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Response of sponges with autotrophic endosymbionts during the coral-bleaching episode in Puerto Rico

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Abstract. An updated list of sponges with algal endosymbionts including new records for Puerto Rico and the Caribbean, indicates that thirty-five species of common Caribbean sponges possess photosynthetic endosymbionts. Of these, 23 (67.6%) species in seven orders, were found with unicellular chroococcoid cyanobacteria (*Aphanocapsa*-like) and 5 (14.7%) hadromerid species were found with zooxanthellae. Sponges with other algae as symbionts occur less frequently (≦6%). Thirty-one common sponge species were inspected for bleaching during coral-bleaching months (July–September 1987; January 1988) in Puerto Rico. *Anthosigmella varians, Xestospongia muta* and *Petrosia pellasarca* bleached partially, but only few individuals within any given population became bleached and the bleaching of sponges was very localized. Adaptations between cyanobacterial symbionts and sponges, acquired during the long evolutionary history of these two taxa may explain the paucity of bleached sponges when compared to the high incidence of bleached corals reported.

Introduction

Many common Caribbean sponges possess photosynthetic endosymbionts including zooxanthellae (Rützler 1974, 1981, in press; Wilkinson 1987; Vicente 1987) like most shollaw coral reef anthozoans. Sponges with photosynthetic endobiotic algae (whether zooxanthellae or cyanobacteria) virtually did not lose their algal endosymbionts in Puerto Rico during the 1987 coral-bleaching episode, even when these were found next to bleached corals. Bleaching or tissue discoloration is usually related to stress conditions, and occurs when hosts (e.g. cnidarians, sponges) expell their endosymbionts (e.g. zooxanthellae, cyanobacteria) and/or the photosynthetic endosymbionts loose their pigments partially (Trench and Blank 1987; Hoegh-Guldberg and Smith 1988).

While there is an increasing amount of information on events that cause aposymbiosis in scleractinian corals (Glynn 1983; Roberts 1987; Williams et al. 1987; Goenaga et al., in press), little, if any reliable information exists on the status of sponge reactions to the environmental conditions which caused bleaching on many cnidarian taxa during the summer of 1987 (Williams et al. 1987). This study lists an updated record of sponges with photosynthetic symbionts in the Caribbean Region; and examines the incidence of bleaching in sponges (Calcarea and Demospongea) during the summer of 1987 and early winter of 1988 in Puerto Rico.

Materials and methods

The updated list (Table 1) of symbiotic associations between Caribbean sponges and photosynthetic autotrophs is based on: 1. information provided to me by K. Rützler (in press; personal communication); 2. the literature; and 3. field observations and light microscopy. The symbionts were identified using transmission electron microscopy. All TEM was done by Dr. T. Pueschel at the State University of New York following standard procedures. TEM is needed to confirm species composition of *Aphanocapsa*-type symbionts in two haplosclerid sponges found in this study (*Petrosia pellasarca* and *Xestospongia rosariensis*).

Sponge populations (31 species) were inspected for bleached tissue during 1 h dives in the sponge habitats described below. All inspections were done during bleaching periods in Puerto Rico (July–September 1987 and January 1988). Different sponge habitats on the north (San Juan) and on the southwest (La Parguera) coasts of Puerto Rico (Fig. 1) were included in this study. The habitats inspected at San Juan were: 1. flat, horizontal, pitted hard ground with small, slightly elevated boulders at Condado Beach (depth = 1–9 m); 2. pitted hard substrate with shifting coarse sand at Condado Beach (4–6 m); 3. generally flat, hard bottom with large boulders (1 m high) north of Las Marias Reef (12–15 m); 4. hard pitted flat ground with thick brown algal cover on San Jorge Reef (6–8 m) and 5. irregular hard ground at Las Marias Reef (4–6 m).

Sponge populations at La Parguera were inspected on the shallow (0.1–3 m) reef front communities of Collado Reef and in deeper reef substrates along the shelf edge (depth = 13–26 m). Photographs ($n=150$) were taken within a 10 × 15 m grid on the reef front of Cayo Enrique Reef during the summer (1987) inspections. This grid encloses the *Acropora palmata* zone (depth = 0.6–4 m), the *A. cervicornis* zone (4–7 m) and the base of the reef (7–12 m). Populations of sponges (e.g. *Chondrilla nucula*) within this grid have been photographed since October 1984, making possible the detection of

