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PRIMARY RESEARCH PAPER

New insights into the ecology and corallivory of *Culcita* sp. (Echinodermata: Asteroidea) in the Republic of Maldives

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Abstract Although corallivory is recognized as a threat affecting the structure and integrity of coral reef habitats, ecological data on most species of coral consumers remain limited, slowing down the development of conservation and restoration strategies of the reef ecosystems. In this study, the population distribution and corallivorous behaviour of the cushion sea star *Culcita* sp. were investigated in the south region of Faafu Atoll, Maldives. Most sea stars were found on reef slopes within 0–10 m depth and in areas characterized by low live coral cover. Several coral genera were preyed on by the sea star. Although most of the consumed corals belong to the genus *Acropora*, a feeding preference for the genera *Pocillopora* and *Pavona* and a consistent avoidance of the genus *Porites* were observed. Furthermore, the majority of the prey corals were small colonies (< 10 cm diameter), even though *Culcita* sp. appeared to be capable of partially consuming larger colonies. Dietary preferences for specific coral colonies or genera have the potential to generate local shifts in coral community composition and structure and may affect reef recovery following natural and anthropogenic disturbance in an already impacted environment such as the Maldivian reefs.

Keywords *Culcita* sp. · Cushion sea star · Corallivory · Feeding preferences · Maldives · *Pocillopora*

Introduction

The role of corallivorous sea stars in coral reef ecology and their impact on coral health have become increasingly important and investigated, due to the devastating effects from outbreaks of the crown-of-thorns sea star (COTS) (*Acanthaster* spp.) (Sweatman & Syms, 2011; De'ath et al., 2012; Pratchett et al., 2017). Under these circumstances, other species of coral-eating sea stars have been neglected, likely due to their apparent inability to cause population outbreaks or to represent an immediate and macroscopic risk to reef integrity. Among these less-recognized corallivorous organisms are the cushion sea stars of the genus *Culcita*.

Culcita spp. (Oreasteridae) are distributed across coral reefs in the Indian and Pacific Oceans. Currently,

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only three species are described; *C. coriacea* (Müller & Troschel, 1842), *C. schmideliana* (Bruzelius, 1805) and *C. novaeguineae* (Müller & Troschel, 1842). In the Indo-Pacific area, the predominant species are *C. schmideliana* and *C. novaeguineae*, with a large abundance of the former in the western Indian Ocean (Yasuda, 2012), whereas *C. coriacea* is considered endemic to the Red Sea (Clark, 1976). Like *Acanthaster* spp., *Culcita* spp. are also coral predators, which feed on corals by everting their stomachs and removing only the coral tissue without affecting the carbonate skeleton. Ultimately, the tissue is digested in situ, and this predation leaves scars that appear as large white spots (Goreau et al., 1972; Glynn & Krupp, 1986). However, both sea stars include a variety of other organisms in their diet (Thomassin, 1976; De'ath & Moran, 1998). The two sea stars also share similar spawning periods and larval ecology in many geographic areas (Yamaguchi, 1977; Yasuda et al., 2010; Ohta et al., 2011).

Nevertheless, differences in the feeding behaviour of *Acanthaster* spp. and *Culcita* spp. have been reported, with cushion sea stars consuming comparatively less coral and at slower rates. For example, while a *Culcita* sea star can remove up to 1 m^2 $year^{-1}$ of *Pocillopora damicornis* (Linnaeus, 1758) or up to 0.9 m^2 $year^{-1}$ of mixed coral prey (Glynn & Krupp, 1986), individual COTS have been estimated to consume an average of 5–6 m^2 $year^{-1}$ of coral surface, reaching values of 12–13 m^2 $year^{-1}$ in some locations (Birkeland & Lucas, 1990).

The main difference between these two sea stars is that *Acanthaster* spp. have a higher fecundity and cause large population outbreaks with disastrous consequences for coral reefs (Birkeland & Lucas, 1990; Kayal et al., 2012; Scott et al., 2017), whereas similar bursts of cushion sea star populations have not yet been reported. Nevertheless, average densities of *Culcita* spp. are typically higher than the number of individuals observed in non-outbreak populations of *Acanthaster* spp. (Goreau et al., 1972; Glynn & Krupp, 1986). This suggests that the cushion sea star, due to its continual removal of living coral, may represent a persistent force in affecting coral cover abundance and composition (Pratchett et al., 2011) and, therefore, similar to COTS, may influence broader ecological processes and interactions in coral reefs.

Although our knowledge of *Acantahster* spp. is continuously increasing (Pratchett et al., 2017), little information about the ecology and corallivorous behaviour of *Culcita* spp. in natural environments is currently available. To date, these often limited and preliminary field observations indicate that dietary preferences are highly variable, with *Culcita* spp. feeding on different coral species depending on location (Goreau et al., 1972; Thomassin, 1976; Glynn & Krupp, 1986; Quinn & Kojis, 2003). However, these studies often report a general preference for small coral colonies and/or recruits, potentially as the size and shape of *Culcita* individuals limit their ability to climb and feed on larger colonies (Glynn & Krupp, 1986; Quinn & Kojis, 2003).

In this study, the dietary ecology and corallivorous behaviour of the cushion sea star were investigated for the first time in a geographic area where this organism is poorly investigated: the Republic of Maldives. In the Maldives, the presence of the genus *Culcita*, and in particular, the species *C. schmideliana*, has been reported (Clark & Rowe, 1971; Jangoux & Aziz, 1984; Moosleitner, 1997; James, 2004); however, the Maldivian morpho-type shares common morphological features with both *C. schmideliana* and *C. novaeguineae* and, without a precise taxonomic identification, should therefore be referred to with the generic name *Culcita* sp.

The Maldivian coral reef is the seventh largest reef system on earth, with 8920 km^2 of total surface area (Spalding et al., 2001). Recently, its health status has been affected by multiple stressors, such as coral bleaching events (Tkachenko, 2015; Ibrahim et al., 2017; Perry & Morgan, 2017), disease outbreaks (Montano et al., 2015, 2016; Seveso et al., 2015, 2017), land reclamation and anthropogenic pressure (Brown et al., 2017; Fallati et al., 2017), algal overgrowth (Montano et al. 2012a, b; Seveso et al., 2012) and COTS outbreaks (Saponari et al., 2015, 2018). Hence, understanding the ecology of coral-consuming animals is of critical importance, in order to identify their role in mediating coral community structure and better predict their ecological impact under changing conditions. To this end, we examined a population of cushion sea stars within a Maldivian coral reef system to determine (a) whether the distribution and size of individuals are related to depth, habitat composition, structural complexity and reef zonation, and (b) what the diet of these sea stars consists of and if they exhibit preferences for specific coral genera, growth forms, or colony sizes.

Materials and methods

Study area and sampling design

Underwater surveys were performed on SCUBA diving during a number of field campaigns between February 2015 and April 2016 in the southern region of the Faafu Atoll, Republic of Maldives (Fig. 1). Our logistic base was the Marine Research and High Education Center (MaRHE) on Magoodhoo Island (3°4′49.08″N, 72°57′57.19″E, WGS84), an inhabited island that measures 900 × 450 m^2 and is located on the south-eastern region of the atoll rim, approximately 140 km south of the capital Malè. Magoodhoo reef is approximately 3 km long and 1.55 km wide (Montano et al., 2012b).

