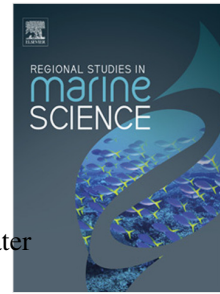


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The highly competitive ascidian *Didemnum* sp. threatens coral reef communities in the Wakatobi Marine National Park, Southeast Sulawesi, Indonesia

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Abstract

Coral reefs in the Wakatobi Marine National Park (WMNP), Indonesia, are protected but have been degrading in several areas due to local anthropogenic stressors. In affected areas, benthic surveys revealed the occurrence of a dominant ascidian species of the genus *Didemnum*, which may negatively impact the benthic community composition and structure. We quantified the abundance, substrate preference, and growth rate of *Didemnum* sp. in non-degraded and degraded reefs to assess its impact on the benthic community. While *Didemnum* sp. occurred in similar high abundances in both, non-degraded (0.66%) and degraded (0.75 %) reef sites, this species showed a substantially (> 10-fold) increased growth rate in degrading reefs ($2.7 \pm 0.98\%$ day⁻¹ increase in colony size, compared to $0.17 \pm 0.39\%$ day⁻¹ in non-degraded reefs). Furthermore, *Didemnum* sp. colonized many different substrates and showed the ability to overgrow live corals quickly. These observations indicate that *Didemnum* sp. can be a severe threat to a reef community by outcompeting live corals and call for further studies on the interaction between environmental pollution and *Didemnum* growth patterns in coral reefs.

Keywords: Didemnidae (ascidian); epibiosis; Coral Triangle; benthic competition; pollution impacts

1. Introduction

Coral reefs are among the most diverse and productive marine ecosystems (Odum and Odum 1955; Crossland et al. 1991). However, they are threatened by a variety of global and local anthropogenic stressors that have repeatedly led to a loss of coral cover (Schroth et al. 2005; Hughes et al. 2010; Bellwood et al. 2011). Local stressors, such as eutrophication, pollution and the overexploitation of marine life modulate the benthic community structure of reef ecosystems by promoting the colonization of benthic organisms on the surfaces of dead corals and other hard substrates (Burkepile and Hay 2006).

Among other opportunistic taxa, particularly colonial ascidians have the potential to colonize and overgrow natural and artificial substrates quickly if the biological characteristics of the habitat (e.g., food availability and predation pressure) are favourable (López-Legentil et al. 2005). Eutrophic conditions enhance their growth by providing an increased supply of food from planktonic primary producers that benefit from elevated levels of nitrate and phosphate (Hughes 1994; Mumby 2009). Overfishing, on the other hand, removes potential predators that structure the benthic community and, either directly or indirectly, controls populations and species dominance (Jackson et al. 2001; Hughes et al. 2007; Kremer and da Rocha 2016). In addition, fast growth and maturation rates (Lambert 2002), high fecundity (Lambert 2002; Shenkar and Swalla 2011) and resilience to environmental changes including temperature, salinity and pollutants (Lambert 2002) make ascidians particularly strong spatial competitors in coral reefs (Nandakumar 1996; Lambert and Lambert 2003; Castilla et al. 2004a). Invasive ascidians may not only colonize bare substrate but also successfully overgrow living benthic organisms (Birkeland et al. 1981; Chang and Marshall 2016), leading to significant changes in the benthic community structure of impacted coral reefs (Lambert 2001; Castilla et al. 2004b; Dijkstra et al. 2007).

The Coral Triangle, situated in the western Pacific Ocean, counts as the world's hotspot for marine biodiversity (Foale et al. 2013). In addition, the Coral Triangle is home to 390 million people, 130 million of which directly rely on its coral reefs for food, income, and protection from storms. Nevertheless, current levels and methods of harvesting fish and other resources are not sustainable and place this important marine area and its people in peril. In recent years, an increasing number of studies (Cabral and Geronimo 2018; Lasut et al. 2018; Teh et al. 2018) and the 'Reefs at Risk Revisited in the Coral Triangle' report (Burke et al. 2011) have highlighted the immediate and potentially fatal threat from a range of factors, including overfishing, destructive fishing, climate change, land-based pollution and coastal development in this area (Burke et al. 2011).

From all countries bordering the Coral Triangle, Indonesia is the most extensive archipelagic country, consisting of nearly 13,500 islands. In this vast area, almost 60 million live on the coast within 30 km of a coral reef, comprising the largest reef-associated population of any country in the world (Burke et al. 2011). However, the dense population and combined pressures leave very few reefs (< 10 %) in Indonesia unthreatened, with more than 35 % in the high or very high threat categories. Among these stressors are watershed-based pollution, coastal development, destructive fishing practices, and the increased occurrence of invasive species (Edinger et al. 1998; Burke et al. 2011; Azmi et al. 2015).

As part of the commitment to the Coral Triangle Initiative, the government of Indonesia agreed to conserve 100,000 sq km of its marine area in MPAs by 2010. Already established in 1996, WMNP in Southeast Sulawesi is the third largest marine park in Indonesia and ranks as one of the highest priorities for marine conservation concerning the diversity of marine life, scale, and reef condition (Clifton 2010). Besides all efforts, marine resources of the WMNP are under

increasing pressure due to many of the above factors (Hopley and Suharsono 2000; Elliott et al. 2001; Caras and Pasternak 2009; Cullen 2010). The WMNP is inhabited by a population of over 100,000 people (Cullen 2010), and the presence of villages is broadly correlated with the presence of degraded coral habitats (Ruppert et al. 2017). The combination of local utilization of marine resources and the multiple-use zoning plan of the park has resulted in a patchwork of degraded and non-degraded coral reef environments in proximity to each other.

