

## Could ‘Ecosystem Atavisms’ Help Reefs to Adapt to the Anthropocene?

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**Abstract.** Reef evolution since the Proterozoic is characterized by a long-term increase of reef system modules (microbial, soft/spiculed sponges, calcifying sponges, heterotrophic metazoans, photosymbiotic metazoans, coralline algae). Scleractinian reef adaptations since the Late Triassic are denoted by perfecting the photosymbiotic system. Jurassic coral reef ecology still reflects a wider set of growth environments, thus larger niche boundaries relative to today, with different types thriving from brackish, mesotrophic and sediment-loaded, to oligotrophic environments. Tipping point-shifts of modern reefs from healthy to sponge/soft-coral/algae to heterotrophic/microbial reefs appear to reflect in-place ‘atavistic’ switches to an evolutionary less complex state with a reduced number of modules. The Caribbean Almirante Bay, Panamá, may be a present-day equivalent of adaptation of reefs to increased terrigenous run off and nutrient levels: Isotope and metabolic studies indicate a nutrition with increase of heterotrophy relative to photosymbiotic activity, and changing dominance of hard coral species and species composition structure resemble Jurassic coral reefs of mixotrophic environments characterized by terrigenous runoff. Whether or not these ‘atavistic’ reef types might firmly establish themselves and might have potential to substitute declining oligotrophic reefs will be strongly governed by the rate and scale of global and local environmental changes. However, owing to their reduced diversity and flat spatial structure these reefs will not be able to substitute all ecosystem services as provided by high-complexity coral reefs. Nevertheless, reef conservation under an anthropocenic view should not only manage and protect oligotrophic ‘healthy’ reef sites but also those under stress, to allow for ‘atavistic’ adaptation.

**Key words:** Reef evolution, Almirante Bay, Atavistic reefs, Jurassic, Anthropocene.

### Introduction

Modern reef systems may be understood as a ‘deep past’ product of a long evolutionary selection and adaptation process. Despite strong spatial and temporal variability of reef abundances and despite long reef lag times following major extinction events, the general complexity of the structure of reefs has increased over Earth history. Reef structure complexity is illustrated by the amount of incremental basic reef modules appearing over time (Leinfelder and Nose 1999). In a simplified manner the following modules occurred from the Precambrian to the Neogene: (1) anaerobic microbial, (2) photoautotrophic microbial, (3) soft/spiculed ‘parazoan’ sponge, (4) ‘parazoan’ sponges, (5) heterotrophic metazoans, (6) photosymbiotic metazoans, (7) coralline algae. During many times in Earth history, e.g. the Jurassic, high-complexity reefs (combined modules 1-6) were accompanied by low or medium complexity reefs (modules 1-2 and 1-3, resp.), resulting in adaptation of reef types to a wide array of different environ-

mental settings. Owing to the imperfection of the photosymbiotic relation (module 6) and the lack of coralline algae (module 7), Late Jurassic high-complexity coral reefs spread across a wider variety of reef settings than modern tropical coral reefs. Several Jurassic coral reef types showed adaptations to elevated sedimentation rate, nutrient influx and even freshwater runoff (Nose and Leinfelder 1997; Leinfelder 2001). Contrasting, modern tropical coral reefs have dominantly entered a very narrow environmental niche, which today is severely challenged by anthropogenic threats.

The Almirante Archipelago of the Caribbean of Panamá shows modern coral reefs with peculiarities in species composition, dominance, reef architectures and energy uptake. This is considered as a reflection of a Holocene naturally fluctuating environment. Long-term observations and monitoring combined with an investigation of the strategies of hard coral species to survive increased sedimentation and eutrophication were applied to study ‘atavistic’

structures (the evolutionary throwback) such as known from Jurassic reefs. These conserved mechanisms may help reefs from the Holocene and modern coral species to compensate accelerated environmental changes from anthropogenic impacts, resulting in low or medium complexity reefs again. The present paper aims to test this hypothesis by interpreting ecological changes of reef ecosystems and niche competences of the most abundant hard coral species of the Almirante Archipelago over the last 20 years as partially ‘atavistic’ reactivation of ancient ecological adaptations to ‘anthropocenic’ environmental change.

