

## Burying behaviour of two sympatric crab species: *Cancer magister* and *Cancer productus*\*

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**SUMMARY:** The mechanics and emergence patterns associated with burying behaviour were investigated in the Dungeness crab, *Cancer magister*, and the red rock crab, *Cancer productus*. *Cancer magister* used both the legs and chelae to excavate the sand, whereas *Cancer productus* used the legs to pull and push itself down into the sediment only using the chelae in a final push beneath the sediment. Several individuals of each species remained buried for over 50 h, which was accomplished by alterations in ventilatory physiology. More commonly, both species exhibited an endogenous rhythm of circadian periodicity, with peak periods of emergence from the sand occurring during nocturnal high tides. Although burial may act as a means of predator evasion and to ambush prey, it appears the primary reason may be to conserve energy. These two species of crabs often occur sympatrically; the difference in behaviours is closely related to previously reported differences in physiological mechanisms between the two species when buried.

**Keywords:** Bury, Behaviour, *Cancer magister*, *Cancer productus*, endogenous rhythm.

**RESUMEN:** COMPORTAMIENTO DE ENTERRAMIENTO EN DOS ESPECIES DE CANGREJOS: *CANCER MAGISTER* Y *CANCER PRODUCTUS*. – Los patrones de comportamiento asociados con la acción de enterramiento de dos cangrejos, *Cancer magister* y *Cancer productus*, fueron investigados. *Cancer magister* usa tanto pereiópodos como quelas para excavar en la arena y enterrarse, mientras que *Cancer productus* empuja su cuerpo contra la arena para enterrarse. Varios individuos de ambas especies se mantuvieron enterrados por más de 50 h debido a alteraciones en su fisiología de respiración. Ambas especies mostraron un ritmo circadiano endógeno de emergencia a la superficie, con la mayoría de emergencias en horas nocturnas. Aunque el comportamiento de enterramiento es un medio para la evasión de predadores y captura de presas, es posible que la razón primaria de este comportamiento sea la conservación de energía. La especie de cangrejo en este estudio se distribuyen simpáticamente; la diferencia en comportamiento entre estas dos especies está asociada con las diferencias en mecanismos fisiológicos en condiciones de enterramiento que han sido reportadas previamente.

**Palabras clave:** enterrar, comportamiento, *Cancer magister*, *Cancer productus*, ritmo endógeno.

### INTRODUCTION

Many species of decapod crustaceans bury in soft sediments (Bellwood, 2002). In small crab species such as *Ovalipes* spp. and *Macrophthalmus* spp., burying behaviour functions primarily as a means to avoid predation (Nye, 1974; McLay and

Osborne, 1985; Barshaw and Able, 1990). However, its exact function in larger species, such as the cancrid crabs, is unknown (Bellwood, 2002).

The mechanics of burial have been investigated in several taxa. The combined use of the legs and the chelae propel the crabs beneath the surface. The legs loosen the sand beneath the crab (Garstang, 1896; Faulkes and Paul, 1997; Schembri, 1981) and pull the animal down into the sediment (McLay and

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Osborne, 1985). At the same time, the chelae thrust outwards, clearing sand that has accumulated in the buccal region (Garstang, 1896; Hartnoll, 1972; Schembri, 1981) and pushing the crab backwards and down into the sand (Caine, 1974; Taylor, 1984). A final push with the whole body drives the animal under the surface, thereby forcing sediment upwards. The displaced sediment settles on top of the body, leaving only the eyes, antennae and exhalant openings visible above the surface (McLay and Osborne, 1985).