Table 1. Caribbean reef demosponges with algal symbionts. Sponge orders: CA = Calcarea; CH = Choristida; DC = Dictyoceratida; DD = Dendroceratid; HD = Hadromerida; HL = Halichondriida; HP = Haplosclerida; P = Poecilosclerida; PT = Petrosiida; VR = Verongida. Algal symbionts: ac = articulated coralline red algae; ch = Chlorophyta; d = diatom; dn = dinophycean; oc = oscillatorian cyanobacteria; rh = rhodophyte; uc = unicellular Cyanobacteria. References: 1 = Rützler in press; 2 = Pang 1973; 3 = Vicente unpublished data; 4 = Vicente 1987; 5 = Rützler 1974; 6 = this study

Species	Algal symbiont
1. *Anthosigmella varians* (HD)	Zooxanthellae (dn-1)
	Zooxanthellae (dn-2)
2. *Anthosigmella* sp. (HD)	Zooxanthellae (dn-3)
3. *Aplysina fistularis* (VR)	*Aphanocapsa feldmanni* (uc-1)
4. *Aplysina fulva* (VR)	*Aphanocapsa feldmanni* (uc-1)
5. *Aplysina lacunosa* (VR)	*Aphanocapsa feldmanni* (uc-1)
6. *Aplysina cauliformis* (VR)	*Aphanocapsa feldmanni* (uc-1)
7. *Chondrilla nucula* (HD)	*Aphanocapsa feldmanni* (uc-4)
	Aphanocapsa feldmanni (uc-1)
8. *Clathrina coriacea* (CA)	*Pleurosigma* sp. (d-3)
9. *Cliona caribbaea* (HD)	Zooxanthellae (dn-5)
	Zooxanthellae (dn-1)
10. *Cliona aprica* (HD)	Zooxanthellae (dn-3)
	Zooxanthellae (dn-2)
11. *Cribochalina vasculum* (PT)	*Aphanocapsa feldmanni* (uc-1)
12. *Cribochalina dura* (PT)	*Aphanocapsa feldmanni* (uc-1)
13. Unidentified (DD)	*Ostreobium* cf. *constrictum* (ch-1)
	Acrochaetium spongicolum (rh-1)
14. *Dysidea janiae* (DC)	*Jania adherens* (ac-1)
15. *Geodia papyracea* (CH)	*Aphanocapsa feldmanni* (uc-1)
16. *Geodia neptuni* (CH)	*Aphanocapsa feldmanni* (uc-1)
17. *Igernella notabilis* (DW)	*Ostreobium* cf. *constrictum* (ch-1)
18. *Ircinia felix* (DC)	*Aphanocapsa feldmanni* (uc-1)
19. *Ircinia campana* (DC)	*Aphanocapsa feldmanni* (uc-1)
20. *Mycale laxissima* (P)	*Ostreobium* cf. *constrictum* (ch-1)
	Acrochaetium spongicolum (rh-1)
21. *Neofibularia nolitangere* (P)	*Aphanocapsa feldmanni* (uc-1)
22. *Oligoceras violacea* (DC)	*Phormidium spongeliae* (oc-1)
23. *Petrosia pellasarca* (PT)	*Aphanocapsa*-like (uc-6)
24. *Spheciospongia vesparium* (HD)	*Aphanocapsa feldmanni* (uc-1)
25. *Spheciospongia cuspidifera* (HD)	Zooxanthellae (dn-3)
26. *Ulosa funicularis* (HL)	*Aphanocapsa raspaigellae* (uc-1)
27. *Ulosa arenosa* (HL)	*Aphanocapsa raspaigellae* (uc-1)
28. *Verongula gigantea* (VR)	*Aphanocapsa feldmanni* (uc-1)
29. *Verongula rigida* (VR)	*Aphanocapsa feldmanni* (uc-1)
30. *Verongula reiswigi* (VR)	*Aphanocapsa feldmanni* (uc-1)
31. *Xestospongia muta* (PT)	*Aphanocapsa feldmanni* (uc-1)
32. *Xestospongia (rosariensis)* (PT)	*Aphanocapsa* -like (uc-6)
33. *Xestospongia portoricensis* (PT)	*Aphanocapsa feldmanni* (uc-1)
34. *Xestospongia subtriangularis* (PT)	*Aphanocapsa feldmanni* (uc-1)
35. *Xytopsues osburnensis* (P)	*Jania capillacea* (ac-1)

chromatic changes in specific individuals ($n > 1{,}000$) before and during the bleaching episode. Specific ecological descriptions of all the habitats surveyed are given elsewhere (Vicente 1987, 1988; Goenaga 1988).

