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DISTRIBUTION AND REPRODUCTION OF INTERTIDAL SPECIES OF *AQUILONASTRA* AND *CRYPTASTERINA* (ASTERINIDAE) FROM ONE TREE REEF, SOUTHERN GREAT BARRIER REEF

Maria Byrne and Simon J. Walker

ABSTRACT

The Asterinidae in tropical regions includes morphospecies complexes in the genera *Aquilonastra* and *Cryptasterina*. Cryptic species in these genera have been discovered based on differences in life histories and by attention to previously poorly investigated habitats. Two species with benthic development occur in the intertidal rubble habitat at One Tree Island, southern Great Barrier Reef. *Aquilonastra byrneae* (O'Loughlin and Rowe, 2006) has oral gonopores and is likely to lay benthic eggs masses. The presence of mature gonads in May and June indicates that egg masses should be present in winter. This species may be a protandric hermaphrodite. *Cryptasterina* sp. is an intragonadal brooder and may be conspecific with the coastal *Cryptasterina hystera* Dartnall and Byrne, 2003. This species broods its young to the juvenile stage in spring and summer. The juveniles emerge through aboral gonopores. *Cryptasterina* sp. is a simultaneous hermaphrodite. *Aquilonastra byrneae* and *Cryptasterina* sp. are distributed in the high shore rubble habitat at One Tree Reef in distinct bands at 1.5 m and 1.1 m above Lowest Astronomical Tide, respectively.

The Asterinidae has the greatest range of life histories known for the Asteroidea and most of what we know about evolution of development in these sea stars is based on research on temperate species (reviewed in Byrne, 2006). In the tropical Indo-Pacific several asterinid genera comprise morphospecies complexes (Marsh, 1977; Dartnall et al., 2003; O'Loughlin and Rowe, 2005, 2006). With the assistance of molecular data, life history traits, and new morphological characters, "cryptic" species have been recognized from within an otherwise widely distributed, single species (Clark and Downey, 1992; Dartnall et al., 2003; Hart et al., 2003; O'Loughlin and Waters, 2004). Problematic taxa include Aquilonastra cepheus (Müller and Troschel, 1842) and Cryptasterina pentagona (Müller and Troschel, 1842), widely distributed Indo-Pacific species (Rowe and Gates, 1995; Dartnall et al., 2003). Aquilonastra cepheus is often mistaken for Aquilonastra burtoni (Gray, 1840) which itself is a difficult species complex (Rowe and Richmond, 2004). The C. pentagona (formerly Patiriella pseudoexigua) species complex includes undescribed species (Dartnall et al., 2003; Hart et al., 2003). Here we investigate species in the A. cepheus and C. pentagona groups from the Great Barrier Reef.

Tropical asterinids have secretive habits occupying the undersides of boulders or reef infrastructure and can be common in intertidal rubble fields (Clark, 1946). Along the Great Barrier Reef, intertidal rubble habitats are not well studied. One Tree Reef in the Capricorn Bunker Group is unusual in having a rubble cay and a continuous rubble bank reef crest surrounding a lagoon system that ponds at low tide (Fig. 1A, Davies et al., 1976). In contrast, most other islands in the Capricorn Bunker Group and elsewhere on the Great Barrier Reef Marine Park are sand cays that lack the habitats utilized by intertidal asterinids. Recent ecological studies of the rubble habitat at One Tree Island

revealed a diverse invertebrate fauna occupying the undersides of boulders (Walker, unpubl. data). Included in this fauna are a number of asterinid sea stars, several of which appear to be new species or new records for the Great Barrier Reef. Detection of oral gonopores in the *Aquilonastra* from One Tree Island prompted a taxonomic revision. *Aquilonastra cepheus* has aboral gonopores. The One Tree Island species was recently described as *Aquilonastra byrneae* (O'Loughlin and Rowe, 2006). Asterinids with oral gonopores lay benthic egg masses (Byrne, 2006) and so *A. byrneae* is expected to be a benthic developer. We investigated the distribution of *Aquilonastra* and *Cryptasterina* in the intertidal rubble habitat at One Tree Reef and describe aspects of the reproduction of *A. byrneae. Cryptasterina* sp. is an intragonadal brooder and may be conspecific with the coastal Queensland species *Cryptasterina hystera* (Dartnall et al., 2003). The viviparous life history of *C. hystera* has been described in detail (Byrne et al., 2003; Byrne, 2005) and so reproduction in the One Tree Reef *Cryptasterina* sp. is only briefly reported here.