In degraded reefs around the stilts village Sampela and the relatively non-degraded reefs of Hoga, a highly competitive Didemnid ascidian was observed during coral reef surveys. Although ascidians have been receiving more scientific attention recently (Mondal et al. 2017; Roth et al. 2017; Stefaniak 2017), we still lack basic data on the presence, distribution and the potential impact of ascidian species in the WMNP. Thereby, the two close reef systems with different health status offer a unique opportunity to study the potential anthropogenic implications for ascidians in coral reefs.

In this study, we quantify the relative abundance, growth rate and the preferred substrate of *Didemnum* sp. in both, degraded and non-degraded reef sites within the WMNP. For this, 2400 m² of coral reef, and the *Didemnum* sp. colonies within, were surveyed to answer the following questions: What is the (i) relative abundance, (ii) preferred substrate and (iii) growth rate of *Didemnum* sp. in a) non-degraded and b) degraded reefs of the WMNP?

2. Material and methods

2.1 Study area

This study was carried out in the WMNP of the Wakatobi archipelago in the Banda Sea, Southeast Sulawesi, Indonesia (Fig. 1). The degraded reef site, Sampela, is located on the northern side of Kaledupa on the fringing reef (5°28'51"S, 123°44'39"E) that surrounds the island. Sampela reef is nearby (400 m) to a Bajau village with around 1,300 people living in 200 stilt houses (Crabbe et al. 2004). Reports describe reefs of Kaledupa as degraded due to local wastewater discharge, destructive fishing practices, and increased sedimentation due to mangrove removal (Bell and Smith 2004; Salinas-de-León et al. 2011). Furthermore, fishing-gleaning activities (collecting of benthic macroinvertebrates) in intertidal areas may prevent seagrass beds from expanding and consequently lead to sedimentation deposits on the Sampela reef (Crabbe and Smith 2002; Crabbe and Smith 2003). Though in proximity (1.5 km to the Sampela reef), reefs of Hoga island (Fig. 1) are less degraded and show enhanced water quality (Crabbe and Smith 2005), lower coral disease prevalence and higher coral cover (Haapkyla et al. 2009). The combination of the stressors on Sampela reef and the isolated situation of Hoga island has resulted in two distinct habitat characteristics that are expressed through a more degraded coral reef system on Kaledupa in comparison to the reefs surrounding Hoga island.

Two non-degraded sites, Buoy and Pak Kasim's, are located on the fringing reef on the western side of Hoga Island (5°28'30"S, 123°45'18"E). Degraded and non-degraded sites were approximately 1.5 km apart and separated by a deep channel (60m) (Salinas-de-León et al. 2013). Field data were collected via scuba diving at these three sites between 8 a.m. and 4 p.m. from August 5 – 28, 2011.

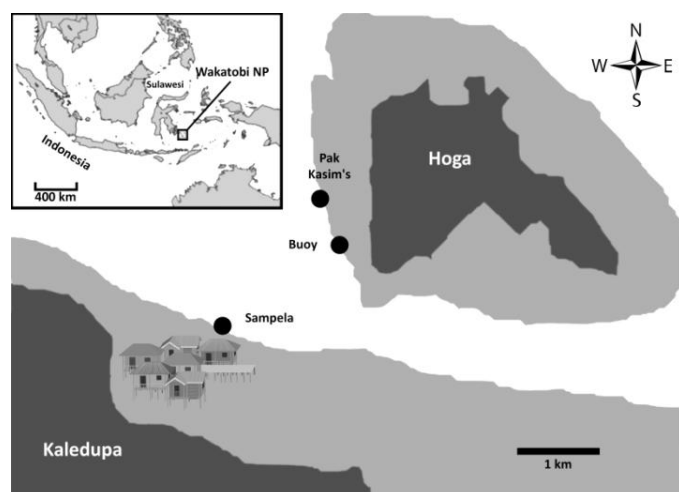


Figure 1. Sampling sites within the Wakatobi Marine National Park (WMNP) in Southeast Sulawesi, Indonesia. The non-degraded sites Buoy, and Pak Kasim's are located within the Hoga Island reef system, while the degraded site Sampela is located within the Kaledupa Island reef system, adjacent to a Bajau village (represented on the map by the houses). Dark areas represent land mass and light grey areas coral reefs. Map modified from Salinas-de-León et al. (2011).

2.2 Relative abundance of *Didemnum* sp. in the benthic reef community

To determine the abundance of *Didemnum* sp. four 50 m transects were laid on the reef crest and four on the reef slope per site (in total 24 transects). The depth of the reef crest transects varied between 3 – 6 meters depending on high and low tide, while the slope transects ranged between 6 – 9 m depth, respectively. Estimates of relative benthic cover from major functional groups (dead corals, living soft corals, living hard corals, rock, coral rubble, sponges, ascidians, and macroalgae) of the same reefs were provided from Operation Wallacea, 2011.

An area of 100 m² was surveyed per transect (one meter to each side of the 50 m transect tape), and every *Didemnum* sp. colony within light-flooded reef areas, but not within hidden / cryptic habitats, was counted and the diameter measured to calculate their area. The ascidian colonies were identified as *Didemnum* sp. via morphological characteristics with visual inspection (e.g. external features of the colony, cloacal channels) (personal communication D. Smith -University of Essex, United Kingdom- and A. Powell -Victoria University of Wellington, New Zealand-), their geographic distribution and possible occurrence in coral reefs in the Indopacific (Shenkar and Swalla 2011).

2.3 Substrate preferences of *Didemnum* sp.

Each *Didemnum* sp. colony within a transect was examined along its edges, and all contacting substrate were identified, recorded and listed according to the following categories: Dead coral; living soft coral; living hard coral; macroalgae; sponges; rock; coral rubble; Ascidiacea; *Tridacna* spp.; and *Dysidea* spp.

