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NOTE

Coral overgrowth by an encrusting red alga (*Ramicrusta* sp.): a threat to Caribbean reefs?

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Abstract An encrusting red alga (*Ramicrusta* sp., Peyssonneliaceae) present in Lac Bay, Bonaire, overgrows and kills corals and other sessile organisms. Living coral tissue comprises 7.2 % of the benthic composition of the shallow reef, while *Ramicrusta* sp. covers 18.7 % of the substratum. Of 1374 coral colonies surveyed, 45.8 % were partially overgrown by *Ramicrusta* sp., with *P. porites*, *P. astreoides* and *M. complanata* being the most susceptible to overgrowth. Mean *Ramicrusta* sp. maximum overgrowth rates ± SD were 0.08 ± 0.05 mm d^{-1}, 0.07 ± 0.03 mm d^{-1} and 0.06 ± 0.02 mm d^{-1} for *M. complanata*, *P. porites* and *P. astreoides*, respectively. None of the 71 coral recruits surveyed were growing on *Ramicrusta* sp. *Ramicrusta* sp. is an immediate threat to corals, reduces the area of suitable substratum for coral settlement and may have the ability to influence coral species composition.

Keywords Alga · Bonaire · Competition · Encrusting macroalgae · Overgrowth · Peyssonnelia · Peyssonneliaceae · *Ramicrusta* · Resilience · Coral

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Introduction

In light of the recent decline in coral reefs worldwide, the resistance of coral reefs to disturbances and the underlying processes of reef resilience have become important areas of research. Phase shifts from coral-dominated to coral-depleted or algal-dominated reefs have occurred on many reefs, particularly in the Caribbean as a result of anthropogenic-induced stressors and natural disturbances (Lewis 1986; Done 1992; Hughes 1994; Hughes et al. 1999; Szmant 2002; McManus and Polsenberg 2004; Burkepile and Hay 2006; Heck and Valentine 2007). As reefs undergo shifts from coral to algae alternate states, knowledge of algal-coral competitive interactions is necessary to understand current reef dynamics and predict future trends.

A variety of mechanisms are employed by sessile reef organisms in their ongoing competition for space (Lang 1973; Jackson and Buss 1975; Wellington 1980; Bak et al. 1981, 1982; Logan 1984; Chornesky 1989; Hughes 1989; Connell et al. 2004; Nugues et al. 2004; Eckrich et al. 2011). Several species of red encrusting macroalgae in the family Peyssonneliaceae overgrow corals (James et al. 1988; Antonius and Ballesteros 1998; Verlaque et al. 2000; Bruckner et al. 2008; Pueschel and Saunders 2009; Ballantine and Ruiz 2011), and one species in particular, *Ramicrusta* sp. (Eckrich et al. 2011), overgrows many species of corals and other benthic organisms in Lac Bay, Bonaire. This particular alga is in the genus *Ramicrusta*, a genus first reported from the Caribbean in 2009 (Pueschel and Saunders 2009). Despite the competitive abilities of *Ramicrusta* sp. and several other Peyssonnelid algae, little is known about the taxonomy, range distributions and abundances of algae in this family. Also poorly understood are the biologic or environmental factors governing competitive outcomes among these encrusting algae and their reef neighbors.

An important indicator of reef resilience is coral recruitment (Bak and Engel 1979; Hughes and Tanner 2000; Grimsditch and Salm 2006; Kuffner et al. 2006; Obura and Grimsditch 2009). Although algae from the *Ramicrusta* genus have a similar growth form and superficially resemble crustose coralline algae, a group that includes many species conducive to coral settlement (Morse et al. 1988; Heyward and Negri 1999; Harrington et al. 2004; Arnold et al. 2010), there is no evidence for successful coral settlement on encrusting algae from this genus.

Because of the recent awareness and abundance of this alga and the apparent threat it poses, we investigated the competitive interactions of *Ramicrusta* sp. in Lac Bay by focusing on the following four factors: the percent benthic cover of the back reef of Lac Bay, the density of coral recruits and the substrates they occur on, the proportion of coral colonies of different species being overgrown by *Ramicrusta* sp. and the rate of coral overgrowth by *Ramicrusta* sp. for three common coral species.

Methods

Coral reefs cover approximately 4 % of Lac Bay, Bonaire (12°5′48″N, 68°13′47″W) and separate the central bay area from the ocean, with sand and seagrass beds comprising the remainder. *Ramicrusta* sp. is abundant on the back reef and is overgrowing corals and other benthic organisms (Eckrich et al. 2011). It forms a thin, crustose layer of variable color (mustard to burgundy) which spreads up from the substrate and grows over living tissues of other organisms.

