Effects of hypoxia on predator–prey interactions between juvenile *Carcinus aestuarii* and *Musculista senhousia*

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ABSTRACT: The impact of hypoxia upon predator–prey interactions between juvenile Mediterranean shore crabs *Carcinus aestuarii* and the mytilid *Musculista senhousia* was investigated in laboratory and mesocosm experiments. These species are among the most abundant macrobenthic organisms in the Sacca di Goro, a lagoon in the Po River deltaic system (Adriatic Sea, Italy). The effect of normoxia and hypoxia on juvenile *C. aestuarii* predatory behaviour was examined in laboratory experiments; factors were prey size (small, medium and large) and oxygen level (normoxic: >6.0 mg $O_2 l^{-1}$; moderately hypoxic: 3.0 to 1.5 mg $O_2 l^{-1}$; severely hypoxic: <1.5 mg $O_2 l^{-1}$). The prey-handling time of crabs was largely increased by hypoxia. In mesocosm experiments, 2 densities of *M. senhousia* (40 and 200 mussels tank^{-1}) were exposed to juvenile *C. aestuarii* (1 crab tank^{-1}) at 2 oxygen levels (normoxic: >6.0 mg $O_2 l^{-1}$; severely hypoxic: <1.5 mg $O_2 l^{-1}$). Consumption rates of *C. aestuarii* were lower under hypoxia, resulting in reduced mortality rates of mussels. Predation was inversely dependent. Short-term hypoxia, therefore, reduced the ability of crabs to forage on mussels efficiently and increased mussel survival, probably reducing the transfer of bivalve prey to predatory crabs.

KEY WORDS: Hypoxia · Predator–prey · *Carcinus aestuarii* · *Musculista senhousia* · Sacca di Goro

INTRODUCTION

Oxygen deficiency events affect coastal and estuarine communities almost worldwide (Diaz & Rosenberg 1995, Gray et al. 2002). The ecological impact of such events ranges from extensive mortality of benthic organisms to the alteration of biological interactions among them (Jørgensen 1980, Justic et al. 1987, Nilsson & Rosenberg 1994, Diaz & Rosenberg 1995, Ritter & Montagna 1999). Fishes are more sensitive to reduced oxygen concentrations than crustaceans, followed by annelids, and bivalves are the most tolerant (Rosenberg et al. 1991, Nilsson & Rosenberg 1994). As an example, in tolerance experiments conducted at 10°C and 0.2 mg $O_2 l^{-1}$, *Mytilus edulis* survived for more than 1000 h, whereas *Nereis diversicolor* survived for ca. 200 h, and *Carcinus maenas* for less than 100 h (Dries & Theede 1974, in Gray et al. 2002). In response to low-oxygen events, behavioural avoidance of unfavourable conditions may result in the migration of mobile organisms (Pihl et al. 1991, Das & Stickle 1994), while sessile and infaunal species, unable to avoid or escape oxygen-depleted waters, initiate a series of responses to hypoxia according to its severity (Diaz & Rosenberg 1995, Gray et al. 2002). A consequence of these behavioural changes is that predator–prey dynamics can also be altered (Taylor & Eggleston 2000, Brante & Hughes 2001, Tallqvist 2001, Seitz et al. 2003).

In the Sacca di Goro, a large, microtidal lagoon in the northern Adriatic Sea (44° 45′ N, 12° 15′ E; NE Italy), small-scale, hypoxic events are common, particularly in summer (Colombo et al. 1994). Bottom water can change quickly from normoxic to hypoxic conditions,

or vice versa, and these changes can be sustained episodically (hours) or chronically (days) (Mistri 2002). The Sacca is a lagoon in which physical disturbance has an overriding influence in structuring benthic communities. As a consequence, animal assemblages are characterised by a small number of species, a strong dominance in abundance by a few of these species, and relatively low diversity (Mistri et al. 2001a,b).

