ABSTRACT: Mass occurrence of seven species of Synaptula (S. sp., S. lamperti, S. madreporica, S. media, S. psara, S. violacea, and S. virgata) was found on large sponges in the Andaman Sea and Gulf of Thailand. From 1 up to at least 1,000 holothuroids could be found on the pinakoderm of a single sponge, but never in the spongocoel even if it was open and very large. The observed holothuroids remained at the same spot all the time. Sometimes they fed on detritus on the sponge surface. We hypothesize that they also take up nutrients that leak out of the sponge on which they thrive.

Key words: Sea cucumbers on sponges, Synaptula, symbiosis, Thailand.

INTRODUCTION

Several observations of mass occurrence of holothuroids of the genus Synaptula on individual sponges, primarily barrel sponges (Petrosia spp.), were made. Similar observations are reported by others. Heding (1928) reported 6 species of Synaptula from sponges. Four of the species were found as single individuals but for two of the species, 3 and 8 specimens in total were found, respectively. SCUBA diving did not exist in his time so, subtidal sampling was therefore done by dredges. Colin and Arneson (1995) show two photos of about 70 and 50 Synaptula individuals, respectively, each on a part of a sponge. Allen and Stone (1996) show the same phenomenon, a photo with at least 50 individuals of Synaptula sp. on a part of a single sponge. Laboute and de Forgès (2004) show Synaptula media Cherbonnier and Féral, 1984 on the sponges Ircinia irregularis (Poléjaeff, 1884) and Dysidea arenaria Bergquist, 1965 from New Caledonia. Purcell and Eriksson (2015) and Purcell et al. (2016) reported S. media and an unidentified species of the same genus from the body wall of Stichopus harrmanni Semper, 1868.

Hammond and Wilkinson (1985) went a step further and showed by experiment that sponges leak nutrients that are directly utilized by Synaptula lamperti (Heding, 1928) living in large numbers on the sponge surface.

MATERIAL AND METHODS

While sampling holothuroids at localities in the Gulf of Thailand and the Andaman Sea, Thailand, we noticed that several Synaptula species were on sponges. We documented these associations photographically and collected the holothuroids involved. We used SCUBA diving and (Canon Digital IXUS 9000 Ti or Canon PowerShot G12) underwater cameras.

The holothuroids were identified by the use of the original descriptions of each species, additional taxonomical literature and the collection of the Zoological Museum, University of Copenhagen, Denmark. Ossicle preparations were made with tissue from all species (AM, supplemented by TC). Voucher specimens of holothuroids are deposited in the Thailand Natural History Museum. Sponges were identified by SP.

RESULTS

All the species found on sponges belonged to the genus Synaptula, apart from single individuals of two species: Opheodesoma grisea (Semper, 1868) and Polyplectana sp.

Seven Synaptula species were found on sponges (Table 1; Figs. 1–2): Synaptula sp.; Synaptula lamperti Heding, 1928; Synaptula madreporica Heding, 1928; Synaptula media Cherbonnier and
Féral, 1984; *Synaptula psara* (Sluiter, 1887); *Synaptula violacea* Heding, 1928; and *Synaptula virgata* Sluiter, 1901. The sponge species on which the holothuroids thrive were large individuals of *Petrosia* sp. (Figs. 1A–F, 2B–C); *Xestospongia* sp. (Petrosiidae) (Fig. 2A); *Clathria* (*Thalysias*) reinwardti Vosmaer, 1880 (Microcionidae) (Figs. 1G, 2H); *Chondrosia* sp. (Figs. 1H, 2F), *Chondrosia reticulata* (Carter, 1886) (Chondrosiidae) (Fig. 2G); *Spheciospongia solida* (Ridley and Dendy, 1886) (Spirastrellidae) (Fig. 2D); and *Haliclona* (*Rhizoniera*) sp. (Chalinidae) (Fig. 2E).

Our observation of occurrence of *Synaptula* spp. on sponges are summarized in Table 1 and shown in Figs. 1–2. Below are some of our general observations of the mass occurrence of *Synaptula* species on sponges:

1. Mass occurrence of *Synaptula* spp. on sponges is a fairly common phenomenon on individual sponges within larger sponge populations.

