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AUTOTOMY, ARM REGENERATION AND CANNIBALISM IN THE SEASTAR *ASTROPECTEN INDICUS*

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ABSTRACT. — Autotomy in seastars is relatively well documented (for certain genera at least), but studies of cannibalism in asteroids are rare. This paper investigates autotomy and cannibalism in *Astropecten indicus* (Döderlein), a common seastar in Singapore. Field surveys showed a low incidence (7.6%) of arm damage under natural conditions. Out of six techniques tested to induce autotomy in *A. indicus*, only "pegging" (being dangled by a clothes peg) was effective. No significant difference in arm regeneration after induced autotomy was recorded between fed and starved individuals. Cannibalism was tested under experimental conditions, i.e. intact pairs, and pairs where one of the conspecifics was injured. Cannibalism occurrence in the laboratory was 10.6%, higher than the natural frequency of arm damage, suggesting that cannibalism is heightened in tank conditions. Injury, however, had no significant effect on the number of cannibalism events observed.

KEY WORDS. — Autotomy, behavior, cannibalism, regeneration, seastar, Singapore

INTRODUCTION

Found in both intertidal and subtidal areas (Sloan, 1980; Menge, 1982), seastars are functionally important components of marine benthic communities due to their ecological roles as predators, scavengers, and prey items (Jangoux, 1982; Menge, 1982; Ganmanee et al., 2003). One of the primary defenses against predation in seastars in their ability to self-amputate (autotomize) an appendage to facilitate escape (Barrios et al., 2008). Other stressors such as heavy wave action or shifting rocks can also induce autotomy (Niesen, 1973; Lawrence & Dehn, 1979; Town, 1979). It is by far the most common proximate cause of structural loss in echinoderms (Wilkie, 2001) and there is no group of animals where autotomy is more widespread (Riggenbach, 1903). The dropping of damaged limbs is considered adaptive if it increases survival, for instance, by reducing infection and/or stopping the leakage of predator-attracting metabolites (Niesen, 1973; Lawrence, 1992). Autotomy, however, can lead to an impairment of locomotion (Ramsay, Kaiser & Richardson, 2001), feeding (Clements, 1985; Barrios et al., 2008), growth (Mathews et al., 1999) and reproduction (Bingham et al., 2000). Allocation of energy to regeneration, which is dependent on food availability, is critical for recovery from the physically compromised state (Díaz-Guisado et al., 2006). When starved, regeneration is slow and seastars allocate most of their resources to their existing arms for growth and reproduction (Lawrence et al. 1986; Ramsay, Kaiser & Richardson, 2001). When fed, allocation of energy is directed towards both their existing and regenerating arms (Lawrence and Ellwood, 1991).

Cannibalism (intraspecific predation) is another phenomenon commonly observed in seastars, being found in all three major orders: Order Platyasterida, Order Spinulosida and Order Forcipulatida (Schaerer, 1981; Sloan, 1979). Cannibalistic behaviour can be an artifact of laboratory systems (Colinvaux, 1973), but it is also a normal and natural occurrence (Fox, 1975a; Polis, 1981; Elgar & Crespi, 1992). There are several factors that promote cannibalism, including reduction of food resources (Fischer, 1960; Smyly, 1952), increase in conspecific density (Fischer, 1960; Twine, 1971; Fox, 1975a), heightened physiological and psychological stress (Clark, 1967) and an increase in the probability of encountering a vulnerable conspecific (Fox, 1975a). Cannibalism can be adaptive and result in greater reproductive success by conferring direct nutritional advantages (Cooper, 1936; Ho & Dawson, 1966). Population-level effects include controlling age structure (Mertz, 1969; Young, 1970) and regulating numbers below the carrying capacity of the environment (Polis, 1980, 1981).

