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RESEARCH

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Root-derived organic matter confines sponge community composition in mangrove ecosystems

Ellard R Hunting*, Selma M Ubels, Michiel HS Kraak and Harm G van der Geest

Abstract

Introduction: Caribbean mangrove-associated sponge communities are very distinct from sponge communities living on nearby reefs, but the mechanisms that underlie this distinction remain uncertain. It has been hypothesized that dissolved organic matter (DOM) leaching from mangrove roots and the ability of mangrove-associated sponge-bacterial consortia to degrade mangrove DOM may cause this distinction.

Methods: This study tested whether mangrove DOM, leaching from mimicry substrates or directly injected in sponge tissue, affected the performance of a reef and a mangrove sponge species.

Results: Controls and the mangrove sponge remained unaffected by mangrove DOM leaching from mimicry substrates or directly injected in sponge tissue, but the reef species showed substantial necrosis when exposed to mangrove DOM.

Conclusions: Results presented in this study suggest that mangrove DOM confines the composition of sponge communities in mangrove ecosystems, explaining the exclusion of typical reef species and the adjacent occurrence of distinct sponge communities.

Keywords: Dissolved organic matter, Mangrove root, Necrosis, Polyphenols, Sponges, Reef

Introduction

Submerged roots of mangroves along (sub-) tropical Caribbean coasts serve as a substrate that is dominated by sponges. Mangrove-associated sponge communities are relatively species poor and distinct from the diverse sponge communities living on nearby reefs (e.g. van Soest 1978, 1980, 1984; Wulff 2004; Diaz et al. 2012). However, the mechanisms that underlie this distinction remain uncertain (for review, see Wulff 2012). Transplantation experiments of typical reef sponges to mangrove roots revealed that reef species deteriorated quickly after transplantation to coastal mangrove roots (Farnsworth and Ellison 1996; Wulff 2004; Pawlik et al. 2007), where the root substrate is critically important in limiting survival of reef species in mangrove systems (Hunting et al. 2013), while mangrove species remain unaffected. However, the question remains what causes the typically observed deterioration of reef species.

Dissolved organic matter (DOM) is a primary food source for sponge-bacterial consortia (de Goeij et al. 2008a, b), and it has been hypothesized that DOM leaching from mangrove roots plays an important role in structuring mangrove sponge community composition (Hunting et al. 2010b). Mangrove DOM consists mainly of tannins and polyphenolic compounds (Maie and Jaffe 2006), which are structurally complex and recalcitrant to biodegradation (Field and Lettinga 1992; Koch et al. 2005; Kristensen et al. 2008), thereby reducing mangrove palatability and inhibiting growth of fouling organisms on mangrove roots (e.g., Schmitt et al. 1998). A limited number of bacterial and fungal species are able to degrade complex polyphenols and tannins (Bhat et al. 1998). Therefore, the ability of mangrove-associated sponge-bacterial consortia to degrade mangrove DOM may explain the persistence of mangrove species in mangrove ecosystems, while the inability to degrade mangrove DOM could potentially hamper fouling of roots by reef species. However, this remains to be proven experimentally. This study therefore aimed to test whether mangrove DOM leachates from roots are responsible for the observed

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deterioration of reef species transplanted to mangrove roots. To this end, we (1) transplanted a typical reef species and a typical mangrove species to mimicry substrates containing mangrove root extract and to control substrates without extract; and (2) injected mangrove DOM directly into tissues of both sponge species.

Methods

Study site and sponge collection

This study was conducted in Curaçao, N.A., southern Caribbean, in February and March 2013. The selected species included the mangrove sponge *Tedania ignis*, collected from the inner bays Spaanse Water and Piscaderbaai, and the reef sponge *Desmapsamma anchorata*, collected at the site where the transplantation experiment was performed: the shallow reefs in front of the research facility of Carmabi (Caribbean Research and Management of Biodiversity). Both species were chosen for their fast growth (Wulff

2005, 2010). For detailed maps of the study sites, see Hunting et al. (2008, 2010a) and De Goeij et al. (2008b).

Transplantation experiment

The effect of mangrove DOM on sponges was assessed with artificial substrates made from agar that allows mangrove root extracts to slowly diffuse into the overlying water (e.g., Henrikson and Pawlik 1995; Browne and Zimmer 2001; Hunting et al., 2010a). Each mimicry gel was prepared in plastic containers (volume 100 cm³) and consisted of 3% agar (Molecular Genetics/Granulated, Roth, Germany) and 1 mL of mangrove root extract, added to the agar suspension at ~50°C. Mangrove DOM was extracted from freeze-dried and ground *Rhizophora mangle* roots (40 g dry weight) with 70% aqueous acetone for 48 h. Root material was subsequently discarded, and the extract-containing acetone was centrifuged (4,000 rpm for 15 min) and air-dried in a flow cabinet.

