

Increased density of the corallivore *Drupella cornus* on *Acropora muricata* colonies overgrown by *Padina boryana*

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Abstract This study investigated the percentage of shallow, lagoonal *Acropora muricata* colonies overgrown by the macroalga *Padina boryana* and the density of *Drupella cornus*, a corallivorous gastropod on those colonies, during summer (March) and winter (August) of 1998 and from 2010 to 2014 at Flic-en-Flac, Mauritius. In 1998, the percentage of *A. muricata* colonies covered by *P. boryana* were $11.11 \pm 2.22\%$ (mean \pm SE) and $8.89 \pm 2.22\%$ for summer and winter, respectively, and *D. cornus* density was low for both summer (0.60 ± 0.55 individuals m^{-2} ; mean \pm SE) and winter (0.80 ± 0.84 individuals m^{-2}). However, from 2010 to 2014, a high percentage of coral colonies were observed to be covered by *P. boryana* with peak in summer 2012 ($93.33 \pm 3.85\%$). Increased macroalgal coverage in summer coincided with high *D. cornus* densities of to 30.60 ± 1.21 individuals m^{-2} in summer 2012. During winters of 2010 to 2014, the percentage of macroalga-covered *A. muricata* colonies and *D. cornus* density on the macroalga-covered colonies were lower as compared to summer. Significant positive correlation was obtained between the percentage of *P. boryana*-covered *A. muricata* and the density of *D. cornus* ($r = +0.967$, $p < 0.01$, Pearson correlation) for both seasons. The effective quantum yield at photosystem II (Φ_{PSII}) of *in hospite* zooxanthellae in *A. muricata* measured in the healthy part of the coral colony was 0.62 ± 0.01 (mean \pm SE) and was significantly higher than in the *P. boryana*-affected section, 0.27 ± 0.01 ($p < 0.001$, One-way ANOVA). These results suggest that overgrowth of *P. boryana* is potentially stressful to the *A. muricata* colonies and that shallow, lagoonal *P. boryana*-covered colonies might be more vulnerable to *D. cornus* predation.

Keywords: *Drupella cornus*, *Acropora muricata*, *Padina boryana*, corallivorous, effective quantum yield, Mauritius

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Introduction

Coral reefs are one of the most important marine ecosystems providing global goods and services of up to US\$29.8 billion per year (Cesar 2000; Cesar et al. 2003). Coral reefs also sustain a high diversity of marine organisms and provide key ecological functions (Moberg and Folke 1999). While global stressors such as global warming, sea level rise (Hoegh-Guldberg et al. 2007; Veron et al. 2009) and ocean acidification (van Woesik et al. 2013) pose major threats to reef-building corals, other site-specific or local stressors, namely, coastal development, marine pollution (Hughes et al. 2003), disease outbreaks (Croquer et al. 2003; Jokiel 2004), overfishing and destructive fishing (Cesar 2000), phase shifts (Hughes et al. 2003; McManus and Polsenberg 2004; Hughes et al. 2007) and predation (Lenihan et al. 2011) also impact coral reefs.

Environmental disturbances may lead to macroalgal growth on coral colonies causing stress and eventually coral mortality (Jompa and McCook 2002). Coral-algal competition, ubiquitous in almost all reefs, may alter the overall structure of the reef system (Barott et al. 2012) if herbivory is controlled or reduced (Rasher and Hay 2010). However, the interaction of corals and macroalgae is recognized to be species-specific (Bender et al. 2012) and the response of corals to this stressor is highly variable depending on coral colony size class (Barott et al. 2012). Moreover, allelochemicals such as lipid-soluble metabolites in macroalgal extracts, transferred to coral tissues by direct physical contact, can have negative impact on coral health and contribute to the decline of coral reefs (Rasher and Hay 2010). Bolton et al. (2012) have reported a high diversity of macroalgae, with some 435 species in

the Mauritian coastal waters and on its reefs, however, potential interactions among macroalgae and corals are yet to be investigated.

Coral predation by vertebrates such as butterflyfish (Chaetodontidae) and parrotfish (Scaridae), and invertebrates such as crown-of-thorns sea star *Acanthaster planci* and sea urchin *Eucidaris thouarsii* presents another important stress on coral reefs (Rotjan and Lewis 2008). Corallivory by marine gastropods *Coralliophila abbreviata* (Bright et al. 2015) and *Drupella* spp. may be one of the contributing factors leading to coral mortality worldwide (McClanahan 1994; Al-Horani et al. 2011). *Drupella* spp. have a preferential diet of stressed coral tissues, especially Acroporids (Morton et al. 2002; Rotjan and Lewis 2008; Al-Horani et al. 2011).

This study aimed at assessing the seasonal effect of *P. boryana* abundance and *D. cornus* density on *A. muricata* colonies in a tropical lagoon for the periods of 1998 and from 2010 to 2014. Specifically, we determined during winter and summer (1) the percentage of *A. muricata* colonies covered and not covered by *P. boryana*, (2) the density of *D. cornus* on *A. muricata* colonies covered and not covered by *P. boryana*, and (3) the effective quantum yield of *in hospite* zooxanthellae of *A. muricata*. Based on the results of this study, we hereby hypothesize that *A. muricata* colonies overgrown by *P. boryana* experience stress and are more susceptible to predation by *D. cornus*.