In the Sacca, a key predator–prey system is constituted by the Mediterranean shore crab *Carcinus aestuarii* and the epibenthic mytilid *Musculista senhousia*; these 2 species are among the most abundant macrobenthic organisms in the lagoon (Mistri et al. 2001b). The non-native *M. senhousia* was accidentally introduced in the 1990s (Mistri et al. 2004). This thin-shelled species fits the classical concept of an opportunist, being short-lived (max. 2 yr), of small body size (max. 35 mm shell length), fast-growing (up to 25 mm in the first year), and experiencing dramatic population fluctuations (Crooks 1996, Mistri 2002). The mussel typically lives on the surface of shallow, subtidal, soft sediments and uses byssal threads to create byssal bags. When occurring in high densities, a mat is formed on the sediment surface. In the Sacca, *M. senhousia* shows very variable abundance, depending on the extension and thickness of the mats, and typically ranges from tens to a few thousand individuals (ind.) m^{-2} (Mistri 2002, Mistri et al. 2004). The native shore crab *C. aestuarii* is a large (up to 70 mm carapace width) epibenthic predator that has a fairly broad diet, comprising many taxa, particularly bivalve molluscs, polychaetes and small crustaceans. The shore crab can live at a wide range of salinities (8 to 35 psu) and temperatures (5 to 30°C) (Mori et al. 1990, author's pers. obs.), and shows very variable abundance, typically ranging between 0.5 and 40 ind. m^{-2} (Mistri et al. 2001a). Adult crabs (>50 mm carapace width) are voracious predators of *M. senhousia*, and are able to break all sizes of mussel within a few seconds (Mistri 2003).

The present study examined juvenile crabs. Although in the Sacca, especially in summer, hypoxia is a common event (Colombo et al. 1994), no information exists on its effects on benthic predator–prey dynamics. By increasing the susceptibility of prey to predators, hypoxia may change the structure of benthic communities (Jørgensen 1980, Pihl et al. 1992). The aim of this study was to examine the effects of hypoxia on predator–prey interactions between juvenile *Carcinus aestuarii* and *Musculista senhousia* through a series of laboratory experiments. The behavioural response of *C. aestuarii* to hypoxia was examined by quantifying and comparing the handling time of crabs presented with *M. senhousia* of different sizes under conditions of normoxia, moderate hypoxia and severe hypoxia. Additionally, in further predator–prey mesocosm

experiments, the foraging behaviour of the crab was examined to ascertain whether or not hypoxia alters predator–prey dynamics.

MATERIALS AND METHODS

Effect of hypoxia on predatory behaviour. Species of the Asian date mussel *Musculista senhousia* were collected with a hand rake in the Sacca di Goro (Po River Delta, Adriatic Sea) in June 2003, and maintained in suspended cages in an outdoor 5000 l tank, in flowing seawater (salinity 27 ± 1 psu, temperature 26 ± 2°C) with natural phytoplankton. I used 50 randomly selected mussels to calculate the relationship between flesh ash-free dry weight, AFDW (mussels dried at 80°C for 48 h and combusted at 450°C for 4 h) and shell length (SL). The relationship had the form AFDW = $0.0039SL^{2.609}$ ($r^2 = 0.88$; $p < 0.05$), and was used to predict the weight of each prey presented to a crab in subsequent trials. Juvenile Mediterranean shore crabs *Carcinus aestuarii* of 30.1 to 34.0 mm carapace width were collected in the Sacca during the same period using dip nets. Crabs were held in flowing seawater in an indoor 500 l, aerated, holding tank, and fed ad libitum with mussel flesh. Sediment, faecal material, and debris were removed from the tank daily. Only intact and actively feeding crabs were utilised for predation trials, and their hunger levels were standardised by a 48 h long starvation.

The effect of normoxia and hypoxia on *Carcinus aestuarii* predatory behaviour was tested through the manipulation of oxygen levels in the water in 4 small (20 l), indoor, Plexiglas aquaria half-filled with seawater. Low oxygen levels were maintained by bubbling air and nitrogen at 97% purity with 2 air stones; normoxic conditions were maintained by bubbling only air. In the severely hypoxic treatment, a sheet of bubble-wrap plastic was placed on the water surface of each aquarium to limit gas exchange. In the experimental design, factors were (1) prey size (small: <15.0 mm SL; medium: 15.1 to 20.0 mm SL; large: >20.1 mm SL) and (2) oxygen level (normoxic: >6.0 mg O_2 l^{-1} [range: 6.0 to 8.3 mg O_2 l^{-1}]; moderately hypoxic: 3.0 to 1.5 mg O_2 l^{-1}; severely hypoxic: <1.5 mg O_2 l^{-1}). Mussels were offered individually, since clumping did not seem to provide refuge to the species from crab predation (Mistri 2004). Each combination of prey size and oxygen treatment was replicated 4 times. Oxygen concentration was continuously monitored by an Oxy-Guard® Mk III oxygen probe. A crab was placed into each aquarium, and nitrogen bubbling was begun; the moderately hypoxic condition was reached within 1 h, the severely hypoxic condition within 2 h. The prey was then introduced into the aquarium. In each feed-

