Synchronized broadcast spawning by six invertebrates (Echinodermata and Mollusca) in the north-western Red Sea

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Abstract

On the evenings of June 11 and 12, 2019, 5 and 6 days before full moon, broadcast spawning by four echinoderm species and two mollusc species was observed on the Marsa Shagra reef, Egypt (25° 14′ 44.2″ N, 34° 47′ 49.0″ E). Water temperature was 28 °C and the invertebrates were observed at 2–8 m depth. The sightings included a single basket star Astroboa nuda (Lyman 1874), 2 large Tectus dentatus (Forskal 1775) sea snails, 14 individuals of the Leiaster cf. leachi (Gray 1840) sea star and 1 Mithrodia clavigera (Lamarck 1816) sea star, 3 Pearsonothuria graeffei (Semper 1868) sea cucumbers, and 2 giant clams, Tridacna maxima (Röding 1798). The observations presented here provide relevant information on broadcast spawning of non-coral invertebrate taxa in the Red Sea, where spawning is considerably less well documented than in other tropical geographical regions such as the Indo-Pacific and Caribbean.

Introduction

The sedentary nature of many invertebrates on coral reefs renders them heavily reliant on dispersal during the pelagic larval period of their life cycle to ensure connectivity amongst reef populations (Atchison et al. 2008; Nunes et al. 2011). Broadcast spawning occurs across most marine phyla (e.g. Hagman and Vize 2003; Ritson-Williams et al. 2005; Hoffman et al. 2011; Bouwmeester 2013) and is a mode of reproduction in which large quantities of male and female gametes are released into the water column within a short period of time. Success of the strategy, however, relies on reproductive synchrony among intraspecific individuals within a few hours of specific nights each year. Such annual spawning events have been shown to be closely tied to factors such as annual temperature variation, lunar cycles and photoperiod length (Boch et al. 2011; Sweeney et al. 2011; Keith et al. 2016). To date, invertebrate species other than scleractinian corals have received noticeably less attention with regard to reproduction and this is particularly relevant for the Red Sea, where only very few studies have been conducted on multi-species broadcast spawning (Bouwmeester et al. 2016). Here we describe spawning observations of 23 non-coral invertebrates belonging to six species and two phyla.
Materials and methods

On the evenings of June 11 and 12, 2019 at 19:00–20:30 h, broadcast spawning by six invertebrate species (Mollusca and Echinodermata) was observed on the Marsa Shagra reef, Egypt (~ 25 km north of Marsa Alam, 25° 14′ 44.2″ N 34° 47′ 49.0″ E). This fringing reef is characterized by a wide (~ 1000 m) and shallow (< 1 m at high tide) reef flat underlain by a large carbonate framework. The reef flat is interrupted by a sand channel (bay) shouldered by gradually downward sloping reefs on both sides, and which transitions into a reef shelf at ~ 20 m depth. All spawning was observed on the sloping edges of the channel at 2–8 m depth (Table 1). The reef slope is characterized by a complex structural morphology and a 60–70% cover of scleractinian coral (mainly Acropora spp., Porites spp. and Pocillopora spp., pers. obs. DdB). Water temperature at 5 m depth was 28 °C, measured with a Suunto D4i dive computer. All observations were made while SCUBA diving and an underwater photographic record was taken for each observation. Species identification, and the identification of sperm or egg spawn, was performed visually in situ. Sperm release was characterized by a “smoky” cloud emitted by the individuals, and egg release was characterized by a “non-smoky” cloud of tiny conspicuous eggs. Taxonomic identifications were later confirmed by Gustav Paulay (FLMNH, USA) based on the extensive photographic and video material. Due to permit limitations and the limited number of individuals that were observed spawning, no voucher specimens were collected for posteriori identification.

Results

Spawning observations

A single basket star, Astroboa nuda (Lyman 1874), was observed on June 11 perched on top of a fire coral releasing female gametes (Fig. 1a, Table 1). When encountered, the individual was in a typical feeding position with arm branches extended and was releasing a vast number of eggs (~ 1 mm diameter) that were dispersed by the prevailing current. When illuminated, it continued spawning but drew in its arms towards the central disk, which is typical for this extremely light-sensitive species (Tsurnamal and Marder 1966; Hendler et al. 1995). A few minutes later, two large top-shell snails (Trochidae), Tectus dentatus (Forskål 1775) were encountered releasing a jet of male gametes into the water column (Fig. 1b). They were found 10 m apart, both perched on top of a coral mound (Table 1).