On the surface of the sand, the crab maintains a ventilatory flow through the branchial chambers by sucking water in through the Milne-Edwards openings at the base of the chelae and legs and expelling it out through apertures adjacent to the mouth. This forward flow is interspersed with brief periods of ventilatory reversals, whereby the scaphognathites beat in the opposite direction pushing water out through the openings at the leg bases (Arudpragasam and Naylor, 1964). However, once crabs have buried, their ventilatory openings are in direct contact with the sediment. They are then faced with the problem of maintaining an adequate flow of water through the branchial chambers. Shallow-burying species fold their chelae close to the body, to form a canal or "exostegal channel" (Garstang, 1897a) that enables water to be drawn down towards the ventilatory openings at the bases of the legs. There is also an increase in the frequency and magnitude of ventilatory reversals (Garstang, 1897b; Cumberlidge and Uglow, 1978), that probably function to expel sediment that has blocked the intake openings (Arudpragasam and Naylor, 1966). In species which have body forms specialised for a sand-dwelling mode of life (*Corystes cassivelaunus*, *Atelecyclus rotundatus*, *Albunea* spp.), the second antennae have become modified to form a tube and the body is fringed with setae (Garstang, 1896, 1897a; Hartnoll, 1972; Taylor, 1984). In these and other sand-dwelling species, a reversed ventilatory current predominates while the crabs are buried (Bridges, 1979; Taylor, 1984; Davidson and Taylor, 1994; McGaw, 2004).

The Dungeness crab *Cancer magister* and the red rock crab *Cancer productus* often occur sympatrically in sandy or muddy bays and estuaries along the west coast of North America. Both species bury in the substrate during periods of inactivity (Stevens *et al.*, 1984; Carroll and Winn, 1989). The aim of the present study was to investigate the mechanics of burial behaviour in *C. magister* and *C. productus*

and determine how patterns of burial behaviour may be related to physiological adjustments that occur while buried (McGaw, 2004).

## MATERIAL AND METHODS

Male and female intermoult Dungeness crabs, *Cancer magister* and red rock crabs, *Cancer productus* of 400–600 g were trapped in Barkley Sound, British Columbia. The crabs were transferred to the Bamfield Marine Sciences Centre and held in running seawater of 10–12 °C and a salinity of  $32 \pm 1\text{‰}$  for at least one week prior to experimentation to ensure any endogenous physiological rhythms were abolished (McGaw and McMahon, 1998). The crabs were fed fish daily, but were starved for 24 h prior to experimentation and were not fed during experiments.

A circular tank of 160 cm diameter x 60 cm depth with a constant flow of aerated seawater was used for behavioural experiments. Coarse sand collected from the intertidal zone in the vicinity of the traps was placed in the bottom of the tank to a depth of 10 cm. This depth allowed the crabs to completely bury in the substrate. During experiments the entire tank was surrounded by a black plastic sheet to avoid any visual disturbance to the animals. All experiments were carried out in constant dim red light. Burying behaviour was recorded for *C. magister* and *C. productus* using a time lapse video system (Panasonic AG-RT600AS VCR and Panasonic WV-BP120 camera). Sixteen crabs of each species were placed individually in the tank and monitored until they had completely buried in the sand. The burying style as well as the total time to bury completely in the sand were recorded.

The time lapse video system was also used to monitor burial and emergence behaviour over several days. In a first series of experiments, emergence and burial times were recorded for freshly collected *Cancer magister* and *Cancer productus* trapped in Sarita Bay (N48°53.869' W125°01.198'). The total time between removal from the traps and transfer to the experimental tank was less than one hour. Four male crabs of each species were introduced into the tank and activity was monitored for 3 days. Wax numbers glued onto the carapace allowed identification of each animal. The times of emergence and burial in the sand were recorded over a 3-day period. In a second series of experiments four arrhythmic crabs (crabs held in captivity for 2 weeks) of

