
The European Zoological Journal

ISSN: (Print) 2475-0263 (Online) Journal homepage: https://www.tandfonline.com/loi/tizo21

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**To cite this article:** C. Roveta, G. Bavestrello, M. Montefalcone, D. Pica & S. Puce (2019) Asymmetrical distribution of *Distichopora violacea* (Cnidaria: Hydrozoa) in four Maldivian atolls, The European Zoological Journal, 86:1, 9-19, DOI: 10.1080/24750263.2018.1551943

**To link to this article:** https://doi.org/10.1080/24750263.2018.1551943

*The European Zoological Journal*, 2019, 9–19
Vol. 86, No. 1, https://doi.org/10.1080/24750263.2018.1551943

# Asymmetrical distribution of *Distichopora violacea* (Cnidaria: Hydrozoa) in four Maldivian atolls

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*(Received 12 September 2018; accepted 19 November 2018)*

**Abstract**
Stylasterids belong to one of the few calcifying hydroid families that are commonly found in shallow tropical coral reefs. Although these corals are accurately described from a taxonomic point of view, information about their ecology is scarce. *Distichopora violacea* is one of the most common stylasterids of the Indo-Pacific region; however, no information is yet available on its distribution and abundance. To fill this gap data we gathered data during three scientific expeditions on four Maldivian atolls. In each atoll investigations were carried out at three depths, both in the ocean and in the lagoon reef, to examine differences in colony density and distribution. *Distichopora violacea* was observed in all the studied atolls; however, its distribution and density were not homogeneous among them. This species was more abundant in the ocean reefs than in the lagoon ones, suggesting a strong influence of water movement. Moreover, we found a high variability in colony density in the eastern ocean reefs that was tentatively attributed to a different topography of the reef: colonies were more abundant on the gentle slopes of Malè atolls than on the steep reefs of Felidhoo. Oceanographic features, mainly due to the seasonal monsoons, are likely to interact with the biological requirements of the species in determining the observed asymmetrical geographical distribution. The present investigation provides new insights on the stylasterid *D. violacea* and, for the first time, quantitative data on its distribution and density that can be useful for conservation and management of this CITES regulated species.

**Keywords:** *Stylasteridae, geographical distribution, coral reefs, Maldives*

## Introduction

Hydrozoans in the Maldives have been studied since 1904 when several expeditions were carried out in this archipelago (Bigelow 1904; Brown 1904; Borradaile 1905). After this period, no additional studies were conducted for many decades, and then the following extensive studies were carried out from 2012 (Gravier-Bonnet & Bourmaud 2012; Montano et al. 2013, 2014, 2015a,b,c; Seveso et al. 2016).

Several papers have also been published on Maldivian calcified hydroids, such as Milleporidae and Stylasteridae. Stylasterids have an important ecological role in both shallow and deep water (Miller et al. 2004; Häussermann & Försterra 2007; Cairns 2011). They are considered habitat-forming species able to build perennial forests (Etnoyer & Morgan 2006; Di Camillo et al. 2017) which, owing to their three-dimensional structure, host a very rich associated fauna (Cairns & Roberts 2011; Pica et al. 2015). Due to their slow-growing calcified skeleton and scarce larval dispersion (Cairns 1992; Miller et al. 2004; Brooke & Stone 2007), they are considered very vulnerable although sometimes the causes of their decline are difficult to identify (Häussermann & Försterra 2013). Stylasterids are subject to many human threats, such as bottom trawling, hydrocarbon drilling, seabed mining (Roberts et al. 2006), scuba diving (Miller et al. 2004; Häussermann & Försterra 2007) and fish farming (Häussermann & Försterra 2007). Moreover, owing to their beautiful colonies, they are harvested for the national and international souvenir markets and for jewel manufacturing (Häussermann & Försterra 2007; Cairns & Roberts 2011). For

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these last reasons, since 1990, the entire family has been listed in the Convention on International Trade of Endangered Species Appendix II (CITES 1975).

The first report of stylasterid hydroids from Maldives dates back to 1947 when the two species *Crypthelia stenopoma* and *C. clausa*, dredged at 229 m and 609–915 m in two stations not far from the Baa Atoll, were described (Broch 1947). Then, in 1964, during an expedition at Addu Atoll, the southernmost atoll in the archipelago, the presence of *Distichopora fisheri* (currently accepted as *Distichopora violacea*) was first reported in the lagoon reef margin of Gan Island (Wells & Davies 1966). Many years later, Scheer and Obrist (1986) discovered large colonies of *Distichopora nitida* at Baa Atoll. The colonies were observed at 22–30 m on the steep slope of the reef, in both the north and south zones of the atoll, but the authors reported records up to 48 m depth. In 1990–1992, small colonies of an unidentified *Distichopora* species were observed in small cavities in several reefs of both the North Malé and Felidhoo atolls (Ciarapica & Passeri 1993). Twenty years later, Gravier-Bonnet and Bourmaud (2012) listed *D. violacea* and *Stylaster roseus* among the hydroids collected at Baa Atoll (even though the known distribution of this last species is Atlantic; Cairns 1983, 1986). Although stylasterids are reported as common in some islands of the South West Indian Ocean (i.e. La Reunion, Glorieuses, Mayotte, Juan de Nova), the present authors note that they were rare in Baa Atoll, being present in only five out of 22 studied stations.

