

## Research



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# Corals hosting symbiotic hydrozoans are less susceptible to predation and disease

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In spite of growing evidence that climate change may dramatically affect networks of interacting species, whether—and to what extent—ecological interactions can mediate species' responses to disturbances is an open question. Here we show how a largely overseen association such as that between hydrozoans and scleractinian corals could be possibly associated with a reduction in coral susceptibility to ever-increasing predator and disease outbreaks. We examined 2455 scleractinian colonies (from both Maldivian and the Saudi Arabian coral reefs) searching for non-random patterns in the occurrence of hydrozoans on corals showing signs of different health conditions (i.e. bleaching, algal overgrowth, corallivory and different coral diseases). We show that, after accounting for geographical, ecological and co-evolutionary factors, signs of disease and corallivory are significantly lower in coral colonies hosting hydrozoans than in hydrozoan-free ones. This finding has important implications for our understanding of the ecology of coral reefs, and for their conservation in the current scenario of global change, because it suggests that symbiotic hydrozoans may play an active role in protecting their scleractinian hosts from stresses induced by warming water temperatures.

## 1. Introduction

Biotic interactions are major drivers for ecosystem functioning and evolutionary processes, being capable of altering ecosystem productivity [1], determining geographical distributions of species [2] and influencing evolutionary processes. In the present context of global environmental crisis, understanding the dynamic interplay between climate and species interactions is crucial to predict how ecosystems will respond to climate change. However, while an increasing body of literature is demonstrating that climate change may have a strong effect on species interactions [3], little is known about how species interaction may shape the responses of ecological communities to environmental stresses.

There are several reasons why this issue is relevant for the future of coral reefs. First, coral reefs are one of the most diverse ecosystems on Earth, and of the richest in terms of species interactions [4]. Second, they support about 500 million people worldwide [5]. Third, they are dramatically challenged by climate change [6,7]. In particular, rising sea temperatures have both direct and indirect detrimental

effects on reefs, by causing extensive mortality due to coral bleaching, and by increasing the frequency of coral diseases and predator outbreaks [8,9].

The commonness of coral–invertebrate interactions suggests that taking them into account could be fundamental for a better understanding of those processes. In fact, although several invertebrates are known to be associated with corals [10], the nature of such associations is mostly unclear. A few works have shown that some associations may increase coral resistance to external disturbances [11–13]. Yet, the overall paucity of information on the matter raises several interesting questions that call for further investigation. Among these, a very timely one is whether, and to what extent, interspecific interactions can mitigate the direct and indirect effects of increasing seawater temperatures on coral reefs, helping them to cope with worsening environmental conditions expected in the near future.

In an attempt to answer this question, we focus here on an invertebrate group whose ecology is largely overlooked. Already known to form symbiotic relationships with many marine taxa [14,15], hydrozoans have also been reported as associates of scleractinian corals with increasing frequency [16–24]. To date, four polymorphic hydrozoans species, all belonging to the genus *Zanclaea* Gegenbaur, 1857, have been recorded on more than 40 scleractinian species (belonging to 26 genera and eight families) from several Indo-Pacific areas, including Australia, Indonesia, Taiwan, Japan, the Maldives, the Red Sea, and the Caribbean [16–20,24–26].

In various known associations, corals identify opportunistic or parasitic invertebrates as a threat, to which they respond with immune reactions and/or tissue inflammation [27]. By contrast, the ability of hydrozoans to creep into coral tissues without triggering any immune reaction suggests that their relationship with corals is more intimate than an opportunistic epibiosis, as also supported by circumstantial evidence of hydrozoans' specific coral preferences [17,23]. This places the coral–hydrozoan association close to other known symbioses characterized by high host specificity, and strong co-evolutionary patterns [28].