Around the island, 17 different sites showing heterogeneous characteristics in terms of reef morphology and exposure were randomly selected among those accessible (Fig. 1). Some sites exhibited typical low-energy reef features with ample growth of coral and gentle slopes, whereas others were characterized by shallow patchy lagoon reefs or steep reef walls. Moreover, some sites were located inside the atoll, either as lagoon-patch reefs or as lagoon-facing sides of the atoll rim (inner reefs), whereas others were positioned on the external, ocean-facing side of the atoll rim (outer reefs), which are often subject to more intense hydrodynamic conditions. The presence of *Acanthaster* spp., whose signs of predation can be confused with those of *Culcita* spp., was not observed on any of the selected sites.

Determination of coral and substrate coverage in the study area

To determine the composition and structure of the benthic community in the study area as well as the diversity and the abundance of the scleractinian corals, a photo-quadrat method was used. For each sampling site, a minimum of 8 PVC quadrats of 1 × 1 m^2 were randomly placed at different depths and spaced

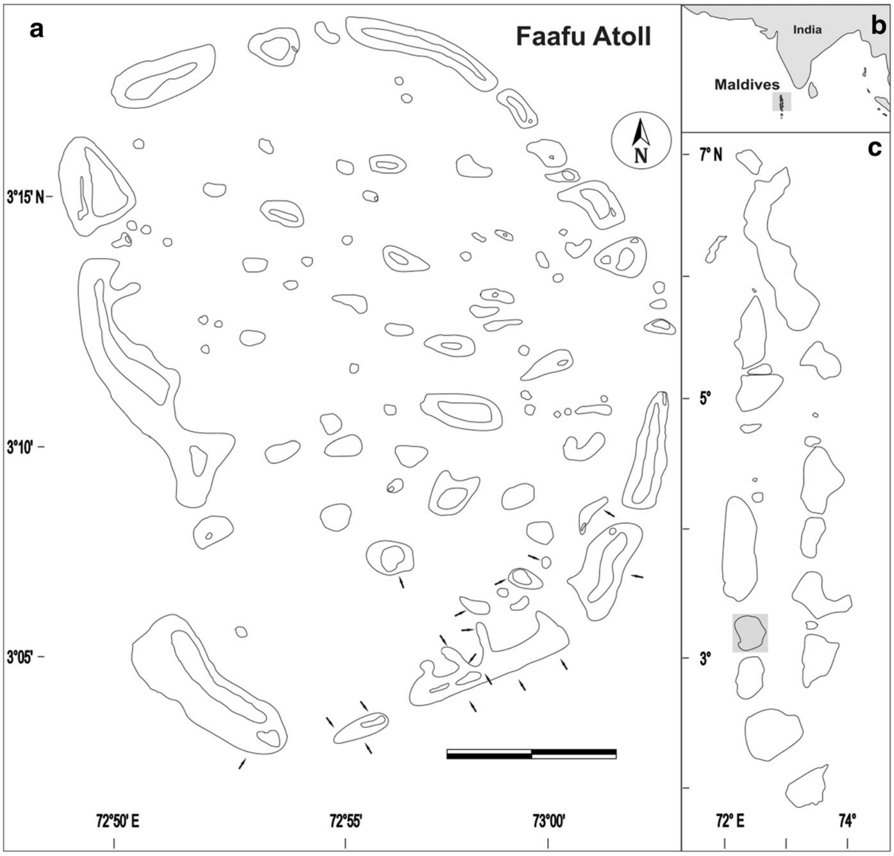

Fig. 1 Map of the study area. Seventeen sites (indicated by arrows) were selected both on the inner and outer side of the Southern part of the Faafu Atoll (**a**), in the Republic of Maldives (**b**, **c**). Scale bar: ~ 10 km. Modified from Montano et al. (2017b)

10–20 m apart. Photographs were taken using a Canon G11 camera in an underwater housing (Canon WP-DC34), and the photographs were analysed using Coral Point Count with Excel extension software 4.0 (CPCe 4.0, Kohler & Gill, 2006). Substrate coverage was estimated through the identification of organisms below 100 randomly distributed points per quadrat. Data relative to each site were collected and analysed together as study areas, using the following benthic categories: corals (scleractinians), rock, sand, coral rubble, dead corals, coralline algae, algae, soft corals, sponges and other sessile invertebrates (tunicates, zoantharians and unknown). In addition, the genus level was added within the benthic category "corals" (identification according to Veron, 2000).

Field observations of *Culcita* sp.

At each study site, the presence of *Culcita* sp. was recorded by applying the roving SCUBA diving technique, which consists of a 1-h dive sampling unit, where the diver moves progressively from the maximum depth (approximately 30 m) to shallower water, swimming freely throughout the dive locality (Hoeksema & Koh, 2009; Montano et al., 2017a). To avoid resampling the same individuals, the divers swam in the same direction without turning back.

Distribution and size

For every cushion sea star encountered, the depth at which it was observed (< 10 m, 10–20 m and > 20 m) and its location in terms of reef zones (reef flat, reef crest, reef slope) were recorded. To determine the coral cover of the area where each individual was found, the living coral cover percentage was evaluated visually within a 2-m radius calculated through a tape measure around each sea star. A coral covering score from 1 to 4 was assigned, where "1" indicated a coral coverage between 0 and 10%, "2" a coral coverage between 10 and 30%, "3" a coral coverage between 30 and 50% and "4" a coral coverage > 50%.

Furthermore, the size of each *Culcita* sp. encountered was noted by measuring with a ruler the maximum diameter of the specimen to the nearest centimetre (cm).

Feeding activity and coral prey preferences

To define the behaviour of the organism, three main activities of the cushion sea star were considered: "moving", when tube feet were visible and the motion of the sea stars was easily detectable; "preying", when sea stars with everted stomachs were feeding on corals or other organic matter; and "stationary," when specimens were not moving or preying.

Within the investigated area (2 m radius around the sea star), we also counted the number of corals consumed by the sea star. In particular, corals showing clear signs of external digestion and the absence of coral tissues were considered as preyed corals (Fig. 2). Importantly, the size of the investigated area (2 m radius) was selected considering the slow movement of the sea stars. This ensured that the coral colonies, showing fresh and bright white scars due to the total removal of living coral tissue as well as a visible thin layer of mucus, had been recently preyed upon by *Culcita* sp. (Fig. 2). The diameter of the targeted colonies was measured to the nearest centimetre (cm) considering their longest axis, and these corals were classified into three size-classes (< 5 cm, 5–10 cm and > 10 cm). Furthermore, the dimensions of scars on the coral surface were noted, and the coral was classified as partially or totally consumed. In addition, the genus of the targeted coral colonies was recorded as well as their growth morphology, according to the following categories: branching, encrusting, massive, foliaceous and mushroom.

Data analysis

Data are presented as the mean ± standard error (SE) unless otherwise stated. Data normality were verified using the Shapiro–Wilk test. Three separate one-way ANOVAs, followed by a Tukey's HSD post hoc test, were used to evaluate significant differences in the abundance of sea stars at different depths, in different reef zones (reef flat, crest and slope) and in relation to different coral cover in the area around the sea star (2 m radius). Likewise, three separate one-way ANOVAs, followed by a Tukey's HSD post hoc test, were used to evaluate significant differences in the sizes of sea stars using the same three previous factors.

