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RESEARCH ARTICLE

Behavioural responses of the Dungeness crab, *Cancer magister*, during feeding and digestion in hypoxic conditions

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Abstract The Dungeness crab, *Cancer magister*, inhabits areas that are frequently subject to periods of hypoxia. This species can employ physiological mechanisms that allow it to cope with acute hypoxic episodes. When crabs feed there is a general increase in physiological variables; these may pose an additional physiological burden on crabs already attempting to maintain adequate oxygen uptake in hypoxia. In Barkley Sound, British Columbia, the inshore habitats of *C. magister* ranged in dissolved oxygen from 28 kPa at the water surface to less than 1.0 kPa just above the sediment–water interface. During short-term hypoxic events, crabs reduced both the amount of food eaten and the amount of time spent feeding. Crabs tended to cease feeding below 3.2 kPa oxygen, but resumed feeding when the dissolved oxygen tensions were rapidly raised to 6 kPa. In a high (10.5–21 kPa) oxygen gradient, both unfed and fed crabs showed no preference for any area of the gradient. In a low (2.5–10.5 kPa) dissolved oxygen gradient, both unfed and fed crabs preferred the highest oxygen regime. In the laboratory, crabs were less likely to enter hypoxic waters (below 3.2 kPa oxygen) to obtain and consume food; those that did moved the food to a higher oxygen regime prior to feeding and settled in higher oxygen regimes for digestion. Crab behaviour was also monitored in the field. Fed and unfed crabs were fitted with ultrasonic telemetry tags and tracked during a tidal cycle. Unfed crabs remained mobile, travelling up to 1,370 m within 6 h, while postprandial crabs settled in areas of high oxygen and moved very little during the first 48 h after release. The present study suggests that *C. magister* exhibits behavioural responses in order to minimise the use of physiological mechanisms, and maximise foraging and digestive processes. Thus the nutritional state of the individual may be important in regulating both its behaviour and distribution in its natural environment.

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Introduction

Episodes of hypoxia are common in the marine environment, particularly in shallow coastal zones. Coastal hypoxia generally follows seasonal patterns directly related to the influx of freshwater and anthropogenic eutrophication (Rabalais et al. 2001). Hypoxic zones are becoming more widespread and are one of the most deleterious human-induced impacts on benthic communities (Rabalais et al. 2001). Ecological effects of hypoxia are dependent in part on its severity and duration (Sagasti et al. 2001), and can disrupt benthic and demersal communities as well as causing mass

mortality of aquatic life (Diaz and Rosenberg 1995). Generally, tolerance levels are higher for organisms residing in the sediments, whereas mobile organisms such as fish and crustaceans may exhibit behavioural responses to avoid hypoxic areas (Diaz and Rosenberg 1995; Hagerman 1998). However, most organisms encountering hypoxic conditions have some physiological means of short-term adaptation.

Many species of decapod crustaceans reside in areas with fluctuating oxygen regimes. Physiological mechanisms enhance the ability of these crustaceans to cope with acute episodes of hypoxia. Many decapods are able to maintain oxygen uptake during hypoxia by increasing the ventilation of the branchial chambers (Airriess and McMahon 1994; McMahon 2001). Below the critical oxygen tension (P_{crit}), however, increases in ventilation rate are unable to compensate for hypoxia, and ventilation frequency decreases together with oxygen uptake (Airriess and McMahon 1994). In hypoxic environments most crustacean species also respond by exhibiting a bradycardia, thus limiting the amount of energy expended by the cardiovascular system (McMahon and Wilkens 1975; Taylor 1982; Airriess and McMahon 1994; Reiber 1995; Reiber and McMahon 1998; McMahon 2001; Guadagnoli et al., in review). Furthermore, crustaceans can alter blood flow during hypoxia, redirecting blood to tissues requiring higher levels of oxygen (Airriess and McMahon 1994; Reiber and McMahon 1998; McGaw and McMahon 2003). However, all the previous research was carried out on unfed animals, because the stimulatory effects of digestion on metabolism (specific dynamic action) are well known (Wang 2001; Robertson et al. 2002). If the specific dynamic action is high it may have significant effects on other systems (Robertson et al. 2002; McGaw 2005a, 2006). The adaptive physiological mechanisms of *Cancer magister* in hypoxia may be compromised during and after feeding (McGaw 2005a). If crabs are unable to balance the demands of these competing physiological systems, the question then arises: do crabs exhibit behavioural responses to minimise the use of physiological mechanisms?

Crabs may respond behaviourally with large-scale changes in distribution and abundance; however, little information is available on fine-scale behavioural responses of mobile species to dynamic hypoxia (Bell et al. 2003a). Apart from migration, other behavioural responses have been noted in crustaceans, which may limit activity as hypoxia increases, thereby decreasing metabolic demands and the need for physiological mechanisms (Johansson 1997). Some intertidal crustaceans, such as the green crab, *Carcinus maenas*, may break the water–air interface in an attempt to breath atmospheric oxygen (Taylor and Butler 1973; Taylor et al. 1977; Hill et al. 1991). Crustaceans residing in sediment, such as *Saduria entomon*, move to the sediment surface to gain additional oxygen (Johansson 1997). The foraging responses of crabs in hypoxic water are diverse. *Callinectes sapidus* tends to feed less frequently and decreases the amount consumed during mild and severe hypoxia (Bell et al. 2003b), while for other crabs, such as *C. maenas*, hypoxia may not have as great an impact on foraging (Brante and Hughes 2001).

