

Effects of periodic hypoxia on distribution of demersal fish and crustaceans*

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Abstract. Effects of periodic hypoxia ($O_2 < 2 \text{ mg l}^{-1}$) on distribution of three demersal fish species, spot (*Leiostomus xanthurus*), hogchoker (*Trinectes maculatus*) and croaker (*Micropogonias undulatus*), and of two crustacean species, mantis shrimp (*Squilla empusa*) and blue crab (*Callinectes sapidus*), were investigated in the lower York River, Chesapeake Bay, USA. Trawl collections were made in four depth strata (5 to 10, 10 to 14, 14 to 20 and $> 20 \text{ m}$) during normoxia and hypoxia from 26 June to 20 October 1989. Three periods with hypoxia in the bottom water (below 10 m depth) occurred in mid-July, early August and early September, each with a duration of 6 to 14 d. The demersal fish and crustaceans studied were all affected by hypoxia, and a general migration from deeper to shallower water took place during July and August. However, when oxygen conditions improved after a hypoxic event all species, except *S. empusa*, returned to the deeper areas. The degree of vertical migration was related to levels of oxygen concentration and varied for the different species. *M. undulatus* was the most sensitive species to low oxygen, followed by *L. xanthurus* and *C. sapidus*. *T. maculatus* and *S. empusa* were more tolerant and survived in 14 to 25% oxygen saturation by increasing ventilation rate and, for *S. empusa*, by also increasing blood pigment (haemocyanin) concentration. Periodic hypoxia driven by the spring-neap tidal cycle may represent a natural phenomenon with which the fishes and crustaceans are in a delicate balance. Areas experiencing periodic short-lived hypoxia may be good nursery grounds for fisheries species, and there is no indication that the habitat value in the study area of lower York River is lessened. However, if eutrophication lengthens the time of hypoxia or brings the system closer to anoxia the system may change and become characteristically stressed. The migratory and physiological responses of these species to hypoxia are good indicators of the severity of oxygen stress and could be used as part of

an early warning monitoring system for changes in environmental quality.

Introduction

Estuaries are highly productive areas functioning as nursery and feeding grounds for many commercially important fish and crustacean species (Setzler-Hamilton 1987). Human activities in and around estuaries are increasing, which in turn increases the sources of stress to fisheries resources. Many of the stresses, particularly those associated with eutrophication, affect the oxygen budget of bottom waters and are implicated in causing hypoxia ($O_2 < 2 \text{ mg l}^{-1}$) and anoxia ($O_2 < 0.2 \text{ mg l}^{-1}$) (Pearson and Rosenberg 1978, Officer et al. 1984, Rosenberg and Loo 1988).

Increased primary production in shallow estuarine systems results in increased organic loading, which is oxidized in the water column or sediment. In areas where the water column stratifies, due to a density cline set up by differences in temperature or salinity, decomposition of organic material in the isolated bottom water could result in hypoxic conditions (May 1973, Degobbi et al. 1979, Falkowski et al. 1980, Turner et al. 1987, Pihl 1989). Hypoxia may act as an added stress for the benthic community, which is already exposed to large changes in temperature, salinity, tidal currents and turbidity.

The purpose of this study was to obtain information about distribution of dominant demersal fish and crustaceans during normoxia and hypoxia in subtidal areas of the lower York River, Chesapeake Bay, USA. The species studied were: Spot (*Leiostomus xanthurus* Lacépède), hogchoker (*Trinectes maculatus* Bloch & Schneider), croaker *Micropogonias undulatus* Linnaeus), mantis shrimp (*Squilla empusa* Say) and blue crab *Callinectes sapidus* Rathburn). In addition, for the crustaceans, blood pigment (haemocyanin) concentrations were monitored to investigate the physiological response to hypoxia of these two species.

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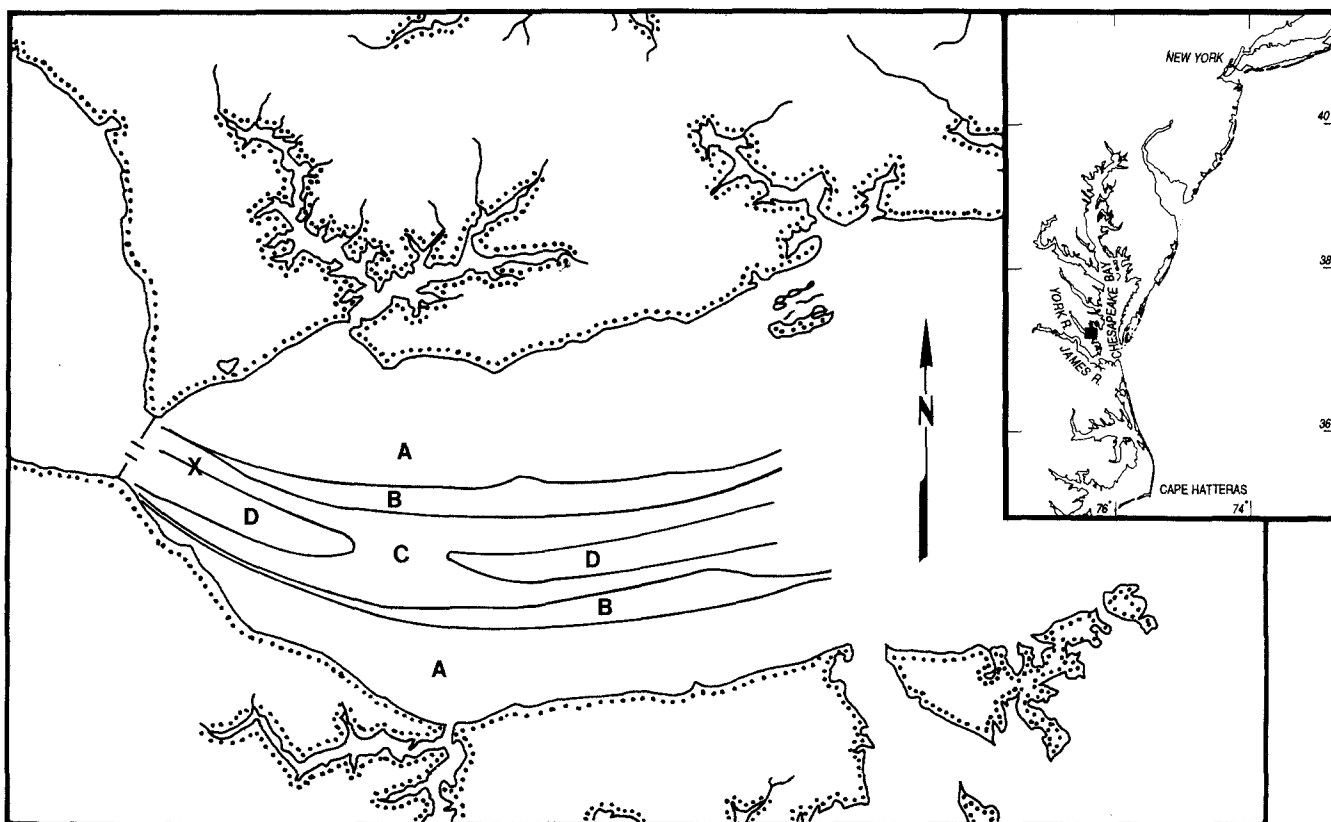


Fig. 1. Lower York River study area, USA, with depth boundaries of strata delineated. Stratum A is 5 to 10 m, Stratum B is 10 to 14 m, Stratum C is 14 to 20 m and Stratum D is > 20 m. Radio-telemetry environmental data buoy was located within Stratum C (indicated by X)

Leiostomus xanthurus and *Micropogonias undulatus* mainly use the study region as a nursery area, with juveniles staying in the river from spring to autumn (Kobyliniski and Sheridan 1979). *Trinectes maculatus* are resident in the York River estuary (Markle 1976), migrating to the more saline lower parts of the river during summer to spawn (Dovel et al. 1969). Burrowing *Squilla empusa* are year-round residents and are territorial (Caldwell and Dingle 1976, Meyers 1979). *Callinectes sapidus* use the study area as a nursery during the summer. Juvenile and adult crabs also utilize the area throughout the year. During late summer adult females migrate to higher-salinity waters at the mouth of the Chesapeake Bay to overwinter and spawn (Schaffner and Diaz 1988).

