

# Vertical movement of mud crab megalopae (*Scylla serrata*) in response to light: Doing it differently down under

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## Abstract

Selective tidal-streaming is a model frequently used to explain how planktonic larvae invade estuaries. The ability of larvae to move vertically in the water column to selectively ride favourable currents and maintain ground gained is critical to this process. The mud crab (*Scylla serrata*) is a widely distributed, commercially and recreationally important portunid crab but little is known about its estuarine recruitment mechanisms or the vertical migration behaviour of its megalopae. In studies of the blue crab (*Callinectes sapidus*), important factors identified in the recruitment mechanism include altered vertical swimming behaviours in estuarine and offshore water and an endogenous circadian rhythm. Using laboratory experiments we examined the vertical displacement response of mud crab megalopae to illumination in estuarine and offshore water during the day and the night. Mud crab megalopae released into 1 m high towers swam higher when illuminated than when in darkness. This behaviour was repeated during the day and the night and in offshore and estuarine water. Given the apparent indifference to water type and the fact that mud crab megalopae are rarely caught in estuaries, we propose the model that these crabs do not invade estuaries as megalopae, but settle and metamorphose into small crabs on the coastal shelf before moving along the sea bed into estuarine habitats.

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## 1. Introduction

Many marine animals have broadly dispersed pelagic larvae associated with large variations in recruitment, which in turn can lead to large fluctuations in population size. Differences in transport whilst in the pelagic larval stage have explained much of the variation in recruitment (Gaines and Bertness, 1992; Hughes et al., 2000). Therefore, understanding the mechanisms of the transport process will help us to understand recruitment and make predictions of future population sizes.

Many adult portunid crabs associated with estuaries migrate seaward to spawn, increasing the chance that their larvae develop in the open coastal region (Hill, 1994; Forward et al., 2003). Seaward transport of larvae may be beneficial as conditions are more thermostatically and chemically stable, providing a more consistent environment for development. Seaward transport would also increase mixing within the population, increase genetic heterogeneity and reduce the risk of total failure of an entire cohort (Pechenik, 1999; Gopurenko and Hughes, 2002). The new generation of crabs must, however, return to the estuary at some stage.

Despite being relatively strong swimmers for invertebrate larvae, crab megalopae tend to be unable to

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maintain swim speeds exceeding flow rates commonly found in tidal estuaries (Luckenbach and Orth, 1992; Lee et al., 2004). Models using selective tidal-stream transport have been used to explain how larvae with an apparent swimming deficit are able to invade estuaries (Forward et al., 2003; Queiroga and Blanton, 2005). The spawning and recruitment characteristics of the portunid crab, *Callinectes sapidus* (the blue crab) have been the focus of considerable research in the USA (e.g. van Montfrans et al., 1995; Pile et al., 1996). The female crabs migrate to the lower estuary to spawn, with subsequent larval development occurring on the coastal shelf through to megalopal stage. Offshore, blue crab megalopae are more abundant in surface waters during the day, utilising wind-generated surface currents to remain near the coast and enter estuaries (Goodrich et al., 1989; Etherington and Eggleston, 2000). In estuaries they ascend into the water column during night-time flood tides and descend during both the daytime and ebb tides. This behaviour reduces their exposure to visual planktivores and allows them to ride the flooding tide to migrate upstream. Upon finding suitable estuarine habitat they settle to the benthos and moult into juvenile crabs (van Montfrans et al., 2003). Stimuli including light, turbulence, salinity and estuary derived chemical cues interact in complex ways with the circadian swimming rhythm of the megalopae to generate this selective tidal streaming behaviour (Forward and Rittschof, 1994; Forward et al., 2003).

The mud crab (*Scylla serrata*) is a portunid crab distributed throughout the Indo-West Pacific region and is generally found in muddy mangrove habitats during adulthood. Like the blue crab, female mud crabs are thought to migrate to the coastal shelf to spawn (Hill, 1994). Their zoea cannot survive low salinities (Hill, 1974) and their megalopae have been caught in offshore waters but rarely within estuaries (Arriola, 1940). Despite a substantial research effort, difficulties in finding significant numbers of megalopae and early-stage crabs (<30 mm carapace width (CW)) have hampered investigations into the mechanisms of their recruitment into estuaries (Heasman, 1980; Hill et al., 1982; Moser and Macintosh, 2001).