The Dungeness crab, *C. magister*, is a commercially important species along the Pacific coast of North America. *C. magister* inhabits sandy and muddy bays and estuaries, where it can encounter hypoxic waters with a PO_2 as low as 1.25 kPa (Airriess and McMahon 1994; Bernatis and McGaw 2004). The physiological responses of *C. magister* to hypoxic exposure have been extensively studied (Airriess and McMahon 1994; McMahon 2001; McGaw and McMahon 2003) and may enhance its ability to cope with hypoxia. However, these previous studies were performed on unfed animals. Digestive processes place an additional burden on animals already attempting to supply tissues with adequate oxygen (Mente et al. 2003; McGaw 2005a, 2006). Because of this, postprandial crabs may alter their behaviour in order to minimise physiological stress. Recently it has been shown that fed *C. maenas* exhibit an emersion response from hypoxic water at a higher oxygen partial pressure than unfed crabs (Robertson et al. 2002). Since *C. magister* is highly mobile they may also exhibit some behavioural mechanism, either reducing food intake during hypoxia and/or moving to areas with higher oxygen tensions to digest food. Therefore, the aim of the present study was two-fold: (1) to determine if crab feeding varies in hypoxic conditions and (2) to investigate if behavioural modification occurs in postprandial *C. magister* in response to hypoxic conditions.

Methods

Adult male intermoult Dungeness crabs, *C. magister*, of 550–850 g were collected in Barkley Sound, British Columbia (latitude 48°49′, longitude 125°08′). The crabs were transferred to Bamfield Marine Sciences Centre and held in running seawater (31–32‰) at a temperature of 10–12°C. Oxygen tension in the holding tanks varied between 16.5 and 17.5 kPa. Crabs were acclimated for 1 week prior to experiments and fed fish muscle ad libitum (*Lepidopsetta bilineata*) every other day. Animals selected for experiments were separated

from the general population and deprived of food for 3 days (hereafter termed unfed) prior to experiments. This starvation period ensured that there was no food residue in the gut, but avoided the effects of long-term starvation (Ansell 1973; Wallace 1973). The water in the experimental tanks was acquired from the same source as the holding tanks. Nitrogen bubbled with ambient air was used to create hypoxic conditions, and oxygen was bubbled with ambient air to generate higher oxygen regimes. Hydrographic measurements (dissolved oxygen, temperature, salinity) were taken with a YSI-85 DO-conductivity meter prior to the start and following completion of each experiment and oxygen tensions were reported as derived partial pressures. During experiments each apparatus was surrounded with black plastic sheeting to minimise external disturbance, and all experiments were carried out in constant dim light. For reference 100% oxygen saturation is approximately 21 kPa or 158 Torr.

Feeding in hypoxia

Crabs (n=25 or 26 per treatment) were held in individual chambers ($45 \times 45 \times 20$ cm^3 depth) in running aerated seawater and allowed to settle for 12 h before experimentation. The oxygen tension was changed during a 4-h period from a baseline level of 16.8 kPa to required test treatments. This time period of 4 h was sufficient to allow changes in internal physiological variables (McMahon 2001). The crabs were then fed a pre-determined mass of fish muscle. They were given 1 h to commence eating, and allowed to continue eating ad lib. When the crabs ceased had feeding for 15 min, the food was removed and weighed for post-consumption mass. If a crab did not eat at all within 1 h, the food was removed and the trial recorded as 0 g consumed, and this value was used in the statistical analysis. The amount of time spent eating was also recorded, with eating defined as the act of inserting food into the mouthparts (Johansson 1997). Trials were carried out in seawater with dissolved oxygen tensions of 21 kPa (100%), 15.75 kPa (75%), 10.5 kPa (50%), 5.25 kPa (25%), 3.15 kPa (15%) and 1.47 kPa (7%). All oxygen tensions were maintained within 0.5 kPa.

Crabs that did not feed in low oxygen tensions were rapidly returned to normoxic conditions by aerating the water, and feeding activity was subsequently monitored, allowing us to establish whether feeding was a direct response to ambient oxygen tensions (i.e. animals would not feed in hypoxia, only in normoxia).

Individual crab mass varied by 300 g; therefore, to remove possible effects of animal mass (Stevens et al. 1982), the data was transformed by dividing the mass of food consumed by the mass of the animal. Data for amount of food consumed as well as the time spent feeding in each oxygen regime was analysed using a Kruskal–Wallis non-parametric ANOVA. Data showing a significant effect were further analysed with a Dunn's pair-wise post-hoc analysis.

Postprandial behaviour in hypoxia

A tank of $240 \times 40 \times 40$ cm^3 was used to monitor oxygen preferences of 20 pre and 20 postprandial crabs (Fig. 1). Bricks located along the length of the tank provided shelter for the crabs (McGaw 2001) and also defined areas for oxygen measurements. The tank was filled with running seawater (approx. 2.5 l min^{-1}) to a depth of 30 cm. Air curtains were placed along the length of the tank, and divided into sections. By manipulating the amount of nitrogen, ambient air and oxygen flowing into each air curtain an approximately 10 kPa difference in oxygen tension could be maintained between each end of the tank for several hours. The first set of trials used a gradient of 10.5 kPa (±0.5 kPa) to 21 kPa (±0.5 kPa). The second set of experiments used oxygen ranges from 2.5 kPa (±0.5 kPa) to 10.5 kPa (±0.5 kPa). Oxygen tensions and the temperature of each area of the tank were recorded at the start and finish of each experiment using the YSI-85 meter.

Twenty postprandial crabs (3-h post-feeding) were placed individually in random areas of the tank. After handling, the crabs were allowed to settle in the tank for 15 min before the experiment began. Time spent in each area of the tank and activity patterns were recorded for 1 h using a time-lapse video system (Panasonic AG-RT600AS VCR and WV-BP120 camera). The experiment was then repeated with 20 unfed crabs (3 days unfed). The high and low oxygen areas were reversed between trials, to avoid any bias for specific areas of the tank. A control group of 20 crabs (unfed 3 days) were tested in the tank at constant oxygen levels of 16.8 kPa. Univariate analysis of variance tests (SPSS) were used to compare the proportion of time the crabs spent in each oxygen tension. Data showing significant effects were further tested using Tukey pair-wise post-hoc analysis.