Materials and methods

Study area

The lower York River, Virginia, USA, a major tributary of the Chesapeake Bay system (Fig. 1), was selected for study because it predictably cycles between hypoxia and normoxia during the summer months. The mechanism that establishes the vertical density stratification-destratification of the water column, and controls the set-up of hypoxia, is the lunar spring-neap tidal cycle (Haas 1977). Periods of stratification occur during neap tide, when tidal currents are reduced. The mechanisms for this have been described in detail for the study area (Haas 1977, Hayward et al. 1986). Variation in freshwater input is thought to have little effect on stratification, and thus on establishment of hypoxia (Hayward et al. 1986). Strong

wind events are able to interrupt the onset of hypoxia and completely mix the river top to bottom 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). Stratum A, from 5 to 10 m, was above the depth at which hypoxia typically occurs. In the York River, only depths > 9 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, was sometimes affected by hypoxia. Strata C, from 14 to 20 m, and D, > 20 m, were always affected by hypoxia when it occurred. The average silt-clay percentage within each stratum was 36, 80, 93 and 78% for A, B, C and D, respectively. During our study bottom temperature ranged between 15 and 26°C and bottom salinity from 17 to 25‰ (Fig. 2).

Field sampling

Eleven trawl collections were made from 26 June to 20 October 1989 (Fig. 2). During each collection all four strata were trawled for demersal fish and crustaceans. The timing of each collection was determined from analysis of changing patterns in bottom oxygen concentration. Physical data were collected by an automated radio-telemetry environmental data buoy located in 18 m depth within the study site (Fig. 1), including dissolved oxygen, salinity and temperature measurements. These data were transmitted from the field to a laboratory receiving station, logged into a computer and displayed every 20 min (see Mountford et al. 1989 and Diaz et al. in press for details). Three of the collections occurred during periods of hypoxia ($O_2 < 2 \text{ mg l}^{-1}$). The remaining eight were conducted when the study area was at higher oxygen concentrations.

The five species investigated were sampled by means of a 4.9-m otter-trawl with a 19-mm stretched mesh size in the wings and a 6.3-mm mesh liner. For each sampling occasion 2 to 3 trawl samples were taken in each depth stratum. The trawl was towed at a speed of 1 to 2 knots for a period of 10 to 20 min. Trawling was carried out during daylight near time of slack current and always against the current. Organisms collected were brought to the laboratory within 5 min, counted and measured. Fish were separated into 50 mm size-classes (by total length). Crustaceans were sexed and separated into 2-mm (*Squilla empusa*) and 10-mm (*Callinectes sapidus*) size-classes by carapace length. Juveniles (0-group) and adults (1- to 2-group) showed little overlap in size and were separated from the length-frequency distribution.

Blood from up to 20 intermoult *Squilla empusa* and *Callinectes sapidus* was sampled on each occasion and from each depth stratum, after cooling to 7°C to prevent rapid blood clotting and to increase ease of handling. Blood from the elongated heart behind the carapace of *S. empusa* and from the arthrothial membrane at the base of the fifth pereopod in *C. sapidus* was taken by hypodermic syringe as soon as possible after capture and frozen for later pigment (haemocyanin) analysis. After thawing, a 100 µl sample was diluted with 1 ml distilled water in a 10-mm cuvette and the absorbance of oxyhaemocyanin measured at 339 nm, using a Shimadzu spectrophotometer model 140 UV. An extinction coefficient of $E_{1\text{cm}}^{mM} = 17.26$ was used to calculate the concentration of oxyhaemocyanin in the blood from the absorbance. This $E_{1\text{cm}}^{mM}$ value was calculated from $E_{1\text{cm}}^{1\%} = 2.83$ given by Nickerson and van Holde (1971) and Antonini and Brunori (1974) on the basis of a functional subunit of haemocyanin with a molecular weight of 74×10^3 .

Experiments

Tolerance to low oxygen concentrations by three of the species studied was investigated in laboratory experiments in autumn 1989. *Leiostomus xanthurus*, *Trinectes maculatus* and *Squilla empusa* were collected by trawl in early October and transported to the laboratory in containers with seawater. Specimens were acclimated to laboratory tanks with running seawater and fed with fresh fish, fish pellets, bivalves and polychaetes for a month prior to experimentation.

The experiments were conducted in 40-litre glass aquaria with recirculating seawater. The water was filtered through an aquaria filter with active carbon to remove particles and reduce bacterial growth. A 3-cm layer of sand was added to each aquarium to allow normal digging and feeding behaviour of the specimens. *Squilla empusa* were also provided with PVC tubes (diameter of 30 and 40 mm) for hiding. Each experimental setup consisted of two test aquaria with the same oxygen concentration and two controls. Nitrogen was used to strip the oxygen in the hypoxia treatment, and bubbling air provided full oxygen saturation in the controls. Stable oxygen tensions in the hypoxic tanks were obtained by adjusting the flow of N_2 . Oxygen concentration was measured continuously with an air- and Winkler-calibrated YSI oxygen meter (Yellow Springs Instruments, model 58). Water temperature ($25 \pm 0.5^\circ\text{C}$) was controlled by aquaria heaters, and salinity varied between 18 and 20‰.

During each experiment oxygen concentration was lowered stepwise at approximately the same rate as observed in the bottom water in York River during periods of stratification. Ventilation activity was measured by counting gill-cover movements of the fish and pleopod movements of *Squilla empusa*. Each aquarium contained six specimens, and during all observations ventilation rate of each individual was recorded as an average of three countings, from which an average value for the aquaria was calculated. For each species ventilation activity was registered for a minimum of five different oxygen concentrations. Oxygen concentration was previously held stable for at least 1 d prior to determining ventilation rates.

Statistical analysis

Analysis of variance was used to test for differences in size of juvenile *Callinectes sapidus* between strata. Only data from 13 September did not conform to test assumptions and was $\log(x+1)$ transformed. Protected mean comparisons were done using the Scheffé procedure (Zar 1984). Sex ratio differences for adult *C. sapidus* and strata-time changes were tested using either χ^2 or G statistics (Sokal and Rohlf 1969). The Mann-Whitney U -test was used for all comparisons of haemocyanin concentration changes in *Squilla empusa* and *C. sapidus*, and for gill beat rates in the oxygen tolerance experiment. The criterion for significance in all tests was $p < 0.05$.