For much of the mud crab recruitment season, Australian estuary mouths within the distribution of the crabs, tend to have similar or in some cases greater salinities than offshore waters (e.g. Wolanski, 1986). Penaeid prawns, which have a similar distribution to the mud crab, also develop offshore before recruiting to estuaries as postlarvae. Falling salinity gradients are not thought to stimulate these postlarvae to invade estuaries in the wild because in some African and Australian estuaries, postlarvae have invaded inverse estuaries (Rothlisberg et al., 1995). Instead, alternative stimuli

have been proposed e.g. changes in pressure due to increasing water depth on flooding tides, the presence of other estuarine plant or animal-derived chemical cues.

There are a number of possible explanations for the lack of success in finding mud crab megalopae and/or early-stage mud crabs in estuaries. Their recruitment to estuaries may be temporally sporadic, making it difficult to detect them. This is the case for the blue crab, however, long term data sets have successfully detected sporadic blue crab recruitment events (Pile et al., 1996; Forward et al., 2004). Mud crabs may also grow rapidly once in estuaries, leaving very little time in which they can be sampled. These are unconvincing reasons, however, given that the efforts of many researchers at different times and places have failed to find significant numbers of mud crab megalopae within estuaries.

Nearly all observations of mud crab megalopae have been made on larvae reared in aquaculture tanks because they are rarely found in the wild. In rearing tanks, mud crab megalopae tend to adopt a benthic habit when observed during the day or under illuminated conditions (Rabbani and Zeng, 2005). This behaviour is consistent with the selective tidal streaming model and similar to field observations of blue crab megalopae in estuaries, which tend to be absent from estuarine surface waters during the day but present during night (De Vries et al., 1994). In offshore waters, however, blue crab (*C. sapidus*) megalopae are found near the surface during the day (Etherington and Eggleston, 2000). Megalopae of *Portunus pelagicus*, another Indo-Pacific portunid, have also been observed to be photopositive and more active when illuminated in offshore water (Bryars, 1997).

Using two laboratory experiments, we tested the model that mud crab megalopae behave in a manner consistent with the field observations of blue crab megalopae and aspects of the selective tidal-streaming model. Specifically, three hypotheses were tested: (1) that megalopae tend to be higher in a water column of offshore water when illuminated than when not and this pattern would be reversed in estuarine water, (2) that megalopae in a column of offshore water tend to ascend after the lighting switches from dark to light but the reverse occurs when in estuarine water, and (3) that the effect of the above treatments will be suppressed or enhanced when exercised during daytime or night-time.

## 2. Materials and methods

### 2.1. Water towers and lightproof rooms

Two lightproof rooms were used for both experiments. Inside each room, straight-sided glass water

towers ( $H \times W \times D$ ;  $100 \times 10 \times 9$  cm) were arranged such that the top of the towers were 10 cm below an unfiltered fluorescent light ( $2 \times$  Osram 35 W Daylight tubes). These lights emit a spectrum with peaks between 400–500 nm, 530–560 nm and 580–640 nm. Light intensity at the water's surface was  $193 \mu\text{mol m}^{-2} \text{s}^{-1} \pm 1.53$  (SE). This spectrum is not equivalent to daylight but the intensity is brighter than during dawn or dusk and includes the 400–500 nm region to which adult *S. serrata* and the larvae of other crab species have been shown to be sensitive (Forward and Cronin, 1979; Leggett, 1979). We considered filtering the light to the 400–500 nm region, however, in the wild megalopae are exposed to a wider range of wavelengths and we saw no detriment in exposing these megalopae to a broad spectrum. The towers were opaque on three vertical sides and arranged such that animals in one tower were not able to see animals in another. Towers were graduated at 10 cm intervals from bottom to top. A small amount of beach sand was added to each tower to cover the glass bottom and reduce light reflection. Although not tested, it was likely that the brightest source of light as seen from inside the towers would be from directly above. We consider that this mimicked the position of the sun at its zenith in a similar manner to that described by Forward et al. (1984).