*Distichopora violacea*, the object of the present investigation, was carefully described by Boschma (1959) and Cairns (1983) who examined several museum specimens; however, the type materials were lost (Cairns 1983). Hickson (1893) investigated the development stages of this species, England (1926) studied its gonophores, and more recently morphological aspects such as the coenosteal canal network (Puce et al. 2012) and the cnidome (Pica & Puce 2017) have been examined.

*Distichopora violacea* has a wide geographic and bathymetric range, being present in the whole Indo-Pacific area (except for Hawaii) from shallow water down to 122 m depth (Boschma 1959; Cairns 1983). This species is frequently reported in papers describing Indo-Pacific reefs and fouling communities, but the provided information is usually qualitative (e.g. Utinomi 1956; Maragos 1974; Jokiel & Maragos 1978; Antonius et al. 1990; Berry & Wells 2000; Joyce & Siang 2012).

The present investigation aims to enlarge the knowledge on the ecology of *D. violacea* in coral reefs of four Maldivian atolls, namely North Malé, South Malé, Felidhoo and Ari. Although oceanographic data about the Maldivian Archipelago are very scarce, information about the ecological preferences of the hydroid can be indirectly obtained by comparing sites characterised by distinct conditions. At a small scale, we compared ocean and lagoon reefs to check the variation of colony densities in two conditions characterised by different intensities of water movement (Kench 1998). Moreover, at a larger scale, we compared the colony densities between western and eastern atolls subjected to a different influence of the seasonal monsoons (Strutton et al. 2015).

## Materials and methods

### *Study area*

The study was carried out in May 2016, 2017 and 2018 during scientific cruises in the North Malé, South Malé, Felidhoo and Ari atolls (Republic of Maldives; Figure 1). North Malé, South Malé and Felidhoo are located on the eastern side of the Maldives archipelago, while Ari is on the western side. Twenty-eight sites were surveyed: 14 ocean reefs (ocean-facing sides of the atoll rim), labelled O1 to O14, and 14 lagoon reefs (lagoon patch reefs or lagoon-facing sides of the atoll rim), numbered L1 to L14. The position of each site was recorded using a global positioning system (GPS; Table I).

North Malé is one of the most populated atolls by Maldivians and tourists (Sathiendrakumar & Tisdell 1989). It includes many faroes without islands and the ocean-ward margin of the atoll rim is characterised by deep erosion (Ciarapica & Passeri 1993). In the southern part, reefs are a combination of passages on the ocean reefs and faroes (McClanahan & Muthiga 2014).

South Malé is oval in shape; reef flats are generally shallow, from 0 to 2 m depth. The maximum depth of the lagoon is 68 m; the lagoon water is connected with the offshore waters by many channels (30–70 m depth) crossing the reefs (Suzuki & Kawahata 1999).

Felidhoo is one of the most pristine atolls of the archipelago (Ciarapica & Passeri 1993). The atoll rim is characterised by continuous reefs, extending without gaps for tens of kilometres; the ocean-ward margin of the eastern atoll rim presents marked erosion and many passages.

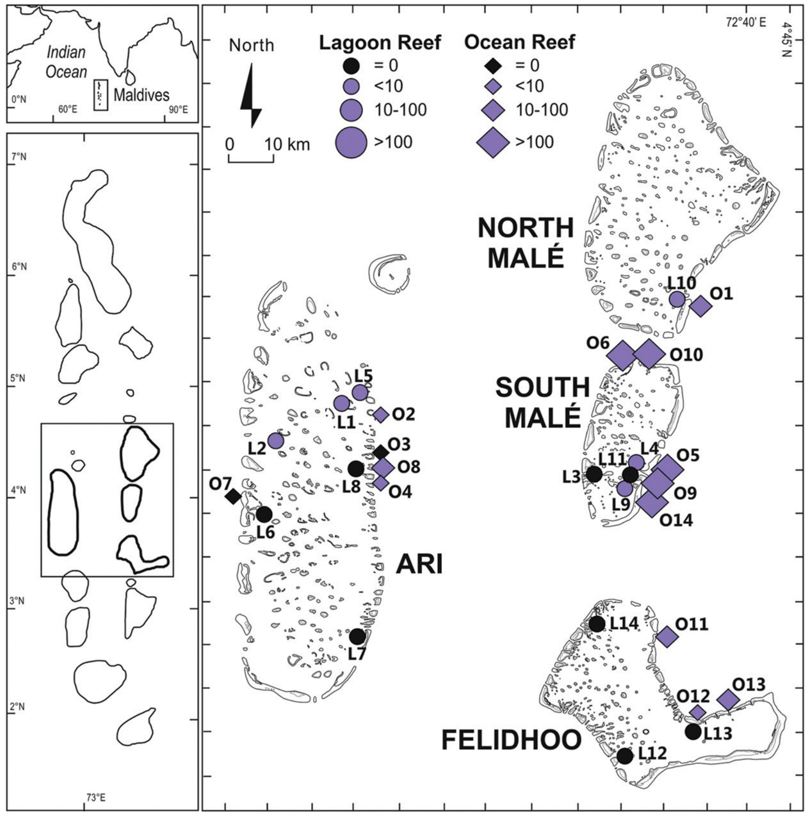


Figure 1. Mean density (number of colonies × 10 $m^{-2}$) of *Distichopora violacea* in the 28 surveyed sites. Refer to Table I for site codes.