Methods

The distribution of A. byrneae and Cryptasterina sp. was investigated in the rubble habitat at One Tree Reef (27°0'S, 152°06'E) at low tide. The sites included either side of the Gutter, Turtle Bay, Entrance Bank, and Two Tree (Fig. 1A). Aquilonastra byrneae was common at Two Tree and this is where the population survey was undertaken. *Cryptasterina* sp. was also common at this locality. The distribution of these sea stars was determined at two stations separated by 200 m. At each station, two shore heights near the rubble pavement interface were estimated at 1.1 m and 1.5 m above Lowest Astronomical Tide (LAT) from previously surveyed shore heights. The mean sea level used for tide predictions at One Tree Reef is 1.52 m above LAT (Australian Hydrographic Service-Seafarer Tides, 2006). At each height on the shore, five quadrats $(2 \text{ m} \times 2 \text{ m})$ were placed haphazardly, with successive quadrats at least 5 m apart. In each quadrat all the coral rubble > 10 cm in diameter was flipped and examined visually to assess whether sea stars were present. If present, the number and species identity was recorded and digital images were taken of the oral and aboral surface of each individual. The digital images were analyzed using image analysis software (Imagetool UTHSCSA) to determine the arm length (R = radius) of each individual. These data were used to determine the size-frequency distribution, with the number of individuals pooled across the sites, and the frequency expressed as the percentage of total individuals sampled.

For the reproductive study, *A. byrneae* was collected from One Tree Reef in November 2004, March, May, and October 2005, and April, June, and November 2006. In each sample 5–6 specimens were examined. Dissected gonads were placed in Bouin's fixative, dehydrated through graded ethanols to Histoclear, and embedded in paraffin wax. Gonad sections (7 µm thick) were stained with haematoxylin and eosin for light microscopy. The eggs were measured with an ocular micrometer.

Results

HABITAT.—The windward margin of One Tree Reef is dominated by a high rubble bank that extends from the southeast corner along the southern and eastern margins of the reef (Fig. 1A). This dynamic rubble habitat consists of dead plate coral skeletons and coral boulders (Fig. 1B) that have been moved onto the reef crest by wave action, predominantly driven by southeast trade winds (Davies et al., 1976). This intertidal habitat extends from a solid algal turf covered pavement at the high-energy zone

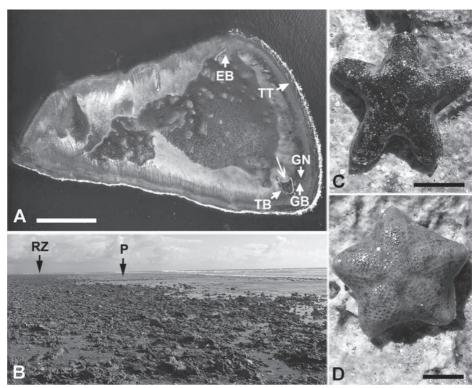


Figure 1. (A) Aerial photograph of One Tree Reef showing location of One Tree Island (arrow) and the sites around the reef, Gutter North and South (GN, GS), Turtle Bay (TB), Two Tree (TT), and the Entrance Bank (EB). (B) Rubble zone (RZ) and pavement (P) habitats. (C) Aquilonastra byrneae (D) Cryptasterina sp. Scales: A = 1 km, C, D = 2 cm.

on the ocean side, to the lagoonal side of the reef rim, where the intertidal rubble is continuous with the shallow subtidal rubble slope.

POPULATION SURVEY.—Four asterinid species were encountered in the rubble habitat including *A. byrneae*, *Cryptasterina* sp., *Disasterina* sp., and *Ailsastra* sp., with the former two species being in sufficient numbers for this study. *Aquilonastra byrneae* has five distinct rays (Fig. 1C). It has bottle green and cream arms with orange and green flecks. The oral surface is cream with occasional olive green patches. Maximum arm radius (R) was 14.4 mm. *Cryptasterina* sp. has a pentagonal cushion-shaped profile (Fig. 1D). It is a consistent pastel-olive green color aborally and has a white oral surface. The maximum arm radius of this species was 14.8 mm.