2.4 Growth Rates

Linear tissue growth of *Didemnum* sp. was calculated using underwater photography (Canon Power Shot G12) and subsequent image processing. Five randomly selected colonies at each site were tagged, frequently revisited (two times/week) and photographed with a measuring reference in the picture. Photographs were taken from straight above the colony with the same distance at all times (50 cm from the camera lens to the colony). Photographs were analysed with the *ImageJ* processing software using the reference in the picture to calculate the projected living tissue area of the colony.

2.5 Statistical Analysis

Statistical analyses were performed using SigmaPlot (Systat) software packages. Data were tested for normal distribution with probability plots (Q-Q-plot) and/or the Shapiro-Wilk-Test. Tests for equal variances were passed in all classes. The non-degraded sites Buoy, and Pak Kasim's were grouped, as data of both reefs represent the non-degraded state and no statistical differences between these were present. Differences between sites were analysed using two-tailed t-tests or one-way analysis of variance (ANOVA) with repeated measures. Response parameters (growth, colony size, frequency of occurrence and relative abundance of *Didemnum* sp.) were summarized as ratios on a logarithmic scale. Hereby, the non-degraded site was set as the standard (1.0), such that values < 1 represent higher and values > 1 represent lower values for non-degraded sites. For example, the ratio 0.2 indicates that the mean of the degraded reef is 20 % of that of the non-degraded reef. The circles mark the calculated ratios, and error bars show lower and upper 95 % confident intervals (CIs). Differences are significant at the 5 % level if the error bars do not include the value 1.0. The logarithmic scale causes different lengths of the upper and lower CIs. Values throughout the manuscript are given as mean with standard error (SE).

3. Results

3.1 Relative abundance and size distribution of *Didemnum* sp. in benthic reef communities

No significant differences in the relative abundance of *Didemnum* sp. were detected between the different reef sites (degraded 0.75 ± 0.41 % and non-degraded 0.66 ± 0.22 % benthic cover) ($p = 0.836$, t-test, 2-sided). However, *Didemnum* sp. colonies grew into significant bigger colonies at degraded reef sites (0.26 ± 0.08 m² compared to 0.04 ± 0.01 m² in non-degraded sites; $p < 0.001$; t-test, 2-sided). In the degraded reef a significant ($p < 0.001$; t-test, 2-sided) lower number of colonies per transect (area of 100 m²) was found (2.8 ± 1.0 compared to 14.1 ± 2.1 in the non-degraded reef) (Fig.2).

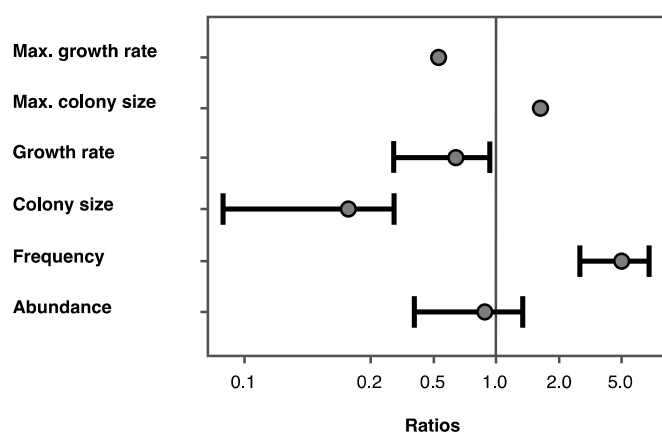


Figure 2. Log ratios (degraded / non-degraded reefs), summarizing the observed biotic changes in growth, colony size, frequency of occurrence and relative abundance of *Didemnum* sp. The non-degraded site was set as the standard (1.0) such that points to the left of the solid vertical line represent higher values at non-degraded sites and values to the right represent lower values for non-degraded sites. For example, the ratio 0.2 indicates that the mean of the degraded reef is 20 % of that of the non-degraded reef. The circles mark the calculated ratios, and error bars show lower and upper 95 % CIs. Differences are significant at the 5 % level if the error bars do not include the value 1.0. The logarithmic scale causes different lengths of the upper and lower CIs.

3.2 Substrate

Didemnum sp. settled and grew mainly on rock substrates (degraded site 34.3 % and non-degraded sites 45.9 %), dead coral (degraded site 11.4 % and non-degraded sites 15.2 %) and on living hard corals (degraded site 25.7 % and non-degraded sites 25.1 %) (Table 1). Coral colonies that were overgrown by *Didemnum* sp. were usually completely covered by the ascidian colony (Fig. 3). Taking the relative benthic cover of major functional groups in the reef into account, living hard corals were associated more frequently with ascidians in comparison to other functional groups in the reef.

Table 1. Benthic community composition in degraded and non-degraded reef sites of the Wakatobi Marine National Park and associations of *Didemnum* sp. with different hard and soft substrates.

Substrate	Degraded		Non-degraded	
	Relative benthic cover [%]	Associations with <i>Didemnum</i> sp. [%]	Relative benthic cover [%]	Associations with <i>Didemnum</i> sp. [%]
Dead coral	1.1	11.4	5.2	15.2
Living soft coral	11.1	2.9	13.6	1.9
Living hard coral total	5.6	25.7	18.8	25.1
<i>Diploastrea heliopora</i>		0.0		0.7
<i>Favia</i> spp.		5.7		0.5
<i>Galaxea</i> spp.		0.0		2.2

<i>Lobophyllia</i> spp.		0.0		0.2
<i>Millepora</i> spp.		2.9		1.4
<i>Pachyseris</i> spp.		0.0		2.9
<i>Pavona varians</i>		0.0		2.4
<i>Pocillopora</i> spp.		0.0		0.5
<i>Stylophora pistillata</i>		0.0		0.2
<i>Tubastrea</i> spp.		5.7		3.6
Other living hard corals		11.4		10.5
Rock	28.5	34.3	26.3	45.9
Coral rubble	32.2	0.0	22.1	2.9
Ascidians	0.1	8.6	0.1	1.9
<i>Tridacna</i> spp.		8.6		1.7
<i>Dysidea</i> spp.		2.9		1.9
Sponges	8.7	0.0	5.6	3.4
Macroalgae	0.9	5.7	3.0	0.2