## 2.2. Megalopae: rearing and selection

Bribie Island Aquaculture Research Centre, Queensland Department of Primary Industries and Fisheries provided the megalopae used in both experiments. Two experiments were completed and the megalopae used were reared from two female mud crabs collected from Pumicestone Passage. Pumicestone Passage is a narrow waterway separated from the Pacific Ocean by Bribie

Table 1

ANOVA results for Experiment 1, testing the effects of treatments on the vertical position of megalopae in towers filled with offshore water, 2 h after being subjected to illumination or darkness

| Source of variation | df | MS     | p      | F versus     |
|---------------------|----|--------|--------|--------------|
| Light regime (LR)   | 1  | 3247.2 | <0.05* | Pooled       |
| Time of day (Ti)    | 1  | 353.9  | <0.05* | Pooled       |
| Date (Da)           | 1  | 21.7   | >0.575 | Pooled       |
| LR × Ti             | 1  | 7.8    | >0.850 | LR × Ti × Da |
| ◆LR × Da            | 1  | 78.3   | –      | –            |
| ◆Ti × Da            | 1  | 84.8   | –      | –            |
| LR × Ti × Da        | 1  | 141.9  | >0.160 | Pooled       |
| Pooled terms        | 18 | 67.6   |        |              |

Data transformed to Arc Sin, Cochran test=*ns*. Some terms were pooled (◆) where  $p > 0.25$  and pooling resulted in a more powerful test.

Table 2

ANOVA results for Experiment 1, testing the effects of treatments on the vertical displacement of megalopae, 2 h after the lighting was changed from Off → On or On → Off

| Source of variation | df | MS    | p      | F versus    |
|---------------------|----|-------|--------|-------------|
| Lighting (L)        | 1  | 2.075 | <0.05* | L × Da      |
| Time of day (Ti)    | 1  | 0.003 | >0.725 | Pooled      |
| Date (Da)           | 1  | 0.008 | >0.605 | Pooled      |
| L × Ti              | 1  | 0.073 | >0.555 | L × Ti × Da |
| L × Da              | 1  | 0.000 | >0.935 | Pooled      |
| ◆Ti × Da            | 1  | 0.002 | –      | –           |
| L × Ti × Da         | 1  | 0.109 | >0.080 | Pooled      |
| Pooled terms        | 17 | 0.030 |        |             |

Water columns were filled with offshore water. Cochran test=*ns*. Terms were pooled (◆) where  $p > 0.25$  and pooling resulted in a more powerful test.

Island, Queensland ( $153^\circ 11' 55''$  E,  $27^\circ 03' 04''$  S). The passage is flanked by intertidal mudflats, seagrass beds and mangroves along most of its length. The rearing protocol followed the ambient day:night cycle (12:12) at temperatures between 27 and 29 °C and salinities between 35 and 36 ppt. Larvae were fed twice per day, generally in the early morning and mid-afternoon. Megalopae were collected from incubation tanks by lifting a bucket (25 cm diameter, 1 mm mesh base) vertically through the water column, sampling a range of swimming and benthic megalopae. The sample ( $\approx 10$  megalopae) was placed into a container partially filled with water. Individual megalopae were haphazardly

Table 3

ANOVA results for Experiment 2, testing the effects of treatments on the vertical position of megalopae, 2 h after being subjected to illumination or darkness