Coral-associated hydrozoans possess specialized polyp morphologies (called 'dactylozooids') dedicated exclusively to defend the colony [17], which are armed with venomous nematocysts capable of injecting a substance whose composition is substantially different from that released by anthozoans [29]. Furthermore, studies on related groups suggest that coral-associated hydrozoans may be unpalatable due to noxious secondary metabolites, which could provide them with an additional, chemical defense against predators [30]. It has been, therefore, hypothesized that hydrozoans may bring benefit to corals by deterring predators. Additional benefits they could bring to corals include removing detritus and/or pathogenic protozoans. On an opposite view, the fact that hydrozoans have sometimes been reported from corals subject to bleaching events and/or diseases has led to speculation that they might instead be detrimental to coral health [17].

In any case, regardless of its nature, the widespread diffusion of the hydrozoan–coral association and the high hydrozoan density observed in colonized corals suggest that this relationship should have an important, yet largely overlooked role in reef ecology. To shed light on this issue, we examined more than 2000 coral colonies in the Western Indian Ocean to investigate the existence of non-random patterns of associations between hydrozoans and coral colonies focusing, in particular, on the potential effects of hydrozoan presence on coral health.

## 2. Material and Methods

### (a) Field work

The study was conducted in the waters of the Republic of Maldives and along the Saudi Arabian coastline of the Red Sea in 2015. We surveyed 33 sites (23 in the Maldives and 10 in Saudi Arabia) taken at random from those accessible among two reef types: inner reefs (lagoon-patches reefs or lagoon-facing sides of the atoll rim) and outer reefs (ocean-facing sides of the reef edge).

We applied the 'roving SCUBA diving technique', which consists of a 1-h dive where the diver moves progressively from the maximum depth to shallower water, swimming freely throughout the dive site [31]. We visually examined every scleractinian colony that was encountered during the dive, searching for the occurrence (i.e. presence/absence) of *Zanclaea*. When maximum depth at the sampling locality was less than 5 m, we applied the same technique by snorkelling (i.e. without SCUBA). We identified each colony at the genus level, also taking note of its depth ( $\leq 5$  m, 5–10 m,  $>10$  m), and size ( $\leq 50$  cm; 50–100 cm,  $>100$  cm).