ing trial, breaking and eating times (Elner & Hughes 1978) were carefully recorded with a stopwatch. The sum of breaking and eating times constituted the prey handling time, which was then used to calculate prey-profitability (Elner & Hughes 1978) by dividing the estimated flesh weight of the prey by handling time.

A 2-way ANOVA, with oxygen level (N: normoxic; MH: moderately hypoxic; SH: severely hypoxic), and prey size (S: small; M: medium; L: large) as fixed factors was used. Before analysis, data were checked for homogeneity of variance (Levene's test), and logarithmic (for behavioural data) and square-root (for profitability data) transformations were used (Underwood 1997). Post hoc pairwise comparisons were made using Tukey's HSD test (Sokal & Rohlf 1981). The components of handling time (breaking and eating time) at each prey size were also analysed by 2-way ANOVA after log-transformation, with oxygen level and prey size as factors.

Effect of hypoxia on predator–prey dynamics. To evaluate crab responses to prey density and oxygen level, 2 densities of medium-sized (15.1 to 20.0 mm SL) *Musculista senhousia* (40 and 200 mussels per tank, corresponding to 66 and 328 mussels m^{-2}) were exposed to juvenile *Carcinus aestuarii* (1 crab per tank, corresponding to 2 crabs m^{-2}) at 2 oxygen levels (normoxic and severely hypoxic). The experimental densities of mussels used in this study represent a low-to-moderate range of natural densities of *M. senhousia* in the Sacca di Goro (Mistri 2002). Episodic hypoxic events in the Sacca (hypoxia may range from a few hours to days: Colombo et al. 1994, Mistri 2002) helped determine a realistic duration for the experiments. I filled 8 outdoor mesocosm tanks ($78 \times 78 \times 15$ cm) with unfiltered seawater. Mussels were introduced into each tank, being at least 10 cm from the sides to avoid edge effects on predation rates (Eggleston et al. 1992). A sheet of bubble-wrap plastic was placed on the water surface of 4 tanks randomly assigned to the severely hypoxic treatment, SH (<1.5 mg O_2 l^{-1}), to limit gas exchange. These 4 SH tanks were then bubbled with nitrogen at 97% purity, monitored by the OxyGuard® Mk III oxygen probe. The hypoxic condition was reached within 5 h of beginning nitrogen bubbling. The remaining 4 tanks were assigned to the normoxic treatment, N (6.0 mg O_2 l^{-1}), and the oxygen level was maintained by bubbling air with 2 Sonic® Premier 3900 air pumps in each tank. *C. aestuarii* were starved for 48 h prior to being released in the centre of each tank. I conducted two 24 h feeding trials at each mussel density. Prey mortality was quantified by counting surviving mussels.

Consumption (no. of mussels eaten 24 h^{-1}) and mortality rates (no. of mussels eaten 24 h^{-1} as a function of mussel density) of *Musculista senhousia* were analysed

by a 2-way, fixed-factor ANOVA using mussel density (LD: low density, 40 ind. $tank^{-1}$; MD: medium density, 200 ind. $tank^{-1}$) and oxygen level (N: normoxia; SH: hypoxia) as factors. Before analysis, data were checked for homogeneity of variance (Levene's test), and logarithmic (for consumption data) and arcsine (for mortality data) transformations were used (Underwood 1997). Post hoc pairwise comparisons were made using Tukey's HSD test (Sokal & Rohlf 1981).

RESULTS

Effect of hypoxia on crab and mussel behaviour

Under severe hypoxia, *Carcinus aestuarii* often raised its cephalotorax towards the water surface by stretching its walking legs. This behaviour enables crabs to oxygenate in suitably shallow water (Taylor et al. 1977). Moreover, crabs often paused for long periods while handling prey under severe hypoxia. Under hypoxia *Musculista senhousia* closed its valves, which interrupted pumping activity.

