Environmental gradients and host availability affecting the distribution of the symbiosis between *Pteroclava krempfi* (Hydrozoa, Cladocorynidae) and alcyonaceans in the Saudi Arabian central Red Sea

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ABSTRACT

Interspecific associations are common in coral reefs, but those involving hydrozoans and octocorals are not widely investigated. The hydroid *Pteroclava krempfi* (Billard, 1919) lives in association with different alcyonacean taxa, showing a widespread distribution. However, very little information is available on the ecology of these relationships. Here, we tested for differences in the taxon-specific prevalence and habitat preference of the symbiosis and we determined ecological traits of the *P. krempfi*-host associations in central Red Sea reefs. *Pteroclava krempfi* was found associated with the alcyonacean genera *Lobophytum*, *Rythisma*, *Sarcophyton* and *Sinularia*, updating its host range and geographic distribution. The symbiosis prevalence was high in the area and especially in the inshore sites compared to the midshore and offshore ones. *Rythisma* was the most common host, while the association with *Lobophytum* showed the lowest taxon-specific prevalence. *Pteroclava krempfi* did not show a clear preference for a specific alcyonacean size and an increase in the host size led automatically to an increase of the surface occupied by hydrozoans, although they rarely colonized more than 50% of the host upper surface. The spatial distribution of the hydroids on the host surface appeared related to the hosts' genus and size as well as to the hydroids' coverage. Despite the nature of this symbiosis requiring further investigations, *P. krempfi* did not seem to play a role in affecting the bleaching susceptibilities of the host colonies. The study shows that the Red Sea coral reef symbioses are more widespread than previously known and therefore should deserve more attention.

KEYWORDS: hydroids, soft coral, association, *Rythisma*, prevalence, cross-shelf gradient

1. INTRODUCTION

Reef corals host a large range of animal species belonging to a multitude of phyla, which can live as endobionts in the coral skeleton or as epibionts on their surface, establishing interspecific associations and symbioses of various nature (Stella et al. 2010, 2011, Hoeksema & Fransen 2011, Hoeksema et al. 2012, 2017, Bos & Hoeksema 2015, Ivanenko et al. 2018, Rauch et al. 2019). Octocorals are considered the second most common group of macrobenthic animals on many shallow reefs, after the reef-building stony corals (Fabricius & Alderslade 2001, Williams & Cairns 2018, Benayahu et al. 2019). Together with stony corals, octocorals play a crucial role in coral reef communities, since they create three-dimensional structures that provide suitable habitat and shelter for other reef dwellers, contributing to increase the total reef biodiversity (Goh et al. 1999, Reijnen et al. 2010, Lau et al. 2019, Denis et al. 2019, Maggioni et al. 2020a).

Among the coral-associated organisms, several hydroid taxa of the subclass Hydroidolina are involved in symbiotic relationships with their host corals (Gili & Hughes 1995, Puce et al. 2002, 2008a, Boero & Bouillon 2005, Pantos & Bythell 2010). To date, the symbioses between hydroids and anthozoans involve six hydrozoan families (Asyncorynidae, Cladocorynidae, Corynidae, Zancleidae, Ptilocodiidae and Tubulariidae), which generally show limited substrate preferences and a high degree of host-specificity (Boero 1980, 1984, Puce et al. 2008a, b). In particular, 13 nominal species of hydrozoans are currently known to live in association with at least 22 species of octocorals (Bo et al. 2011, Maggioni et al. 2016), while 61 scleractinian species belonging to 31 genera and 9 families have been confirmed as hosts (Montano et al. 2015a, b, Bonito et al. 2019), even if the information on scleractinian-associated hydrozoans is constantly updated (e.g. Manca et al. 2019, Maggioni et al. 2020b). In this context, most of the efforts have focused on hydroids of the genus *Zancklea* (family Zancleidae), whose patterns of host-specificity, distribution, ecology and evolution of the interactions with reef-building corals and other hosts have been thoroughly investigated (Boero et al. 2000, Pantos & Bythell 2010, Hirose & Hirose 2011, Pantos & Hoegh-Guldberg 2011, Fontana

1 et al. 2012, Montano et al. 2013, 2014, Maggioni et al. 2017a 2018, 2020c). In contrast, the symbiotic
2 relationship between hydroids and octocorals has received less attention.

