NOTE

Effect of hypoxia on the prey-handling behaviour of *Carcinus maenas* feeding on *Mytilus edulis*

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ABSTRACT: The shore crab (green) *Carcinus maenas* commonly occurs in tide pools and channels where temporary hypoxia is experienced. Under such conditions, aerobic metabolism is limited, with possible consequences to prey-handling behaviour. We investigated this possibility by measuring the prey-handling times of *C. maenas* fed mussels *Mytilus edulis* under normoxic (5.9 ± 0.1 mg O_2 l^{-1}) and hypoxic conditions (1.08 ± 0.12 mg O_2 l^{-1}). The prey-handling time of smaller crabs (5.0 to 5.3 cm carapace width) feeding on relatively small, medium and large mussels was increased by hypoxia. The prey-handling time of larger crabs (7.1 to 7.3 cm carapace width) was increased by hypoxia only when feeding on relatively large mussels. Increases in prey-handling time were largely due to increases in the time taken to glean and ingest flesh, except for large mussels, for which time taken to break the shell became more important. The results show that hypoxia reduces prey-handling efficiency, presumably by limiting the capacity to increase aerobic metabolism, and that susceptibility to this decreases with increasing body size. Reduced prey-handling efficiency could place individuals at greater risk to competition and predation when subjected to hypoxia in the field.

KEY WORDS: Shore crab · Mussels · Behavioural ecology · Physiological constraint · Prey profitability

The shore crab *Carcinus maenas* (L.) is a common resident of estuaries and open coasts of the temperate North Atlantic. Although omnivorous (Crothers 1968), *C. maenas* is an important predator of mussels *Mytilus edulis* L. (Dare & Edwards 1976), and the corresponding prey-handling behaviour has been well studied under normoxic conditions (reviewed in Hughes & Seed 1995). When inhabiting stagnant conditions in estuaries, harbours and tide pools, however, *C. maenas* is likely to experience periods of hypoxia (Taylor & Butler 1973). Although *C. maenas* possesses behavioural and physiological means of reducing the effect of hypoxia (Taylor 1976, Taylor et al. 1977), aerobic metabolism is inevitably restricted and this could limit physical exertion. For example, hypoxia experienced by *C. maenas* in tide pools reduces fighting capacity (Sneddon et al. 1999). Although metabolic expenditure on handling mussels amounts to a mere 2% of the energy gain to *C. maenas* (Rovero et al. 2000a), shell-breaking capacity might still be constrained by the limitation of aerobic metabolism through hypoxia. Such constraint could influence the feeding behaviour of *C. maenas* when hypoxia is encountered. To assess the above possibilities, we compared the prey-handling behaviour of *C. maenas* presented with *M. edulis* under normoxic and hypoxic conditions.

Materials and methods. *Carcinus maenas* were collected in June to July 1997 from the Menai Strait, Anglesey, North Wales, UK. Only green males were used, obviating potential effects of gender and carapace colour, which indicates moulting schedule, on prey-handling capability (Kaiser et al. 1990, Hughes & Seed 1995, Sneddon et al. 1998). The crabs were maintained in aerated seawater, held at a salinity of 34 ± 1‰ and a temperature of 15 ± 1°C, within a 30 l holding tank. *Mytilus edulis* of 1.5 to 5.0 cm shell length were also collected from the Menai Strait. A sample of 36 mussels was used to derive the relationship between flesh content and shell length by drying excised flesh for 36 h at 60°C. A power function was fitted to the data and used to predict the approximate yield of each mussel subsequently presented to a crab: $y = 0.0078 \, e^{1.0962x}$ ($R^2 = 0.87$; p ≪ 0.0005), where y = dry flesh weight, x = shell length.