### Material and Methods

A recent field study on the rebuilding of reef ecosystems and the adaptation potential to anthropogenic impacts of some abundant hard coral species was conducted from 2010-2011 in Bahía Almirante Bay in Bocas del Toro, Panama (Fig. 1). This area is a well documented example of an ecosystem naturally exposed to high sedimentation, river runoff and terrigenous effluence, accompanied by an increase of anthropogenic impacts over the last 20 years (Guzmán and Jiménez 1992; Greb et al. 1996; Guzmán and García 2002; Guzmán 2003; Collin 2005; Guzmán et al. 2005). Coral reefs within the bay are exposed to various impacts from land based changes as well as effluences into the marine environment. Deforestation for banana plantations, pasture land and teak plantations, shipping traffic and dredging results in increased erosion, sedimentation, nutrification and pollution, constituting a fundamental change of the marine bay systems (Collin 2005).

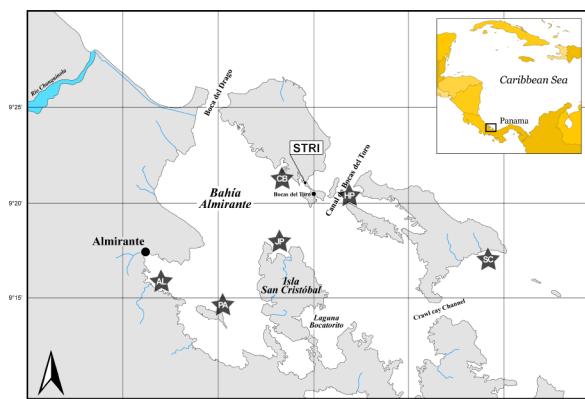


Figure 1: Sampling sites and Smithsonian field station (STRI), AL=Almirante, PA=Pastores, CB=Casa Blanca, JP=Juan Point, HP=Hospital Point, SC=Salt Creek.

To assess niche competences of recent reefs in highly disturbed environments, environmental and biological surveys were conducted. Physical environmental data as secchi depth, water chlorophyll *a* content as well as the size fractions of reef

sediments were measured. The biological reef monitoring was based on international Reef Check methods (Hodgson 2000; Hodgson et al. 2004). Furthermore, changes in biodiversity of hard coral species were recorded using the method from Guzmán and Guevara (1998) and compared with data from Greb et al. (1996).

To assess adaptation capacities of hard corals being impacted by the increased sedimentation and eutrophication, the relation of autotrophy and heterotrophy of the coral symbiosis were assessed by using natural  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios, which are tracers for the trophic level and the food source an organism relies on (Peterson and Fry 1987; Vander Zanden and Rasmussen 2001). Furthermore, they are indicators if carbon and nitrogen was fixed through primary production or if it has been metabolized in the heterotrophic pathway (Minagawa and Wada 1984).

Isotope measures also provide a proxy for the functionality of the symbiosis and the ability to use given food and nutrition sources i.e. to constitute energy reserves such as lipids (Seemann et al. 2012), which can be used as an indicator for resilience and the adaptive capacity of corals (Anthony and Connolly 2004; Grimsditch and Salm 2006). The two most abundant species *Porites furcata* (Lamarck 1816) and *Agaricia tenuifolia* (Dana 1848) were directly sampled from the field from 3 sites within the bay (Almirante, Pastores, Juan Point) and one site outside the bay (Salt Creek). Samples were analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , separately for zooxanthellae and animal tissue, using stable isotope mass spectrometry (IRMS, DELTA V Advantage) with an elemental analyzer (Thermo Flash EA 1112).

Comparison with reef evolution and fossil reefs is based on evaluation and reassessment of previously published work.

### Results

Our case study in the Almirante bay showed several adaptation patterns and rebuilding processes of the reefs inside the bay.

The environmental monitoring demonstrated atypical reef conditions. Main reasons were the turbid marine waters loaded with sediments and nutrients entering at the Boca del Drago, resulting in low secchi depth ( $3.9 \pm 3$  m). Also, according to Håkanson (1994) chlorophyll *a* at sites close to the bay inlet and the harbor would not be considered as oligotrophic environment (chlorophyll *a*  $>1\text{ mg l}^{-1}$  and secchi depth  $<6$  m). In addition, sediment composition changed from bigger reef-typical grain size ( $>1\text{ mm}$  and  $>0.5\text{ mm}$ ), which is settling fast, to small grain sediments ( $<63\text{ }\mu\text{m} - 0.25\text{ mm}$ ), which resuspend more easily.