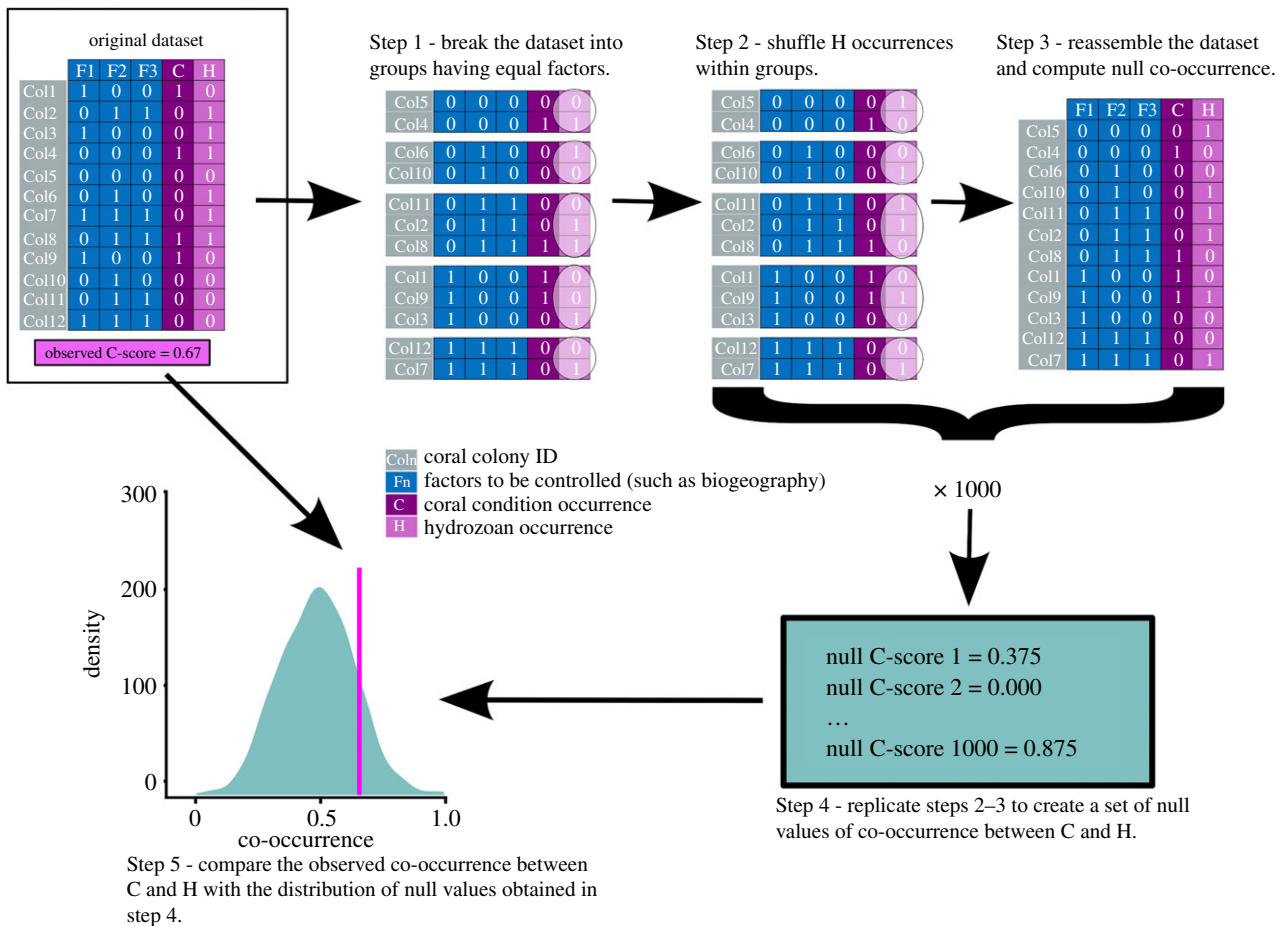
Additionally, for each coral colony, we searched for (and recorded) signs of one or more of the following conditions: coral bleaching, algal overgrowth, predation by fish, predation by coral-livorous gastropods of the genus *Drupella*, and four different diseases (white syndrome, brown band disease, skeletal eroding band disease, black band disease) [32]. Note that, in all cases, we focused on live corals only. Since the prevalence of black band disease was extremely low (0.5% on average), we excluded it from subsequent analyses. The complete dataset is provided as electronic supplementary material (SM1).

### (b) Co-occurrence analysis

We quantified co-occurrence between hydrozoans and the different coral conditions using the C-score [33], which is computed as  $(N_1 - S) \times (N_2 - S)$ , with  $N_1$  and  $N_2$  being the respective number of occurrences for the two entities under study (in our case, total number of hydrozoan occurrences, and number of times we detected the target coral condition), and  $S$  being the number of shared occurrences (i.e. the number of times we found hydrozoans and the target coral condition on the same coral colony). The number of occurrences for the two entities creates an upper boundary for the C-score, which makes comparison of C-scores between different pairs of entities problematic. For this, following [34], we rescaled C-scores between 0 and 1 by quoting them for  $N_1 \times N_2$ . Low C-scores (either rescaled or not) indicate high co-occurrence, while high C-scores indicate segregation. Here we quantified co-occurrence between two entities as 1 minus their standardized C-score, with 0 indicating total lack of shared occurrences between entities, and 1 indicating complete co-occurrence, that is full overlap between the occurrences of the two entities. Hereafter, we refer to this quantity as 'co-occurrence' for simplicity.