The analysis of handling time (Fig. 1) revealed that both factors, oxygen level and prey size, were statistically significant, but their interaction was not (Table 1). Crabs took longer to handle medium and large mussels than small mussels (Tukey HSD test: S vs M, $p < 0.05$; S vs L, $p < 0.001$; M vs L, $p = 0.09$). Moreover, handling time was shorter under normoxia than under moderate and severe hypoxia (N vs MH, $p < 0.001$; N vs SH, $p < 0.0005$; MH vs SH, $p < 0.001$). The components of handling time, breaking time (Bt) and eating time (Et) also varied significantly (Fig. 1, Table 2). Breaking time varied as a function of oxygen level (N vs MH, $p = 0.07$; N vs SH, $p < 0.001$; MH vs SH, $p < 0.001$) but not of prey size. Eating time varied as a function of prey size (S vs M, $p = 0.23$; S vs L, $p < 0.0005$; M vs L, $p < 0.05$), and of oxygen level (N vs MH, $p < 0.05$; N vs SH, $p < 0.0005$; MH vs SH, $p = 0.08$), but their interaction was not significant.

Under normoxic conditions, prey-profitability ranged from about 0.03 mg s^{-1} for small and medium mussels to 0.05 mg s^{-1} for large mussels. Under mod-

Table 1. *Carcinus aestuarii* preying on *Musculista senhousia.* Results of 2-way ANOVA of handling time with fixed factors prey size (Lprey) and oxygen level (Oxy)

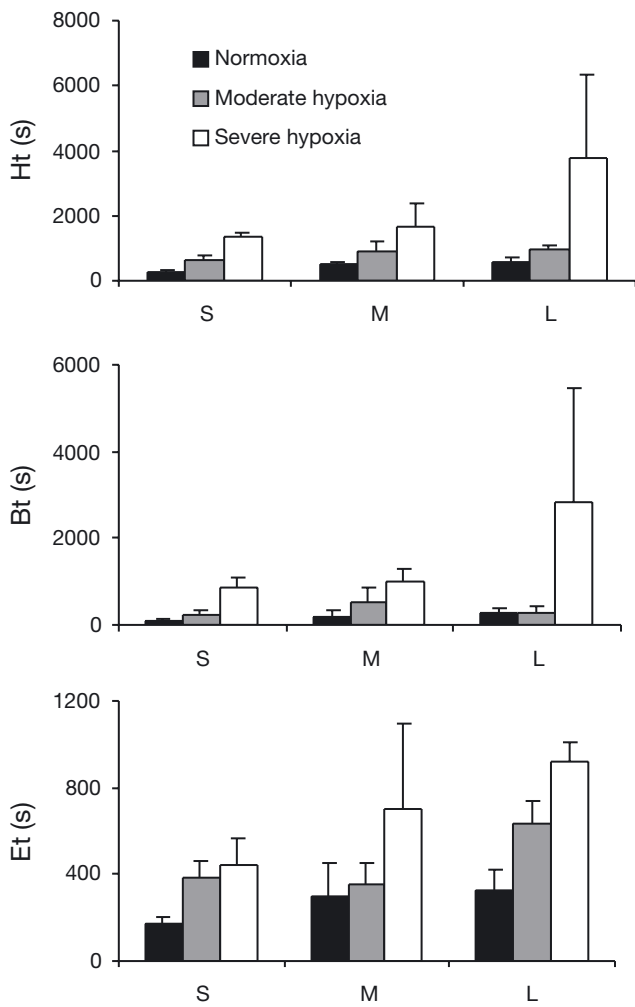| Factor	df	MS	F	p
Lprey (L)	2	1.402	11.502	0.0002
Oxy (O)	2	6.470	53.091	0.0001
L × O	4	0.135	1.105	0.374
Error	27	0.122		

Fig. 1. *Carcinus aestuarii* preying on *Musculista senhousia*. Duration of prey handling time (Ht), breaking time (Bt), and eating time (Et) under conditions of normoxia, moderate hypoxia, and severe hypoxia. Data are means (+SD) of 4 trials. S: small prey; M: medium prey; L: large prey
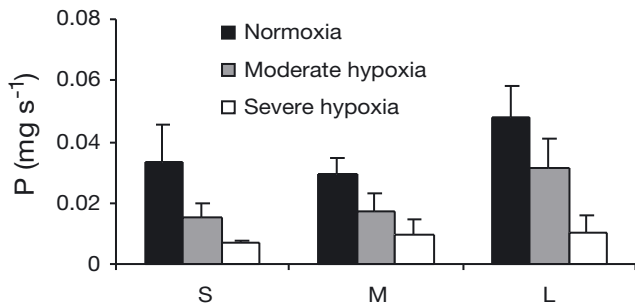