Members of the seastar genus *Astropecten* are generalists, feeding on a wide variety of prey such as crustaceans, polychaetes, sipunculids, pennatulids, ascidians, fish, and sediments (Sloan, 1980; Jangoux, 1982; Wells and Lalli, 2003). They are most abundant in subtropical and tropical regions, especially in the Indo-Pacific (Christensen, 1970). Autotomy in *Astropecten* has only been recorded for *A. articulatus* (Hopkins et al., 1990, 1994) although (unpublished) studies have been conducted on *A. americanus* and *A. duplicatus* (Lawrence, 1992). Even though seastars of the genus *Astropecten* have been observed to ingest other echinoderms (Wells et al., 1961), cannibalism has only been recorded for *A. aranciacus* and *A. irregularis*, and only anecdotally (Kisch, 1958; Schmid & Schaerer, 1981). None of these *Astropecten* species, however, are found in Southeast Asia. The sand star *Astropecten indicus* (Döderlein, 1888) is possibly the most common seastar in Singapore waters, but very little is known of its autecology (Loh & Todd, 2011) and no published studies exist on autotomy, arm regeneration and cannibalism in this species. There is a need for more rigorous experimental data to understand these phenomena in *Astropecten*. To help fill this knowledge gap, we conducted surveys to determine the natural occurrence of arm damage in *A. indicus*. In addition, the following hypotheses were tested: *A. indicus* can autotomise and rate of regeneration is dependent on food availability; *A. indicus* are cannibalistic and an injured or damaged seastar will induce cannibalism more than an intact seastar.

MATERIAL AND METHODS

Collection site and seastar maintenance. — *Astropecten indicus* individuals were collected by hand between July 2008 and February 2009 from the intertidal flat at Pasir Ris (103°56'21.03"E, 1°23'21.91"N), located along the East Johor Strait of Singapore where *A. indicus* was abundant. Experiments were conducted at the marine aquaculture facility in the Tropical Marine Science Institute (TMSI) (103°50'59.76"E, 1°13'03.37"N) on St John's Island, Singapore. Seastars were maintained in rectangular clear plastic tanks (45 × 26 × 30 cm; length × width × height) with aerated and filtered seawater in a flow-through system (flow rate 256.9 ± S.E. 16.1 ml min^{-1}). Stocking density was twelve seastars per tank. The mean ambient water temperature was 29.4 ± S.E. 0.3°C (TidbiT temperature loggers) and the salinity range was 29 to 32 ppt (handheld refractometer, Aquafauna Bio-Marine). Each tank contained a 3 cm layer of fine beach sand as substrate for the seastars to burrow in.

Natural occurrence of arm damage. — To ensure the sandy intertidal flat was exposed, the field study at Pasir Ris was conducted during tide levels lower than 0.5 m above chart datum. The natural occurrence of arm damage (arm loss and partial arm loss) in *A. indicus* was examined by sampling individuals from eleven 2 × 30 m belt transects (3 m apart) that were aligned perpendicular to the shoreline. Every seastar was counted and their maximum radius measured (distance from center of oral disk to tip of longest arm, R) (Wells and Lalli, 2003). Seastars were considered damaged if the length of an arm was ≥20% shorter than the maximum radius of that individual. The survey was completed within one day to avoid any re-sampling of specimens.

Regeneration experiment. — To induce autotomy for the regeneration experiment, seastars were subjected to various manipulations used previously by others (Hotchkiss et al., 1991; Bingham et al., 2000; Díaz-Guisado et al., 2006; Barrios et al., 2008). These were: snipping (5 mm from tip of arm with sterilised scissors), pegging (dangled by clothes peg), crushing (with pliers), pulling (straight off), wiggling (by hand) and electrocution (12 v battery). Three specimens were used for each manipulation. As pegging was the only method that autotomized the arm of the seastar (beyond the exact location of snipping, crushing, wiggling or electrocution), it was used for all subsequent autotomy induction (Fig. 1.). Pegging was meant to simulate a seastar being trapped by a crab's chela (Bingham et al., 2000) or fallen rock.