Results

Oxygen, salinity and temperature

Three periods of hypoxia occurred in mid-July, early August and early September (Fig. 2). Daily mean oxygen concentration (measured at 18 m depth) was below 2 mg l^{-1} (28% O_2 saturation) for 6 d during the first period, for 14 d during the second period (below 1 mg l^{-1} , 14% O_2 saturation, for 4 d), and for 6 d during the third period. These events coincide with stratification of the water masses and an increase in salinity of the bottom water by 4 to 7‰. When the water column was stratified oxygen concentration decreased from full saturation in the surface to $1\text{--}3\text{ mg l}^{-1}$ at about 15 m depth (Fig. 3). During the two first hypoxic events in July and August oxygen concentrations were rather constant in the bottom water from ca. 15 to 27 m. During the first period with low

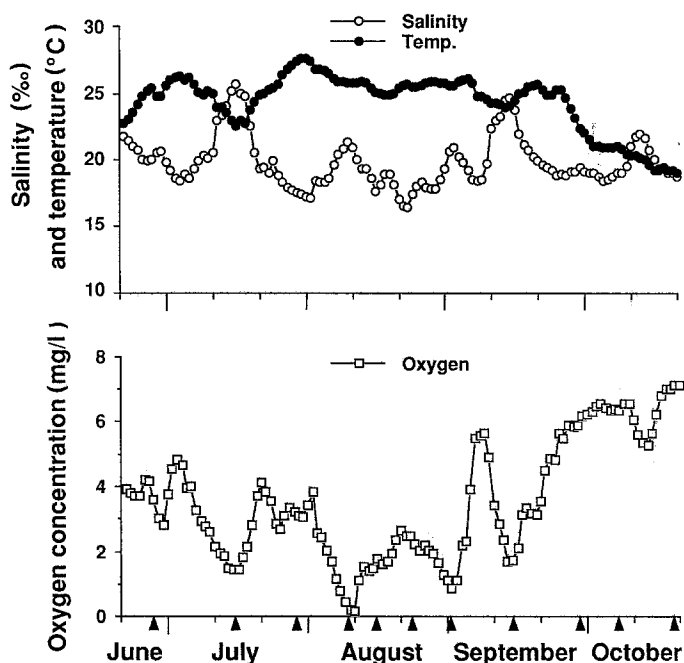


Fig. 2. Daily mean salinity, temperature, and oxygen concentration in the bottom water (18 m depth) in York River, 21 June to 20 October 1989. Means are calculated from measurements recorded continuously every 20 min by an automated radio-telemetry data buoy. Filled triangles indicate the dates when trawl collections were made

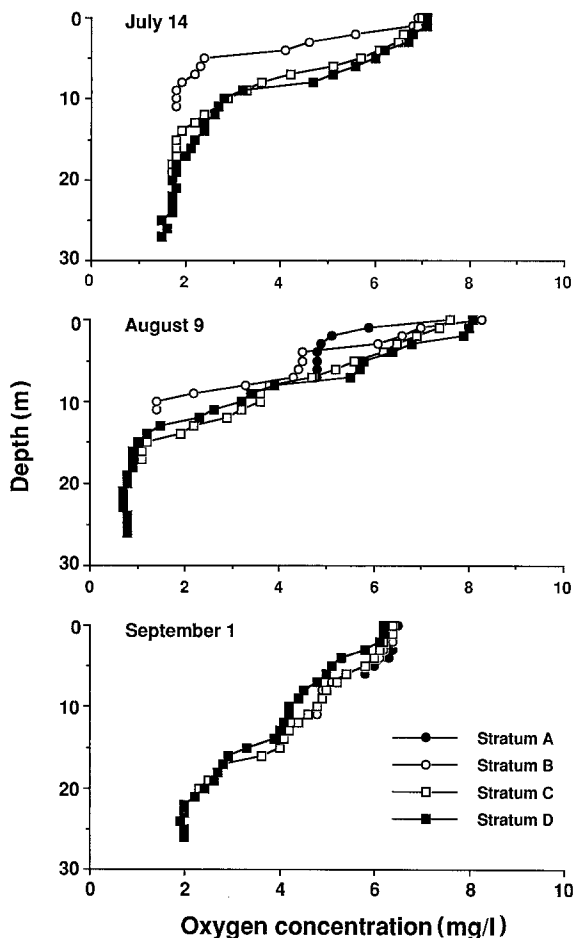


Fig. 3. Vertical distribution of oxygen concentration (mg l^{-1}) in the four depth strata in York River during the periods of hypoxia in July, August and September 1989. Oxygen was measured with an air- and Winkler-calibrated YSI oxygen meter at every meter from surface to bottom

oxygen a decrease in bottom-water temperature was also observed. In the first week of September the stratification was disrupted by a storm, which resulted in a rapid increase in oxygen concentration in the bottom water. After 3 d the water stratified again and the oxygen decreased.

Size distribution

Most of *Leiostomus xanthurus* caught from late June to mid-July were 5 to 10 cm long (Fig. 4) and corresponded mainly to 0-group fish (McCambridge and Alden 1984); subsequently, 10- to 15-cm *L. xanthurus* dominated the catch. Larger *L. xanthurus* were few in this investigation, which probably is due to their capability to avoid the trawl (Kjelson and Johanson 1978, McCambridge and Alden 1984). A general increase in the length of *L. xanthurus* was found during the study period, due to seasonal growth of the 0-group fish.

Trinectes maculatus of 5 to 10 cm and 10 to 15 cm were the dominant size-classes, corresponding to 1-, 2- and 3-group fish (Dovel et al. 1969) (Fig. 4). No general trend

in size distribution over time was observed for this species. However, during the severe hypoxic ($\text{O}_2 = 0.2 \text{ mg l}^{-1}$, 3% saturation) event of the first week in August, the importance of small (5 to 10 cm) *T. maculatus* increased significantly ($p < 0.002$, χ^2 -test), making up ca. 80% of the individuals.

Most *Micropogonias undulatus* were 10 to 15 cm in late June (Fig. 4). By mid-July length increased to 10–20 cm, and later in the season all individuals were 15 to 20 cm. *M. undulatus* sampled were juvenile 0- and 1-group fish (Sheridan et al. 1984), dominated by the older age-group.

The carapace length of adult *Squilla empusa* ranged from 12 to 24 mm (65 to 124 mm total length) (Fig. 5). Mean carapace length increased from 17 to 19.5 mm (80 to 102 mm total length) from late June to late September. Juvenile *S. empusa*, occurring from September, ranged from 6 to 16 mm in carapace length (Fig. 5), and mean carapace length increased from 11 to 13.5 mm (60 to 72 mm total length) during the 5 wk from 1 September to 6 October. Sex composition of adult *S. empusa* varied between 50 and 71% females, with no pronounced temporal pattern. For juvenile shrimp the percentage of females varied from 58 to 62% during sampling in September and October.

Adult *Callinectes sapidus* sampled had a carapace length which ranged from 10 to 70 mm (Fig. 5), and mean length varied from 33 to 58 mm with no apparent temporal trend. Juvenile crabs occurred from the first of September and were numerically dominant (Fig. 5). Juvenile crabs were always larger at the shallowest Stratum A (5 to 10 m) ($p \leq 0.01$). On 13 September juvenile crabs from Stratum C were larger than those from Stratum D ($p \leq 0.01$). For adult *C. sapidus* the percentage of females increased from 53–56% in late June and mid-July up to 74–78% in August ($p < 0.01$), coinciding with the severe hypoxia during that month. In September the population was similar to that in June, with between 46 and 53% females. Overall the percentage of female juvenile crabs varied from 53 to 59% during sampling in September and October.

