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Importance of heterotrophic adaptations of corals to maintain energy reserves

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Abstract. We examined the ability of the two hard coral species *Agaricia tenuifolia* and *Porites furcata* to store lipids under natural conditions, under experimental starvation (weekly vs. daily feeding) and under heat stress. *P. furcata* fed more and accumulated greater lipid quantities than *A. tenuifolia*. Overall, lipid levels *in situ* showed an inverse relationship to turbidity and eutrophication with highest values at the least anthropogenically impacted site. Although zooxanthellae, chlorophyll *a* concentrations and heterotrophy increased in low light, the adaptive response was insufficient to maintain high energy acquisition levels. In the feeding experiment, corals fed weekly contained higher lipid levels than corals fed daily, suggesting that intermittent periods of starvation induce lipid storage. When transplanted to low light conditions *P. furcata* profited from feeding and were able to restore zooxanthellae and chlorophyll *a* levels after an initial reduction. Generally, lipid accumulation in both species was higher when fed with phytoplankton (≤1 µm), suggesting phytoplankton could be a more efficient food source than zooplankton (>180 µm). Temperature stress led to a reduction of lipids and a 100 % mortality of *A. tenuifolia*, while *P. furcata* exhibited the ability to rebuild lipid reserves through heterotrophy. This ability of *P. furcata* to rebuild energy for both host and symbiont resulted in lower mortality and strong fitness and resistance of this species, making it an important umbrella species to maintain reefs in areas strongly impacted by anthropogenic activities and increasing sea water temperatures.

Key words: energy reserves, lipid, starvation, high temperature stress, heterotrophy.

Introduction

In reef building corals (Scleractinia) energy is obtained from a symbiotic interaction between the endodermic zooxanthellae and heterotrophy from the host polyps (Anthony and Fabricius 2000). Energy reserves are used in times of starvation (Grottoli et al. 2004; Houlbrèque and Ferrier-Pagès 2009). Conversely, when photosynthesis and food ingestion is optimized energy reserves are accumulated (Rodrigues and Grottoli 2007). Whether a coral survives a stress event that reduces autotrophic nutrition is largely determined by the quantity of its stored lipid reserves and its heterotrophic competences (Anthony 2000; Anthony et al. 2009). The amounts of lipid reserves provide a physiological proxy for fitness and are a good bioindicator of the coral health (Anthony and Connolly 2004; Anthony 2006). Coral fitness and health is reflected by the animal's ability to grow, reproduce and survive over time, to absorb disturbances and the capacity to offset stress (Anthony and Connolly 2004).

This study combined various determining factors that result in fluctuations of lipid reserves: regular feeding vs. starvation, zooplankton feeding vs. phytoplankton feeding, and heterotrophic food ingestion during a bleaching event induced by heat stress. The aim was to determine the energetic potential of nutrition through heterotrophy, in particular when photosynthetic carbon fixation is reduced or interrupted, and to examine the ability of corals to store lipids under starvation and heat stress conditions.

Material and Methods

The study was carried out in 2011 in the Bocas del Toro Archipelago in Panama. Sampling was conducted at four sites subjected to different intensities of turbidity and eutrophication from river run off, wastewater discharge and shipping traffic. Sites were chosen based on differences in biological and physiological parameters (Table 1). Three of the study sites were located within Bahía Almirante

(Almirante bay): Almirante (AL), which was exposed to the port and the city of Almirante, Pastores (PA), a site exposed to the port and the sediment plume from the Boca del Drago bay inlet and Juan Point (JP), exposed to the sediment plume from the bay inlet. Site Salt Creek (SC) was situated outside the bay in a location more exposed to the open ocean (Fig. 1). Anthropogenic impacts, such as the observed differences in turbidity and eutrophication of bay water could be factors influencing significant differences in the hard coral cover (Table 1), between sites inside and the site outside the bay (paired t-test, $P<0.01$).

Table 1: Site description: Main environmental parameters for turbidity (total suspended solids [TSS], irradiance at 3 m depth of photosynthetic active radiation [PAR] and visibility [secchi depth]), eutrophication seen in phytoplankton growth (chlorophyll a [Chl a], and reef composition (hard coral [HC] diversity and cover).