3 Among these hydrozoans, *Pteroclava krempfi* (Billard, 1919) (family Cladocorynidae) appears to be
4 an obligate symbiont of alcyonaceans, associated with eight genera belonging to 3 families, namely,
5 *Cladiella*, *Lobophytum*, *Sarcophyton*, *Sinularia* (Alcyoniidae), *Astrogorgia*, *Paraplexaura*,
6 *Plexaurella* (Plexauridae) and *Antillogorgia* (Gorgoniidae). In addition, *P. krempfi* shows a
7 circumtropical distribution, since it has been observed in reefs of the Indo-West Pacific (Indonesia,
8 Japan, La Reunion, Maldives, Papua New Guinea, Vietnam) including the Red Sea (Egypt, Israel),
9 as well as in the Caribbean (Cuba, Panama, St. Eustatius), (Billard 1919, Hirohito 1988, Boero et al.
10 1995, Puce et al. 2008b, Varela & Caballero 2010, Seveso et al. 2016, Montano et al. 2016, 2017a,
11 Miglietta et al. 2018). *Pteroclava krempfi* colonies arise from the alcyonacean surface and show a
12 perisarc-covered hydrorhiza embedded in the host coenenchym, elongated hydranths about 1 mm
13 high, moniliform tentacles and eurytele patches in the polyp body walls (Boero et al. 1995, Bouillon
14 et al. 2006, Seveso et al. 2016). In addition, recent phylogenetic analyses demonstrated a host-related
15 cryptic genetic diversification for *P. krempfi*, which appears to be a species complex (Maggioni et al.
16 2016, Montano et al. 2017b). However, little information is still available regarding the ecological
17 aspects of the symbiosis between *P. krempfi* and their hosts (Montano et al. 2016).

18 The Red Sea is a hotspot for marine biodiversity, with a high level of endemism and with new species
19 continuously being discovered and described (Hughes et al. 2002, Roberts et al. 2002, Terraneo et al.
20 2014, Arrigoni et al. 2016, DiBattista et al. 2016, Prudkovsky et al. 2016, 2017, Conradi et al. 2018).
21 Approximately 160 hydrozoans species are currently known from the Red Sea (Prudkovsky et al.
22 2016, 2017, Pica et al. 2017), but a limited number of taxonomical accounts is available for this
23 region, especially for hydrozoans living in association with corals (Montano et al. 2014, Pica et al.
24 2017, Maggioni et al. 2017a). Furthermore, the ecology of the Red Sea reefs remains relatively
25 understudied in comparison to other biogeographical regions (Berumen et al. 2013). In particular,
26 comparatively little information is available from the central and southern Red Sea, although these

1 areas show the greatest reef concentration and the highest abundance and diversity of stony and soft
2 corals (Sheppard et al. 1992, Benayahu et al. 2002, Haverkort-Yeh et al. 2013).

3 In this study, the association between *P. krempfi* and alcyonacean hosts is analyzed for the first time
4 in reefs along the central Red Sea coast, near Thuwal (Saudi Arabia) in order to provide new
5 ecological details on this poorly investigated relationship. To this end, we determined the prevalence
6 and host range of the symbiosis to test for differences in its taxon-specific prevalence and habitat
7 preference in terms of reef type and depth. In addition, we took advantage of the occurrence of a coral
8 bleaching event to assess the hypothesis that *P. krempfi* may play a role in affecting the bleaching
9 susceptibility of its hosts, as previously suggested for other coral-associated hydrozoans (Pantos &
10 Bythell 2010, Montano et al. 2017b). Finally, we determined whether *P. krempfi* showed a preference
11 for a specific host size and we analyzed the abundance and distribution of the hydroids on the host
12 surface to test whether all these factors were related.

14 2. MATERIALS AND METHODS

16 2.1. Study area and sampling design

18 The sampling activities were carried out in reefs of the central Red Sea near Thuwal, a small town
19 approximately 90 km north of Jeddah (Saudi Arabian Red Sea coast), on November/December 2015.
20 In this region, a series of reefs 100–300 m wide and several km long surrounded by smaller patches
21 and pinnacles are aligned parallel to the shore on a North-South axis and extend up to 20 km offshore,
22 giving rise to cross-shelf environmental gradients (Pineda et al. 2013, Roik et al. 2016, Khalil et al.
23 2017). In total, nine sites were selected haphazardly among those accessible and were surveyed by
24 SCUBA diving. They were located in three different zones varying in distance from the shore along
25 a cross-shelf gradient off the coast, and they were characterized by different exposure and

1 environmental conditions: three offshore sites, placed in a zone ~ 15–20 km far from the coast, a zone
2 with three midshore sites (~ 8–9 km) and a zone consisting of three inshore sites (~ 2–4 km), (Fig.
3 1).

