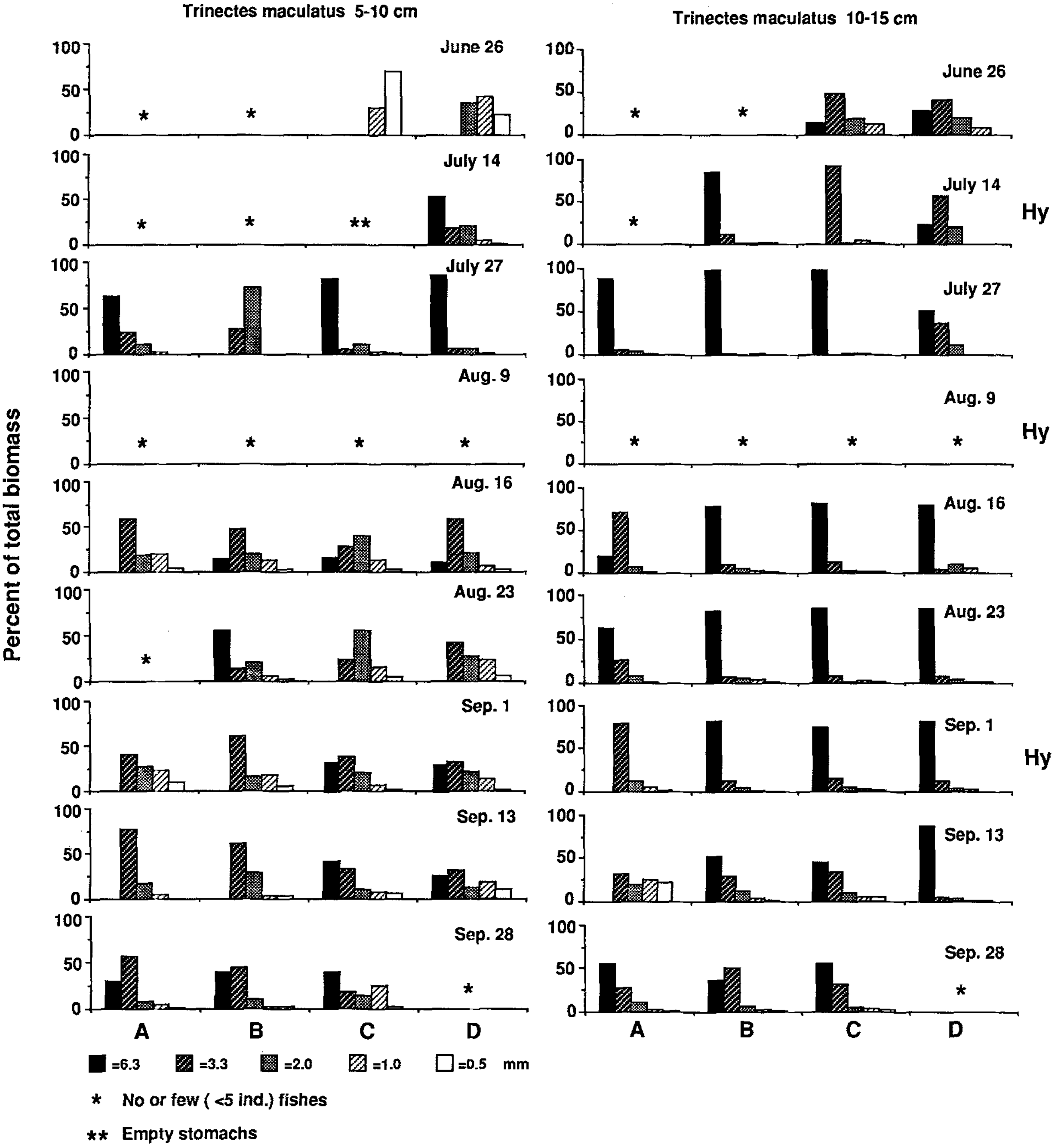

Fig. 7. *Trinectes maculatus.* Size distribution (percent of total biomass) of food taken by two size-classes (5–10 and 10–15 cm) of hogchoker in the four depth strata (A, B, C, D) in the lower York River (26 June to 28 September 1989). All stomach contents were sieved on nested 6.3, 3.3, 2.0, 1.0 and 0.5 mm sieves. Hy indicates period with hypoxia