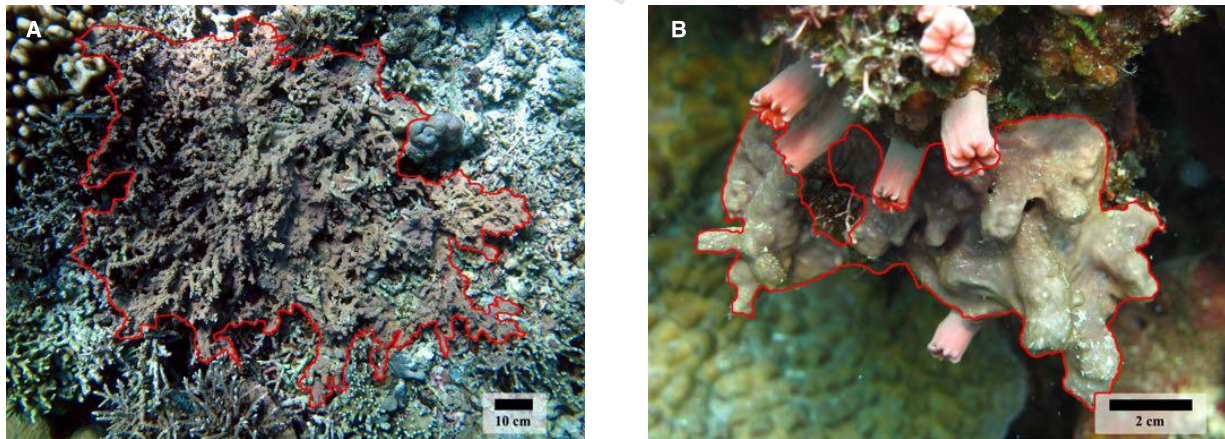


Figure 3. Images of *Didemnum* sp. in the Wakatobi Marine National Park. *Didemnum* sp. (encircled in red) covering a wide area of the coral *Acropora* sp. (A) and living polyps of *Tubastrea* sp. (B).

3.3 Growth Rate

The growth rate of *Didemnum* sp. colonies was significantly different between study sites. In degraded reefs, colonies of *Didemnum* sp. grew significantly faster than in the non-degraded reef sites (2.717 ± 0.984 % day⁻¹ compared to 0.172 ± 0.388 % day⁻¹; $P = 0.017$, repeated measures ANOVA, $F(1, 2.544) = 5.986$) (Fig. 4). However, average initial colony size of the degraded

($1019.3 \pm 441.9 \text{ mm}^2$) and non-degraded ($876.6 \pm 348.7 \text{ mm}^2$) did not differ from the average colony size (degraded 1516.7 and non-degraded 1023.7 mm^2) after 23 days, due to a large variation in colony sizes within habitats.

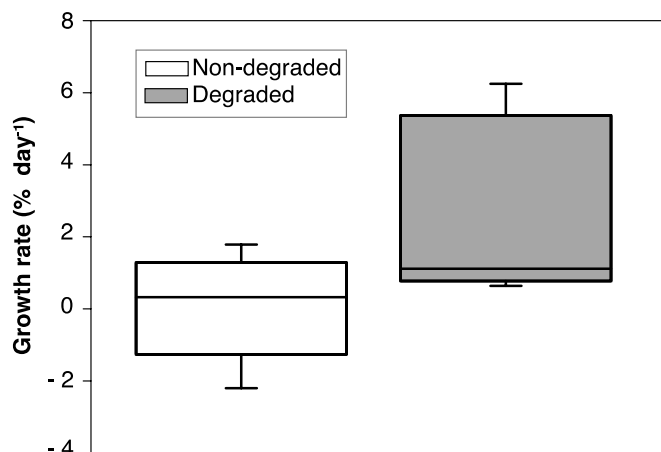


Figure 4. Boxplots showing the median (line across a box), quartiles (upper and lower bounds of each box), and extremes (upper and lower whisker) for growth rates of *Didemnum* sp. colonies in non-degraded and degraded reef habitats of the Wakatobi Marine National Park.

4. Discussion

The results of this study concur with other reports that highlight ascidians as a potential threat for benthic coral reef communities (Bullard et al. 2007; Kremer et al. 2010; Smale and Childs 2012; Kopllovitz et al. 2016; Roth et al. 2017). Extremely high growth rates in degraded reefs of the WMNP and the ability to overgrow living hard corals further emphasize the importance of studying potentially harmful ascidians and include them in outreach and awareness activities, as well as in monitoring programs of the national park. In this study, colonial ascidians were identified based on external morphological features, their geographic distribution, and their possible occurrence in tropical coral reefs in the Indopacific. However, many members of the family Didemnidae show similarities in morphological characteristics, including shape and color of the colony, and the size of zooids, larvae, and spicules. Hence, DNA barcoding involving the sequencing of the COI gene is recommended for the identification of ascidians (Jaffar Ali and Ahmed 2016). It is likely that it might be *Didemnum perlucidum* (Monniot 1983), as it is known to be present in these areas and shows similar invading characters (Dias et al. 2016; Simpson et al. 2016), however without DNA sequencing it is not certain to identify. Thus, to prevent any misinformation, the nomenclature *Didemnum* sp. is used, indicating that the specimen is believed to be within the genus *Didemnum*, but the actual identification cannot be certain. Importantly, the study assesses the impacts of a non-indigenous organism on coral reefs under anthropogenic influence, and is not a record of an ascidian species in a certain region. The large size of the colonies, their rapid growth rates and ability to overgrow living substrates make the ascidian *Didemnum* sp. a highly effective spatial competitor. However, the overall distribution, biology,