4 For each site, an extensive pre-survey was conducted to detect the occurrence of *Pteroclava krempfi*
5 on different alcyonacean genera (family Alcyoniidae), focusing on those previously reported to host
6 the hydroid (Seveso et al. 2016, Montano et al. 2016). Only the alcyonacean genera found as hosts
7 were considered and sampled for the following analyses. Three 50 × 2 m belt transects (100 m² each)
8 spaced 10 to 20 m apart and placed at two different depth ranges (0-10 m and 11-20 m) were randomly
9 laid at each site to obtain the overall and taxon-specific prevalence of the association. Furthermore,
10 since the study was conducted a few months after the beginning of a coral bleaching event (Monroe
11 et al. 2018, Seveso et al. 2020), all alcyonacean colonies in the transects (either hosting hydrozoans
12 or not) were classified as “healthy” or “bleached” using a color reference card (coral watch color
13 card, Siebeck et al. 2006, Montano et al. 2010). Specifically, colonies showing tissues and polyps
14 strikingly pale corresponding to color categories 1–2 of the reference card were defined as bleached
15 (Anthony & Kerswell 2007, Richardson et al. 2020, Seveso et al. 2020).

16 In addition, the preference of *P. krempfi* for specific host-size classes, the abundance of the hydroids
17 colonizing the host surface and their spatial distribution on the alcyonacean tissue, were also
18 collected. In this regard, for each alcyonacean colony found within transects, the size was determined
19 as the longest colony disk diameter using calipers and measurement tape. Measurements were made
20 to the nearest cm, after touching the colonies to cause contraction (as described in Fabricius 1995,
21 Hellström & Benzie 2011). Soft coral colonies were then grouped in 4 size classes: ≤ 5 cm, 6-10 cm,
22 11-15 cm and > 15 cm. Moreover, the abundance of the hydroids, when present, on their hosts, was
23 estimated by determining the percentage of coral surface covered by hydroids. In particular, the
24 surface area of the octocorals was divided into 4 quadrants in order to determine 3 different coverage
25 % categories: ≤ 25%, 26-50% and > 50%. Finally, the spatial distribution of hydroids over the host
26 surface was qualitatively evaluated, and scored as “clustered”, if the hydroid polyps formed one or

multiple groups, or “dispersed”, when *P. krempfi* polyps were randomly dispersed over the octocoral surface, without creating defined and clear groups.

2.2. Data analysis

2.2.1. Prevalence, host range and habitat preference of the symbiosis

For each transect, the prevalence of the association was calculated as the ratio between the number of alcyonacean colonies hosting *P. krempfi* and the total number of alcyonacean colonies. By averaging the corresponding prevalence values measured on the three random belt transects for each site, both an overall and a series of taxon (host genus)-specific prevalence values were determined.

To examine the habitat preference of the symbiosis, differences in the overall prevalence of the *P. krempfi* – alcyonacean symbiosis among reef types and depths were analyzed with a two-way ANOVA, using the distance from the shore (inshore, midshore and offshore) and depth (0-10 m and 11-20 m) as factors. Tukey’s honestly significant difference (HSD) post hoc tests for multiple pairwise comparisons of means were performed to assess significant differences in the overall prevalence of the association. The prevalence of the symbiosis was compared among the different host genera and, for each genus, among the different reef types, using the Kruskal-Wallis test followed by multiple pair-wise comparisons, because the data did not meet the assumption of normality (Zar 1999). Similarities among sites based on the taxon-specific prevalence values were illustrated using a non-metric multidimensional scaling plot (nMDS), performed using Primer v7 (Primer-E Ltd., Plymouth, UK). nMDS was done using normalized Euclidean distance, without transformation.

To examine a possible role of *P. krempfi* in affecting the bleaching susceptibility of the host, the taxon-specific prevalence of the symbiosis in bleached and healthy colonies was calculated and compared. Differences in the % of bleached alcyonacean colonies between reef types and depths were

analyzed with a two-way ANOVA, using the distance from the shoreline (inshore, midshore and offshore) and depth (0-10 m and 11-20 m) as factors. Tukey's HSD post hoc tests for multiple pairwise comparisons of means were performed to assess significant differences.

2.2.2. Characteristics of the *P. krempfi*-host association

Hydroids' preference for different alcyonacean size classes (≤ 5 cm, 6-10 cm, 11-15 cm and > 15 cm) was determined analyzing all the alcyonacean genera together, with two indices usually employing to assess the organisms' feeding behaviour and preferences (Saponari et al. 2018, Montalbetti et al. 2019): the Standardized Forage Ratio (S_i) (Chesson 1983) and the Ivlev's electivity index (E_i) (Ivlev 1961). The Standardized Forage Ratio is 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, in this rearranged version of the index, P_i is the relative abundance (%) of the host size classes in the environment, r_i is the relative abundance (%) of the size classes of the hosts in symbiosis with *P. krempfi* and n is defined as the number of groups in the system. The values of the standardized forage ratio range between 0 and 1, with $S_i = 0$ indicating avoidance and $S_i = 1$ indicating exclusiveness for a size class.