### (c) Null model analysis

To investigate whether the observed patterns deviated from a random expectation, we compared the actual co-occurrence between hydrozoans and different coral conditions with null scenarios obtained by randomly redistributing hydrozoan occurrences on coral colonies. In doing this, we designed a null model controlling for biogeographical, ecological and taxonomical factors potentially influencing hydrozoan occurrence independently from coral condition. This consists of a randomization procedure where hydrozoan occurrences can only be moved to and from coral colonies belonging to the same biogeographical areas, found at the same site and depth, having comparable size, and belonging to the same genus (figure 1). The original database consists of a set of entries, each corresponding to a coral colony. Columns in the dataset report three different types of information,



**Figure 1.** Schematic representation of the null modelling approach used to assess the significance of co-occurrence patterns. The original database consists of a set of entries each corresponding to a coral colony. Columns in the dataset report potential 'confounding' factors (F1, F2, F3); presence/absence of a specific coral condition (C); presence/absence of hydrozoans (H). At *Step 1*, the dataset is broken apart into sub-datasets having identical entries in columns F1, F2, F3. At *Step 2*, column H is shuffled within each sub-dataset. At *Step 3*, the sub-datasets are merged again into a complete dataset, and the co-occurrence between H and C is computed. At *Step 4*, *Steps 2 and 3* are reiterated 1000 times, providing a set of null C-scores to be compared with the corresponding ones observed in the original dataset (*Step 5*). (Online version in colour.)

and particularly, the five potential 'confounding' factors (as indicated above); six binary fields indicating the presence/absence of a specific coral condition (see previous paragraph); a binary field indicating presence/absence of hydrozoans.

In the first step of the randomization procedure, the dataset is broken apart into sub-datasets having identical entries in the factor columns (i.e. including coral colonies from the same region, sampled at the same site and depth, belonging to the same size class and genus). In the second step, the column corresponding to the hydrozoan presence/absence field is reshuffled within each sub-dataset. In the third step, the sub-datasets are merged again into a complete dataset, and the co-occurrence between the randomized hydrozoan occurrences and the various coral conditions is computed. Steps 2 and 3 are reiterated 1000 times, providing a set of null C-scores to be compared with the corresponding ones observed in the original dataset. We computed a  $p$ -value as the fraction of null C-scores higher than the corresponding observed ones. In addition, we quantified effect sizes using Z-values, which we computed as the difference between the observed C-scores and the mean of the 1000 corresponding null values, quoted by their standard deviation.

### 3. Results and discussion

In both investigated regions (Maldives and Saudi Arabia), both the occurrence of hydrozoans and of the target coral conditions (corallivory, disease, bleaching and algal overgrowth) were

