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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.

Keywords: Estuary; Phototaxis; Recruitment; Selective tidal-streaming; Vertical migration

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