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**No evidence of top-down control on
sponges by vertebrate predators in a
Philippine reef system.**

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Abstract

Hermatypic corals are demising in many reef systems worldwide. In ecosystem where the substrate availability is limited, guarantee space is essential for the growth of organisms, sometimes overgrowing other living organisms. Sponges are relevant benthic organisms which perform relevant functions in coral reefs. Where regulation of their abundance is missing, they are facing competition with corals and other benthic organisms for the substrate. Still unclear, is if sponges are Top-Down controlled by the presence of their predators, or Bottom-up regulated (nutrient availability). Herein it is analysed if spongivore fishes regulate sponge abundance in 4 Philippines small scaled MPAs. Comparison of sponge abundances with spongivore abundances across 4 MPA and likewise overfished sites, showed no relationship between spongivore and sponge abundance. The MPAs guaranteed higher spongivore abundance than in the overfished sites (Shapiro-Wilk's $p = 1.38 \times 10^{-9}$). A generalised linear model showed influence from sponge on spongivore abundance ($p = 8.46 \times 10^{-15}$). Over a five year period in one site, sponge abundance was lower outside the MPA but no correlation with spongivore were significant. In another site, sponge morphological assemblages were observed. They did not differ in the fished and the protected zone, although were influenced by a spongivore family (Pomacanthidae). In the same site, coral-sponge interaction were recorded. Inside the MPA coral overgrowth was higher, mostly due to cryptic sponges. Sponges overgrowing corals were positively correlated with spongivores ($p = 0.0013$). Therefore, in the surveyed reefs no evidence of Top-down control has been recorded. It is likely that other factors influence sponge abundance.

Key words: Top-down; Bottom-up; Predation; Benthic competition; Coral reefs; Sponges; MPAs; Indo-Pacific.

Abbreviation list:

CCC = Coral Cay Conservation

MPA= Marine protected area

SE= Standard error

UTM= Universal Transfer Mercator

1. Introduction

Worldwide coral reefs are in serious degradation. During the last decades, direct and indirect anthropogenic impacts, simultaneously contributed to the demising of these extremely biodiverse and socio-economically relevant ecosystems (Braekman and Daloze, 1986; Burke, 2011). These resilient habitats cannot continue to withstand these extreme anthropogenic pressures (Mora *et al.*, 2016). The total area of coral reefs worldwide is estimated to have decreased by 19% (Wilkinson, 2004). The habitat loss of these ecosystems, that support an elevated abundance of economically important invertebrate and vertebrate species, has important consequences on the well-being of more than 275 millions of people relying on coral reefs for food sources (Burke, 2011). Decreasing coral-cover, following disturbance events, often lead to a change in the dominant benthic community (Ledlie *et al.*, 2007; Steneck *et al.*, 2014), determining at the long run a decreasing in the habitat functionality (Ledlie *et al.*, 2007). When the dominant community of the benthos shifts, the ecosystem is found in an alternative stable state. The Top-down control from predators may be crucial to prevent such phase-shift by regulating the abundance of the benthic component likely to become the predominant. As instance, where herbivore are abundant, often, the macro-algal cover is restrained. Overfishing is the principle cause of decreasing herbivore abundance and biomass, resulting in a permanent shift of the ecosystem into an algae dominated state (Norstrom *et al.*, 2009). In synergy with the top-down control, the nutrient enrichment have a likewise influence on the benthic communities (Hughes, 1994). For algae this is ascertained, for other organisms, like sponges, whereas the top-down or the bottom-up control is more effective, it is often debated and objective of studies (Pawlik *et al.*, 2018). Although, the most discussed phase-shift is often correlated with macroalgae, also common are urchin, soft coral, corallimorph and sponge shifts.

In the Caribbean, coral-sponge shifts are reported in numerous reefs. These events are likely to occur after disruptive and/or prolonged events, Caribbean reefs have been extensively overexploited since the European colonization. An example for the Pacific, is the Palmyra Atoll, after the US navy occupation during the WWII it presented extensively damaged reefs, corals were highly impacted and sponges became the benthic dominant community (Knapp *et al.*, 2016). In coral reefs, sponges contribute to the highest benthic biomass after scleractinian corals (Diaz and Rutzler, 2001). Although the their substrate competition with scleractinian corals, sponges are relevant benthic organisms that perform important roles in coral reefs and in many marine ecosystems (Bell, 2008b; Rützler, 2004). Herein is present a brief summary of the most relevant roles of sponges in coral reefs.

1.1 *Sponge functional roles*

Sponges are widespread at all the latitudes in polar, temperate and tropical regions (Van Soest *et al.*, 2012; Worheide *et al.*, 2005). They are found along all the vertical gradient from the deep sea (Vacelet and Boury-Lesnaut, 1995) to shallow waters (Hartman and Goreau, 1970), in intertidal and subtidal zones (Becking *et al.*, 2013), in mesophotic reef (Lesser *et al.*, 2009) and in mangrove ecosystems (Hunting *et al.*, 2013; Becking *et al.*, 2013). The origin of sponges, phylum Porifera, date back to the Precambrian. Sponges are the first evolved pluricellular organism, conferring this taxonomic group the name as living fossil (Li *et al.*, 1998). These organisms have a vast species diversity (Van Soest *et al.*, 2012). Many new species are continuously described, moreover, cutting edge molecular tools may unveil discrepancies with the previous taxonomical classification, hence sponge taxonomy is constantly slightly rearranged (e.g. Calcinaï *et al.*, 2005; Pacheco *et al.*, 2018; Esteves *et al.*, 2018).

One of the primarily observed and described ecological function, was the ability of sponges to erode the calcareous substrate (Goreau and Hartman, 1963). Boring sponges actively chip away small portion of the calcareous substrate by physical and chemical action in a coral reef

(Perry, 1998), the removed portion from the reef skeleton contributes to the fine sediment and the formation of rubble. Rocks and rubble can be important in a coral reef as they function as a platform of adhesion for coral larvae (Victor, 2008). Sponges are considered the most relevant invertebrates contributing to bioerosion, except for grazers (Chazottes *et al.*, 1995). Relevant external bioeroders are parrotfish, they erode an higher portion of the substrate compared to invertebrate bioeroders, although their bites involve just the surface of the coral whereas sponge erosion intact up to the base of the carbonate skeleton, engaging a major portion of rock (Wulff, 2016). An environmental factor that also have a noteworthy impact on the reef frame are storms and typhoon, although these events are far less common than the continuous biological erosion by sponges, parrotfish and other small bioeroders (Bivalves, Barnacles, Polychaetes, Sipunculans). Other factors that contribute to reef erosion are of anthropogenic origin, such as dynamite fishing, anchor damage, tourism impacts (resort construction, reckless divers). However Sponges still have a major role in controlling the reef carbonate budget (Perry *et al.*, 2015). Indeed, in an accreting coral reef, the rate of bioerosion has to be lesser than the rate of accretion of new calcium carbonate. For this reason bioeroders sponge abundance have to be kept under monitoring. Ocean warming is one of the principal factors contributing to the demising of corals. On reefs where bleaching event occurred, it has resulted an increasing of bioeroding sponge abundance (Carballo *et al.*, 2013; Chaves-Fonnegra *et al.*, 2018). Likewise corals, recent research observed that bioeroding sponges like the common *Cliona viridis* that host the unicellular algae symbionts (Zooxanthellae), are subjected to blanching due to temperature anomalies. Hence, a possible decrease of the bioerosion rate and an increased mortality of this class of sponges is likely to occur in reefs dominated by sponges hosting an algal symbionts (Fang *et al.*, 2018). On the other hand, the other important consequence of the climate change is decreasing water pH due to increasing $p\text{CO}_2$ atmospheric concentration. All the calcium carbonate structures present in the Ocean are docile to this phenomenon and the resulting trend is weakened carbonate structures. The class of sponge *Calcarea* synthetize a

carbonate skeleton, thus they are affected by ocean acidification. However, the majority of sponges secrete spongin fibers and/or silicate spicules which have a function of defence and skeletal sustainment and any of these substances are affected by lower pH. Boring sponges therefore, are not affected by acidified waters at contrary of the hermatypic corals, this may determine an increment in the reef bioerosion in a projected more acid ocean (Duckworth *et al.*, 2012).

