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Biodiversity of the community associated with *Pocillopora verrucosa* (Scleractinia: Pocilloporidae) in the Red Sea

T. A. Britayev[1] · V. A. Spiridonov[2] · Y. V. Deart[1] · M. El-Sherbiny[3,4]

Abstract The symbiotic community associated with a scleractinian coral *Pocillopora verrucosa* has been studied along the Red Sea coast of Saudi Arabia from Al Wajh to the entrance of the Gulf of Aqaba. Forty colonies have been sampled from 2- to 15-m depth in 2 areas, southern and northern. Thirty-six associated species were found, including 15 symbionts and 21 species with uncertain status (SUS). The number of recorded symbiotic species was close to the statistically expected value, while SUS were rare and did not reach the value expected from the Chao 2 model. Species number and abundance positively correlated with the colony volume. Mean abundance of all species and symbionts and the number of SUS per covariate colony volume were higher in the northern area than in the southern area. This may be related to a higher habitat diversity of the surrounding reefs and to the presence of colonies with partially dead tissues in the north.

These two factors have a weak impact on symbionts, but strongly affect SUS. The diversity of the pocilloporid-associated communities range from 36 to 127 species along the Indo-Pacific and Tropical East Pacific, with 9 to 19 of them being symbionts. The total species diversity varies owing to the SUS number, while the core of true symbionts includes much fewer species and is less variable. The diversity of *Pocillopora* symbionts in the Saudi Arabian coast (15 species) is among the highest for the studied areas in the Indo-Pacific.

Keywords Symbiotic community · Coral reefs · Pocilloporidae · Trapeziidae · Palaemonidae · Alpheidae · Indo-Pacific · Saudi Arabia

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✉ T. A. Britayev
   britayev@yandex.ru

✉ V. A. Spiridonov
   vspiridonov@ocean.ru

[1] A.N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russia

[2] P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow, Russia

[3] Faculty of Marine Science, King Abdulaziz University, Jeddah, Saudi Arabia

[4] Department of Marine Science, Faculty of Science, Suez Canal University, Ismailia 41522, Egypt

Introduction

Coral reef biodiversity is mainly associated with fish, corals, large mollusks and echinoderms, while a large amount of hidden biodiversity resides in the harder-to-see holes and crevices (Glynn and Enochs 2011; Goldberg 2013). The symbionts living on or in free-living hosts contribute significantly to this hidden biodiversity (Hoeksema et al. 2012, Molodtsova et al. 2016; Stella et al. 2011b).

All scleractinian corals harbor a great variety of associated symbionts. According to the latest review (Stella et al. 2011b), there are about 900 invertebrate species described as coral associates. However, most probably, this is just a small portion of their real diversity (Bouchet 2006). Many symbionts of Cnidaria are host-specific. For example, 69 out of 107 polychaetes (64.48%) are known from a single host species (Molodtsova et al. 2016), which lead them to be more vulnerable. Degradation of coral reefs leads to a change in the ratio of coral species and local extinctions of the most vulnerable

ones. This causes habitat losses for coral symbionts, changes in symbiotic community structure and, eventually, even local extinction of highly specialized species with one or limited range of hosts (Munday 2004; Stella et al. 2011a; Tsuchiya and Yonaha 1992). Taking into account the current situation of coral reefs worldwide, a comprehensive inventory of coral symbionts, with special attention to the host specific and rare species, is certainly required.

The most diverse symbiotic communities are associated with branching corals, mainly with acroporids and pocilloporids, which contribute significantly to the formation of a three-dimensional reef structure (Sheppard et al. 2009) and provide symbionts with well-protected microhabitats (Stella et al. 2011b). During recent decades, the fauna associated with the pocilloporid corals *Pocillopora damicornis* (Linnaeus, 1758), *P. verrucosa* (Ellis et Solander, 1768), *P. meandrina* Dana, 1846 and *Stylophora pistillata* Esper, 1797 have been described from different areas of the Indian and Pacific Oceans, from the eastern coast of Africa to the western coast of Central America, but mainly in the tropical West Pacific (e.g., Abele 1976; Abele and Patton 1976; Austin et al. 1980; Black and Prince 1983; Coles 1980; Edwards and Emberton 1980; Patton 1966; Stella et al. 2010, López-Pérez et al. 2016). However, only one paper reported on the fauna associated with a pocilloporid coral in the Red Sea (Edwards and Emberton 1980).

Species composition and species richness of pocilloporid-associated communities greatly varies from area to area without marked latitudinal gradient; the number of species can vary as much between geographically adjacent samples as between extremely separated ones (Black and Prince 1983), probably because these differences are more related to the respective environmental conditions than to the hosts' characteristics (Abele 1976). This variability mainly concerns facultative symbionts and occasional coral associates, while obligate symbionts are much less variable. If so, the differences between sites may simply reflect the species composition and microhabitat diversity of the surrounding reef (Black and Prince 1983).

The aim of this paper is to document the species composition and structure of the community associated with the scleractinian coral *P. verrucosa* (so far, the only species of the *P. damicornis* complex recorded with certainty for the Red Sea; Schmidt-Roach et al. 2014), along the north-west coast of Saudi Arabia. These results are compared with the known data on pocilloporid-associated communities from other tropical areas. Additionally, we have tested the Black and Prince (1983) hypothesis, which postulates that the variability of symbiotic communities mainly concerns facultative symbionts, which simply mirrors the differences in species and habitat diversity of the surrounding reef, while the symbiotic community core consisting of obligate symbionts is more conservative.