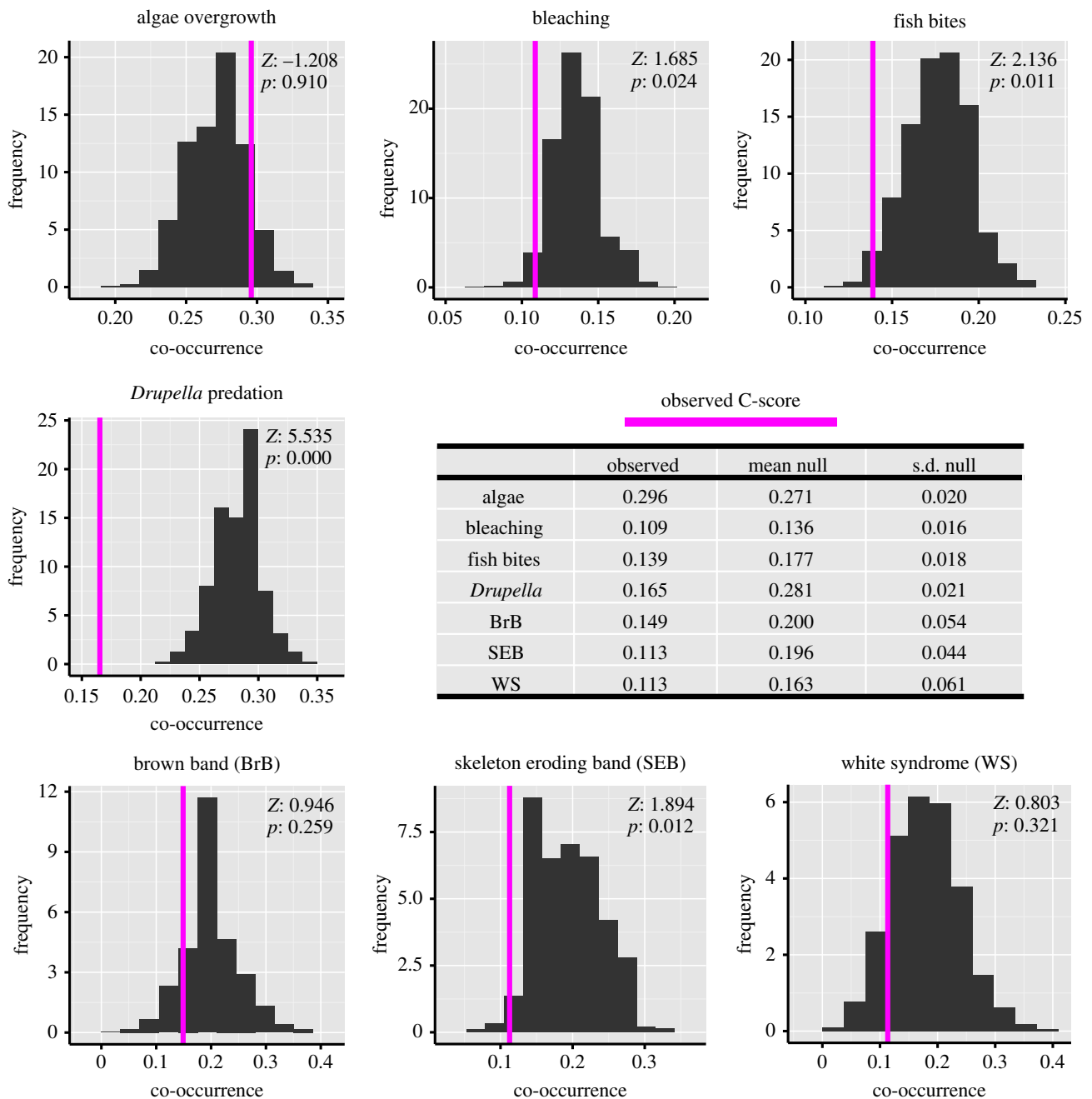
quite common. Nevertheless, in most of the reef localities, corals were, in general, in good health, with more than 50% of the investigated colonies being, on average, free from any sign of disturbance (table 1). Bleaching was much lower in the Maldives than in Saudi Arabia (with an average of 1.9% of bleached colonies in the first region, and of more than 17% in the latter), while the scenario was reversed as regards predation by *Drupella* gastropods, with more than 11% of colonies affected in the Maldives, and only 0.4% in Saudi Arabia. The same applies to diseases, which were much more frequent in the first region than in the second one, while algal overgrowth affected colonies in Saudi Arabia almost double the percentage of investigated corals than in the Maldives (16.9% versus 9.5%).

Co-occurrence levels between hydrozoans and, respectively, partial algal overgrowth, brown band disease and white syndromes were not different from the null expectation ( $p > 0.05$ ). By contrast, coral colonies hosting hydrozoans were significantly less susceptible to predation by *Drupella* ( $p = 0.000$ ), fish bites ( $p = 0.011$ ), and skeletal eroding band disease ( $p = 0.012$ ) than corals without hydrozoans. Furthermore, hydrozoans were found on bleached corals less frequently than expected ( $p = 0.024$ ) (figure 2).