Ari is the largest atoll of the Maldives archipelago. The marginal reef, being discontinuous, is characterised by numerous passages. The fore-reef slope has an erosional origin, whereby it is usually characterised by a spur and groove pattern, and it ends in a vertical drop-off. The lagoon is over 100 m deep and includes about 140 major patch reefs and faroes (Gischler 2006).

### *Field and laboratory activities*

The target organism of this study was the stylasterid *Distichopora violacea*. The morphometric features of the Maldivian colonies were studied on 50 specimens randomly collected and preserved in alcohol 95% (CITES Permission 17-MV/0008/E8). The height of the colonies was measured, and the number of branch apexes was counted in order to assess the variation of the branching pattern according to the growth of the colonies.

For species identification the colonies were observed under a stereomicroscope, and some branches were prepared for scanning electron microscope (SEM) analysis (see Pica et al. 2015 for the method). The careful morphological description provided by Cairns (1983) allowed us to identify our specimens as *Distichopora violacea*, despite the pore row being sometimes wider and the elements of the ring palisade slightly taller and wider (Figure 2).

Data of abundances (i.e. density) of the colonies were recorded by scuba diving in both lagoon and ocean reef sites at three depths: (i) flat (f), 4–6 m; (ii) upper slope (u), 9–11 m; and (iii) lower slope (l), 14–16 m. For each depth, three 5 m × 2 m belt transects (Bianchi et al. 2004) were laid parallel to the reef edge from an arbitrarily selected starting point. A total of 252 transects were surveyed. Densities of *D. violacea* were expressed as number of colonies per transect (10 $m^2$).

Photos of the colonies were taken underwater with a Canon 600D camera with an INON Z240 external flash.

### *Data analysis*

Mean density values (± standard error) of *Distichopora violacea* were computed for each of the 28 sites and at each depth. Due to the low density of colonies recorded in many sites, we preferred to

Table I. List of the 28 sites surveyed during the 2016, 2017 and 2018 annual scientific cruises in the Maldives.

| Site name | Site code | Reef typology | Atoll | Coordinates |
|---|---|---|---|---|
| Hulumale Beyru | O1 | Ocean | North Malé | 04°13′39″N, 73°33′07″E |
| Ellahidoo Beyru | O2 | Ocean | Ari | 04°03′13″N, 72°54′44″E |
| Fushi Faru Reef | O3 | Ocean | Ari | 04°01′39″N, 72°57′33″E |
| Faru Madugau | O4 | Ocean | Ari | 03°59′21″N, 72°46′41″E |
| Kandhooma Beyru | O5 | Ocean | South Malé | 03°56′49″N, 72°46′41″E |
| Velassaru Caves | O6 | Ocean | South Malé | 04°07′34″N, 73°26′18″E |
| Maavaru Faru | O7 | Ocean | Ari | 03°52′35″N, 72°42′17″E |
| Faanu Madugau Beyru | O8 | Ocean | Ari | 03°55′31″N, 72°57′28″E |
| Maadu Faru Beyru | O9 | Ocean | South Malé | 03°52′49″N, 73°28′04″E |
| Vaadhoo Caves | O10 | Ocean | South Malé | 04°07′43″N, 73°27′23″E |
| Bolikey Falhu | O11 | Ocean | Felidhoo | 03°36′17″N, 73°30′20″E |
| Kashavaru Falhu Beyru | O12 | Ocean | Felidhoo | 03°26′49″N, 73°35′46″E |
| Fushi Falhu | O13 | Ocean | Felidhoo | 03°27′57″N, 73°39′06″E |
| Kandhooma Beyru | O14 | Ocean | South Malé | 03°54′00″N, 73°28′34″E |
| Halaveli Reef | L1 | Lagoon | Ari | 03°54′29″N, 72°57′28″E |
| Fesdu Reef | L2 | Lagoon | Ari | 03°54′39″N, 73°22′37″E |
| Vaagali Faru | L3 | Lagoon | South Malé | 03°54′21″N, 73°27′21″E |
| Guraidoo Lagoon Reef | L4 | Lagoon | South Malé | 03°54′04″N, 73°28′33″E |
| Bathala Maaga | L5 | Lagoon | Ari | 04°03′32″N, 72°56′31″E |
| Maavaru Faru Lagoon | L6 | Lagoon | Ari | 03°50′34″N, 72°44′11″E |
| Dangethi House Reef | L7 | Lagoon | Ari | 03°36′10″N, 72°56′06″E |
| Kubulabhi | L8 | Lagoon | Ari | 03°55′01″N, 72°55′59″E |
| Villivaru Giri | L9 | Lagoon | South Malé | 03°54′15″N, 73°26′40″E |
| Kuda Banana Reef | L10 | Lagoon | North Malé | 04°13′59″N, 73°32′01″E |
| Villivaru Reef | L11 | Lagoon | South Malé | 03°54′14″N, 73°26′41″E |
| Anabara Reef | L12 | Lagoon | Felidhoo | 03°22′17″N, 73°26′25″E |
| Kashavaru Falhu Etere | L13 | Lagoon | Felidhoo | 03°26′18″N, 73°36′01″E |
| Goro Giri | L14 | Lagoon | Felidhoo | 03°37′58″N, 73°23′13″E |