Activity levels of unfed and postprandial crabs were also analysed. If a crab remained motionless for more than 10 s (time taken to walk through an area of tank) this was counted as inactivity. If the crab was motionless for less than 10 s the data were not used in the analysis. All other movement was counted as activity. Activity levels of unfed and postprandial crabs in the

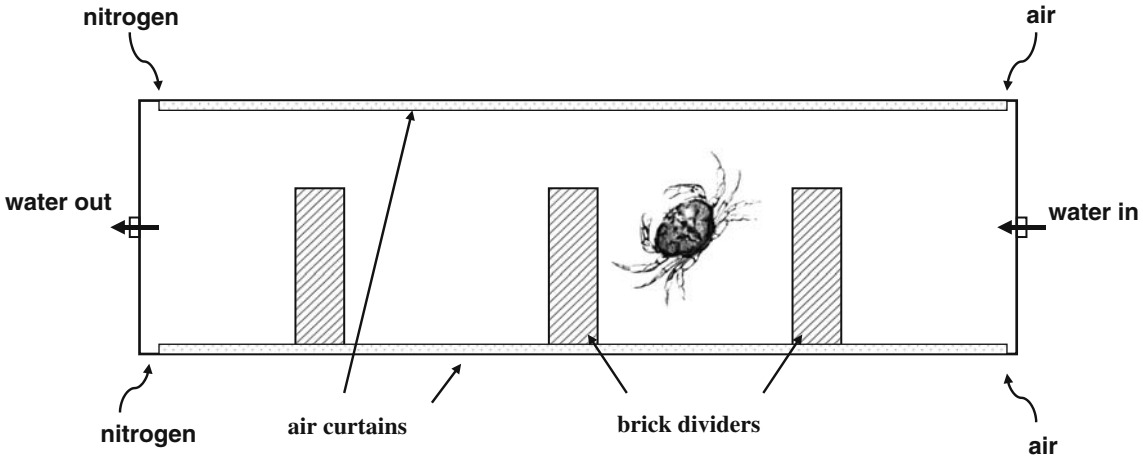

Fig. 1 Diagram of apparatus used for oxygen gradient experiments. A constant flow of seawater (2.5 l min^{-1}) maintained the salinity at 31–32‰ and the temperature at 10–12°C. Separate air curtains placed along the length of the tank allowed varying mixes of nitrogen, ambient air and oxygen to be infused into the tank. Bricks divided the tank into compartments, and also provided corners into which the crabs could retreat

high and low oxygen gradients were compared using Mann–Whitney rank sum tests.

Foraging behaviour

Foraging behaviour of unfed crabs (3 days) was examined in the oxygen gradient apparatus (2.5–10.5 kPa range). Individual crabs ($n = 32$) were randomly placed in the gradient and given 15 min to settle after handling. Food (fish muscle) was then introduced into the tank by lowering it from the outside of the plastic sheeting. Food was placed in the high oxygen area (10.5 kPa) of the chamber for 16 trials. The experiment was then repeated with the food in the low oxygen area (2.5 kPa). Food handling and consumption and movement within the chamber were recorded for 1 h with a time-lapse video system. A control group of 16 crabs was tested using constant oxygen levels of 16.8 ± 0.5 kPa. For the controls, eight trials had food placed at one end, and then food was placed in the opposite end for another eight trials to ensure that there was no preference for a certain area of the tank. The amount of time that crabs spent in each area of the tank when food was present was analysed using a univariate analysis of variance test.

Field work

Dissolved oxygen, temperature and salinity were recorded at various depths during a number of tidal cycles in the Bamfield Inlet, British Columbia (Canadian Hydrographic Chart 3671). The YSI-85 DO/salinity probe was attached to a circular weighted plate (0.5 m diameter) and lowered to the bottom, ensuring that the probe was approximately 2 cm above the sediment surface, but did not sink into the sediment. Depth was recorded at each location using a depth sounder (Lowrance 3500) and a position (latitude and longitude) obtained by GPS.

The movements of fed and unfed crabs ($n = 3$ each) were also tracked in the field. Ultrasonic coded tags (IT85-2, Sonotronics Inc., Tucson, AZ, USA) were attached to the carapace of each crab with epoxy glue. The animals were then allowed to settle in the holding tanks for 1 day prior to experiments. Three postprandial crabs (3-h post-feeding) and three unfed crabs (3 days) were then released into Bamfield Inlet. The time between removal from the experimental tanks and release in the inlet was less than 15 min. The crabs were tracked from a small boat using a DR-4 directional hydrophone and a receiver (Sonotronics Inc., Tucson, AZ, USA). When the maximal signal from the ultrasonic tag was obtained a position reading was taken. Dissolved oxygen, temperature and depth were also recorded in the vicinity of the crab. The crabs were located at hourly intervals for 6 h, then at 24 and 48 h after release. The hydrographic variables for unfed and postprandial crabs were compared using a repeated measures ANOVA test.

Results

Feeding in hypoxia

Oxygen tension had a significant effect on the amount of food that the crabs consumed (Kruskal–Wallis, $P < 0.001$). The greatest amount of food was eaten in

15.8 kPa oxygen, where crabs consumed 17.95 ± 1.94 g of food (Fig. 2a). There was a steady decrease in food consumption at lower oxygen tensions with only 1.98 ± 0.6 g of food consumed in 1.5 kPa oxygen. This level was significantly lower than the amount of food consumed by crabs in 5.3, 10.5, 15.8 and 21 kPa (Dunn's test, $P < 0.05$). Crabs in 3.2 kPa oxygen only consumed 6.37 ± 1.12 g food, significantly less than in 10.5 and 15.8 kPa oxygen (Fig. 2a).