Methods

Field survey

The present study was conducted at Flic-en-Flac, a 13 km long highly frequented white sandy beach located on the west coast of Mauritius (20°17' S, 57°35' E; Fig. 1), during summer (March) and winter (August) 1998 and 2010 to 2014. Three shallow, lagoonal stations, 30 m apart and with depths ranging from 1.0 m to 1.5 m, were surveyed by snorkeling. Fifteen random *A. muricata* colonies were studied at each station within a belt transect of 30 m x 10 m. The number of *A. muricata* colonies covered by *P. boryana* (at least 70% macroalgae coverage) was enumerated and expressed as the percentage of coral colonies covered and not covered by *P. boryana*. Out of the 15 coral colonies, 5 random colonies covered by the macroalga and 5 colonies without macroalgal growth were selected for determining *D. cornus* density. This was achieved by counting the number of *D. cornus* individuals using a 1 m² quadrat placed on each coral colony. *P. boryana* growing on the coral colonies was

removed to count *D. cornus* individuals. The density of *D. cornus* was expressed as the mean number of individuals \pm standard error (mean \pm SE) per m² for coral colonies both covered and not covered by *P. boryana*.

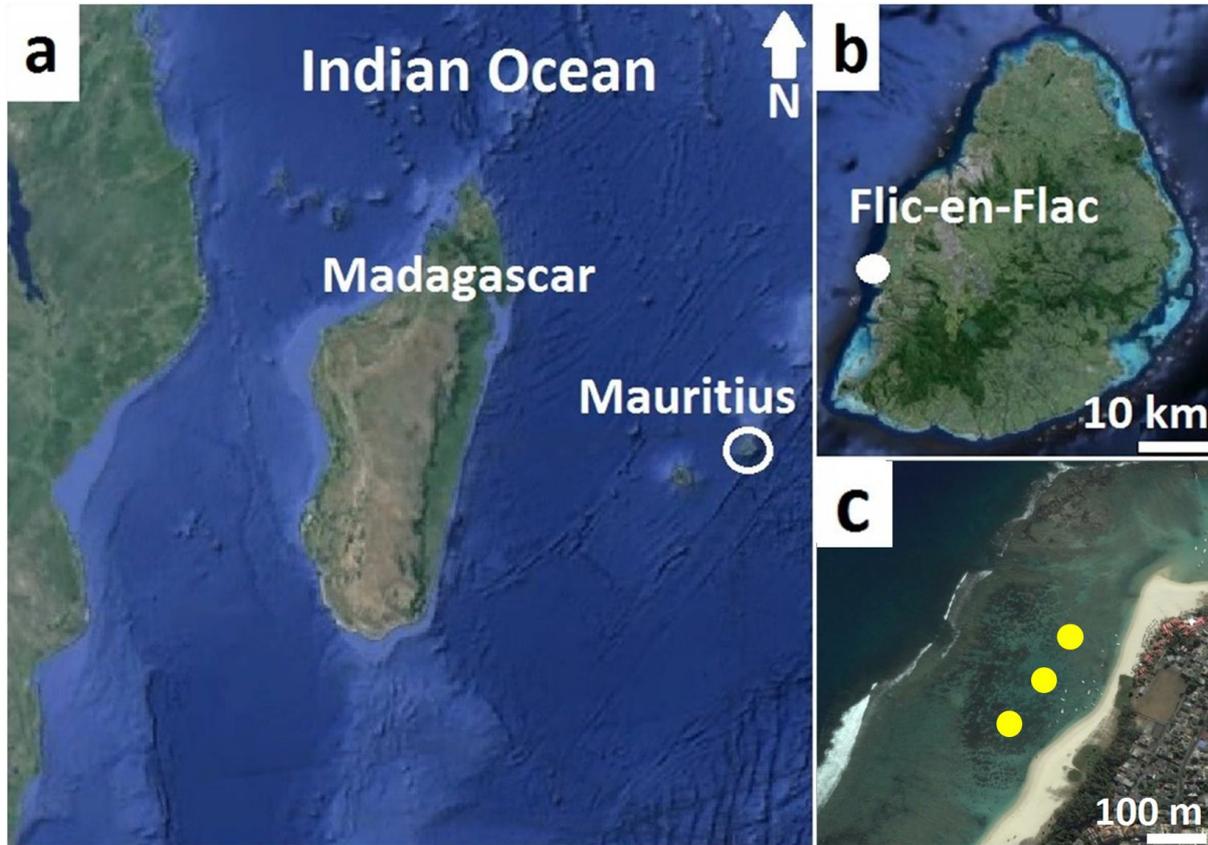


Fig. 1 a) Location of Mauritius in the Indian Ocean. b) Map of Mauritius showing location of Flic-en-Flac. c) The study site in the Flic-en-Flac lagoon with the yellow dots indicating the location of the three lagoon stations (Source: Google Earth 2016)

Physico-chemical analyses

Seawater samples were collected from each station in triplicate per season per year for determination of nitrate and phosphate concentrations using the cadmium reduction and the ascorbic acid methods, respectively, following the standard methods of Greenberg et al. (1992). The monthly mean rainfall data for March and August for 1998 and 2010 to 2014 was acquired from the Mauritius Meteorological Services. In 1998, a thermometer was used to record sea surface temperature (SST) for summer (March) and winter (August), while from 2010 to 2014, temperature data was acquired every 15 minutes using data loggers (HOBO, Pendant).