Abundance

Leiostomus xanthurus

On the first sampling in late June oxygen concentration in the bottom water averaged 3 mg l^{-1} and *L. xanthurus* were found at approximately the same densities at depth Strata A, B and C, but were about twice as abundant in the deepest area D (Fig. 6). When the average oxygen concentration in the bottom water (measured at 18 m) declined to 1.4 mg l^{-1} in mid-July, *L. xanthurus* abundance significantly decreased in Stratum C ($p < 0.05$). After reoxygenation of the bottom water later in July the density of *L. xanthurus* increased in Stratum C but decreased in both Strata A and D ($p < 0.01$). While abundance in Stratum B was lower, it was not significantly different. During the second hypoxic event ($\text{O}_2 = 0.2 \text{ mg l}^{-1}$) in the first week of August, *L. xanthurus* were absent in the two deepest strata. Densities recorded in Stratum

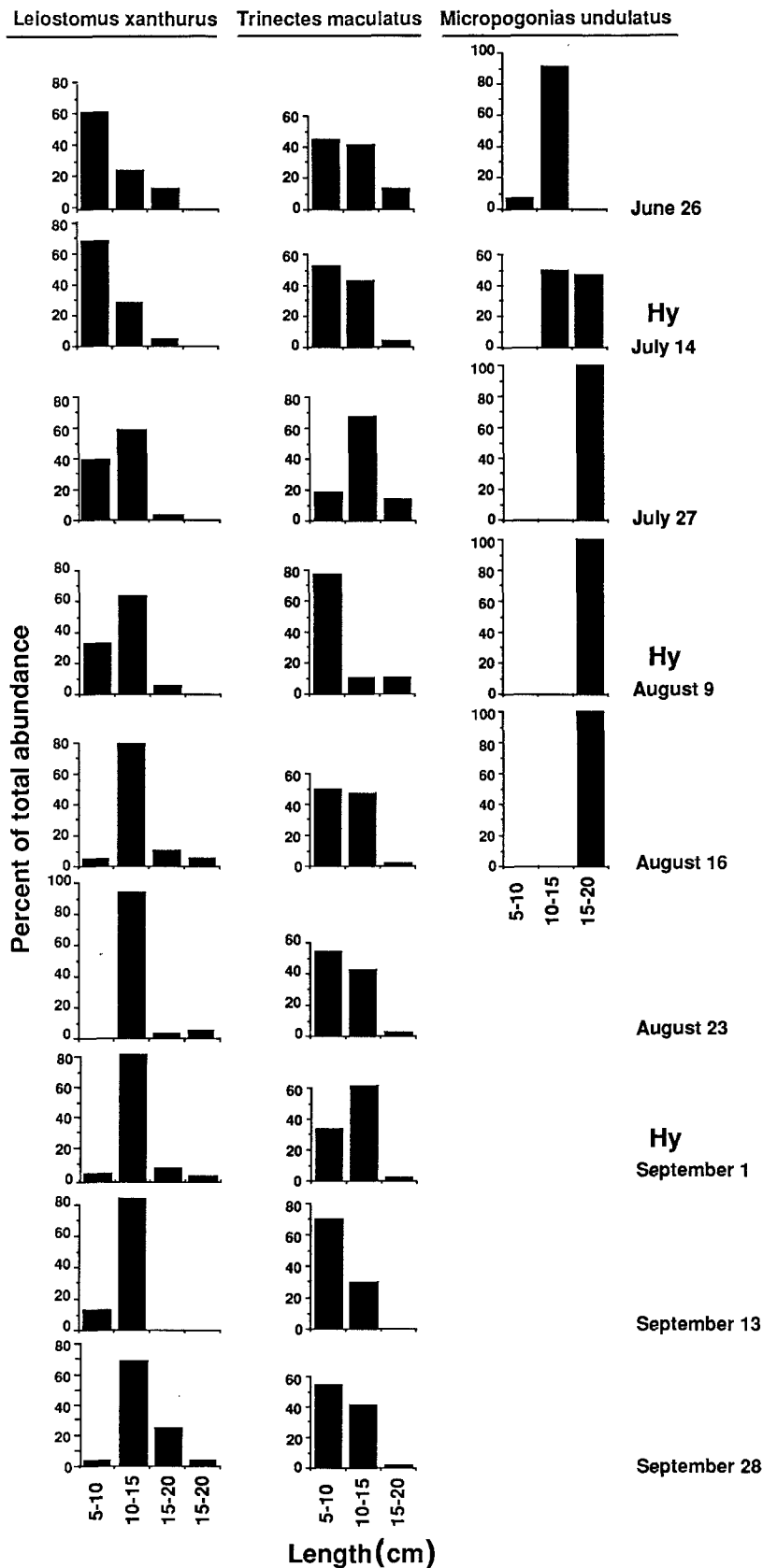


Fig. 4. *Leiostomus xanthurus*, *Trinectes maculatus*, *Micropogonias undulatus*. Abundance, as % of total abundance, for the size-classes 5–10, 10–15, and 15–20 cm (total length) of fish in York River during each sampling occasion from 26 June to 28 September 1989. Fishes from all strata are pooled. Hy: samples taken during hypoxia

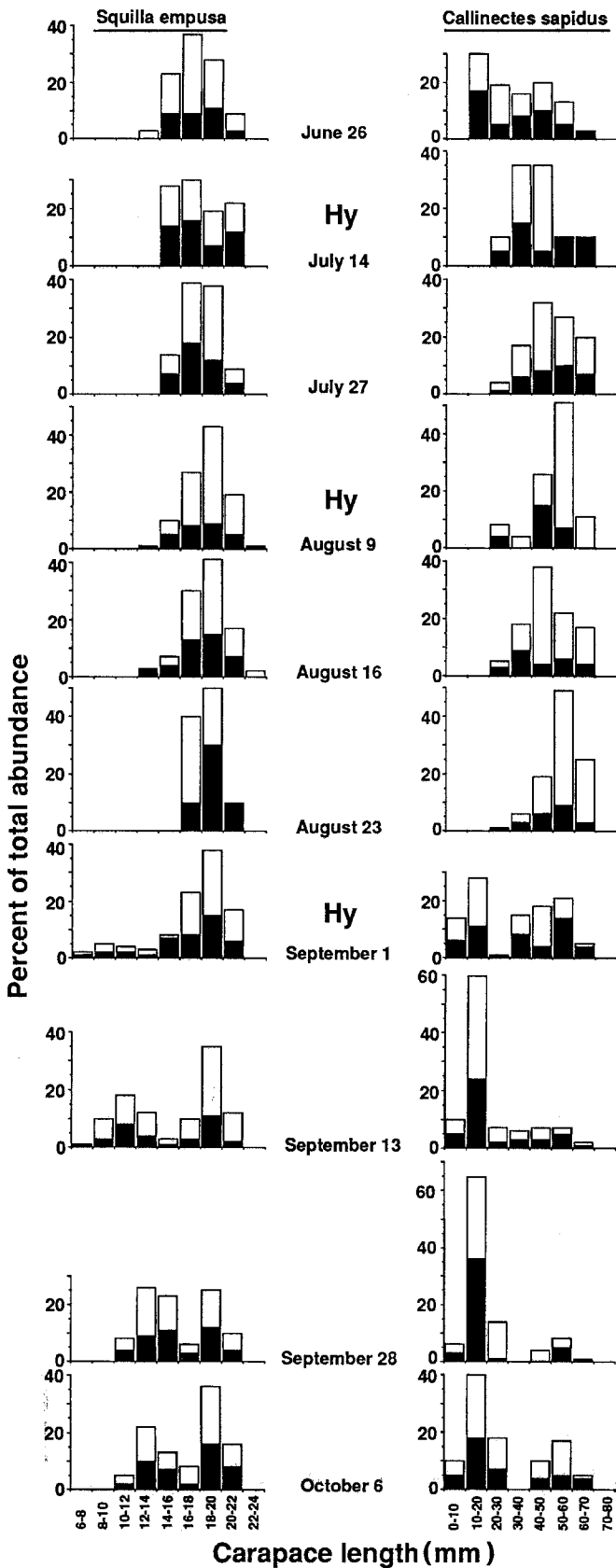


Fig. 5. *Squilla empusa*, *Callinectes sapidus*. Abundance, as % of total abundance, for the size-classes 6–8 to 22–24 mm (shrimp) and 0–10 to 70–80 mm (crab) carapace length in York River during each sampling occasion from 26 June to 6 October 1989. Shrimp and crab from all depth strata are pooled. Open portion of bars: female; filled portion: male; Hy: samples taken during hypoxia