The time spent feeding was also affected by oxygen tension (Kruskal–Wallis, $P < 0.001$). Maximum feeding times of 89.4 ± 10.6 min were observed in 15.8 kPa oxygen (Fig. 2b); this time was significantly greater than that recorded in all other oxygen regimes, except 10.5 kPa. There was a trend towards a decrease in feeding time with decreasing oxygen levels. The lowest feeding time of 2.19 ± 0.52 min was recorded in 1.5 kPa oxygen and was significantly less than feeding times recorded in 5.3, 10.5, 15.8 and 21 kPa (Dunn's test, $P < 0.05$). Crabs in 3.2 kPa oxygen only fed for 14.35 ± 2.21 min, significantly less than in 10.5 and 21 kPa oxygen (Fig. 2b). Not all crabs fed in the lower oxygen regimes: 5 out of 25 crabs in 5.3 kPa, 5 out of 25 crabs in 3.2 kPa and 11 out of 26 crabs in 1.5 kPa did not feed at all. However, all of these crabs fed within 30 s of raising oxygen levels to 5.8–6.3 kPa.

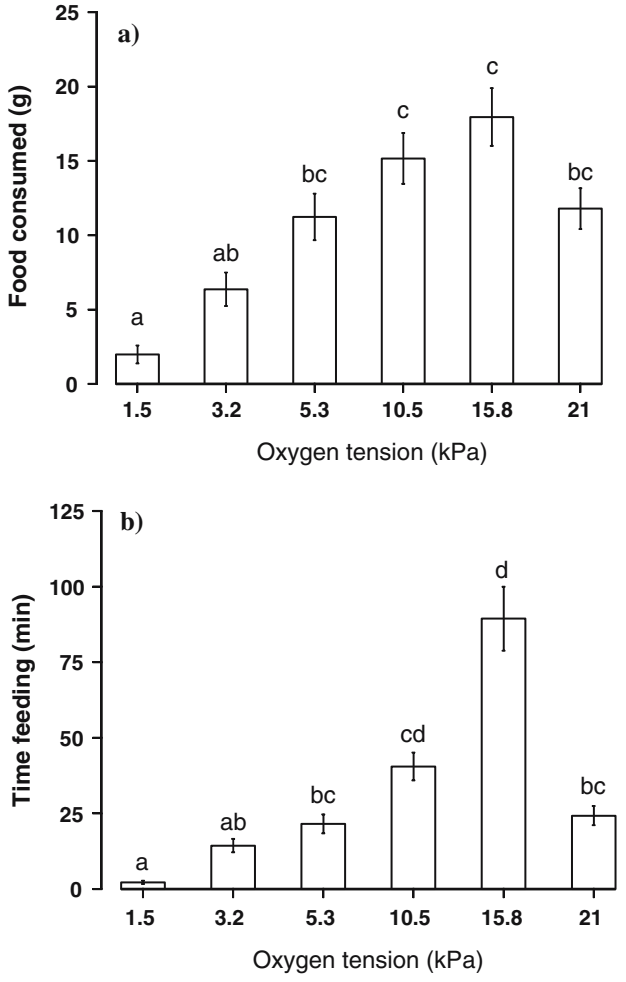

Fig. 2 Feeding behaviour of *Cancer magister* ($n = 25$ or 26) in dissolved oxygen tensions of 1.5–21 kPa. **a** Wet mass of food consumed (g) and **b** time spent feeding (min). Values are means ± SEM. *Bars* with like *letters* are not significantly different at the $P = 0.05$ level

Foraging behaviour

When foraging behaviour was observed in an oxygen gradient (2.5–10.5 kPa), 22 of the 32 crabs (69%) consumed food. When food was placed in the higher oxygen end (10.5 kPa), 13 of the 16 crabs (81%) entered this area of the chamber and all of these crabs fed. Twelve of the crabs (92%) consumed the food in the area. Only one crab (8%) moved the food into a lower oxygen regime to feed. In contrast, when food was placed in the low oxygen end (2.5 kPa), only nine crabs (56%) entered this area of the gradient. Of these nine crabs, only six (67%) actually fed. Two crabs (33%) remained in the 2.5 kPa oxygen to feed, while four crabs (77%) picked up food and moved it to higher oxygen regimes to feed. By the end of the experiment 23 of the 32 crabs (72%) had moved to the highest oxygen area of the tank.

Although some of the crabs ventured into the low oxygen area (2.5 kPa) to obtain food, the presence of food in the gradient apparatus did not alter their overall behaviour. The time that the crabs spent in each area of the gradient was independent of the presence or absence of food (Fig. 3b) (univariate analysis of variance, $F = 2.53$, $P = 0.114$). In control conditions (16.8 kPa), when no oxygen gradient was present, 15 of the 16 crabs (94%) fed during the experiment. All of these (100%) fed in the area where the food was located.