Fig. 2. *Carcinus aestuarii* preying on *Musculista senhousia*. Prey-profitability (P) on small (S) medium (M) and large (L) prey

erate hypoxia, prey-profitability values ranged from about 0.02 mg s^{-1} for small and medium prey to 0.03 mg s^{-1} for large prey, while under severe hypoxia, the values were 0.007 for small, 0.009 for medium and 0.01 mg s^{-1} for large mussels (Fig. 2). Oxygen level and prey size were significant, but their interaction was not (Table 3). Prey-profitability was significantly higher for large mussels than for small or medium mussels (Tukey HSD test: S vs M, p = 0.89; S vs L, p < 0.005; M vs L, p < 0.01), and decreased greatly from normoxic to moderately and severely hypoxic conditions (N vs MH, N vs SH, MH vs SH: all p < 0.0005).

Effect of hypoxia on predator–prey dynamics

Consumption rates of individual *Carcinus aestuarii* differed significantly according to oxygen level and mussel density (Fig. 3a); the interaction effect was not significant (Table 4). Crabs ate more mussels under normoxia than hypoxia (Tukey HSD test: N vs SH, p < 0.001). In addition, significantly more *Musculista senhousia* were consumed at the moderate (200 mussels per tank) density than at the low (40 mussels per tank) density (LD vs MD: p < 0.001).
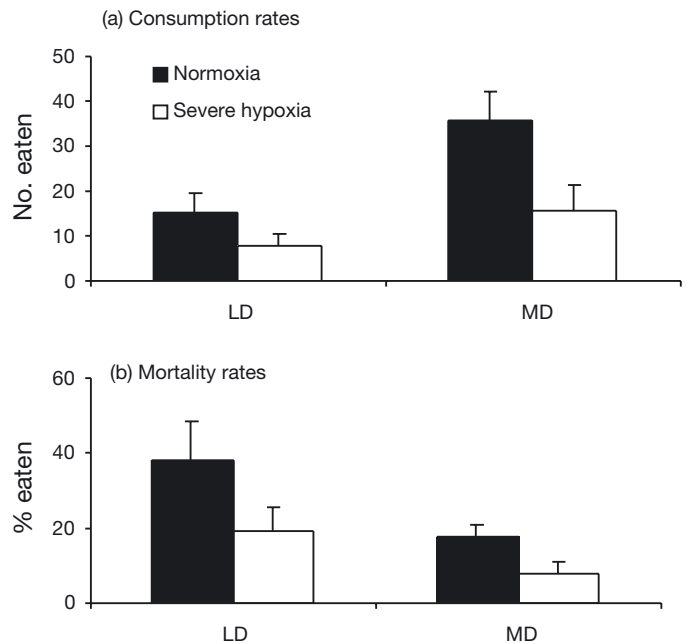

Fig. 3. *Carcinus aestuarii* preying on *Musculista senhousia*. (a) Consumption rates (no. of mussels eaten 24 h^{-1}) and (b) mortality rates (no. of mussels eaten 24 h^{-1} as a function of mussel density under conditions of normoxia and severe hypoxia. LD, MD: light (40 mussels per tank) and medium (200 mussels per tank) densities respectively. Data are means (+SD) of 4 trials

Mortality rates of *Musculista senhousia* also differed significantly as a function of oxygen level and mussel density (Fig. 3b), while the interaction effect was not significant (Table 5). Mortality rates were higher under normoxia (N vs SH, p < 0.001) and at low mussel density (LD vs MD: p < 0.001).