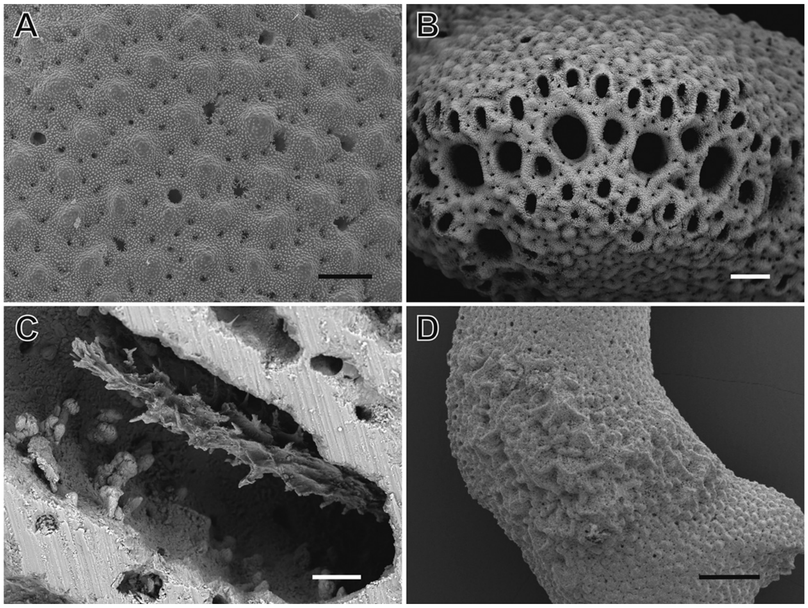


Figure 2. *Distichopora violacea* scanning electron microscope (SEM) micrographs. (a) coenosteal texture; (b) rows of gastropore and dactylopores; (c) gastrostyle and elements of the ring palisade; (d) ampullae. Scale bars: A, D = 400 μm; B = 500 μm; C = 100 μm.

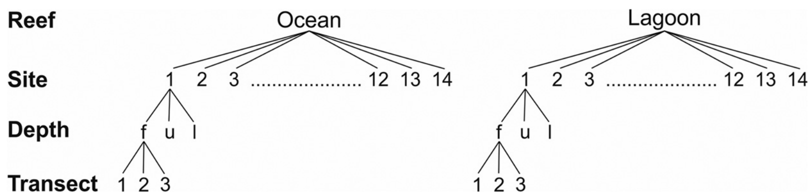


Figure 3. Hierarchical sampling design used in the statistical analyses. Numbers from 1 to 14 indicate sites, which are nested within reef typologies (ocean and lagoon). At each site, three depths were surveyed: flat (f), between 4–6 m; upper slope (u), between 9–11 m; and lower slope (l), between 14–16 m. Three replicated transects (1, 2, 3) were done at each depth.

express the mean density in tens of square metres (10 m$^2$) rather than in square metres (1 m$^2$).

Differences among densities of the colonies at each site were analysed by three-way analysis of variance (ANOVA) with reef typology as a fixed factor with two levels (lagoon and ocean), site as random and nested within the reef typology factor with 28 levels (sites O1 to O14 and L1 to L14), and depth as a fixed and orthogonal factor with three levels (f, u, l), with the transects as replicates (n = 252; Figure 3).

Prior to analysis, homogeneity of variances was tested by Cochran's test. In the case of non-homogeneous variances, ANOVA was nevertheless used after setting $\alpha$ = 0.01 in order to compensate for the increased likelihood of Type I error (Underwood 1997). When a treatment factor was significant, the