Increased sedimentation and eutrophication is reflected by changing reef composition over the last decades. Hard coral cover declined compared to what was found 15-20 years ago (Greb et al. 1996; Guzmán and Guevara 1998) to values of <10 % in some areas (i.e. Pastores, 10 m depth). Also, the described impacts led to local differences, comparing reefs in-and outside the bay. Hard coral cover was significantly higher outside the bay ( $44 \pm 5\%$ ) than inside (down to  $23 \pm 11\%$ ). A loss in hard coral biodiversity was significant comparing the site outside (35 species) and inside (between 7 and 23 species), so as there was a loss of hard coral species within the last two decades from 58 (Guzmán and Guevara 1998) to 35 species. *Acropora* spp., which used to be abundant species within the bay (Greb et al. 1996; Saric 2005) are close to be eradicated. Instead, sponges (up to  $26 \pm 4\%$ ) (Fig. 2) and zoanthids (up to  $20 \pm 7\%$ ) became dominant. Sedimentation furthermore led to a high percentage coverage of sand and silt in reefs within the bay (up to 26 %), which was minimal (2-3 %) outside the bay.

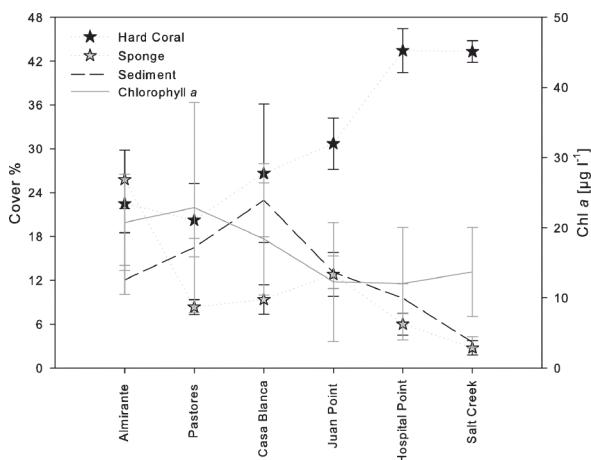


Figure 2: Dependences of hard coral and sponge cover to sediment cover and eutrophication (chlorophyll *a* in water column). Hard coral and sponge negatively correlate to each other. Sponge cover positively correlates with sediment cover and chlorophyll *a*.

In fact, today two hard coral species are most dominating within the bay, obviously able to adapt their niche competence to the bay conditions: *Porites furcata* (usually >30 % of hard coral cover) and *Agaricia tenuifolia* (usually >40 %). Some reefs were found to be dominated by one species, e.g. the site close to the harbor with a *P. furcata* coverage >90 % or Hospital Point with an *A. tenuifolia* coverage >80 %. However, both species seem to be in competition recently resulting in a competitive advantage for *P. furcata*.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios from the coral host and the zooxanthellae of *P. furcata* varied between -14 to -16 ‰ and 1 and 5 ‰ respectively. (Fig. 3). The difference of the  $\delta^{15}\text{N}$  ratio goes up to 2.7 ‰ in Pastores (*P. furcata*) (Fig. 3),

which is indicating a ‘decoupling’ between zooxanthellae and host, since they are separated by a whole trophic step ( $\delta^{13}\text{C}$  1 ‰ and  $\delta^{15}\text{N}$  3 ‰, resp. (Peterson and Fry 1987)). Also, *A. tenuifolia* was found to be able to ‘decouple’ host and symbiont, visible in a difference of  $\delta^{13}\text{C}$  of 1.1 ‰ at Salt Creek. At the same time strong interdependences between symbiont and host are evident through strongly overlapping values of host and zooxanthellae ( $\delta^{15}\text{N}$   $4.0 \pm 0.1$  and  $4.1 \pm 0.5\%$ , resp.) in Almirante.