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Four crabs were chosen in each of 2 size classes: 5.0 to 5.3 and 7.1 to 7.3 cm carapace width. Hunger levels were standardised by depriving the crabs of food for 2 d (Elner & Hughes 1978). Each crab was then placed in an individual 3.8 l tank containing seawater held at $15 \pm 1°C$ and $34 \pm 1‰$ S and presented with small, medium and large mussels. Prey size was defined relative to the size of the predator as follows: smaller crabs, small mussels = 2.0 to 2.5 cm shell length, medium = 2.5 to 3.0 cm, large = 3.0 to 3.5 cm; larger crabs, small mussels = 2.0 to 3.0 cm, medium = 3.0 to 4.0 cm, large = 4.0 to 5.0 cm. Every 2 d, each crab was presented with a mussel placed loosely on the floor of the tank, thus receiving 3 mussels of each size class under both normoxic and hypoxic conditions (below) over a period of 40 d. Combinations of mussel size and oxygen condition were assigned to each crab in random sequence.

Each crab was exposed to both normoxic and hypoxic conditions. To present normoxic conditions, the seawater was aerated using 2 air stones placed at 1 end of the tank. Oxygen concentration, continuously monitored by an oxygen meter (pHOX62) positioned at the opposite end of the tank from the air stones, was maintained at 5.9 ± 0.1 mg O_2 l^{-1} (100% saturation). To generate hypoxic conditions, oxygen concentration was reduced over a period of 4 h to 1.08 ± 0.12 mg O_2 l^{-1} (18 ± 2% saturation) by aeration of the seawater using a mixture of 3% oxygen and 97% nitrogen. The position of the tanks was changed daily to avoid potential bias due to location (Hurlbert 1984).

Following Elner & Hughes (1978), the following behavioural acts were recorded in each feeding trial: breaking time (Bt), time (s) from the first physical contact with the prey to the first bite of flesh; eating time (Et), time (s) from the first bite of flesh to the completion of the meal and subsequent abandonment of the empty shell; handling time (Ht), the sum of Bt and Et. Profitability of the prey (mg s^{-1}), representing the flesh ingested per unit Ht, was calculated by dividing the estimated dry weight of the prey (above) by the Ht.

Log$_e$ (behavioural data) or square root transformation (profitability) was used to homogenise variances before applying ANOVA. Oxic condition and prey size were specified as fixed factors and crabs as a random factor. *A posteriori* pairwise comparisons were made using the Scheffé test (Zar 1996). Data for larger and smaller crabs were analysed separately in order to simplify interpretation. This was justified because there was an order-of-magnitude difference in prey-handling times between the 2 size classes, whereas the effects of the experimental factors showed similar trends in both cases.

Results. *General behaviour:* Under hypoxia, crabs tended to pause while handling prey, adopting a characteristic posture in which the front part of the

cephalothorax was raised toward the water surface, while the master chaela held the prey. This behaviour enables *Carcinus maenas* to breathe air when in sufficiently shallow water, thereby increasing the oxygenation of arterial blood (Taylor et al. 1977). Elevation in beating rate of the third maxillipeds also occurred. This response is characteristic of decapod crustaceans on exposure to hypoxia, indicating hyperventilation in an attempt to increase oxygen delivery to the gills (Taylor 1982).

Larger crabs: Neither the random factor crabs, nor any of its interactions was statistically significant (Table 1). Larger crabs took significantly longer to handle large mussels when under hypoxia than when under normoxia (Tables 1 & 2), but oxygen availability had no significant effect on ht for medium or small mussels (Table 2, Fig. 1a). Data for Bt and Et showed similar patterns to Ht and so are not presented in

Table 1. *Carcinus maenas*, *Mytilus edulis.* Larger crabs: log$_e$ (handling time). ANOVA with random factor crabs (C), fixed factors prey size (S) and oxic condition (O)

Factor	df	MS	*F*	p
C	3	0.079	0.393	0.758567
S	2	7.940	163.764	**0.000006**
O	1	0.838	19.656	**0.021325**
C × S	6	0.048	0.242	0.96008
C × O	3	0.043	0.213	0.886881
S × O	2	0.899	13.383	**0.00614**
C × S × O	6	0.067	0.336	0.914694
Error	48	0.200		

Table 2. *Carcinus maenas*, *Mytilus edulis.* Larger crabs: log$_e$ (handling time). *A posteriori* Scheffé test for pairwise comparisons within the interaction S × O (s, small prey; m, medium prey; l, large prey; h, hypoxia; n, normoxia). S critical = 3.428 (α = 0.05)