Sponges feed filtrating the water column, thus an nutrient's increment may influence the abundance of sponges, according to Holmes *et al.*, (2000) enriched reefs resulted in an increment of boring sponge abundance. Hence anthropogenic impact that increase nutrient concentration in the waters, like terrestrial run-offs due to construction, cutting down mangroves forests and general costal overexploitation may contribute to the creation of a negative reef carbonate budget (Schonberg *et al.*, 2017).

Field observation reported sponge having a role in stabilizing the substrate by binding the coral fragments together (Wulff, 1984). Some sponges, borer excluded, may therefore contributing to the reef accretion. The capacity of encrusting sponge of binding rubble together may be a useful tool to apply to coral restoration (Bell, 2008b). Studies are reported mostly for the Caribbean with less observation in the Indo-Pacific. Recruits of *Pocillopora sp.* were found on pieces of rubble in sandy patches in a Philippine coral reefs, they were stabilized on the sandy substrate by encrusting sponges. Other pieces of rubble were bind together by cryptic sponges on the covered side, whereas the exposed side was mostly covered by sand (personal observation). This undervalued role is still poorly studied and require more attention for implementing some sponge species in conservation efforts (Biggs, 2013). Although sponge are not an ideal substrate for their chemical defences, some sponge function as substrate for other organisms blowing across the coral reefs. These benthic organisms like bryozoans, ascidians, coralline algae, often encrust some sponges, as it has been observed for the demosponge *Agelas clathrodes* observed by Bell (2008).

Sponges have a relevant role in nutrient recycling. Sponges feed on suspended nutrients available in the water, with some exception of the deep-sea carnivorous sponges (Vacelet and Bouryèsnault, 1995), hence the majority of species prefer vertical surface to better use the water flow and avoid sedimentation (Bell and Smith, 2004). Sponges have the ability to filter suspended sediment. Their role as filter feeders is largely described. Consequently, it is retained that bottom-up control of the availability of nutrients dissolved in the water column may control sponge abundance. Dissolved organic carbon (DOC) and detritus, are the main nutrient source for sponges (Pawlik *et al.*, 2018). Recent researches described the sponge-loop, the indication that sponges feed on dissolved organic matter (DOM) processing it, and releasing it as detritus to be available for the benthic detritivorous (de Goeij *et al.*, 2013; Rix *et al.*, 2018), this novel hypothesis is at present argument of investigation (McMurray *et al.*, 2018).

Sponges take part in the primary production as some species hosts photosynthetic unicellular algae (Wilkinson, 1987). Many of these photo-symbionts are transient in the sponge tissue, assimilated during the filtration of salt water. Cyanobacteria are the most abundant symbionts in sponges (Usher, 2008), with *Synechococcus spongiarium* as best representative (Erwin and Thacker, 2007). Sponge symbionts seem to confer tolerance to sponges for adapting to highly turbid and sediment habitats (Biggerstaff *et al.*, 2015). Symbiosis makes sponges contributing to the primary production of coral reefs. Although many boring sponges that contain Zooxanthellae, as described herein above, are vulnerable to ocean warming, hence this class of sponges can perish after a bleaching event.

Sponges, like many organisms at basal trophic levels, develop chemical defences to be protected by predators, some sponges use mechanical defences, producing siliceous or calcareous spicules, whereas others secrete secondary metabolites (Braekman and Daloze, 1986).

These metabolites often have antimicrobial properties to defend sponges by colonization of bacteria and fouling organism (Helber *et al.*, 2018), sponge secondary metabolites production is effective against other benthic organism with whom sponge compete for the substrate, moreover they are effective as defence from predators. With more than half of the described sponges species producing these deterring compounds, sponges present a primary role in the pharmaceutical industry (Laport *et al.*, 2009) and other sectors of the industry, as instance in the naval industry for the antifouling properties (Fusetani, 2004).

Despite their ubiquitous presence in many marine habitats and the important functional roles they performs, there is a paucity of information, attention and conservation efforts of sponges compared to Hermatypic corals. In the last decade, a particular attention has been reserved to sponges in the Caribbean, where coral cover is low and in many reef, the total substrate cover of sponges is higher than hermatypic corals (Villamizar *et al.*, 2014; Burke, 2011). In 69 sites surveyed across all the Caribbean, sponge covered an average of 15.9% of the total surface available, a result comparable with the cover of hermatypic corals (Loh and Pawlik, 2014). A recent thoroughly review from Pawlik *et al.*, (2018), illustrates the researches and opinions developed in the recent decades concerning if sponge abundance in the coral reefs is controlled by bottom-up or top-down controls process. The authors of the review sustain in some own publications, an evidence that the abundance of predatory fishes that grazes on sponges, regulates sponge biomass and benthic cover. And that there are no evidences for a strictly bottom-up process (Pawlik *et al.*, 2013; Pawlik *et al.*, 2015). Contradictorily Slattery & Lesser (2015), sustain that both bottom-up with top-down control are likely to regulate growth, biomass and abundance of sponges. From the debate resulted, it is likely that chemical defeated sponge are not affected by predation, as predators usually avoid this category of sponges, thus bottom-up process seems influence the abundance of this sponges (Pawlik *et al.*, 2013). Whereas, chemical undefeated sponges, considered palatable, are likely to be subjected to top-down

control (Leong and Pawlik, 2010; Pawlik *et al.*, 2015). The studies object of debate, were conducted merely in the Caribbean using as main sample the common demosponge *Callyspongia vaginalis* (Lamarck, 1814), Slattery and Lesser sustained the abundance of the vase sponge increased with depth in a Bahamian reef (Slattery and Lesser, 2015), whereas Pawlik's group support no evidence of increasing cover with depth in the Florida Keys (Cabral *et al.*, 2014). None of the authors considered a possible more intrinsic mechanism of sponge feeding preference. A recent study revealed a phylogenetic disruptions between population of this sponges in the Bahamas and Florida and seemed clustered between Western and Eastern central Caribbean (DeBiasse *et al.*, 2016). This sponge may, therefore, present different adaptation and selective feeding behaviour. Recent new studies unveiled some complexity in sponge feeding mechanisms. As instance, different sponges species displays different assumption rates and different cellular mechanisms of picoplankton (Maldonado *et al.*, 2010). The preference of resources for food assumption is determined by the localization of the sponge in the reef (Wulff, 2017). Below the mesophotic level, plankton availability is limited and sponge community seems to be adapted to the availability of the carbon source, preferring the POC. Deep sponges of the class Hexactinellida are found at depth, whereas Demosponge abundance diminishes increasing with depth (Kahn *et al.*, 2015). Sponge able to uptake microorganisms from the water column may also present selective feeding for their food income (Ribes *et al.*, 1999; Wehrl *et al.*, 2007). Although, new findings are contributing to understand sponge growth in relationship with nutrient availability, some intrinsic mechanisms are lively study argument. Whereas, for the Caribbean, it still not appear fully clear how bottom-up process regulates sponge growth, many evidence are present for Top-down controls (Hill, 1998; Pawlik *et al.*, 2013). A clear demonstration of sponge increasing their biomass when predators are removed, is the yellow sponge *Mycale laevis* (Carter, 1882). In overfished reef, *M. laevis* displayed a massive form, overgrowing corals, whereas in normal conditions it uses corals as a refugee from predators growing in a cryptic form (Loh and Pawlik, 2009; Loh and Pawlik, 2012). For the