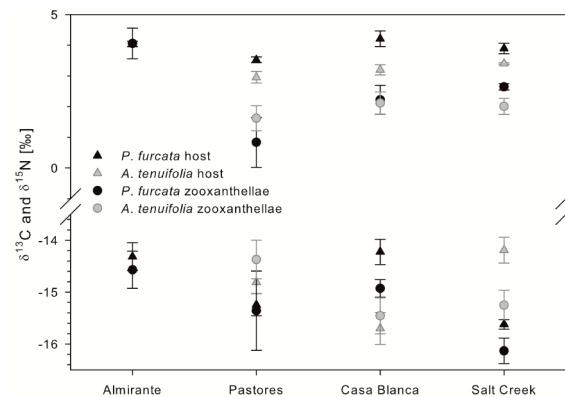


Figure 3: Natural C and N isotope signatures from the two hard coral species *P. furcata* (black) and *A. tenuifolia* (grey) sampled at 4 different sites in the Bocas Archipelago (n=5). In the site Almirante only *P. furcata* occurs.

## Discussion

The Almirante bay used to host shallow *Acropora palmata* and extensive *A. cervicornis* stands and the typical *Montastrea-Colpophyllia-Siderastrea*-community in slightly deeper waters, widespread low-energy *Porites furcata*-meadows in the shallowest part, and *Agaricia tenuifolia*-thickets in different growth forms, but largely confined either to shallow patch reefs or to the slightly deeper *Montastrea* zone (Greb et al. 1996; Guzmán and Guevara 1998).

However, Almirante reefs have always been different from other reefs: most of them grow in a relatively unusual semi-enclosed setting on ramp-type morphologies, with a strong dominance of *Porites* meadows. Despite severe anthropogenic impact Almirante reefs still appear relatively robust. This is tentatively interpreted as an adaptation of the relatively young, several thousand year old reef system to an environment continuously exposed to natural stress. The highly active geological setting in a tectonic ‘piggy-back’-basin within a thrust belt (Greb et al. 1996), together with the semi-enclosed character, heavy tropical rainfall and coastal currents reimporting fine sediment, causes severe runoff of sediments and nutrients into the bay. Obviously the Almirante reefs developed an ‘immune system’ - which is not a classical redundancy system - by being continuously challenged by many natural disturbance

events. Slightly elevated overall nutrients are also reflected by a very high proportion of shallow water sponges, brittle stars and terebellid worms in this reef environment.

Comparison with the situation 15 to 20 years ago when we started surveying shows that accelerating anthropogenic disturbance pays its toll, as described above. Bottom core samples reveal sediment disturbances and resettling of *Porites* meadows more often already in earlier, natural times of development (Greb et al. 1996, cf. Aronson et al. 2004).

High differences between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  host-symbiont-values (up to 1 trophic step) show that *P. furcata* is benefiting most from this situation, being able to cope with elevated food supply, and profit from heterotrophic nutrition. These results were confirmed by ex situ experiments (Seemann et al. 2012), which found that the competence of *P. furcata* to maintain nutrition through heterotrophy is higher than in *A. tenuifolia*, thus having a stronger competence to maintain and constitute lipid reserves under dark light conditions. It appears that starting with the late 1990's Agariciidae frequently replaced *A. cervicornis* thickets as well as the outermost part of the *Porites* spp. zone (Aronson et al. 2004). We interpret this as a pull up of *A. tenuifolia* to shallower waters owing to stronger turbidity as well as to its good morphological adaptation potential to mobile sediments. Especially the funnel-shaped morphologies act as a good baffling and sediment-bypass system (Greb et al. 1996). Based on fieldwork undertaken in 2000/2001 Aronson et al. (2004) noted an increasing dominance of *A. tenuifolia* on costs of the dominating *P. furcata*, foreseeing the complete disappearance of *P. furcata* in the future. Based on our present data, this trend cannot be confirmed. This possibly initial shift to a stronger dominance of *A. tenuifolia* in very shallow water appears now counterbalanced by the better adaptation of *Porites* to eutrophication and freshwater influx, and by greater vulnerability of *A. tenuifolia* to the frequent bleaching events in this region (NOAA 2010).