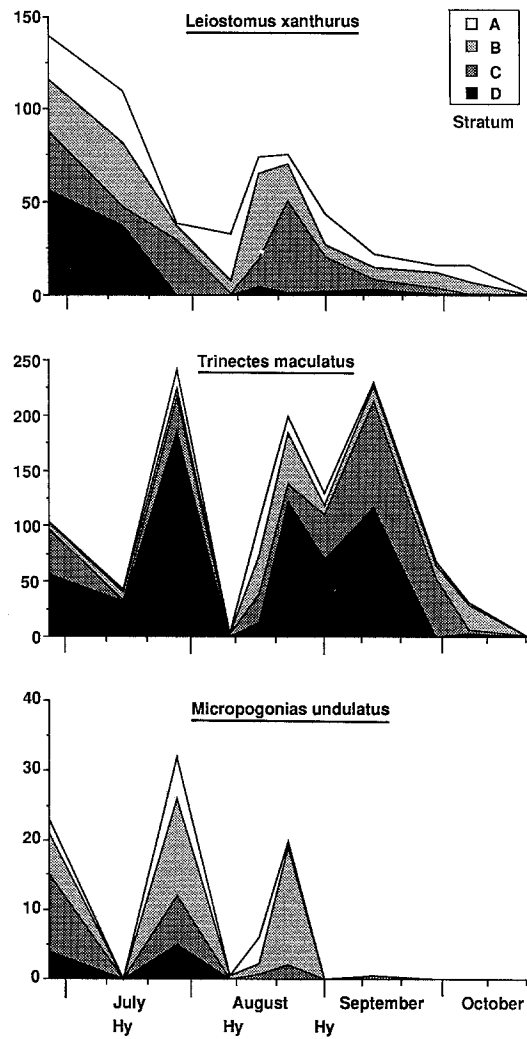


Fig. 6. *Leioostomus xanthurus*, *Trinectes maculatus*, *Micropogonias undulatus*. Abundance (ind. per 10 min trawling) of fish in Strata A (5 to 10 m), B (10 to 14 m), C (14 to 20 m), and D (> 20 m) in York River from 26 June to 20 October 1989. Figure shows general response to hypoxia and is not intended to show absolute changes in abundance. Each estimate is a mean of 2 to 3 trawl samples. Standard errors (SE) as percent of the mean ranged from 12 to 62% for the study species, but were on most occasion less than 35%. Hy: samples taken during hypoxia

B continued to be low, and in Stratum A densities increased ($p \leq 0.01$). When oxygen conditions improved *L. xanthurus* returned to Strata B and C but not to Stratum D, where densities of *L. xanthurus* remained low for the rest of the investigation period. The third hypoxic event ($O_2 = 0.9 \text{ mg l}^{-1}$) in late August and early September resulted in an increase of *L. xanthurus* abundance in Stratum A ($p \leq 0.01$). After this, numbers of *L. xanthurus* at all strata remained low for the rest of the study.

Trinectes maculatus

In late June *T. maculatus* occurred mainly in the two deeper Strata C and D (Fig. 6). During the first hypoxic event in mid-July densities were reduced in Strata C and D ($p < 0.01$). When oxygen concentration increased the

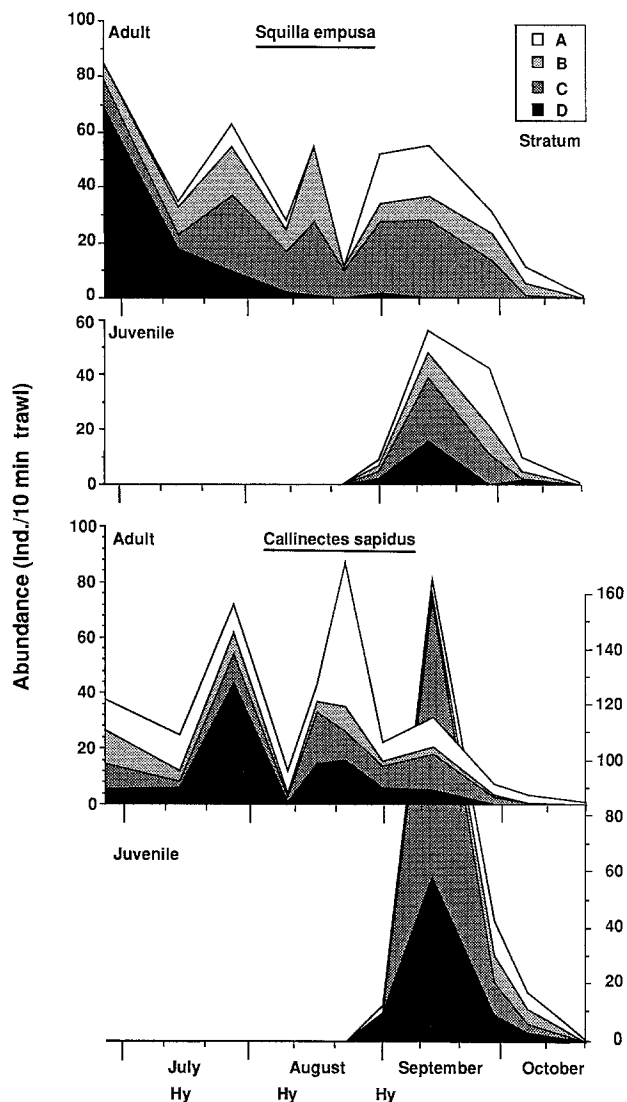


Fig. 7. *Squilla empusa*, *Callinectes sapidus*. Abundance (ind. per 10 min trawling) of crustaceans in depth Strata A (5 to 10 m), B (10 to 14 m), C (14 to 20 m) and D (>20 m) in York River from 26 June to 20 October 1989. Figure shows general response to hypoxia and is not intended to show absolute changes in abundance. Each estimate is a mean of 2 to 3 trawl samples. Standard errors (SE) as percent of the mean ranged from 14 to 68% for the study species, but were on most occasion less than 35%. Hy: samples taken during hypoxia

overall abundance of *T. maculatus* increased ($p < 0.01$), except for a decrease in Stratum B ($p \leq 0.01$). With the second hypoxic event few if any *T. maculatus* were caught in all strata. As oxygen concentration increased again (16 August) *T. maculatus* were found in all strata. With continued high-oxygen conditions (23 August; see Fig. 2) *T. maculatus* were much more abundant than expected in Stratum D ($p \leq 0.01$). The third hypoxic period did not significantly reduce abundance in Stratum D or increase abundance in Stratum A. High numbers were found throughout all strata during most of September. In October densities decreased at all strata and on the last sampling occasion no *T. maculatus* were caught.