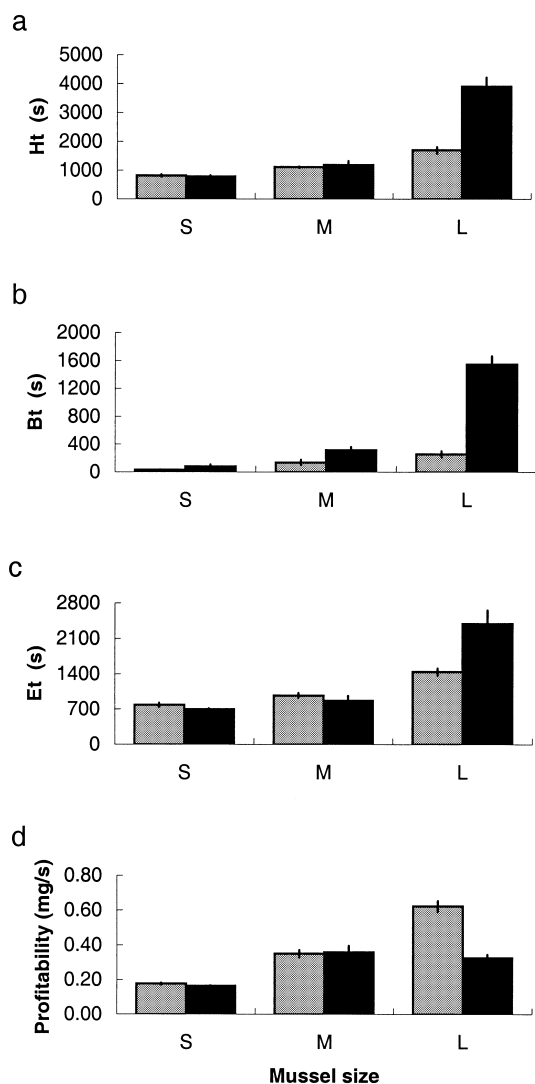| Comparison	(Mean difference)	SE	S
sn × sh	0.057	0.106	0.537
sn × mn	0.301	0.106	2.848
sn × mh	0.347	0.106	3.276
sn × ln	0.767	0.106	**7.247**
sn × lh	1.425	0.106	**13.474**
sh × mn	0.403	0.106	**3.812**
sh × mh	0.403	0.106	**3.812**
sh × ln	0.824	0.106	**7.784**
sh × lh	1.482	0.106	**14.011**
mn × mh	0.045	0.106	0.428
mn × ln	0.465	0.106	**4.400**
mn × lh	1.124	0.106	**10.626**
mh × ln	0.420	0.106	**3.972**
mh × lh	1.079	0.106	**10.198**
ln × lh	0.659	0.106	**6.227**

Fig. 1. *Carcinus maenas*, *Mytilus edulis.* Larger crabs: duration of components of prey-handling behaviour under normoxia and hypoxia. (a) Handling time (*Ht*), (b) breaking time (*Bt*), (c) eating time (*Et*), (d) prey profitability. Data are means with standard errors (S, small prey; M, medium prey; L, large prey; grey bars, normoxia; black bars, hypoxia)

Table 3. *Carcinus maenas*, *Mytilus edulis.* Larger crabs: square root (prey value). ANOVA model as in Table 1

Factor	df	MS	*F*	p
C	3	0.003004	0.33692	0.79869
S	2	0.420409	91	**0.000033**
O	1	0.09945	33.46496	**0.010274**
C × S	6	0.004621	0.51835	0.791504
C × O	3	0.00972	0.33334	0.801262
S × O	2	0.087505	18.25867	**0.00281**
C × S × O	6	0.004793	0.53757	0.776995
Error	48	0.008915		

Table 4. *Carcinus maenas*, *Mytilus edulis.* Larger crabs: square root (prey value). *A posteriori* Scheffé test for pairwise comparisons within the interaction S × O, as in Table 2