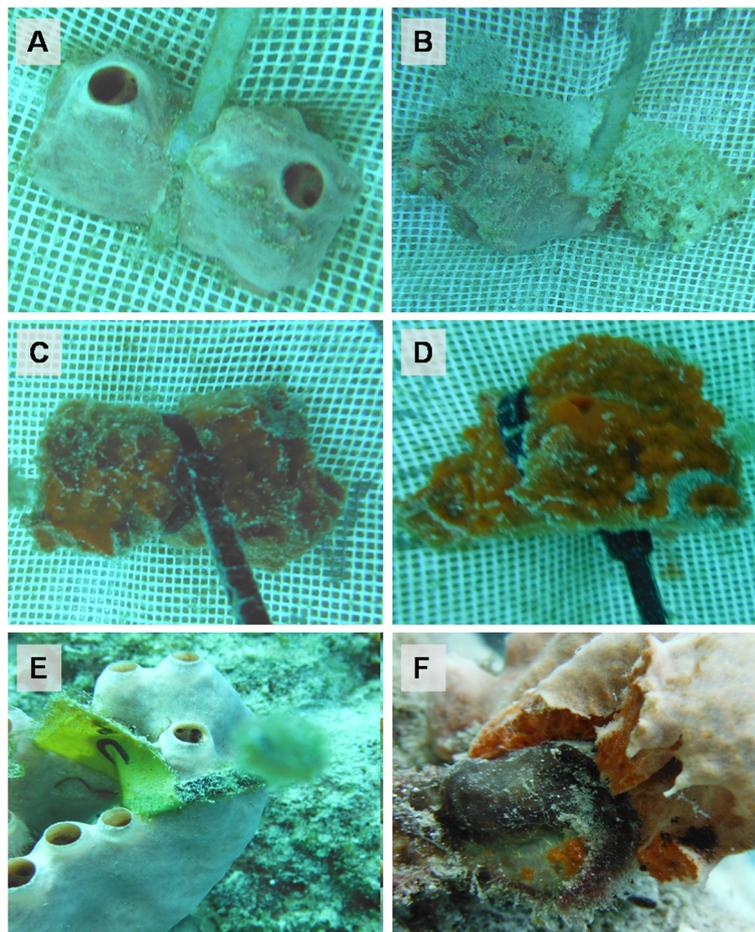


Figure 1 Responses of mangrove and reef sponges to mangrove-derived organic matter. Photographic recordings of the development of the reef sponge *D. anchorata* after transplantation to (A) control gels without mangrove root extract and (B) mimicry gels containing mangrove root extract. *T. ignis* after transplantation to (C) control gels without mangrove root extract and (D) mimicry gels containing mangrove root extract. Direct effects of the injection of (E) seawater and (F) dilute mangrove root extract on *D. anchorata*. Photographs were taken on day 7. The photographs are representative for each treatment ($n = 5$).

The remaining pellet was subsequently resuspended in 100 mL deionized water. Gels were covered with plankton net (mesh size 2.0 mm) to facilitate attachment of sponge transplants with plastic cable ties (Ellison et al. 1996). Five specimens of both *T. ignis* and *D. anchorata* (2–3 cm³) were transplanted to gels containing mangrove DOM, while an additional five specimens of both species were transplanted to gels without mangrove DOM as control. Transplants were evaluated for percent tissue necrosis (formation of white and black lesions) after 1 week and compared with a two-sample *z*-test.

Injection experiment

An additional experiment was performed to assess the direct effect of mangrove DOM on sponges by injecting mangrove DOM in sponge tissues. Five specimens of both *T. ignis* and *D. anchorata* were in situ injected with dilute (1:50) mangrove extract, and an additional five specimens of both species were injected with seawater as control. Injected sponges were evaluated for percent tissue necrosis (formation of white and black lesions) after 1 week and compared with a two-sample *z*-test.

Results and discussion

All specimens of the typical reef species *D. anchorata* transplanted to control substrates without mangrove DOM developed very well (Figure 1A). In contrast, 60% of the specimens transplanted to substrates containing mangrove DOM showed substantial (40–100% of the tissue) necrosis (white lesions) after 1 week (Figure 1D), suggesting that mangrove DOM significantly affected the performance of *D. anchorata* (two-sample *z*-test, $z = 2.1$, $p = 0.0384$). This response is in agreement with previous observations on reef sponges transplanted to mangrove roots (Farnsworth and Ellison 1996; Wulff 2004; Pawlik et al. 2007; Hunting et al. 2013). The mangrove sponge *T. ignis* did not reveal any sign of necrosis on substrates containing mangrove DOM or on the control substrates (Figure 1B,D). Similarly, injection of dilute mangrove extract in *D. anchorata* resulted in necrosis in all specimens, primarily various degrees of black lesions surrounding the site of injection, and altered shape in two specimens, while controls injected with seawater remained unaffected (Figure 1C,F). All *T. ignis* specimens remained unaffected by the injection of both dilute mangrove DOM and seawater (not shown). Injection of mangrove DOM also significantly affected the performance of *D. anchorata* (two-sample *z*-test, $z = 3.2$, $p = 0.0016$).

The present study provided experimental evidence that mangrove DOM can exert negative effects on reef sponges, while mangrove-associated sponges remain unaffected. It has been demonstrated that mangrove-derived organic matter is a major carbon source for sponges living in mangrove ecosystems (Granek et al.

2009), while reef species feed mainly on DOM derived from crustose coralline algae and coral mucus (van Duyl et al. 2011). Sponges attached to mangrove roots are in the direct vicinity of root leachates and exposed to high concentrations of DOM when DOM accumulates in the surrounding water. Our observations thus suggest that mangrove DOM prevents typical reef species from thriving in mangrove ecosystems and support the notion that the composition of DOM can be of general importance to the performance of sponge-bacterial consortia (Hunting et al. 2013).

Conclusions

This study aimed to test whether mangrove DOM leachates from roots are responsible for the typically observed deterioration of reef species transplanted to mangrove roots. We observed that mangrove DOM induced necrosis in a reef sponge, while a mangrove-associated sponge remained unaffected. The inability of reef species to cope with mangrove DOM may therefore confine the composition of mangrove-associated sponge communities, explaining the exclusion of typical reef species and the adjacent occurrence of distinct sponge communities.

Competing interests

The authors declared they have no competing interests.

Authors' contributions

EH conceived the study. SU performed the experiment. EH, SU, MK and HG wrote the paper. All authors read and approved the final manuscript.

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