and ecological implications of *Didemnum* sp. in the WMNP and the Coral Triangle are mostly unknown, and demand urgent investigation. Given that anthropogenic disturbances can lead to a range of alternative states, including Didemnid ascidian dominance (Chadwick and Morrow 2011), we strongly recommend for future management plans that the appearance of *Didemnum* sp. on coral reefs is incorporated. Although we assessed reefs in the WMNP only for restricted periods of time, this limitation indicates that further research is essential to provide more details and information for stakeholders, the local population, and managers. Further studies have to determine if the abundance of *Didemnum* sp. is increasing, and extra efforts to reduce pollution and prevent illegal fishing within the WMNP could reduce the potential for this species to threaten non-degraded reefs in the WMNP.

4.1 Abundance

A species of colonial ascidian of the genus *Didemnum* was found in coral reefs of the WMNP at high abundances. The relatively high numbers we observed on well-lit surfaces highlights the potential of these ascidians to compete for space with other benthic reef taxa under favourable environmental conditions, as ascidians usually occur in cryptic habitats (i.e., not typically found in the light-exposed benthic coral reef community (Nydam et al. 2017)). Locally, the proximity to the wooden stilts and the rocky bases of the Bajau village may provide substrates for propagules to settle (Simkanin et al. 2017), increasing the number of larvae to the surrounding area. Additionally, illegal fishing practices have been recorded (von Heland and Clifton 2015), which reduce the number of predators and may promote the growth of *Didemnum* sp. (Rogers et al. 2016; Roth et al. 2017). Interestingly, the relative cover of *Didemnum* sp. was similar on degraded and non-degraded reefs, but the size of the colonies was dramatically different. The largest colony of *Didemnum* sp. found in degraded reefs occupied twice the space of the largest colony found in non-degraded reefs. Eutrophic conditions resulting from untreated sewage and land-based pollution (Riisgård et al. 1995; Shenkar et al. 2008) from adjacent villages are likely favourable for ascidian growth (Rodríguez-Martínez et al. 2012) due to an increase in food resources resulting from an increase in phytoplankton and subsequent organic matter (Herbert 1999). Such conditions may also lead to an earlier fusion of colonies in degraded waters (Petersen et al. 1995; Shenkar et al. 2008). Despite constant recruitment in non-degraded waters, colonies may be restrained from fusion by environmental factors such as resource availability or competing invertebrate species (Lambert 2005; Dias et al. 2008; López-Legentil et al. 2013). Fusion of ascidian colonies may be evolutionarily beneficial and is likely to be lethal for overgrown species (Rinkevich and Weissman 1987).

4.2 Substrate

Concurrent with other studies, most *Didemnum* sp. colonies in the WMNP grew on the surfaces of dead corals and rock (Bullard et al. 2007; Miller and Etter 2011). However, a significant proportion (one quarter) of recorded *Didemnum* sp. colonies settled on living hard corals, with no differences between sites. These findings emphasize results of several cases where the potential to kill living corals using allelochemicals has been shown (Jackson and Buss 1975; Bak et al. 1996; Bak et al. 1998; Lambert 2002), and highlight the competitive strength of Didemnid

ascidians in the WMNP. Only recently, discoveries from Li et al. (2016) revealed that specific ascidians were even capable of eroding coral skeleton. All of these cases display the high potential of endangerment for the corals in the WMNP. The loss of coral cover can be particularly harmful to the reef community, as scleractinian corals are involved in many biogeochemical cycles and provide stable substrates and structural complex habitats for associated organisms (Wild et al. 2011). As the structural complexity is an integral component of coral reef ecosystems, a loss of such may result in a loss of associated biodiversity, resilience and even shoreline protection (Graham and Nash 2013). Moreover, the degradation of reefs may result in significant social and economic impacts, particularly on small islands like Kaledupa and Hoga, where livelihoods depend on reefs and related resources, and the capacity to adapt to reef loss is limited. A proportional substrate preference relative to the benthic cover indicates that the substrate choice of *Didemnum* sp. did not occur randomly. Since a relatively high percentage of living hard corals was covered, we conclude that the defence mechanism of hard corals is inefficient to repel *Didemnum* sp. The observation that no differences in the type of overgrown substrate were detected between the degraded and non-degraded habitat suggests that *Didemnum* sp. can recruit on most substrates regardless of the environmental conditions, which makes *Didemnum* sp. a particularly competitive ascidian.

4.3 Growth rate

Taking into account each colony's initial size, there was no apparent difference in growth rates between smaller and larger colonies. However, the significant increase in growth rates of *Didemnum* sp. in degraded reef communities deserves particular notice. A study of Roth et al. (2017) highlighted that *Didemnum* sp. grew faster in a coral reef when exposed to high nutrient concentrations and simulated overfishing. Concordant, Chadwick and Morrow (2011) showed that ascidians can successfully compete with stony corals under eutrophic conditions. Growth rates in the degraded reefs reported here outnumber those reported by Rius et al. (2014) by a factor of seven and may be explained by a lack of predators (Osman and Whitlatch 2007; Roth et al. 2017) and an excessive supply of food (Shenkar et al. 2008; Sawall et al. 2013; Roth et al. 2017). Illegal fishing activities (von Heland and Clifton 2015) and other unsustainable activities endangering the WMNP are well known in the studied area (Szuster and Albasri 2010). Additionally, a higher food supply for filter feeders may be provided by unfiltered sewage discharge and nutrients (Shenkar et al. 2008; Sawall et al. 2013) from villages at Kaledupa island, undermining the reef's resilience against opportunistic species.