On June 12, 14 starfish Leiaster cf. leachi (Gray 1840) were seen broadcast spawning. Several individuals released sperm, while other individuals were observed releasing a cloud of eggs (Table 1). Individuals were several meters apart from each other (i.e. no clustering) and generally on top of coral mounds. Most of them exhibited the same spawning behaviours with raised discs and perched on the tips of their arms (Fig. 1c). Another sea star species, Mithrodia clavigera (Lamarck 1816), was encountered releasing male gametes in a flattened position on top of a coral mound (Table 1).

During the same evening, spawn was observed emanating from three Pearsonothuria graeffei (Semper 1868) sea cucumbers (Table 1). One was observed on a sandy bottom with half of its body lifted off the seafloor in a vertical position. It swayed with the waves’ surging motion while releasing a cloud of male gametes. The two other individuals were encountered briefly emerging from the cryptic reef environment to release a single cloud of male gametes before rapidly retreating into the reef (ESM_1). Lastly, two giant clams (Tridacna maxima, Röding 1798) were encountered, releasing a cloud of male gametes. Discharge lasted for only a few seconds and occurred through the excurrent siphons. The two individuals were in close proximity (1 m apart), embedded in the same coral mound. They spawned within seconds of each other (ESM_1).

Discussion

Spawning times of four out of the six species encountered here were not yet described for the Red Sea and to our knowledge, this is the first field observation of a basket star releasing female gametes. Relatively little is known about the life

| Days before full moon | Species                  | Number of individuals | Time of spawning | Type of gametes | Depth (m) |
|-----------------------|--------------------------|-----------------------|-----------------|-----------------|-----------|
| 6 (June 11)           | Astroboa nuda            | 1♀                    | 19:45           | Eggs            | 8         |
|                       | Tectus dentatus          | 2♂                    | 20:00–20:10     | Sperm           | 3–5       |
| 5 (June 12)           | Leiaster cf. leachi      | 5♂ & 9♀              | 19:30–20:15     | Sperm & eggs    | 3–8       |
|                       | Mithrodia clavigera      | 1♂                    | 20:15           | Sperm           | 2         |
|                       | Tridacna maxima          | 2♂                    | 19:50           | Sperm           | 3         |
|                       | Pearsonothuria graeffei  | 3♀                    | 19:50–20:10     | Sperm           | 2–5       |
history of *A. nuda*, but our observations suggest that this species—like many Ophiuroids—relies on broadcast spawning. Apart from our description of mass egg release in the northwestern Red Sea, the only other in situ description of spawning appears to be a single *A. nuda* individual releasing sperm two nights before the full moon (July 2012) on the Red Sea reef Al Fahal (Saudi Arabia) (Bouwmeester 2013). *Astroboa nuda* are known to return to the same location on the reef at night to feed (Tsurnamal and Marder 1966), and this behaviour did not appear to be affected by their spawning activity.

**Fig. 1** Nocturnal spawning of non-coral invertebrates on the shallow reef of the Egyptian Red Sea. *a* *Astroboa nuda* releasing eggs. *b* Continuous jet-like release of male gametes from the siphon of a *Tectus dentatus* sea snail. *c* *Leiaster cf. leachi* discharging female gametes in typical upright position. Video footage of all observed species is provided as Supplementary Resource 1 (ESM_1)
Observations of natural spawning of the two sea star species have previously been described in the Red Sea on Al Fahal Reef (Bouwmeester et al. 2016). They found a single individual of M. clavigera and four individuals of L. leachi that released sperm in April, 4–5 days after the full moon, and a single L. leachi that spawned two days after the May full moon in 2014 (Bouwmeester et al. 2016). Together with our observations in June, this might indicate that both species have a relatively extended period of potential spawning, yet a more thorough assessment is needed to support this hypothesis. Other sea star species from the Red Sea have been observed to spawn in winter, spring and summer (Pearse 1968). Although both species have a relatively broad distribution range, observations of spawning are scarce. Komatsu (1973) describes a single L. leachi sea star in an aquarium, which released eggs for ~1 h from the dorsal–lateral parts of the arms (August 11, 1972, at 10:00 h). Very little is known about the reproduction and development of these sea stars—and tropical sea stars in general (Bos et al. 2008)—except that both species appear to produce relatively small eggs (~140 µm diameter) and have a planktonic-feeding larval stage (Yamaguchi 1975; Chia et al. 1993).