| Source of variation | df | MS       | p      | F versus          |
|---------------------|----|----------|--------|-------------------|
| Light regime (LR)   | 1  | 14,232.3 | <0.05* | Pooled            |
| Water type (WT)     | 1  | 352.3    | >0.070 | Pooled            |
| Time of day (Ti)    | 1  | 398.8    | >0.055 | Pooled            |
| Date (Da)           | 1  | 863.8    | <0.05* | Pooled            |
| LR × WT             | 1  | 26.8     | >0.500 | LR × WT × Da      |
| LR × Ti             | 1  | 2.2      | >0.955 | LR × Ti × Da      |
| ◆LR × Da            | 1  | 20.7     | –      | –                 |
| WT × Ti             | 1  | 81.3     | >0.540 | WT × Ti × Da      |
| ◆WT × Da            | 1  | 60.5     | –      | –                 |
| ◆Ti × Da            | 1  | 9.9      | –      | –                 |
| LR × WT × Ti        | 1  | 53.3     | >0.685 | LR × WT × Ti × Da |
| LR × WT × Da        | 1  | 26.9     | >0.610 | Pooled            |
| LR × Ti × Da        | 1  | 524.3    | <0.05* | Pooled            |
| WT × Ti × Da        | 1  | 105.7    | >0.310 | Pooled            |
| LR × WT × Ti × Da   | 1  | 184.3    | >0.185 | Pooled            |
| Pooled terms        | 35 | 101.4    |        |                   |

Data transformed to Arc Sin, Cochran test=*ns*. Some terms were pooled (◆) where  $p > 0.25$  and pooling resulted in a more powerful test.

collected using a pipette and randomly allocated to a vial within an array of vials that corresponded to the number of towers used until each vial contained 10 live megalopae. These megalopae were added to their respective tower at the start of each experiment.

2.3. Experimental design

Experiment 1 used three towers per room, all were filled with offshore water collected 100 m offshore from the ocean side of Bribie Island. In the second experiment an additional factor being Water Type (2 levels, offshore and estuarine; salinities 36.0 ppt and 35.7 ppt respectively) was introduced. Experiment 2 used 6 towers per room, three with offshore water and three with estuarine water collected from the seagrass beds of Pumicestone Passage (153° 07' 45" E, 27° 03' 52" S). In both experiments, the lights in one room were turned off (Dark) whilst they were turned on (Light) in the other. Ten megalopae were added to each tower and after 2 h, the position of each megalopa within each tower was recorded. For towers in darkness, observations were made using a dim incandescent torch covered with red cellophane because crab larvae are less responsive to far-red light (Cronin and Forward, 1988). Position recordings were completed within 1 min per tower. After collecting these data, the light within the rooms were reversed (Light→Dark and Dark→Light). Megalopae were left for a further 2 h to adjust to the new

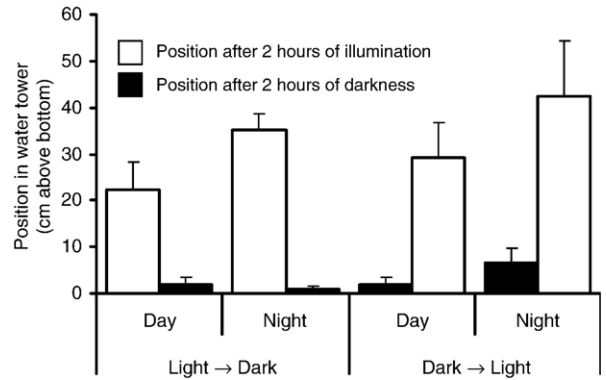


Fig. 1. Mean (SE) vertical position of megalopae in towers filled with offshore water (Experiment 1), for treatments Light to Dark, Dark to Light during both day and night.

lighting conditions after which their positions were recorded again before they were discarded. This 4 h protocol was completed during day and night (Factor: Time of day, 2 levels) on two days (Factor: Date, 2 levels) for both experiments. The experiments were started at different times during the day and the night so that the potentially confounding effects of the larval rearing protocol or lighting regimes were reduced. Water temperatures (25.8 °C±0.1 SE) were similar for all treatments during both experiments.

2.4. Data analyses

The data for hypothesis 1 were the mean vertical position of all megalopae within a tower after 2 h. Data for hypothesis 2 were the change in mean vertical position 2 h after changing the light regime (mean position after 2 h – mean position after 4 h). These variables provided independent data and equal sample sizes across all treatments (refer to Tables 1–4 for relevant *df* for tests of different factors). The hypotheses were tested using ANOVA (GMAV, Underwood and Chapman, 2001). For hypothesis 1, data were arcsin transformed as values were constrained between 0 and 100. We examined heterogeneity of variance using plots of the data and Cochran’s test. After the initial ANOVA, terms were pooled if they were not significant at  $\alpha=0.25$  and pooling provided a more powerful test of higher terms (Quinn and Keough, 2002).