2. Some sponges host a single *Synaptula* individual. Other sponges host numerous individuals, up to at least 1000.

3. All the photographed apodids stick close to the sponge surface. They do not stretch any body part above the sponge surface. It gives them a close contact to the sponge.

4. The apodid population on the sponge is usually very dense. No territoriality or aggressive behavior between the individuals was observed.

5. When many holothuroids were found on the same sponge individual, they seem to be of approximately the same size.

6. We have also observed that the holothuroids remain seemingly inactive, attached to the same spot on the sponge. They do not move around but sometimes they move their anterior side with the feeding tentacles sideways a little bit and occasionally feed on detritus settled on the sponge surface. The body shape of the holothuroids is usually curved. It shows that it is not moving around very much but remains on the same spot. An actively moving holothuroid would expose a more stretched body.

7. Sponges allow only small particles (<50 μm) to enter their ostia (Reiswig, 1971). Larger particles will be left outside and can be seen as detritus on the surface of the sponge. Such detritus was occasionally observed to be fed on by the holothuroids.

8. The holothuroids are always positioned on the outside of the sponge, on the pinacoderm, never in the spongocoel, even if it is open and very large.

9. The occurrence of *Synaptula* is very patchy. A sponge individual with a dense population of *Synaptula* is usually surrounded by numerous other sponges without any holothuroids. It is striking that *Synaptula* spp. prefer sponges over other organisms as their substratum.

10. We have dissected over a 100 *Synaptula* individuals but never found any ripe gonads or brooding of juveniles in any of them.
Mass occurrence of Synaptula spp. (Holothuroidea: Apodida) on sponges

Figures 2. Synaptula spp.: A. Synaptula media on Xestospongia testudinaria (Lamarck, 1815), Gulf of Thailand; B. Synaptula media on Petro sia (Petrosia) sp., Gulf of Thailand; C. Synaptula psara on Petro sia (Petrosia) sp., Gulf of Thailand; D. Synaptula violacea on Spirastrel la solida (Ridley and Dendy, 1886), Gulf of Thailand; E. Synaptula virgata on Haliclona (Rhizoniera) sp., Gulf of Thailand; F. Synaptula virgata (the white individual) on Chondrosia sp., Gulf of Thailand; G. Synaptula virgata (the white individual) and Synaptula madreporica (individuals with patterns) on Chondrosia reticulata (Carter, 1886), Gulf of Thailand; H. Synaptula virgata on Clathria (Thalysias) reinwardt Vosmaer, 1880, Gulf of Thailand. Photos A–D, F and H by Arom Mucharin. Photos E and G by Sumaitt Putchakarn.
Table 1. Observations of *Synaptula* spp. on sponges in Thai waters.