Chlorophyll *a* fluorescence measurements

A Diving Pulse-Amplitude-Modulated fluorometer (D-PAM, Heinz Walz GmbH) was used *in situ* to photo-physiologically assess the health status of zooxanthellar symbionts (Smith et al. 2006) associated with *A. muricata* in 2013-2014. This was quantified as the effective quantum yield (Φ_{PSII}) which is a unitless measure of the efficiency of photosystem II (PSII) within light-adapted photosynthetic organisms generally ranging from 0.0-1.0 (Smith et al. 2006; Rasher and Hay 2010). Typically, the range for healthy corals is from 0.5 to 0.7 while for severe stress/ bleaching and mortality it is \sim 0.0 to 0.2 (Smith et al. 2006; Bhagooli and Hidaka 2006). PAM measurements were taken in ambient light conditions between 1000 to 1400 hrs on (1) *P. boryana*-affected region on the coral, (2) the coral section adjacent to the *P. boryana*-affected region, and (3) a healthy-looking coral segment not affected by *P. boryana*. The effective quantum yield was determined by the expression $(F'_m - F_o)/F'_m$, where F_o is the initial fluorescence measured by applying weak pulses, and F'_m is the fluorescence obtained by applying a saturated pulse in a light-adapted sample when PSII reaction centres are partially closed/ open (Genty et al. 1989).

Statistical analyses

The normality of the data was determined by the Shapiro-Wilk test using SPSS (PASW Statistics 18.0.0). The data was arcsine (square root) transformed before conducting further statistical analyses. Density data was log (base-10) transformed. A three-way ANOVA was applied to evaluate the significant differences in inter-annual variations, seasonal variations and coral condition (covered and not covered by *P. boryana*) for the density of *D. cornus*. Correlations among *D. cornus* density on the percentage of colonies covered by *P. boryana*, nutrient levels and rainfall were expressed as Pearson's correlation coefficient (r). One-way ANOVA was used to test the significant differences in mean values of effective quantum yield among the macroalga-affected region on the coral, the part adjacent to the macroalga-affected region and in the healthy coral segment, followed by Tukey's post hoc analysis for comparison of means.

Results

Percentage of coral colonies covered by *P. boryana* and *D. cornus* density

In 1998, the percentage of *A. muricata* colonies covered by *P. boryana* was $11.11 \pm 2.22\%$ (mean \pm SE) in summer and $8.89 \pm 2.22\%$ in winter (Fig. 2a). An opposite trend was observed for the summer months of 2010 to 2014 wherein higher percentage of *A. muricata* colonies were covered by *P. boryana* with mean percentages ranging from $62.22 \pm 5.88\%$ to $93.33 \pm 3.85\%$. During the winter months of 2010 to 2014, the percentage of coral colonies covered by macroalga declined drastically ranging from $15.56 \pm 5.88\%$ to $26.67 \pm 3.85\%$. Summer 2012 experienced the highest percentage of *P. boryana*-covered *A. muricata* colonies ($93.3 \pm 3.85\%$).

In summer 1998, the density of *D. cornus* on *P. boryana*-covered *A. muricata* colonies was 0.60 ± 0.55 individuals m^{-2} (mean \pm SE) and 0.40 ± 0.24 individuals m^{-2} on non-covered coral colonies (Fig. 2b), whereas in winter 1998, *D. cornus* density on the *P. boryana*-covered colonies was 0.80 ± 0.84 individuals m^{-2} and 0.80 ± 0.49 individuals m^{-2} on non-covered coral colonies. From 2010 to 2014, the density of *D. cornus* on *P. boryana*-covered *A. muricata* colonies (Fig. 2b) was significantly higher ($p < 0.001$, One-way ANOVA) in the summer months with values of 17.60 ± 2.71 , 17.00 ± 2.63 , 30.60 ± 1.21 , 17.4 ± 2.16 and 19.6 ± 2.25 individuals m^{-2} during 2010, 2011, 2012, 2013 and 2014, respectively. During the winter months of these years, their densities were 6.40 ± 0.98 , 6.20 ± 1.59 , 6.20 ± 0.98 , 5.20 ± 0.86 and 5.40 ± 0.92 individuals m^{-2} , respectively. The density of *D. cornus* on the coral colonies not covered by *P. boryana* was comparable during 1998 and 2010 to 2014, with the exception of summer 2012 (Fig. 3) where it peaked considerably reaching a density of 5.20 ± 0.86 individuals m^{-2} .

Both separate and combined effects of year, season and coral colony condition (covered and not covered by *P. boryana*) had a significant interaction on *D. cornus* density ($p < 0.001$, Three-way ANOVA) (Table 1). There was a significant positive correlation between the percentage of *A. muricata* colonies covered by *P. boryana* and the density of *D. cornus* on *P. boryana*-covered *A. muricata* colonies ($r = +0.97$, $p < 0.01$, Pearson's correlation) for summer and winter (Table 2).

Physico-chemical measurements

The mean SST in summer was $29.03 \pm 0.22^\circ\text{C}$ (mean \pm SE), $26.52 \pm 0.02^\circ\text{C}$, $29.29 \pm 0.01^\circ\text{C}$, $28.27 \pm 0.02^\circ\text{C}$, $28.55 \pm 0.01^\circ\text{C}$ and $29.33 \pm 0.01^\circ\text{C}$ for 1998, 2010, 2011, 2012, 2013 and

2014, respectively. During winters of these years, SST was recorded as $24.95 \pm 0.26^{\circ}\text{C}$, $23.50 \pm 0.01^{\circ}\text{C}$, $24.55 \pm 0.01^{\circ}\text{C}$, $24.13 \pm 0.01^{\circ}\text{C}$, $23.84 \pm 0.01^{\circ}\text{C}$ and $24.75 \pm 0.01^{\circ}\text{C}$, respectively.