Material and methods

Sampling areas

Samples were collected during an expedition to Saudi Arabia, framed within the Red Sea Biodiversity Survey (http://redseabiodiversity.senckenberg.de/; Fig. 1; Electronic Supplement 1), and the respective specific habitat types have been described according to Bruckner et al. (2012). The southern area, located to the north of Al-Wajh Bank, has been sampled to the south (stations 1 and 12) and facing [station 4 (6)] the city of Al-Wajh. Station 1 was characterized by a shallow, relatively exposed fringing reef seaward of a 50–100-m wide reef flat (Fig. 2a) that has inside numerous canals and one lagoon adjacent to a small southern peninsula. There was a moderate reef slope with a 70 to 100% coverage of living stony corals and, occasionally, columnar structures built by *Porites*. The reef slope extended to a 4–5-m depth and was followed by a shallow sand sheet (Fig. 3a, b). The colonies of *Pocillopora* occurred both in groups and isolated, the latter mostly in the median part, near the reef foot (Fig. 4a, b). Station 12 was located in the southern side of the mentioned small peninsula, in a less exposed conditions, and was characterized by a ca. 50–70-m wide reef flat with a low coverage of living coral colonies, followed by a fringing reef extending to about 5-m depth and having a significant coverage of dead coral colonies and mostly isolated living colonies (coverage 30–40%; Fig. 3c). From 6 to 8 m depth, there was a sandy and rubble bottom with patchy residual died reefs at depth. Isolated colonies of *Pocillopora* were collected at the median and lower reef slope (Fig. 4c, d). Station 4(6) was well exposed, with a relatively narrow (about 30 m depth) reef flat and a reef wall falling to 26 m depth, followed by a gently sloping sandy bottom with patches of coral limestone and isolated living colonies or coral rubble. The reef slope was almost entirely (90–100%) covered by a high diversity of living coral colonies (Fig. 3d), but those of *Pocillopora* were most common (and, thus, sampled) in the median reef slope (13–15 m; Fig. 2c, d).

The northern area, located near the entrance to the Gulf of Aqaba, was represented by two localities: Duba, with station 29 to the south and station 21 (3) facing the city (Fig. 2b); and stations 22 and 33 located to the north (Fig. 1; Electronic supplement). The Duba reefs were within protected inlets. At station 29, the reef was characterized by rocky points interspersed within a moderately broad (about 100 m) reef flat showing a relatively deep depression and an elevated leeward coral crest covered with living corals. The fringing reef had a moderate slope with marked ledges. The colonies of *Pocillopora* were sampled at 6–8-m depths (Fig. 3e), from the upper margin to the reef terraces, where living coral colonies showed 90–100% coverage (Table 1; Fig. 4e, f). The reef foot was at ca. 20-m depth

Fig. 1 Map of the study area with indication of station numbers
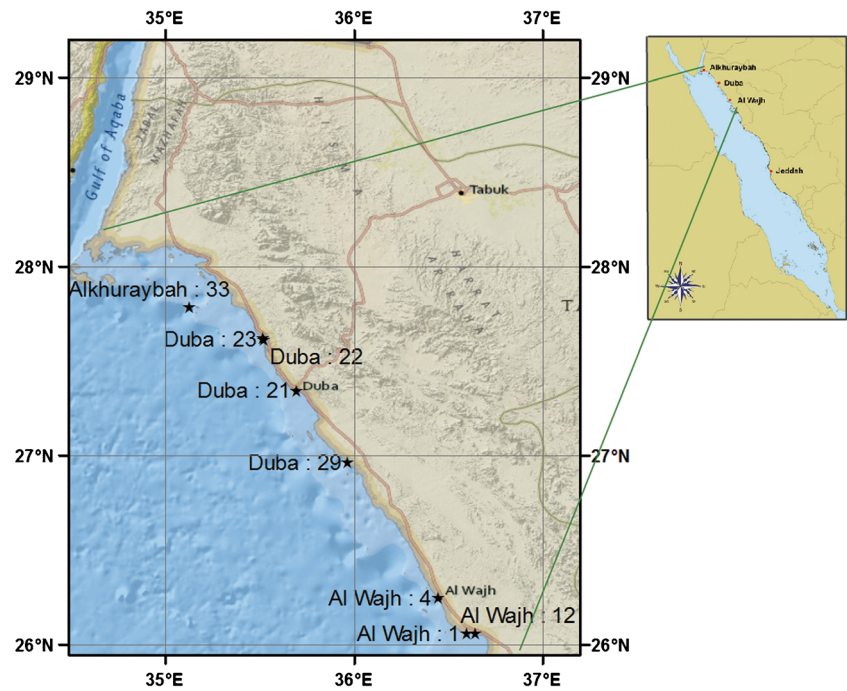
and showed a continuum of sparse corals, rubble and sandy bottom. Station 21 (3) was sampled inside an inlet having an extensive reef flat and a fringing reef similar to that of station 29 (Fig. 2b). Station 22 was located in a relatively exposed continental coast emarginated by a narrow reef flat and a terraced fringing reef extending to 16–17-m depth, with a significant coverage of dead coral colonies, coral limestone and alcyonarians (Fig. 3f, h). Isolated colonies of *Pocillopora* occurred at different depths (Fig. 4g), but the coverage was higher below 10-m depth. Station 33 was in