Reduction of predation by *Drupella* and fish bites could be a direct consequence of the deterring action of hydrozoan nematocysts (figure 2*b*). Of course, this is not due to the exiguous quantity of venom that can be injected by a single

**Table 1.** Summary of coral diversity and health status in the 33 sites included in this study. We report the number of sampled colonies, number of observed coral genera, percentage of colonies hosting hydrozoans, percentage of colonies showing no apparent sign of the investigated conditions and percentage of colonies showing signs of: corallivory (either by fish or by *Drupella* gastropods); percentage of various types of coral disease (white syndrome, WS; brown band disease, BrB; skeleton eroding band disease, SEB; black band disease, BBD), algal overgrowth and bleaching. Data for each site are provided in electronic supplementary material, table S1.

region	sampled colonies	coral genera	hydrozoans (%)	no sign (%)	corallivory (%)			disease (%)				other (%)	
					fish	<i>Drupella</i>	WS	BrB	SEB	BBD	algae	bleaching	
Maldives (23 sites)	mean	12.0	15.0	58.8	12.0	11.2	2.2	3.4	3.3	0.7	9.5	1.9	
	s.d.	51.7	14.3	24.9	9.9	16.2	3.7	6.0	4.7	2.2	6.5	2.5	
	min	11.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	max	272.0	20.0	57.7	97.7	35.4	50.0	13.6	27.3	15.2	9.1	20.4	8.5
Saudi Arabia (10 sites)	mean	97.0	9.3	56.2	18.5	0.4	0.6	0.0	0.2	0.0	16.9	17.4	
	s.d.	64.8	7.3	21.0	10.6	0.9	1.3	0.0	0.4	0.0	5.7	29.7	
	min	46.0	2.9	17.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	
	max	216.0	28.0	28.3	75.5	31.5	2.3	3.9	0.0	0.9	0.0	27.1	76.5
both	mean	74.4	13.3	58.0	14.0	7.9	1.7	2.4	2.4	0.5	11.7	6.6	
	s.d.	57.0	5.8	23.5	10.4	14.3	3.2	5.2	4.1	1.9	7.1	17.4	
	min	11.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
	max	272.0	28.0	57.7	97.7	35.4	50.0	13.6	27.3	15.2	9.1	27.1	76.5



**Figure 2.** Epibiotic hydrozoans protect corals from predation and disease. Histograms show the frequency distribution of co-occurrence values of the considered coral conditions in null models, while magenta lines indicate the observed co-occurrence values. Numerical values (observed co-occurrence values, average and standard deviation of null co-occurrence values) are summarized in the central table. (Online version in colour.)

hydrozoan polyp, but to the density of hydrozoans on coral hosts, which, in the areas of study, typically ranges between about 10 and 30 polyps per  $\text{cm}^2$ , with peaks of more than 50 polyps per square centimetre [21] (figure 3a).

The effect size ( $Z$ ) observed for *Drupella* was much higher than that for fish bites (figure 2). This may reflect the fact that, differently from fish, *Drupella* gastropods need to crawl on the coral surface to feed, which would put them in continuous contact with the poisonous hydrozoan carpet. The smaller incidence of skeletal eroding band disease could be explained both as an indirect effect of the reduced coral susceptibility to bite wounds (because these can open doors to infection, with predators acting as spreaders [35,36]), and as a direct consequence of hydrozoan predation upon pathogenic protozoans.

Among all described hydrozoan species of the genus *Zanclaea*, there have been no reports of this species on dead coral or abiotic substrate [16]. Consistently we found that

hydrozoans tend to be less common than expected on bleached corals ( $p = 0.024$ ), thus supporting the idea that hydrozoans receive more benefits from their coral hosts than just a substrate, and that those can be provided only by a healthy host, as hypothesized by previous work [21]. Another possible explanation for the observed pattern is that the co-evolution between corals and hydrozoans may have led them to have overlapping thermal niches, and hence doomed hydrozoans to share corals' vulnerability to warming waters.

#### 4. Caveats

Our field survey presents a trade-off in pros and cons when compared to a strictly experimental study. On the one hand, our sampling design permitted us to take simultaneously into account a wide range of disturbance factors whose



**Figure 3.** *Zanclea*–scleractinian association. (a) High density of *Zanclea gallii* on *Acropora muricata*; (b) close up of the *Zanclea* sp. polyp on *Leptastrea purpurea*; (c) colony of *Zanclea* sp. on *Dipsastraea* sp.: arrowhead shows the defense-modified polyps called dactylozooids. Scale bars: *a* ~ 5 mm, *b* ~ 200  $\mu\text{m}$ ; *c* ~ 1 mm. All pictures were taken in the Maldives.