Indo-Pacific an example of influence by sponge predators on sponge abundance was observed in the Wakatobi National Park, in the centre of the Coral Triangle (Powell *et al.*, 2015). In coral reefs where substrate availability is limited competition among benthic organisms is often documented (McCook *et al.*, 2001). Coral-sponge competition for space is a concern, particularly considering the decreasing coral cover trend. Few cases are reported for coral overgrowing sponges (Aerts, 1998; Aerts and vanSoest, 1997; Garcia-Hernandez *et al.*, 2017), often sponges tend to overgrow the competitor coral (Gonzalez-Rivero *et al.*, 2011; Loh *et al.*, 2015), particularly the excavating sponges (Marulanda-Gomez *et al.*, 2017; Elliott *et al.*, 2016). The consequences are often the demising of the coral. The regulation of predators of massive form sponges is fundamental to delimit substrate competition, particularly in demised reefs supported by lower biodiversity. The Philippines are a primary centre of endemism and are considered the top endemism spots undergoing anthropogenic impacts (Roberts *et al.*, 2002). In this Region not such coral-sponge competition and top-down regulation has ever been studied. Philippines are placed in the heart of the Indo-Pacific. This region, present a lush biodiversity compared to the Caribbean. Principally in zones like the Coral Triangle, where Philippines resides, retained one of the biggest hotspot for biodiversity, which also appear more resilient to climate change. Sponge Top-down control is chiefly been discussed for the Caribbean, any studies for the Philippines are reported. The Visayan region of the Philippines are known for the establishment of MPAs to support fish larval supplies in an area where enhanced tourism and international fishing vessel are recurrent (Burke, 2011). MPAs worldwide are widely accepted as a low effort conservation tool (Selig and Bruno, 2010). Although, their effectiveness is discussed (70). In the Philippines MPAs are often of small dimension, < 1 Km² (catlas.reefbase.org, 2018). Local managed MPAs appear more efficient and the proximity of the MPAs should be sufficient to provide larval connectivity (Weeks *et al.*, 2010). Many reefs in this region are subjected to disruptive natural and anthropogenic disasters, hence damaged reef may present increased levels of sponge-corals competition and a possible shift to the dominant benthic community.

Herein, I analyse if Visayan Philippine reefs located in the Coral Triangle, may face a sponge phase-shift. The aim of this study is comprehend if small scaled MPAs, supply increased spongivore abundance, heling prevent a shift in the dominant benthic community from coral to sponge dominated reef. Showing top-down controls evidence in the Philippines. Therefore, it will be assessed: 1. If small No-take areas maintain increased spongivore abundance; 2. Sponge-coral interactions and growth form assemblages of sponges in an overfished and protected site, in order to evaluate the effect of spongivore in preventing outcompetition of coral by sponges; 3. Coral and sponge cover across 4 reefs, in order to compare their abundances with coral's in sites where spongivore have a low abundance and NTAs.

2. Material and methods

2.1 Study sites

This study was conducted in the Philippine province of Southern Leyte in Sogod Bay. The province is divided in 11 municipalities which in turn are divided in barangays. The reefs surveyed were situated in front of the barangay of Napantao of the municipalities of San Francisco; Bahay, Cagbungalon, Catig, Tabugon Gudan of the municipality of Liloan (Figure 1). The two municipalities have a total population of more than ten thousands inhabitants each, many of which rely on fishing activities for their income. In the area of Sogod Bay, in accordance with the Philippine Fisheries code of 1998 that require that 15% of all the Philippines water have to be protected areas (Philippines Republic Act No. 8550), MPAs have been established since the 2002 from the NGO Coral Cay Conservation (CCC) in partnership with the Philippines Reef and Rainforest Conservation Inc. (Dallison, T & Ferguson, A, 2017). All the MPAs are locally managed by the barangay adjacent to the reef. Napantao, Catig, Bahay and Tabugon are the reef considered protected as they have established MPAs. As control site were used transects outside Napantao and Catig; whereas Cagbungalon and Gudan were used as control site for

Bahay and Tabugon respectively. All the reef surveyed are fringing reef. The MPA of Napantao has been established in the 1996 and has a No-take area extended for 5380 m². The reef appear in a good state with healthy corals, it present a gentle slope that ends with a wall that drop to 50m deep, mean horizontal visibility is 16.62 ± 6.49 m. The site is slightly exposed, clear marks of typhoon in some area of the reef are lastly reported in 2014 after the typhoon Yolanda. In the protected area is evident and reported in the recent years a moderate level of poaching and use of rocks to capture fishes that damaged the corals. Catig and Bahay are considered as site of moderate protection for the young age of the MPAs, merely instituted in the 2016, their total NTA area is respectively 2601 and 27314 m² . Both are situated on the eastern side of Panaon island, facing the Surigao strait. For both sites, the population centre resides in proximity of the reef but the anthropogenic impact is generally low. Catig's reef is exposed to the northeastern monsoon (Amihan) during the winter season (November-March). Catig's reef surveys were conducted on the slope, most of the MPAs is covered in branching hard coral with an high abundance of *Porites* sp. (Dallison, T & Ferguson, A, 2017). Bahay's reef is sheltered from the monsoon during all the year. The overall anthropogenic impact on this site is generally low. Cagbungalon is localized on Sogod Bay. The population size of the barangay is below one thousand people but the anthropogenic impact on the reef is moderate. There is actually no control on the area which is used for fishing, although no highly disruptive fishing practices are ever been recorded. The MPA of Tabugon is been established in the 1993 and it is extended for 22770 m². The site is sheltered from storms, the anthropogenic impact is overall low although poaching is recorded. Gudan is situated north to Napantao. The site is often exposed to typhoon being lastly impacted in 2014, the site is used for fishing and recreational diving activity by locals and it is never been protected.

2.2 Data collection

All the surveys were performed using SCUBA, using transects. The surveys were conducted at 6 and 12 m. The data for spongivores abundance and substrate type were conducted with the

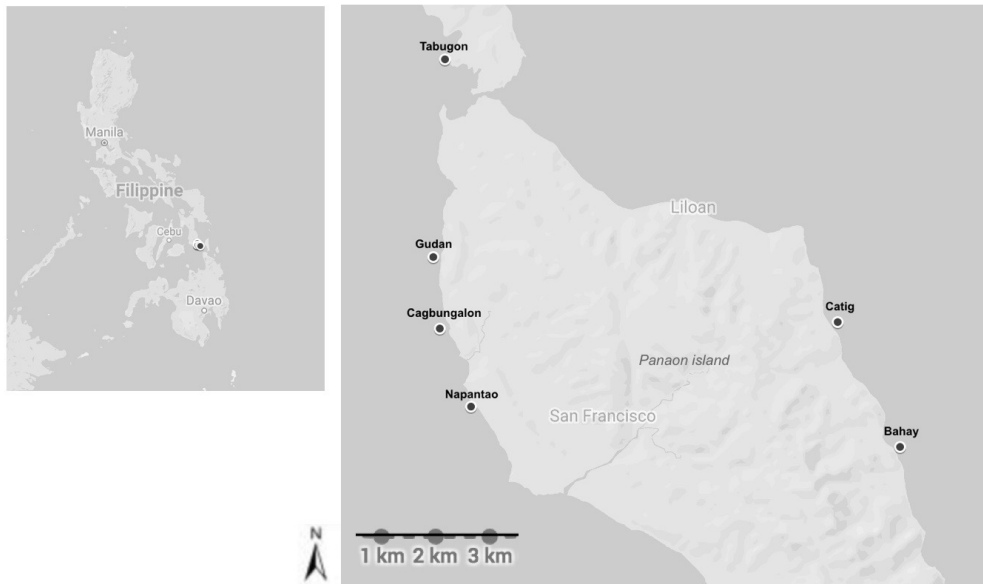


Figure 1. Map Showing the location of the surveyed sites in Sogod Bay, Southern Leyte, Philippines.

methodology used by CCC of an augmented reef check (Dallison, T & Ferguson, A, 2017). CCC uses this methodology to assess the reef status prior the establishment of an MPA (Leopold *et al.*, 2009). Spongivore and substrate data were collected with the help of volunteers and local staff, therefore the data collected for fish were the same used for CCC's MPA assessment. Fish data are collected within a 5 m belt transect along 20 m of each replicates of the 100 m transect. Substrate data are recorded along the same replicates of the point-intercept transect at intervals of 0.5 m. A deepened review of the literature was performed to identify the spongivore families for the Indo-Pacific region that have sponges as part of the diet: Acanthuridae, Chaetodontidae (Nagelkerken *et al.*, 2009), Nemipteridae, Pomacanthidae, Siganidae (Hoey *et al.*, 2013), Scaridae, Tetraodontidae (Moreno *et al.*, 2009) and Zanclidae were the families selected for this study (Powell *et al.*, 2015; Cole *et al.*, 2008; Pawlik, 1998). Pomacanthidae is the only family that reportedly feed chiefly on sponges (Randall, 1967). Due to shortage of survey time,