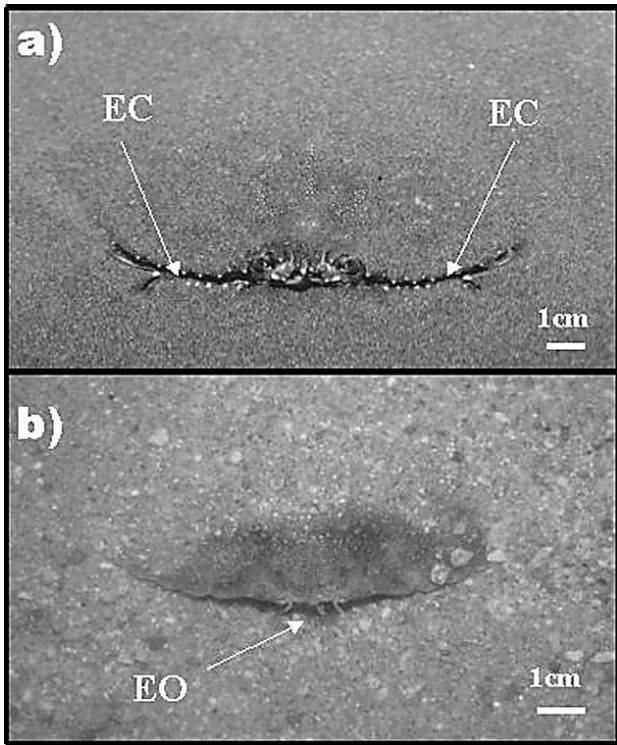


FIG. 1. – Photograph showing burial in the sand for a) *Cancer magister* and b) *Cancer productus*. In *C. magister* the exostegal channels (EC) are visible. *C. productus* shows the typical burial depth of this species, with the mouthparts, antennae and exhalant openings (EO) visible above the surface.

each species were introduced into the tank and allowed to settle for 1 h. Activity was recorded as the percentage of time emerged from the sand per 15 min interval, and as a function of the number of animals emerged; for example, 100% activity would represent all four crabs of one species being on the surface for an entire 15 min period. Significant periodicity within the data was tested for using a periodic regression analysis (deBruyn and Meeuwig, 2001) (Periodogram statistical software; Aagaard *et al.*, 1995).

## RESULTS

Both species of crabs started the burying process by probing the sand with the dactyls of the walking legs. *Cancer magister* used the legs and chelae simultaneously while burying. *Cancer magister* rapidly loosened the sand by flicking their legs outwards and upwards and at the same time the chelae pushed the sand outwards in front of the animal. The combined actions of these appendages produced a pit that the animal submerged into and at the same time threw sand upwards onto the dorsal surface of the carapace. A final push with the body submerged