3. Results

In the first experiment using only offshore water, megalopae tended to be higher in the water towers when the lights were on (Fig. 1). The factors Light Regime

Table 4  
ANOVA results for Experiment 2, testing the effects of treatments on the vertical displacement of megalopae, 2 h after the lighting was changed from Off→On or On→Off

| Source of variation | <i>df</i> | MS     | <i>p</i> | <i>F</i> versus |
|---------------------|-----------|--------|----------|-----------------|
| Lighting (L)        | 1         | 10.343 | >0.095   | L×Da            |
| Water type (WT)     | 1         | 0.034  | >0.250   | Pooled          |
| Time of day (Ti)    | 1         | 0.527  | >0.180   | Ti×Da           |
| Date (Da)           | 1         | 0.028  | >0.300   | Pooled          |
| L×WT                | 1         | 0.000  | >0.905   | L×WT×Da         |
| L×Ti                | 1         | 0.009  | >0.850   | L×Ti×Da         |
| L×Da                | 1         | 0.254  | <0.05*   | Pooled          |
| WT×Ti               | 1         | 0.003  | >0.825   | WT×Ti×Da        |
| ◆WT×Da              | 1         | 0.003  | –        | –               |
| Ti×Da               | 1         | 0.047  | >0.180   | Pooled          |
| L×WT×Ti             | 1         | 0.001  | >0.895   | L×WT×Ti×Da      |
| L×WT×Da             | 1         | 0.020  | >0.375   | Pooled          |
| L×Ti×Da             | 1         | 0.169  | <0.05*   | Pooled          |
| WT×Ti×Da            | 1         | 0.004  | >0.705   | Pooled          |
| L×WT×Ti×Da          | 1         | 0.026  | >0.310   | Pooled          |
| Pooled terms        | 33        |        |          |                 |

Cochran test=*ns*. Terms were pooled where *p*>0.25 and pooling resulted in a more powerful test.

and Time of Day had a significant effect ( $p < 0.05$ ,  $df = 1, 18$  and  $p < 0.05$ ,  $df = 1, 18$  respectively: Table 1). There were no significant interactions. This supported the hypothesis that megalopae tend to be higher in the water column when illuminated, however, they tend to be higher during the night than the day.

Changing the factor Lighting, from dark to light, caused the megalopae to ascend while changing from light to dark elicited the reverse behaviour ( $p < 0.05$ ,  $df = 1, 1$ : Table 2). There was no significant effect of Time of Day and no interactions.

In the second experiment, megalopae tended to be higher in the illuminated water columns for both estuarine and offshore water (Fig. 2). The ANOVA to test hypothesis 1 showed a significant three-way interaction between Lighting Regime, Time of Day, and Date ( $p < 0.05$ ,  $df = 1, 35$ : Table 3). A series of pairwise SNK tests found a complex pattern of interaction among levels of the three terms, without a clearly discernible trend. These differences were, in any case, considerably smaller than changing the lighting regime (Fig. 2). Lighting Regime and Date, were also significant ( $p < 0.05$ ,  $df = 1, 35$  and  $p < 0.05$ ,  $df = 1, 35$  respectively: Table 3), but Time of Day was not. There was no main effect of Water Type (estuarine, offshore), nor did this factor interact with any other (Table 3). The hypothesis that megalopae tend to be higher in a water column of offshore water when illuminated than when not and that this pattern would be reversed in estuarine water was rejected.