The Ivlev's Electivity index 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 range between -1 and 1, with $E_i = -1$ representing total avoidance, $E_i = 0$ non-selectivity and $E_i = 1$ exclusive choice of a given alcyonacean size class.

A Kruskal-Wallis test followed by multiple pair-wise comparisons was performed in order to detect significant differences in the coverage percentages of hydroids on the surface of the soft corals. The

Spearman's rank correlation order test was used to determine whether the coverage % of hydroids on the host surface was correlated to the size of the host.

Finally, a binomial logistic regression was performed to analyze the relationship between the size of the soft coral, the coverage of hydroids on the host surface, the alcyonacean health status (healthy or bleached) and the spatial distribution of *P. krempfi* on the host surface. Linearity of the continuous variables with respect to the logit of the dependent variable was assessed via the Box & Tidwell (1962) procedure, applying a Bonferroni correction for statistical significance (Tabachnick & Fidell 2014). Based on this assessment, all continuous independent variables were found to be linearly related to the logit of the dependent variable.

All the statistical analyses were performed using SPSS ver. 24 (IBM, New York). Statistical significance was defined as $p < 0.05$ and all data are presented as arithmetic means $\pm$ standard error (SE) unless stated otherwise.

3. RESULTS

3.1. Prevalence, host range and habitat preference of the symbiosis

Four alcyonacean genera were found in association with *Pteroclava krempfi*: *Lobophytum*, *Rhytisma*, *Sarcophyton* and *Sinularia* (Fig. 2). In total, 1122 colonies belonging to these genera were sampled and the overall prevalence of the symbiosis was $20.3\% \pm 4$.

Significant differences in the overall prevalence of the *P. krempfi*-alcyonaceans symbiosis were detected depending on the distance of the sites from the shoreline (Table 1), with inshore sites displaying a significantly higher overall prevalence compared with the midshore and offshore ones (Fig. 3a). The prevalence of the symbiosis was not affected neither by depth (21.1% at 0-10 m deep; 19.5% at 11-20 m deep), nor by the combination of depth and distance offshore (Fig. 3b and Table 1). In the whole study area, at genus level, *Rhytisma* showed the highest symbiosis prevalence,

followed by *Sinularia* and *Sarcophyton*, even if no statistically significant differences were found among them (Kruskal-Wallis test, $p \geq 0.05$, Fig. 4a). Instead, *Lobophytum* displayed a prevalence significantly lower than that of the other alcyonacean genera (Kruskal-Wallis test, $p < 0.05$, Fig. 4a). *Lobophytum* was also the only genus showing a higher symbiosis prevalence in offshore sites, whereas for the other genera the relationship was more prevalent at inshore sites; for *Sinularia* and *Rhytisma* the prevalence differences among the three reef zones across the shelf were significant (Kruskal-Wallis test, $p < 0.01$, Fig. 4b and 5).

Signs of bleaching were detected in $8.3\% \pm 2.4$ of the sampled colonies ($n=1122$) and the percentage of bleached colonies was higher at depths < 10 m and in inshore sites (Fig. S1, Supplementary materials), although no significant differences were detected depending on the distance of the sites from the shoreline, the depth, and the combination of these factors (Table S1, Supplementary materials). Only *Sinularia* and *Sarcophyton* were affected by bleaching (Fig. S1) and the prevalence of the symbiosis in their healthy and bleached colonies was similar (Fig. 6).

3.2. Characteristics of the *P. krempfi*-host association

Most of the alcyonacean colonies had a diameter of 6-10 cm, followed by those with size ≤ 5 cm, size between 11-15 cm and size > 15 cm (Table 2a). A similar abundance pattern was also observed for the symbiosis prevalence for each size class (Table 2a). However, the S_i and E_i indices allowed to compare the abundance of the size classes with that of the colonies hosting the hydrozoans. The values obtained for both these indices are comparable, showing the same trend. In fact, the E_i values for the size classes 6-10 cm and 11-15 cm were very close to zero (0.137 and 0.017, respectively) meaning a low selectivity. This is also confirmed by the intermediate S_i values (0.389 and 0.306, respectively), (Table 2b). On the other hand, the values for the class size ≤ 5 cm indicated a slight avoidance ($E_i=0.146$ and $S_i=0.220$) and those of the size class > 15 cm revealed a clear avoidance ($E_i=-0.554$ and $S_i=0.075$) (Table 2b).