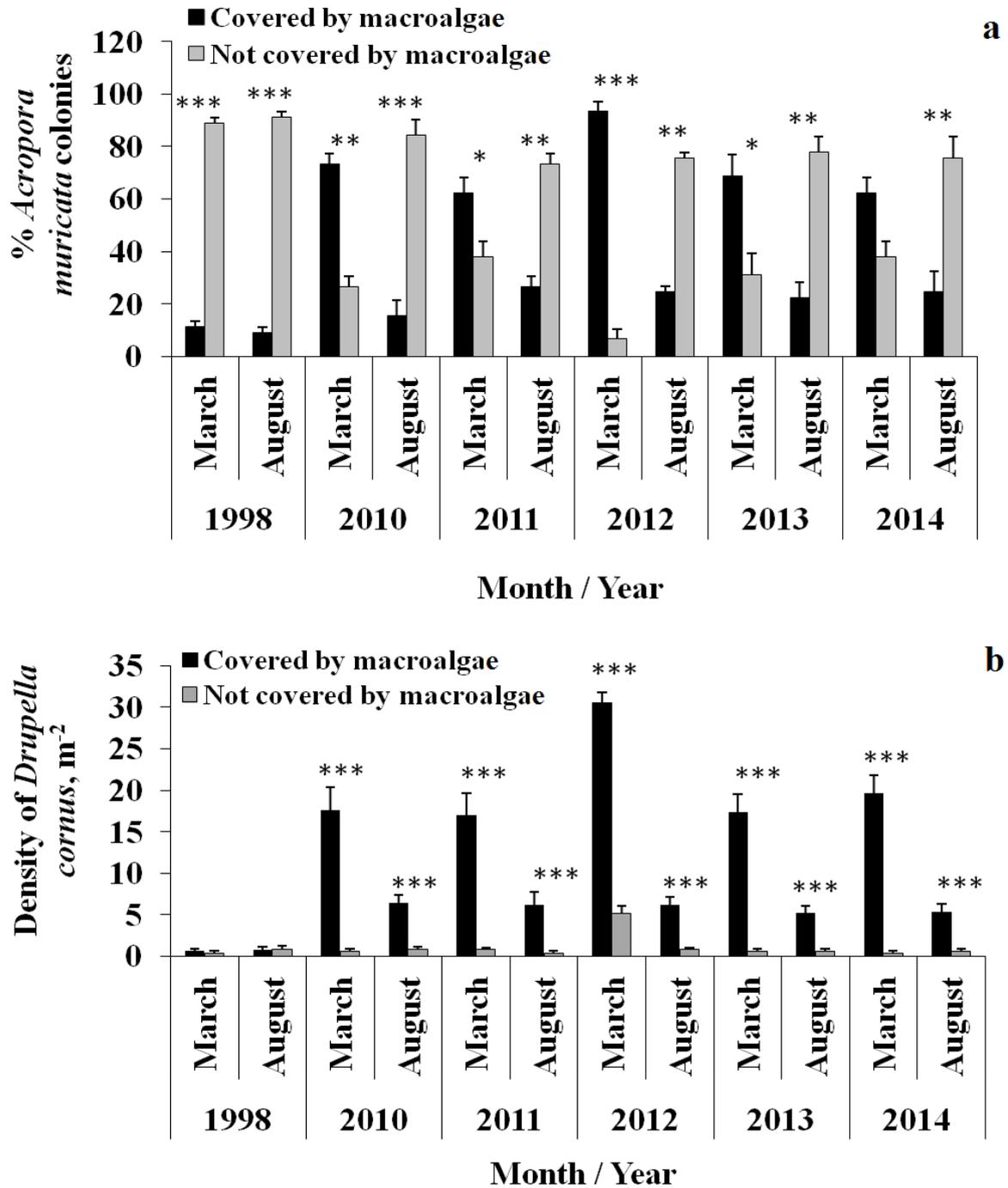


Fig. 2 a) Percentage of *A. muricata* colonies covered and not covered by the macroalgae, *P. boryana*, b) Density of *D. cornus* on coral colonies covered (at least 70% coverage by macroalgae) and not covered by *P. boryana*. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ (Tukey's post hoc) representing comparison between *D. cornus* density on coral colonies covered and not covered by *P. boryana*