Comparison	(Mean difference)	SE	S
sn × sh	0.013	0.028	0.459
sn × mn	0.170	0.028	**6.000**
sn × mh	0.173	0.028	**6.121**
sn × ln	0.359	0.028	**12.701**
sn × lh	0.146	0.028	**5.149**
sh × mn	0.183	0.028	**6.459**
sh × mh	0.186	0.028	**6.580**
sh × ln	0.372	0.028	**13.160**
sh × lh	0.158	0.028	**5.607**
mn × mh	0.003	0.028	0.121
mn × ln	0.189	0.028	**6.701**
mn × lh	0.024	0.028	0.851
mh × ln	0.186	0.028	**6.580**
mh × lh	0.027	0.028	0.973
ln × lh	0.213	0.028	**7.552**

Table 5. *Carcinus maenas*, *Mytilus edulis.* Smaller crabs: $\log_e$ (handling time). ANOVA with random factor crabs (C), fixed factors prey size (S) and oxic condition (O)

Factor	df	MS	*F*	p
C	3	0.07106	0.529	0.664267
S	2	8.114	229.974	**0.000002**
O	1	11.124	1723.341	**0.000003**
C × S	6	0.035	0.263	0.951472
C × O	3	0.006	0.048	0.985863
S × O	2	0.101	4.029	0.077751
C × S × O	6	0.025	0.187	0.979065
Error	48	0.134		

detail. In summary, for large prey *Bt* and *Et* were significantly greater under hypoxia than under normoxia (Fig. 1b,c). Moreover, this differential was relatively greater for *Bt* than for *Et*, reflecting the greater effort required to break the shell of large mussels.

Prey profitability under normoxia ranged from 0.16 mg s^{-1} for small prey to 0.65 mg s^{-1} for large prey, and under hypoxia from 0.16 to 0.35 mg s^{-1} respectively (Fig. 1d). The interaction between factors prey size and oxic condition was significant (Table 3). All pairwise comparisons for normoxia were statistically significant, but for hypoxia profitability was significantly different only between small and medium prey (Table 4).

Smaller crabs: Neither the random factor crabs, nor any of its interactions was statistically significant (Table 5). Smaller crabs took longer to handle prey of all sizes when under hypoxia than when under normoxia (Tables 5 & 6, Fig. 2a). *Bt* and *Et* followed similar trends to *Ht* (Fig. 2b,c). However, the differential responses suggest that the effect of oxygen availability on *Ht* derived principally from *Et* for small and med-

Table 6. *Carcinus maenas*, *Mytilus edulis.* Smaller crabs: $\log_e$ (handling time). Scheffé test for pairwise comparisons within the factor O (Table 5). Symbols as in Table 2

Comparison	(Mean difference)	SE	S
$s \times m$	0.440	0.054	**8.148**
$s \times l$	0.710	0.054	**13.148**
$m \times l$	1.150	0.054	**21.296**

Table 7. *Carcinus maenas*, *Mytilus edulis.* Smaller crabs: square root (profitability). ANOVA model as in Table 1

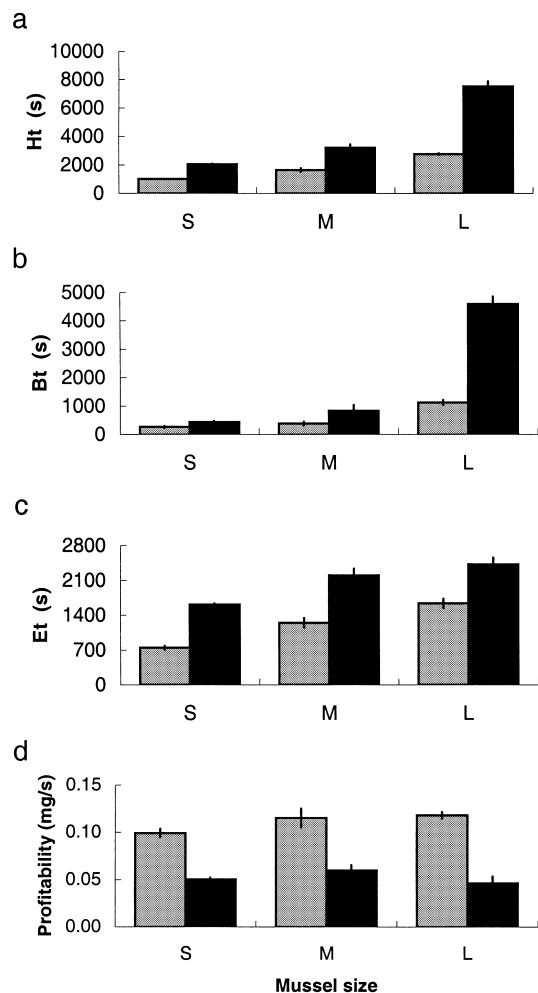| Factor	df	MS	*F*	p
C	3	0.000598	0.671	0.573807
S	2	0.002612	1.300	0.339508
O	1	0.197573	104.794	**0.001987**
$C \times S$	6	0.002008	2.255	0.05368
$C \times O$	3	0.001885	2.117	0.110444
$S \times O$	2	0.003099	3.276	0.109212
$C \times S \times O$	6	0.000946	1.062	0.398453
Error	48	0.000891		