Spearman's rank correlation order test was used to examine whether the size of the scars produced by *Culcita* sp. on the preyed coral colonies was correlated

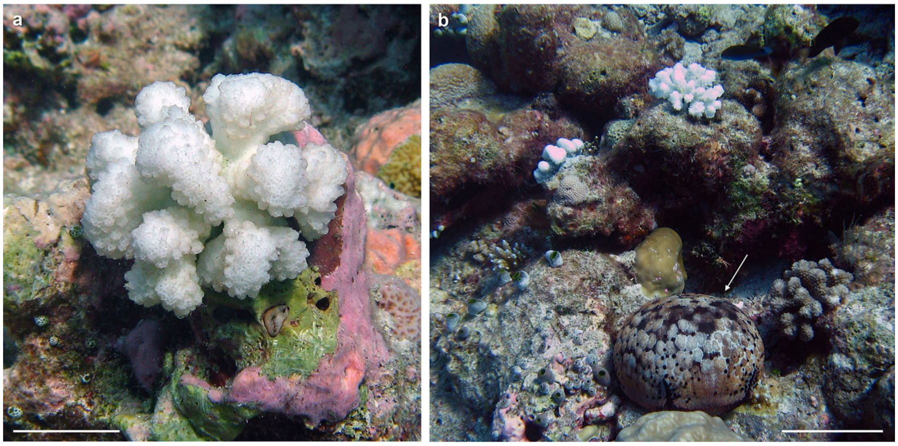

Fig. 2 Small adult colony of *Pocillopora* spp. consumed by *Culcita* sp. (**a**). Note the absence of living tissue. Cushion sea star (indicated by the arrow) close to recently consumed coral colonies (**b**). Scale bars: ~ 4 cm in (**a**) and ~ 10 cm in (**b**)

with the size of the colonies. All statistical analyses were performed using SPSS version 24 (IBM, New York) and R version 3.2.3 (R Development Core Team, 2015).

Sea stars' preferences for different groups of prey, here considered as coral genera, were calculated following Chesson (1983), as the standardized forage ratio (S_i) and defined for a group i as:

$$S_i = \frac{\left(\frac{r_i}{P_i}\right)}{\sum_1^n \left(\frac{r_i}{P_i}\right)}$$

where P_i is the prey relative abundance in the environment, r_i is the relative abundance of the prey in the predators' diet, and n is defined as the number of groups in the system. The values of the standardized forage ratio ranged between 0 and 1, with S_i= 0 indicating avoidance and S_i = 1 indicating exclusiveness for a group of prey. We calculated P_i as the mean percentage cover for a coral genus in all the sites obtained from photo-quadrats analysis and r_i as the percentage of predatory actions on a coral genus in relation to all preyed colonies.

The Ivlev's electivity index, E_i (Ivlev, 1961), was obtained by the following calculation:

$$E_i = (r_i - P_i)/(r_i + P_i)$$

where r_i and P_i are defined as above. Values of E_i ranged between − 1 and 1, such that $E_i = -1$ represents total avoidance, E_i= 0 means non-selective feeding ,and E_i = 1 represents exclusive feeding on a given prey item. As reported by many authors, this index is not independent of prey density and thus has a major shortcoming for comparative purposes versus the standardized forage ratio (Jacobs, 1974; Chesson, 1983). Both indices have been used in feeding studies on Asteroidea and hence provide an efficient tool for the comparative analyses of sea star feeding behaviour (Farias et al., 2012; Saponari et al., 2018).

Results

Coral and substrate coverage in the study area

Considering the community structure and composition of the investigated area (Fig. 3a), benthic community composition was dominated by corals (29.9 ± 3.6%), followed by rock (18.9 ± 2.1%) and sand (13.5 ± 1.6%). The coral genus *Acropora* was the most abundant (13.2 ± 6.4%), followed by *Porites* (6.7 ± 4%), *Pocillopora* (1.2 ± 1%), *Favites* (0.9 ± 0.7%), *Montipora* (0.8 ± 1.3%), *Pavona* (0.8 ± 0.5%) and other less represented genera (Fig. 3b).

Distribution and size of *Culcita* sp.

During the study period, 163 specimens of *Culcita* sp. were found in the area examined.

The abundance of sea stars showed significant variations depending on the depth (one-way ANOVA, $F_{(2,50)} = 24.825$, $P = 0.000$), with the majority of organisms (approximately 70%) found between 0 and 10 m. Below 10 m, the number of observed sea stars decreased progressively with increasing depth, even if no significant difference was detected between the depth ranges 10–20 m and > 20 m (Fig. 4a). No

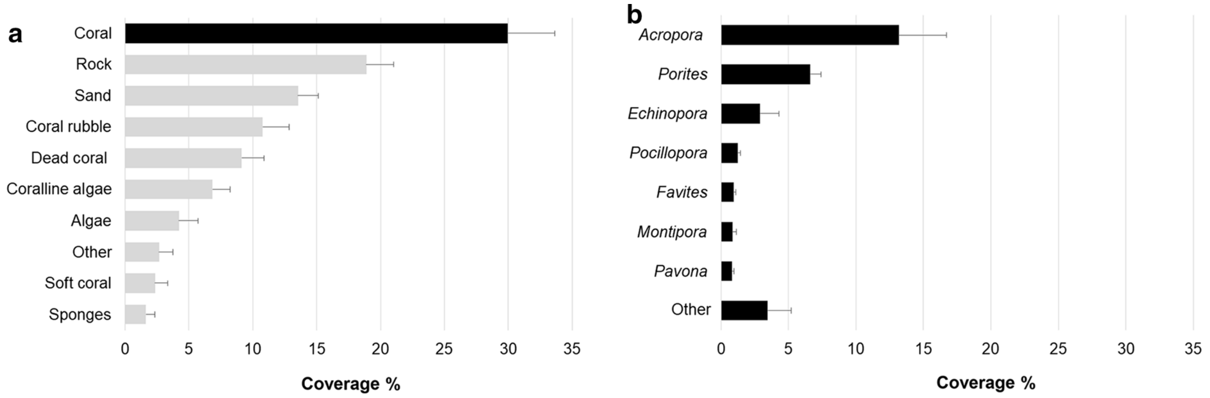

Fig. 3 Overall coverage of the benthic categories (**a**) and coral genera (**b**) in the whole study area. Coral genera showing a coverage % lower than 0.5 were included in the category “Other” (represented by 30 coral genera). Data are expressed as the mean ± SEM