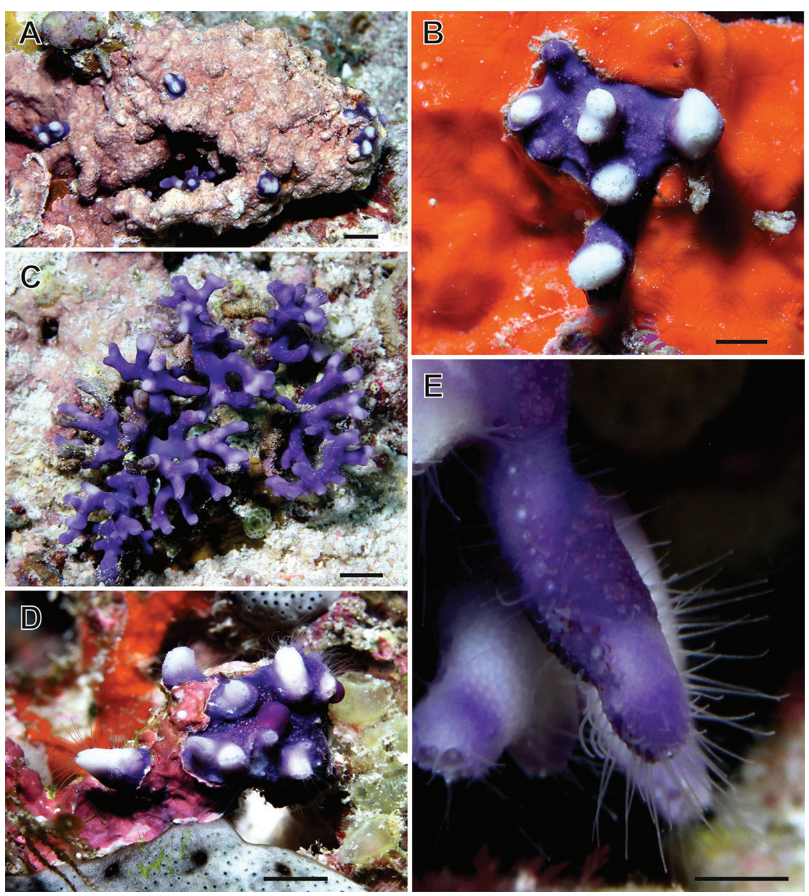


Figure 4. Field images of colonies of *Distichopora violacea*. (a) cluster of small, unbranched colonies settled on a coral rubble covered by coralline algae, at 15 m depth in Maadu Faru Beyru (site O9); (b) colony surrounded by an encrusting sponge, at 10 m depth in Velassaru Caves (site O6); (c) branched colonies forming a dense cluster, at 5 m depth in Velassaru Caves (site O6); (d) small branches arising from a common encrusting plate, in Maadu Faru Beyru (site O9); (e) close up of a branch showing the rows of extended dactylozooids (about 2 mm) on the two sides of the gastropores. Scale bars: A = 5 mm; B = 3 mm; C = 1 cm; D = 4 mm; E = 2 mm.

differences between levels were determined using the Student–Newman–Keuls test (SNK test).

Differences between eastern and western ocean reefs and between eastern ocean reefs (i.e. North and South Malè considered together, and Felidhoo) were investigated using a one-tiled Student *t* test.

Topography of the ocean reefs in Malè and Felidhoo atolls was described using nine depth transects laid perpendicular to the reef edge (Lasagna et al. 2010), from the reef flat to about 20 m depth according to the site, where the depth and the distance from the edge of the reef were recorded.

## Results

On the reef flat and the upper slope, colonies of *Distichopora violacea* were mainly settled inside small crevices of the reef, while on the lower slope they were recorded on a substratum covered by coralline algae or on coral rubbles, sometimes surrounded by encrusting sponges (Figure 4). Generally, the colonies were clustered in groups and their size ranged from 1 to about 30 mm in height. Although quantitative data are not available, colonies appeared larger in shallow waters. Moreover, the colonies observed in Ari Atoll were smaller than the ones recorded in Felidhoo, North and South Malè atolls.

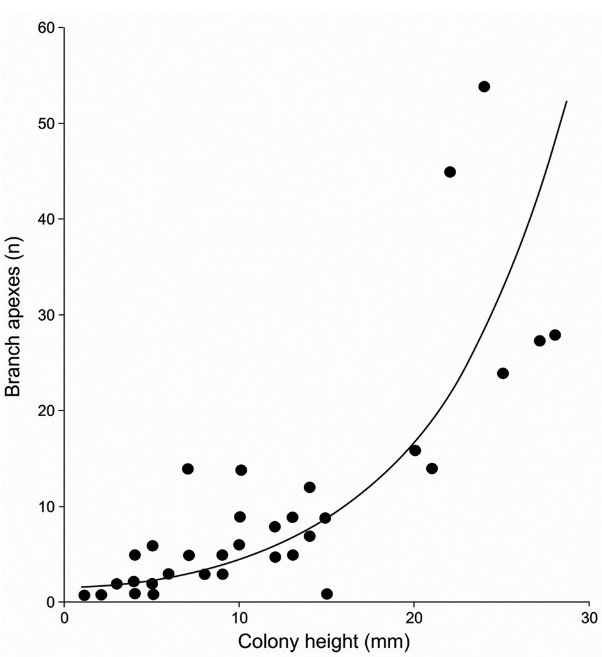


Figure 5. Relationship between colony height and number of branch apexes in 30 colonies of *Distichopora violacea* with different size ($R^2 = 0.7$).