Results

A total of 34 species of Caribbean reef sponges possess one (the rule) or more (the exception) types of endosymbiotic, photosynthetic symbionts (Table 1). Zooxanthellae, similar to those occuring in corals and many other tropical cnidarians, were found in 5 (15%) demosponge species, all of which belong to two related families (Spirastrellidae and Clionidae) of the order Hadromerida. On the other hand, 23 (68%) species within 7 orders were found with *Aphanocapsa* spp., a chroococcoid cyanobacteria which usually imparts a reddish tinge to the peripheral region of their sponge host. These photosynthetic endosymbionts are shown in Fig. 2. Associations between sponges and photosynthetic algae other than *Aphanocapsa* or zooxanthellae were found less frequently: coralline reds = 2 (6%); other red algae + chlorophytes = 2 (6%); diatoms = 1 (3%); and filamentous cyanobacteria = 1 (3%) (Fig. 2a).

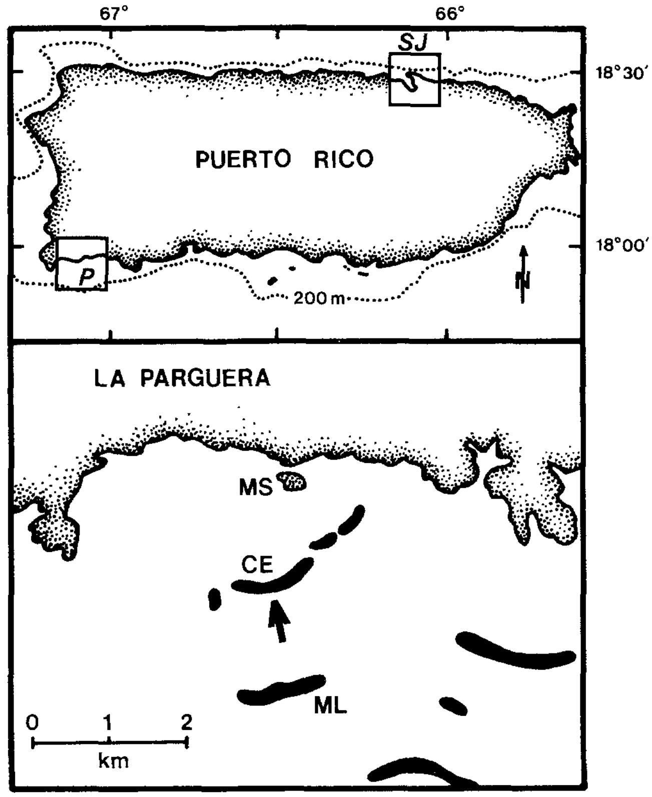

Fig. 1. Map of Puerto Rico showing the sites of San Juan (SJ) (north coast) and La Parguera (P) (southwest coast), inspected during the 1987 bleaching event. Cayo Enrique Reef (CE) is located at La Parguera between the Marine Station (MS) and Media Luna Reef (ML) about 1.6 km from shore. The arrow points to the reef front where a 150 m^2 grid is located

The common chicken liver sponge *(Chondrilla nucula)* as well as other reef sponges with *A. feldmanni* as endosymbionts (e.g. *Aplysina* spp., *Ircinia* spp.) did not bleach (Fig. 2b). Sponges bearing zooxanthellae as endosymbionts on the reef front of Cayo Enrique, such as *Cliona aprica* and *Anthosigmella varians* (Corredor et al. 1988) also maintained their normal color (light brown in the former, dark brown in the latter) even when these were found next to bleached corals. Sponges without photosynthetic endosymbionts (e.g. *Iotrochota birotulata, Ircinia strobilina*) retained their normal coloration.

Fig. 2 a, b. Common photosynthetic endosymbionts of Caribbean sponges. **a** Zooxanthella (*Gymnodinium microadriaticum*) in the sponge *Anthosigmella varians*. Notice the large pyrenoid (P) body and chloroplasts (CL) characteristic of this species (× 5800). **b** Cyanobacterial symbionts (C) (*Aphanocapsa feldmanni*) in *Chondrilla nucula*. F = collagen fibrils; 2 = Spherulous cells; IN = crystalline inclusion; B = bacteria