Fig. 2 Sampling conditions and procedures. **a**: A broad and shallow walkable reef flat and a shallow fringing reef where shore diving was undertaken (station 1); **b**: a deepened reef flat with complex topography and a steep relatively deep fringing reef where boat diving was undertaken (station 21 (3) in Duba); **c**: preparation for sampling of the colony # 23, station 4 (6); **d**: sampling of the colony # 25, station 4 (6). Photo: V. Spiridonov
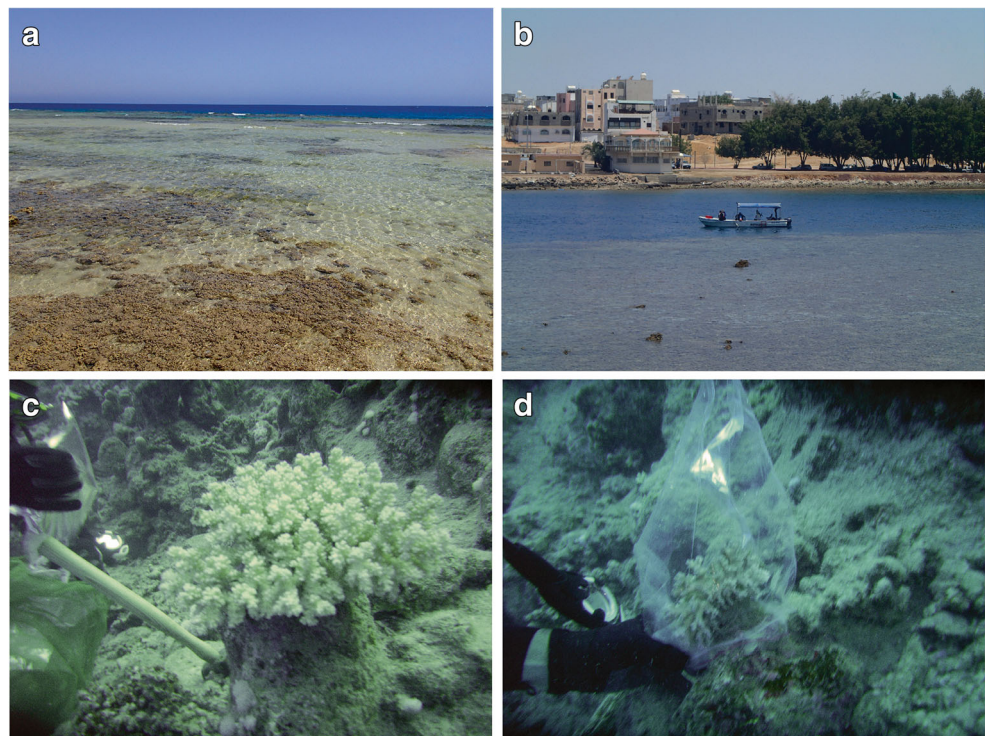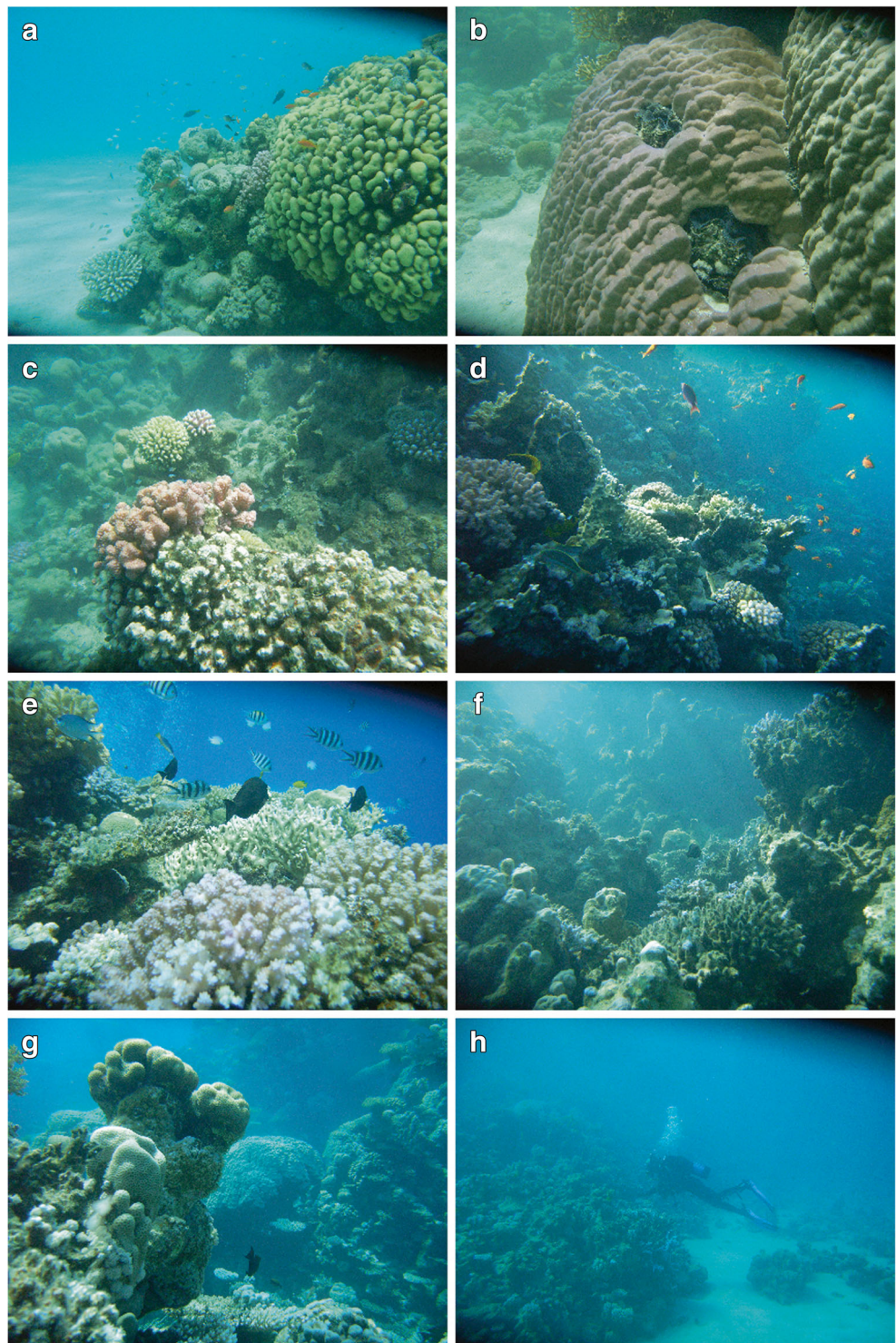
Fig. 3 Images of sampled reef landscapes. **a**: shallow fringing reef at station 1; **b**: same as A; **c**: reef at station 12; **d**: steep fringing reef in Al-Wajh, station 4 (6); **e**: terraced fringing reef relatively protected at station 29, south of Duba; F: terraced fringing reef at station 22; **g**: complex insular reef at station 33; **h**: same reef as F, foot of the reef. Photo: V. Spiridonov


the northern end of a reef bordering a small island, which showed structurally complex construction with scoured channels and a high diversity of coral colonies (Fig. 3h) that extended towards the fringing reef of the larger neighboring island. The colonies of *Pocillopora* occurred at different depths (Table 1), both isolated (Fig. 4h) and in groups.