The perhaps most interesting feature of the Almirante reefs is the similarity of the *Porites*-meadow dominance with the widespread branching coral meadows from the Late Jurassic. During this period the photosymbiotic system was, though in place, not yet fully established, as shown by Nose & Leinfelder (1997) and Leinfelder (2001), (cf. Stanley 2006). This is deduced from the existence of typical growth form reactions of microsolenid brain corals which exhibit close morphological similarities with Agariciidae (e.g. horizontal flattening in deeper waters), and from the existence of high-/low density bands in nearly all corals, which are interpreted as annual growth rings related to photosymbiotic activity. However, strongly

reduced annual growth, as compared with today, and especially a ratio of low to high density bands of only 1 (in contrast to 3:1 to 5:1 in modern zooxanthellate corals) points to nearly identical importance of heterotrophic and photosymbiotic energy uptake in most Jurassic reef corals (Nose and Leinfelder 1997). This explains why Upper Jurassic coral communities such as *Calamophylliopsis* spp. meadows or *Actinastrea crassoramosa* thickets grew in near-shore muddy settings with reduced but noticeable terrigenous sedimentation with additional fauna, such as annelid worms, mollusks and calcareous sponges, supporting the interpretation of mesotrophic conditions (Leinfelder 2001). Modern *P. furcata* settings from Almirante bay appear quite similar to these ancient reef types, notwithstanding modern sea grass which did not yet exist during the Jurassic.

We suggest that niche narrowing by complexity increase of scleractinian reef structure from the Triassic till the Holocene is not as confined and unidirectional as it might appear (Fig. 4). The close similarity of *Porites*-dominated Almirante settings with Late Jurassic coral reef settings from Iberia, India and other places, such as the dominance of a combined autotrophic and heterotrophic feeding strategy, abundance of sponges and other plankton feeders, high proportion of terrigenous sediments and indicators of reduced salinities may give hope that some modern coral reefs may have the potential to adjust to the Anthropocene by 'atavistically' recombining to lower-complexity reefs with different nutrition strategies, given they have a chance for adjusting. The readjusted reefs would however be impoverished and would not comprise the same ecosystem goods and services, neither would they esthetically compensate for the highly structured reefs we still have in some places of the world. It is nevertheless worth noting that the changes of the Almirante reefs are not (yet?) in a tipping point situation, where all reef types would suddenly shift into a completely new and nearly irreversible state. It is even imaginable that present Almirante reefs might represent 'transition time' reefs, with a chance that high-complexity, oligotrophic reef development might reappear once anthropogenic threats have been minimized.

The Almirante reefs are a good example how the understanding of reef evolution helps to identify reef growth potential during the Anthropocene. A major possible lesson to learn is that partially damaged reefs should not be given up but are also worth being protected since adaptive strategies might develop best here.

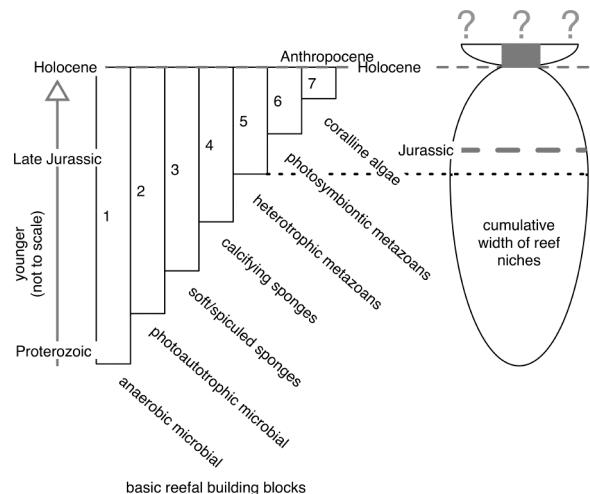


Figure 4: Deep Past history of reefs and future prospects. Reef Evolution is characterized by increase of structural reef modules (see text), which first allowed reefs to conquer new environmental settings, then threw them to narrower niches, resulting in the Holocene dominance of oligotrophic, narrow niche tropical reefs. The Almirante reefs show that despite threatening the oligotrophic reef niche other reef types might persist and develop into areas previously occupied by other reef communities. These reefs are structurally very similar to certain Jurassic reef associations, hence appearing as 'ecologically atavistic'.

### Acknowledgement

We would like to thank the staff from the Smithsonian Tropical Research Institute (STRI) Bocas del Toro, in particular Eric Brown, Plinio Gondola, Gabriel Jacome and Rachel Collin for their invaluable help, great support in organization and space acquisition at the field station. Thanks to Kathryn Berry and Cindy Gonzalez for help with monitoring. Further thanks to Ewgenija Kuhl for assistance with isotope analysis and field trip preparations.

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