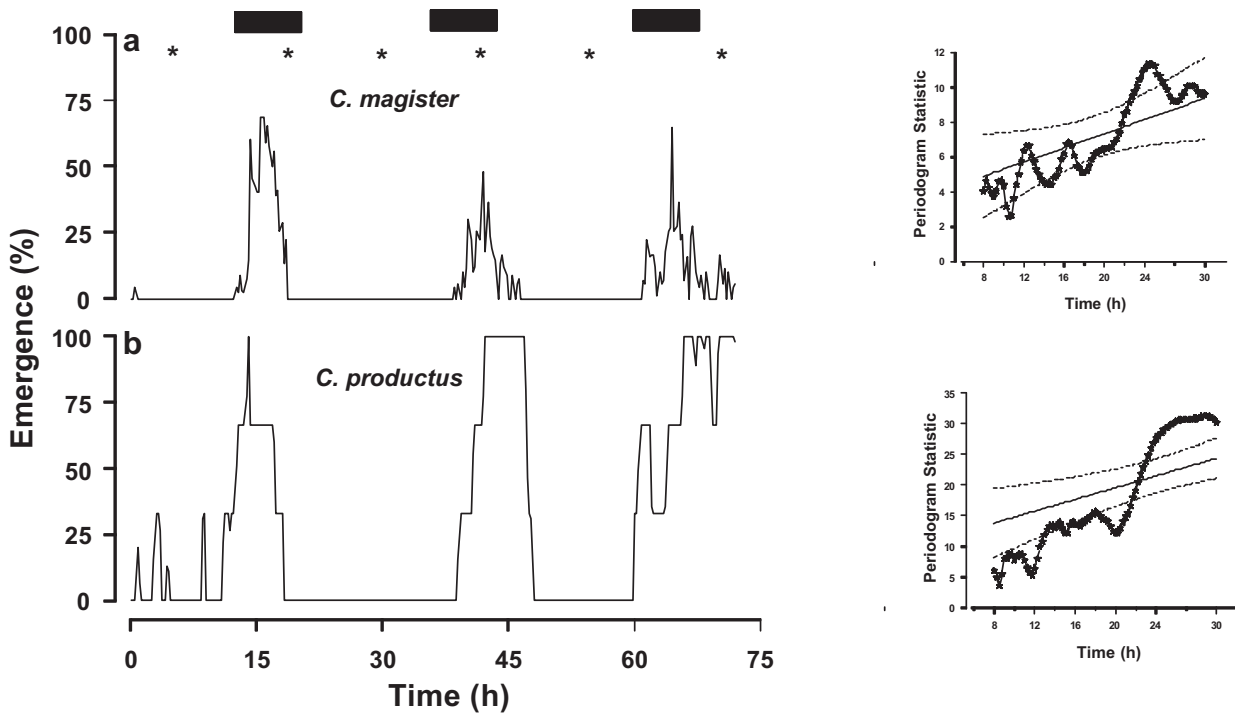


FIG. 2. – Percentage activity (per 15 min interval, with no averaging between intervals) of a) *Cancer magister* and b) *Cancer productus* (n=4 of each species) freshly collected from Sarita Bay when high tide predominated during the hours of darkness and recorded for 3 days in constant dim red light. Bars represent times of expected darkness and asterixes represent times of expected high tide in the field. Periodogram statistics are shown for each species on the right side of the graph. The periodogram graph represents data from periodic regression. The X axis is the period time in hours and the Y axis is the amplitude of the rhythm. Deviation outside 95% confidence limits (dashed lines) is shown.

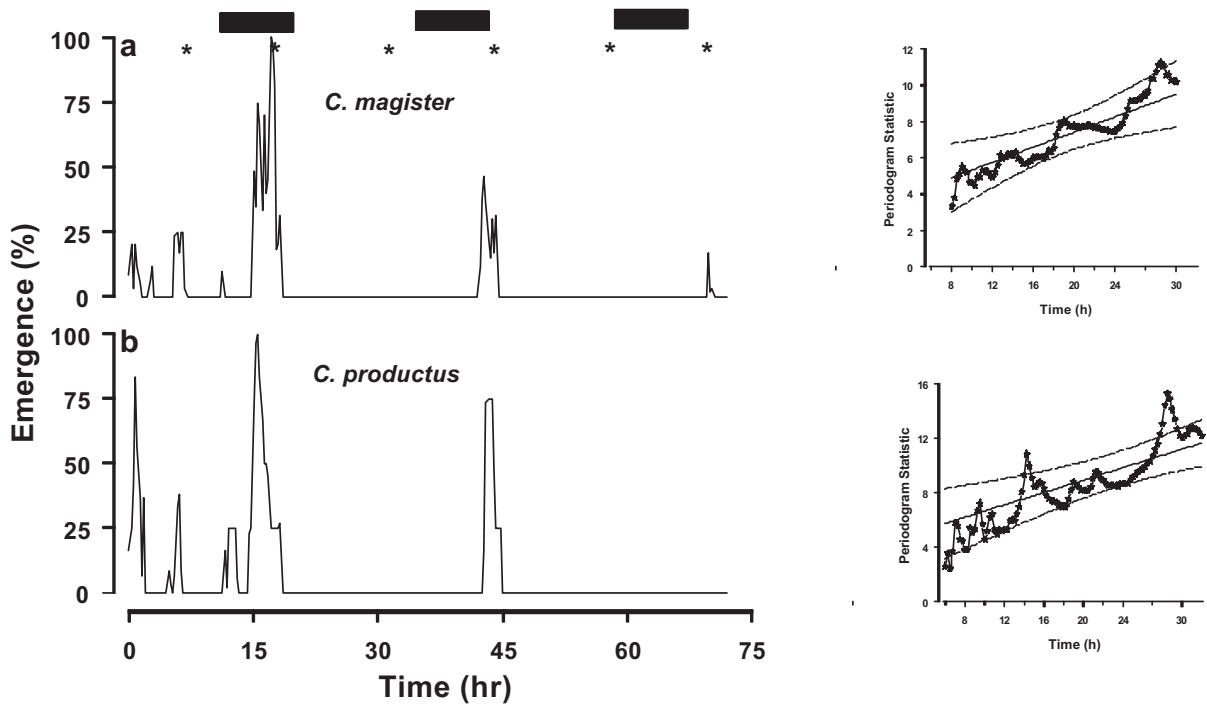


FIG. 3. – Percentage activity (per 15 min interval, with no averaging between intervals) of **a**) *Cancer magister* and **b**) *Cancer productus* (n=4 of each species) freshly collected from Sarita Bay when high tides occurred during daylight hours and recorded for 3 days in constant dim red light. Bars represent times of expected darkness and asterixes represent times of expected high tide in the field. Periodogram statistics are shown for each species on the right side of the graph.