identification at each site for fishes that include sponge in their diet would not have been possible. To positively avoid the exclusion of fish that potentially feed on sponges, without being showed in the literature, spongivores were considered at family level. And to avoid bias of fish species included that not fed on sponges, the same analyses were repeated considering just Pomacanthidae. The Napantao reef has been considered one of the healthiest reef across all Sogod Bay, the site is surveyed yearly since 2013 during March-April and September-October. The temporal series of data for Napantao has been granted by CCC. The methodology is the aforementioned used for all the surveys by CCC. A total of six fixed 100m transect (12 m depth) inside and likewise outside the MPA boundaries are surveyed annually (see supplementary material A. for coordinates). For Bahay and Cagbungalon, 6 transects (6 and 12 m depth) were surveyed between June and July of the present year (appendix A), Tabugon and Gudan have been surveyed in February and June respectively with a total of four transects at each site. Data for sponge interaction with corals and sponge growth forms were collected at Catig during August, in addition to data for spongivores and substrate at a depth of 12m, with 3 transect inside and 3 outside the no-take area (Schonberg, 2015). The number of transects was decided evaluating the extent of the MPA and in concession with CCC. To determine sponge-coral interaction a number was used as code: 0 meant no interaction with the hard coral, 1 meant the sponge grew adjacent to the coral but the tissue was not covering the corallites, 2 meant the sponge was overgrowing the coral and sponge tissue was completely or partially covering the coral skeleton. To determine sponge growth, a visual assessment of the reef was performed with an explorative dive, with a 12m, 60' maximum bottom time profile, covering great part of the reef allowing to evaluate the possible growth forms of sponges present in the reef. Subsequently 11 growth form were selected: aborescent, barrel, boring, encrusting, digitate, fistulose, globular, tubular, thick encrusting (> 5mm thick), vent, other/massive (massive with an amorphous form). Moreover, two volunteer were given an additional lecture to the skills development program, regarding the methodology, the biology and ecology of sponges to make

them able to survey (Bell, 2007). Both data for interactions and growth forms were collected along the same transects for fish and substrate data, along a 2 m belt transect.

2.3 Statistical analyses

All the statistical analyses were performed using the software R (R Development Core Team, 2018). Prior all the analysis, it is been verified the normality of the distribution with graphical visualization and the Shapiro-Wilkinson test for normality (Shapiro and Wilk, 1965). The homogeneity of variance was tested with the Brown-Forsythe Levene test. Non-parametric analyses were performed were the distribution was not normal using the “MASS” library, parametric tests were used within the “vegan” library.

Coral-sponge interaction and growth forms data

A Paired sample t-test was used to verify the difference of spongivore abundance between the protected and non-protected area. A non-metric multidimensional scaling (nMDS) using the Bray-curtis distances of the growth form abundances matrix was performed to visualize the differences of sponge morphological assemblages between the protected area and outside. Permutational multivariate analysis of variance (PERMANOVA) was used to test the null hypothesis of difference between the fished and the protected sites. The same approach was used to compare sponge-corals interactions. A linear model to show if spongivore had an influence on sponge overgrowing corals and the type of relationship was performed.

Sponge abundances across all sites

To visualize the substrate composition across all the sites were performed an nMDS. Prior to substrate analyses a Wilcoxon Signed-ranks Test was performed to determine a difference in spongivore abundance between the protected and the fished sites. In the same way was tested the sponge and hard coral abundance. A general linear model was performed to investigate

difference in sponge abundance across sites and an effect of spongivore on sponge abundance.

Napantao Marine protected area

The Akaike's Information Criterion (AICc) was used to identify the best model for a linear regression considering as factors the protection, spongivore abundance and time with % sponge cover. The lower AICc value was considered as the more parsimonious and was used for a linear regression. The change in abundances for sponge as % cover between the two conditions of protection and for the different years was testified using a Two-way ANOVA followed by the Tukey's HSD *post-hoc* test.

3. Results

3.1 Spongivore abundance

The mean spongivore abundance for the years 2017-2018 was 42.33 ± 8.39 inside the MPAs and 17.20 ± 0.41 outside (mean and standard error). The lowest value was recorded in Gudan 16.19 ± 4.84 , the highest spongivore abundance was in Napantao MPA 59.33 ± 19.42 (mean and standard error). The spongivore abundance was significantly different between protected and non-protected sites (Shapiro Wilk's test, $w = 777$, $p = 1.38 \times 10^{-9}$). The mean spongivore abundance in Napantao from 2013 to 2017, ranged from 43.35 ± 5.78 inside the MPA to 24.29 ± 3.59 outside. Spongivore abundance was significantly different in the transects inside and outside the MPA for all the surveyed years (1-Way ANOVA, $f_{1,118} = 29.31$, $p = 3 \times 10^{-7}$). In Catig's MPA, spongivore abundance was 50.25 ± 13.08 and outside was 18.08 ± 7.55 (mean and standard error). Hence, the abundance resulted different inside and outside the MPA (1-Way ANOVA, $f_{1,22} = 18.14$, $p = 0.00032$). Pomacanthidae was also significantly different between

MPAs and outside in all the sites ($p=0.0052$), for all the years in Napantao ($p=0.0426$), and for Catig ($p=0.0019$), the same statistical tests for all the spongivore were used.

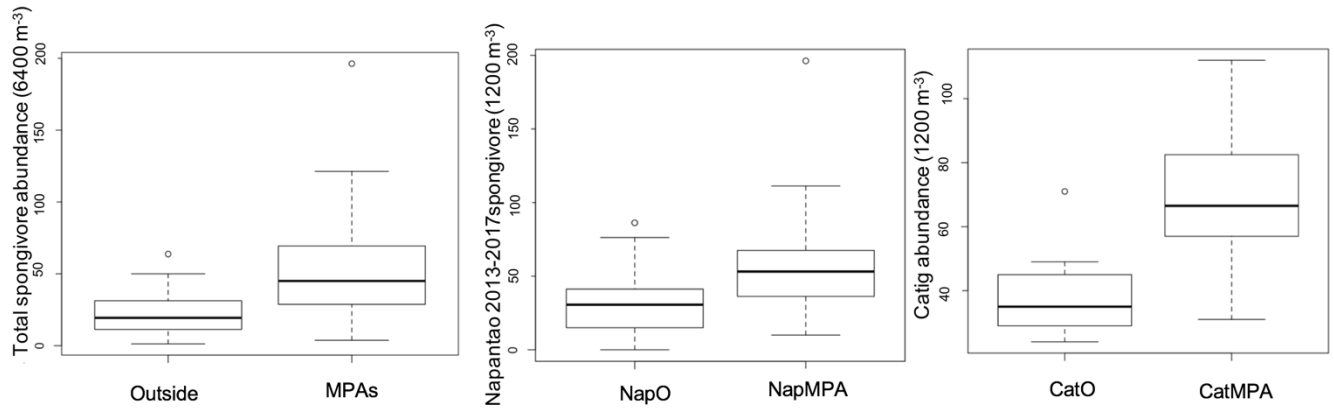


Figure 2. Difference of spongivore abundance inside and outside the MPAs. On the left, considering all the survey sites, Shapiro Wilk's test, $w=777$, $p=1.38 \times 10^{-9}$; in the centre only Napantao, years 2013-2017, 1-Way ANOVA, $f_{1,118}=29.31$, $p=3 \times 10^{-7}$; on the right, only Catig, 1-Way ANOVA, $F_{1,22}=18.14$, $p=0.00032$.

3.2 Morphological assemblages

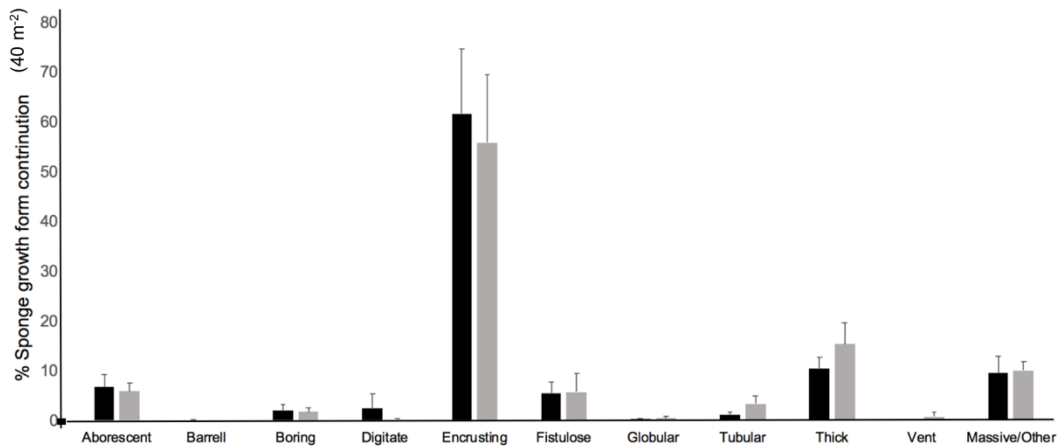


Figure 3. Growth form assemblages between MPA and fished area in Catig. Mean % abundance for the 11 selected growth form is represented with error bars. Black bar represent the % abundance of growth form inside the MPA. Grey bar outside. The error bars are for the standard error.