Fig. 2. *Carcinus maenas*, *Mytilus edulis.* Smaller crabs: duration of components of prey-handling behaviour under normoxia and hypoxia. Symbols as for Fig. 1

were consumed readily, it is unlikely that the observed increase in handling time originated from reduced appetite of the experimental subjects. Neither was increased handling time caused by altered foraging behaviour, since handling techniques followed the normal repertoire previously described for crabs attacking mussels of different sizes (Elner & Hughes 1978). Instead, the negative effect of hypoxia on prey-handling efficiency appears to have resulted from limited capacity to increase aerobic metabolism above basal rates (aerobic scope). This was more severe for smaller crabs, whose prey-handling efficiency was reduced for all prey sizes, than for larger crabs, whose efficiency was reduced only for large prey. Of the 2 components of prey-handling time, eating time showed the greater response to hypoxia when small and medium prey were consumed by smaller crabs, whereas breaking time showed the greater response for large prey consumed by both smaller and larger crabs. The gleaning and ingestion of flesh, therefore, must account for a substantial proportion of prey-handling effort, only to be overshadowed by the effort of breaking the shell in the case of large, robust prey. Although in the longer term the energetic cost of handling prey is trivial, representing only some 2 to 3% of ingested energy when crabs feed on mussels (Rovero et al. 2000a), in the shorter term it is important under hypoxic conditions because of limited aerobic scope, which constrains the speed of handling prey. Although not addressed in the present study, hypoxia may depress overall feeding rate, with significant effect on a crab's energy budget in the longer term (Das & Stickle 1993).

Hypoxia exacerbates aerobic constraints on prey-handling time, especially in smaller crabs. Houlihan et al. (1984) reported similar effects of hypoxia on the walking performance of *Carcinus maenas*, and an increased anaerobic scope with increasing body size is also known, for example, in brown trout *Salvelinus fontinalis* (Kieffer et al. 1996) and rainbow trout *Oncorhynchus mykiss* (Ferguson et al. 1993). *C. mae-*

ium prey but principally from *Bt* for larger prey. For all prey sizes, profitability was significantly greater under normoxia than under hypoxia (Table 7, Fig. 2d).

Discussion. Hypoxia substantially reduced prey-handling efficiency of *Carcinus maenas*, increasing handling time by as much as 2 to 3 times. Since all prey

nas commonly occurs in tide pools and temporally stagnating channels, where the oxygen availability could become critical, especially in warmer periods (Dare & Edwards 1981, Hill et al. 1991). By increasing prey-handling time, hypoxia increases the length of exposure of the forager to competitors and predators (Cunningham 1983). Moreover, the inverse relationship between the effect of hypoxia and body size will place larger individuals at an even greater competitive advantage than normal (Rovero et al. 2000b).

Many physiological responses to hypoxia have been reported. The most important response is L-lactate accumulation in the tissue and haemolymph as an end product of anaerobic metabolism (Burke 1979, Morris & Greenway 1989, Hill et al. 1991). Behavioural implications of the physiological consequences of hypoxia are, however, relatively unknown. Sneddon et al. (1998) demonstrated that oxygen availability could influence fight duration in *Carcinus maenas* and that fighting was energetically more expensive under hypoxia. Moreover, hypoxia increased the percentage of contests won by larger opponents. Both fighting and prey-handling behaviour, therefore, show similar trends, indicating the potential importance of hypoxia to the behavioural ecology of *C. maenas*.

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