1 Most of the host colonies had 26 to 50% or less than 25% of their surface occupied by *P. krempfi*,
 2 whereas colonies showing more than 50% of their surface covered by hydrozoans were significantly
 3 fewer (Kruskal-Wallis test, $p < 0.01$, Fig. 7a). This coverage pattern was observed for all the
 4 alcyonacean genera investigated (Fig. S2). An overall slight but significant positive correlation was
 5 found between the size of the hosts and the surface occupied by hydrozoans (Spearman's rho, $\rho =$
 6 0.206 , $p < 0.01$). At the genus level, this positive correlation was observed only for *Rhytisma* and
 7 *Sinularia* (Spearman's rho, $\rho = 0.309$, $p < 0.05$ and $\rho = 0.249$, $p < 0.01$ respectively; for *Sarcophyton*
 8 and *Lobophytum* no significant correlation was detected).
 9 The spatial distribution of *P. krempfi* on the host surface appeared to be mostly "clustered" in
 10 *Rhytisma* and "dispersed" in *Lobophytum*, whereas *Sinularia* and *Sarcophyton* did not show a
 11 prevailing type of distribution (Fig. 7b). Overall, the hydroid spatial distribution appeared almost
 12 equally divided between "clustered" ($53.5\% \pm 9.6$) and "dispersed" ($46.5\% \pm 9.8$). The logistic
 13 regression model suggested that the spatial distribution of hydroids was significantly affected by the
 14 host size and the host surface occupied by the hydroids (Table 3). Specifically, an increase in the host
 15 size and hydroid coverage was associated with an increased likelihood of exhibiting a dispersed
 16 spatial distribution of *P. krempfi* (Table 3).

17

18 4. DISCUSSION

19

20 Alcyonacean soft corals are among the most common members of many coral reef habitats, including
 21 the Red Sea (Benayahu & Loya 1981, Stobart et al. 2005, Haverkort-Yeh et al. 2013, Lau et al. 2019).
 22 Nevertheless, although information on the ecology of soft corals is increasing (Edmunds et al. 2016),
 23 very few studies have examined the distribution patterns of their associated species. Our study
 24 explored the ecology of the poorly studied but relatively abundant interaction between *Pteroclava*
 25 *krempfi* and alcyonaceans.

1 On the reefs of the Saudi Arabian central Red Sea, *P. krempfi* was observed in symbiosis with four
2 alcyonacean genera (*Lobophytum*, *Rhytisma*, *Sarcophyton*, and *Sinularia*), all belonging to the
3 family Alcyoniidae, and the association was recorded in all of the nine explored sites and in both
4 depth ranges considered. However, it is important to point out that, considering the high species
5 diversity of these alcyonacean genera, we cannot exclude that different species within each taxa may
6 have been analyzed.

7 Our results indicate that the symbiosis appeared to be very abundant in the study area. In the Maldives
8 the association involved only three alcyonacean genera (*Lobophytum*, *Sarcophyton* and *Sinularia*),
9 and was not observed in all of the investigated sites, showing a much lower overall prevalence of
10 only 6.4% (Montano et al. 2016). Nevertheless, a real comparison between the prevalence obtained
11 in the two studies does not appear reliable, since in the two areas, which are characterized by diverse
12 habitat structure and ecological traits, different alcyonacean species may have been sampled.
13 Moreover, the genus *Rythisma* has never been observed in the Maldives and this may have contributed
14 to the lower symbiosis prevalence found in this area.

15 The *P. krempfi* host range was updated with an additional genus, *Rhytisma*, raising the number of
16 host genera worldwide to nine. Furthermore, the geographic distribution of the association was
17 extended to the central Red Sea, contributing to increase the ecological and biodiversity value of this
18 little studied area, and the reports of benthic symbiotic hydrozoans (Maggioni et al 2017a, b, 2018).
19 Given the high diversity and abundance of alcyonaceans in the Red Sea, and especially in its central
20 region (Fabricius & Alderslade 2001, Benayahu et al. 2002, Haverkort-Yeh et al. 2013), it remains
21 unclear why other octocoral taxa, including other alcyoniid genera, have not been recorded as *P.*
22 *krempfi* hosts. In this regard, the maximum sampling depth of this study, set at 20 m deep, may have
23 been a limiting factor, considering that some *Pteroclava* records were observed at even greater depths
24 (Maggioni et al. 2016) and that the Red Sea possesses rich mesophotic octocoral communities
25 (Shoham & Benayahu 2017, Benayahu et al. 2019). Furthermore, small organisms, such as *P. krempfi*,

1 may be easily overlooked in the field because of their size (0.5–2 mm) (e.g. Giorgi et al. 2016,
2 Montano et al. 2017a).