The holothurian P. graeffei is found throughout the wider tropical Indo-Pacific and has been recorded spawning in various locations, including Thailand (Scott et al. 2015), the South China Sea (Purwati 2003), Great Barrier Reef (Purcell et al. 2012), the Maldives, the Seychelles and Mozambique (Friedman 2008). Described individuals are generally found exhibiting the typical characteristics of sea cucumber spawning, with the anterior part of the body stretched and in a vertical position, while the posterior part of the body remained on the substrate. Similar to our observation, this species has been described spawning simultaneously with other echinoderms (Scott et al. 2015) and in most recordings two or more individuals were encountered a few meters apart. The observed P. graeffei on the Marsa Shagra reef are the first to our knowledge to be found exhibiting spawning behaviour in the Red Sea. Previously described encounters in other geographical regions occurred between 15:00 h and sunset, and the lunar phase was usually between waning crescent and new moon. The individuals encountered in the Red Sea differ from these previous sightings at they were found releasing gametes in full darkness around 20:00 h and under a waxing gibbous moon.

The only description of reproduction in T. dentatus is a case of stimulated egg release by exposing several individuals to variable temperatures in a controlled aquarium environment (Eisawy 1970). Each female released approximately 1 million eggs. The same article provides some details regarding observations of T. dentatus spawning in its natural environment, but extensive descriptions are essentially absent. Eisawy (1970) described a spawning period ranging from April until July with an approximate lunar periodicity (and at an optimum water temperature of 27–28 °C), which complies with our observations in June. The reproduction in T. dentatus appears to be comparable to other Trochidae species. Trochus niloticus males have also been observed to release sperm in the evening (18:00–22:00 h), and for an extended period of time (10 min to an hour) on the Great Barrier Reef, while females spawned for up to 15 min (Heslinga and Hillmann 1981). Although the sexes of T. dentatus are separate (Eisawy 1970), we did not observe any females releasing eggs. Spawning in Trochidae species is generally initiated by males, although females do not always spawn in response to sperm release (Heslinga and Hillmann 1981).

It is possible that T. dentatus females released eggs later in the night or even several days later. Until our spawning observation, T. dentatus snails had rarely been observed on top of the reef of Marsa Shagra. Like many of the closely related Trochidae species, T. dentatus are known to spend most of their time hidden. Their increased activity and displacement to the reef surface at nights around the full moon, however, has also been described for T. niloticus (based on anecdotal evidence from fishermen).

The spawning behaviour of T. maxima appears to correspond to previous descriptions of natural gamete release in the Red Sea. The reproductive strategy of T. maxima is relatively well described (See Roa-Quiaoit 2005 and references therein). This is partly because these clams are fished and cultured for commercial purposes (food, shell craft industry and the aquarium trade) (Lucas 1994). Throughout the Red Sea, T. maxima spawn June–December (Kilada et al. 1998), although the length of the spawning season can differ due to latitudinal variations in water temperature or the availability of food (Roa-Quiaoit 2005). Female gametes reach their largest diameter in June (~95 µm) shortly before spawning—which coincides with the timing of our observations—and are generally released within hours after the male gametes. Like many hermaphroditic broadcast spawners, this strategy reduces the chance of self-fertilization (Lucas 1994).

Spawning observations reported here contribute to the still poorly documented spawning of non-coral invertebrates in the Red Sea and shed light on their spawning behaviour. Previous reports combined with our findings provide evidence for synchronized inter-taxa mass spawning on the coral reefs of the Red Sea. Only a few dedicated surveys to document spawning in invertebrates have been conducted in the Red Sea, and it is to be expected that many more species spawn around the same period.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-021-03871-6.
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Author contribution Conceptualisation: AEW and DMdB. Methodology: AEW, AHE, and DMdB. Data collection: AEW, AHE, IvD, EG, JL, DE, BSdB, and DMdB. Writing—original draft preparation: AEW and DMdB. Writing—review and editing: AEW, AHE, JB, IvD, EG, JL, DE, BSdB, and DMdB. Funding acquisition: AHE. Supervision: AEW, JB, and DMdB.

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Availability of data and materials All data and relevant footage collected during this study are presented in this article or the accompanying electronic supplementary materials. Additional photographs are available on request.

Code availability Not applicable.

Declarations

Conflict of interest The authors have no conflict of interest to declare.

Ethical approval Access to the study site was provided under the authorisation of the Ecological Team of the Red Sea Diving Safari dive centre. All precautions were taken to minimise the impact on the marine habitat at the study site. As this study was purely observational, no additional permits or ethical approval were required.

Consent to participate Not applicable.

Consent for publication Not applicable.

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