Hogchokers are nocturnal selective predators that utilize chemical sensors on the ventral side of the head (O'Connor 1972) for locating prey such as large polychaetes. Similar mechanisms involving selective feeding are known for other flatfish such as sole (*Solea solea;* de Groot 1971). In the present study hogchokers typically ingested deep-dwelling organisms (Table 3). The predominance of whole prey in the stomachs suggests that hogchokers are able to remove infauna intact from the sediment. Following hypoxia, this species foraged opportunistically on apparently stressed benthos emerged from the sediment by ingesting larger polychaetes and a greater proportion of bivalve siphons.

Stomatopods mainly ingest epibenthic organisms (Caldwall and Dingle 1976) but can also consume infaunal polychaetes (Hamano and Matsuura 1986, present study). Crustaceans are the preferred prey but in the present study hydroids (predominantly *Sertularia cupressina*) made up a large part of the diet, and on one occasion a green macroalga (likely *Ulva lactuca*) was consumed. In September newly recruited juvenile blue crabs were eaten. No published information on the diet of western Atlantic

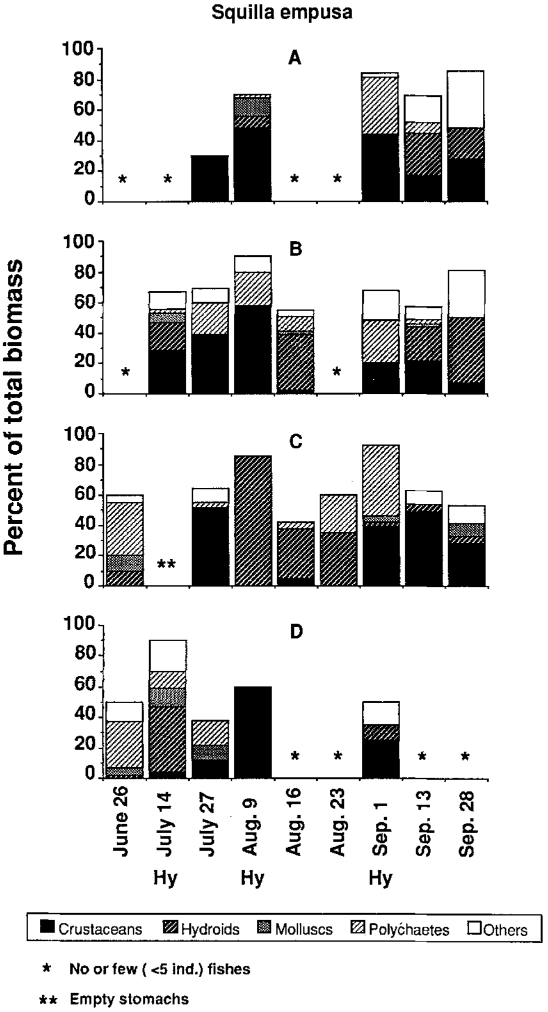

**Fig. 8.** *Squilla empusa.* Percent of total biomass for identified food items taken by mantis shrimp in the four depth strata (A, B, C, D) in the lower York River (26 June to 28 September 1989). Food is separated into the following groups: crustaceans, hydroids, molluscs, polychaetes and others. Hy indicates period with hypoxia

mantis shrimp was found for comparison with this study. The diet of the Japanese mantis shrimp, *Oratosquilla oratoria* (similar in size to *Squilla empusa*), consists of crustaceans (62%, mainly macruran shrimps), molluscs (38%, mainly bivalves), fish (14%) and polychaetes (5%) (Hamano and Matsuura 1986). Hydroids or algae were not reported as food items.