Sites	TSS [mg L^{-1}] n=14	Secchi [m] n=7	PAR [µmol m^{-2} s^{-1}] n=7	Chl *a* [µg L^{-1}] n=7	No of HC species	HC Cover [%]
AL	4.21 ± 3.3	5.9 ± 1.4	507 ± 252	0.88 ± 0.3	7	23 ± 4
PA	3.65 ± 3.1	7.5 ± 2.7	537 ± 274	0.97 ± 0.9	11	21 ± 5
JP	4.74 ± 3.3	7.3 ± 2.9	457 ± 261	0.52 ± 0.4	23	31 ± 4
SC	4.00 ± 2.5	7.4 ± 2.9	540 ± 296	0.58 ± 0.3	35	44 ± 2

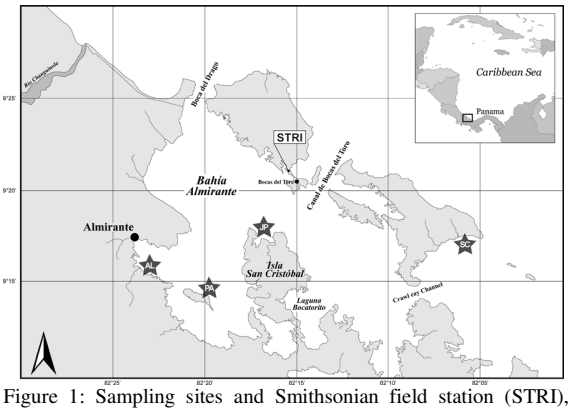
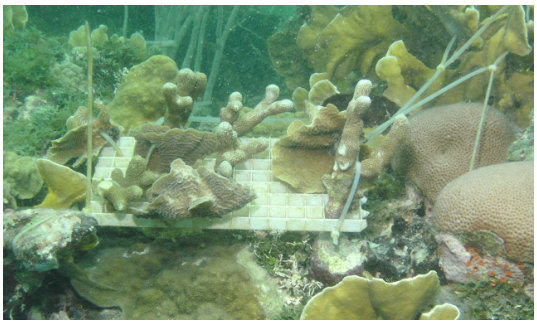


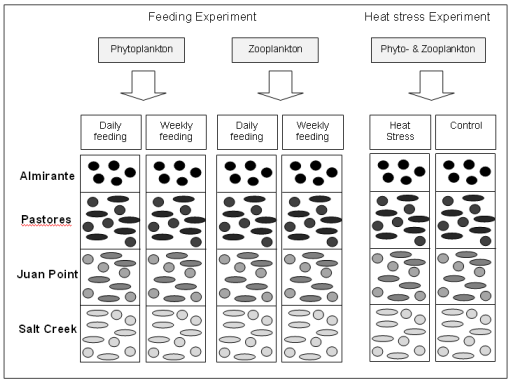
Figure 1: Sampling sites and Smithsonian field station (STRI), AL=Almirante, PA=Pastores, JP=Juan Point, SC=Salt Creek.

Aquaria set up and sampling design

The studied species *Porites furcata* (Lamarck 1816) and *Agaricia tenuifolia* (Dana 1848) are the most abundant shallow water coral species in Almirante bay (Guzmán and Guevara 1998a). Coral fragments from both species were collected from the reef flat at depths of 1-4 m. The average fragment size was approximately 20 cm² (5 – 10 cm length). Five fragments of both *P. furcata* and *A. tenuifolia* were directly sampled from the field at each site and immediately frozen until processing *(*samples referred to as field initials). An additional 18 fiber glass aquarium racks containing five fragments from each species (90 fragments total) were fixed with cable ties (Fig. 2A) at each site (Almirante only contained *P. furcata*).

A)





B)

Figure 2: A) Fiber glass aquarium racks remained 10 days at each sampling site for healing from breakage before being transported to the aquaria for the feeding and heat stress experiment (B). Each aquarium had five fragments of *P. furcata* (circles) and *A. tenuifolia* (ovals) from each sampling site: Almirante [AL] (only *P. furcata*), Pastores [PA], Juan Point [JP] and Salt Creek [SC]. Each treatment was conducted in replicates of three. Three aquaria were fed daily and three were fed weekly with phytoplankton (*Nannochloropsis* spp.), while three aquaria were fed daily and three were fed weekly with zooplankton (*Artemia salina* larvae). The aquaria from the heat stress experiment were fed with both phyto- and zooplankton. Three aquaria were heated (31.2 ± 0.1 °C), whereby three control aquaria had ambient water temperatures (27.5 ± 0.3 °C).