Table 2. *Carcinus aestuarii* preying on *Musculista senhousia*. Results of 2-way ANOVA of breaking time (Bt) and eating time (Et) with fixed factors prey size (Lprey) and oxygen level (Oxy)

Factor	df	MS	F	p
Bt				
Lprey (L)	2	1.270	3.049	0.064
Oxy (O)	2	12.175	29.215	0.0001
L × O	4	0.448	1.075	0.388
Error	27	0.417		
Et				
Lprey	2	1.207	9.459	0.0008
Oxy	2	2.513	19.683	0.0001
L × O	4	0.114	0.896	0.480
Error	27	0.128		

Table 3. *Carcinus aestuarii* preying on *Musculista senhousia*. Results of 2-way ANOVA of prey-profitability with fixed factors prey size (Lprey) and oxygen level (Oxy)

Factor	df	MS	F	p
Lprey (L)	2	0.0045	8.179	0.0017
Oxy (O)	2	0.0285	52.071	0.0001
L × O	4	0.0008	1.499	0.230
Error	27	0.0005		

Table 4. *Carcinus aestuarii* preying on *Musculista senhousia*. Results of 2-way ANOVA of consumption rates with fixed factors oxygen level (Oxy) and prey density (DP)

Factor	df	MS	F	p
Oxy (O)	1	0.454	25.461	0.00029
DP	1	0.461	25.848	0.00027
O × DP	1	0.006	0.336	0.573
Error	12	0.018		

Table 5. *Carcinus aestuarii* preying on *Musculista senhousia*. Results of 2-way ANOVA of mortality rates with fixed factors oxygen level (Oxy) and prey density (DP)

Factor	df	MS	F	p
Oxy	1	0.089	19.494	0.00084
DP	1	0.109	23.753	0.00038
O × DP	1	0.009	2.048	0.178
Error	12	0.005		

DISCUSSION

Hypoxia significantly affected predator–prey interactions between juvenile *Carcinus aestuarii* and *Musculista senhousia*. In laboratory experiments, hypoxia (both moderate and severe) reduced prey-handling efficiency of *C. aestuarii*, as observed in *C. maenas* feeding on *Mytilus edulis* under hypoxia (ca. 1 mg O_2 l^{-1}: Brante & Hughes 2001). In the present study, of the 2 components of prey-handling time, breaking time responded to severe hypoxia, increasing nearly 3-fold, while eating time also responded to moderate and severe hypoxia; time spent ingesting and digesting mussels therefore also accounted for a proportion of prey-handling effort. Crabs compensate for short-term hypoxia by increasing ventilation, and this requires energy that is drawn from the energy available for locomotion and feeding (Taylor et al. 1977). Therefore, under severe hypoxia, crabs are less active because they are energy-limited (Das & Stickle 1994). Through this energetic limitation, and by significantly increasing its prey-handling time, hypoxic events in the natural environment may place juvenile *C. aestuarii* at greater risk to competition and predation, due to the increase in the time of exposure during foraging (in the Sacca, competitors and predators are mostly larger conspecific crabs or shorebirds such as *Larus argentatus* and *Ardea cinerea*; G. Pagnoni pers. comm., author's pers. obs.).

In the outdoor mesocosm experiments, when *Carcinus aestuarii* foraged upon *Musculista senhousia* under normoxia, mussels suffered a higher risk of mortality at low than at medium density, which is indicative of a Type II functional response. This pattern of inversely density-dependent mortality of mussel prey under normoxia is consistent with previous findings regarding predatory dynamics of adult (>50 mm carapace wt) crabs (Mistri 2003), and is characteristic of predator–prey interactions between crabs and many bivalve species (Seitz et al. 2001). Under hypoxia, the proportional mortality of mussels was also inversely density-dependent but lower, indicating that mussels attained a partial refuge from crab predation. Seitz et al. (2001) suggested 2 strategies of antipredator defence in bivalve prey (i.e. armour or avoidance): thin-shelled prey avoid predators by reducing encounter rates through deep burial, and/or living at low density; thick or ornamented-shelled prey, which are epibenthic or shallow-burrowers, reduce predation by reducing the handling efficiency of predators. *M. senhousia* is a thin-shelled (i.e. not armoured), epibenthic (i.e. not avoidant) species and no size refuge (Mistri 2003). Under normal conditions, it must rely on aggregative behaviour as a refuge from predation by shore crabs. In the mesocosm experiments, hypoxia

promoted a partial refuge for mussels by reducing the handling efficiency of crabs. Thus, hypoxia apparently reduced the transfer of benthic production from mussels to epibenthic predators such as *C. aestuarii.* In the Sacca di Goro, this potential loss of trophic transfer from mussel to crabs under hypoxia is likely to be significant, since *C. aestuarii* shows a marked preference for *M. senhousia* compared to other bivalve prey (Mistri 2004).