Samples of *Ramicrusta* sp. were sent to three independent laboratories specializing in Peyssonneliaceae taxonomy. Morphological analysis placed this alga in the genus *Ramicrusta* (D. Ballantine pers. comm.). The genus was confirmed with molecular techniques including rbcL sequence data and COI-5P genetic barcoding and genetic sequencing of this alga did not match either of the described *Ramicrusta* species, *R. nanhaiensis* or *R. textilis* (S. Fredericq pers. comm.; G.W. Saunders pers. comm.).

Fifty random sites were surveyed in the back reef area of Lac Bay (<3 m deep) from January to August 2010. Benthic cover was determined along a 10-m transect line using the line intercept method. Categories included live stony coral (by species), gorgonian (by growth form), non-encrusting macroalgae (by genus), *Ramicrusta* sp., turf algae, sand, bare hard substrate and 'other'. To determine density of coral recruits and the substrates they were growing on, 25 × 25 cm quadrats were surveyed at meter intervals along each 10-m transect line. Within each of the quadrats, visible corals <5 cm in diameter and the substrate they were growing on were recorded. Frequency of *Ramicrusta* sp. overgrowth of living corals was determined by surveying an area 2.5 m on either side of each 10-m transect line. Coral colonies greater than 10 cm diameter were identified, and presence of overgrowth of any part of the colony by *Ramicrusta* sp. was recorded. *Ramicrusta* sp. overgrowth was defined as the presence of a thin crustose layer of *Ramicrusta* sp. growing over living coral tissue.

A minimum of 8 colonies of three coral species susceptible to *Ramicrusta* sp. overgrowth (*Millepora complanata*, *Porites astreoides* and *P. porites*) were marked, and zip ties or nails were used for measurement reference. Of these colonies, monthly photos were taken from November 2009 to January 2011 using a Sony HD SR7 6.1 MP camcorder in an Ocean Images housing. For each photo, a 25 × 25 cm quadrat was placed vertically or horizontally over the coral to standardize the camera angle and a ruler was placed alongside the coral/*Ramicrusta* boundary. Colonies were photographed for a minimum sampling period of 147 days and a maximum sampling period of 447 days. Sampling periods were not equal for all marked colonies due to complete *Ramicrusta* sp. overgrowth of individual corals, overturned corals and lost rebar stakes. *Ramicrusta* sp. maximum overgrowth rates were determined using CPCe 3.6 software and were based on the distance of maximum *Ramicrusta* sp. growth. The Kruskal–Wallace rank sum test was used to determine whether *Ramicrusta* sp. maximum overgrowth rates were different for the three coral species. Using the same coral colonies and methods described above, linear coral growth rates were measured for *M. complanata* and *P. porites* for a period of 325 days. Growth rates for *P. astreoides* were not measured due to the spherical colony form of this species.

Results and discussion

Benthic cover at 15 of the 50 locations was without live coral and was more than 50 % sand. Data from these 15 locations were excluded in the analysis of benthic cover and coral recruits. The dominant benthic substrates of the back reef of Lac Bay were turf algae (growing on bare hard substrates) and sand. Mean percent cover ± SD was 26.6 ± 27.4 for turf algae and 26.4 ± 24.8 for sand (Table 1). *Ramicrusta* sp. (mean percent cover ± SD of 18.7 ± 20.9) was more than twice as abundant as stony corals (6.9 ± 11.6 %). The remainder of the area surveyed was comprised of bare hard substrate with no apparent turf algae (mean percent cover ± SD of 13.4 ± 34.5), non-encrusting macroalgae (7.4 ± 8.8 %), gorgonians (0.3 ± 1.1 %), and zoanthids, seagrass and sponges (0.7 ± 1.5 %). The mean density ± SD of coral recruits was 3.2 ± 4.2 m^{-2} ($n = 71$). All of the recruits were found on bare hard substrate, and none were found on *Ramicrusta* sp.

Table 1 Mean percent benthic cover ± SD by substrate category using line intercept method (10 m) in 2010 in Lac Bay Bonaire ($n = 35$)

Substrate type	Mean percent cover	±SD
Turf algae	26.6	27.4
Sand	26.4	24.8
Ramicrusta sp.	18.7	20.9
Bare hard substrate	13.4	34.5
Macroalgae (non-encrusting)	7.4	8.8
Stony corals	6.9	11.6
Gorgonians	0.3	1.1
Other	0.7	1.5

Bare hard substrate includes pavement, rubble and dead coral colonies

Table 2 Percent coral colonies being overgrown by *Ramicrusta* sp. in 2010 in 10 × 5 m belt transects in Lac Bay Bonaire ($n = 50$)