Aquilonastra byrneae was found on the underside of coral rubble at both Gutter sites and at Two Tree (Fig. 2A). This species was found on rubble plates or boulders with surface areas between 200 cm² and 780 cm². Rarely, more than one specimen was found under an individual boulder or rubble plate. Aquilonastra byrneae was patchily distributed between the replicate quadrats, with an average abundance of 1-1.4 individuals per 4 m² at each station respectively (which equates to 0.9-1.5 individuals per 100 rubble plates flipped).

Only one individual *A. byrneae* was sampled from the highest intertidal sites, and these sea stars were also rarely found on rubble plates from areas lower on the shore (0.8 m above LAT), which were sampled in a different study to assess the distribution of sessile invertebrates at several sites around the reef rim (Walker, unpubl. data).

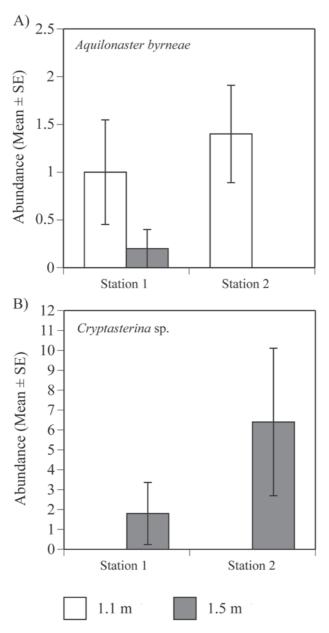


Figure 2. The mean abundance per 4 m² (\pm SE) of (A) *Aquilonastra byrneae* (n = 13) and (B) *Cryptasterina* sp. (n = 40) at two heights on the shore, 1.1 m (white bar) and 1.5 m (grey bar) above LAT.

These results suggest that the species distribution is limited to a narrow band at the rubble zone–algal pavement interface, approximately 1.1 m above LAT. In total, 23 *A. byrneae* were sampled across both stations. While the number of individuals is low, the size-frequency distribution shows a slight peak at R = 10.1-12.0 mm with the majority of the individuals (51%) falling between R = 8.1 mm and R = 12 mm (Fig. 3A).

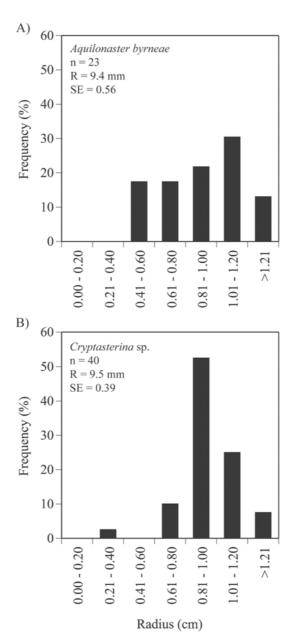


Figure 3. Size-frequency distribution of (A) Aquilonastra byrneae and (B) Cryptasterina sp. Frequency is expressed as the percent of total individuals in each radius size-class. The mean radius $(R) \pm SE$ and sample size (n) is given for each species.

Cryptasterina sp. is locally common, with populations found on either side of the Gutter, the Entrance Bank, Turtle Bay, and Two Tree. In the survey *Cryptasterina* sp. dominated the coral rubble habitat high on the shore (1.5 m above LAT). An average abundance between 1.8 and 6.4 individuals per 4 m² was recorded at each station respectively (3.8–9.3 species per 100 pieces of rubble flipped; Fig. 2B). This species was often found in aggregations with a maximum of 21 individuals found in one quadrat,

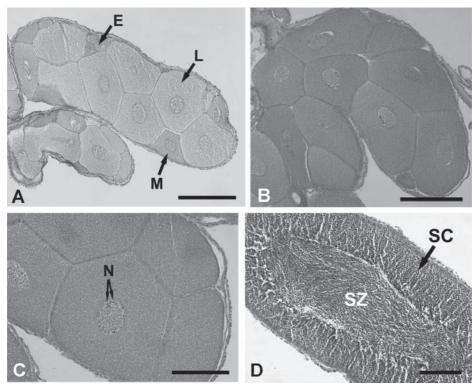


Figure 4. Gonad histology of *Aquilonastra byrneae* (A) May: Ovary with eggs at different stages of development including early (E), mid (M), and late (L) vitellogenic oocytes. (B) June: Ovary is filled with fully grown late vitellogenic oocytes. (C) June: Large eggs have a strongly eosinophilic cytoplasm with scattered lipid droplets. The nucleus has distinct bead like nucleoli (N). (D) June: Mature testis with spermatozoa (SZ) and developing sperm in spermatocyte columns (SC). Scales: A, B = $200 \,\mu$ m, C, D = $100 \,\mu$ m.

and up to 4 individuals on a single rubble plate. Individuals of this species were not present on rubble pieces lower on the shore, and were not found on the same piece of rubble as *Aquilonastra*. *Cryptasterina* sp. has a normal size-frequency distribution with 52% of individuals having a radius between 0.81 mm and 10.0 mm (Fig. 3B).