After 10 days of healing, all racks were transported in water filled buckets to the aquaria. One rack from each site was transferred into one of 18 glass aquaria (30 l), which were supplied with filtered sea water. Twelve aquaria (feeding experiment) were darkened with black plastic foil to reduce photosynthesis as much as possible (PAR <10 µmol m^{-2} s^{-1}). Six aquaria (heat stress experiment) were supplied natural light (PAR <80 µmol m^{-2} s^{-1}) through the roof of the aquarium building (Fig. 2B).

Feeding Experiment: Six tanks (phytoplankton aquaria) were fed with pure cultures of *Nannochloropsis* spp. (≤1 µm) while six tanks

(zooplankton aquaria) were fed with freshly hatched *Artemia salina* larvae (>180 µm) for a period of 60 days. Three of the phytoplankton and zooplankton aquaria were fed daily with 1l phytoplankton (density: 6.25 ± 1.32 [Mio cells ml-1] equals 0.32 ± 0.04 g dry weight) and 2g zooplankton (2g wet weight equals 0.16 ± 0.0001 g dry weight), respectively, whereby three were fed weekly with seven-times the amount of daily food given.

Heat stress experiment: Another six tanks (three heat stress aquaria and three control aquaria) were fed for 45 days with both phytoplankton and zooplankton cultures (1/2l phytoplankton, 2g zooplankton). Corals were fed daily under high temperature stress (31.2 ± 0.1 °C) in three aquaria heated with 50 W heaters (JBL Pro Temp s50). An additional three tanks were kept at ambient (27.5 ± 0.3 °C) seawater temperatures (control).

Fragments were sampled after the 10 day acclimatization period before the feeding and heat-stress treatment started (aquarium initial fragments, n=5 for each site from feeding and heat stress aquaria). Fragments of corals fed daily and weekly were sampled after 30 (10 days acclimatization + 20 days treatment), 50 and 70 days. Furthermore, after 30 and 45 days fragments were sampled from the heat stress and control aquaria. **At e**ach sampling period three fragments from each site and each treatment (daily and weekly feeding of phytoplankton and zooplankton, heat-stress and control) were sampled.

Coral processing

Coral tissue was standardized to the surface area (cm²) of each coral fragment (Naumann et al. 2009) and analyzed for chlorophyll *a* (Aminot and Rey 2000), zooxanthellae density and lipid content (Folch et al. 1957).

Statistical analysis

All data were tested for normality and homogeneity of variance using the Kolmogorov-Smirnov test and Levene's test, respectively. Differences between treatments, sites, species and time were tested by comparing means with a parametric t-test. To explore possible interdependences between lipid, zooxanthellae and chlorophyll *a* values regression analysis was applied. The software JMP 9.0.2 (SAS Institute) was used for analyses. All values are presented as means ± standard errors, if n>2.

Results

Summarizing all sites (field initials), *P. furcata* had a significantly higher competence for lipid accumulation (ANOVA; F = 32, P = 0.0383, $n_{P. furcata}$ = 15, $n_{A. tenuifolia}$ = 19) (Fig. 3). Field initials showed highest accumulation of lipids in fragments from SC (*P. furcata* 0.35 ± 0.09, *A. tenuifolia* 0.21 ± 0.09 mg cm^{-2}), the site outside the bay. Lipid values from sites close to the port were lower in (AL: *P. furcata* 0.20 ± 0.03; PA: *P. furcata* 0.22 ± 0.05; *A. tenuifolia* 0.10 ± 0.01 mg cm^{-2}) but higher than at JP (*P. furcata* 0.09 ± 0.02; *A. tenuifolia* 0.08 ± 0.01 mg cm^{-2}).

No significant differences were found in zooxanthellae or chlorophyll *a* values between species. They were lower at SC (1.8 ± 0.2 Mio cm^{-2}, 4.9 ± 0.4 µg cm^{-2}) than at sites close to the port (AL: 3.9 ± 0.6 Mio cm^{-2}, 6.7 ± 1.9 µg cm^{-2}, PA: 4.2 ± 0.9 Mio cm^{-2}, 6.7 ± 1.2 µg cm^{-2}). The site with corals containing the lowest lipid reserves, JP, also presented lowest zooxanthellae (1.2 ± 0.3 Mio cm^{-2}). However, these parameters were not generally correlated to each other (R^2<0.2).

