Ecology, 100(6), 2019, e02668

Filamentous turf algae on tube worms intensify damage in massive *Porites* corals

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Manuscript received 3 December 2018; revised 17 January 2019; accepted 4 February 2019. Corresponding Editor: John Pastor.

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Citation: Hoeksema, B. W., R. J. van der Schoot, D. Wels, C. M. Scott, and H. A. ten Hove. 2019. Filamentous turf algae on tube worms intensify damage in massive *Porites* corals. Ecology 100(6):e02668.

Key words: associated fauna; Christmas tree worm; coral injury; coral reef; epibiont; Gulf of Thailand; Okinawa; Serpulidae; Spirobranchus.

Christmas tree worms of the genus *Spirobranchus* (Polychaeta: Serpulidae) are common associates of reef corals. Regarding host selection, they are known to be generalists, both on Caribbean and Indo-Pacific coral reefs (Hoeksema and ten Hove 2017, Perry et al. 2018*a*). They rarely settle on other invertebrates, such as giant clams (Van der Schoot et al. 2016), but when the original host becomes overgrown by sponges or soft corals, the latter can act as secondary hosts (Hoeksema et al. 2015, García-Hernández and Hoeksema 2017).

The serpulid excretes a calcareous tube, which usually becomes incorporated within the host coral, except for its opening (Nishi and Nishihira 1999). When it senses danger, it retracts inside its tube, which becomes shut by a calcified operculum (Pezner et al. 2017). This operculum is adorned with antler-shaped spines and may become covered by epibiotic algae and invertebrates (Hoeksema et al. 2018, Perry et al. 2018*b*). After the serpulid dies and disappears, its empty tube can become occupied by hermit crabs or fish (Fig. 1a; Schuhmacher 1977, Böhm and Hoeksema 2017).

Despite the wide distribution range, common occurrence and striking appearance of *Spirobranchus* species, little attention has been given to their impact on corals,

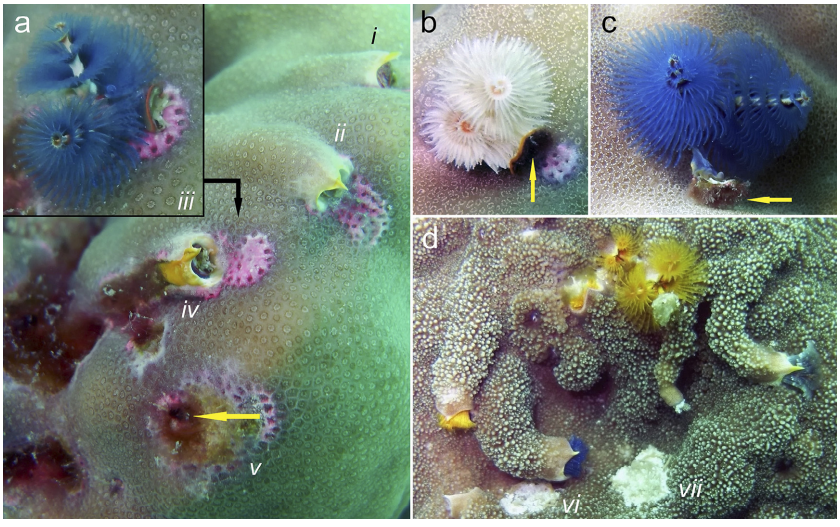

Fig. 1. Christmas tree worms in host corals at Koh Tao, Gulf of Thailand. (a) Coral injuries with pink discolorations next to tube openings on a *Porites* coral: worms retracted in tubes overgrown by coral tissue (i, ii); expanded worm with operculum touching a damaged spot (iii); same worm retracted showing its algae-covered tube (iv); vacated tube, now inhabited by a hermit crab, *Paguritta* sp. (*v*, arrow). (b, c) *Porites* with (b) and without injury (c) next to worm opercula covered by turf algae (arrows), (d) the rough surface of *Montipora informis* may provide protection against damage, but not always (vi, vii).

although some studies indicate benefits for the hosts (DeVantier et al. 1986, Ben-Tzvi et al. 2006). Recently it was discovered that opercula of *Spirobranchus* in the Red Sea can cause injuries in massive *Porites* corals and that some of these opercula serve as substrate for filamentous turf algae (Hoeksema et al. 2018). It was unclear whether this impact is widespread, if other coral species are affected, and what is the role of the algae herein.

To study coral damage caused by *Spirobranchus* opercula with and without algae, we surveyed 10 reef sites around Koh Tao, an island in the Gulf of Thailand (Appendix S1: Fig. S1). The survey took place February–March 2015 by using the roving diver technique within a depth range of 4–10 m, allowing 1 h of dive time per site. Each worm was counted as a single association, but no more than 10 worms per host coral colony were counted in order to limit any possible sampling bias.