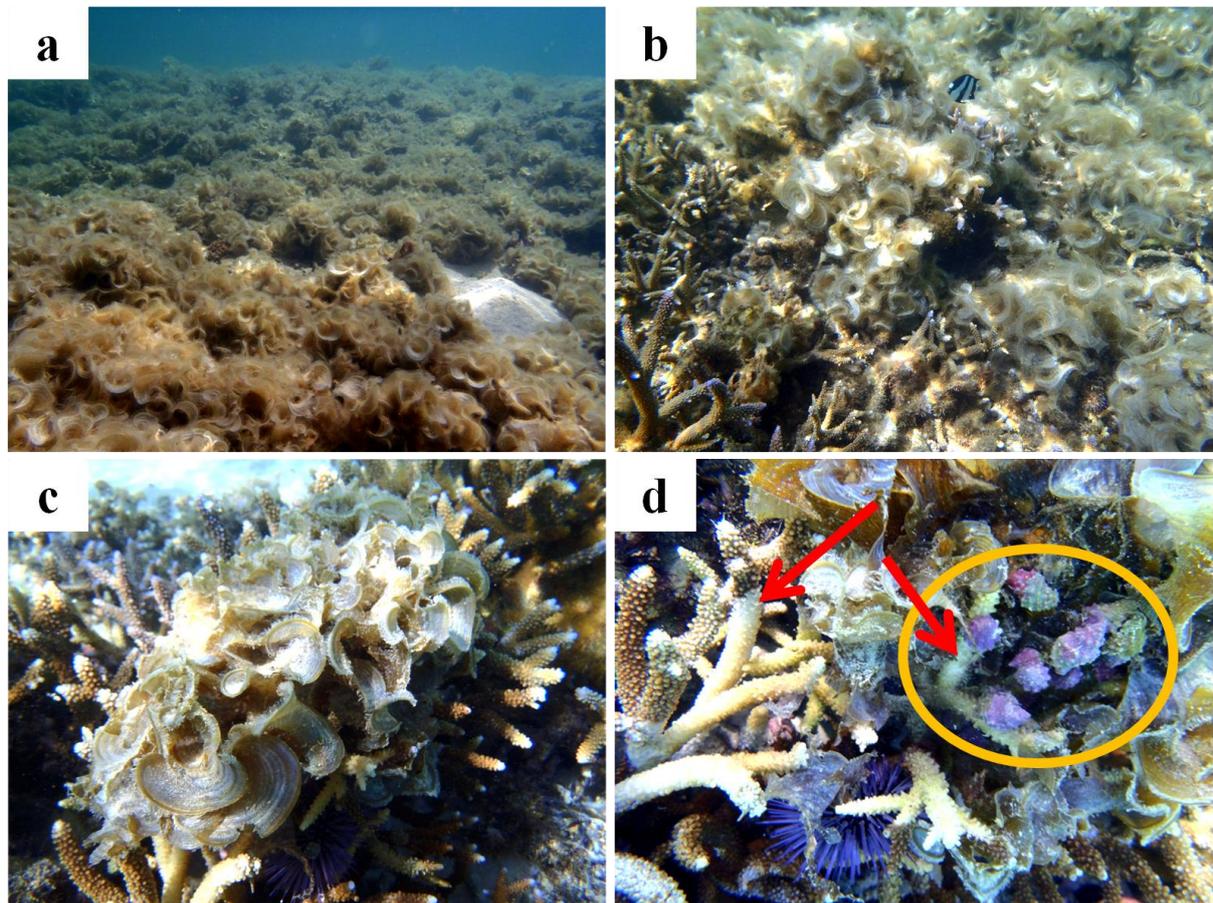


Fig. 3 a) *P. boryana* bloom in March 2012. b) *P. boryana* overgrowing a large *A. muricata* colony. c) Close-up view of an *A. muricata* colony covered by *P. boryana*. d) *P. boryana* removed to reveal *D. cornus* individuals feeding on *A. muricata* tissues (yellow) and predation scars (red arrows)

Except for the year 1998, nitrate and phosphate levels were in general higher in summer as compared to winter (Fig. 4a). It is noteworthy that in summer 2012 nitrate and phosphate concentrations showed a considerable increase up to $13.70 \pm 0.70 \mu\text{M}$ and $3.77 \pm 0.15 \mu\text{M}$, respectively, and that the highest monthly mean rainfall was recorded in summer 2012 (350 mm) (Fig. 4b).

Significant positive correlations between the rainfall, the percentage of *A. muricata* colonies covered by *P. boryana* and the density of *D. cornus* on *P. boryana*-covered *A. muricata* colonies were obtained for the summer and winter months ($r = +0.93$, $p < 0.01$ and $r = +0.95$, $p < 0.01$, respectively) (Table 2). The aforementioned variables also displayed positive correlations with nitrate and phosphate concentrations (Table 2).

Photo-physiological measurements of chlorophyll *a*

One-way ANOVA revealed significant differences in means of effective quantum yield among the three coral parts tested ($p < 0.001$; One-way ANOVA, Tukey's post hoc). The macroalga-affected part of *A. muricata* exhibited the lowest effective quantum yield with