3 A progressive increase in the prevalence of the *P. krempfi*-alcyonaceans symbiosis was observed with
4 decreasing distance from the coast, with inshore sites showing the highest prevalence. This appears
5 significant considering that the number of colonies sampled in inshore sites was considerably lower
6 than that of the midshore and offshore sites. In addition, a cross-shelf gradient of biodiversity and
7 coverage of benthic communities was previously observed in these reefs, with offshore and midshore
8 communities relatively richer and more homogenous than inshore communities (Ellis et al. 2017,
9 Khalil et al. 2017). The same pattern is generally observed in other geographical areas and reef
10 systems (Clearly et al. 2005, 2016, Hoeksema 2012, Waheed & Hoeksema 2014), although in some
11 cases wave energy can partially reverse it (Waheed & Hoeksema 2013). The highest symbiosis
12 prevalence in inshore reefs contrasts to previous observations in the Maldives, where the prevalence
13 was highest in the outer reefs (Montano et al 2016). Both soft corals and hydrozoans are suspension
14 feeders and their access to food mostly rely on moderately strong currents for maximum food
15 encounters, which are typically found in an exposed habitat (Dinesen 1983, Gili & Hughes 1995, Gili
16 & Coma 1998, Fabricius & Alderslade 2001). Furthermore, hydroids rely on moving water for the
17 supply of dissolved gases, dispersal of waste products, medusae, larvae, and to prevent the sediment
18 accumulation (Boero 1984). In the study area, inshore reefs are subjected to an annual average current
19 speed slightly lower than that of mid- and offshore reefs. This implies a reduced water mixing close
20 to shore, resulting in higher salinity, chlorophyll-a concentration and turbidity compared to midshore
21 and offshore reefs (Roik et al. 2016). These environmental conditions could play a role in promoting
22 the symbiosis. For example, turbidity is a proxy for suspended particulates in the water column, which
23 are used as source of nutrition by heterotrophic biota (Anthony & Fabricius 2000) and a high turbidity
24 may therefore reflect a food rich environment. In addition, mid- and offshore sites, being fully
25 exposed to the open sea, are likely to receive cooler water input through upwelling (Davis et al. 2011)
26 and are often subjected to very strong currents, which in offshore reefs can reach maxima of 0.3 m/s

1 (over all reefs, current speeds mostly ranged between 0 and 0.1 m/s, Roik et al 2016). It is known that
2 too strong currents may negatively affect the hydroids feeding efficiency, since potential preys may
3 escape, and that hydroids are expected to be more numerous in areas where the water movement is
4 sufficient but not violent enough to cause damage (Gili & Hughes 1995).

5 Among the octocoral hosts, the prevalence of the symbiosis was highest for *Rhytisma* and lowest for
6 *Lobophytum*, oppositely to what observed in the Maldives where *Lobophytum* was the genus most
7 frequently associated with *P. krempfi* (Montano et al. 2016). However, as previously highlighted, we
8 cannot exclude that different *Lobophytum* species may have been sampled in the two different
9 geographic location. In addition to the host abundance in the area, the morphology of the soft coral
10 polyps and tissues have been suggested to play a role in the selection of suitable substrates for the
11 settlement of hydrozoans (Montano et al. 2016). In this context, *Rhytisma* colonies are thin-encrusting
12 mats or ribbons of irregular shape, about 2-4 mm thick, which overgrow the substrate (Fabricius &
13 Alderslade 2001), and thus they may provide an almost flat and smooth tissue surface on which the
14 hydrozoan polyps can easily settle. Also *Lobophytum* colonies often show an encrusting morphology,
15 with a flat upper surface devoid of lobes and ridges (Fabricius & Alderslade 2001); however, despite
16 this, very few colonies were found in association with *P. krempfi*. The genus *Sinularia* showed a high
17 symbiosis prevalence, comparable to that of *Rhytisma*, despite being characterized by completely
18 different colony morphologies. Therefore, a clear pattern of symbiosis prevalence related to the host
19 morphology is not identifiable, and a host-reliant relationship seem to be more likely (Montano et al.
20 2016). Alternatively, the bioactive compounds and secondary metabolites produced by soft corals
21 and used for chemical communication in symbiotic relationships (Farak et al. 2017, Dokalahy et al.
22 2019) may also have a role in hydroids settlement. Soft corals also produce chemical compounds as
23 a defense mechanism from predation, competition for space or parasitism (Khalesi 2008, Farak et al.
24 2017, Dokalahy et al. 2019) and they could affect the establishment of the symbiosis too.

25 The ecological outcomes of the *P. krempfi*-alcyonaceans association are still not completely
26 elucidated. Previous reports suggested a trophic relationship since the polyps of *P. krempfi* appeared