A total of 2125 sponges were counted inside Catig MPA and 1791 outside. Encrusting was the most abundant growth form, accounting for 61.67 ± 13.02 and 55.90 ± 13.58 of the total % abundance for inside and outside the MPA respectively (Figure 3). The majority of the encrusting sponges were found on rubble patches, binding rubble fragments together. The total sponge abundance was not significantly different between the two condition. Growth form

richness was 7 ± 0.38 and 6.91 ± 0.30 inside and outside Catig's MPA. nMDS analyses showed the morphological assemblages did not differ between the protected and non-protected area of Catig, as it is evidenced in the figure showing different growth form based on Bray-curtis distances (Stress = 0.04; Figure 4). The PERMANOVA analyses with 999 permutation confirmed there were not a significant difference in morphological assemblages in the two zones (Table 1). All the spongivore considered did not have an effect, but Pomacanthidae alone did influence the sponge morphologies between the two sites.

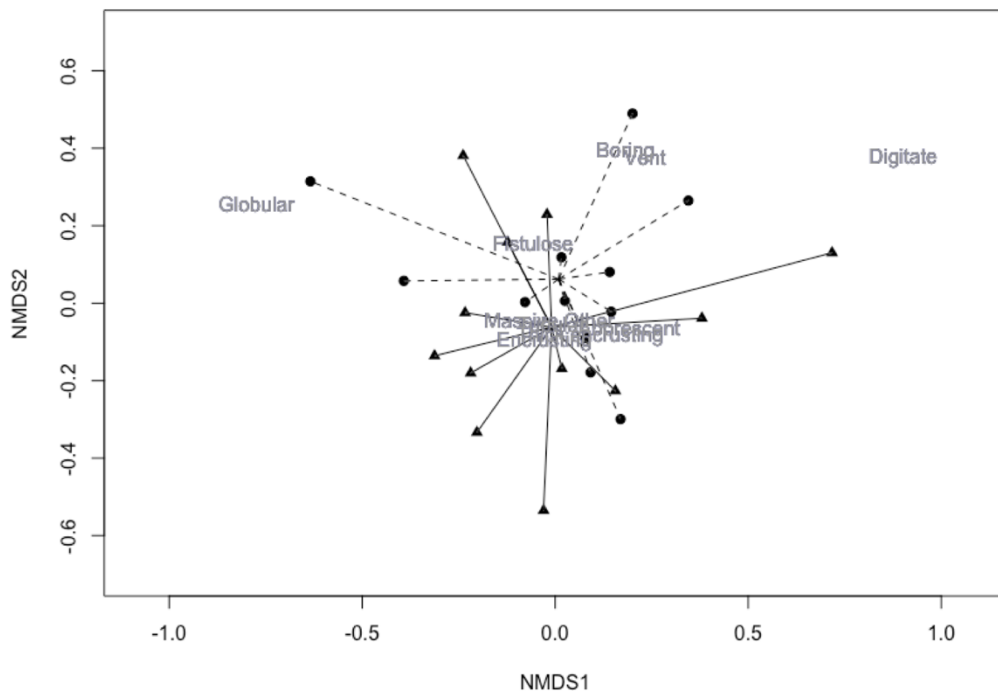


Figure 4. Non-metric multidimensional scaling (nMDS) showing the different morphological assemblages in Catig. The ordination is based on Bray-curtis dissimilarities of abundances for $p=11$ sponge morphologies obtained for three different 100m transects at 12m depth inside and outside the protected area of Catig. Triangles shows the assemblages inside the MPA, circles outside's. In grey are the growth forms. Stress= 0.04

Factors	Df	Sum	Sq	Pseudo-F	R2	P
Pomacanthidae	1	0.35	0.36	3.028	0.12	0.022*
Protection	1	0.048	0.048	0.4	0.016	0.87
Pomacanthidae x Protection	1	0.21	0.21	1.8	0.071	0.12
Residuals	20	2.34	0.12		0.79	
Total	23	2.96			1	

Table 1. PERMANOVA table showing differences in the sponge morphological assemblages with different abundance of Pomacanthidae, a family almost exclusively feeding of sponges.

3.3 Hard coral interactions

In Catig, a total of 2548 sponge that had no interaction with corals were counted across all the survey area. 797 were overgrowing corals and 571 were growing adjacent to hermatypic corals. The major representative of sponge overgrowing corals inside the MPA, was the purple excavating sponge *Chalinula nematifera* (identification by visual observation, Figure 5). The nMDS showed the different interaction coral-sponge inside and outside Catig's protected area (stress= 0.025; Figure 6). PERMANOVA confirmed an interplay of total spongivore on coral-sponge interactions. The same results were obtained when considered the effect of Pomacanthidae alone out of all the spongivore (Table 2). The linear regression between spongivore abundance and sponge overgrowing corals abundance showed a positive correlation (adjusted $r^2 = 0.35$, $p=0.0013$; Figure 7a), Pomacanthidae alone were also considered a good model according to the AICc showing a positive correlation with sponge overgrowth (adjusted $r^2 = 0.35$, $p=0.0012$; Figure 7b).

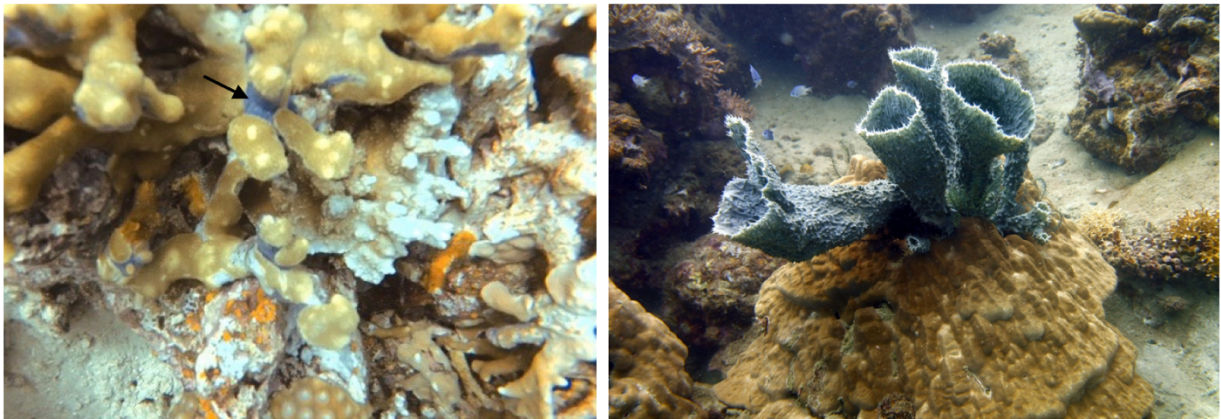


Figure 5. Sponge overgrowing corals in Catig. On the left, arrow indicates the cryptic purple sponge *Chalinula nematifera* overgrowing a branching colony of *Porites* sp. inside the MPA; On the right a vase sponge overgrowing a massive form of the same coral outside the MPA.