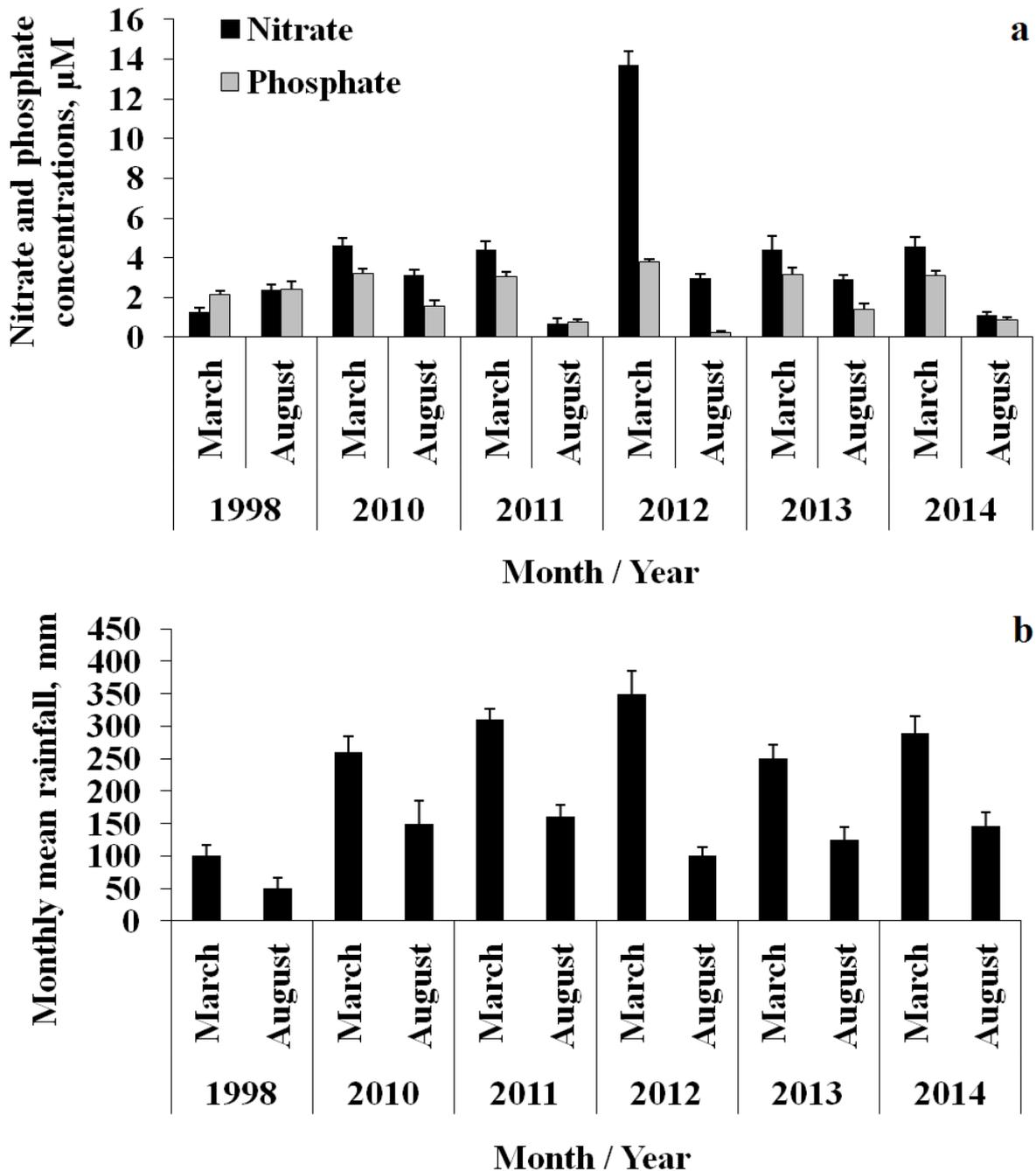


Fig. 4 a) Nitrate and phosphate levels for the months of March and August of the years 1998, 2010, 2011, 2012, 2013 and 2014. b) Monthly mean rainfall for the months of March and August of the years 1998, 2010, 2011, 2012, 2013 and 2014

Φ_{PSII} values of 0.27 ± 0.01 (mean \pm SE, n=5), while the adjacent *P. boryana*-affected and healthy-looking parts displayed higher Φ_{PSII} values of 0.41 ± 0.02 and 0.62 ± 0.01 , respectively.

Table 1 Three-way ANOVA for the effects of year, season (summer and winter) and condition (*A. muricata* colony covered and not covered by *P. boryana*) on the density of *D. cornus*. *** = p<0.001, NS = not significant

Parameter	Source of variation	df	MS	F	p-value	
<i>D. cornus</i> density	Year	5	204.348	29.456	5.2×10^{-18}	***
	Season	1	1222.408	176.203	1.9×10^{-23}	***
	Condition	1	3050.208	439.670	1.3×10^{-37}	***
	Year*Season	5	110.788	15.969	2.0×10^{-11}	***
	Year*Condition	5	134.308	19.360	2.7×10^{-13}	***
	Season*Condition	1	980.408	141.320	1.4×10^{-20}	***
	Year*Season*Condition	5	52.508	7.569	4.9×10^{-6}	***
Nitrate level	Year	5	0.032	97.985	5.4×10^{-24}	***
	Season	1	0.117	354.392	8.4×10^{-24}	***
	Condition	1	0.000	0.000	1.000	NS
	Year*Season	5	0.023	69.539	8.2×10^{-21}	***
	Year*Condition	5	0.000	0.000	1.000	NS
	Season*Condition	1	0.000	0.000	1.000	NS
	Year*Season*Condition	5	0.000	0.000	1.000	NS
Phosphate level	Year	5	0.002	9.034	4.2×10^{-6}	***
	Season	1	0.095	384.131	1.5×10^{-24}	***
	Condition	1	0.000	0.000	1.000	NS
	Year*Season	5	0.008	33.766	1.3×10^{-14}	***
	Year*Condition	5	0.000	0.000	1.000	NS
	Season*Condition	1	0.000	0.000	1.000	NS
	Year*Season*Condition	5	0.000	0.000	1.000	NS

Table 2 Pearson correlation (r) values for studied parameters. ** = p<0.01, * = p<0.05

	Percentage of <i>A. muricata</i> colonies covered by <i>P. boryana</i>	<i>D. cornus</i> density on <i>P. boryana</i> -covered <i>A. muricata</i> colonies	Rainfall	Nitrate	Phosphate
Percentage of <i>A. muricata</i> colonies covered by <i>P. boryana</i>	-	0.967**	0.933**	0.820**	0.660**
<i>D. cornus</i> density on <i>P. boryana</i> -covered <i>A. muricata</i> colonies	0.967**	-	0.953**	0.808**	0.566
Rainfall	0.933**	0.953*	-	0.701*	0.637*
Nitrate	0.820**	0.808**	0.701*	-	0.651*
Phosphate	0.660*	0.566	0.637*	0.651*	-

Discussion

The present study, based on field observations, provides insights into the association of a corallivore with macroalga-covered coral colonies, focusing on the coral – predator – macroalga (*A. muricata* - *D. cornus* - *P. boryana*) association in Mauritian waters. Numerous authors have previously documented the occurrence of *Drupella cornus* on *Acropora* spp. (Turner 1994; Zuschin et al. 2001; Schoepf et al. 2010; Al-Horani et al. 2011).