	Total colonies surveyed	No. colonies being overgrown by *Ramicrusta* sp.	Percent of colonies being overgrown
Porites porites	37	27	73.0
Porites astreoides	730	374	51.2
Millepora complanata	139	71	51.1
Montastraea annularis	130	61	46.9
Sea rods	46	21	45.7
Diploria strigosa	118	50	42.4
Sea fans	22	7	31.8
Porites branneri	28	8	28.6
Siderastrea sidereal	29	6	20.7
Agaricia sp.	5	1	20.0
Diploria clivosa	11	2	18.2
Acropora cervicornis	41	1	2.4
Acropora palmata	33	0	0.0
Diploria labyrinthiformis	1	0	0.0
Siderastrea radians	4	0	0.0
Total	1,374	629	45.8

Overgrowth was defined as *Ramicrusta* sp. overgrowing living coral tissue on any part of the colony

Ramicrusta sp. was overgrowing 12 species of stony corals, a hydrocoral, sea rods and sea fans (Table 2). *P. astreoides* was the most abundant coral species ($n = 730$) followed by *M. complanata* ($n = 139$) and *Montastraea annularis* ($n = 130$). Of 1,374 coral colonies surveyed, 45.8 % were being overgrown by *Ramicrusta* sp. Coral species that had more than 50 % of their colonies overgrown by *Ramicrusta* sp. included *P. porites* (73.0 %), *P. astreoides* (51.2 %) and *M. complanata* (51.1 %). One out of 41 *Acropora cervicornis* colonies was being overgrown and no *Acropora palmata* ($n = 33$), *Diploria labyrinthiformis* ($n = 1$) or *Siderastrea radians* ($n = 4$) colonies were being overgrown by *Ramicrusta* sp.

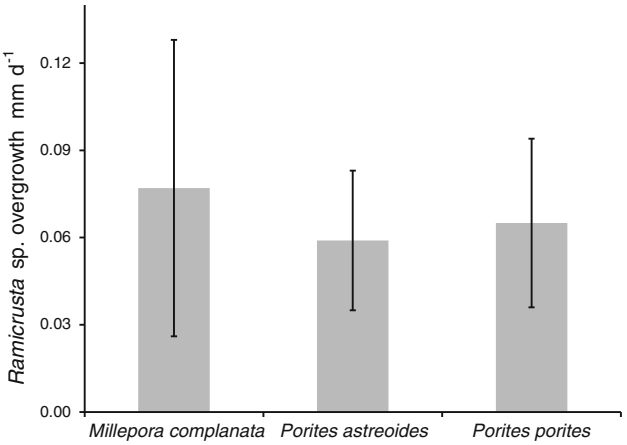

Fig. 1 Mean rate of *Ramicrusta* overgrowth ± SD in 2010 for three of the most common species of corals in Lac Bay, *Millepora complanata* ($n = 9$), *Porites astreoides* ($n = 10$) and *Porites porites* ($n = 8$)

The mean rate ± SD of live tissue overgrowth by *Ramicrusta* sp. was 0.08 ± 0.05 mm d^{-1} for *M. complanata* ($n = 9$), 0.06 ± 0.02 mm d^{-1} for *P. astreoides* ($n = 10$) and 0.07 ± 0.03 mm d^{-1} for *P. porites* ($n = 8$, Fig. 1). There was no difference in the rates of live tissue overgrowth by *Ramicrusta* sp. for the 3 coral species (Kruskal–Wallis Chi squared $= 0.178$, df $= 2$, p value $= 0.9149$). The mean linear growth rates ± SD of *M. complanata* ($n = 4$) and *P. porites* ($n = 5$) being monitored were inferior to the *Ramicrusta* sp. overgrowth rates for each species: 0.04 ± 0.02 mm d^{-1} and 0.05 ± 0.02 mm d^{-1}, respectively. During the sampling period, 1 of each of the 3 species of corals being monitored was completely overgrown. By July 2012 (18 months later), 1 additional *M. complanata*, 4 more *P. porites* and 2 more *P. astreoides* colonies had been completely overgrown by *Ramicrusta* sp.

In conclusion, *Ramicrusta* sp. is locally abundant, offers unsuitable substratum for settlement of coral larvae, and some species of scleractinians (*P. astreoides*, *P. porites* and *M. complanata*) are more susceptible than others (*D. clivosa*, *A. cervicornis*, *A. palmata*) to *Ramicrusta* sp. overgrowth. *Ramicrusta* sp. has the rare ability to overgrow a wide variety of benthic organisms (Eckrich et al. 2011), and this overgrowth is rapid and complete for the species monitored in this study. It decreases the resilience of the

reef and has the potential to alter coral species composition. This may lead to a coral-algae phase shift. The coral-algal dynamics of the back reef of Lac Bay may be a result of recent anthropogenic or natural disturbances (Slijkerman et al. 2011). Monitoring and further study are needed.