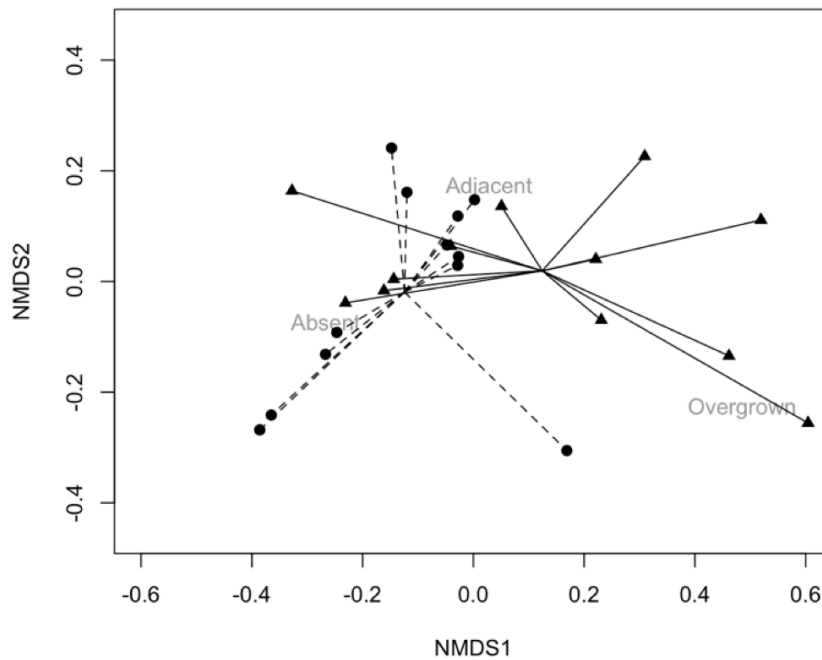


Figure 6. Non-metric multidimensional scaling (nMDS) ordination of $p=3$ type of interaction coral-sponge for the protected and fished area of Catig. The ordination is based on the Bray-curtis dissimilarities. The $n=12$ replicates at 12m inside the MPA are reported as triangles and were compared with the $n=12$ replicates outside the MPA reported as circles. PERMANOVA showed a difference in the interactions just when spongivore abundance where considered. Stress= 0.025

Factors	Df	Sum	Sq	Pseudo-F	R2	P
a) Total spongivore	1	0.42	0.42	3.67	0.14	0.021*
Protection	1	0.042	0.042	0.36	0.014	0.779
Total spongivore x Protection	1	0.19	0.19	1.71	0.066	0.177
Residuals	20	2.29	0.11		0.77	
Total	23	2.95			1	
b) Pomacanthidae	1	0.49	0.49	4.41	0.16	0.08*
Protection	1	0.099	0.099	0.89	0.033	0.43
Pomacanthidae x Protection	1	0.13	0.13	1.18	0.044	0.32
Residuals	20	2.23	0.11		0.75	
Total	23	2.95			1	

Table 2. PERMANOVA table showing different sponge-coral interactions with different abundances of a) all the spongivore, b) angelfish. The interactions were not different inside and outside the MPA.

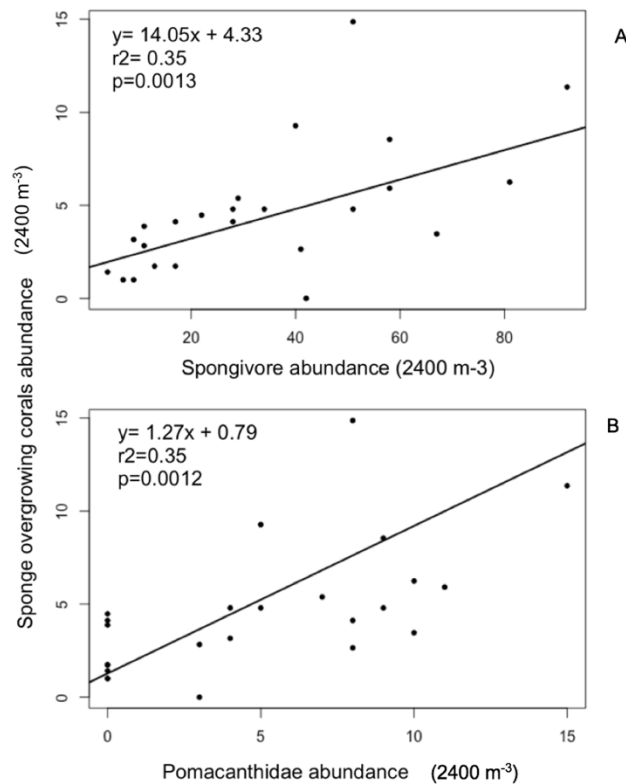


Figure 7. Correlation between spongiivore and coral overgrowth. The dots represent abundance for each replicate of the total transects surveyed at Catig, n=24. The equation with the R² and p-value are reported.

3.4 Substrate analysis

The nMDS for the benthic assemblages showed a difference of the benthic composition among sites and in protected and non-protected sites (Table 3, figure 8; stress= 0.19). Bahay was dominated by rubble and sand (8.85 ± 0.2 and 42.91 ± 1.81 % abundance and SE), Cagbungalon by hard corals (31.77 ± 1). The MPA of Napantao is mainly dominated by hard coral (53.33 ± 2.09) and Zoanthid (13.54 ± 1.18 ; reported in the OT category for substrate). The area outside the MPA is mainly dominated by hard coral (41.66 ± 3.01) with patches of rubble, a similar substrate type is showed for the Catig of MPA (38.95 ± 4), whereas the outside is prevailed by macroalgae (9.16 ± 0.72). The MPA of Tabugon is dominated by sand (41.56 ± 2.10) and rubble (15.93 ± 0.84). The fished area of Gudan is dominated by hard corals ($27.18 \pm$

1.25) and sand (22.81 ± 2.45). The % Sponge abundances appeared being equal to 0 in 49 replicates, the distribution presented a non-normal fit. Consequently the data were analysed as a negative binomial distribution. The Wilcox-test showed a significant difference for the % sponge cover in the MPAs and outside ($w=2634.5$, $p=0.0037$), but not for the % coral abundance (Figure 9).

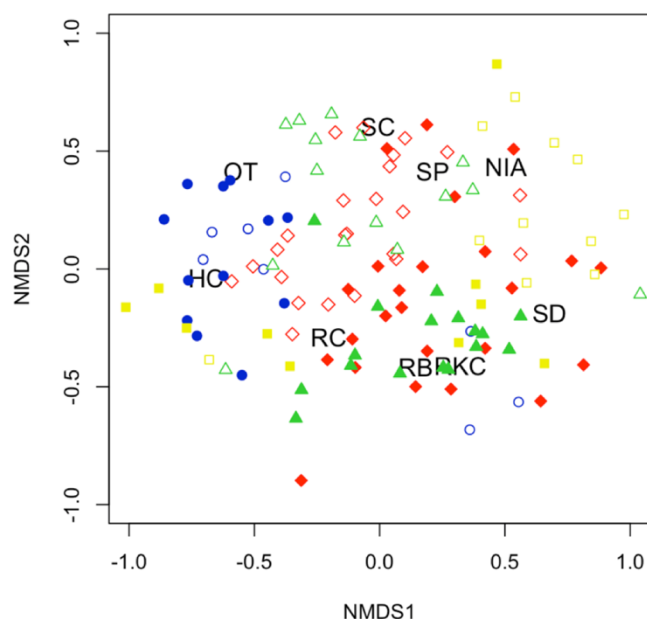


Figure 8. Non-metric multidimensional scaling (nMDS) ordination showing the benthic assemblage composition at the sites surveyed. Distances are obtained with the Bray-curtis method. Full shapes represent the MPAs, empty shapes the equivalent control sites. The study sites are: red diamonds, Bahay; empty diamonds, Cagbungalón; Blue circles, Napantao MPA; empty circles, Napantao control; Yellow square, Catig MPA; empty squares, control for Catig; Green triangles Tabugon MPA, empty triangles Gudan. Stress=0.19

Factors	Df	Sum	Sq	Pseudo-F	R2	P
Protection	1	0.59	0.59	9.28	0.033	0.001*
Sites	30	10.81	0.36	5.67	0.62	0.001*
Residuals	96	6.099	0.063		0.35	
Total	127	17.5			1	

Table 3. PERMANOVA table showing the difference of benthic assemblages among sites and between MPA and fished sites.