Feeding Experiment

For both *P. furcata* and *A. tenuifolia*, mean values of fragments fed weekly contained higher lipid contents than those fed daily (Fig. 3A&B). Lipid values of corals fed weekly were always highest at PA for both, phytoplankton aquaria (*P. furcata* 0.13 ± 0.06 mg cm^{-2}, *A. tenuifolia* 0.06 ± 0.01 mg cm^{-2}) and zooplankton aquaria (*P. furcata* 0.11 ± 0.03 mg cm^{-2}, *A. tenuifolia* 0.04 mg cm^{-2}). *P. furcata* as well as *A. tenuifolia* fed daily showed highest lipid values in SC (phytoplankton: *P. furcata* 0.06 ± 0.02 mg cm^{-2}, *A. tenuifolia* 0.01 mg cm^{-2}, zooplankton: *P. furcata* 0.10 ± 0.02 mg cm^{-2}).

Lipid, zooxanthellae and chlorophyll *a* values were significantly higher in initials than in fragments fed daily and weekly for both species (paired t-test, P<0.01) (Fig. 3C-F). The transplantation to low light aquaria conditions (from day 0 day 10) led to a decrease of zooxanthellae and chlorophyll *a* for all sites and both species (Fig. 3C-F). *P. furcata* sampled from AL and PA exhibited a significant loss in zooxanthellae (AL from 3.90 ± 0.6 to 1.47 ± 0.4 Mio cm^{-2}, PA from 4.25 ± 0.9 to 1.19 ± 0.3 Mio cm^{-2}) and in chlorophyll *a* (AL from 6.72 ± 1.9 to 1.49 ± 0.4 µg cm^{-2}, PA from 6.75 ± 1.2 to 1.86 ± 0.2 µg cm^{-2}) (paired t-test, P<0.01) During the experiment, *P. furcata* zooxanthellae and chlorophyll *a* values increased in corals fed both daily and weekly with phytoplankton and zooplankton. At the end of the experiment (70 days) zooxanthellae in *P. furcata* approached initial values from the field, while *A. tenuifolia* suffered from a loss in zooxanthellae and chlorophyll *a*, which lead to a 100 % die off in fragments after 50 days.

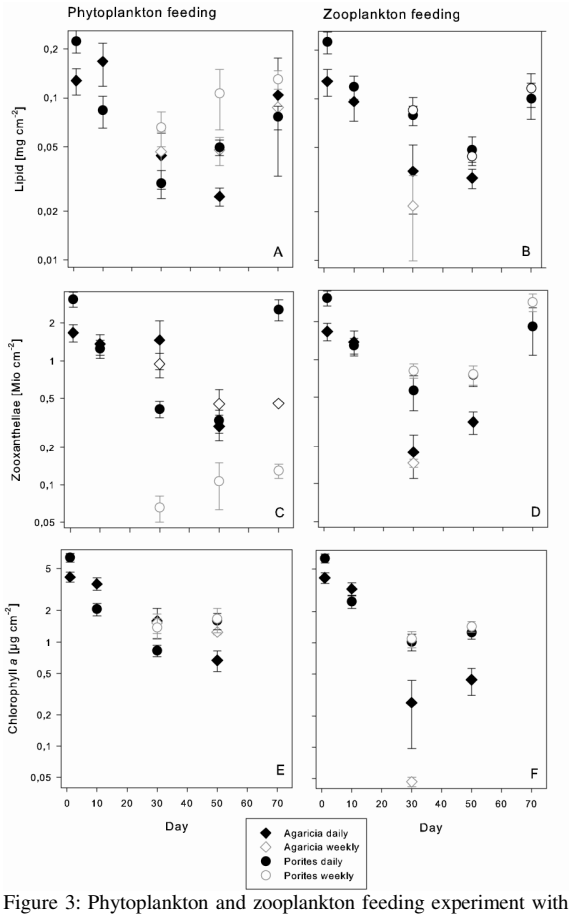


Figure 3: Phytoplankton and zooplankton feeding experiment with *P. furcata* and *A. tenuifolia* (day 0 = f*ield initials*). After a 10 day aquarium acclimatization period corals were fed daily and weekly for a 60 day period. Fragments fed weekly accumulated higher amounts of lipids (A&B) than those fed daily, which was most distinct in *P. furcata*. In the beginning of the experiment lipid (A&B), zooxanthellae (C&D) and chlorophyll *a* (E&F) values dropped (day 30) under low light aquarium conditions and increased again after 50 and 70 days, respectively, in particular for *P. furcata*. *A. tenuifolia* showed a lower competence for recovery, which led to a die off. Fragments fed weekly with zooplankton were all dead after 50 days.