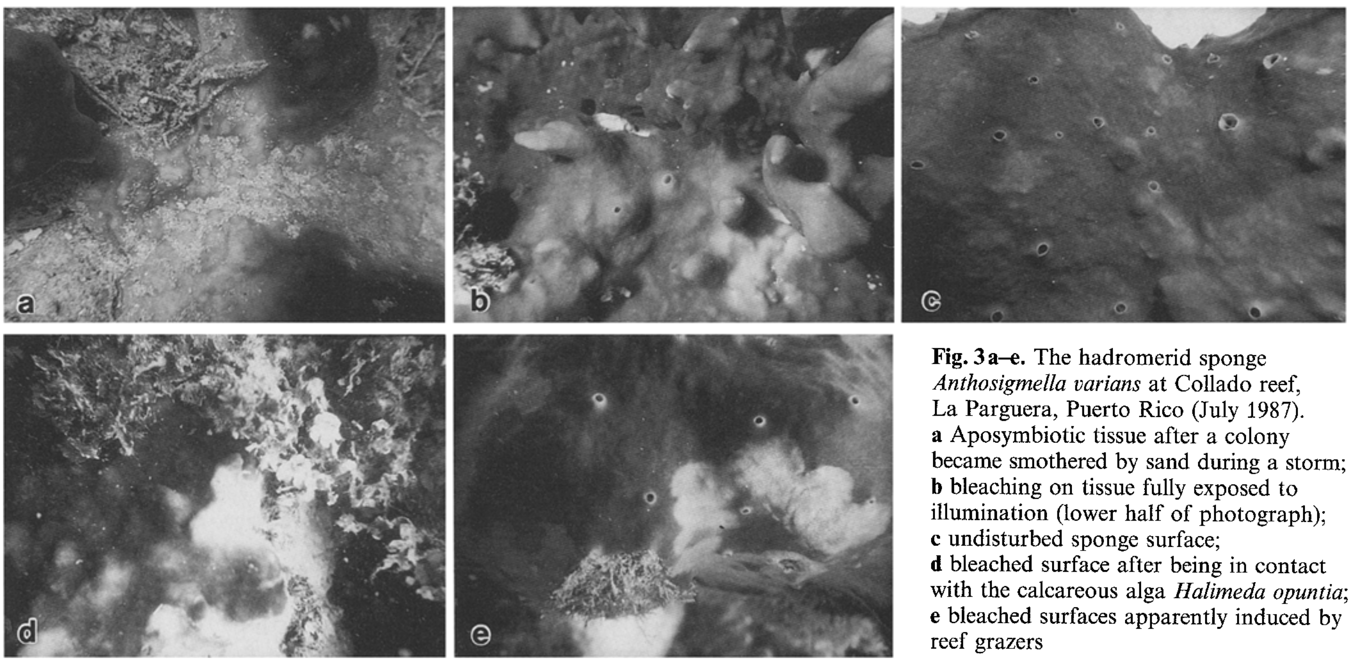

Fig. 3 a–e. The hadromerid sponge *Anthosigmella varians* at Collado reef, La Parguera, Puerto Rico (July 1987). **a** Aposymbiotic tissue after a colony became smothered by sand during a storm; **b** bleaching on tissue fully exposed to illumination (lower half of photograph); **c** undisturbed sponge surface; **d** bleached surface after being in contact with the calcareous alga *Halimeda opuntia*; **e** bleached surfaces apparently induced by reef grazers

Bleaching of sponges in other reefs at La Parguera was very localized and rare. For example, only three specimens of the encrusting sponge *A. varians* on Collado Reef became yellow on surfaces exposed to full illumination (Fig. 3 b). Bleached sponge tissue was also seen in isolated sponges that either were exposed to sand (Fig. 3 a), or were in contact with calcareous green algae (Fig. 3 d) or apparently were grazed on their surface (Fig. 3 e). One other species (*Petrosia pellasarca*, $n = 10$) was found bleached on the shelf edge reef of La Parguera. Exposed surfaces were very pale, sometimes white, instead of their normal color (pink of reddish-brown).

All sponges except one species *(X. muta)* inspected on hardgrounds of the Atlantic coast of Puerto Rico (San

Juan) did not bleach, even when corals (e.g. *A. palmata*, *Porites astreoides*) and anemones (*Condylactis gigantea*) were notably discolored in this region (Vicente 1988). Between 10–30% of *X. muta* at depths of 4–15 m were white or pale. This sponge looks dark brown at these depths, but becomes reddish-brown to pink when brought to the surface. In deep habitats (> 60 m) they are always white (personal observations). The surfaces of *X. muta* suggested that the red colored endosymbiotic algae were lost. Specimens of *X. muta* on the shelf edge reef of La Parguera, however, did not bleach. Other common or dominant sponges on the north coast (*Anthosigmella varians*, *Cliona aprica*, *Ircinia campana*) did not bleach, even when they occured next to bleached animals.