Sample collection and processing

The colonies of *Pocillopora* were collected by SCUBA diving, either from the shore (Fig. 2a) or from a boat (Fig. 2b), depending on the reef accessibility. Entire individual coral colonies were covered with a fine mesh net to prevent animals

Fig. 4 Underwater images of selected sampled *Pocillopora verrucosa* colonies. **a**: colony # 6, station 1; **b**: colony # 7, station 1; **c**: colony # 15, station 12 (2); **d**: colony # 20, station 12 (2); **e**: colony # 32, station 29; **f**: colony # 33, station 29; **g**: colony # 29, station 22; **h**: colony # 39, station 33. Photo: V. Spiridonov
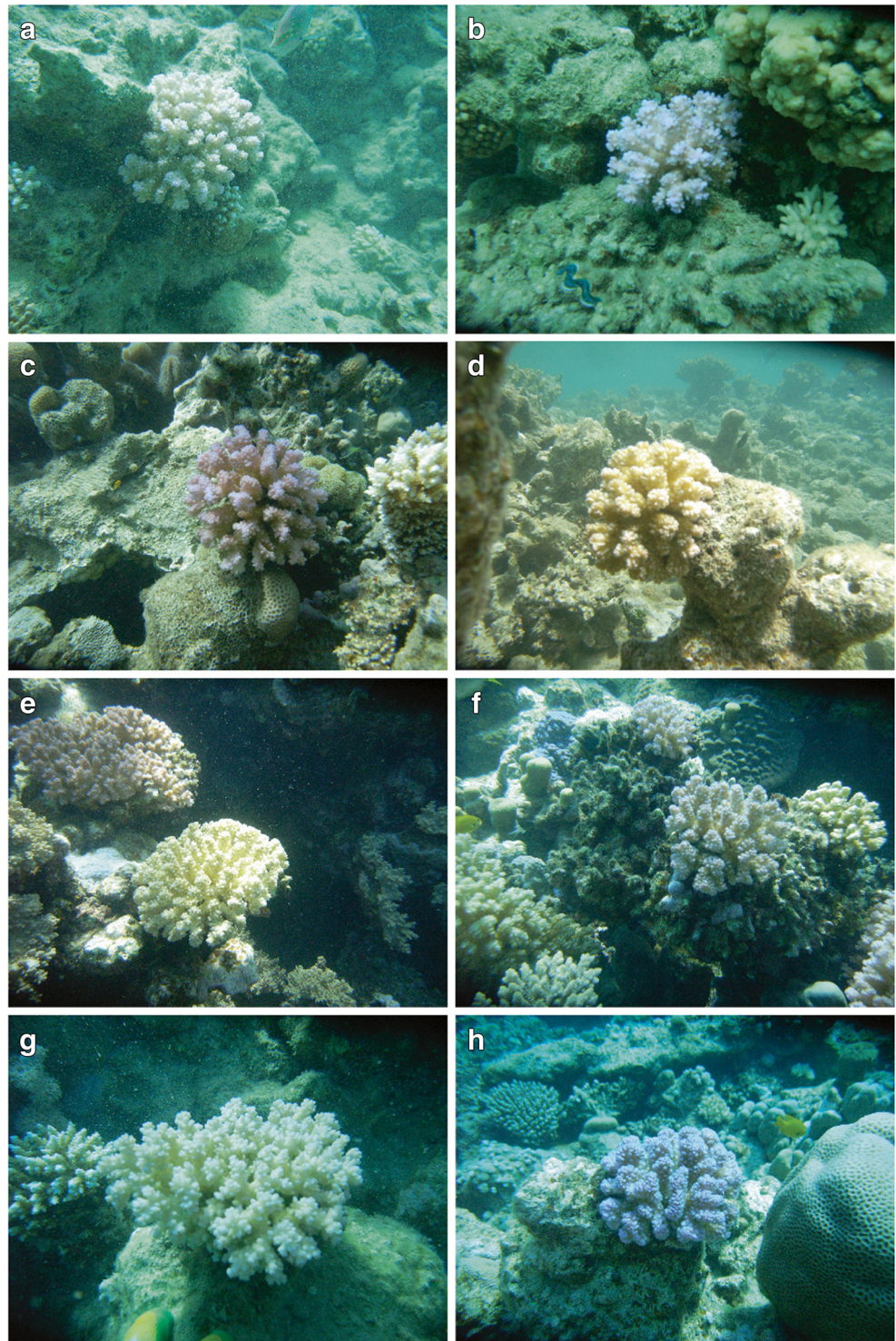
from escaping, carefully detached from the substrate (Fig. 2a, b), placed in individual buckets of fresh filtered seawater and immediately delivered to a temporal camp or a coastal laboratory. Each colony was photographed and the maximum and perpendicular diameters and the height were measured to determine the volume. Following that, each colony was submerged for 3 min into an emulsion of 0.5 ml of clove oil in 1000 ml of filtered seawater to anesthetize the associated fauna. Corals were then divided with a hammer into several fragments, which were carefully inspected to remove the associated animals visible to the naked eye, using blunt probes and forceps. Then, the colonies were intensively washed with

Table 1 Taxa associated with *Pocillopora verrucosa* in the northwest coast of the Saudi Arabian Red Sea. O: obligate symbiont; F: facultative symbiont; SUS: species of uncertain status