High temperature stress experiment

The heat stress experiment showed metabolic responses visible in changing lipid, zooxanthellae and chlorophyll *a* values. After 30 days aquaria treatment (20 days heat stress), lipid, zooxanthellae and chlorophyll *a* values were significantly lower (Table 2) than in fragments sampled after the 10 day acclimatization (Fig. 3) (paired t-test, $P<0.01$). Also, lipid values remained significantly higher in control fragments of both species than in fragments exposed to heat stress (ANOVA, $F = 75$, $P = 0.0013$, $n = 40$). However, *P. furcata* heat stress fragments had higher lipid, zooxanthellae and chlorophyll *a* values than *A. tenuifolia* (Table 2). After 45 days lipid and zooxanthellae values of *P. furcata* were higher than at the first sampling (30 days).

After 5 days heat stress 19 % bleaching was observed in *A. tenuifolia*, while *P. furcata* started to bleach after 12 days (20 %). After 26 days heat stress, 97 % of *A. tenuifolia* were dead and 65 % of the *P. furcata* fragments were bleached. After 45 days all *A. tenuifolia* fragments were dead.

Table 2: Lipid, zooxanthellae and chlorophyll *a* values of *P. furcata* and *A. tenuifolia* after 30 and 45 days exposure to high temperature stress. Chlorophyll values were not measured for the fragments sampled after 45 days.

		30 days			
Species		Control (n=3)		Heat stress (n=3)	
A. tenuifolia	Lipid [mg cm^{-2}]	0.017	±0.01	0.005	±0.00
P. furcata		0.040	±0.01	0.015	±0.00
A. tenuifolia	Zooxanthellae [Mio cm^{-2}]	0.41	±0.39	0.11	±0.05
P. furcata		0.45	±0.06	0.44	±0.10
A. tenuifolia	Chlorophyll *a* [µg/cm²]	1.92	±0.90	0.13	±0.03
P. furcata		0.91	±0.28	0.42	±0.11
		45 days			
A. tenuifolia	Lipid [mg/cm²]	dead		dead	
P. furcata		0.076	±0.02	0.037	±0.01
A. tenuifolia	Zooxanthellae [Mio/cm²]				
P. furcata		0.63	±0.05	0.90	±0.05
A. tenuifolia	Chlorophyll *a* [µg/cm²]				
P. furcata		n.a.	n.a.	n.a..	n.a.

Discussion

Within the natural site specific conditions (field initials), lipid reserves, zooxanthellae and chlorophyll *a* per coral surface were not correlated to each other. In fact, lipid accumulation was highest at the site SC, outside the bay, which was least affected from anthropogenic impacts, whereby zooxanthellae and chlorophyll *a* were lowest there. This leads to the assumption that the coral symbiosis is most efficient in low stress environments with an optimized autotrophy-heterotrophy-interaction (Anthony and Fabricius 2000). Sites within the bay exhibited lower lipid reserves. Besides a less efficient symbiosis, the loss in lipid values might be the result of a high energy demand due to stress from sedimentation (Riegl and Branch 1995) and/or high competition from other reef organisms due to the combination of anthropogenic impacts (Aerts 2000; Foster et al. 2008).

It is possible that corals from sites close to the port and Almirante city (AL, PA) could compensate part of the higher energy demand by profiting from high nutrient availability from eutrophication, hence high plankton availability for heterotrophy (Table 1). This was confirmed by lowest lipid values at JP, a site which was characterized by high suspension load (TSS) but lower eutrophication (Table 1). Since zooxanthellae and chlorophyll *a* abundances did not

correlate with lipid values they could be excluded as a determining factor for lipid accumulation. Rather, it is suggested that photosynthetic compounds were increased to compensate reduced light availability and to maintain photosynthetic efficiency (Sawall et al. 2011). This compensatory mechanism is also profiting from eutrophication (Borell and Bischof 2008).