Discussion

This study confirms that many common shallow-water Caribbean sponges, like corals, have photosynthetic endosymbionts. Rützler (in press) reported that 45% of the 42 conspicuous sponges of Bermuda and Belize contain small unicellular cyanobacteria of the *Aphanocapsa feldmanni*-type as symbionts. Wilkinson (1987) also stated that approximately 40% of Caribbean sponge species have a thin layer of tissue containing cyanobacteria that overlies the bulk of the sponge. Furthermore, Wilkinson (1983) demonstrated that the association between cyanobacteria and sponges is similar to that between corals and zooxanthellae as far as biotrophic translocation of nutrients are concerned. Only hadromerid sponges (spirastrellids and clionids) of shallow reefs in the Caribbean were found in this study to have zooxanthellae as endosymbionts.

The specific mechanism which prevented sponges in general from bleaching remains unknown. However, the early evolutionary symbioses between sponges and cyanobacteria (Wilkinson 1984) might have allowed a more stable interaction to evolve between them, than in corals with their zooxanthellae. The sponge-cyanobacteria symbiosis are considered to have evolved 650 million years ago, whereas the coral-zooxanthellae symbiosis evolved during the Middle Triassic, about 200 million years ago (Newell 1972; Oliver 1980).

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References

Corredor JE, Wilkinson CR, Vicente VP, Morel JM, Otero E (1988) Nitrate release by Caribbean reef sponges. Limnol Oceanogr 33:114–120

Glynn PW (1983) Extensive "bleaching" and death of reef corals on the Pacific Coast of Panama. Environ Conserv 10:149–154

Goenaga C (1988) The distribution and growth of *Montastrea annularis* in near shore Puerto Rican Coral reefs. Ph D thesis, University of Puerto Rico, Mayagüez, Puerto Rico, p 214

Goenaga C, Vicente VP, Armstrong R (1989) Bleaching induced mortalities in reef corals from La Parguera, Puerto Rico: a precursor of change in the community structure of coral reefs. Carib J Sci 25:59–65

Hoegh-Guldberg O, Smith GJ (1988) Physiological correlates of light and temperature stress in two pocilloporid corals. Abstracts. 21st Annual Mtg Assoc Mar Labs Caribb, p 57

Newell ND (1972) The evolution of reefs. Sci Am 226:54–65

Oliver WA (1980) The relationship of the scleractinian corals to the rugose corals. Paleobiology 6:146–160

Roberts L (1987) Corals remain baffling. Science 239:256

Rützler K (1974) The burrowing sponges of Bermuda. Smith Contr Zool 165:1–32

Rützler K (1981) An unusual bluegreen alga symbiotic with two new species of *Ulosa* (Porifera: Hymeniacidonidae). PSZNI Mar Ecol:35–50

Rützler K (in press) Associations between Caribbean sponges and photosynthetic organisms. In: Rützler K (ed) New perspectives in sponge biology. Smithsonian Institution Press

Trench RK, Blank RJ (1987) *Symbiodinium microadriaticum* Freudenthal, *S goreauii* sp nov, *S kawagutii* sp nov and *S pilosum* sp nov: gymnodinioid dinoflagellate symbionts of marine invertebrates. J Phycol 23:469–481

Vicente VP (1987) The ecology of the encrusting demosponge *Chondrilla nucula* (Schmidt) in a coral reef community in Puerto Rico. Ph D thesis, University of Puerto Rico, Mayaguez, Puerto Rico, pp 118

Vicente VP (1988) Marine environmental data, inner sublittoral. In: Walton A (ed) Environmental Impact Statement: AT&T, Proposed construction and operation of the Florico II and Transcaribbean Cable System No. 1 (TCS-1) submarine fiber optic cables system within the Coastal Management Zone of the Commonwealth of Puerto Rico, vol II, pp 1–33

Wilkinson CR (1983) Net primary productivity in coral reef sponges. Science 219:410–412

Wilkinson CR (1984) Immunological evidence for the Precambrian origin of bacterial symbiosis in marine sponges. Proc R Soc Lond Ser B 220:509–517

Wilkinson CR (1987) Interocean differences in size and nutrition of coral reef sponge populations. Science 236:1654–1657

Williams EH, Goenaga C, Vicente VP (1988) Mass bleachings on Atlantic coral reefs. Science 238:877–878