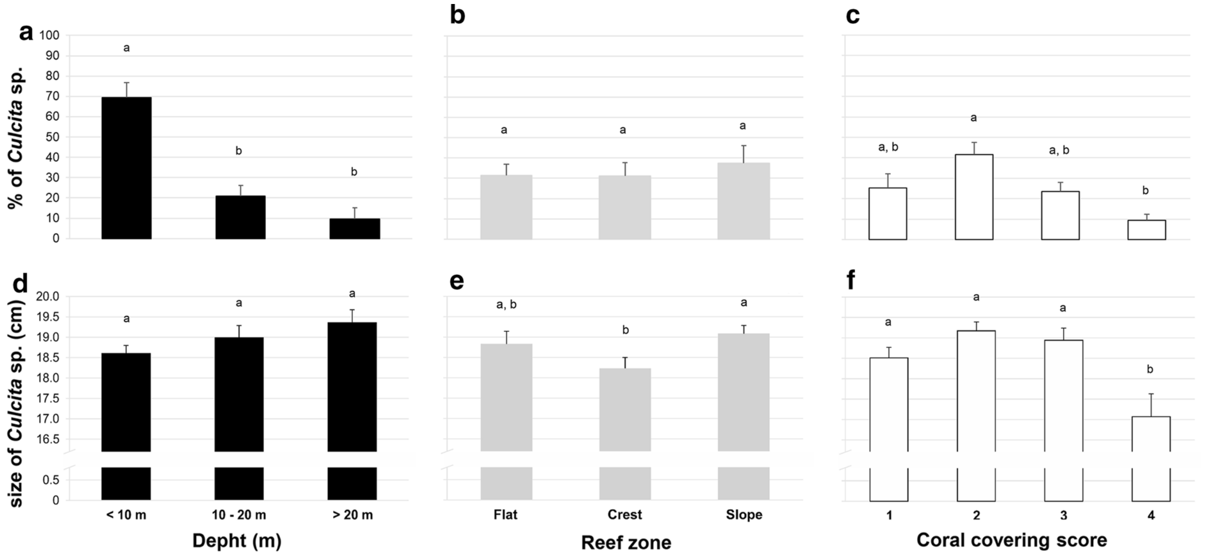

Fig. 4 Mean percentage of abundance of *Culcita* sp. in three depth ranges (**a**), in three reef zones (**b**), and in 2 m radius areas around sea stars, showing 4 different coral cover percentages (1: coral coverage between 0 and 10%, 2: 10–30%, 3: 30–50%, 4: > 50%) (**c**). Data from 17 sites were analysed and percentages expressed as the mean ± SEM (one-way ANOVA followed by Tukey’s HSD multiple pair-wise comparisons). Average size of *Culcita* sp. (cm) in three depth ranges (**d**), in the three reef zones (**e**) and in areas showing different coral cover percentages (**f**). Data are expressed as the mean ± SEM (one-way ANOVA followed by Tukey’s HSD multiple pair-wise comparisons). In each graph, letters denote Tukey’s significant difference among the different groups ($P < 0.05$); thus, the same letter indicates no significant difference ($P \geq 0.05$)

significant difference was observed in the number of sea stars in the different reef zones (one-way ANOVA, $F_{(2,50)} = 0.268$, $P = 0.766$, Fig. 4b), whereas their abundance varied significantly depending on the coral cover percentage recorded in the 2 m radius area around the sea star (one-way ANOVA, $F_{(2,66)} = 6.219$, $P = 0.001$). In particular, significant differences were detected between areas characterized by a coral coverage between 10 and 30%, where the highest number of *Culcita* sp. was found (~ 41.5%) and those with a coral coverage > 50%, where the lowest abundance of specimens was observed (~ 9.5%), (Fig. 4c).

The average size of all sea stars sampled was 18.74 ± 0.15 cm, which did not show significant variation depending on the depth (one-way ANOVA, $F_{(2,153)} = 1.624$, $P = 0.107$, Fig. 4d). However, the average size of the individuals showed significant variation depending on the location of the organisms in the different reef zones (one-way ANOVA, $F_{(2,153)} = 3.217$, $P = 0.0427$, Fig. 4e) and the coral cover abundance in the 2-m radius area around each sea star (one-way ANOVA, $F_{(3,153)} = 5.933$, $P = 0.000$, Fig. 4f). In particular, significant differences in average sizes were detected between the reef crest and the reef slope (Tukey HSD post hoc, $P < 0.05$; Fig. 4e) and between areas where the coral coverage was more than 50% compared to areas where this percentage was less than 50% (Tukey HSD post hoc, $P < 0.05$; Fig. 4f).

Feeding activity and coral prey preferences of *Culcita* sp.

Only 14 sea stars (∼ 9%) out of a total of 163 were observed to perform feeding activities during the sampling, and all were found to be preying on scleractinian corals. Most sea stars (∼ 68%) were found stationary on the reef, whereas approximately 23% of the specimens were moving.

Scars typical of predation by *Culcita* sp. were found on 433 coral colonies belonging to 16 different coral genera (Table 1). Most of the preyed corals belonged to the genera *Acropora* (38.1%) and *Pocillopora* (∼ 36.3%). A considerable number of colonies belonging to the genus *Pavona* were also found to be preyed upon by sea stars (∼ 12.5%), whereas predation on other reef-building genera represented only a small percentage of the total predation (Table 1). Considering the growth morphology of the consumed colonies, *Culcita* sp. predation was highest on corals with a branching growth morphology, whereas the predation on massive forms was less intense, although it encompassed nine different coral genera (Table 1).

Most of the sampled sea stars consumed small adult corals with a diameter between 5 and 10 cm (260 colonies out of 433, ∼ 60%) followed by juvenile corals with a diameter < 5 cm (129 colonies out of 433, ∼ 30%), whereas large adult colonies with a diameter > 10 cm (average size: 15.6 ± 0.84 cm; maximum size: 38 cm) appeared to be the least predated (44 colonies out of 433, ∼ 10%).

Furthermore, considering all the preyed colonies, both totally and partially, a significant positive correlation (Spearman's rho = 0.897, $P < 0.001$) was detected between the size of these colonies and the size of the scars created by the predatory activity of the sea star (Fig. 5). However, as the size of the predated corals increased, the number of partially consumed colonies also increased. In fact, partial predation by *Culcita* sp. occurred on only approximately 7% of all consumed juvenile colonies and on approximately 19.5% of small and 25% of the larger (> 10 cm) predated colonies (Fig. 6a). As shown in Fig. 6b, the coral genus *Montipora* was the most partially consumed (three colonies out of 7, ∼ 42%) followed by *Pavona* (17 colonies out of 54, ∼ 31%), *Porites*, *Acropora*, *Galaxea* and finally *Pocillopora* (only 12 colonies out of 157, ∼ 8%).

The use of the standardized forage ratio (S_i) and the Ivlev's index (E_i) allowed us to compare the abundance of prey categories in the environment and in the predator's diet. The values obtained for both of these indices are shown in Table 2. Remarkably, the standardized forage ratio produced values that indicate a preference for corals of the genus *Pocillopora* and *Pavona*, with values of 0.592 and 0.298, respectively. In contrast, the value generated for the genus *Porites* (0.005) was close to zero, indicating avoidance. The Ivlev's index showed a similar pattern, with values corresponding to preferences for *Pocillopora* and *Pavona* (0.761 and 0.576, respectively) and a negative value, indicating strong avoidance for *Porites* (− 0.885), (Table 2).

Discussion

The direct consumption of live coral, or corallivory, represents an important biotic stressor for reef-building corals that can accelerate the rate of coral reef decline (Knowlton et al., 1990; Rotjan et al., 2006; Lenihan et al., 2011). However, although a wide variety of species from numerous taxa consume living coral (Carpenter et al., 1997; Cole et al., 2008; Rotjan & Lewis, 2008), to date, most studies have focused on a few specific organisms (e.g., COTS, butterflyfishes and *Drupella* spp.), indicating that the actual impact of corallivores on reefs may be underestimated. This study increases the knowledge of the little-investigated cushion sea star *Culcita* sp. in the Maldives, showing how this sea star is widely distributed over the reef, although exhibiting a preference for a specific depth range, reef zone and coral coverage of the habitat, and has a predilection for specific colony sizes and genera.