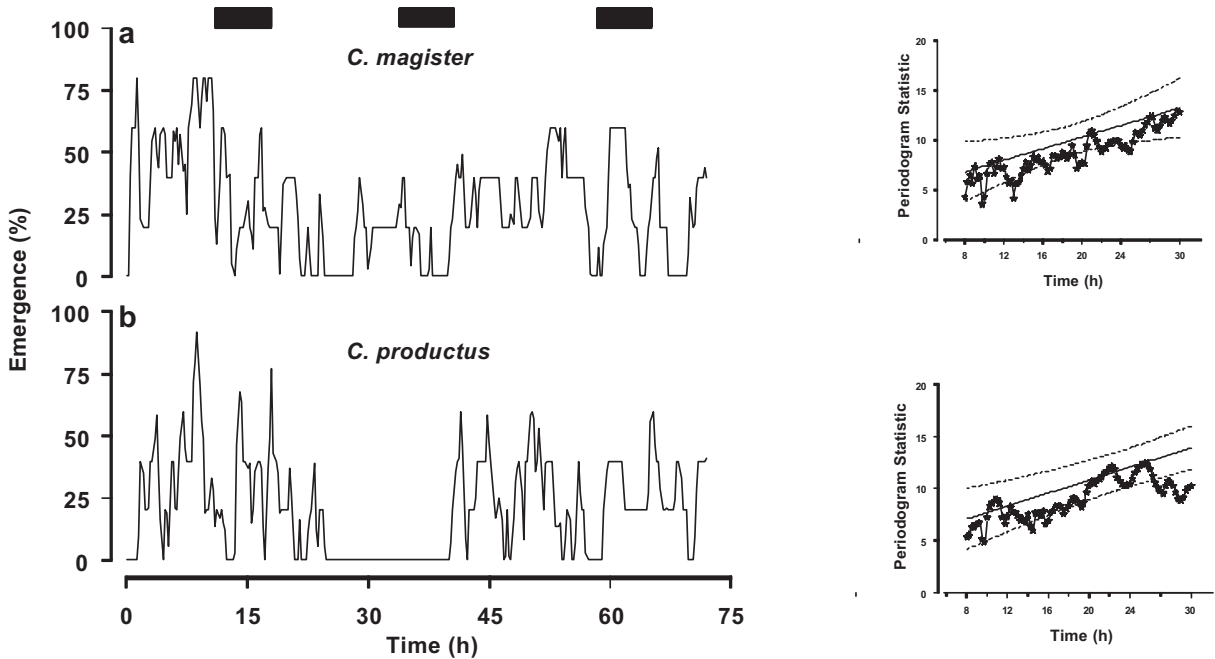


FIG. 4. – Percentage activity (per 15 min interval, with no averaging between intervals) of **a**) *Cancer magister* and **b**) *Cancer productus* (n=4 of each species) previously maintained for 2 weeks in constant conditions at the Bamfield Marine Sciences Centre. Recordings were made during a 3-day period in constant dim light. Bars represent times of expected darkness. Periodogram statistics are shown for each species and the right side of the graph.

the animal below the surface of the sand (Fig. 1a). *Cancer productus* used a different burying style, often with several short pauses. The legs were worked slowly into the sand, pulling from the outside toward the centre of the body and drawing the

animal down into the sand. *C. productus* only used the chelae in the final stage of the burying process to push the body down into the sand at a 45° angle. Once in the sand, a few pushes of the body completed the process (Fig. 1b). Both species settled in



the sand in the horizontal position. *C. magister* tended to bury slightly deeper, with only the antennae and exhalant opening visible, while in the majority of *C. productus* part of the anterior margin of the carapace was still visible above the sand (Fig. 1). However, individual animals of both species did bury deeply, so that only an exhalant water jet was visible above the sand. The average time for *C. magister* to bury completely was  $26.8 \pm 3.1$  s, which was significantly faster than the  $59.5 \pm 7.5$  s recorded for *C. productus* ( $t$  test,  $P < 0.001$ ).