Postprandial behaviour in hypoxia

In the high oxygen gradient (10.5–21 kPa) fed and unfed crabs exhibited similar behaviour (Fig. 3a; univariate analysis of variance, $F = 0.67$, $P = 0.42$) and showed no preference for any area of the tank (univariate analysis of variance, $F = 2.1$, $P = 0.11$), spending mean times of 9.5 ± 2.9 to 23 ± 5.3 min within each area of the tank. In the low oxygen gradient (2.5–10.5 kPa) there was also no difference in preference between fed and unfed crabs (univariate analysis of variance, $F = 0.19$, $P = 0.66$). However, both fed and unfed crabs did prefer (Tukey test, $P < 0.05$) the highest oxygen

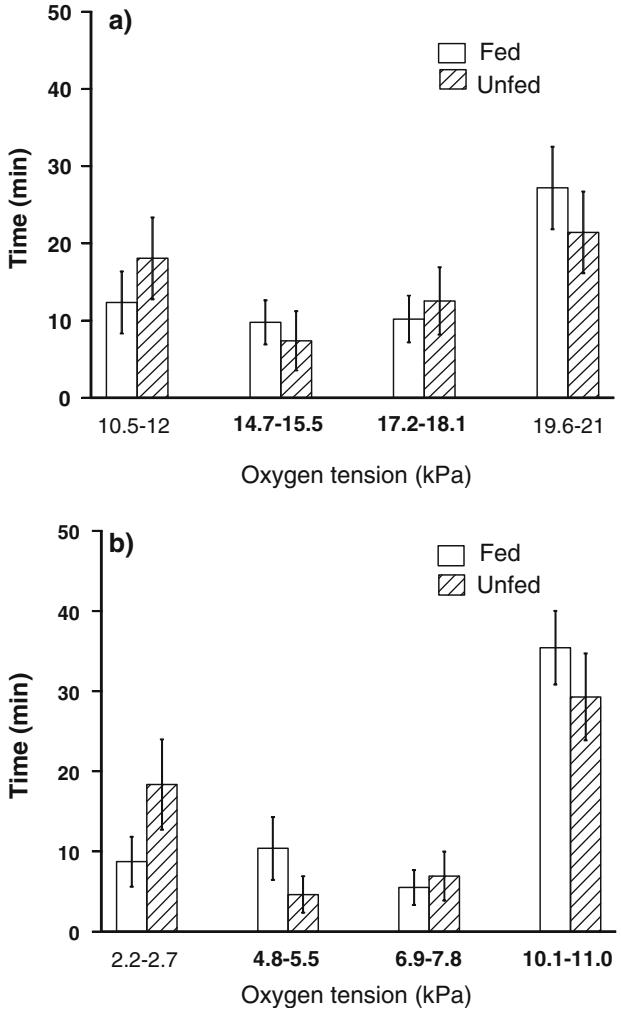

Fig. 3 Behaviour of unfed crabs (*hatched bars*) and postprandial crabs (*open bars*) in a dissolved oxygen gradient. Data represents mean times (±SEM) that 20 crabs spent in each area of the gradient. **a** High oxygen gradient of 10.5–21 kPa and **b** a low oxygen gradient of 2.5–10.5 kPa

area of the tank (Fig. 3b; univariate analysis of variance, $F = 12.37$, $P<0.001$), spending between 29.3 ± 5.25 and 34.5 ± 4.75 min of the hour in this area. When considering activity levels of crabs (movements between individual chambers in the gradient) there was no difference in activity levels between unfed and fed crabs in either the high oxygen gradient (Mann–Whitney, $U = 237.5$, $P = 0.85$) or the low oxygen gradient (Mann—Whitney, $U = 432$, $P = 0.56$).

In control conditions (16.8±0.5 kPa) crabs did not prefer any area of the tank (univariate analysis of variance, $F = 0.55$, $P = 0.65$). The crabs moved around the tank during the first 10 min of the acclimation period, before settling in one area and exhibiting very little movement thereafter.

Field work

Oxygen measurements were taken approximately 2–3 cm above the sediment. The shallow water (<3 m) close to the shoreline was hyperoxic (Fig. 4), with oxygen tensions as high as 28.5 kPa. Normoxic levels were reached at about 3 m depth, although several pockets of hyperoxic water (22–23 kPa) were observed as deep as 5 m. As depth increased there was a decrease in dissolved oxygen tension. The deeper areas (>7 m) were hypoxic (<13 kPa) with several areas being nearly anoxic (<1.5 kPa). Water temperature was more uniform and only varied between 11 and 15°C.

Postprandial crabs exhibited very little movement during the first 24 h after release (Fig. 5a). All three individuals were found within 12–20 m of the original release site. In contrast, the three unfed crabs all moved away from their release site (Fig. 5b). The approximate distance covered by the three unfed crabs within the first 6 h (assuming linear movement), was 1,035, 805 and 1,370 m, respectively. At the hourly intervals when crab position was noted, unfed crabs had moved into shallower, warmer (5.4 ± 2.1 m SD, 13.1 ± 0.7°C) water than postprandial crabs (7.1 ± 1.8 m, 12.6 ± 0.7°C) (ANOVA, $P = 0.005$ and 0.015, respectively). However, there was no significant difference in the oxygen regimes that unfed (12.1 ± 3.3 kPa SD) and postprandial crabs (11.9 ± 2.5 kPa) experienced at each of the hourly measurement intervals (ANOVA, $P = 0.88$). None of the crabs moved into water greater than 17.5 kPa oxygen.