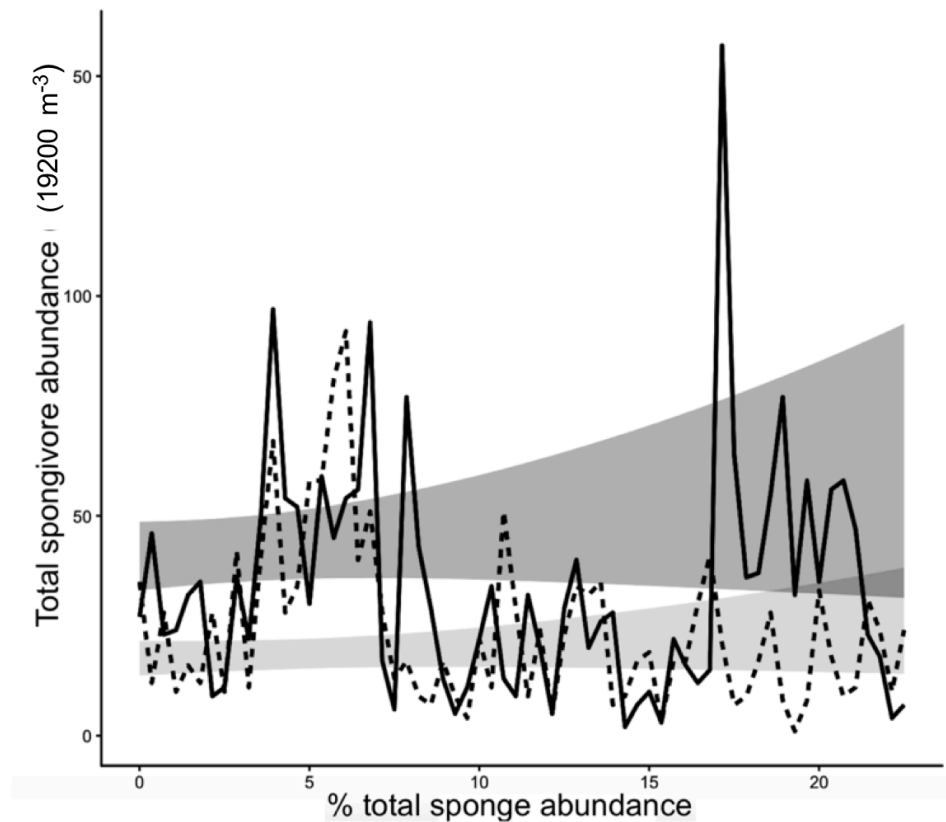


Figure 9. Correlation for %sponge abundance and spongivore in the MPAs. The general Linear Model for the negative binomial distribution shows a positive relationship between sponge and spongivore abundance in four MPAs (dotted line), the continuous line is for the control sites. The dark grey bar represent the 95% confidence interval for the MPAs, the lower light bar is for the controls

The linear model showed no influence from spongivore or angelfish on % sponge abundance.

To evaluate the possibility of an opposite effect the general linear model for a negative binomial distribution was performed for a possible effect of sponges on their vertebrate predators. The result showed that sponge % cover was positively correlated with spongivores in the protected areas ($p=8.46e10^{-15}$; figure 9). In Napantao, the mean total sponge abundance was 3.50 ± 0.48 in the MPA and 4.65 ± 0.57 outside. The highest % sponge cover was recorded for the year 2014 at both the fished area and the protected area (6.56 ± 0.88 and 5.64 ± 0.98). The average hard coral % abundance was not different inside and outside the MPA's boundaries (37.49 ± 3.07 and 29.94 ± 2.69).

The Akaike's Information Criterion allowed to identify two models for the linear regression for the temporal series of data from Napantao. The model with the lower AICc score were selected, and two models were considered the most parsimonious. One model identified was correlating the total %sponge abundance for all the years with time. The second model had as responsive factors the spongivore abundance and the time (expressed in years). In both models the liner regression identified any significant correlation of sponge abundance with the two variables. The % sponge abundance was different inside and outside the MPA (ANOVA, $F_{1,116}=5.21$, $p=0.0243$; Figure 10.), the post-hoc Tukey test evidenced higher sponge abundance outside the MPA .

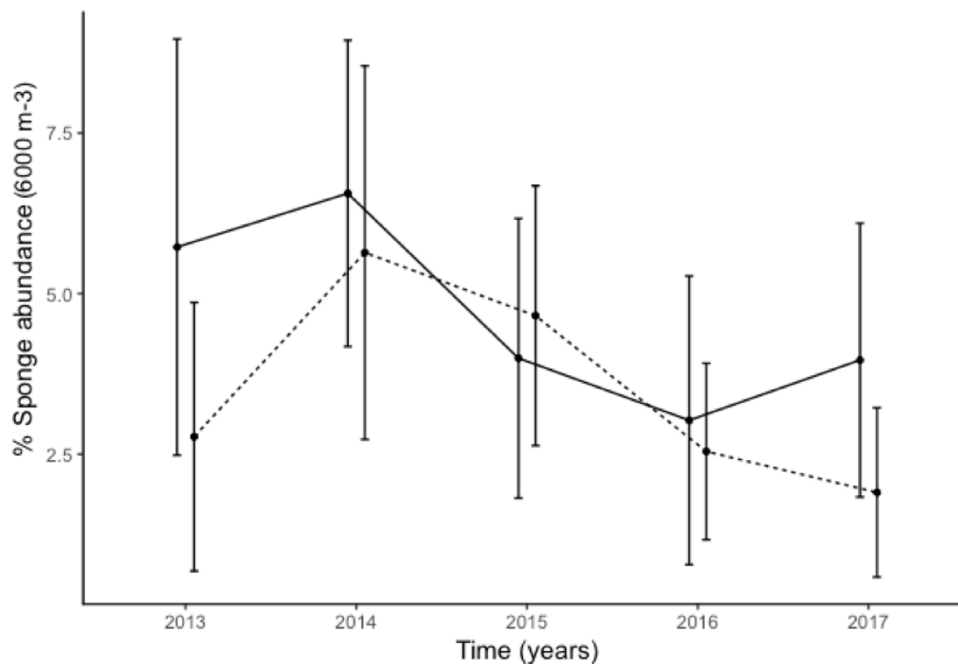


Figure 10. Line plot of the 2-Way ANOVA, showing difference of % sponge abundance between Napantao NTA's (dotted line) and the adjacent fished area (continuous line). $p=0.0238$.

4. Discussion

Approximately 60% of the World's reef is damaged from overfishing (Burke, 2011). Reefs in Sogod Bay in the Philippines, have evident signs of exploitation due to usage of the reef resources by the local population. Sponges are important benthic organisms, but their thriving could negatively affect coral reefs by outcompeting reef building corals and lowering the reef carbonate budget for the action of excavating sponges. Understanding mechanisms of regulation of sponge growth, is fundamental to prevent a possible shift of the dominant benthic community into a sponge-dominated reef.

Results showed no evidence of top-down controls by sponge vertebrate predators. But demonstrated the possible efficacy of forbidding any fishing practice in incrementing fish abundance, at least for the selected fish families of this study, underlining the relevance of No-Take areas in maintaining adequate fish abundance. In Catig and Napantao, the transects for the fished zones were not much distant than the transects inside the MPA boundaries (<1 Km), but still showed a significant difference in spongivore abundances (Figure 2.). The families of spongivores herein selected, usually shows a territoriality (Kuitert and Tono-zuka, 2001). Moreover, in Catig, fish cages were found in two transects. The Barangay captain, responsible for the MPA management, affirmed that was the fishing technique broadly used in the site, nearly outside the MPA, hence it is plausible a difference in fish abundance. The MPAs were established in order to protect the portion of the reef with highest coral cover (Dallison, T & Ferguson, A, 2017; Mumby and Harborne, 2010), hence the portion surveyed outside the MPAs, presented an highest sand and rock cover (%) which supported lower fish abundance (Figure. 6). In opposite with studies sustaining the top-down control (e.g. Pawlik *et al.*, 2013), here spongivore abundance was positively correlated with % sponge cover. In Catig, sponge overgrowing corals were positively correlated with the fish, even when just considering the Pomacanthidae. The pearl-scaled angelfish *Centropyge vrolikii* (Bleker, 1853), was found at all

