NOCTURNAL MOVEMENT AND POSSIBLE GEOTAXIS IN THE FLUTED GIANT CLAM (TRIDACNA SQUAMOSA)

Pamela Soo
Tropical Marine Science Institute, National University of Singapore, 18 Kent Ridge Road, Singapore 119227, and Experimental Marine Ecology Laboratory, Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Blk S2 #02-02, Singapore 117543.

Peter A. Todd
Tropical Marine Science Institute, National University of Singapore, 18 Kent Ridge Road, Singapore 119227, and Experimental Marine Ecology Laboratory, Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Blk S2 #02-02, Singapore 117543.

ABSTRACT. — Giant clams (Bivalvia: Tridacnidae) inhabit the shallow waters of tropical Indo-Pacific coral reefs. Despite their economic and biological significance, surprisingly little is known about their behaviour. To add to knowledge regarding locomotion and geotaxis in juvenile fluted giant clams, Tridacna squamosa L., we examined day-night locomotive activity as well as their movement up or down a slope.

In the day-night experiments (single clams, and clams in a group) locomotion away from initial positions was limited to the period between 20:30 h and 05:00 h. When tested on three slope treatments (0°, 30° and 60°) the clams moved preferentially down the length of the steeper (60°) slope, while those on the 30° slope did not exhibit any clear directional response to gravity (Chi square test: $p = 0.0255$, d.f. = 4). Locomotive behaviour, both horizontally and vertically, probably facilitates the search of ecological environments (e.g., stable substrata, optimal light levels), that will increase the clams’ survival.

KEY WORDS. — Behaviour, geotaxis, giant clam, locomotion, Singapore, Tridacna squamosa

INTRODUCTION

Giant clams (Bivalvia: Tridacnidae) inhabit the shallow waters of tropical Indo-Pacific coral reefs (e.g., Rosewater, 1965; Othman, et al. 2010.). Despite their economic and biological significance, surprisingly little is known about their behaviour—although some recent studies have shed light on their defenses (e.g. Ling et al., 2008; Todd, et al., 2009; Neo & Todd 2011a, b) and larval biology (e.g., Neo et al., 2009, 2011). Reports of locomotion, however, are limited to anecdotal observations (e.g. Yonge, 1936), descriptions of early juveniles (Reid et al., 1992; Suzuki, 1998) and a single detailed study of aggregation (Huang et al., 2007).

In general, giant clam larvae are actively planktonic for approximately one week before settling down on the benthos to metamorphosize into juveniles, which become less mobile over time. This general decline in locomotory activity with age reflects both anatomical constraints (Heslinga, 1989), as well as ecological needs, where more energy is channelled into growth and reproduction. Retention of the ciliated foot allows for crawling, and rapid contraction of the valves can generates a force that supplements horizontal movement (Stasek, 1962; Ansell, 1969; Huang et al., 2007). Small individuals of Tridacna crocea and T. squamosa are also known to climb vertical surfaces with the aid of byssal threads (Yonge, 1936; Huang et al., 2007). Reid & King (1988) highlighted that observations of locomotion in byssate juveniles are numerous, but casual. Vertical locomotion may continue until the organism reaches the water-air surface (Reid et al., 1992), however, no studies have examined geotaxis experimentally.

There has been only one attempt to quantify giant clam locomotive activity under light-dark conditions. In a small experiment on juvenile boring clams, T. crocea, Suzuki (1998) set up two regimes from 18:00 to 06:00 h (2 h light–8 h dark–2 h light), and constant illumination. The $T. crocea$ were more active at night in terms of mean locomotion (mm/h), especially from 22:00 to 02:00 h in the first regime. Given that shell length increases disproportionately in relation to foot length, it is not surprising that Suzuki (1998) found locomotive ability was gradually lost with time. Juveniles smaller than 20 mm manoeuvred the foot in a vertical
position for locomotion, while larger individuals relied on sudden valve closure for movement as the foot could not extend sufficiently.

Here we present three small experiments designed to add to knowledge regarding locomotion and geotaxis in juvenile fluted giant clams, *T. squamosa*. In the first, we investigated day-night locomotive activity in single specimens. In the second, we examined day-night locomotive activity of clams in a group. Finally, we tested for geotaxis (movement up or down a slope) in single specimens. As the experiments were preliminary, the methods and results are presented together.

MATERIAL, METHODS AND RESULTS

All experiments were conducted in the marine aquaculture facility at the Tropical Marine Science Institute (TMSI) on St John’s Island, Singapore, between September 2008 and March 2009.

**Day-night locomotive activity (individuals).** — Eight juveniles (size range 16.5 to 46.4 mm) were placed in the centre of eight separate 30 L tanks and, starting at 17:00 h, filmed for 24 h using a Philips SPC900NC web camera (infra-red filter removed). An infra-red illuminator was used at night and natural light conditions used during the day. Locomotion only occurred at night. Half (four) of the clams exhibited translation (the lateral movement of the clam away from its original position) and this was facilitated by pedal locomotion and valve closure, similar to the behaviour described in the aggregation experiments carried out by Huang et al. (2007). There was no clear relationship between locomotion and clam size other than the largest individual travelled the furthest (the 17 mm clam moved 168 mm, the 22 mm clam moved 102 mm, the 43.5 mm clam moved 174 mm and the 43.9 mm clam moved 342 mm). The direction of movement for all the clams appeared to be random. Vertical climbing was also observed, but only for the 17 mm clam which travelled across the bottom and, upon reaching the tank wall, crawled upwards at least 70 mm and remained there during the daytime. The remaining four clams exhibited either only rotation (a change of orientation about the approximate centre of the clam without it shifting from its initial position) or did not move. All of these latter four clams were found byssally attached to the tank bottom by the end of the experiment.