5. Conclusions

This study is the first to provide quantitative data on a dominant ascidian in the WMNP in Indonesia and identifies it as a potential threat toward the local coral reef ecosystem. Locally in the WMNP, a strong correlation between anthropogenic pressures and the extent of ascidians in coral reefs is apparent. However, enforcing national park regulations and effectively managing anthropogenic threats in these vast areas is an ongoing challenge, and, therefore, has to be readdressed. One step towards improving the effectiveness of protected areas is a recently developed new protocol to strengthen marine protected area management in Indonesia and across

all six countries of the Coral Triangle Initiative. Here, the Coral Triangle Support Partnership and the Ministry of Marine Affairs and Fisheries are compiling ideas to distribute responsibilities to local governments and communities. This step has to be used as a chance to include changes in the abundance of ascidians in reef monitoring programs, as ascidians have often been grouped with other benthic organisms and, therefore, have been widely overlooked. This is highly unfortunate since ascidians may function as indicator species for degrading marine ecosystems, particularly for highlighting harmful consequences of species introduction (Rocha and Kremer 2005), eutrophication and overfishing (Roth et al. 2015; Stuhldreier et al. 2015). Moreover, distribution vectors, such as recreational and fishing vessels that tend to account for most ascidian introductions and spreads (Kauano et al. 2016), need to be monitored and evaluated for their potential to spread ascidians among the islands. While diversity and live coral cover have declined, many reefs in the WMNP still have a good complement of species and could be resilient in the face of future change if local threats can be reduced, no-take zones are extended, and regulations are strictly enforced.

6. Acknowledgements

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7. References

- Azmi F, Hewitt CL, Campbell ML (2015) A hub and spoke network model to analyse the secondary dispersal of introduced marine species in Indonesia ICES Journal of Marine Science: Journal du Conseil 72:1069-1077
- Bak RPM, Joenje M, Jong I, Lambrechts DYM, Nieuwland G (1998) Bacterial suspension feeding by coral reef benthic organisms Marine Ecology-Progress Series 175:285-288
- Bak RPM, Lambrechts DYM, Joenje M, Nieuwland G, Van Veghel MLJ (1996) Long-term changes on coral reefs in booming populations of a competitive colonial ascidian Oceanographic Literature Review 11:1145
- Bell JJ, Smith D (2004) Ecology of sponge assemblages (Porifera) in the Wakatobi region, south-east Sulawesi, Indonesia: richness and abundance Journal of the Marine Biological Association of the UK 84:581-591
- Bellwood DR, Hoey AS, Hughes TP (2011) Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs Proceedings of the Royal Society of London B: Biological Sciences:rsob20111906
- Birkeland C, Cheng L, Lewin RA (1981) Motility of didemnid ascidian colonies Bulletin of Marine Science 31:170-173

- Bullard SG et al. (2007) The colonial ascidian *Didemnum* sp. A: Current distribution, basic biology and potential threat to marine communities of the northeast and west coasts of North America *Journal of Experimental Marine Biology and Ecology* 342:99-108
- Burke L, Reytar K, Spalding M, Perry A (2011) Reefs at risk revisited in the Coral Triangle. World Resources Institute, Washington, DC,
- Cabral RB, Geronimo RC (2018) How important are coral reefs to food security in the Philippines? Diving deeper than national aggregates and averages *Marine Policy* 91:136-141
- Caras T, Pasternak Z (2009) Long-term environmental impact of coral mining at the Wakatobi marine park, Indonesia *Ocean & Coastal Management* 52:539-544
- Castilla JC, Guíñez R, Caro AU, Ortiz V (2004a) Invasion of a rocky intertidal shore by the tunicate *Pyura praeputialis* in the Bay of Antofagasta, Chile *Proceedings of the National Academy of Sciences of the United States of America* 101:8517-8524
- Castilla JC, Lagos NA, Cerda M (2004b) Marine ecosystem engineering by the alien ascidian *Pyura praeputialis* on a mid-intertidal rocky shore *Marine Ecology Progress Series* 268:119-130
- Chadwick NE, Morrow KM (2011) Competition among sessile organisms on coral reefs. In: *Coral Reefs: an ecosystem in transition*. Springer, pp 347-371
- Chang CY, Marshall DJ (2016) Spatial pattern of distribution of marine invertebrates within a subtidal community: do communities vary more among patches or plots? *Ecology and Evolution* 6:8330-8337
- Clifton J (2010) Introduction to the Wakatobi National Park. Chapter 1 In: Clifton J, Unsworth RKF, Smith DJ (eds) *Marine Conservation and Research in the Coral Triangle: The Wakatobi National Park*. Nova Publishers, New York,
- Crabbe JM, Smith DJ (2002) Comparison of two reef sites in the Wakatobi Marine National Park (SE Sulawesi, Indonesia) using digital image analysis *Coral Reefs* 21:242-244
- Crabbe MC, Karaviotis S, Smith DJ (2004) Preliminary comparison of three coral reef sites in the Wakatobi Marine National Park (SE Sulawesi, Indonesia): estimated recruitment dates compared with Discovery Bay, Jamaica *Bulletin of Marine Science* 74:469-476
- Crabbe MJC, Smith DJ (2003) Computer modelling and estimation of recruitment patterns of non-branching coral colonies at three sites in the Wakatobi Marine Park, SE Sulawesi, Indonesia; implications for coral reef conservation *Computational Biology and Chemistry* 27:17-27
- Crabbe MJC, Smith DJ (2005) Sediment impacts on growth rates of *Acropora* and *Porites* corals from fringing reefs of Sulawesi, Indonesia *Coral reefs* 24:437-441
- Crossland CJ, Hatcher BG, Smith SV (1991) Role of coral reefs in global ocean production *Coral reefs* 10:55-64
- Cullen LC (2010) Marine resource dependence and natural resource use patterns in a small Indo-Pacific island community: implications for management. Chapter 10 In: Clifton J, Unsworth RKF, Smith DJ, editors. *Marine Research and Conservation in the Coral Triangle: the Wakatobi Marine National Park* *Marine Research and Conservation in the Coral Triangle: the Wakatobi Marine National Park* Nova Publishers, New York:171-192
- Dias GM, Delboni CGM, Duarte LFL (2008) Effects of competition on sexual and clonal reproduction of a tunicate: the importance of competitor identity *Marine Ecology Progress Series* 362:149-156