The data for hypothesis 2 showed that where the factor Lighting was changed from dark to light, megalopae tended to ascend the water column. When changed from light to dark megalopae tended to descend (Fig. 3). There were significant three-way and two-way interactions (Table 4, Fig. 3), however the factor Water Type was not significant and did not interact with any

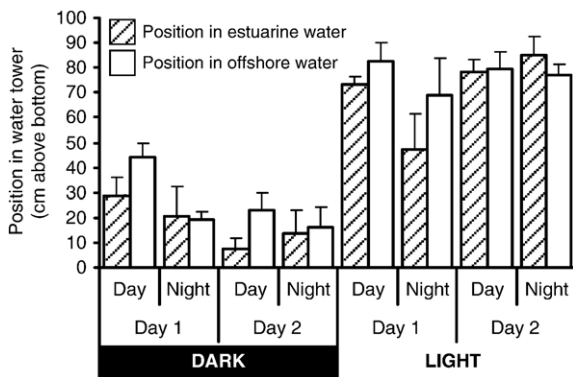


Fig. 2. Mean (SE) vertical position of megalopae in towers after 2 h of darkness or illumination, on two different days during both the daytime and night-time (Experiment 2).

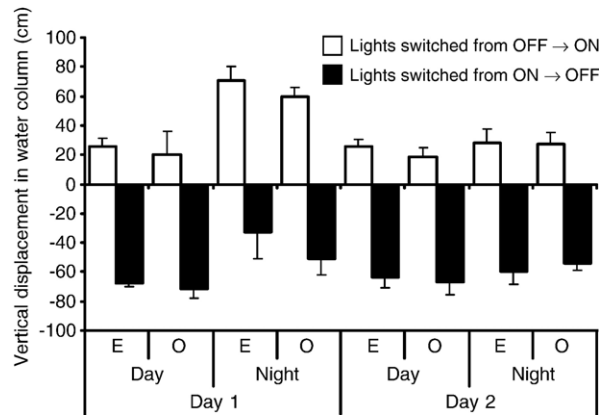


Fig. 3. Mean (SE) vertical displacement after changing the lighting (ON → OFF, OFF → ON) on two days, during daytime and night-time, for towers filled with estuarine (E) or offshore (O) water (Experiment 2).

other factor (Table 4). Therefore the hypothesis that megalopae in a column of offshore water tend to ascend after the lighting changes from dark to light but the reverse occurs in estuarine water was rejected. Time of Day was not significant but interacted with Lighting and Date (Table 4).

#### 4. Discussion

In offshore and estuarine water, during the daytime and night-time, mud crab megalopae tended to swim higher in the water towers when illuminated. For offshore water, this was consistent with the hypothesis, however the ascent in illuminated estuarine water was not predicted. Contrary to the results obtained here, swimming was suppressed in estuarine water for fiddler crab (*Uca* spp.) and blue crab (*C. sapidus*) megalopae (Forward and Rittschof, 1994).

It is possible that the mud crab megalopae had the capacity to, but did not distinguish between the two water types. This is unlikely as the estuarine water was collected over seagrass beds and no doubt contained many chemical cues associated with an estuary. Salinity of the estuarine water was only slightly lower than offshore water. This was expected as salinities at the mouth of Pumicestone Passage are usually within this range (EPA Qld, personal communication). Mud crab megalopae are rarely caught in estuaries and if this is because they are rarely there, rather than the result of ineffective sampling, mud crab megalopae in offshore or coastal waters would rarely encounter estuarine salinity gradients, ruling out salinity as a natural stimulus (Rothlisberg et al., 1995). The offshore water may have contained small traces of estuarine derived chemicals, however the behaviour exhibited by the megalopae in

our experiment is consistent with the behaviour of other portunid megalopae in offshore waters. This behaviour would be beneficial in maintaining them close to the coast during their pelagic larval phase. Surface currents generated by on-shore winds assist the ingress of blue crab megalopae to estuaries. In offshore waters, migrating to the surface during the day enhances the utilisation of these currents, thus increasing the probability of remaining near or penetrating estuaries (Goodrich et al., 1989; Morgan et al., 1996). Exhibiting this behaviour inside estuaries would expose megalopae to a suite of estuarine visual predators (Forward and Rittschof, 1994). For these reasons, we consider that the megalopae behaved as expected in offshore waters and the combined differences between the water types were sufficient to elicit any natural behavioural response due to water type if one was forthcoming.