Taxa	Group	Prevalence (%)	Mean intensity (SD), ind./colony	Intensity range (min-max), ind./colony
Trapezia bidentata (Forskål, 1775)	O	82.5	3.0 (1.95)	1–10
Alpheus lottini Guérin-Méneville, 1838	O	72.5	1.83 (0.38)	1–2
Harpiliopsis depressa (Stimpson, 1860)	O	52.5	3.1 (6.42)	1–31
Periclimenes madreporae Bruce, 1969	O	52.5	4.0 (3.82)	1–13
Trapezia tigrina Eydoux et Souleyet, 1842	O	40	1.8 (0.75)	1–3
Trapezia digitalis Latreille, 1828	O	32.5	1.8 (0.44)	1–2
Trapezia guttata (Rüppell, 1830)	O	17.5	2.4 (3.78)	1–11
Trapezia cymodoce (Herbst, 1801)	O	10	1.75 (05)	1–2
Yemenicaris trullicauda Bruce, 1997	O	10	1.6 (0.89)	1–3
Hapalocarcinus marsupialis Stimpson, 1859	O	7.5	9.3 (13.58)	1–25
Harpilius cf. *consobrinus* De Man, 1902	O	5	1	1
Coralliophila sp.	O	5	1	1
Domecia hispida Eydoux et Souleyet, 1842	F	35	1.9 (2.20)	1–9
Palaemonella rotumana (Borradaile, 1898)	F	10	2.5 (0.58)	2–3
Calcinus sp.	F	7.5	1.7 (0.58)	1–2
Ophiocoma sp.	SUS	40	1.6 (0.89)	1–4
Alpheidae gen.sp. juv	SUS	17.5	1.8 (1.17)	1–4
Brachyura gen. spp. megalopae	SUS	12.5	1.4 (0.54)	1–2
Perinia tumida Dana, 1852	SUS	10	1.3 (0.58)	1–2
Galatheidae sp.1	SUS	7.5	2.3 (2.31)	1–5
Lophozozymus sp. juv	SUS	7.5	1.3	1–2
Actaea sp. juv	SUS	5	1	1
Chlorodiella sp. juv	SUS	5	1	1
Zozymoides sp. juv	SUS	2.5	1	1
Hyastenus sp. juv	SUS	2.5	1	1
Majoidea sp. 1 juv	SUS	2.5	1	1
Periclimenaeus arabicus (Calman, 1839)	SUS	2.5	1	1
Tanaidacea gen sp. 1	SUS	2.5	1	1
Cirripedia gen sp. 1	SUS	2.5	1	1
Priapulida gen sp. 1	SUS	2.5	1	1
Conus sp.	SUS	2.5	1	1
Nudibranchia gen sp. 1	SUS	2.5	1	1
Cidaridae gen sp. 1	SUS	2.5	1	1
Asteroidea gen sp. 1	SUS	2.5	1	1
Ophiuroidea gen sp. 1	SUS	2.5	1	1
Pseudocheilinus hexataenia (Bleeker, 1857)	SUS	2.5	1	1
Polychaeta gen spp.	SUS	62.5	4.2 (3.56)	1–11
Amphipoda gen spp.	SUS	35	3.3 (3.29)	1–12
Gastropoda gen spp.	SUS	17,5	1.8 (1.16)	1–4
Bivalvia gen spp.	SUS	5	1.5	1–2

the clove oil/seawater emulsion and the obtained water was poured through a 1 × 1-mm pore net to retain the washed off animals. Boring animals and, generally, those measuring less than 1 mm in length are not collected using this method. The coral fragments were carefully inspected again to maximize the detection of small cryptic macrofauna and then returned to the sea. Associated animals were also photographed and then preserved in 70% or 100% alcohol for further processing.

Identification and categorization of the species

Each individual animal was identified to the lowest possible taxonomic level based on specialized literature and with the assistance of taxonomic consultations. The Palaemonidae (except the easily recognizable *Harpiliopsis depressa* and *Palaemonella rotumana*) were identified by Dr. Zdenek Ďuriš (Ostrava University, Faculty of Science, Department of Biology and Ecology, Ostrava, Czech Republic; Ďuriš 2017). The associates with uncertain taxonomic status (i.e., polychaetes, amphipods, gastropods and bivalves) were identified at these high taxa levels and counted to provide lump abundances (i.e., number of individuals per colony; Table 1, 2S).

The identified material was deposited in the Senckenberg Museum (Senckenberg Biodiversity Centre), Frankfurt on Main, Germany (SMF) and in the King Abdulaziz University Marine Museum, Jeddah, Saudi Arabia (KAUMM). The material that was not identified to the species level has been stored in SMF in the crustacean, mollusk, polychaete and echinoderm sections, respectively.

All specimens associated with the colonies of *Pocillopora* were divided into three main groups: obligatory symbionts, facultative symbionts and species with uncertain status (SUS), according to the existing literature (Black and Prince 1983; Britayev and Mikheev 2013; Coles 1980; Patton 1966; Stella et al. 2011b; Ďuriš 2017). These three groups were used to compare the biodiversity, species richness, intensity and abundance, mean intensity and mean abundance of the coral associated communities. The terms were used with minor changes following Bush et al. (1997): prevalence (ratio between number of infested and total number of hosts); intensity (number of symbiont individuals in each infested host); mean intensity (mean number of individuals of a particular symbiotic species per infested host in a sample); abundance (number of symbiont individuals in each host, independent of whether the host is infected or not); mean abundance (mean number of symbionts per examined host, infested and non-infested); species richness (mean number of symbiotic species per infested host). The assemblage formed by all symbionts from the different species harbored by the same host individual is the infracommunity, while all infracommunities from a target host population are considered as the component community (Holmes and Price 1986).

Statistical analysis

The variability in species richness was assessed by cumulative abundance curves, as well as by the expected total number of species, based on the Chao2 bias correction for the occurrence of rare species (Chao 1987).

The volume of coral colonies was calculated using a formula: maximum diameter x perpendicular diameter x height of the colony. Each community associated with a given coral colony was characterized by: the species number [taxa not-identified to species level (see Table 1) were not counted if they occurred in several colonies, such as Polychaeta and Amphipoda, but a taxon was counted as one species if recorded in a single colony, such as Tanaidacea]; symbiotic species (obligate and facultative) per colony; abundance of all species (including taxa not identified to species level); and abundance of symbiotic species. Additionally, we estimated the Shannon diversity index and the Berger–Parker index of dominance (Magurran 2004) for each infracommunity, based on the abundance of species, but excluding the taxa not identified to species level (see Table 1).

Observed distributions of symbiont species and individual numbers per colony were significantly different from normal and better fitted the log-normal model (Shapiro–Wilk test, $p > 0.05$), so log-transformed data were employed for statistical tests.

To check how the coral head volume correlate with the abundance and the number of associated species in both areas, we have built regression lines and computed correlation coefficients for southern and northern areas separately (see Hammer 2009 and references therein). The regressions were compared for all species, symbionts and SUS. As abundance and diversity of associated species are related with the colony's volume, we compared the mean abundance and the number of species per colony in southern and northern areas using analysis of covariance (ANCOVA).