REPRODUCTION.—Aquilonastra byrneae has oral gonopores and so has benthic development. Although looked for, egg masses were not located under the adults. The eggs (ca. 420 μ m diam) are negatively buoyant. Histological examination of the gonads revealed the presence of mid and late vitellogenic oocytes in the ovaries in April, May, and June (Fig. 4A,B). Ovaries in the June sample were large and packed with late stage oocytes (Fig. 4B,C). They appeared to be at a pre-spawning stage indicating the presence of a period of enhanced reproductive activity in winter. In October, the ovaries were reduced in size, although late vitellogenic oocytes were still present. By November, the gonads were very small and no gametes were evident. Only six males were encountered out of thirty specimens dissected. The males were the smaller sized individuals (R \leq 8.0 mm). Three males in the June sample had mature testes (Fig. 4D).

Cryptasterina sp. is a simultaneous hermaphrodite and is a viviparous brooder incubating its young through brachiolaria larval stage to the juvenile in the gonads during the summer. The juveniles leave the parent though aboral gonopores. Intrago-

nadal juveniles occasionally cannibalise their siblings and so can differ in size when they leave the parent. The life history of the One Tree Reef *Cryptasterina* sp. is similar to that described for the coastal *C. hystera* in Byrne (2005).

DISCUSSION

In the revised taxonomy of the Asterinidae (O'Loughlin and Waters, 2004) *Aquilonastra* and *Cryptasterina* are among six major clades of this asteroid family. Species divergence in asterinid genera is often associated with evolutionary change in life history traits resulting in the presence of conspecifics with similar adult morphologies but markedly different modes of reproduction and development (Byrne, 2006). The difference in gonopore location of the *Aquilonastra* species from One Tree Island indicated that this was a new species with a different life history compared to *A. cepheus* with which it was formerly confused (O'Loughlin and Rowe, 2006). All *Aquilonastra* species for which we have life history data have sexual reproduc-

All *Aquilonastra* species for which we have life history data have sexual reproduction with production of lecithotrophic developmental stages or have asexual reproduction by splitting in half (fission). *Aquilonastra* includes several multiarmed (more than five arms) fissiparous species (O'Loughlin and Waters, 2004). These include a number of tropical species including *Aquilonastra corallicola* (Marsh, 1977), *Aquilonastra anomala* (H. L. Clark, 1921), *Aquilonastra heteractis* (H. L. Clark, 1938), and what appear to be several species in the *Aquilonastra burtoni* (Marsh, 1977) complex. *Cryptasterina* species have planktonic or brooded lecithotrophic larvae (Komatsu et al., 1990; Chen and Chen, 1992; Byrne et al., 2003; Byrne 2005, 2006). A full understanding of the diversity of these tropical asterinids requires taxonomic investigation (Dartnall et al., 2003; O'Loughlin and Waters, 2004; Rowe and Richmond, 2004). There is a recent systematic revision of *Aquilonastra* (O'Loughlin and Rowe, 2006).

Life history diversity is a characteristic feature of the Asterinidae (Byrne, 2006) and this is well illustrated by *Aquilonastra* and *Cryptasterina*. *Aquilonastra coronata* (Martens, 1866), *Aquilonastra batheri* (Goto, 1914), and at least one species in the *A. burtoni* complex are known to have planktonic brachiolaria larva, while *Aquilonastra minor* (Hayashi, 1974) has a benthic brachiolaria that is not brooded (James, 1972; Komatsu, 1975; Komatsu et al., 1979). Like *A. byrneae* from One Tree Island, *A. minor* from Japan has orally directed gonopores (Komatsu et al., 1979). Asterinids with oral gonopores lay egg masses and have benthic larvae (Komatsu et al., 1979; Byrne, 1995, 2006). *Aquilonastra byrneae* is likely to deposit egg masses but these were not found in the field. This species has negatively buoyant eggs, also characteristic of asterinids with benthic development (Komatsu et al., 1979; Byrne, 1995; Prowse et al., in press). The small individuals examined were all male, suggesting that this sea star may be a protandric hermaphrodite. This, however, has to be assessed though examination of specimens across the size range of *A. byrneae*. It remains to be determined where this sea star deposits its eggs and whether the adults remain with the developing progeny. A brooding species has yet to be found in *Aquilonastra*.