Unfed crabs had moved from their previous locations when tracked at 24 and 48 h. Postprandial crabs were found in the vicinity (< 20 m) of the release site

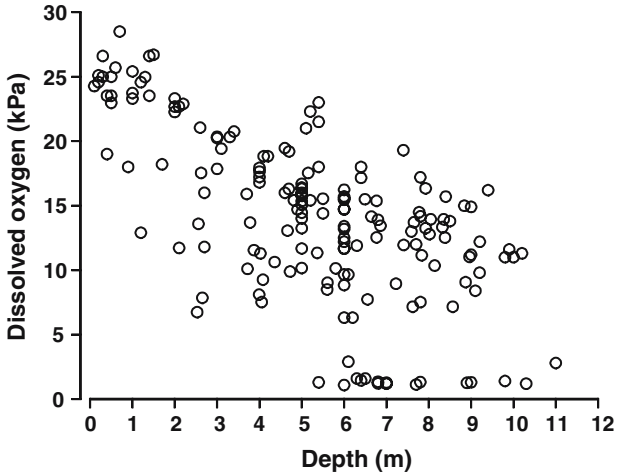

Fig. 4 Dissolved oxygen tensions (kPa) as a function of depth (m) in the Bamfield Inlet, British Columbia. Measurements were taken approximately 2 cm above the sediment surface at varying states of the tidal cycle during July and August 2004

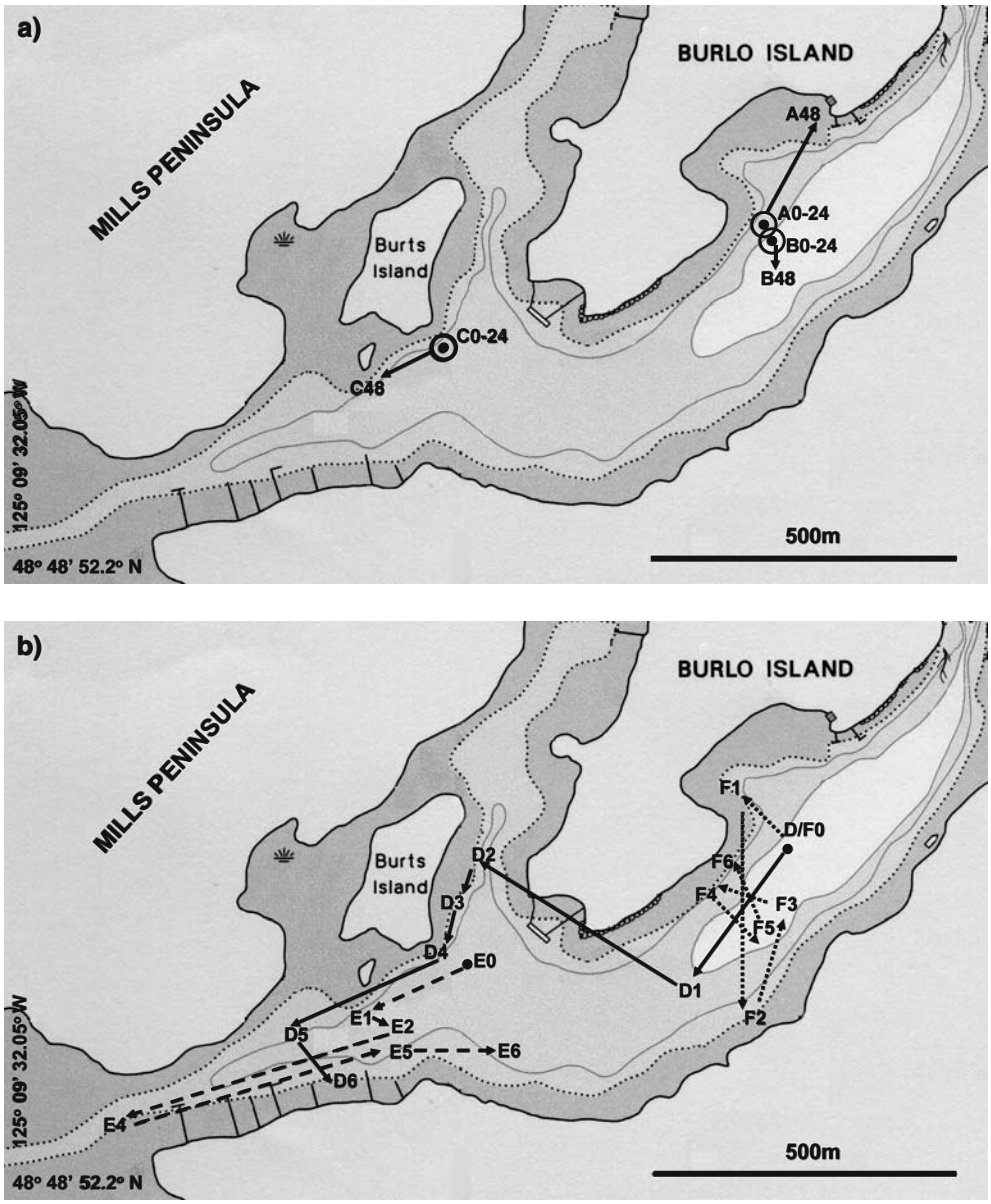

Fig. 5 Movement of *Cancer magister* in the Bamfield Inlet, British Columbia; each crab was fitted with an ultrasonic tag and tracked at hourly intervals for 6 h and at 24 and 48 h after release. Data show the position of each crab after set time intervals (each *number* denotes time in hour after release). **a** Postprandial crabs *A–C* ($n = 3$); *rings* around release site show that the crabs were located in the same area; movement away from the release site is shown at 48 h. **b** Movement of unfed crabs *D–F* ($n = 3$) during 6 h after release. If a certain time is not shown on the figure, that individual crab could not be located at that time

at 24 h; it was only after 48 h that each of the three postprandial crabs exhibited noticeable movement (> 50 m) away from the release site.