The reduced importance of crustaceans in the diet of mantis shrimp after the second hypoxia in July was also observed in spot. During normal oxygen levels and the onset of hypoxia the species of crustaceans that spot consumed were predominantly epifauna associated with hydroid colonies (McCain 1965). Mantis shrimp were most likely also preying upon these epifaunal species. With the first occurrence of hypoxia, epifaunal crustaceans may have been more susceptible to predation by the mantis shrimp but subsequently the hypoxia-induced decline of hydroid-associated crustaceans may have left only hydroids for consumption.

The successful exploitation of the stressed benthic resources in the York River by bottom-feeding predators is related to the reduced severity and short duration of the hypoxic events as well as the relatively small size of the affected area. In the York River, oxygen in bottom water predictably declines to hypoxic levels, but anoxia tends not to occur, at least not in the water (Haas 1977, Kuo and Neilson 1987). The duration of hypoxia is also relatively short when compared to other areas of Chesapeake Bay (Officer et al. 1984), lasting only between 6 and 14 d per occurrence during the present study. However, oxygen condition in the sediment can be more severe and last for longer periods, forcing infauna to stay on the sediment surface. These features of York River oxygen oscillations allow spot and hogchoker to energetically benefit from the periodic exploitation of lethargic, emerged and easily accessible prey during hypoxic events through migrations into and out of affected areas (Pihl et al. 1991). Similar behaviour is known for the galatheid crab *Munida quadrispina* which follows the movement of the hypoxic water layer in order to exploit food resources (Burd and Brinkhurst 1984). During moderate hypoxia the mantis shrimp also benefit via easy exploitation of prey. However, under severe hypoxic conditions ($O_2$ saturation $<1$ mg $l^{-1}$) haemocyanin is metabolized for short-term survival and feeding appears to be greatly reduced (Pihl et al. 1991). Eventually, mantis shrimp, which are stationary during normoxia, migrate to shallower water with more favourable oxygen conditions (Pihl et al. 1991). Such a behavioural response has also been described for *Munida quadrispina* (Burd and Brinkhurst 1984). Tolerance under laboratory conditions to low oxygen by the three species investigated supports field evidence of observed feeding behaviour and predatory exploitation of infauna during hypoxia (Pihl et al. 1991).

This study demonstrates the opportunistic exploitation by both mobile transient and resident burrowing predators of benthic prey sublethally affected during hypoxic events. Each of the predators investigated appears to use different mechanisms for prey resource exploitation. Spot apparently move into stressful hypoxic bottom water for short time periods to easily prey on lethargic and emerged large-sized infauna which are otherwise unavailable due to their normal burial depth in the sediment. Less mobile hogchoker are unable to forage in areas of prolonged hypoxia but apparently return to affected areas to exploit slowly recovering benthic prey (Llanso 1990). Similarly, mantis shrimp, which are relatively tolerant to low oxygen levels, are capable of exploiting benthic prey during the onset of hypoxia but are unable to remain in affected areas for long time periods. Thus, it appears that these predators forage optimally on weakened prey of the largest size to maximize energy intake (Pianka 1978). A similar pattern of prey exploitation in oxygen-stressed ($<2$ mg $l^{-1}$) benthic communities was evident in diets of demersal fishes in the Kattegat, Sweden, where emerged large polychaetes (*Aphrodite aculeata*) and lethargic hermit crabs (*Pagurus bernhardus*) were consumed by cod (*Gadus morhua*) only during hypoxia (Pihl unpublished data). Further, the importance of other crustaceans decreased in the diet of demersal fish during hypoxia in the Kattegat, similar to the pattern observed in Chesapeake Bay. Though hypoxia may not cause direct mortality of the benthos, sublethal consequences apparently have important implications for energy flow in affected areas, which remains to be quantified.

*Acknowledgements.* This work was part of a broad program designed to evaluate the effects of hypoxia and anoxia on living resources. We thank J. van Montfrans, L. Haas and R. Seitz for their discussion of ideas and manuscript review. This work was supported by the National Oceanic and Atmospheric Administration and Virginia Sea Grant (Grant no. 5-592-46) and by the Swedish National Science Research Council.

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