In 1998, the density of *D. cornus* on *A. muricata* colonies did not vary greatly between the two seasons, irrespective of macroalga coverage which was lower compared to the period from 2010 to 2014. It is likely that herbivory was controlling the growth of *P. boryana* in 1998. Leckraz (2015) observed a decrease in herbivorous fish density in the coastal waters of Mauritius from 1998 to 2015 at Bel Ombre, southwest coast and Anse La Raie, northeast coast of Mauritius. During 2010 to 2014, a higher percentage of coral colonies were covered by *P. boryana* in summer compared to winter, possibly owing to the seasonality of *P. boryana*, which is observed to proliferate during the summer season. Higher concentrations of nitrate and phosphate are known to promote the growth of the macroalga (McManus and Polsenberg 2004). Higher nutrient levels were recorded in the summers of the years from 2010 to 2014.

High *P. boryana* coverage in summer months also coincided with higher *D. cornus* density occurring underneath *P. boryana*-covered colonies. This could be attributed to increased growth of macroalga on the coral resulting in a decreased resistance to stress and a higher vulnerability to *D. cornus* predation (Morton et al. 2002, Rotjan and Lewis 2008, Al-Horani et al. 2011, Bright et al. 2015). Macroalgae release labile dissolved organic carbon (DOC) from live and decomposing tissues reaching up to 39% of the gross production in brown algae (Khailov and Burlakova 1969). The release of DOC by macroalgae could cause an increase in microbial growth on corals, resulting in coral stress and, eventually, coral mortality (Kline et al. 2006; Smith et al. 2006).

The amount of rainfall and SST were higher in summer compared to winter in 1998 and from 2010 to 2014. Bhagooli and Taleb-Hossenkhan (2012) reported high SST (> 30°C) during the summer in Flic-en-Flac lagoon, while the average SST for summer and winter reported from Belle Mare by Louis et al. (2016) were 30.5°C and 25.5°C, respectively. The trend in our temperature data is consistent with published literature.

Our results (Fig. 5) suggest that macroalgal overgrowth coupled with corallivory, may affect the future growth and survival of corals. Consistent with our observations, Wolf and

Nughes (2013) first reported the synergistic impacts of corallivorous fireworm *Hermodice carunculata* and macroalga *Halimeda opuntia* on the reef-building coral *Orbicella faveolata* in the Caribbean, whereby, they observed algal-induced corallivory in aquaria and *in situ* experiments. It was speculated that decaying coral tissue results from macroalgal contact with the coral, and this attracts the coral-eating organism and increases its aggregation behaviour.