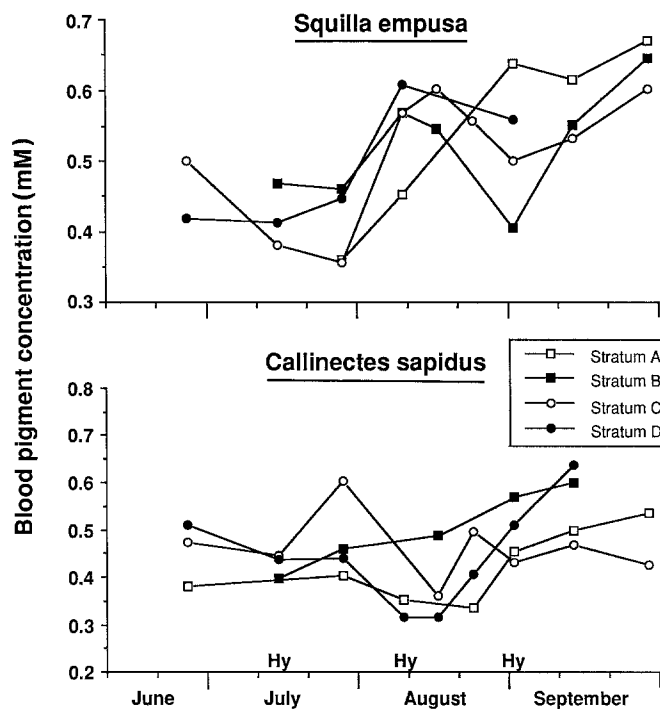


Fig. 8. *Squilla empusa*, *Callinectes sapidus*. Blood pigment (haemocyanin) concentration (mM) of crustaceans in depth Strata A (5 to 10 m), B (10 to 14 m), C (14 to 20 m), and D (>20 m) in York River from 26 June to 28 September 1989. Each estimate is a mean of 10 to 20 individuals. Standard errors (SE) as percent of the mean ranges from 4 to 15% and 8 to 21% for *S. empusa* and *C. sapidus*, respectively, but were on most occasion less than 10 and 15% for the two species. Hy: samples taken during hypoxia

Micropogonias undulatus

In late June *M. undulatus* were found in all strata, with the highest densities in Stratum C (Fig. 6). During the three hypoxic periods *M. undulatus* were absent at all depths. After the first two hypoxic events a recovery was observed at all depths, except at Stratum D, with highest densities in Stratum B. In September and October only two *M. undulatus* were taken in the whole area investigated.

Squilla empusa

Adult *S. empusa* were found in Strata B, C and D in late June, with highest densities in the deepest stratum (Fig. 7). When the first hypoxic period occurred in mid-July, combined abundance in Strata A and B increased ($p < 0.01$). At Stratum D the decline in *S. empusa* was almost significant. When oxygen returned to the bottom water decreased densities of *S. empusa* continued to occur in Stratum D ($p < 0.01$). Few adult *S. empusa* were found for the rest of the investigation in Stratum D. Immediately after the second hypoxic period (16 August) there was no change in *S. empusa* distribution. On 23 August few *S. empusa* were caught. During the last hypoxic event *S. empusa* densities increased in Stratum A ($p \leq 0.01$). Later in September, after hypoxia, abundance

patterns in Strata A, B and C did not change. In October a decline in adult *S. empusa* was observed, and none was found during the last sampling occasion. During September a recruitment of juvenile *S. empusa* occurred, with peak abundance in mid-September in Strata B, C and D, and in late September in Stratum A (Fig. 7).

Callinectes sapidus

Adult (1- and 2-group) *C. sapidus* were found in approximately the same densities at all sampling depths in late June (Fig. 7). No significant change in abundance was observed during the first hypoxic period in mid-July. In Stratum D higher densities were observed after oxygen concentrations increased later in July ($p < 0.05$). During the second period of hypoxia crab density declined in Stratum D ($p < 0.01$). When oxygen increased again *C. sapidus* were caught in all strata and exhibited increased density in Stratum A ($p < 0.01$). Later in September and October the abundance of adult crabs declined and no crabs were caught in late October. At the begin-

ning of September recruitment of juvenile (0-group) *C. sapidus* was observed in Strata A and D. Two weeks later juvenile crabs were found within all strata, with highest abundance in the two deepest areas. Densities declined later in September and October and no juvenile crabs were found during the last sampling.

Blood haemocyanin concentration

Mean blood haemocyanin concentration of *Squilla empusa* was between 0.35 and 0.5 mM in Strata B, C and D in late June and early July (Fig. 8). No significant change in haemocyanin concentration was observed after the first hypoxic period in mid-July, when *S. empusa* were exposed to oxygen concentrations of 1.5 to 2 mg l⁻¹ (20 to 30% saturation, 23°C) for 6 d. During the second hypoxic event in August, when oxygen concentration was <1.5 mg l⁻¹ for 1 wk and <2 mg l⁻¹ for 2 wk (Fig. 2), mean haemocyanin concentration increased significantly ($p < 0.02$ to 0.002, *U*-test) to 0.45–0.6 mM in all depth strata. From mid-August to 1 September haemocyanin

Table 1. *Leiostomus xanthurus*, *Trinectes maculatus*, *Squilla empusa*. Oxygen tolerance experiments. Ventilation rate (beats min⁻¹) at different levels of oxygen saturation (% sat) for spot (*L. xanthurus*), hogchoker (*T. maculatus*) and mantis shrimp (*S. empusa*). Each control and experiment is a mean from two replicate aquaria with six specimens each. Temp. = 25 ± 0.5°C, salinity = 18 to 20‰. Expt 3 performed for *T. maculatus* only

Species	Time (d)	Control			Expt 1			Expt 2			Expt 3		
		Oxygen (% sat)	Beats (mean)	Beats (high/low)	Oxygen (% sat)	Beats (mean)	Beats (high/low)	Oxygen (% sat)	Beats (mean)	Beats (high/low)	Oxygen (% sat)	Beats (mean)	Beats (high/low)
<i>L. xanthurus</i>	1	92	55	74/42	92	50	56/44	91	52	58/44	–	–	–
	2	91	53	70/40	90	49	55/46	44	78	86/66	–	–	–
	3	92	52	58/44	40	92	108/86	28	104	108/98	–	–	–
	4	93	52	62/42	30	98	104/50	26	118	124/100	–	–	–
	5	93	54	66/44	47	62	64/56	20	132	144/120	–	–	–
	6	93	55	68/42	36	80	88/74	11	124	166/98	–	–	–
	7	93	50	60/44	34	92	110/80	–	–	–	–	–	–
	8	93	56	62/40	33	90	98/82	–	–	–	–	–	–
	9	93	58	64/40	24	122	136/118	–	–	–	–	–	–
	10	93	54	60/38	13	150	160/139	–	–	–	–	–	–
<i>T. maculatus</i>	1	92	41	52/26	92	48	56/30	88	44	50/36	90	48	58/34
	2	93	42	54/28	41	84	118/72	64	85	102/64	62	55	64/47
	3	94	41	56/26	27	88	122/64	38	112	136/98	48	74	98/64
	4	92	40	56/26	14	116	114/85	34	88	114/82	70	46	64/36
	5	92	38	54/28	13	123	138/98	38	107	110/62	58	46	52/28
	6	93	35	42/26	14	128	164/110	30	128	130/126	56	48	64/40
	7	94	35	48/26	14	124	134/106	12	128	170/102	62	42	60/26
	8	93	33	48/24	14	122	132/108	8	114	166/86	54	58	78/32
	9	93	34	48/26	14	112	120/104	8	134	164/118	28	79	138/58
	10	93	34	48/28	14	110	120/94	8	130	144/124	26	82	124/72
	11	93	30	42/26	14	108	112/92	8	132	142/124	30	83	128/64
	12	93	28	38/24	13	110	120/98	4	114	134/94	30	81	116/56
	13	94	28	38/26	14	106	110/88	–	–	–	–	–	–
	14	94	28	36/24	14	108	112/84	–	–	–	–	–	–
	15	93	28	38/26	8	110	128/106	–	–	–	–	–	–
	16	93	28	38/26	5	80	86/56	–	–	–	–	–	–
<i>S. empusa</i>	1	90	30	38/20	91	26	31/22	91	31	36/24	–	–	–
	2	92	24	24/24	45	20	24/18	32	29	30/28	–	–	–
	3	91	27	28/24	25	52	55/46	25	47	56/40	–	–	–
	4	91	31	36/24	16	48	52/44	25	24	32/20	–	–	–
	5	92	24	38/22	10	64	80/56	–	–	–	–	–	–
	6	93	25	28/24	7	41	60/40	–	–	–	–	–	–

concentration decreased significantly in Strata B ($p < 0.001$, U -test) and C ($p < 0.02$, U -test). During the third hypoxic period in late August and early September, with 1 wk of oxygen concentrations $< 2 \text{ mg l}^{-1}$ and 4 d $< 1.5 \text{ mg l}^{-1}$, haemocyanin concentrations increased in Strata A, B and C, although the changes were not significant.