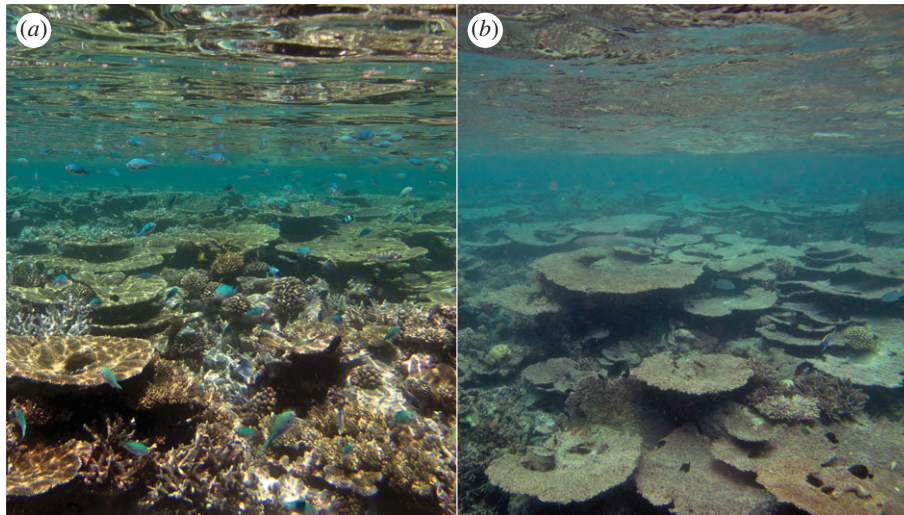
replication in a laboratory (both singularly and in combination) would have been difficult. On the other hand, our results do not necessary imply a causation. Nevertheless, our interpretation of the observed patterns can be considered conservative in light of the hypothesized ‘protective’ action of hydrozoans.

Our main result is the strong negative co-occurrence pattern between hydrozoans and corals subjected to predation by *Drupella* spp., which supports our claim that ‘hydrozoans may protect corals from predatory gastropods’. The alternative interpretation of the observed pattern would be that whenever a coral is predated by a gastropod, it loses its hydrozoans, and that it does not recover them for a while (at least until the feeding signs of *Drupella* are visible). Yet, this scenario sounds much less reasonable than the one we hypothesize. That is, it is much easier to imagine that a gastropod would be discouraged from crawling over a poisonous nematocyst carpet, rather than a widespread mortality of hydrozoans in a colony following a predation event (or that colonizers avoid colonizing corals showing predation signs). A similar reasoning may apply to the less-than-expected co-occurrence between hydrozoans and skeleton eroding band (SEB) disease.

As for the less-than-expected occurrence of hydrozoans on bleached coral colonies, the concrete evidence provided by

recent worldwide events of mass coral mortality [6] urged us to restrain from the appealing conclusion that hydrozoans may protect corals from warming waters. Nevertheless, the potential positive effect on coral health may play an important role in areas subjected to nearly lethal bleaching intensity: there, even a small advantage in terms of resilience can make a difference between life and death. And our findings suggest that hydrozoans may have the potential to provide corals with that advantage.