- Dias J et al. (2016) Investigating the cryptogenic status of the sea squirt *Didemnum perlucidum* (Tunicata, Ascidiacea) in Australia based on a molecular study of its global distribution *Aquatic Invasions* 11:239-245
- Dijkstra J, Harris LG, Westerman E (2007) Distribution and long-term temporal patterns of four invasive colonial ascidians in the Gulf of Maine *Journal of Experimental Marine Biology and Ecology* 342:61-68
- Edinger EN, Jompa J, Limmon GV, Widjatomoko W, Risk MJ (1998) Reef degradation and coral biodiversity in Indonesia: effects of land-based pollution, destructive fishing practices and changes over time *Marine Pollution Bulletin* 36:617-630
- Elliott G, Mitchell B, Wiltshire B, Manan IA, Wismer S (2001) Community participation in marine protected area management: Wakatobi National Park, Sulawesi, Indonesia *Coastal Management* 29:295-316
- Foale S et al. (2013) Food security and the Coral Triangle initiative *Marine Policy* 38:174-183
- Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems *Coral Reefs* 32:315-326
- Haapkyla J, Unsworth RKF, Seymour AS, Melbourne-Thomas J (2009) Spatio-temporal coral disease dynamics in the Wakatobi Marine National Park, south-east Sulawesi, Indonesia *Diseases of Aquatic Organisms* 87:105-115
- Herbert RA (1999) Nitrogen cycling in coastal marine ecosystems *FEMS microbiology reviews* 23:563-590
- Hopley D, Suharsono H (2000) The status of coral reefs in eastern Indonesia *Australian Institute of Marine Science, Townsville*
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef *Science-AAAS-Weekly Paper Edition* 265:1547-1551
- Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS (2010) Rising to the challenge of sustaining coral reef resilience *Trends in Ecology & Evolution* 25:633-642
- Hughes TP et al. (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change *Current Biology* 17:360-365
- Jackson JBC, Buss L (1975) Alleopathy and spatial competition among coral reef invertebrates *Proceedings of the National Academy of Sciences* 72:5160-5163
- Jackson JBC et al. (2001) Historical overfishing and the recent collapse of coastal ecosystems *science* 293:629-637
- Jaffar Ali HA, Ahmed NS (2016) DNA barcoding of two solitary ascidians, *Herdmania momus* Savigny, 1816 and *Microcosmus squamiger* Michaelsen, 1927 from Thoothukudi coast, India *Mitochondrial DNA Part A* 27:3005-3007
- Koplovitz G, Shmuel Y, Shenkar N (2016) Floating docks in tropical environments-a reservoir for the opportunistic ascidian *Herdmania momus*
- Kremer LP, da Rocha RM (2016) The biotic resistance role of fish predation in fouling communities *Biological Invasions* 18:3223-3237
- Kremer LP, Rocha RM, Roper JJ (2010) An experimental test of colonization ability in the potentially invasive *Didemnum perlucidum* (Tunicata, Ascidiacea) *Biological invasions* 12:1581-1590
- Lambert CC (2005) Historical introduction, overview, and reproductive biology of the protochordates *Canadian Journal of Zoology* 83:1-7

- Lambert CC, Lambert G (2003) Persistence and differential distribution of nonindigenous ascidians in harbors of the Southern California Bight Marine ecology Progress series 259:145-161
- Lambert G (2001) A global overview of ascidian introductions and their possible impact on the endemic fauna. In: The biology of ascidians. Springer, pp 249-257
- Lambert G (2002) Nonindigenous ascidians in tropical waters Pacific Science 56:291-298
- Lasut MT et al. From Coral Triangle to Trash Triangle—How the Hot spot of Global Marine Biodiversity Is Threatened by Plastic Waste. In: Proceedings of the International Conference on Microplastic Pollution in the Mediterranean Sea, 2018. Springer, pp 107-113
- Li S, Chen T, Xu L, Hu M (2016) Ascidians (*Diplosoma* sp.) kill *Acropora* corals in a deteriorating reef environment (Luhuitou, Sanya, northern South China Sea) Bulletin of Marine Science 92:527-528
- López-Legentil S, Ruchty M, Domenech A, Turon X (2005) Life cycles and growth rates of two morphotypes of *Cystodytes* (Asciacea) in the western Mediterranean Marine Ecology Progress Series 296:219-228
- López-Legentil S, Erwin PM, Velasco M, Turon X (2013) Growing or reproducing in a temperate sea: optimization of resource allocation in a colonial ascidian Invertebrate Biology 132:69-80
- Miller RJ, Etter RJ (2011) Rock walls: small-scale diversity hotspots in the subtidal Gulf of Maine Mar Ecol Prog Ser 425:153-165
- Mondal J, Raghunathan C, Venkataraman K (2017) New records of Aplousobranch ascidians to Indian waters from Andaman Islands Journal of Threatened Taxa 9:9874-9880
- Mumby PJ (2009) Herbivory versus corallivory: are parrotfish good or bad for Caribbean coral reefs? Coral Reefs 28:683-690
- Nandakumar K (1996) Importance of timing of panel exposure on the competitive outcome and succession of sessile organisms Marine ecology progress series Oldendorf 131:191-203
- Nydam ML, Giesbrecht KB, Stephenson EE (2017) Origin and Dispersal History of Two Colonial Ascidian Clades in the *Botryllus schlosseri* Species Complex PloS one 12:e0169944
- Odum HT, Odum EP (1955) Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll Ecological Monographs 25:291-320
- Osman RW, Whitlatch RB (2007) Variation in the ability of *Didemnum* sp. to invade established communities Journal of Experimental Marine Biology and Ecology 342:40-53
- Petersen JK, Schou O, Thor P (1995) Growth and energetics in the ascidian *Ciona* in *testinalis* Mar Ecol Prog Ser 120:175-184
- Riisgård HU, Bondo Christensen P, Olesen NJ, Petersen JK, Møller MM, Andersen P (1995) Biological structure in a shallow cove (Kertinge Nor, Denmark)—Control by benthic nutrient fluxes and suspension-feeding ascidians and jellyfish *Ophelia* 41:329-344
- Rinkevich B, Weissman IL (1987) A long-term study on fused subclones in the ascidian *Botryllus schlosseri*: the resorption phenomenon (Protochordata: Tunicata) Journal of Zoology 213:717-733