The colonies were usually three-dimensional, stout and without a main stem. Often several branches arose from an encrusting plate, and rarely planar colonies were observed (Figure 4). The number of apexes ranged from 1–2 in the smallest colonies to more than 50 in the largest ones (Figure 5). The coenosteum was usually violet with white tips, but also orange-yellow specimens were rarely recorded, representing 1.72% of the total number of the observed colonies. Rows of dactylozooids (about 2 mm long) extending on the two sides of the gastropores have been often observed (Figure 4(e)).

*Distichopora violacea* occurred in 18 out of 28 sampling sites, with a total of 7947 recorded colonies. Most colonies (98%) were observed in the eastern sites of North Malè, South Malè and Felidhoo, while only 2% of the colonies occurred in the Ari sites. Despite a large variability among sites, density of *D. violacea* was higher in ocean reefs than in lagoon ones ($p < 0.001$; Table II), as almost all the colonies (99%) were observed in the former (Figures 1 and 6).

The highest density was recorded at Vaadhoo Caves (site O10), an ocean reef in South Malè (Figure 1 and Table III), with a mean value among the three depths of 234.2 ± 46.6 colonies/10 $m^2$. Density is usually higher on the reef flat at 4–6 m depth ($p < 0.001$), except for three sites, namely O1, O6 and O14 (Table III).

A significant difference in colony density was found between the eastern and the western ocean reefs ($p < 0.001$, Student's *t* test). In the eastern ocean reefs, a significant difference between Malè and Felidhoo atolls ($p < 0.001$, Student's *t* test) was also recorded. Moreover, we observed differences in the topography of the reef slope that decreases gently in Malè (slope between 10–60°) and steeply in Felidhoo (slope between 60–90°) (Figure 7).

## Discussion

Stylasterids have been widely studied from a taxonomic point of view, but field studies providing quantitative data are still scant (Miller et al. 2004; Häussermann & Försterra 2007; Wagner et al. 2014). These hydrozoans are known to be distributed especially around small oceanic islands and atolls, and on seamounts (Cairns 1992; Cairns & Roberts 2011); therefore, it is not surprising that they are present around Maldivian atolls. Literature data indicate that four species, *Crypthelia stenopoma*, *C. clausa*, *Distichopora nitida* and *Stylaster roseus*, have been recorded from Baa Atoll and the surrounding area, while *Distichopora violacea* has also been reported from Addu Atoll

Table II. Three-way analysis of variance (ANOVA) to test differences in the densities of *Distichopora violacea*. Significant values (** = $p < 0.001$) are in bold.

| Source | df | SS | MS | F | *P* |
|---|---|---|---|---|---|
| Reef (R) | 1 | 285.2536 | 285.2536 | 13.87 | **0.0010**[a] |
| Site (S) | 26 | 534.7761 | 20.5683 | 86.32 | **0.0000** |
| Depth (D) | 2 | 5.3275 | 2.6637 | 1.83 | 0.1702 |
| R × D | 2 | 4.8825 | 2.4413 | 1.68 | 0.1965 |
| D × S | 52 | 75.5980 | 1.4538 | 6.10 | **0.0000**[b] |
| Res | 168 | 40.0287 | 0.2383 | | |
| Total | 251 | 945.8665 | | | |

Cochran's C-test C = 0.2000
Transformation Ln(x+1)
SNK test [a] Ocean > Lagoon**
[b] Ocean: O1 f < u**, f < l*; O5 u < f*, l < f*; O6 f < u**; O11 u < f**, l < f**; O13 u < f*, l < f**; O14 f < u**, f < l*, l < u**

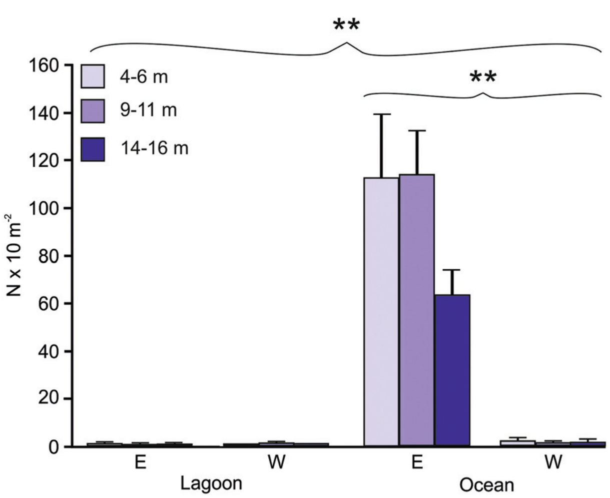


Figure 6. Mean density (number of colonies × 10 $m^{-2}$) (+ standard error) of *Distichopora violacea* at the three depths (reef flat, upper slope and lower slope) in the ocean and lagoon reefs of the eastern (E, North Malè, South Malè and Felidhoo atolls) and western (W, Ari Atoll) side of the Maldives archipelago. ** = $p < 0.001$.