1 to be denser at the base of the octocoral polyps and were observed touching the tentacles of the host,
2 similarly to what observed for numerous other symbiotic hydroids (Boero et al. 1995, Gili et al. 2006,
3 Puce et al. 2002, 2007, 2008a). A mutualistic relationship was also hypothesized, since the hydroid
4 may benefit from food provided by the increased water flow and protective mucus on the alcyonacean
5 surface and could in turn provide protection to their hosts (Montano et al. 2016), similarly to what
6 observed for Scleractinia-associated hydroids (Montano et al. 2017b). Montano et al. (2017b)
7 highlighted that the hydroids presence was associated with a reduction in coral susceptibility to
8 corallivory and diseases caused by pathogenic organisms, probably due to the hydroids' defense
9 specialized polyps ('dactylozooids') armed with venomous nematocysts. Additionally, hydroids could
10 remove detritus from the host surface. A possible role of coral-associated hydrozoans in affecting
11 host susceptibility to bleaching has also been previously discussed (Pantos & Bythell 2010, Montano
12 et al. 2017b). In particular, the fact that *Zanclaea* hydrozoans were reported from corals subjected to
13 bleaching events has led to speculation that they might be detrimental to coral health, by increasing
14 the host bleaching susceptibility (Pantos & Bythell 2010). On the contrary, Montano et al. (2017b)
15 found that these hydrozoans tended to be less common than expected on bleached corals, suggesting
16 that the positive effects of hydroids on coral health (deter predators and diseases) may increase the
17 coral resistance and tolerance in areas subjected to nearly lethal bleaching intensity. In September
18 2015, the reefs of the study area were affected by a coral bleaching event (Monroe et al. 2018, Seveso
19 et al. 2020) and, contrary to what observed for scleractinian corals, a clear spatial and depth pattern
20 of bleaching was not detectable for the considered soft coral genera. Moreover, the symbiosis
21 prevalence in the bleached host colonies was similar to that recorded in the healthy ones. This may
22 indicate that *P. krempfi* hydroids had no effect on the susceptibility of their hosts to environmental
23 stresses causing bleaching and that they may receive the same benefits from the hosts regardless of
24 their health condition.

25 The hydroids' preference for specific host size classes and their abundance and spatial distribution
26 on the host surface have so far rarely been addressed for symbiotic hydrozoans. *Pteroclava krempfi*

1 did not show clear preference patterns for a specific alcyonacean class size. However, small
2 alcyonacean recruits (< 5 cm) were not particularly targeted by hydroids, possibly due to the limited
3 space available, but the same was observed also for the large colonies (> 15 cm), which seemed to be
4 generally avoided by hydrozoans despite having a larger available surface area. Alcyonaceans with
5 an intermediate size (6-15 cm) appeared to be slightly more selected by *P. krempfi*. Moreover, with
6 the increase of the host diameter, the surface covered by the hydrozoans also increased, although *P.*
7 *krempfi* rarely colonized more than half of the host upper surface. A clear general pattern of spatial
8 distribution of the hydroids on the host surface was not detected too, since they appeared to be
9 clustered or dispersed depending on the host genus. However, regardless of the host genus, *P. krempfi*
10 showed a clustered distribution on coral colonies with small size and low hydroid coverage, whereas
11 it had a dispersed distribution in colonies with large diameter and high hydroid coverage.
12 Nevertheless, it is necessary to underline that the distribution pattern of hydroids such as *P. krempfi*
13 on their hosts could also be affected by their complex life cycle, characterized by both sexual and
14 sexual reproduction (Bouillon et al. 2006).

15 This study represents the first report of the *P. krempfi*-alcyonacean association in the central Red Sea.
16 Overall, our findings suggest that this intimate relationship is more frequent and widespread than
17 previously known and provide new insights on its ecological significance and nature, increasing the
18 knowledge on coral reef symbioses. Moreover, they may represent the basis for future studies on the
19 ecology and biodiversity of Saudi Arabian reefs and alcyonaceans. Finally, our study could support
20 conservation decisions in this Red Sea region, as coastal development and climate change continue
21 to represent an important threat in this area and reef degradation might disrupt these symbiotic
22 relationships exacerbating the loss of biodiversity (Caley et al 2001).

23

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25

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TABLES (WITH LEGEND)

Table 1 - Two-way analysis of variance (ANOVA) of the overall prevalence of the *Pteroclava krempfi* – alcyonacean symbiosis among reef zones (inshore, midshore and offshore) and depths (0-10 m, 11-20 m). Significant values ($p < 0.05$) are in bold.

Factors	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Reef zone	2	1240.272	620.136	12.424	P < 0.0001
Depth	1	15.466	15.466	0.31	0.584
Reef zone x Depth	2	73.917	36.959	0.74	0.489
Residuals	21	1048.225	49.915		

Table 2 – A. Percentage of alcyonacean colonies belonging to each size class and percentage of colonies found in symbiosis with *P. krempfi* for each size class. **B.** Ivlev's index (Ei) and standardized forage ratio (Si) values indicating the preferences of *P. krempfi* for host colonies size classes.