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>Depth (m)</th>
<th>Date</th>
<th>Type of sponge</th>
<th>Number of holothuroid individuals</th>
<th>Figure no.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Opheodesoma grisea</em></td>
<td>Gulf of Thailand, Chang Islands, Hin Keak Ma</td>
<td>8</td>
<td>6 May 2013</td>
<td><em>Petrosia</em> (<em>Petrosia</em>) sp.</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td><em>Polyplectana</em> sp.</td>
<td>Andaman Sea, Lanta Islands, Rok Nok Island</td>
<td>6</td>
<td>4 May 2013</td>
<td>Unidentified sponge</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td><em>Synaptula</em> sp.</td>
<td>Gulf of Thailand, Chang Islands, Hin Keak Ma</td>
<td>8</td>
<td>16 May 2013</td>
<td><em>Petrosia</em> (<em>Petrosia</em>) sp.</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td><em>Synaptula lamperti</em></td>
<td>Andaman Sea, Lanta Islands, Ngai Island</td>
<td>6</td>
<td>6 May 2013</td>
<td><em>Petrosia</em> (<em>Petrosia</em>) sp.</td>
<td>ca 200–300</td>
<td>1A–B</td>
</tr>
<tr>
<td></td>
<td>Andaman Sea, Lanta Islands, Rok Nok Island</td>
<td>6</td>
<td>4 May 2013</td>
<td><em>Petrosia</em> (<em>Petrosia</em>) sp.</td>
<td>ca 200–1000</td>
<td>1C–F</td>
</tr>
<tr>
<td><em>Synaptula madreporica</em></td>
<td>Gulf of Thailand, Pattaya, Lan Island</td>
<td>6</td>
<td>11 June 2013</td>
<td><em>Clathria</em> (<em>Thalysias</em>) <em>reinwardti</em></td>
<td>ca 10 (with other species)</td>
<td>1G–H</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Chondrosia</em> sp.</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Chondrosia reticulata</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Synaptula media</em></td>
<td>Gulf of Thailand, Chang Islands, Kra-Tean Island</td>
<td>6</td>
<td>16 May 2013</td>
<td><em>Xestospongia testudinaria</em></td>
<td>ca 20–30</td>
<td>2A–B</td>
</tr>
<tr>
<td></td>
<td><em>Petrosia</em> (<em>Petrosia</em>) sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Synaptula psara</em></td>
<td>Gulf of Thailand, Chang Islands, Hin Keak Ma</td>
<td>6</td>
<td>16 May 2013</td>
<td><em>Petrosia</em> (<em>Petrosia</em>) sp.</td>
<td>2</td>
<td>2C</td>
</tr>
<tr>
<td><em>Synaptula violacea</em></td>
<td>Gulf of Thailand, Chang Islands, Wai Island</td>
<td>9</td>
<td>15 May 2013</td>
<td><em>Spheciospongia solida</em></td>
<td>1</td>
<td>2D</td>
</tr>
<tr>
<td><em>Synaptula virgata</em></td>
<td>Gulf of Thailand, Pattaya, Lan Islands, Lan Island</td>
<td>6</td>
<td>11 June 2013</td>
<td><em>Haliclona</em> (<em>Rhizoniera</em>) sp.</td>
<td>1 or 2 13–16 (with or without other species)</td>
<td>2E–H</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Chondrosia</em> sp.</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Chondrosia reticulata</em></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>Clathria</em> (<em>Thalysias</em>) <em>reinwardti</em></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
DISCUSSION

The holothuroid – sponge relation

Other sea cucumbers have been reported to occur in large densities in some areas (Rutherford, 1973; Costelloe and Keegan, 1984; Sewell and Levitan, 1992; Massin, 1999; Lane and Vandenspiegel, 2003; Ng et al., 2015). However, these species were not involved in symbiosis with sponges.

Our observations as well as lacking evidence from the literature give us the impression that the species Opheodesoma grisea and Polyplectana sp. found on sponges were just cases of coincidence. There is probably not a symbiotic relation between them and the sponges. At least O. grisea is commonly found also on other substrates.

Coral reef habitats are nutrient-poor environments (Sheppard et al., 2009). Sponges are very effective filter feeders that trap enormous amounts of plankton as food (Gill and Coma, 1998; Lesser, 2006; de Groeij et al., 2008). Sponges, contrary to the Eumetazoa (Epitheliozoa), lack tight cell junctions or gap junctions, but have only adherence junctions (Schmidt-Rhaesa, 2007). One consequence of this is that sponges “leak” more dissolved organic matter (DOM) into their surroundings than eumetazoans (Thompson, 1985; Walker et al., 1985). The DOM can include compounds that are useful for nutrition and others that are toxic and thus would be a deterrent to other organisms (Hammond and Wilkinson, 1985). This leakage can thus modulate interactions between sponges and other organisms.

Representatives of many phyla can absorb DOM through the body surface (Wright and Ahearn, 1995). For example, Asteroidea and Echinoidea, are able to absorb DOM nutrients by epidermal absorption (Ferguson, 1967; Fontaine and Chia, 1968). A related phenomenon called “skin digestion” has also been demonstrated in the echinoderms Asteroidea and Echinoidea. These animals transport digestive trypsine-like enzymes by externalized cells to the body surface where they digest and take up nutrient particles by epidermal absorption (Péquignat, 1966, 1972; de Burgh, 1978; de Burgh et al., 1977; Stephens et al., 1978).

Conclusions about the holothuroid - sponge relation

1. Toxins, spongin, and spicules are the main protection a sponge has against predators and epibionts. The leakage of toxins has probably been an important evolutionary selective advantage that has allowed them to survive predation and successfully diversify since the beginning of the Paleozoic (Clarkson, 1998).

2. Another consequence of the “leaky” body and leakage of compounds from sponges is that also other compounds than toxins leak out: substances which can be considered nutrients for organisms such as holothuroids.