(Broch 1947; Wells & Davies 1966; Scheer & Obrist 1986; Gravier-Bonnet & Bourmaud 2012). The collected specimens of *D. violacea* presented pore rows 1.3–1.6 mm in width (0.8–1.0 in Cairns 1983) and ring palisade elements 56–100 µm tall (up to 54 µm in Cairns 1983) and 24–48 µm in width (16–18 µm in Cairns 1983). Despite these differences, the general morphology and the other microscopic characters match with the description provided by Cairns, leading us to identify our specimens as *D. violacea*. Therefore, our surveys showed that this species is present also around North Malé, South Malé, Felidhoo and Ari atolls. Moreover, it was recorded also in Faafu Atoll (S. Puce, unpublished), suggesting that the known pattern of distribution is probably affected by the scarce sampling efforts.

Ecological studies about stylasterids are scant, and no data are available about colony density of *D. violacea* or of other tropical species. The mean density of colonies reported in the present study ranges from 0.022 to 23 colonies/$m^2$, values of the same order of magnitude as those recorded for *Errina antarctica* in Patagonian fjords, Pacific coast, Chile (20 colonies/$m^2$; Häussermann & Försterra 2007), but lower than those observed for *Errina aspera* in the Messina Strait (101.4 colonies/$m^2$; Salvati et al. 2010).

Salvati et al. (2010) pointed out that *E. aspera* increases rapidly the number of apexes during growth, reaching 50 apexes in colonies almost 5 cm high. Maldivian *D. violacea* increases its colony complexity even more rapidly; in fact, colonies that are 3 cm in height already have 50 apexes.

Our investigation showed that the distribution of *D. violacea* is not homogeneous in the four studied atolls. In fact, colony density was higher in the eastern ocean reefs of North Malé, South Malé, and Felidhoo atolls, while only a few colonies have been observed in the western ocean reefs of Ari Atoll and in lagoon reefs of both the eastern and western atolls. The scarcity of colonies in the reefs of Ari Atoll is in agreement with the observations reported by Gravier-Bonnet and Bourmaud (2012), who noticed that colonies of

Table III. Mean density (number of colonies × 10 $m^{-2}$) (± standard error) of *Distichopora violacea* at the three depths (4–6 m, 9–11 m and 14–16 m) in the 28 surveyed reefs. Refer to Table I for site codes.

| Site | 4–6 m | 9–11 m | 14–16 m |
|---|---|---|---|
| O1 | 5.33 ± 1.76 | 24.33 ± 2.03 | 11.33 ± 3.28 |
| O2 | 0.33 ± 0.33 | 0 | 0.33 ± 0.33 |
| O3 | 0 | 0 | 0 |
| O4 | 1.67 ± 1.67 | 0 | 0 |
| O5 | 279.00 ± 17.78 | 197.67 ± 19.68 | 145.00 ± 23.00 |
| O6 | 47.00 ± 15.89 | 183.00 ± 13.58 | 97.67 ± 11.29 |
| O7 | 0 | 0 | 0 |
| O8 | 14.00 ± 6.11 | 7.67 ± 3.84 | 10.33 ± 10.33 |
| O9 | 152.00 ± 69.01 | 178.00 ± 24.27 | 77.67 ± 21.09 |
| O10 | 347.00 ± 101.45 | 186.33 ± 15.93 | 142.33 ± 20.87 |
| O11 | 86.00 ± 23.07 | 2.00 ± 2.00 | 0 |
| O12 | 1.00 ± 1.00 | 0.33 ± 0.33 | 0.67 ± 0.67 |
| O13 | 53.33 ± 13.12 | 9.00 ± 2.52 | 0 |
| O14 | 15.67 ± 2.33 | 234.67 ± 20.67 | 86.00 ± 17.69 |
| L1 | 0.33 ± 0.33 | 0.67 ± 0.67 | 0.33 ± 0.33 |
| L2 | 0 | 4.33 ± 2.96 | 0.33 ± 0.33 |
| L3 | 0 | 0 | 0 |
| L4 | 4.67 ± 0.67 | 5.33 ± 1.76 | 5.0 ± 3.00 |
| L5 | 2.67 ± 2.67 | 0 | 0 |
| L6 | 0 | 0 | 0 |
| L7 | 0 | 0 | 0 |
| L8 | 0 | 0 | 0 |
| L9 | 0 | 0.33 ± 0.33 | 0.67 ± 0.67 |
| L10 | 0 | 0 | 0.67 ± 0.67 |
| L11 | 0 | 0 | 0 |
| L12 | 0 | 0 | 0 |
| L13 | 0 | 0 | 0 |
| L14 | 0 | 0 | 0 |