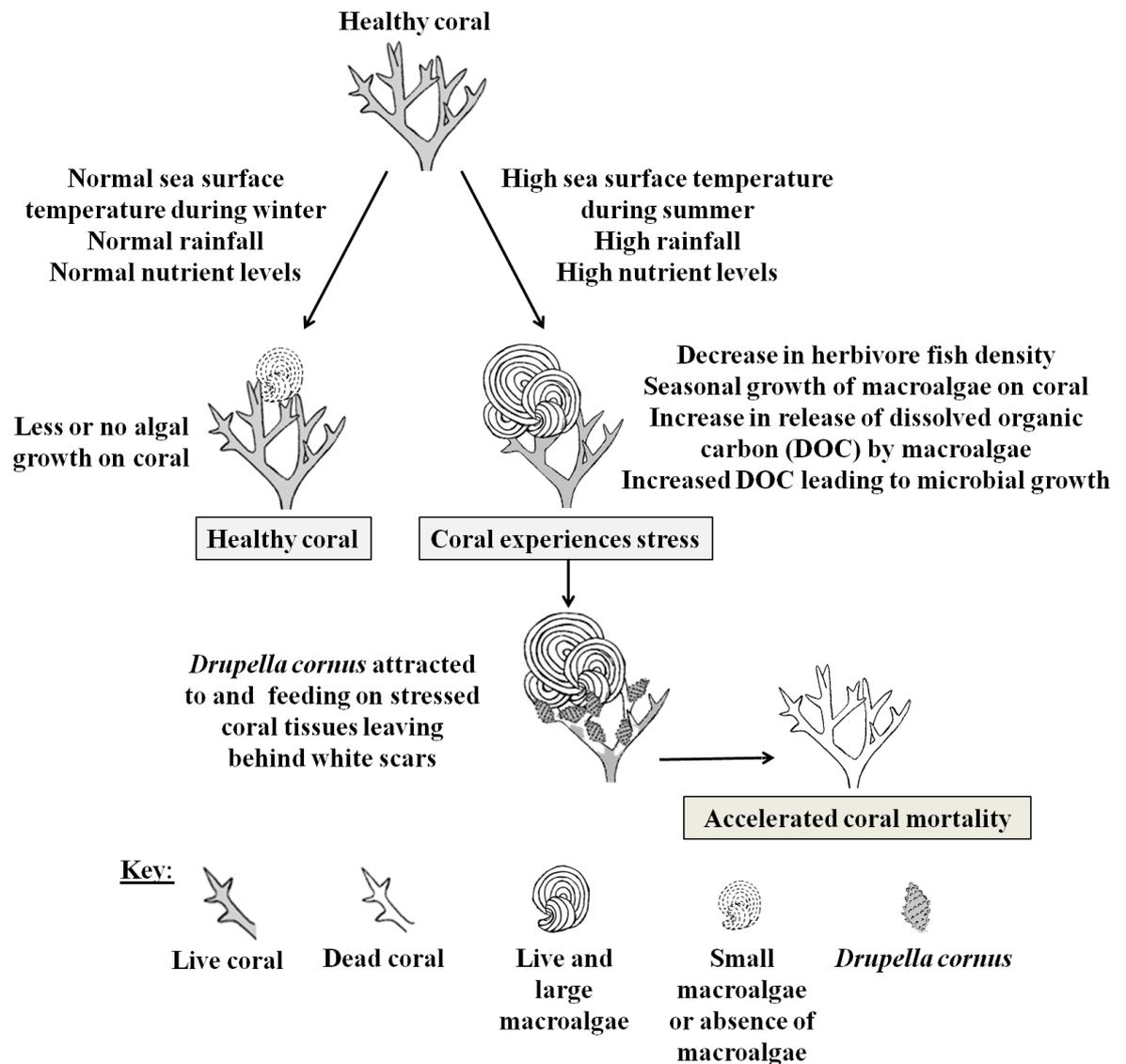


Fig. 5 Proposed scenario depicting the combined effect of macroalgae overgrowth and gastropod corallivory on the health of corals

Previous studies have demonstrated the adverse effects of algal growth on corals, such as competition (McCook et al. 2001; Barott et al. 2012), leading to stress in corals. Morton et al. (2002) demonstrated that *D. rugosa* individuals preferred a diet composed of stressed *A.*

pruinosa live tissues, while Bright et al. (2015) reported the preference of *C. abbreviata* for diseased or mechanically damaged *A. cervicornis*.

Photo-physiological measurements on *A. muricata* revealed evident variations in the effective quantum yield of *in hospite* zooxanthellae, indicative of varying levels of stress in the coral holobiont. *A. muricata* photo-physiology was indeed most compromised at the *P. boryana*-affected region, indicating that the coral was stressed by *P. boryana*. A decrease of 56% in the *in hospite* zooxanthellae photosynthetic efficiency in *A. muricata* was observed upon direct contact with *P. boryana* leading to shading and abrasion effects and also possibly due to the occurrence of a large amount of soluble allelopathic metabolites on the macroalga surface (Rasher and Hay 2010). *A. muricata*, when subjected to *in situ* bioassays, has been found to be susceptible to macroalgal extracts and it experienced visual bleaching upon contact with the extracts leading to impairment in the coral (Vieira et al. 2016).

Decreased effective quantum yield of *in hospite* zooxanthellae in corals can be due to environmentally-induced damage to PSII (Warner et al. 1999) and/or damage to dark reaction of photosynthesis (Jones et al. 1998), or even repair mechanism of PSII (Yakovleva and Hidaka 2004, Bhagooli 2013) leading to bleaching. This has often been linked to thermal anomalies or high irradiance levels. *A. muricata* has been reported to be vulnerable to thermal stress and subsequently, bleaching (Mattan-Moorgawa et al. 2012). It has also been demonstrated that horizontal branches of *A. muricata* tend to be more susceptible to bleaching than upright ones (Bhagooli 2012), leading to a higher level of stress in horizontally positioned *A. muricata* branches. In this investigation, reduced effective quantum yield of *in hospite* zooxanthellae in corals covered by *P. boryana* might not be directly associated with environmentally-induced factors such as elevated sea SST or high solar irradiance as different parts of the same coral branch occurring at the same location were used for photo-physiological evaluation.

Although shallow, lagoonal *A. muricata* colonies at Flic-en-Flac (Bhagooli and Taleb-Hossenkhan 2012) and at Belle Mare (Bhagooli and Taleb-Hossenkhan 2012; Louis et al. 2016) have been reported to possess enhanced physiological capacities through acclimatisation and thus are potentially less susceptible to bleaching compared to the reef flat colonies, the occurrence of *D. cornus* on these colonies indicates that these colonies may not be spared from corallivore predation. In an effort to conserve live coral cover, a few studies (Miller 2001, Williams et al. 2014) have demonstrated that the removal of the corallivorous snail *C. abbreviata* allowed the coral *A. palmata* to maintain more live tissue area compared to corals which were not subjected to snail removal. Thus, the management strategy of partial

active removal of such gastropods from the reef system is suggested to considerably reduce corallivore densities and associated impacts on live corals. Though it is impossible to entirely eliminate overgrowing macroalgae from a reef system, non-destructive mechanical removal of invasive macroalgae, as well as management efforts to increase the numbers of herbivorous fish is another option to be considered (Kamalakaran et al. 2014).

To thoroughly understand the interaction between algal overgrowth and corallivory on *A. muricata* in Mauritian waters, further experimental studies are warranted. Appropriate efforts by relevant authorities could potentially focus on sustainable ways to improve coral reef management by minimizing the impacts of multiple stressors such as corallivory and algal overgrowth.

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