	Size class (cm)			
	≤ 5	6-10	11-15	> 15
A				
Total colonies	29%	42%	20%	9%
Colonies in symbiosis with <i>P. krempfi</i>	22%	55%	21%	3%
B				
Index Ei	-0.146	0.137	0.017	-0.554
Index Si	0.220	0.389	0.306	0.075

Table 3 - Binary logistic regression model to analyze the relationship between the spatial distribution of *P. krempfi* on the host surface (clustered and dispersed) depending on the size of the host, the coverage % of hydroids on the host surface and the host health status (healthy or bleached).

Source	B	S.E	Wald	d.f	P-value	Exp (B)
Size	0.064	0.031	4.371	1	0.036	1.066
Coverage %	0.036	0.009	17.22	1	0.002	1.036
Health status	- 0.15	0.564	0.071	1	0.789	0.86
Constant	- 1.737	0.413	17.686	1	0	0.176

FIGURES (WITH LEGENDS)

Fig. 1 - Map of the 9 reefs located off the coast of Thuwal, Saudi Arabia, in the central Red Sea in which the samplings were performed. Abbreviations are as follows: OF (offshore), MI (midshore) and IN (inshore). OF1: Shib Nazar N, OF2: Shib Nazar S, OF3: Abu Madafi, MI1: Al Fahal, MI2: Shaab Al-Sheek, MI3: Umm-Al-Kathel, IN1: Abu Shosha, IN2: Abu Gishaa, IN3: Tahla

Fig. 2 – *Pteroclava krempfi* polyps in association with alcyonacean colonies of the genera *Rythisma* (A, B) and *Sinularia* (C). *P. krempfi* polyp growing on the soft coral (D). Scale bars: 1 mm for A, B and C. 0.2 mm for D.

Fig. 3 – A. Box plots summarising the prevalence (%) of *P. krempfi*-alcyonaceans symbiosis in inshore, midshore and offshore reefs. Boxes show the first and third quartiles, whiskers show range values, and horizontal lines indicate median values. Numbers above each box plot indicate the total number of alcyonacean colonies (both with and without *P. krempfi*) per reef zone. Two-way ANOVA followed by Tukey’s HSD multiple pairwise comparisons was performed between the reef zone (* $p < 0.05$). **B.** Symbiosis prevalence (%) at the two depth ranges considered (0-10 m and 11-20 m) for each reef zone (inshore, midshore and offshore).

Fig. 4 – Prevalence (%) of *P. krempfi*-alcyonaceans symbiosis by genus in the whole study area (**A**) and in the inshore, midshore and offshore reefs (**B**). Kruskal-Wallis tests followed by multiple pairwise comparisons were performed and asterisks denote significant differences in the prevalence among host genera (A) and reef zones within each genus (B) ($p < 0.05$).

Fig. 5 – Non-metric multidimensional scaling plot (nMDS) showing the prevalence of *P. krempfi*-alcyonaceans symbiosis by site, with vectors (Pearson's correlations > 0.7) representing the variables that drive similarities among sites (*P. krempfi*-taxon-specific prevalence).

Fig. 6 – Star plot showing the mean prevalence (%) of the *P. krempfi* symbiosis with both healthy and bleached colonies of the genera *Sinularia* and *Sarcophyton*.

Fig. 7 – A. Abundance (%) of the alcyonacean colonies in symbiosis with *P. krempfi* based on the surface coverage (%) by the hydrozoans. A Kruskal-Wallis test followed by multiple pairwise comparisons was performed (* $p < 0.05$). **B.** Relative abundance (%) of alcyonacean colonies per genus showing a clustered or dispersed spatial distribution of *P. krempfi* polyps of their surface. Numbers above each bar indicate the total number of soft coral colonies per genus found in symbiosis with *P. krempfi*.

Supplementary Materials

Table S1 - Two-way analysis of variance (ANOVA) of the % of bleached alcyonacean colonies between reef zones (inshore, midshore and offshore) and depths (0-10 m, 11-20 m). Significant values ($p < 0.05$) are in bold.

Factors	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Reef zone	2	131.674	65.837	1.591	0.227
Depth	1	121.668	121.668	2.941	0.101
Reef zone x Depth	2	81.481	40.740	0.985	0,39
Residuals	21	868.850	41.374

Fig. S1 – Overall abundance (%) of bleached alcyonacean colonies belonging to the four considered genera in the three different reef zones (**A**), at the two depth ranges (**B**) and at different depths per reef zone (**C**). Abundance (%) of bleached colonies for each alcyonacean genus considered (**D**). Kruskal-Wallis tests followed by multiple pairwise comparisons were performed without detecting significant differences.

Fig. S2 - Abundance (%) of the alcyonacean colonies of the different genera in symbiosis with *P. krempfi* based on the surface coverage (%) by the hydroids. A Kruskal-Wallis test followed by multiple pairwise comparisons was performed for each genus. Asterisks denote significant differences between hydroid coverage categories ($p < 0.05$).