Freshly collected crabs exhibited an endogenous circadian rhythm of emergence. Peak periods of activity occurred during hours of expected darkness (Fig. 2a, b) and both species remained buried during times of expected daylight. Tidal changes exerted some influence on emergence from the sand. The endogenous rhythm was absent in *C. magister* when a high tide did not occur during the hours of darkness and it was not clearly defined in *C. productus* (Fig. 3a, b).

Results from several trials showed that rhythmic *C. magister* emerged more often from the sand (mean  $\pm$  SEM =  $16.6 \pm 2.6$ ) during the 3-day period compared with *C. productus* (mean  $\pm$  SEM =  $5.9 \pm 0.8$ ) ( $t$  test = 3.36,  $P = 0.003$ ). The average time that *C. magister* remained buried was  $3.7 \pm 0.6$  h, which was significantly less than the  $8.8 \pm 1.3$  h recorded for *C. productus* ( $t$  test = -3.8,  $P < 0.001$ ). However, 3 *C. magister* and an individual *C. productus* remained buried for over 50 h.

The endogenous rhythm of burial and emergence started to break down after 5 days in constant conditions. Crabs maintained for 2 weeks in captivity showed no significant periodicity in activity (Fig 4 a,b). Both species were active for the duration of the 3 days, spending about 50% of the time emerged from the sand.

## DISCUSSION

Representative species in ten families of the Brachyura have been reported to exhibit burying behaviour, though comparatively little is known about the mechanics of this behaviour (Bellwood, 2002). The burying style exhibited by *Cancer productus* is similar to that reported for the paddle crab, *Ovalipes catharus*, where the legs pull the animal down and a final push with the chelae submerges the animal in the sediment (McLay and Osborne, 1985). Unlike *C. productus*, *Cancer magister* excavates the

sand with its legs. This "shovelling" of the sediment is also employed by the sand crabs, *Blepharipoda occidentalis* and *Emerita analoga*, which use the walking legs to dig up sand from under the body (Faulkes and Paul, 1997). In conjunction with the legs, *C. magister* also uses the chelae to shovel sand in a similar fashion to *Corystes cassivelaunus* (Garstang, 1896) and *Ovalipes guadalupensis* (Caine, 1974), which creates a depression for the animal to submerge into.

The time it takes for different species of crabs to bury ranges from a few seconds (Garstang, 1896; Dugan *et al.*, 2000) to several minutes (Schembri, 1981). The size of the animal affects the burial time, with larger animals taking longer to bury. *Ovalipes catharus* of comparable size to the crabs used in the present study have similar burial times (24 s; McLay and Osborne, 1985) to those observed for *C. magister* (26.1 s). Although *C. magister* buries significantly faster than *C. productus* (59.5 s), it is not without cost: a much larger increase in cardiac parameters and blood flow is necessary to assist this process (McGaw, 2004).

Several of the crabs remained buried in the sand for over 50 h. However, this is a comparatively short period, since during the winter ovigerous *C. magister* may remain buried in the mud for up to 2 weeks at a time (Jensen, pers. comm.). Though they are buried for long periods, oxygen is not considered to be limiting for animals buried in the sand (Webb, 1969; Bellwood, 2002). This may be because changes in ventilatory patterns compensate during burial (McGaw, 2004). *C. magister* maintains water flow over the gills by increasing the amount, magnitude and duration of ventilatory reversals (McGaw, 2004). In some cases, these ventilatory reversals are so frequent in deeper buried crabs that a reversed water flow through the branchial chambers predominates for several hours (McGaw, 2004). This is a typical response of sand-dwelling species of crabs (Bridges, 1979; Taylor, 1984; Davidson and Taylor, 1994). In contrast, buried *C. productus* made frequent shifts within the sediment, which loosened the sand between the body and chelae and maintained the opening of the exostegal channels (Garstang, 1897a). The use of dye tracers confirmed that even deeply buried *C. productus* maintained a more-or-less constant forward flow through the branchial chambers by sucking water down through the sand and by moving the chelae slightly and blowing sand out from between chelae and body by way of several ventilatory reversals. Because *C. magister* did not

maintain the exostegal channels, eventually blockage of the Milne-Edwards openings occurred. The crabs then emerged briefly from the sand in order to clear the openings; this accounted for the lower mean burial times of *C. magister* compared with those of *C. productus*.