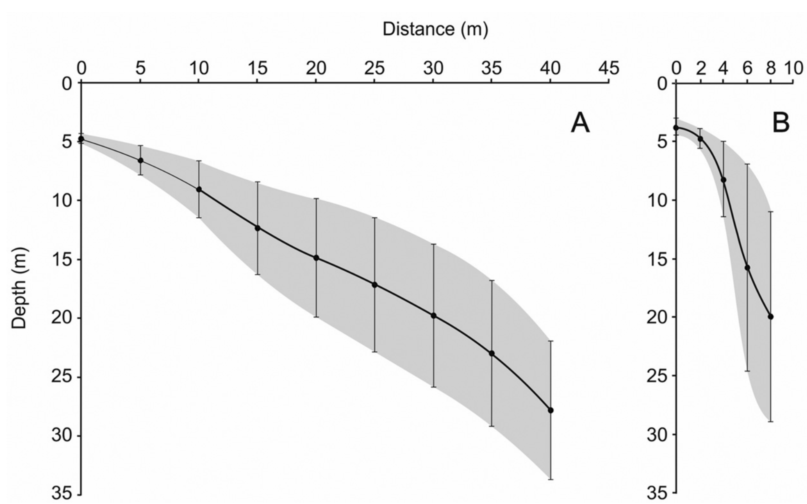


Figure 7. Mean reef profile (± standard error) of the ocean sites in (a) North and South Malè (n = 6), and (b) Felidhoo (n = 3). The variability among transects is represented by the grey area.

*D. violacea* were rare in Baa Atoll, located the farthest north but at the same longitude as Ari.

The Maldives area is dominated by monsoon winds (Strutton et al. 2015). Analyses in the literature indicate that no detailed hydrological data for the shallow water of the whole Maldivian area or single atolls are currently available. Furthermore, the only information about winds provided by Maldives Meteorological Services concern exclusively a few spotted locations of the archipelago. Therefore, the observed distribution pattern is not easily interpretable. Nevertheless, it is possible to hypothesise that biotic and abiotic factors may act synergistically in determining this distribution.

Monsoons move westward during winter, while they are directed eastward during summer and completely drive the marine currents (Strutton et al. 2015). If planula release occurs in summer, this may represent an insuperable obstacle for a westward dispersal. Moreover, studies conducted on stylasterid planulae demonstrated that they are lecithotrophic with a very short planktonic stage (Ostarello 1973, 1976; Fritchman et al. 1974; Brooke & Stone 2007). The Maldivian colonies show a patchy distribution and sometimes are clustered in dense aggregates. As already noticed for other stylasterids, the planula settling occurs very close to the mother colony, representing a possible obstacle to the dispersal of these hydroids at a wide scale (Ostarello 1973; Fritchman et al. 1974; Miller et al. 2004). Wells and Davies (1966, p. 9), referring to Addu Atoll, stated, "marine currents in this area are variable with the monsoon circulation, but under the influence of the Equatorial countercurrent the predominant current direction appears to be eastward or north-eastward". If this condition is present also in the northernmost atolls, it could contribute to explain the observed asymmetrical distribution. In addition, the few colonies recorded in Ari Atoll were very small, generally with only one or two branches, indicating they were young. This evidence could support the hypothesis of a short survival of the colonies due to possibly unsuitable conditions in the western atolls.

Cairns (1992, 2011) reported that, from a hydrologic point of view, stylasterids are sensitive to fluctuations of salinity and high levels of sedimentation, and prefer oligotrophic waters. Moreover, several observations strongly suggest a preference for intense water movement (Häussermann & Försterra 2007; Salvati et al. 2010). The differences in the density of colonies of *D. violacea* between lagoon and ocean sites may be related to differences in water circulation. In fact, in lagoons, the rate of sedimentation and the suspended organic matter are high and currents are generally weaker than in ocean sites (Done 1983; Kench 1998; Morri et al. 2015), thus creating a habitat unfavourable for the settling of stylasterids. The few specimens recorded in lagoons could be transported by entering currents from the oceanic water, which drive larvae in the inner parts of the atoll. However, due to the unsuitable conditions, the larval survival is very low and only a few of them, settled in particularly favourable habitats, can develop. The unusual lower density recorded on the reef flat of some ocean sites could be similarly explained by the low current intensity observed (C. Roveta, pers. obs.).

Differences in colony density recorded in the ocean reefs of Malè and Felidhoo atolls could be related to the reef topography. Ocean reefs in Malè North and South are characterised by a gentle slope, while those in Felidhoo are represented by almost vertical walls, with a lower three-dimensionality of the reef. On the reef flat of Felidhoo sites, density was comparatively higher, while no or only a few colonies were observed on the slope between 9 and 16 m depth. Maragos and Jokiel (1986) observed a similar pattern in the north-west ocean reef of Johnston Atoll (eastern Indo-Pacific Ocean), an area characterised by a steep reef and strong waves, reporting the presence of very few corals among which were small encrusting colonies of *D. violacea*.

These quantitative data, obtained for the first time in the Maldivian archipelago, improves the knowledge on the ecology of Stylasteridae, in particular of the well-known and common species *D. violacea*. Moreover, we stress the importance of future ecological studies, which could provide crucial information for the protection and management of this CITES regulated group.

## Acknowledgements

Albatros Top Boat (Verbania, Milan and Malé) organised our scientific cruises in the Maldives: we especially thank Donatella 'Dodi' Telli, Massimo Sandrini and Herbert Fontana for their support and all the staff of Conte Max and Duke of York boats for assistance during field work. We also thank all participants in field activities that helped with collecting data and Save the Beach Maldives. A special thank to Annalisa Azzola for the underwater pictures of *Distichopora violacea*.

## Disclosure statement

No potential conflict of interest was reported by the authors.

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