The fact that *P. furcata* was able to accumulate more lipids than *A. tenuifolia*, in particular within the bay suggests that food sources can be used more efficiently via heterotrophy. This was validated within the *ex situ* aquarium experiments, in which *P. furcata* also accumulated more lipids than *A. tenuifolia* through heterotrophy.

In the beginning of the feeding experiment zooxanthellae and chlorophyll *a* declined more distinctly in *P. furcata* from sites close to the harbor (AL and PA). This could be related to a strong competence in corals from those sites to regulate the density of zooxanthellae through host digestion (Titlyanov et al. 1996). This mechanism provides energy from zooxanthellae digestion and may help to maintain lipid reserves in case of bleaching stress by reducing unnecessary energy consuming compounds (Titlyanov et al. 1996). The competence to regulate the density of zooxanthellae through host digestion and expulsion (Titlyanov et al. 1996) also reduces stress from superoxide radicals (O_2^-) incrementally formed during heat stress (Lesser et al. 1990), thus providing better survival chances in periods of bleaching.

Additionally, *P. furcata* seemed to be able to buffer the loss in autotrophy via heterotrophy by using the alternative food sources from phyto- and zooplankton (Anthony and Fabricius 2000). This was seen in an acclimatization process, thus a re-accumulation of lipids during weekly feedings (Fig. 3) and after bleaching from heat stress (Table 2). These results support other studies (Houlbrèque and Ferrier-Pagès 2009) that found certain coral species enhance their heterotrophic input during reduced photosynthesis (low light conditions, bleaching), and have a better capacity to maintain and restore lipid reserves (Grottoli et al. 2006; Rodrigues and Grottoli 2007). Heterotrophic acclimatization also led to a recovery of zooxanthellae and chlorophyll *a* abundance after 50-70 days of feeding experiments, which could be related to the positive nutrition feedback for the zooxanthellae (Titlyanov et al. 2001; Houlbrèque et al. 2003). In contrast *A. tenuifolia* seemed to have the ability to compensate the lack of light availability by increasing their zooxanthellae abundance (Fig. 3C), however not by a compensation through heterotrophy. Low heterotrophic competence might also explain the low recovery after bleaching, as seen in high mortality during heat stress and the bleaching event that occurred in 2010 (NOAA 2010 and personal communication). Their low capability to recover after a bleaching event was observed in big areal die offs, compared to the fast recovery of *P. furcata*.

Additionally, *P. furcata* were able to accumulate lipids in times of starvation and irregular food supply. They seemed to have the ability to 'remember' stress from previous starvation (weekly feeding) and 'learn' from it through a higher accumulation of lipid reserves. This could be an important mechanism to survive many natural and anthropogenic disturbances from i.e. bleaching, sedimentation, and heavy metal pollution.

The feeding experiment furthermore supported that nanoplankton (≤1 µm) are important food source for energy acquisition (Ferrier-Pagès et al. 1998; Houlbrèque and Ferrier-Pagès 2009), and is even preferred to microplankton (>50 µm). Thus, is should be considered that hard corals can procure nutrition from herbivory (Fabricius et al. 1995; Glynn 2004), providing a similar nutrition as zooxanthellae, in particular in fatty acid composition, which makes it easy to metabolize (Treignier et al. 2009).

In summary, considering energy reserves such as lipids as indicators to assess the resistance and the adaptive capacity of a coral (Anthony and Connolly 2004; Grimsditch and Salm 2006), *P. furcata* has a higher fitness than *A. tenuifolia*. The higher competence to accumulate and rebuild energy reserves resulted in higher survival rates and recovery from bleaching. Furthermore, the lipid accumulation competence enabled them to 'remember' stress such as starvation and to develop a so called Yo-Yo effect (Brownell et al. 1986).

Thus, *P. furcata* could be more resistant to future anthropogenic impacts such as increased eutrophication, sedimentation and climate changes, profiting from their ability for heterotrophy. However, the described natural acclimatization mechanisms cannot maintain the functionality of the coral symbiosis on a long term basis. Hence, the combination of all anthropogenic impact factors will result in a reduction of both species and a substantial loss of reef cover in Almirante bay, Panama.

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