In our survey, we recorded only presence–absence of hydrozoans on coral colonies, without quantifying their density. Our choice was driven by difficulties in obtaining reliable estimates of hydrozoan density in the field because of their very small size and transparent body. These features make it very difficult to spot hydrozoans on a coral colony, let alone counting them to obtain density estimates. Forced also by the limited time to sample a site by SCUBA diving, we preferred to maximize the number of surveyed colonies at the expense of the information on hydrozoan density, in order to have a sample size large enough to explore a broad range of ecological hypotheses. Furthermore, the same features making hydrozoans very hard to spot in the field also ensure that their detection on a coral indicates the presence of a population of non-negligible size (in terms of potential effect) compared to that of the coral (that is,



**Figure 4.** Evidence of coral reef decline. (a) Pristine coral reefs of Maaga, Maldives ( $3^{\circ}04' N 72^{\circ}57' E$ ) showing a complete live coral community dominated by *Acropora* plate coral in February 2015. (b) Overview of identical coral reef system of Maaga showing coral mortality to nearly 90% after a mass bleaching event occurred in April 2016 (photo October 2016). (Online version in colour.)

the chances of spotting an hydrozoan on a coral decrease rapidly with their density, making detection very unlikely when there are only a few individuals present, with respect to the size of the colony). Nevertheless, more specific future work, possibly oriented by the preliminary findings we report in this paper, will certainly benefit from precise quantitative data on hydrozoan–coral associations.

A fundamental value of the present study is that it simultaneously takes into account a broad range of ecological, environmental and geographical factors, clearly not reproducible in a controlled setting. Nevertheless, our results identify several interesting questions that could be individually addressed by targeted laboratory and/or mesocosm experiments. Although a detailed discussion about specific research lines goes far beyond the purpose of this work, we hope that our findings could promote the exploration of neglected areas in reef ecology, and shed new light on the complex, elusive mechanisms controlling coral reef functioning.

## 5. Conclusion

Coral reefs are among the most diverse and most threatened ecosystems on Earth [6,7]. In particular, the extraordinary richness of species interactions that could be key to reef diversity [37] may also increase their vulnerability to global change, providing local perturbations with countless paths for propagation [38]. Thus, improving our knowledge on the complex networks connecting the fates of reef species is of paramount importance to identify key vulnerabilities, to predict possible responses to species loss, and hence to address effective conservation actions [39].

The hydrozoan–coral association has been documented only recently [16,17]. Thus, it is virtually impossible to establish whether this association has emerged in recent times, or whether it has been simply ignored in the past, possibly due to the very small size of the hydrozoan polyps (having length  $< 1$  mm), which makes their detection very difficult. Patterns of host specificity, however, suggest the existence of a longstanding co-evolutionary history, which supports the second hypothesis [12,40].

How complexity emerges and is maintained in natural communities is one of the most important open ecological

questions. The trade-off between consumer specialization and resource dependability (with consumers avoiding specialization on risky resources) may play a key role in permitting species coexistence [38,41]. In this perspective, the specialization of hydrozoans on corals could represent evidence of the long-term stability of reef systems, and of the high dependability of corals. Global change is now rapidly modifying this scenario, depleting coral communities at an unprecedented rate [42,43], so that we may not even have time to fully understand what is going on [44].

Although our findings suggest that symbiotic hydrozoans may help corals to resist environmental stress, they cannot preserve coral reefs from the dramatic consequences of current anthropogenic impacts: despite the documented abundance and diversity of symbiotic hydrozoans on the reefs we have surveyed for the present study, most of them have recently experienced a dramatic and possibly irreversible bleaching event (figure 4). Unfortunately, their fate is shared by most of world's reefs [6]. In a dark, yet realistic final consideration, as in other fields of biodiversity research [45], global change is reducing our chances to achieve a proper understanding of the ecological significance of the intimate relationships between corals and symbiotic hydrozoans faster than we can cope with. Although we hope that this study will pave the way for future field investigations, we also fear that it may be just another testament of something we lost long before we got to know.

**Data accessibility.** All relevant data are within the paper and its electronic supplementary material files.

**Authors' contributions.** S.M. led the field activities. D.M., D.S. and R.A. helped with the sampling. P.G. and M.L.B. contributed materials and supervised field activities. G.S. and S.F. designed and performed the analyses. G.S., S.M., S.F. and V.P. led the writing. All authors contributed to the writing and approved the final version.

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