Table 1 Relative percentages of colonies belonging to each coral genus that have been eaten by *Culcita* sp. and their average size (± SE)

Coral genus	% Eaten (genus)	Average size (± SE) eaten colonies (cm)	Growth form	% Eaten (growth form)
Acropora	38.11	8.91 (± 0.62)	B	74.37
Pocillopora	36.26	6.97 (± 0.34)		
Pavona	12.47	7.44 (± 0.61)	E	15.01
Montipora	1.62	8.43 (± 2.22)		
Leptoseris	0.92	8.25 (± 0.85)		
Porites	1.62	11.71 (± 3.18)	M	9
Galaxea	1.62	8.57 (± 0.92)		
Favia	1.62	5.71 (± 8.5)		
Hydnopora	1.15	6.8 (± 0.37)		
Platygyra	0.92	6.75 (± 1.03)		
Coeloseris	0.69	7.33 (± 1.2)		
Isopora	0.69	9 (± 3.51)		
Favites	0.46	7 (± 2)		
Gardinoseris	0.23	4		
Fungidae	1.39	8.5 (± 2.22)	MSH	1.39
Pachyseris	0.23	9	F	0.23

The growth morphology (*B* branching, *E* encrusting, *M* massive, *MSH* mushroom, *F* foliaceous) and the relative percentage of the eaten colonies by growth morphology are also reported. The data shown in the table were obtained analysing 433 coral colonies eaten by *Culcita* sp.

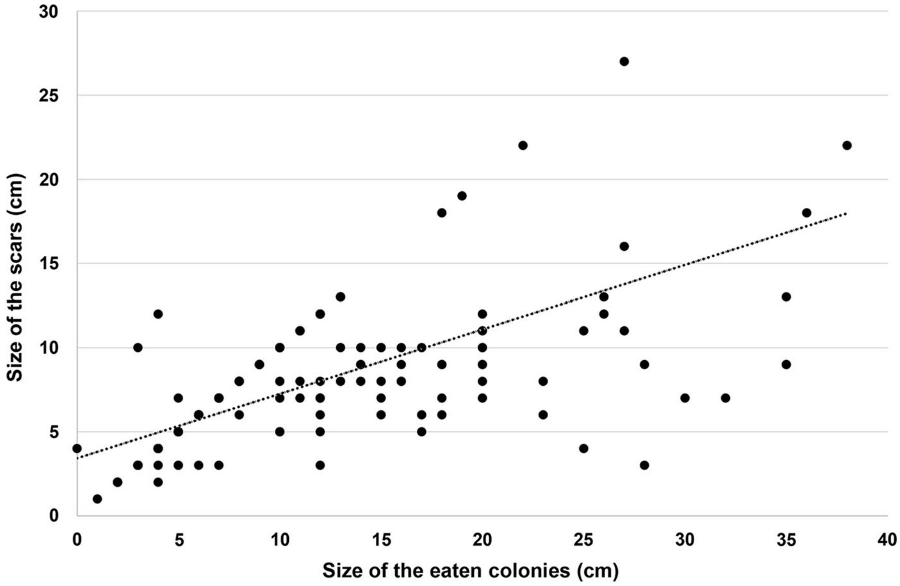

Fig. 5 Relationship between the size of the scars produced by *Culcita* sp. on the preyed coral colonies and the size of the eaten colonies

Regarding the distribution patterns of the cushion sea star, our results indicate that in the study area *Culcita* sp. can be found at a wide depth range (from 0 to at least 30 m) and in all reef zones (flat, crest, slope), even though a preference for reef slopes characterized by a shallow depth, within 10 m, was evident. In previous studies, *C. novaeguineae* was observed on reef slopes to 20 m depth, on reef flats, and on patch

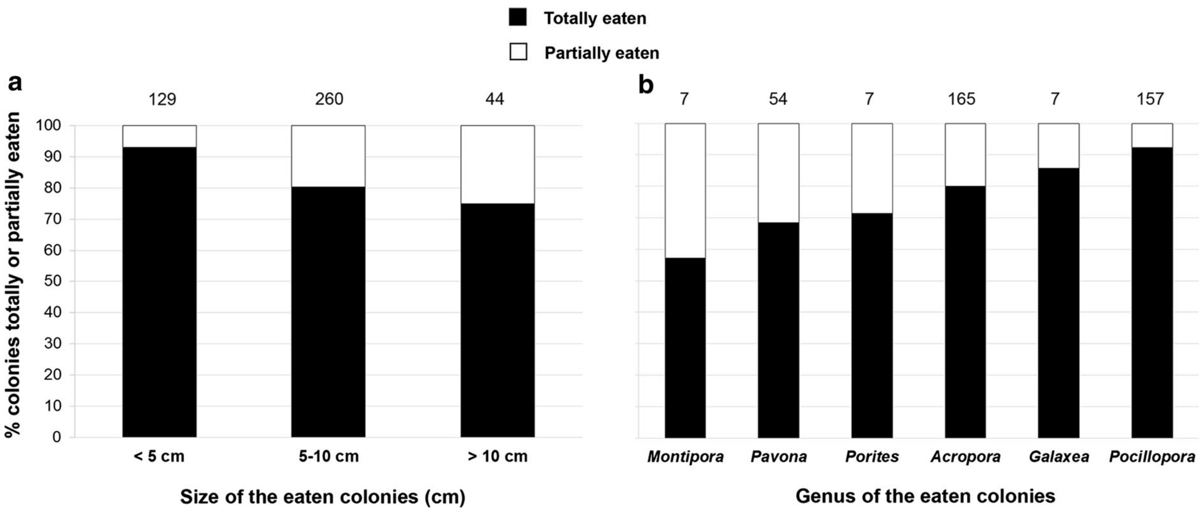

Fig. 6 Relative abundance (%) of coral colonies eaten totally (in black) or partially (in white) by *Culcita* sp. based on their size range (diameter < 5 cm, between 5 and 10 cm and > 10 cm) (**a**). Numbers above each bar indicate the total number of eaten colonies (both totally and partially) per size range. Relative abundance (%) of coral colonies eaten totally or partially by *Culcita* sp. based on their genus (**b**). The coral genera reported in the graph are the only ones for which partially consumed colonies were observed. Numbers above each bar indicate the total number of eaten colonies (both totally and partially) per coral genus

Table 2 Ivlev's index (E_i) and standardized forage ratio (S_i) referring to the six-most abundant coral genera in the study area

Index	Coral genus					
	Acropora	*Porites*	*Pocillopora*	*Favites*	*Montipora*	*Pavona*
E_i	− 0.173	− 0.885	0.761	− 0.779	− 0.352	0.576
S_i	0.057	0.005	0.592	0.01	0.039	0.298

reefs in protected areas (Goreau et al., 1972; Yamaguchi, 1975; Grosenbaugh, 1981; Glynn & Krupp, 1986). However, in line with our observations, *C. novaeguineae* always displayed a higher density on the reef slopes below 3 and 7 m (Goreau et al., 1972; Glynn & Krupp, 1986). In contrast, *C. schmideliana* mainly colonizes coral reef flats (Thomassin, 1976). In this study, the reef slope may have been preferred over the reef flats and crests due to lower water movement and light exposure, a higher presence of palatable coral prey, or an abundance of coralline algae that induce the recruitment of sea star larvae and provide juveniles with food and shelter, which has been proposed to explain similar patterns of distribution of COTS (Johnson et al., 1991; De'ath & Moran, 1998; Pratchett, 2005; Kayal et al., 2012). Variations in seawater temperature could also affect cushion sea star distribution. For example, *C. novaeguineae* was observed in areas characterized by a temperature of between 29°C and 31°C, with highest abundances recorded at approximately 29°C (Yokley, 2016), which corresponds to the average surface temperature recorded in our study area (Seveso et al., 2015, 2017). Our data also showed that most of the sea stars were located on substrates characterized by a low live coral coverage (10–30%), whereas fewer specimens were located in reef zones with a coral coverage > 50%. This observation suggests that *Culcita* sp. may prefer areas where in addition to corals, several types of prey are found, increasing the food resource diversity. In fact, *Culcita* spp. are not obligate corallivores because they feed on other organisms, such as the epilithic algal matrix growing on dead coral, sponges, soft corals, bryozoans, small fauna (nematodes, crustaceans) and algae (Thomassin, 1976; Glynn & Krupp, 1986).