Regeneration was investigated using forty seastars (mean R= 27.6 ± 2.3 mm), where each seastar was held in a separate 2.2 L tank (21 × 13 × 12 cm; length × width × height) with flow-through sand-filtered seawater. The seastars were divided into four groups (n=10): two control and two treatment groups (control starved, control fed, autotomised starved, and autotomised fed) in a Latin square arrangement. Seastars were first conditioned by starving for a week (following Ramsay, Kaiser & Richardson, 2001). During the experiment, fed seastars were given 0.4 g of minced squid twice a week whereas starved seastars were only fed once a week. Individuals were buoyant weighed (under water) to ± 0.01g (Yamaguchi, 1974) with a portable electronic balance (Ohaus SPS602) and their radius (only the arm opposite of the seastar's madreporite was measured) re-calculated after one month. Mean survivorship (in days) was also tested. Single-

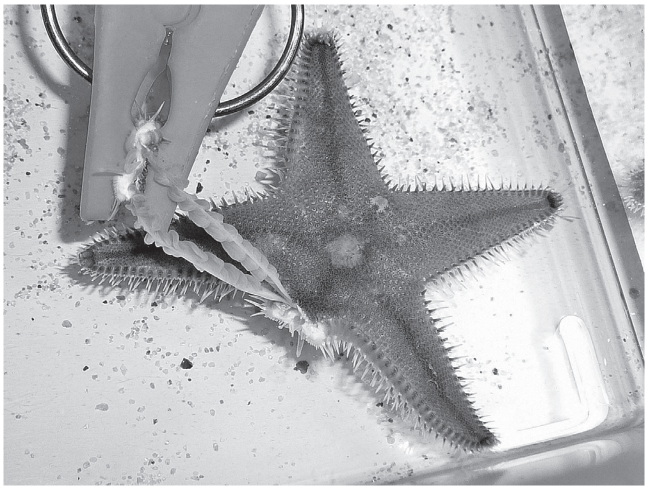

Fig. 1. *Astropecten indicus* autotomising its arm after being dangled by a clothes peg.

factor analysis of variance (ANOVA) was used to check for significant changes in buoyant weight and mean survivorship among the four groups whereas, due to failure to meet the ANOVA assumptions, a Kruskal Wallis test was used to test for changes in mean R. All statistical analyses were performed with SPSS version 17.0 (SPSS Inc, Chicago, Ill).

Cannibalism experiment. — While in their holding tanks, *A. indicus* would occasionally eat conspecifics (Fig. 2). To investigate this cannibalistic behaviour, their interactions were monitored on video. As a closely related species, *Astropecten aranciacus*, is nocturnal (Burla et al., 1972) and is known to be affected by lighting (Ferlin-Lubini and Ribi, 1978), and our own observations suggested *A. indicus* is also more active from dusk to dawn, the experiments were conducted overnight (16 h) and filmed using a modified USB web camera (Philips SPC 900NC PC Camera) with an infrared illuminator (10 m range). The camera lenses were modified to capture infrared light and the cameras mounted under the transparent tank facing the seastars' oral surface. Eight 2.2 L replicate tanks (two rows of four tanks) were set up with two size-matched (± 3 mm) seastars in each. Experiments were run over six days. There were two groups (n = 23): starved but intact, and starved but injured (the tips of all arms were excised from one of each pair of seastars). Fed states were excluded because trial runs (n = 8) with fed seastars did not reveal any cannibalism. All seastars were first starved for a week. Cannibalism events were searched for among the 736 h of video recordings using VLC Media Player Software.

RESULTS

Natural occurrence of arm damage. — A total number of 568 seastars (mean radius = 23.0, S.E. 4.8 mm) were surveyed within the 11 belt transects and of these 43 (7.6%) exhibited some degree of arm loss. Out of all the damaged seastars, 86.0% had one injured arm, 9.3% had two injured arms, where as those with damage to three or four arms accounted for 2.3% each. No seastars had five damaged arms.

Regeneration experiment. — No significant differences were found among the four groups for mean change in arm length between the first and second month (Kruskal Wallis, $P > 0.05$, $d.f. = 3$). Nevertheless, regeneration of arms was recorded in seven out of ten seastars for each of the two groups where the arms had been autotomised (although new growth was generally < 2 mm). There was also no significant difference in the mean change in buoyant weight or mean survivorship among the four groups (ANOVA, $P > 0.05$, $d.f. = 3$).