3. Nutrients leaking out from the sponge can be utilized by other organisms if they can cope with the sponge toxins.

4. Larvae and adults of holothuroids might utilize such leaking compounds as a kind of pheromone and use them to locate a sponge. However, as juvenile holothuroids were not observed on the sponges, it is improbable.

5. The holothuroids on the sponge surface are exposed to potential predators but seemingly not preyed upon. A possible explanation could be that they, themselves are poisonous, either by their own toxin or due to toxins taken up from the sponge, or both.

6. Among holothuroids only Apodida have been reported to live in such a close association with sponges. The extremely thin body wall of Apodida, compared with other holothuroids, is probably an important factor behind the evolution of this kind of symbiosis as it facilitates the uptake of nutrients.

7. We hypothesize that DOM nutrients could be utilized by many holothuroids of the genus Synaptula in the same way as has been demonstrated for S. lamperti by Hammond and Wilkinson (1985).

8. The large sponges are probably much longer lived than the holothuroids living on them. This type of symbiosis is therefore probably just a short moment in a sponge’s long life.

9. Another possible explanation is that the sponges with holothuroids are slowly dying, leaking organic matter or dead cells, and by the “smell” attract planktonic larvae. This is, however, less likely as Hammond and Wilkinson (1985) showed the connection between the actively filtering of plankton by the sponge with the consecutive direct uptake of the same nutrients by the holothuroids.

10. There are two basic mechanisms that Synaptula spp. may use for feeding: 1) using tentacles to feed on adherent detrital material accumulated on the sponge surface (because of the size limit of ostia), and 2) dissolved organic matter (DOM) leaked by the sponge. The first mechanism is
probably most important, because the holothuroids are mainly on the outside of the sponge where detritus accumulates but absent from large spongocoels where detritus is lacking but DOM should be more abundant as that part of the sponge is bathed in excurrent water.

Colonization of sponges

The reproduction, larval biology, and dispersal are virtually unknown in holothuroids of the genus *Synaptula* in the Indo-Pacific region (Sewell and McEuen, 2006). There are, however, a few small notes in the literature. Mortensen (1937) found *Synaptula reciprocans* (Forskål, 1775) and *Synaptula vittata* (Forskål, 1775) spawning in his aquaria in Egypt. (*Synaptula vittata* is a nomen dubium (Paulay, 2015)). The development of the embryos and larvae of both species resembled each other. They developed to an auricularia in three days and continued to develop for two weeks. They did not develop any further but survived for another week. *S. reciprocans* is an invasive species coming from the Red Sea to the Mediterranean Sea. It is now well established in the eastern Mediterranean Sea (Bianchi et al., 2014; Streftaris et al., 2005). It shows that it has an effective dispersal. *Synaptula hydriformis* (Lesueur, 1824) lives in the Caribbean region southwards to the Brazilian coast (Alvarado and Solí-Marín, 2013), and its reproductive biology is extensively investigated. *Synaptula hydriformis* is a simultaneous hermaphrodite that broods its juveniles in the perivisceral coelom (Frick et al., 1996; Frick, 1998; Hadel et al., 1998). Matrotrophy, transfer of nutrient from the mother to the progeny during gestation, exists in this species (Ostrovsky et al., 2015). Another apodid species, *Chiridota rotifera* (Pourtalès, 1851), (family Chiridotidae) was also collected when it was brooding numerous embryos in its coelom (Clark, 1910; Hadel et al., 1998).

The very patchy occurrence of holothuroids on sponges shows that settling on a sponge might be a quite rare phenomenon, but when it occurs it might be followed by mass reproduction on the same spot, probably by fissipary.

The pattern of occurrence on sponges give some clues to an understanding of the holothuroid reproduction. The patchy occurrence of *Synaptula* on some sponges, while it is absent on most others in the surroundings, indicate the existence of a rare larval stage capable of planktonic dispersal. It could be lecithotrophic or planktotrophic. On the other hand, the mass occurrence of *Synaptula* of fairly similar size on single sponges indicate the possibility of some kind of brooding or more probably, asexual reproduction, fissipary. Better knowledge about holothuroid reproduction is needed in order to understand this symbiotic relation.

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