Mean haemocyanin concentration of *Callinectes sapidus* was between 0.3 and 0.6 mM. No significant changes in haemocyanin were observed after the three hypoxic events, with one exception. In Stratum D, a significant increase ($p < 0.02$) occurred after the second hypoxic period, and the increase remained through the third hypoxic period.

Experiments

During normoxia (91 to 94% O_2 saturation) mean ventilation rate of *Leiostomus xanthurus* ranged from 50 to 58 beats min^{-1} (Table 1) for the 10-d experiment. When O_2 saturation was below 50% ventilation rate increased almost linearly with decreasing oxygen. At 30 to 40% O_2 saturation ($\text{O}_2 = 2.4$ to 3.0 mg l^{-1}) ventilation rate was about doubled compared to the controls. *L. xanthurus* survived for at least 6 d at this level. When O_2 saturation was decreased to 11–13% ($\text{O}_2 = 0.8$ to 1.0 mg l^{-1}) ventilation rate was about three times higher compared to the controls, and all fish died within 4 h.

Mean ventilation rate for *Trinectes maculatus* in the control series (92 to 94% O_2 saturation) ranged from 33 to 42 beats min^{-1} initially and from 28 to 30 beats min^{-1} at the end of the experiment (Table 1). Large variation in ventilation rate among individuals was observed (range from 24 to 56 beats min^{-1}), and the rate was inversely related to how much the gill cover was used for pumping water over the gills. Ventilation rate was similar to that of the control when oxygen was lowered to 50–70% O_2 saturation, but at lower oxygen concentration ventilation was significantly higher ($p < 0.01$ to 0.001 , U -test) than that of the controls and was inversely related to oxygen concentration. When O_2 saturation was held at 13 to 14% ($\text{O}_2 = 1.0$ to 1.1 mg l^{-1}) for 10 d (Expt 1) a 15% reduction in mean ventilation rate (from 128 to 108 beats min^{-1}) was observed, whereas fish kept in 8% O_2 saturation ($\text{O}_2 = 0.7 \text{ mg l}^{-1}$) for 4 d (Expt 2) did not show any decline in mean ventilation. A decrease in O_2 saturation from 8 to 4–5% ($\text{O}_2 = 0.3$ to 0.4 mg l^{-1}) resulted in a decline in ventilation, after which all fish died within 5 to 22 h.

During normoxia (83 to 89% saturation) mean ventilation rate of *Squilla empusa* ranged from 20 to 38 beats min^{-1} (Table 1). Ventilation rate was not significantly different ($p < 0.05$, U -test) from that of the control at oxygen concentrations down to 32% (Expt 2). At 25% O_2 saturation ventilation rate was about double that of the controls (Expts 1 and 2). Individuals were at first very actively swimming and cleaning gills but adapted when kept in this concentration for a longer time, as seen in Expt 2. Ventilation rate increased further at 10% O_2 saturation to 59–66 beats min^{-1} (Expt 1). At 8% O_2 satura-

tion individuals were immobile while maintaining an elevated body position with pereopods and raptorial claws fully extended, and ventilation decreased to 42–48 beats min^{-1} at this oxygen level.

Discussion

In the York River study area, hypoxia ($\text{O}_2 < 2 \text{ mg l}^{-1}$) occurred in the bottom water during three major periods in summer 1989. These events had a duration of 1 to 2 wk and coincided with stratification-destratification of the water mass driven by the spring-neap tide cycle (Haas 1977). During stratification approximately the same low oxygen concentration was recorded in the whole water column below ca. 15 m depth (Fig. 3). A general decrease in dissolved oxygen in the bottom water was also observed from late June to early September, occurring during both spring- and neap-tide cycles, resulting in increased severity of hypoxia. From this it would be expected that the third hypoxic period would be the most severe. However, the water column was completely mixed with respect to oxygen by a storm in early September, and oxygen conditions in the bottom water improved rapidly (Diaz et al. in press). The declining trend in oxygen concentration during the summer was due, in part, to intruding less oxygenated bottom water from the Chesapeake Bay and to increased water-column and sediment oxygen demand within the river (Kuo and Neilson 1987).

The demersal fish and crustaceans studied were all affected by hypoxia in the bottom waters. A general migration of all species from deep to shallow strata took place during July and August hypoxic events. The degree of vertical migration in the study area was related to level of oxygen concentration and time of exposure. All species seemed to react to oxygen concentrations below 2 mg l^{-1} , but differences in oxygen tolerance were found among species. When oxygen conditions improved all these species, except for the *Squilla empusa*, returned to the deeper areas.

Migration and physiological response related to hypoxia

Micropogonias undulatus was the most sensitive species and was absent from the whole area during hypoxia. After the second hypoxic period it was absent in the deepest stratum even during normoxia.

In the York River, *Leiostomus xanthurus* were absent when oxygen concentration dropped below 2 mg l^{-1} , which is their lower limit of oxygen tolerance in St. Marks, Florida, USA (Subrahanyam 1980). After the first hypoxic event *L. xanthurus* left the deepest stratum and occurred later at highest densities in Strata B and C. *L. xanthurus* died within 4 h when experimental oxygen concentrations were reduced to $< 1.4 \text{ mg l}^{-1}$ (20% saturation). Survival for at least 4 d was observed at 1.8 to 2.7 mg l^{-1} (24 to 36% saturation). Both the magnitude of gill-cover movement and ventilation rate in *L. xanthurus* were inversely related to low oxygen concentration.

Trinectes maculatus were tolerant to low oxygen and showed only slight density reductions during the first and third hypoxic periods. Following hypoxia, high numbers of *T. maculatus* were seen returning to the deepest stratum. During destratification in late August, between the second and third hypoxic periods, daily mean oxygen concentration in the bottom water ranged from 2.0 to 2.6 mg l⁻¹. Despite this weak recovery in oxygen, *T. maculatus* returned to deep water (Stratum D). The laboratory experiment showed that ventilation rate of *T. maculatus* increased two- to three-fold when oxygen concentration was lowered from 92 to 14% (O₂ = 1 mg l⁻¹) saturation. This species could survive in oxygen concentrations of 1 mg l⁻¹ (14% saturation) for at least 10 d and also acclimated to low oxygen levels, as evidence by a decrease in ventilation rate (Table 1). During normoxia only about 1/3 of the gill cover was lifted when pumping water over the gills. As oxygen decreased gill-cover movement increased, and the entire cover was elevated at oxygen concentrations of 1 mg l⁻¹. Thus, increase in actual ventilation when exposed to hypoxia may be five- to six-fold. *T. maculatus* died within 1 d of exposure to oxygen concentrations of 0.4 mg l⁻¹ (5% saturation).