The structure of the communities associated with *Pocillopora* was assessed by non-metric multidimensional scaling (nMDS) based on the abundance of all recorded taxa (including those not identified to species level) and on Bray and Curtis (1953) similarity test.

The differences in abundance and species richness between the southern and northern areas were assessed by non-parametric Mann–Whitney test and *t* tests (based on log-transformed mean values), while their similarity was assessed by ANCOVA, adjusted for the covariance of colony volumes.

Similarity percentage (SIMPER) analysis was performed to identify the species most substantially contributing to the observed differences between the northern and southern areas. The data from Abele and Patton (1976) were used to compare the relationships between the volume of the colonies of *Pocillopora* and the characteristics of its associated communities in the Red Sea and the Eastern Tropical Pacific (eastern coast of Panamá), based on linear regressions of log-transformed data and ANCOVA. All analyses were done using software packages: PAST (Hammer 2009) and STATISTICA (10) v. 10.

Results

Taxonomic composition

Thirty-six species were found in the 40 coral heads examined. Sixteen of them were identified to species level, 10 to genus level, and 10 to family or higher levels. Crustaceans were the most diverse group, including 27 species, most of them Decapoda. They were followed by echinoderms (four species), mollusks (three), priapulids (one) and fish (one). There were 12 obligate symbionts, 3 facultative symbionts and 21 SUS. Among obligate symbionts, the most diverse were trapeziid crabs (five species) and palaemonid shrimps (four species; Table 1, Fig. 5).

The total number of species was much lower than expected from the Chao 2 model (36 and 54, respectively) and the cumulative abundance curve did not reach an asymptote (Fig. 6a). Conversely, the number of symbiotic species (both obligate and facultative) appeared to be saturated, as the observed species number almost coincided with that expected from the Chao 2 model and the accumulative abundance curve was close to the asymptote (Fig. 6b).

Structure of the symbiotic community

All coral colonies were populated by symbionts (prevalence 100%), but the specific prevalence ranged from 2.5 to 82.5%. Obligate symbionts were most common (prevalence ranged from 5 to 82.5%), particularly the trapeziid crab *Trapezia bidentata* (82.5%), and the palaemonid shrimps: *Alpheus lottini* (72.7%), *Harpiliopsis depressa* (52.5%) and *Periclimenes madreporae* (52.5%; Table 1). The prevalence was lower for facultative symbionts, ranging between 7.5 and 40%, and never exceeding 17.5% for SUS (Table 1).

The number of species that inhabit the same colony ranged from 2 to 14, while that of symbionts from 1 to 10 and for SUS from 0 to 9. The species richness was 5.7 ± 2.74, (4.8 ± 2.11 for symbionts, and for SUS 2.3 ± 2.20).

The total number of specimens living in a single coral colony varied from 3 to 80, while that of symbionts ranged from 2 to 68, and for SUS, from 0 to 22. The mean abundance was 18.25 (±14.82) individuals per colony (11.93 ± 11.51 for symbionts and 6.5 ± 6.40 for SUS).

The mean intensity of the symbionts was relatively low, ranging from 1 to 3.85 individuals per colony, except for *Hapalocarcinus marsupialis*, which typically exhibits aggregated distributions (Mohammed and Yassien 2013). It reached a mean value of 9.3 individuals per colony in our samples due to the high number of juveniles found in colony # 2.

Several decapod species, like trapeziid crabs and the shrimps *A. lottini* and *H. depressa*, usually form heterosexual pairs when occupying coral colonies. Large (i.e., carapace 10–

14 mm wide) *Trapezia* crabs live in pairs in 95% of the colonies, most of them being female and male adults of *T. bidentata* and, less frequently, being replaced by either *T. tigrina* or *T. cymodoce* (Table 2). However, these species practically never occurred on the same host, except for the single finding of heterosexual pairs of *T. bidentata* and *T. tigrina* living together. Pairs of large shrimps *A. lottini* and *H. depressa* were also common (Table 2).

The number of species and individuals per colony were positively correlated with the coral head volume (Table 3).

The Shannon diversity (H) varied from 0.6 to 2.34 bits, but was usually moderate (1.0–1.9; Table 2). The Berger–Parker index ranged from 0.167 to 0.8, being usually relatively low (0.2–0.5; Table 2), indicating a low level of numerical dominance in the infracommunities.

The nMDS revealed no clear grouping of the infracommunities according to location or depth (Electronic supplement 3). Although, the presence of *T. cymodoce* instead of *T. bidentata*, and a specimen of a relatively rare species *Yemenicaris trullicauda* in colony # 13 makes this infracommunity an outlier (see Electronic supplement 2 and 3).

## Sub-regional variation of the symbiotic community structure

Twenty-nine species were found in the southern area (29 species) and 26 species in the northern one. Both areas shared only 19 out of 36 species (52.8%), but they shared 13 out of 15 symbiotic species (86.7%), both obligate and facultative. The two symbiotic species found only in the southern area were *T. cymodoce* and a gastropod *Coralliophila* sp. The mean number of SUS in the southern area was 5 (0–20), and in the northern 9.3 (from 0 to 22).

H, the Berger–Parker dominance index and the species richness did not show significant sub-regional differences, neither for all species nor for the symbionts, while the mean abundance (both total and that of symbionts), was significantly higher in the northern area (non-parametric Mann–Whitney test, Table 2). The percentage of infracommunities including only symbiotic species was 25% in the southern area, while they were absent in the northern one (see Electronic supplement 2).

Generally, the number of species and individuals per colony were positively correlated with the coral head volume in both studied areas, and the regression line for the northern part was above the line for the southern area (Fig. 7). The only exception was SUS abundance in the northern area tended to decrease with the increasing volume, but the relationship was not statistically significant (Fig. 7e).