Discussion

Feeding in hypoxia

Cancer magister consumed the greatest amount of food in 15.8 kPa oxygen (75% oxygen saturation). In their natural environment, crabs appeared to prefer an oxygen tension range between 12 and 16 kPa. In addition, the water source to which the crabs were acclimated (16.5–17.5 kPa oxygen) was close to 15.8 kPa, which may also account for the observed behaviour. Crabs exhibited atypical behaviour in 21 kPa (100% oxygen saturation); attempting to climb out of the test chamber and becoming more aggressive assuming an offensive posture. Because the crabs remained active in 21 kPa oxygen they spent shorter periods of time actually feeding and thus consumed less food. *C. magister*

showed a trend towards a reduction in food intake in oxygen tensions below 15.8 kPa, largely due to a decrease in the amount of time the crabs spent feeding. A number of other articles discuss a reduction in food intake in hypoxia due to a reduction in activity levels (Das and Stickle 1993; Brante and Hughes 2001; Bell et al. 2003b; Mistri 2004). It has been suggested that crabs reduce activity and channel energy towards maintenance of an increased ventilation rate (Das and Stickle 1994; Mistri 2004). The size of a meal increases both the magnitude and duration of the specific dynamic action (Wang et al. 1995; Fu et al. 2005). Therefore, rather than a reduction in activity during hypoxia, it is possible (although less likely) that the crabs may have been able to anticipate the specific dynamic effects and were able to reduce the amount of food consumed accordingly.

The crabs often paused while feeding in the lower oxygen tensions (< 5.25 kPa), holding the food under the thorax. This pausing behaviour has also been observed in *C. maenas* (Brante and Hughes 2001) and *Carcinus aestuarii* (Mistri 2004), but whether this behaviour serves to conserve energy, remains unclear. Some of the crabs did not feed in the lower oxygen regimes, especially at 1.5 kPa. Airriess and McMahon (1994) report the P_{crit} for this species to be below 3 kPa and we have found that ventilation starts to become erratic after about 30–45 min in 1.4 kPa oxygen (J.L. Bernatis and I.J. McGaw, unpublished observation). The marked reduction in feeding in the lowest oxygen regime could therefore be a result of the inability of the crabs to obtain enough oxygen, which would restrict movement involved with feeding activities. However, when the oxygen tension of the water was raised rapidly (30 s) all crabs began eating at approximately 6 kPa. Previous authors have suggested that a change in internal physiology is the limiting factor, causing a reduction in activity and thus feeding (Das and Stickle 1994; Johansson 1997; Sneddon et al. 1998; Brante and Hughes 2001; Mistri 2004). This may not be the case for *C. magister*. The presence of external oxygen receptors in the branchial chambers has been suggested for the crayfish, *Procambarus simulans* (Larimer 1964), the shore crab, *C. maenas* (Taylor and Butler 1978) and the lobster, *Homarus americanus* (McMahon and Wilkens 1975). The ability of *C. magister* to resume feeding within 30 s when the oxygen tension of the water is raised only slightly, may provide additional evidence of external oxygen receptors. In support of the use of external oxygen receptors, rather than internal chemoreceptors, crabs maintain a low tissue oxygen strategy (Massabuau 2001) and blood oxygen tensions remain relatively stable, independent of changes in the external environment (Legeay and Massabuau 1999, 2000). The crabs in the present study were acclimated to hypoxia for a 4-h period, before feeding. During this time, their tissue biochemistry may change substantially (Taylor and Butler 1973; McMahon and Wilkens 1975; Wilkes and McMahon 1982; Hill et al. 1991; Zou et al. 1996; McMahon 2001), but these parameters are not altered significantly (within 30 s) when raising the oxygen tension by approximately 4 kPa (Taylor and Butler 1973; Butler et al. 1978; Lowrey and Tate 1986; Hill et al. 1991; Zou et al. 1996; McMahon 2001). This ability of *C. magister* to return to full activity levels and feed, without waiting for their internal physiological status to return to normal would allow them to exploit comparatively small or transient changes in environmental oxygen.

Hypoxic waters cause sediment-dwelling organisms such as molluscs and annelids to migrate towards the sediment–water interface (Diaz and Rosenberg 1995), thereby increasing the amount of available prey for crabs (Pihl et al. 1992; Taylor and Eggleston 2000). Although hypoxia reduces feeding efficiency (Das and Stickle 1993; Taylor and Eggleston 2000; Brante and Hughes 2001; Mistri 2004; Fig. 2), the present study has shown that crabs can detect differing oxygen tensions and move the food to higher oxygen tensions to feed. The presence of localised areas of hypoxia in the field, where the *C. magister* forages, provides a rationale for such behaviour. Coupled with rapid detection of the oxygen tension of the water, *C. magister* would be able to increase their foraging efficiency by exploiting severely hypoxic microhabitats while taking food to more favourable locations for feeding and digestion (Pihl et al. 1992; Diaz and Rosenberg 1995).

Postprandial behaviour in hypoxia

Once crabs have fed they exhibit a specific dynamic action: oxygen uptake increases rapidly, reaching a maximum within 2–5 h (McGaw and Reiber 2000; Robertson et al. 2002; Mente et al. 2003). In *C. magister* an increase in heart rate occurs almost immediately, reaching maximal levels 2 h after feeding (McGaw 2005a). Heart rate and ventilation rate remain elevated up to 10 h (McGaw 2005a), while oxygen uptake can take 40–50 h to return to pre-feeding levels (Legeay and Massabuau 1999; McGaw and Reiber 2000; Robertson et al. 2002). Thus, digestion places additional energy demands on animals. Because of this increase in physiological variables, we hypothesised that postprandial crabs would seek out higher oxygen regimes for digestion. Although the time spent in each oxygen regime was similar for unfed and postprandial

crabs, the behaviour observed, was different. Unfed crabs moved through the lower oxygen areas exploring the corners before leaving an area or choosing to remain in the area. Postprandial crabs were active in the low oxygen tensions and frequently tried to break the air–water interface, presumably attempting to increase oxygen uptake (Taylor and Butler 1973; Taylor et al. 1977). *C. sapidus* and *Callinectes similis* (Das and Stickle 1994) and *C. maenas* (Taylor et al. 1977) become more active and move the mouthparts more frequently when exposed to gradual changes in hypoxia. While hypoxic environments can be tolerated and are often not avoided by the crabs, behaviour does change, presumably in an attempt to increase the uptake of available oxygen (Taylor and Butler 1973; Das and Stickle 1994). This suggests that physiological compensatory mechanisms may have limitations and/or that behavioural responses reduce the necessity for physiological adjustments.