Although several individual crabs buried for a prolonged period, most of the freshly collected crabs exhibited a circadian pattern of activity with peak periods of activity at night (Fig. 2). Most of the species of crab that bury remain inactive during the day, emerging at night to forage (Garstang, 1896; Hartnoll, 1972; Caine, 1974; Schembri, 1979; Stevens *et al.*, 1984; Taylor, 1984; McLay and Osborne, 1985; Skinner and Hill, 1986; Sumpton and Smith, 1990; Abelló *et al.*, 1991). However, only one of these works discusses an endogenous component of burying behaviour (Abelló *et al.*, 1991). The endogenous circadian activity rhythm in *C. magister* and *C. productus* (Fig. 2a,b) is somewhat surprising, since cardiovascular parameters in *C. magister* exhibit an endogenous rhythm of tidal periodicity (McGaw and McMahan, 1998) and cardiac and locomotor rhythms are closely coupled in decapod crustaceans (Aguzzi *et al.*, 2004). However, water depth can affect periodicity of emergence rhythms in burrowing decapods (Aguzzi *et al.*, 2003). The animals in the present study were collected at approximately 35 m depth, where they may not have been strongly influenced by the tide. The crabs in the previous study (McGaw and McMahan, 1998) were trapped in a shallow bay of 5-7 m where they are known to forage intertidally (Zaklan and Ydenberg, 1997). Nevertheless, tidal changes had some influence on burying behaviour because the endogenous emergence rhythm was not as clearly defined when a high tide did not occur during the hours of darkness, especially for *C. magister* (Fig. 3). It is also worth noting that when the nocturnal high tide shifts from darkness to daylight hours peak splitting of the emergence rhythm occurs (Fig. 2a, b; day 3).

Burying behaviour in smaller crab species is thought to be an anti-predator mechanism (Bellwood, 2002). The crabs used in the present study were too large to fall prey to most animals. The main predators in the area that would tackle crabs of this size (400-600 g) are visual feeders such as seals and sea lions (Tollit and Thompson, 1996; Calkins, 1998), so burying during the day may help avoid capture by these animals.

Burying in substrate may also enable these large crabs to ambush prey. The antennae were usually

the only structures protruding from the sand when the crabs were buried and an increased blood flow to the musculature of these structures is reflective of their increased flicking activity (McGaw, 2004). The crabs may use the antennae to detect food whilst buried (Caine, 1974), since they will emerge from the sand in response to prey or prey odours (Caine, 1974; Schembri, 1981; pers. obs.). Nevertheless, the primary advantage of burying appears to be an energy-saving mechanism. When they are buried, there is a decrease in blood flow rates to the musculature, resulting in a decrease in cardiac output (McGaw, 2004). Periods of unilateral ventilation also predominate once the crabs are buried (McGaw, 2004). *C. magister* and *C. productus* cease ventilating the branchial chambers for up to 30 min, coupled with periods of cardiac arrest (McGaw, 2004). These act as an energy-saving mechanism, when oxygen levels in the haemolymph are optimal and only basal metabolic activities have to be supplied (Bridges, 1979; Burnett and Bridges, 1981; Naylor and Taylor, 1999). This time may be ideal for digestion and absorption because haemolymph flow to the digestive organs via the anterolateral and hepatic arteries is maintained while the crabs were buried (McGaw, 2004).

The behavioural responses as well as the physiological changes (McGaw, 2004) observed in *C. magister* resemble those reported in the sand-dwelling crabs, *Corystes cassivelaunus*, *Atelecyclus rotundatus* and *Ovalipes catharus* (Bridges, 1979; Taylor, 1984; Davidson and Taylor, 1994). Indeed, *C. magister* is largely confined to sandy or muddy bottoms (Pauley *et al.*, 1986), whereas the habitat of *C. productus* is broader and although they inhabit muddy or sandy areas they also occur commonly on rocky bottoms (Carroll and Winn, 1989). In addition, the underside of the carapace of *C. magister* is covered in setae, which could function in maintaining a pathway for water delivery to the ventilatory openings (Garstang, 1896; Taylor, 1984; Davidson and Taylor, 1994). In *C. productus* the underside is bare. Along with the faster burial times observed in *C. magister*, these findings suggest that *C. magister* may be better adapted for a burying existence compared with *C. productus*.

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