The numbers of both species and specimens per covariate colony volume were higher in the northern than in the

Fig. 5 Common symbiotic species associated with *Pocillopora verrucosa* colonies. **a**: *Trapezia bidentata*, male, colony # 3; **b**: *Alpheus lottini*, female, colony # 1; **c**: *Trapezia tigrina*, male, colony # 4; **d**: *Harpiliopsis depressa*, female, colony # 2; **e**: *Trapezia digitalis*, male, colony # 19; **f**: *Hapalocarcinus marsupialis*, female ov, colony # 39; **g**: *Trapezia guttata*, juvenile, colony # 25 (preserved material); **h**: *Ophiocoma* sp., colony # 22. Scale bar 10 mm. Photo: T. Britayev (**a–d**, **h**), V. Spiridonov (**e–g**)
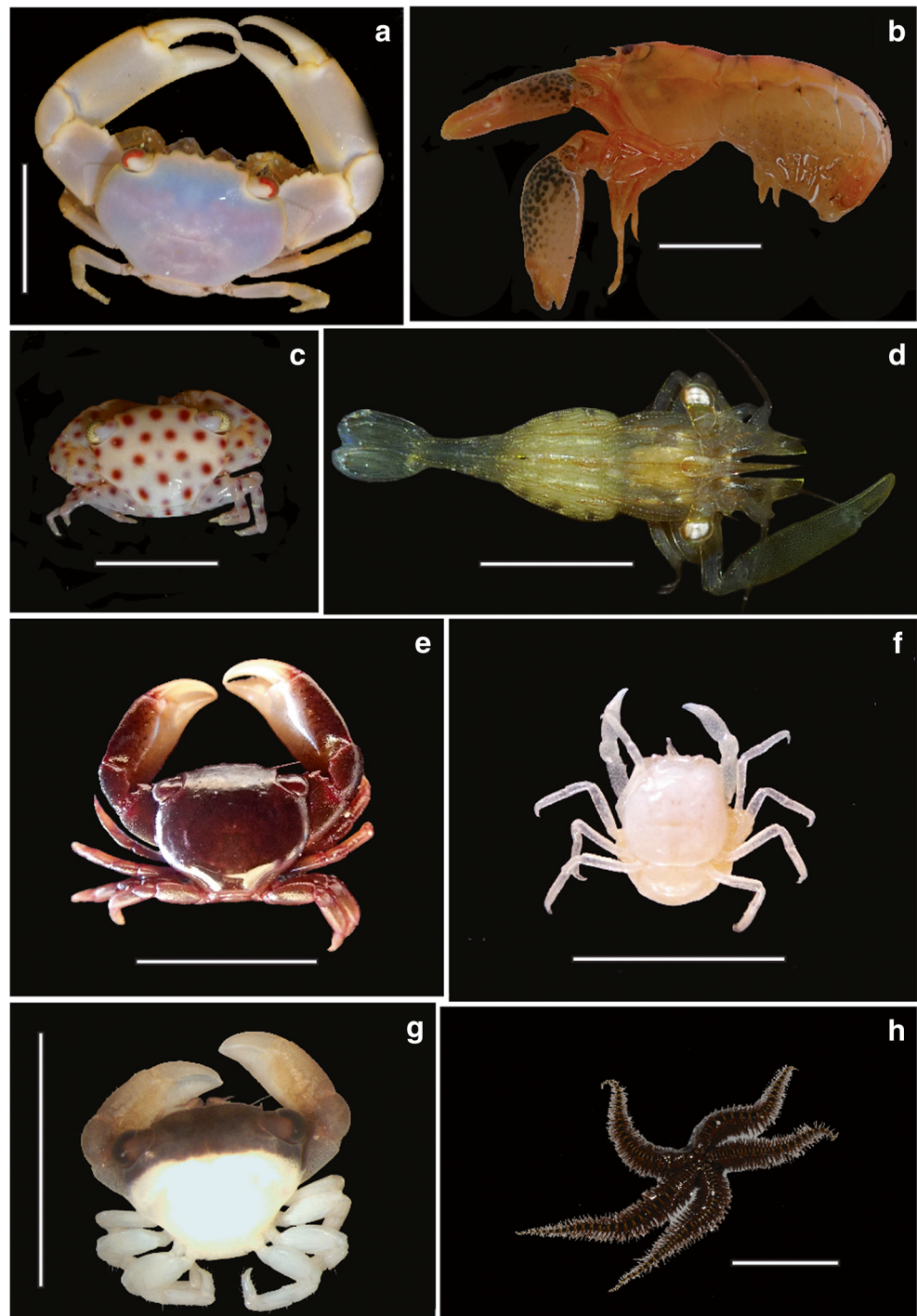
southern area, but were only significant for the abundance of SUS ($p = 0.04$), all species ($p = 0.007$) and symbionts ($p = 0.01$; ANCOVA, Table 4).

The most important contributors to the differences in abundance were polychaetes, shrimps (i.e., *P. madreporae*) and amphipods that were more abundant in the northern than in the southern area (SIMPER analysis, Table 5).

Discussion

Symbiotic versus species of unknown status (SUS)

The species harbored by living coral colonies can be classified according to their relationships with the host (e.g., Abele 1976; Black and Prince 1983; Patton 1974; Stella et al. 2011b). Black and Prince (1983) proposed five groups:
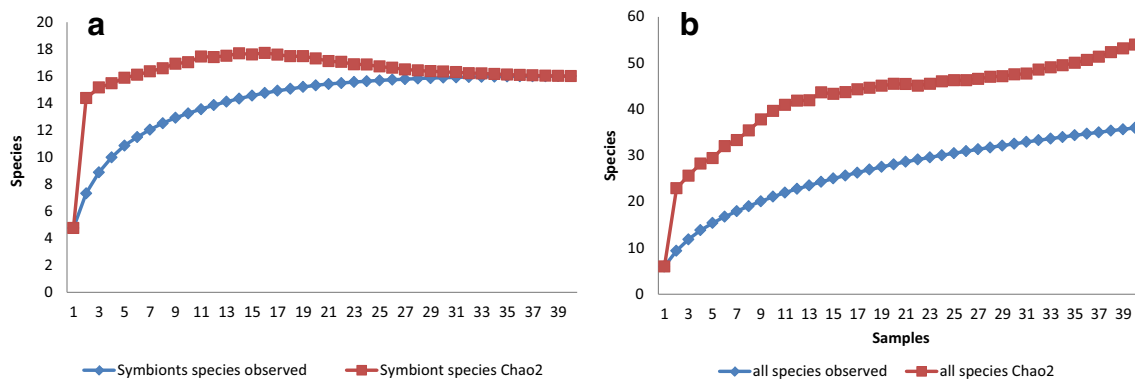
Fig. 6 Species accumulation curves for all *Pocillopora*-associated species (**a**) and for symbionts (**b**) collected along the north-western coast of Saudi Arabia. Chao2: expected species number derived from Chao2 model; obs.: observed species number