The reduced predation impact of *Carcinus aestuarii* on *Musculista senhousia* under hypoxia agrees with the consumer stress model (Menge & Sutherland 1987) observed in recent studies on predator–prey interactions under hypoxia (Taylor & Eggleston 2000, Seitz et al. 2003). Hypoxia affected the predator–prey interaction between the blue crab *Callinectes sapidus* and the infaunal, soft-shelled clam *Mya arenaria* by hindering crab foraging despite the clams′ migration towards the sediment surface (Taylor & Eggleston 2000). Similarly, the Baltic clam *Macoma balthica* showed a reduced mortality under hypoxia rather than normoxia, indicating that blue crabs were more adversely affected by hypoxia than the clams (Seitz et al. 2003). If, in areas subjected to hypoxia, such a disturbance is more stressful to the predator than to its prey, these areas may serve as a refuge from predation. Such a refuge, however, may depend on the duration of the hypoxic disturbance event, since prolonged hypoxia can cause mass mortality of benthic fauna (Stachowitsch 1984, Ueda et al. 2000). For instance, an unusual, prolonged (more than 1 wk) hypoxic event during summer 1999 in the Sacca di Goro triggered mass mortality of *M. senhousia* (over 90% of the mussel population: Mistri 2002).

Benthic organisms respond to declining oxygen concentrations in several ways, depending on their taxonomic and ecological position (Rosenberg et al. 1991). Sessile and infaunal species may increase their ventilation rates (DeFur et al. 1990), extend siphons upwards into the water column, or migrate vertically towards the sediment surface (Diaz & Rosenberg 1995); and they may reduce their activity and shift towards anaerobic metabolism (Kluytmans et al. 1983, Hochachka 1997, Greenway & Storey 1999). In contrast, more mobile organisms, such as crustaceans and fishes, migrate away from oxygen-depleted waters (Pihl et al. 1991, Das & Stickle 1994, Lenihan et al. 2001). Predators may also follow the spatially dynamic transition zone between normoxic and hypoxic zones, and exploit prey that have been stressed by hypoxic events (Pihl et al. 1991). Since benthic organisms vary in their ability to tolerate hypoxia and in their vulnerability to predators, hypoxia can thus lead to selective predation on some taxa. In Chesapeake Bay, bottom-feeding fishes and crabs increase prey exploitation of

some infauna during or after hypoxia as a result of increased prey availability due to their shallower depth distribution (Pihl et al. 1992). Under moderate hypoxia, annelid worms emerge from their burrows and begin undulatory body movements in an attempt to increase the surrounding oxygen levels (Llansò 1991). Following an hypoxic event, the likelihood of predation upon the hypoxic-stressed worm *Glycera americana* by epibenthic predators (the blue crab *Callinectes sapidus* and the spot *Leiostomus xanthurus*) increased with decreasing dissolved oxygen concentration (Nestlerode & Diaz 1998). Hence, transfer of benthic production to higher trophic levels can either be reduced (e.g. mussels: this study; soft-shelled clams: Taylor & Eggleston 2000; Baltic clams: Seitz et al. 2003) or increased (e.g. polychaetes: Pihl et al. 1992, Nestlerode & Diaz 1998) by hypoxia. The experiments described here suggest that in tha Sacca di Goro hypoxia has the potential to alter (perhaps greatly) the importance of trophic pathways by altering predation patterns in individual predator species; interestingly, neither mussel nor crab abundance declined over the long term (C. Munari & M. Mistri unpubl. data). The results also suggest that shifts in predator–prey interactions probably depend on the behaviour and the susceptibility to hypoxia of the individual interacting species. In the Sacca, the most common potential prey of crabs are *Nereis* (*Neanthes*) *succinea* (up to 140 ind. m^{-2}), Oligochaeta (up to 250 ind. m^{-2}), *Chironomus salinarius* (up to 900. ind. m^{-2}), *Cerastoderma glaucum* (up to 20 ind. m^{-2}) and *Ruditapes philippinarum* (up to 400 ind. m^{-2} in shellfish farming areas) (Mistri et al. 2001a). Being different in their susceptibility to hypoxia, and thus their vulnerabilty to crabs, predator–prey relationships in the Sacca are expected to be altered in a complex manner by hypoxic events.

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