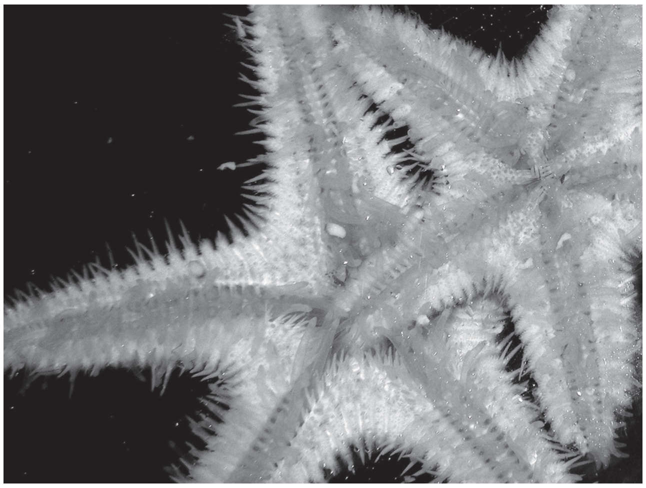

Fig. 2. Evidence of cannibalism in *Astropecten indicus.*

Cannibalism experiment. — Cannibalism was recorded for five out of forty six (i.e. 10.6%) *A. indicus* pairs; two cannibalism events for the starved and intact group and three events for the starved and injured group. In all instances, the arm tip of one seastar entered the mouth of the other. The duration of the cannibalistic interactions ranged from 120 to 1545 s (mean = 622, S.E. = 247). None of the cannibalism events resulted in the death of the damaged individual.

DISCUSSION

Autotomy in asteroids is adaptive because it can prevent mortality if the seastar is attacked or trapped (Bingham et al., 2000): it is sub-lethal, a "disturbance" resulting in the loss of biomass (Lawrence, 1991). But, as autotomy may disrupt the functionality of an asteroid (Pomory & Lares, 2000; Barrios et al., 2008), regeneration is crucial (Díaz-Guisado et al., 2006; Barrios et al., 2008). The natural occurrence of arm loss in asteroids ranges from 0% to 86% (Lawrence, 1992) and is a response to both anthropogenic and natural causes (Lawrence, 1992; Lawrence and Vásquez, 1996; Pomory & Lares, 2000; Ramsay et al., 2001). The *A. indicus* population at Pasir Ris appears to experience relatively low arm damage (7.6%), when compared to the 16.7% observed in an *A. articulatus* population in Japan (Hopkins et al., 1990). Arm loss has been associated with fishing (Kaiser, 1996; Ramsay et al., 2001) and such activities at Pasir Ris may account, to a certain extent, for the arm damage in *A. indicus*. Strong wave action (Niesen, 1973; Bingham et al., 2000) and rolling boulders (Town, 1979) can crush or trap arms and also lead to autotomy (Lawrence, 1992). The average tidal velocity along East Johor Strait is low (≤50 cm s^{-1}) (Chou & Lee, 1997) and there were no rocky habitats at the sampling sites. Hence, these abiotic factors may play only a small role in *A. indicus* arm loss of at the sites studied.

The relatively low occurrence of arm loss in *A. indicus* could be due to a lack of predation pressure. Even though one was observed to be attacked by a flower crab (*Portunus pelagicus*) during a field survey (pers. obs.), the spines along the arms of *A. indicus* may be a deterrance to predators. This species could also contain chemicals that make it distasteful, as documented in *A. articulatus* (Bryan et al., 1992). Our autotomy manipulations suggest *A. indicus* has a high threshold level (the point that needs to be exceeded before the stimulus neurones that leads to autotomy are fired)(Fleming et al., 2007) and this resistance towards autotomy may also account for the low occurrence of arm loss in natural conditions. Interestingly, the diffuse autotomy region of most asteroids is near the base of their arms (Emson & Wilkie, 1980; Hotchkiss et al., 1991). However, the induced autotomy in *A. indicus* occurred anywhere along the arm's length (but rarely was the entire appendage lost).