Blue crab megalopae are found in significant numbers in estuaries and complex models have been developed to explain their upstream migration (Forward et al., 2003). Mud crab megalopae, however, have proved difficult to find in estuarine surveys (Macintosh et al., 1999; Moser and Macintosh, 2001). Given the extensive efforts to collect mud crab megalopae from estuaries, the most parsimonious alternative model explaining their apparent absence is that mud crab megalopae tend not to occur within estuaries. This model explains why estuarine water did not suppress their swimming activity. In the wild, mud crab megalopae may rarely occur in estuaries and therefore have not evolved an alternative swimming behaviour more suited to the estuarine environment as the blue crab has. If the megalopae tend not to enter estuaries they must settle out of the plankton along the coast before metamorphosing into small crabs. This settlement process may be controlled ontogenetically or stimulated by coastal cues. Migration to estuarine habitats would occur shortly after settlement, since juveniles found in estuaries and mangroves are typically >30 mm CW (Hill et al., 1982). This new model requires mud crabs to settle out of the plankton on the coastal shelf and invade estuaries, not as planktonic larvae, but as small, benthic juvenile crabs. This coastal settlement model is analogous with the mechanism of estuarine invasion of the prawn *Penaeus plebejus* (Rothlisberg et al., 1995). In their model, the postlarval prawns become epibenthic on the coastal shelf before invading estuaries during flooding tides. Water pressure changes, generated by increasing depth on flooding tides, stimulates the epibenthic prawn postlarvae to selectively ride tidal currents and opportunistically invade estuaries whilst being swept along the coast by alongshore drift.

Megalopae in Experiment 1 swam significantly higher in water towers during the night than the day and this behaviour was almost significant in Experiment 2 ( $p=0.055$ ). However, this effect was small compared to the effect of light. Blue crab megalopae have been shown to have an endogenous circadian rhythm (Tankersley and Forward, 1994) and this may also be the case for mud crab megalopae, although it was not tested here. The experiment could have been improved by using a gradient of light intensities. The intensities used here were greater than at dawn and dusk, spanning the time at which we considered changes to the swimming behaviour of megalopae most likely to occur.

We used hatchery-reared megalopae because collecting them from the wild is rarely successful. Whether the behaviour exhibited by hatchery-reared mud crab megalopae can be generalised to wild populations is not known. Behaviours exhibited by hatchery-reared animals are not always consistent with their wild conspecifics. For example, hatchery-reared blue crabs are preyed upon at higher rates than wild crabs (Davis et al., 2004). The behaviour of larvae can also vary spatially (Manuel et al., 1996), therefore all of these factors should be considered when generalising to wild populations.

Whilst laboratory experiments can be useful, by their nature they remove many potentially interactive factors (Carpenter, 1996) and perhaps the most obvious issue in the current experiment is that the water depth was limited by the height of the tower. These mud crab megalopae could swim from the bottom to the top in a single burst. They then tended to swim at the surface for a short period before sinking 30–60 cm after which they resumed swimming back to the top. The stimuli for this swimming/sinking pattern are unknown, however, blue crab megalopae respond to changes in pressure (Tankersley et al., 1995). The resumption of swimming may be a response to exceeding a pressure threshold whilst sinking. If this is the case, then it is important to ensure that the water column is deep enough to trigger this response. In shorter towers, megalopae may be inactive and benthic, not because they are exhibiting their natural behaviour, but because they have not crossed the pressure/depth threshold and consider themselves to be in surface waters. The fact that the sinking megalopae observed here tended to resume swimming before reaching the bottom of the tower indicates that the towers were tall enough.

The blue crab recruitment model is unlikely to be wholly applicable to mud crabs as the swimming behaviour of the mud crab megalopae does not change in estuarine water and they have rarely been found in estuaries. The combination of (1) the apparent absence of mud crab megalopae from estuaries, (2) the

consistency in vertical swimming behaviour in offshore and estuarine water and (3) that mud crabs smaller than 30 mm CW are rarely found in estuaries prompts us to propose an alternative model to explain how mud crabs invade estuaries. We postulate that mud crab megalopae tend to settle from the plankton on the coastal shelf and invade estuaries by moving along the sea bed as early-stage crabs, before migrating further upstream and inhabiting the intertidal shallow estuarine habitats.

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