Regarding the size of *Culcita* individuals in relation to the coverage of live coral, our results suggest as in areas characterized by elevated coral coverage, the average size of the *Culcita* sp. population appeared to be the lowest. Considering that corals represent the main framework builders of the Maldivian reef systems, areas characterized by a high coral abundance generally also show a high structural complexity. Small sea stars may prefer a complex three-dimensional habitat that allows them to reduce both the pressure of predation, through hiding and crypsis, and the effects of waves and currents that could easily transport them away from the corals into deeper parts of the reef. During the sampling activities conducted in daylight conditions, very few *Culcita* sp. specimens were actively feeding upon corals, in line with previous evidence suggesting that this animal is preferentially a nocturnal feeder (Glynn & Krupp, 1986), and the majority of individuals were observed hidden and stationary inside ravines, crevices or under coral colonies.

In addition to habitat preferences, our study suggests that *Culcita* sea stars on Maldivian reefs exhibit strong patterns of prey preference and feeding behaviour. Based on previous observations, the feeding preferences of *Culcita* spp. appear to vary depending on geographical area. *C. novaeguineae* in Guam fed mainly on small heads of *Acropora, Pocillopora,* various faviids, *Porites lichen,* and possibly *Hydnopora* and *Montipora* (Goreau et al., 1972). In Hawaii, the same sea star species mainly preyed on *Pocillopora meandrina* (Dana, 1846), followed by *Montipora verrucosa* (Lamarck, 1816) and *Porites lobata* (Dana, 1846), showing the same food preferences when offered a single coral prey species in captivity (Glynn & Krupp, 1986). In Madagascar, *C. schmideliana* has been observed to more frequently eat coral colonies of small sizes and large polyps, such as *Galaxea fascicularis* (Linnaeus, 1767) or *Goniopora stokesi* (Milne Edwards & Haime, 1851), and less commonly small *Acropora* (Thomassin, 1976). Our results showed that in the Maldives a wide range of coral genera are preyed upon by *Culcita* sp.; however, the majority of predation occurred on *Acropora* and *Pocillopora* corals, which are both characterized by a branching growth morphology. Interestingly, no predatory event on colonies of *Acropora* displaying a tabular morphology was observed. All other corals preyed on had either an encrusting (*Pavona*) or massive growth form; however, this accounted for only ~ 25% of total predation events. The preference for particular coral morphologies may be in part due to the surface complexity of the coral (De'ath & Moran, 1998). For example, Keesing (1990) found that branching forms of *Acropora* have the greatest complexity, thereby providing the sea star *A. planci* (Linnaeus, 1758) with greater surface area and hence more tissue per feeding. However, the availability in the investigated area of the different coral genera targeted as prey should be considered in order to detect real food preferences. While sea stars fed on a number of coral general, Si and Ei values suggest that sea stars have a preference for the genus *Pocillopora* followed by *Pavona*, which are both characterized by a low abundance in the area. Considering that *Culcita* sp. has a small stomach and low feeding rate (Glynn & Krupp, 1986; Birkeland, 1989), its preference for *Pocillopora* could be related to the high digestibility or nutritional quality of this coral genus. In fact, the tissues of *Pocillopora* are very thin and, because they are not intricately connected and deeply penetrating in the skeleton, they form a superficial layer that makes them easily available for the sea star (Glynn & Krupp, 1986; Loya et al., 2001). Moreover, this genus is characterized by a low level of protective mucus, absence of large nematocysts and ineffective protection of the juvenile colonies by the *Trapezia* spp. symbiotic crabs, which often fail to prevent the predatory action of *C. novaeguineae* (Glynn & Krupp, 1986; Rouzé et al., 2014).

The genus *Pavona* showed a high index of preference but also a high percentage of partially eaten colonies. The genus *Acropora*, despite the large number of predatory acts, did not appear to be preferentially chosen by *Culcita* sp., and therefore, its high rates of predation may be due to the large abundance of this genus in the study area. The genus *Porites*, although one of the most abundant in the area, was among the least eaten, and all these few colonies targeted by *Culcita* showed a massive growth form. *Porites* could be less palatable due to its thick tissue, which penetrates deeply into the skeleton and is characterized by a low protein content, as well as the numerous and large nematocysts that can cause arm rearing, tube feet retraction and stomach withdrawal in sea stars (Brauer et al., 1970; Moore & Huxley, 1976; Glynn & Krupp, 1986; Keesing, 1990; Lough & Barnes, 2000; Loya et al., 2001). *Porites* is also known to host organisms that may prevent feeding (DeVantier et al., 1986; DeVantier & Endean, 1988). In addition, *Porites* is generally considered a large growing genus, and it is possible that *Culcita* sp. would have difficulties climbing it (Glynn & Krupp, 1986). Not surprisingly, the average size of the few colonies of *Porites* eaten by *Culcita* sp. was relatively small and the largest ones were only partially consumed.

In this context, small colonies (< 10 cm in diameter) have been found to be preferred by *Culcita* sp., which is in line with previous studies, suggesting that the lack of prehensile arms prevents *Culcita* spp. from climbing onto large or high growing corals (Goreau et al., 1972; Thomassin, 1976; Glynn & Krupp, 1986). However, *Culcita* sp. also preyed upon larger coral colonies, which were only partially eaten. In general, we observed that as the size of the colonies targeted by the sea stars increased, both the size of the scars on the colonies as well as the amount of partially consumed colonies increased. This result suggests that *Culcita* sp. is seldom able to kill an entire large colony at one time, perhaps preferring to change coral once a certain amount of its tissue has been assimilated, rather than consuming an entire large colony during multiple feeding attacks. We hypothesized that *Culcita* sp. might be more easily deterred by the developed defensive mechanisms of large adult colonies, which could also be more effective in their defence than smaller colonies due to the higher number of host symbiotic organisms (Abele & Patton, 1976; Glynn, 1980). However, even the partial mortality of coral colonies can affect reef health because it reduces coral growth rate and reproduction, due to the expenditure of the energy stores used for tissue regeneration processes (Veghel & Bak, 1994; Henry & Hart, 2005). In addition, if tissue regeneration is incomplete, portions of the colony could become susceptible to colonization by spatial competitors such as algae, sponges, other colonial invertebrates or disease-causing agents (Bak & Van Es 1980; Nugues & Bak, 2009).

Conclusion

This study provides an overview of the feeding behaviour of a corallivorous organism, *Culcita* sp., that has received scarce attention, but whose impact on coral reef composition and health should not be underestimated. Considering its preferential predation on recruits and juvenile coral colonies and its predilection for some specific coral genera, *Culcita* sp. may affect reef recovery and resilience following other stress events and generate local shifts in coral community composition and structure. In this regard, further ecological investigations on larger scales and quantitative analyses on population dynamics should be considered.

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References

Abele, L. G. & W. K. Patton, 1976. The size of coral heads and the community biology of associated decapod crustaceans. Journal of Biogeography 3: 35–47.

Bak, R. P. M. & Y. Van Es, 1980. Regeneration of superficial damage in the scleractinian corals *Agaricia agaricites*. *F. purpurea*, and *Porites astreoides*. Bulletin of Marine Science 30: 883–887.