We hypothesized that arm regeneration would be dependent on food availability but no significant differences in arm length change or buoyant weight change were observed among the four groups (control starved, control fed, autotomised starved, and autotomised). This was possibly due to the relatively short duration of the study, or perhaps because only one arm was autotomised (in others studies, e.g. Ramsay, Kaiser & Richardson, 2001, multiple arms were removed). Further, individuals in the starved treatments were still fed once a week, which may be enough for them to regenerate arms. Seastars in the experiment began showing signs of deterioration such as loss of plates from their body surface and the disintegration of arm tips after approximately one month. Similar symptoms were also observed in *A. irregularis*, although only after they were starved for more than a year (Christensen, 1970). Mortality among controls and treatments were not significantly different, suggesting the loss of one arm did not greatly add to their general deterioration. Results from transects showed that the majority (86.0%) of injured *A. indicus* had only one damaged arm. By not experiencing multiple arm loss, regeneration should be less energetically costly and possibly not affect the seastar's overall fitness (Lawrence, 1992; Ramsay, Kaiser & Richardson, 2001).

We first observed cannibalism in *A. indicus* while they were being maintained in their holding tanks. Injured individuals appeared to be preyed upon more often (pers. obs.) — potentailly because chemical signals can carry information about the seastars' condition (Kidawa, 2001). The overnight experiment, however, did not demonstrate that cannibalism increased significantly with injury in conspecifics; possibly an artifact of sample size or insufficient monitoring time. No obvious behaviour pattern or sequence was observed to be associated with the cannibalism events, other than they always entailed the arm tip of one seastar entering the mouth of the other. The only injury sustained by the preyed-upon individuals was the loss of a single arm tip and this did not result in any mortality. The duration of the cannibalism events was highly variable (ranging from 2 to 25 min) but, as there are no other experimental studies on cannibalism in Asteroidea, it is not possible to compare these results across species.

The cannibalism occurrence observed during the overnight experiment was higher (10.6%) than the natural occurrence of arm damage (7.6%), suggesting that cannibalism is heightened in tank conditions. Cannibalism of vulnerable conspecifics (such as those that are damaged) is known to both help the attacker gain energy and to eliminate weaker individuals (Bragg, 1964; Polis, 1980). Such a homeostatic regulation helps maintain populations below the carrying capacity of the environment (Andrewartha, 1971; Polis, 1980) and, therefore, cannibalism remains potentially important for *A. indicus* as it can increase the probability of a population's persistence and stability (Fox, 1975a; Polis, 1980).

Cannibalism is one of the factors contributing to asteroid arm loss and it becomes more common when prey availability is low (Sloan, 1980). For instance, a decline in mussel population can lead to different responses in seastars, including feeding on alternative prey types (Town, 1980), migration to other sites (Himmelman et al., 2005) and also cannibalism of conspecifics (Harris et al., 1998). No conspecific body part was recovered during Loh and Todd's (2011) diet analysis of *A. indicus* in Singapore; this, nonetheless, does not mean that cannibalism in the natural environment does not exist in this species. Most cannibalistic predators are generalist feeders and the rate of cannibalism may be variable across short periods of time (Fox, 1975b), hence, it would probably be necessary to examine gut contents over a year in order to identify cannibalism via diet in *A. indicus* (Lawton, 1970; Eliot, 1973).

Autotomy and cannibalism in *A. indicus* are likely to play crucial roles, not only in relation to the seastar's behaviour and life history, but also in the ecology of the soft sediment communities that they live in. Rates of natural arm damage in *A. indicus* were relatively low and our efforts to induce autotomy suggest this species has a high threshold level. Further investigations on arm loss could test whether natural predators such as fish and crabs can induce autotomy as a defensive mechanism. Furthermore, the effects of multiple arm loss on regeneration, feeding, and mobility in *A. indicus* should be examined. The experimental study of cannibalism in asteroids is new and demonstrates unequivocally that *A. indicus* will prey upon conspecifics. However, video recording for longer periods of time and under different conditions (density for instance) will be needed too identify what stimulates this behaviour. Due to their abundance, *A. indicus* are excellent research subjects (Hopkins et al., 1994) and should be further investigated to help understand the ecology of marine soft sediment habitats in Singapore.

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