- Rocha RMd, Kremer LP (2005) Introduced ascidians in Paranaguá Bay, Paraná, southern Brazil *Revista Brasileira de Zoologia* 22:1170-1184
- Rodríguez-Martínez RE, Jordán-Garza AG, Baker DM, Jordán-Dahlgren E (2012) Competitive interactions between corals and *Trididemnum solidum* on Mexican Caribbean reefs *Coral reefs* 31:571-577
- Rogers TL, Byrnes JE, Stachowicz JJ (2016) Native predators limit invasion of benthic invertebrate communities in Bodega Harbor, California, USA *Marine Ecology Progress Series* 545:161-173
- Roth F, Stuhldreier I, Sánchez-Noguera C, Carvalho S, Wild C (2017) Simulated overfishing and natural eutrophication promote the relative success of a non-indigenous ascidian in coral reefs at the Pacific coast of Costa Rica *Aquatic Invasions* 12:435-446
- Roth F, Stuhldreier I, Sánchez-Noguera C, Morales-Ramírez Á, Wild C (2015) Effects of simulated overfishing on the succession of benthic algae and invertebrates in an upwelling-influenced coral reef of Pacific Costa Rica *Journal of Experimental Marine Biology and Ecology* 468:55-66
- Ruppert JLW, Vigliola L, Kulbicki M, Labrosse P, Fortin MJ, Meekan MG (2017) Human activities as a driver of spatial variation in the trophic structure of fish communities on Pacific coral reefs *Global Change Biology*
- Salinas-de-León P, Costales-Carrera A, Zeljkovic S, Smith DJ, Bell JJ (2011) Scleractinian settlement patterns to natural cleared reef substrata and artificial settlement panels on an Indonesian coral reef *Estuarine, Coastal and Shelf Science* 93:80-85
- Salinas-de-León P, Dryden C, Smith DJ, Bell JJ (2013) Temporal and spatial variability in coral recruitment on two Indonesian coral reefs: consistently lower recruitment to a degraded reef *Marine biology* 160:97-105
- Sawall Y, Jompa J, Litaay M, Maddusila A, Richter C (2013) Coral recruitment and potential recovery of eutrophied and blast fishing impacted reefs in Spermonde Archipelago, Indonesia *Marine pollution bulletin* 74:374-382
- Schroth W, Ender A, Schierwater B (2005) Molecular biomarkers and adaptation to environmental stress in moon jelly (*Aurelia* spp.) *Marine Biotechnology* 7:449-461
- Shenkar N, Bronstein O, Loya Y (2008) Population dynamics of a coral reef ascidian in a deteriorating environment *Marine Ecology Progress Series* 367:163-171
- Shenkar N, Swalla BJ (2011) Global diversity of Ascidiacea *PLoS One* 6:e20657
- Simkanin C, Davidson IC, Therriault TW, Jamieson G, Dower JF (2017) Manipulating propagule pressure to test the invasibility of subtidal marine habitats *Biological Invasions*:1-11
- Simpson TS, Wernberg T, McDonald JI (2016) Distribution and Localised Effects of the Invasive Ascidian *Didemnum perlucidum* (Monniot 1983) in an Urban Estuary *PLoS one* 11:e0154201
- Smale DA, Childs S (2012) The occurrence of a widespread marine invader, *Didemnum perlucidum* (Tunicata, Ascidiacea) in Western Australia *Biological Invasions* 14:1325-1330
- Stefaniak LM (2017) Mechanisms for invasion success by *Didemnum vexillum* (Chordata: Ascidiacea): observations versus manipulations *Biological Invasions*:1-13
- Stuhldreier I, Bastian P, Schönig E, Wild C (2015) Effects of simulated eutrophication and overfishing on algae and invertebrate settlement in a coral reef of Koh Phangan, Gulf of Thailand *Marine pollution bulletin* 92:35-44

- Szuster WB, Albasri H (2010) Site selection for grouper mariculture in Indonesia
International Journal of Fisheries and Aquaculture 2:87-92
- Teh LSL, Teh LCL, Jolis G (2018) An economic approach to marine megafauna conservation
in the coral triangle: Marine turtles in Sabah, Malaysia Marine Policy 89:1-10
- von Heland F, Clifton J (2015) Whose Threat Counts? Conservation Narratives in the
Wakatobi National Park, Indonesia Conservation and Society 13:154
- Wild C et al. (2011) Climate change impedes scleractinian corals as primary reef ecosystem
engineers Marine and Freshwater Research 62:205-215

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Highlights

- A dominant ascidian species was observed locally in coral reefs of Indonesia
- Anthropogenic disturbances promoted the growth and abundance of *Didemnum* sp.
- Ascidiaceans were observed to outcompete major ecosystem engineers
- Urgent need for further studies on ascidiaceans in the Wakatobi National Park