Oxygen tensions above 10 kPa are not physiologically stressful for *C. magister* (Airriess and McMahon 1994; McGaw and McMahon 2003) and there was no significant avoidance of these regimes in the present study. Likewise, *C. similis* does not avoid oxygen tensions above 12 kPa (Das and Stickle 1994). In lower oxygen regimes (2.5–10 kPa) the crabs moved to the higher oxygen tension suggesting they prefer oxygen tensions higher than about 8 kPa. This fits well with field data, where crabs spent less than 20% of their time in oxygen tensions below 8 kPa.

Avoidance behaviour is usually the first response to hypoxia, but such responses may not always be feasible (Das and Stickle 1994; Bell et al. 2003a). *C. magister* is able to survive in severe hypoxia by increasing ventilation rate, facilitating an increase in oxygen uptake, while a pronounced bradycardia conserves energy (Guadagnoli et al., in review). When postprandial crabs encounter hypoxia the effectiveness of some of these mechanisms may be reduced (McGaw 2005a), and the crabs attempt to compensate for the effects of digestion by diversion of blood away from the hepatopancreas (McGaw 2005a), and by slowing of food processing in the gut (McGaw 2006).

Field work

A layer of hyperoxic water in Bamfield Inlet extended down to 2–3 m, with occasional pockets found as deep as 5 m; this extensive area of hyperoxic water is probably caused by algal blooms, vascular plants releasing oxygen, and surface water run-off entering the system (Rabalais et al. 2001). These shallow waters with higher oxygen tensions increase prey abundance as organisms seek refuge from hypoxic waters, and therefore provide better foraging for predators such as crustaceans (Pihl et al. 1992). Although a significant portion of Bamfield Inlet had high oxygen levels, *C. magister* was predominately found at greater depths with lower oxygen levels (12–15 kPa) and avoided these normoxic and hyperoxic areas. The oxygen tensions just above the sediment surface varied from 15.8 to 1.5 kPa. As *C. magister* routinely buries in the sediment for up to 50 h (McGaw 2005b), measurements were also taken at the sediment–water interface and the water was found to be anoxic. This range of oxygen tension requires the resident animals to be very tolerant of hypoxia and the P_{crit} for *C. magister* is very low (Airriess and McMahon 1994; Bernatis 2005). Indeed, there was little evidence that this species attempted to avoid hypoxic environments to the same degree as other crab species (Taylor and Butler 1973; Taylor et al. 1977; Das and Stickle 1994; Bell et al. 2003a, b), and they appear to prefer mildly hypoxic water to normoxia.

Field data showed that there was no significant difference in the oxygen tensions that fed and unfed crabs encountered. This supported our laboratory experiments and led us to reject our original hypothesis that postprandial crabs select higher oxygen regimes. Nevertheless, there were noticeable differences in activity levels between unfed and postprandial crabs. Unfed crabs covered distances of up to 1.3 km during the first 6 h after release, while postprandial crabs remained relatively motionless for the first 48 h. Although it could be argued that fed crabs were satiated, while unfed crabs were actively foraging, this behavioural response was also seen in the laboratory when no food cues were present. Unfed crabs remained active in the tanks, but as soon they had fed, they became quiescent. This suggests that postprandial crabs cannot balance the simultaneous energy requirements of activity and digestion; by remaining inactive the crabs would be able to prioritise energy for digestive processes (Bennett and Hicks 2001; Hicks and Bennett 2004). A reduction in activity also occurs in larval fish following feeding; digestive processes exert an extra demand on their metabolism and they cannot swim for as long as unfed fish (Von Herbing and White 2002). Postprandial crabs started to exhibit significant movement after 48 h, which corresponds to the time when postprandial oxygen uptake has decreased to pre-feeding levels (McGaw and Reiber 2000; Robertson et al. 2002; I.J. McGaw, unpublished observation).

Although the laboratory experiments showed the crabs were able to detect oxygen gradients and orientate in response to oxygen tension, one must be cautious about extrapolating reactions in the field from

laboratory-based experiments. In the laboratory sharp gradients were created over small spatial scales (<3 m), and behavioural responses were only followed for short periods (1 h). Although the ability to detect oxygen gradients may allow crabs to exploit some of the oxygen microhabitats within the Bamfield Inlet, orientation on a larger spatial scale is questionable. This assumption is upheld by similar work on blue crabs; which can detect and avoid hypoxic water but are unable to orientate over large spatial oxygen gradients (Bell et al. 2003a).

Laboratory and field experiments showed that the preferred oxygen tension range of *C. magister* was approximately 8–17 kPa (approx. 40–80% oxygen saturation), but they would enter into, and feed in, severe hypoxia. The Dungeness crab may be one of the more hypoxia tolerant species of crab (Airriess and McMahon 1994; Bernatis 2005); nevertheless, feeding in hypoxia poses an additional physiological burden for animals already attempting to maintain adequate oxygen uptake (McGaw 2005a). Although *C. magister* is able to use physiological mechanisms to control digestive processes in hypoxia (McGaw 2005a), the present study has shown that behavioural responses may be the first mechanism used to balance the demands of simultaneously competing systems, thus maximising foraging ability, growth and reproduction. Clearly neither behavioural nor physiological mechanisms can be considered in isolation.

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