Squilla empusa seem to first adapt physiologically to hypoxia and then migrate as hypoxia becomes more severe. This is consistent with its more stationary and territorial way of living (Caldwell and Dingle 1976, Myers 1979). During the first hypoxic period, when *S. empusa* experienced 6 d of moderate hypoxia (20 to 30% O₂ saturation), no increase in blood haemocyanin was observed. Crustaceans can compensate for effects of moderate short-term hypoxia in ways other than increasing haemocyanin concentration. Besides doubling the ventilation rate at 25% O₂ saturation and becoming more active, as we observed, some crustaceans [*Carcinus maenas* (L.)] exhibit increased pH and urate concentration in the blood, increasing haemocyanin oxygen affinity during hypoxia (Lallier et al. 1987). The 'delayed' reaction of increasing haemocyanin concentration during exposure to hypoxia was also found in experiments with the Norway lobster, *Nephrops norvegicus* (L.) (Baden et al. 1990 b). The second hypoxic event was prolonged and more severe than the first and *S. empusa* compensated by increasing haemocyanin concentration by 20 to 30%. At this time *S. empusa* appear to have migrated to shallow water, as evidenced by unexpectedly high haemocyanin concentration in Stratum-A individuals and the delayed increase in haemocyanin concentrations in Stratum-A individuals relative to individuals in other strata. Oxygen concentrations were never critical at these shallow depths, indicating that shrimp migrated from deeper areas where they had been exposed to low oxygen, resulting in an increase in blood pigment concentration. Migration was strongest from Stratum D, where densities decreased rapidly after the first hypoxic event. The second and most serious hypoxic period did not, however, last long enough for *S. empusa* to reach the exhaustion phase (Seyle 1976), and catabolism of haemocyanin did not take place as found for *N. norvegicus* (Hagerman and Baden 1988, Baden et al. 1990 b). The increase in *S. empusa* haemocyanin cannot be explained by change from

the postmoult stage (when the blood is diluted with water) to the intermoult stage, as no increase in mean carapace length was observed in this period (Fig. 5). Between the second and third hypoxic periods, the increase in haemocyanin stopped and a significant decrease took place in Strata B and C. This can be explained by a recovery of haemocyanin during slightly better oxygen conditions or by a migration from Strata B and C of *S. empusa* with high haemocyanin concentrations to Stratum A, where an increase in mean haemocyanin was observed in the same period. The third hypoxic period seemed to halt this recovery, expressed as a decline in haemocyanin concentration.

A two-fold increase in ventilation rate was observed for *Squilla empusa* at 25% O₂ saturation (2 mg l⁻¹) in the laboratory experiment. Both hypoxia and an observed increase in activity might explain the doubling in beat rate at this O₂ level and could give an indication of the O₂ concentration below which *S. empusa* start migrating away from the hypoxic area or adapt by increasing beat rate. The sex ratio of adult *S. empusa* was dominated by females, a condition also observed under normoxia in the Gulf of Mexico by Rockett et al. (1984).

With the exception of some individuals in Stratum D, the strategy of *Callinectes sapidus* for withstanding hypoxia is, as indicated by the trawl data, to migrate from the hypoxic area and return when conditions improve.

Juvenile *Squilla empusa* and *Callinectes sapidus* occurred in trawl samples during September and October. Young *S. empusa* were found in densities as similar to those of adults, whereas newly recruited *C. sapidus* were numerically dominant over adults. Both species were found at highest densities in the deepest area (Strata C and D), where hypoxia occurred early in the season (July and August). The size of juveniles in early September suggests that recruitment took place a month earlier (Van Engel 1987), but they were not sampled effectively by the trawl. It is therefore impossible to evaluate how hypoxia in the bottom water may affect recruitment of these species. It is possible that the recruitment occurred in other habitats and that juvenile *S. empusa* and *C. sapidus* migrated into the study area during September.

Seasonal migration

A general decrease in density was observed for all species at all depths during September and October. During this time oxygen concentration in the bottom water was increasing and full saturation was recorded in mid-October. Thus, the decline in abundance was not due to hypoxia but rather to natural migration patterns of the species studied. *Leiostomus xanthurus* and *Micropogonias undulatus* are seasonal residents. They use the York River as a nursery area during spring and summer (Markle 1976) and migrate offshore during autumn for spawning on the continental shelf in winter (Markle 1976, Kobylinski and Sheridan 1979). *Trinectes maculatus* are resident in the York River estuary and migrate upstream in autumn to spend the winter in low-salinity waters (Dovel et al. 1969, Markle 1976). *Squilla empusa* are resident,

and they burrow in U-shaped tubes ranging from 0.15 to 0.5 m in the sediment during summer and hibernate in straight vertical-tube burrows, with a maximum extension of 4 m (Myers 1979). A transition from summer to winter burrows occurs in Narragansett Bay, USA (41.7°N) when temperature falls below 8°C during November and December (Myers 1979). Our findings indicated that *S. empusa* did not appear in the trawl in October, when the temperature was still about 20°C. This was likely due to the previous hypoxia and was not related to any overwintering behaviour. The low abundance of *Callinectes sapidus* during trawling from the middle of September can be explained by spawning migrations of female *C. sapidus* in late summer from the estuary towards more saline bay water (Van Engel 1987), and by burrowing of male *C. sapidus* within the estuary for overwintering (Schaffner and Diaz 1988).

Conclusion

The effect of periodic hypoxia on the demersal species studied appears to be related to their oxygen tolerance, mobility and feeding habits. The fishes and *Callinectes sapidus* moved quickly into and out of the deeper parts of the river, depending on the level of dissolved oxygen. *Squilla empusa* seemed to remain in the deep hypoxic strata until their tolerance was exceeded, and then they migrated to and remained in shallower water. The attraction causing all species to stay as long as they could in the deeper strata may have been food availability. With the onset of hypoxia, many infaunal species change their behaviour and come to the sediment surface, where they can be easily preyed upon (Jørgensen 1980, Diaz et al. in press). Gut content analysis of the study fishes confirms that with hypoxia there was an increase in the size of prey taken (Pihl et al. unpublished). This opportunistic feeding behaviour may be a characteristic response to hypoxia and could be used as an early warning that a bottom is under stress. The consequences of continued hypoxia or anoxia are well documented and catastrophic to all faunal elements (Harper et al. 1981, Stachowitsch 1984, Rosenberg and Loo 1988, Pihl 1989, Baden et al. 1990 a).

The key issue involved in areas that become hypoxic is one of energy flow. Basically, it is whether or not the fishes survive in the long term. If hypoxia is prolonged or leads to anoxia, fish and invertebrates die and energy is dissipated by microbenthos, a condition we tend to associate with severely stressed systems (Stachowitsch 1984). If hypoxia is short-lived, as in the York River, then benthic invertebrate prey are retained by the fishes and the system is thought of as productive (Diaz and Schaffner 1990). The possibility exists that areas experiencing periodic short-lived hypoxia may actually be good nursery grounds for fisheries species. There is no indication that the habitat value of the lower York River is lessened by periodic hypoxia for the species studied.

This phenomenon of periodic hypoxia driven by the spring-neap tidal cycle has been known for over ten years (Haas 1977). It may represent a natural phenomenon with

which the fishes are in a delicate balance. Even brief hypoxia bring a species to its physiological limits, and if eutrophication lengthens the time of hypoxia or brings the system closer to anoxia the system may change and become characteristically stressed.

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