Birkeland, C., 1989. The influence of echinoderms on coral-reef communities. In Jangoux, M. & J. M. Lawrence (eds), Echinoderm Studies. AA Balkema, Rotterdam: 1–79.

Birkeland, C. & J. S. Lucas, 1990. *Acanthaster planci*: a major management problem of coral reefs. CRC Press, Boca Raton: 257.

Brauer, R. W., M. J. Jordan & D. J. Barnes, 1970. Triggering of the stomach eversion reflex of *Acanthaster planci* by coral extracts. Nature 228: 344.

Brown, K. T., D. Bender-Champ, D. E. P. Bryant, S. Dove & O. Hoegh-Guldberg, 2017. Human activities influence benthic community structure and the composition of the coral-algal interactions in the central Maldives. Journal of Experimental Marine Biology and Ecology 497: 33–40.

Carpenter, K. E., P. L. Harrison, G. Hodgson, A. H. Alsaffar & S. H. Alhazeem, 1997. The corals and coral reef fishes of Kuwait. Kuwait Institute for Scientific Research, Kuwait.

Chesson, J., 1983. The Estimation and analysis of preference and its relatioship to foraging models. Ecology 64: 1297–1304.

Clark, A. M., 1976. Echinoderms of coral reefs. In Jones, O. A. & R. Endean (eds), Biology and geology of coral reefs. Academic Press, New York: 99–123.

Clark, A. M. & F. W. E. Rowe, 1971. Monograph of the shallow water Indo-Pacific echinoderms. British Museum of Natural History. Pitman Press, Bath.

Cole, A. J., M. S. Pratchett & G. P. Jones, 2008. Diversity and functional importance of coral-feeding fishes on tropical coral reefs. Fish and Fisheries 9: 286–307.

De'ath, G. & P. J. Moran, 1998. Factors affecting the behaviour of crown-of-thorns starfish (*Acanthaster planci* L.) on the Great Barrier Reef: 1: patterns of activity. 2: Feeding preferences. Journal of Experimental Marine Biology and Ecology 220: 83–126.

De'ath, G., K. E. Fabricius, H. Sweatman & M. Puotinen, 2012. The 27–year decline of coral cover on the Great Barrier Reef and its causes. Proceedings of the National Academy of Science of the United States of America 109: 17995–17999.

DeVantier, L. M. & E. Endean, 1988. The scallop *Pedum spondyloideum* mitigates the effects of *Acanthaster planci* predation on the host coral *Porites*: host defense facilitated by exaptation. Marine Ecology Progress Series 47: 293–301.

DeVantier, L. M., R. E. Reichelt & R. H. Bradbury, 1986. Does *Spirobranchus giganteus* protect host *Porites* from predation by *Acanthaster planci*: predator pressure as a mechanism of coevolution? Marine Ecology Progress Series 32: 307–310.

Fallati, L., A. Savini, S. Sterlacchini & P. Galli, 2017. Land use and land cover (LULC) of the Republic of the Maldives: first national map and LULC change analysis using remote-sensing data. Environmental Monitoring and Assessment 189: 417.

Farias, N. E., P. E. Meretta & M. Cledón, 2012. Population structure and feeding ecology of the bat star *Asterina stellifera* (Möbius, 1859): omnivory on subtidal rocky bottoms of temperate seas. Journal of Sea Research 70: 14–22.

Glynn, P. W., 1980. Defense by symbiotic crustacea of host corals elicited by chemical cues from predator. Oecologia 47: 287–290.

Glynn, P. W. & D. A. Krupp, 1986. Feeding biology of a Hawaiian sea star corallivore, *Culcita novueguineae* (Mulller and Troschel). Journal of Experimental Marine Biology and Ecology 96: 75–96.

Goreau, T. F., J. C. Lang, E. A. Graham & P. D. Goreau, 1972. Structure and ecology of the Saipan reef in relation to predation by *Acanthaster planci* (Linnaeus). Bulletin of Marine Science 22: 113–152.

Grosenbaugh, D. A., 1981. Qualitative assessment of the asteroids, echinoids and holothurians in Yap Lagoon. Atoll Research Bulletin 255: 49–54.

Henry, L. A. & M. Hart, 2005. Regeneration from injury and resource allocation in sponges and corals—a Review. International Review of Hydrobiology 90: 125–158.

Hoeksema, B. W. & E. G. L. Koh, 2009. Depauperation of the mushroom coral fauna (Fungiidae) of Singapore (1860–2006) in changing reef conditions. Raffles Bulletin of Zoology 22: 91–101.

Ibrahim, N., M. Mohamed, A. Basheer, H. Ismail, F. Nistharan, A. Schmidt, R. Naeem, A. Abdulla & G. Grimsditch, 2017. Status of coral bleaching in the Maldives in 2016. Marine Research Centre, Malé: 47.

Ivlev, V. S., 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven.

Jacobs, J., 1974. Quantitative measurement of food selection. Oecologia 14: 413–417.

James, D. B., 2004. Echinoderms of the Maldives. Records of the Zoological Survey of India 102: 121–125.

Jangoux, M. & A. Aziz, 1984. Les astérides (échinodermes) du centre-ouest de l'océan Indien (Seychelles, Maldives et îles Mineures). Bulletin du Muséum national d'histoire naturelle. Section A, Zoologie, biologie et écologie animales 4: 857–884.

Johnson, C. R., D. C. Sutton, R. R. Olson & R. Giddins, 1991. Settlement of crown-of-thorns starfish: role of bacteria on surfaces of coralline algae and a hypothesis for deepwater recruitment. Marine Ecology Progress Series 74: 143–162.

Kayal, M., J. Vercelloni, T. Lison de Loma, P. Bosserelle, Y. Chancerelle & S. Geoffroy, 2012. Predator crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. PLoS ONE 7(10): e47363.

Keesing, J. K., 1990. Feeding biology of the crown-of-thorns starfish, *Acanthaser planci*, (Linnaeus). Ph.D. thesis, James Cook University of North Queensland, Townsville, 197 pp.

Knowlton, N., J. C. Lang & B. D. Keller, 1990. Case study of natural population collapse: post-hurricane predation on Jamaican staghorn corals. Smithsonian Contributions to the Marine Sciences 31: 1–25.

Kohler, K. E. & S. M. Gill, 2006. Coral point count with excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. Computers & Geosciences 32: 1259–1269.

Lenihan, H. S., S. J. Holbrook, R. J. Schmitt & A. J. Brooks, 2011. Influence of corallivory, competition, and habitat structure on coral community shifts. Ecology 92: 1959–1971.

Lough, J. M. & D. J. Barnes, 2000. Environmental controls on growth of the massive coral *Porites*. Journal of Experimental Marine Biology and Ecology 245: 225–243.

Loya, Y., K. Sakai, K. Yamazato, Y. Nakano, H. Sambali & R. van Woesik, 2001. Coral bleaching: the winners and the losers. Ecological Letters 4: 122–131.

Montano, S., D. Seveso, R. Arrigoni & P. Galli, 2012a. *Acropora muricata* mortality associated with extensive growth of *Caulerpa racemosa* in Magoodhoo Island, Republic of Maldives. Coral Reefs 31: 793.

Montano, S., G. Strona, D. Seveso & P. Galli, 2012b. First report of coral diseases in the Republic of Maldives. Disease of Aquatic Organisms 101: 159–165.