the sites, in Catig, was the more abundant representative of his family. Hypothetically, this angelfish has a too small biomass to contribute the limitation of sponge abundance, having a maximum length of 12 cm (Kuitert and Tono-zuka, 2001). The Hawksbill turtle, a primary spongivore (Leon and Bjorndal, 2002), was not considered in this study due to lack of previous direct observations of feeding behaviour and abundance measures. Although, it is known that populations of this turtle inhabit the reef of Catig and Napantao, which recently hatched on the shore near the latter (CCC staff observation). Therefore, this important spongivore could have a role in determining sponge abundance, although in Bahay, Cagbungalon, Gudan and Tabugon, Hawksbill have never been recorded and sponge cover (%) was not significantly different then in Napantao and Catig. The absence of sponge abundance control by predators in all the survey sites may explain the lack of different morphological assemblages in Catig. There was an interaction of morphological assemblages with the angelfish, although they were not successful in reducing spongivore abundance, probably for the highest abundance of cryptic sponges. Indeed, encrusting sponges were observed being the main sponges overgrowing corals inside the MPA. *Chalinula nematifera* was found overgrowing branching forms of *Porites* sp. . This fast growing sponge has been reported abundant across Sulawesi, Indonesia, from the Lembeh strait to the Wakatobi Marine National Park, overgrowing and killing different corals of different growth forms (Rossi *et al.*, 2015). This sponge is also considered invasive in the Caribbean where principally overgrows *Pocillopora* sp. and branching coral forms (Avila and Carballo, 2009). The coral reef in Catig shows a predominance of branching coral cover but supported by low species diversity (Dallison, T & Ferguson, A, 2017). In this reef were evident marks of invertebrates predation. Along the transects, during the surveys, numerous *Drupella* sp. were observed, *Drupella* is a known gastropod grazing Scleractinian corals. The Barangay captain confirmed crown of thorns outbreaks happened in the recent years. Considering the brittleness of Catig's reef, the abundance of *C. nematifera* has to be monitored and it is considerable

implementing monitoring of this sponge during the MPA surveys of Catig, since protection from fishing may be not sufficient to seek the health of the reef.

Sediment has been reported been an environmental factor influencing sponge abundance in an Indonesian reef system (Powell *et al.*, 2015). Herein, sediment was not considered due to lack of equipment, although, considering sedimentation for similar studies may underline it as a crucial driving factor for sponge abundance. Sponges are relevant filter feeding, hence water turbidity may also perform a role in sponge growth. In the surveyed reefs, the visibility was often less than 20 m and a moderate current was often recorded during the survey time. Water quality have an impact of sponge growth: in increased turbid environment, particularly in proximity of the coast in shallow water, sponges are negatively affected. Moreover different sponge taxa seem recover and have different tolerance to a turbid environment (Wulff, 2013). In the Philippines are present a conspicuous number of endemic species (Bakus and Nishiyama, 2000), endemism in sponge is common for the limited swimming ability of the larvae (Van Soest *et al.*, 2012). Hence, in the Indo-Pacific different sponge assemblages might respond differently to turbidity and sedimentation, these response might stand back from the observations in other geographical areas. For example, sponges in the Indo-Pacific are commonly phototrophic, some hosts the unicellular photo-symbiotic dinoflagellate *Zooxanthellae*, hence, likewise corals, are affected by poor light conditions (Fang *et al.*, 2018). In a Sulawesi reef system, Indonesia, has been observed how sponges preferred to grow on vertical surfaces to avoid sediment deposition (Bell and Smith, 2004). The availability of nutrients in the water and the type of environment, seem influence sponge growth rates (Wulff, 2017). Seasonality has never been considered as a sponge abundance driving factor in the tropics. It has been observed for three temperate sponge in the Eastern Atlantic that size of sponge patches increased during warmer seasons (Bell, 2008a).

Findings of the current studies showed it is likely sponges have a role in increasing spongivore abundance. Recently, the concept of the sponge-loop (de Goeij *et al.*, 2013) showed the role

sponges have in the reef trophic interactions, although it is not clear at which extent different sponge taxa are involved in detritus production and what are the environmental factors driving this process. To assess the effect nutrient availability have on sponge and how sponge reorganize the carbon matter, it has to be considered all the variation in sponge feeding mechanism and how it varies among species. Hence considering the sponge assemblages of a reef and the concentration of DOM, DOC, POC and detritus (Pawlik *et al.*, 2016). Evidence for bottom-up and top-down regulations are both valid for different geographical area, but it is more likely that together are relevant for controlling sponge communities (Pawlik *et al.*, 2018). Multiple factors have to be considered when accounting for sponge control. Besides predators abundance and nutrient availability, reef position, turbulence, light, seasonality and sponge feeding mechanisms are relevant factors to possibly have a role in regulating sponge growth.

I observed if Top-down control was verified for sponges living at shallow depth, as it seems bottom-up process are more relevant for deeper sponges. For example observation of influence of the living particulate organic matter (LPOC) in limiting sponge abundance have been reported for deep habitat and mesophotic reefs, where picoplankton is more abundant (Trussell *et al.*, 2006). Studies that sustain increased concentration of food affects filter feeding sponges, did not considered the particulate organic matter (DOC). Recent field manipulation and laboratory experiments revealed DOC being an important component of nutrition for some sponges (McMurray *et al.*, 2018), as instance, high microbial abundance (HMA) sponges seemed prefer the DOC (Hoer *et al.*, 2018). Hence Bottom-up process have to be revised considering inter-specific DOC assumption, also including DOC-flux rates and the heterogeneity of the carbon source available in the environment . Significant bottom-up studies, observed the feeding mechanism of single or few species, like the giant barrel *Xestospongia sp.* (Pawlik *et al.*, 2018), this sponge is chemical defeated thus is likely its growth rate is affected by the availability of nutrient in the water column, since it process a big portion of the water column, overturning the total volume of water every 2.3 to 18 d (McMurray *et al.*, 2015). Broadly, sponge feeding seems

influenced by the morphology, total volume, thickness, tissue density, photosynthetic symbiosis, the holobiont and tissue concentration of bacteria (Pawlik *et al.*, 2015). Therefore, it is important to study how different sponges respond their preferred nutrient source. Also attention has to be reserved to comprehend and define the composition of the DOC which seem refractive (Rix *et al.*, 2016) and the different methods of assumption, comprehending inter-specific sponge feeding behaviour. It seems more likely an elaborate mechanism, where the energetic level of the reef influence sponge assemblages and their resulting morphological assemblages have as consequences different feeding mechanisms, which interest impact in turn the nutrient availability for other organisms (de Goeij *et al.*, 2013).

Herein was not possible to observe bottom-up control for different reasons: limited survey time with no previous data of sponges present for the site, impeded monitoring sponge growth; missing equipment, the CCC base of Napantao is not supported by laboratory facilities and instrumentation to determine precise estimation of sponge growth, density and nutrients availability. Hence just Top-down process were considered. For the purpose of this research it would have been more accurate to survey corals-sponge interactions and morphological assemblages in an MPA with a better ecological status and increased coral diversity than Catig to compare it with an overfished reef, as instance Napantao with Gudan . The surveyed period was during the rainy season, although weather conditions were acceptable, Napantao reef is subjected to strong winds during this season generating high waves, hence was not possible to survey at that site. This also justify data for Napantao being only present up to the year 2017. Direct observation of fish grazing on sponges would have been more accurate, but once more, time was not adequate. All the surveys had to be coordinated with the CCC survey schedule, which also affected the choice of survey sites.

The results of this research suggest coral reefs in the Indo-Pacific are characterized by other process that regulate sponge abundance than top-down control by spongivore. Contrary to previous studies (Loh *et al.*, 2015; Powell *et al.*, 2015), here spongivore seems positively

influencing sponge overgrowing corals, this finding furtherly support that sponges in these reefs are not subjected by top-down regulations and may suggest an evidence of the sponge-loop, which would require further study in the area. Indo-pacific reefs seem display different sponge assemblages than in the Caribbean, with a major abundance of cryptic sponge than massive forms. I suggest further research of mechanism of control of cryptic excavating sponge abundance and growth is necessary in this geographical area, particularly concerning the nutrient availability and the carbon sources. This is relevant to understand mechanism of expansion of some cryptic sponges, acknowledged hostile competitors with corals. In the Caribbean both Top-down and Bottom-up control seems influence sponge abundance (Pawlik *et al.*, 2018). Further research should be focused in the Indo-Pacific as from this study appears other factors influence sponge assemblages than predation pressure.