In a subsample of 61 *Spirobranchus* individuals (n_{tot} = 749) collected from 21 host species, *S. corniculatus* (Grube, 1862) was the most common associate (77%), followed by *S. richardsmithi* Pillai, 2009 (16%) and *S.* cf. *tetraceros* (Schmarda, 1861; 7%; Appendix S1: Table S1). A few worm tubes were not entirely embedded in the coral skeleton but either remained bare or became covered by filamentous algae (Fig. 1a). Vacated tubes became inhabited by other organisms and surrounded by filamentous algae, hindering the coral's capacity to regenerate (Fig. 1a). A *Spirobranchus* operculum was considered harmful when it caused wounds visible as tissue discoloration or as tissue loss on the adjacent coral surface (Fig. 1a, b), which may prevent polyps to function properly. Among the 749 *Spirobranchus* opercula, 157 (21%) caused such injuries. Pink discoloration may indicate an inflammatory-like reaction (Palmer et al. 2008). When polyps lose soft tissue, the exposed coral skeleton may become covered by algae or sponges that prevent regeneration (Meesters et al. 1997). Eventually, the injuries may cause the whole coral to become more susceptible to deadly diseases (Lamb et al. 2014).

A comparison of the occurrence of operculum-induced injuries in the four most frequently observed host species (n > 50 worm counts) showed significant interspecific variation (Appendix S1: Table S2: P < 0.0001, Fisher's exact test). After post hoc Bonferroni correction, *Porites lobata* Dana, 1846, showed more damage than *P. lutea* Milne Edwards and Haime, 1851 (P < 0.0001), *Montipora informis* Bernard, 1897 (P < 0.0001), and *M. spumosa* (Lamarck, 1816) (P < 0.0001), whereas *P. lutea* only showed more wounds than *M. spumosa* (P < 0.001). The surface of *Porites* polyps is generally smooth (Fig. 1a–c), not offering much resistance to moving opercula, whereas the solid papillae on the rough surface of *Montipora* corals may provide the calices with protection against abrasion, but not always so (Figs. 1d, 2). Variation in damage can also be explained by the worm's position in the coral. If a coral fails to overgrow the worm tube entirely, the tube grows over the coral surface and the worm's operculum may touch the coral surface more easily (Fig. 1a, d) than if it grows perpendicularly to the coral surface, as observed in massive *Porites* corals in Okinawa (Appendix S1: Figs. S2 and S3).

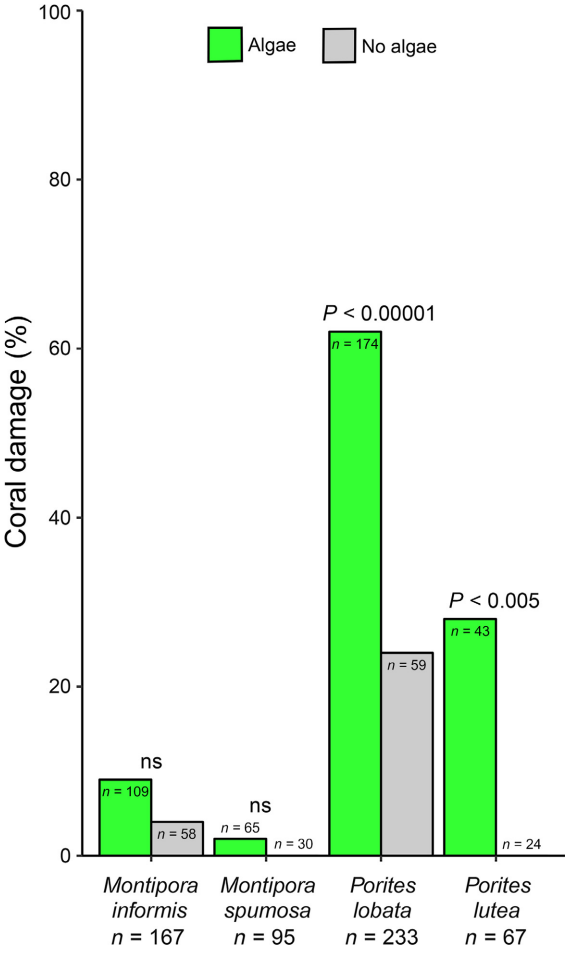

FIG. 2. Proportions of *Spirobranchus* opercula causing coral damage with or without algae in four host coral species at Koh Tao. Interspecific variation was significant (P < 0.0001). More damage was caused by opercula with algae in two massive *Porites* species; ns, not significant (Fisher's exact test).

Opercula covered by filamentous turf algae caused significantly more damage than opercula without algae in the massive corals *Porites lobata* and *P. lutea*, while the two *Montipora* species did not show such a difference (Fig. 2). These results confirm the hypothesis that opercula with algae can be more harmful than those without (Hoeksema et al. 2018), although this may only count for massive *Porites* corals. This finding is consistent with the observation that these corals are susceptible to harm

caused by turf algae (Gowan et al. 2014). It also shows that this phenomenon is not only occurring in the Red Sea (Hoeksema et al. 2018).

Acknowledgments

We thank staff of New Heaven Reef Conservation Program at Koh Tao for hospitality and logistic support and Rahul Mehrotra for his constructive comments on the manuscript. The second and third author received financial support from the Jan-Joost ter Pelkwijk Fund and the Alida B. Buitendijk Fund. The first author is grateful to James D. Reimer for hosting him in Okinawa (Appendix S1: Figs. S2 and S3). We thank two anonymous reviewers and the editor for their constructive remarks.

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