Montano, S., G. Strona, D. Seveso, D. Maggioni & P. Galli, 2015. Widespread occurrence of coral diseases in the central Maldives. Marine Freshwater Research 67: 1253–1262.

Montano, S., A. Giorgi, M. Monti, D. Seveso & P. Galli, 2016. Spatial variability in distribution and prevalence of skeletal eroding band and brown band disease in Faafu Atoll, Maldives. Biodiversity and Conservation 25: 1625–1636.

Montano, S., S. Fattorini, V. Parravicini, M. L. Berumen, P. Galli, D. Maggioni, R. Arrigoni, D. Seveso & G. Strona, 2017a. Corals hosting symbiotic hydrozoans are less susceptible to predation and disease. Proceedings of the Royal Society B 284: 20172405.

Montano, S., V. Allevi, D. Seveso, D. Maggioni & P. Galli, 2017b. Habitat preferences of the *Pteroclava krempfi*-alcyonaceans symbiosis: inner vs outer coral reefs. Symbiosis 72: 225–231.

Moore, R. J. & C. J. Huxley, 1976. Aversive behaviour of crown-of-thorns starfish to coral evoked by food-related chemicals. Nature 263: 407.

Moosleitner, 1997. Shallow water Asteroidea (Echinodermata) from the coral reef of the Maldives Islands. Revue Francaise de Aquariologie 24: 3–14.

Nugues, M. M. & R. P. M. Bak, 2009. Brown-band syndrome on feeding scars of the crown-of-thorn starfish *Acanthaster planci*. Coral Reefs 28: 507–510.

Ohta, K., N. Yasuda, S. Nagai, K. Oki, C. Taquet & K. Nadaoka, 2011. Observations of *Culcita novaeguineae* spawning events. Galaxea 13: 1–2.

Perry, C. T. & K. M. Morgan, 2017. Bleaching drives collapse in reef carbonate budgets and reef growth potential on southern Maldives reefs. Scientific Reports 7: 40581.

Pratchett, M. S., 2005. Dynamics of an outbreak population of *Acanthaster planci* at Lizard Island, northern Great Barrier Reef (1995–1999). Coral Reefs 24: 453–462.

Pratchett, M. S., M. Trapon, M. L. Berumen & K. Chong-Seng, 2011. Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia. Coral Reefs 30: 183–193.

Pratchett, M. S., F. C. Caballes, C. J. Wilmes, S. Matthews, C. Mellin, P. H. Sweatman, E. L. Nadler, J. Brodie, A. C. Thompson, J. Hoey, R. A. Bos, M. Byrne, V. Messmer, A. S. Fortunato, C. C. Chen, C. A. Buck, C. R. Babcock & S. Uthicke, 2017. Thirty years of research on crown-of-thorns starfish (1986–2016): scientific advances and emerging opportunities. Diversity 9: 41.

Quinn, N. J. & B. L. Kojis, 2003. The dynamics of coral reef community structure and recruitment patterns around Rota, Saipan, and Tinian, Western Pacific. Bulletin of Marine Science 72: 979–996.

Rotjan, R. D. & S. M. Lewis, 2008. Impact of coral predators on tropical reefs. Marine Ecology Progress Series 367: 73–91.

Rotjan, R. D., J. L. Dimond, D. J. Thornhill, J. J. Leichter, B. Helmuth, D. W. Kemp & S. M. Lewis, 2006. Chronic parrotfish grazing impedes coral recovery after bleaching. Coral Reefs 25: 361–368.

Rouzé, H., G. Lecellier, S. C. Mills, S. Planes, V. Berteaux-Lecellier & H. Stewart, 2014. Juvenile *Trapezia* spp. crabs can increase juvenile host coral survival by protection from predation. Marine Ecology Progress Series 515: 151–159.

Saponari, L., S. Montano, D. Seveso & P. Galli, 2015. The occurrence of an *Acanthaster planci* outbreak in Ari Atoll, Maldives. Marine Biodiversity 45: 599–600.

Saponari, L., E. Montalbetti, P. Galli, G. Strona, D. Seveso, I. Dehnert & S. Montano, 2018. Monitoring and assessing a 2-year outbreak of the corallivorous seastar *Acanthaster planci* in Ari Atoll, Republic of Maldives. Environmental monitoring and Assessment 190: 344.

Scott, C. M., R. Mehrotra, M. Y. Hein, M. S. Moerland & B. W. Hoeksema, 2017. Population dynamics of corallivores (*Drupella* and *Acanthaster*) on coral reefs of Koh Tao, a diving destination in the Gulf of Thailand. Raffles Bulletin of Zoology 65: 68–79.

Seveso, D., S. Montano, G. Strona, I. Orlandi, M. Vai & P. Galli, 2012. Up-regulation of Hsp60 in response to skeleton eroding band disease but not by algal overgrowth in the scleractinian coral *Acropora muricata*. Marine Environmental Research 78: 34–39.

Seveso, D., S. Montano, M. A. L. Reggente, I. Orlandi, P. Galli & M. Vai, 2015. Modulation of Hsp60 in response to coral brown band disease. Disease of Aquatic Organisms 115: 15–23.

Seveso, D., S. Montano, M. A. L. Reggente, D. Maggioni, I. Orlandi, P. Galli & M. Vai, 2017. The cellular stress response of the scleractinian coral *Goniopora columna* during the progression of the black band disease. Cell Stress Chaperones 22: 225–236.

Spalding, M. D., C. Ravilious & E. P. Green, 2001. World Atlas of Coral Reefs. University of California Press, Berkeley.

Sweatman, H. & C. Syms, 2011. Assessing loss of coral cover on the Great Barrier Reef: A response to Hughes et al. (2011). Coral Reefs 30: 661.

Thomassin, B. A., 1976. Feeding behaviour of the felt-, sponge-, and coral-feeder sea stars, mainly *Culcita schmideliana*. Helgoländer wissenschaftliche Meeresuntersuchungen 28: 51–65.

Tkachenko, K. S., 2015. Impact of repetitive thermal anomalies on survival and development of mass reef-building corals in the Maldives. Marine Ecology 36: 292–304.

Van Veghel, M. L. J. & R. P. M. Bak, 1994. Reproductive characteristics of the polymorphic Caribbean reef building coral *Montastrea annularis*. III. Reproduction in damaged and regenerating colonies. Marine Ecology Progress Series 109: 229–233.

Veron, J. E. N., 2000. Corals of the World. Australian Institute of Marine Science, Townsville.

Yamaguchi, M., 1975. Coral-reef asteroids of Guam. Biotropica 7: 12–23.

Yamaguchi, M., 1977. Estimating the length of the exponential growth phase: growth increment observations on the coral-reef asteroid *Culcita novaeguineae*. Marine Biology 39: 57–59.

Yasuda, N., 2012. Genetic structure of *Culcita sp.* pincushion sea star in the Coral Triangle. Proceedings of the 12th International Coral Reef Symposium, Cairns, Australia, 9-13 July 2012.

Yasuda, N., K. Ogasawara, K. Kajiwara, M. Ueno, K. Oki, H. Taniguchi, S. Kakuma, K. Okaji & K. Nadaoka, 2010. Latitudinal differentiation in the reproduction patterns of the crown-of-thorns starfish *Acanthaster planci* through the Ryukyu Island Archipelago. Plankton and Benthos Research 5: 156–164.

Yokley, A. G., 2016. The thermal range of the cushion sea star, *Culcita novaeguineae*, distribution and its behavioral response to warmer waters. PeerJ Preprints 4: e2653v1.