Cryptasterina is a new genus erected for pantropical asterinids formerly known as *Patiriella* including various forms called *P. pseudoexigua* (Dartnall et al., 2003). Several species remain to be described (Dartnall et al., 2003). The species of *Cryptasterina* from One Tree Reef has intragonadal development to the juvenile stage similar to that described for the coastal species *C. hystera* (Byrne et al., 2003; Byrne, 2005). *Cryptasterina hystera* is a narrow range endemic (< 100 km). Although the

One Tree Island form appears morphologically different from *C. hystera*, clarification of its taxonomic status awaits molecular sequence data. Resolution of its identity will determine whether its presence on One Tree Reef represents a new record or a new species for the Great Barrier Reef.

Cryptasterina sp. and *A. byrneae* were restricted to the high intertidal rubble habitat on the outer margin of One Tree Reef. Few mobile species are able to tolerate the harsh physical conditions found in this habitat with most species seeking refuge during low tides to escape extreme temperatures and desiccation (Walker, unpubl. obs). Other mobile invertebrates in this habitat included brittle stars, small crustaceans, and gastropods. A few sessile species occupy the underside of the rubble plates including spirorbids, encrusting *Cliona* sponges, and didemnid ascidians, in addition to biofilm and algal species. The coral slabs in the band occupied by *Cryptasterina* sp. had a thin algal-cyanobacterial cover. Both *Cryptasterina* sp. and *A. byrneae* are surface grazers utilizing the biota attached to the undersides of boulders as a food source (Byrne, pers. obs.).

The two species were found along distinct bands with *Cryptasterina* sp. higher on the shore than *A. byrneae*. The latter species was restricted to a narrow band at the interface between the high rubble habitat and the hard algal pavement. As an egg layer likely to have a benthic brachiolaria larva, *A. byrneae* may have high fidelity to this narrow band. It is unlikely that their benthic larvae would tolerate the desiccation stress or extreme temperatures that occur higher on the shore. The pavement habitat below the narrow band occupied by *A. byrneae* is wave-scoured and would also be unsuitable habitat for this asteroid. The ability of *Cryptasterina* sp. to dominate the high shore environment may be due to the reduced exposure of young to environmental extremes in their internal gonad habitat to the crawl away juvenile stage. Viviparous asterinids are specialists of high intertidal environments (Byrne et al., 2003).

Cryptasterina sp. was a conspicuous component of the high rubble habitat and its presence in the Gutter and elsewhere around the reef suggests that this species may extend to the inner lagoon margin. It is also possible that *Cryptasterina* sp. excludes *A. byrneae* from areas higher on the shore. Further work is required to determine the extent of the interaction between these two species, their diet preferences, and whether *A. byrneae* egg masses, juveniles, and adults are capable of surviving conditions further up the shore. This could be done using a series of mesocosm and manipulative translocation experiments and by determining whether juveniles are present at other shore heights.

Life history evolution involving various modes of sexual and asexual reproduction appears more prevalent in the Asterinidae than other asteroid families (Byrne, 2006). As diverse modes of development are discerned in cryptic species complexes, new insights into life history evolution in the Asterinidae are being generated and substantial, previously undetected species diversity, is being realized. In their high intertidal habitat, the two species investigated here are likely to be deleteriously impacted by the rising sea level associated with climate change. It seems unlikely that the physical processes that created this habitat at One Tree Reef would keep pace with rising water levels.

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ADDRESSES: (M.B.) One Tree Island Research Station and Department of Anatomy and Histology, F13, University of Sydney, NSW 2006, Australia. (S.J.W.) School of Integrative Biology, University of Queensland, Brisbane, QLD 4072, Australia. CORRESPONDING AUTHOR: (M.B.) E-mail: <mbyrne@anatomy.usyd.edu.au>.