**Day-night locomotive activity (group).** — Only the initial and final positions were noted at the end of the 3 d aggregation experiment by Huang et al. (2007). To gain a better understanding of the locomotive behaviour involved, we tracked juveniles over a period of 24 h using time-lapse photography (HandyAvi 4.3). A total of 63 *T. squamosa* juveniles (size range 20 to 60 mm) were placed in a 9 × 7 grid spaced ~40 mm away from each other, and 5971 images were taken at a rate of four frames per minute. Comparing the clam positions before (Fig. 1a) and 24 h later (Fig. 1b) clumping was apparent. Locomotion away from the initial position was observed in 81% of the clams, and this was limited to the period between 20:30 h and 05:00 h. Among the clams that translocated, the mean distance travelled was estimated to be 280 ± S.E. 34.9 mm (based on a haphazardly selected sub-sample of 20 individuals).

**Geotaxis.** — Single *T. squamosa* juveniles were allowed to form byssal attachment at the mid-line (with the anterior-posterior axis aligned perpendicular to the slope) of individual rectangular custom-made cement tiles (L 25.0 cm × W 15.5 cm × H 0.5 cm) over 48 h. Their locomotive response to gravity was tested with three slope treatments set up in individual 30 L tanks: 0, 30 and 60° (n=16). No clam was used more than once. Clam movement was recorded after 24 h as follows: up the tile, remain at the mid-line, or down of the tile. In the control, the direction of the clam movement was tagged according to the slope direction in its two neighbouring test tanks. A clam was considered to have moved in a particular direction if it exhibited translational movement ≥5 mm. Results were analyzed using a Chi Square test on a 3 × 3 contingency table (three possible responses × three treatments). We found a significant difference in geotactic response between the treatments (Chi square test: *p*=0.0255, d.f.=4). Significantly more (10 out of the 16)
clams moved down the length of the steeper (60°) slope, while those on the 30° slope did not exhibit any clear directional response to gravity.

**DISCUSSION**

The first two experiments suggest strongly that *T. squamosa* juveniles exhibit locomotion only at night—possibly an adaptation to reduce the risk of visual predation (Suzuki, 1998). Similar to Suzuki (1998), the clams moved to their final positions before dawn and remained there during the day. More locomotion was observed when the clams were grouped with con-specifics (81% compared to 50% when the clams were single); this is not unexpected as Huang et al. (2007) demonstrated positive chemotaxis in giant clam juveniles. Huang et al. (2007) suggested chemical signalling was a proximate mechanism for non-random aggregation, the benefits of which may include lower individual risk of predation (e.g. Reimer & Tedengren, 1997; Krause & Ruxton, 2002), higher reproductive success during mass spawning (Adams et al., 1988; Downing et al., 1993) and physical stabilization against abiotic stresses (Seed, 1969; Bertness & Grosholz, 1985). The amount of movement was considerable, with the mean distance travelled during 5.5 night time hours a surprising 28 cm. As Huang et al. (2007) only looked at initial and final positions they had no way of calculating this metric. Much of this locomotion was due to rapid valve closure propelling the clams across the substrate. It should be noted, however, that mobility in giant clams would eventually be constrained by shell size (rather than age per se); likely due the reduction in the foot size to shell weight ratio as the clam grows bigger (Yonge, 1936; Uryu et al., 1996).

Previous observations of vertical climbing did not satisfactorily demonstrate geotaxis as clams were generally spatially constrained in aquaria and therefore may simply have been exploring their environment or trying to escape. The results of our geotaxis experiment indicate significant downward movement, lending support to Vaillant’s (1865) brief observation that *T. maxima* individuals do not remain permanently attached to the substrate but travel to deeper, calmer waters which experience less wave action. Clams on the 30° slope, however, did not exhibit any significant directional response to gravity. As highlighted by Huang et al. (2007), the energetic costs in breaking the byssus to move could possibly explain the tendency to remain in the original position or display rotation. Unfortunately, if the clams are not allowed to attach basally first, they roll off the slope (pers. obs.). Hence, designing a robust experiment for geotaxis in giant clams remains a challenge.

As with other broadcast spawning species, giant clam larvae have limited control over where they settle on a coral reef. Hence, locomotive behaviour, both horizontally and vertically, should enable juvenile clams to search for ecological environments that will increase their survival (Tan, 1975), such as those that provide stable substrates for attachment, shelter from wave action, or optimal light conditions for photosynthesis. High levels of sedimentation due to human activities continues to be a major issue for Singapore’s reefs (Todd et al., 2010) and interferes both with giant clam larval settlement and subsequent byssal attachment (Guest et al. 2008; Neo & Todd, 2012a). The ability to move away from sediment-covered substrates is a clear example of how locomotion can increase fitness in giant clams. Future studies, however, could investigate the navigational cues for longer-term crawling patterns and nocturnal behaviour in general, two important categories for which there are scant data. Knowledge of these will help direct appropriate site selection for restocking projects (Tan & Yasin, 1999), such as those presently underway in Singapore (Neo & Todd, 2012a). Clam restoration programmes may also benefit from transplanting clams as clusters to replicate the ecological advantages of aggregation (Huang et al., 2007). More work on geotaxis is needed, but if giant clams do move vertically in their natural environment this also has implications for restocking efforts. It would clearly be desirable to position transplanted clams at a depth that they will not immediately try and move away from. Presently, giant clam populations in Singapore are spatially dispersed and sparse (Guest et al., 2008; Neo & Todd, 2012b), therefore setting up nurseries with the aim of aggregating introduced giant clams at an optimal depth may be a cost-effective method to encourage local recruitment and enhance survival.

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**LITERATURE CITED**


Nocturnal movement in juvenile giant clam