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References

Antonius A, Ballesteros E (1998) Epizoism: a new threat to coral health in Caribbean reefs. Rev Biol Trop 46:145–156

Arnold SN, Steneck RS, Mumby PJ (2010) Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. Mar Ecol Prog Ser 414:91–105

Bak RPM, Engel MS (1979) Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Mar Biol 54:341–352

Bak RPM, Sybesma J, van Duyl FC (1981) Ecology of the tropical compound ascidian *Tridemnum solidum*. II. abudance, growth and survival. Mar Ecol Prog Ser 6:43–52

Bak RPM, Termaat RM, Dekker R (1982) Complexity of coral interactions: influence of time, location of interaction and epifauna. Mar Biol 69:215–222

Ballantine DL, Ruiz H (2011) *Metapeyssonnelia milleporoides*, a new species of coral-killing red alga (Peyssonneliaceae) from Puerto Rico, Caribbean Sea. Bot Mar 54:47–51

Bruckner AW, Bruckner RJ, Hill R (2008) Improving restoration approaches for *Acropora palmata*: lessons from the Fortuna Reefer grounding in Puerto Rico. Proc 11th Int Coral Reef Symp 2:1199–1203

Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128–3139

Chornesky EA (1989) Repeated reversals during spatial competition between corals. Ecology 70:843–855

Connell JH, Hughes TP, Wallace CC, Tanner JE, Harms KE, Kerr AM (2004) A long-term study of competition and diversity of corals. Ecol Monogr 74:179–210

Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. Hydrobiologica 247:121–132

Eckrich CE, Engel MS, Peachey RBJ (2011) Crustose, calcareous algal bloom (*Ramicrusta* sp.) overgrowing scleractinian corals, gorgonians, a hydrocoral, sponges, and other algae in Lac Bay, Bonaire, Dutch Caribbean. Coral Reefs 30:131

Grimsditch GD, Salm RV (2006) Coral reef resilience and resistance to bleaching. IUCN, Gland, Switzerland, p52

Harrington L, Fabricius K, De'ath G, Negri A (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. Ecology 85:3428–3437

Heck KL, Valentine JF (2007) The primacy of top-down effects in shallow benthic ecosystems. Estuaries Coasts 30:371–381

Heyward AJ, Negri AP (1999) Natural inducers for coral larval metamorphosis. Coral Reefs 18:273–279

Hughes TP (1989) Community structure and diversity of coral reefs: the role of history. Ecology 70:275–279

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551

Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81:2250–2263

Hughes T, Szmant AM, Steneck R, Carpenter R, Miller S (1999) Algal blooms on coral reefs: what are the causes? Limnol Oceanogr 44:1583–1586

Jackson JBC, Buss L (1975) Allelopathy and spatial competition among coral reef invertebrates. Proc Natl Acad Sci USA 72:5160–5163

James NP, Wray JL, Ginsburg RN (1988) Calcification of encrusting aragonitic algae (Peyssonneliaceae): implications for the origin of late Paleozoic reefs and cements. J Sediment Petrol 58:291–303

Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. Mar Ecol Prog Ser 323:107–117

Lang JC (1973) Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. Bull Mar Sci 23:260–279

Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. Ecol Monogr 56:183–200

Logan A (1984) Interspecific aggression in hermatypic corals from Bermuda. Coral Reefs 3:131–138

McManus JW, Polsenberg JF (2004) Coral–algal phase shifts on coral reefs: ecological and environmental aspects. Prog Oceanogr 60:263–279

Morse DE, Hooker N, Morse ANC, Jensen RA (1988) Control of larval metamorphosis and recruitment in sympatric agariciid corals. J Exp Mar Biol Ecol 116:193–217

Nugues MM, Delvoye L, Bak RPM (2004) Coral defence against macroalgae: differential effects of mesenterial filaments on the green alga *Halimeda opuntia*. Mar Ecol Prog Ser 278:103–114

Obura DO, Grimsditch G (2009) Resilience assessment of coral reefs—Assessment protocol for coral reefs, focusing on coral bleaching and thermal stress. IUCN, Gland, Switzerland, p 70

Pueschel CM, Saunders GW (2009) *Ramicrusta textilis* sp. nov. (Peyssonneliaceae, Rhodophyta), an anatomically complex Caribbean alga that overgrows corals. Phycologia 48:480–491

Slijkerman DME, Peachey RBJ, Hausmann PS, Meesters HWG (2011) Eutrophication status of Lac, Bonaire, Dutch Caribbean including proposals for measures. IMARES Wageningen UR, Report C093(11):40

Szmant AM (2002) Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries 25:743–766

Verlaque M, Ballesteros E, Antonius A (2000) *Metapeyssonnelia corallepida* sp. nov. (Peyssonneliaceae, Rhodophyta), an Atlantic encrusting red alga overgrowing corals. Bot Mar 43:191–200

Wellington GM (1980) Reversal of digestive interactions between Pacific reef corals; Mediation by sweeper tentacles. Oecologia 47:340–343