obligate pocilloporid symbionts; symbionts of pocilloporids and other living corals; inhabitants of living and dead corals; facultative symbionts; and SUS. However, the limited information on coral associates' biology, as well as the controversial classifications proposed in different papers impedes proper comparison. In this paper, we following the simplified classification by Stella et al. (2011a), which includes three groups: obligate symbionts, facultative symbionts and SUS. Based on the extensive literature on species composition of pocilloporid-associated communities (e.g., Abele and Patton 1976, Castro 2015, Coles 1980, Patton 1966, Stella et al. 2011b) and our own observations, we included in SUS free-living species inhabiting mainly dead parts of the colony, the numerous fouling organisms (e.g., sponges, bryozoans and ascidians) attached to corals and a limited number of possibly

symbiotic, but rare and poorly known taxa. Dead coral tissue creates additional microhabitats within the colony which allow non-specialized species to utilize new resources that, in turn, may lead to the increase of species richness and intensity in coral infracommunity (Coles 1980; Stella et al. 2010). For example, dead colonies of *Stylophora* may frequently host portunid crabs that are rare (Spiridonov and Neumann 2008; V. Neumann, pers. comm.) or absent (Edwards and Emberton 1980) in living colonies. These are often opportunistic species that do not have relationships as close as those of a symbiont with its host coral colony. Moreover, their abundance and composition are driven by external environmental factors (e.g., diversity of surrounding habitats, wave action, predators' pressure, etc.), while symbiotic species are more influenced by the host characteristics, as well as by biological

Table 2 Comparison of the symbiotic communities associated with *Pocillopora verrucosa* in the southern and northern areas of the Saudi Arabian coast of the Red Sea. Mean (±standard deviation, range) communities characteristics and frequency (%) of heterosexual pairs of the decapod symbionts are provided

Characteristics	Southern area; $n = 25$	Northern area; $n = 15$	Mann–Whitney U (p)
Depth (m), range	2–15	3–13	NA
Colony volume (cm^3)	3300 (±1870, 800–7100)	2400 (±1240, 300–4400)	135 (0.15)
Number of all species per colony	5.7 (±2.88, 2–14)	6.2 (±2.76, 2–13)	158 (0.41)
Number of symbiotic species per colony	4.8 (±2.13, 1–10)	4.9 (±2.07, 1–8)	169 (0.61)
Abundance of all species	15.6 (±15.84, 3–80)	23.1 (±12.11, 8–47)	95 (0.01)**
Abundance of symbiotic species	10.8 (±12.32, 2–68)	13.9 (±8.27, 2–32)	114 (0.041)*
H (Shannon diversity index)	1.45 (±0.479, 0.64–2.32)	1.53 (±0.392, 0.6–1.93)	158.5 (0.54)
Berger–Parker Index	0.38 (±0.160, 0.167–0.80)	0.36 (±0.139, 0.214–0.714)	171 (0.65)
Large *Trapezia* pairs (% of colonies)	92	100	NA
T. bidentata pairs (% of colonies)	68	87	NA
T. tigrina pairs (% of colonies)	16	13	NA
T. cymodoce pairs (% of colonies)	12	0	NA
Alpheus lottini pairs (% of colonies)	60	60	NA
Harpiliopsis depressa pairs (% of colonies)	32	44	NA

NA not applicable

* and ** statistically significant differences at level of 0.05 and 0.01, respectively

Table 3 Correlation coefficients (r) and linear regressions for number of associated species (S) and their abundance (A) vs. volume (V, in cm^3) of colonies for *Pocillopora*-associated communities in the Red Sea (present study) and Panamá (Abele and Patton 1976)

Region	Characteristics	r	p	Linear regression	N
Red Sea	S	0.60	0.001	S = 2.524 + 0.009 V	40
	A	0.55	0.003	I = 0.743 + 0.004 V	40
Panamá	S	0.40	0.045	S = 6.604 + 0.008 V	27
	A	0.54	0.004	I = 10.278 + 0.004 V	27

interactions within the host colony (Abele and Patton 1976; Coles 1980; Huber 1987; Vannini 1985).

Colony volume and associated infracommunities

The relationships between colony volume and the characteristics of their associated infracommunities are at the basis of the methodological comparison of diversity and abundance patterns at different scales. In our study, the whole sample revealed positive correlation between the colony volume and the associated species and individuals. Conversely, the subregional and symbionts vs. SUS comparisons did not show such a clear pattern (Fig. 7). Nevertheless, a significant positive correlation between colony volume and associated species number and abundance in most cases stands for the southern area (Fig. 7a–e), where the sample of colonies is larger and conditions have been more uniform (see Methods). However,

Fig. 7 Relationships between the colony volume (V in cm^3) and the characteristics of associated communities in the southern (S; *blue circles*) and the northern (N; *red quadrates*) areas. **a**: Ln (natural logarithm) of abundance of all species (TA); TAS = 1.8326 + 0.0002*V; $r = 0.5865$; $p = 0.0021$; TAN = 2.7898 + 0.0001*V; $r = 0.2538$; $p = 0.3614$; **b**: Ln of total species number per colony (TS); TSS = 1.4776 + 0.0001*V; $r = 0.5670$; $p = 0.0031$; TSN = 1.8322 + 0.0001*V; $r = 0.4013$; $p = 0.1382$; **c**: Ln of abundance of symbiotic species (AS): ASS = 1.6368 + 0.0002*V; $r = 0.5491$; $p = 0.0045$; ASN = 2.1009 + 0.0002*V; $r = 0.3608$; $p = 0.1865$; **d**: Ln of number of symbiotic species (SN): SNS = 1224 + 0.0001*V; $r = 0.6636$; $p = 0.0004$; SNN = 1.4399 + 0.0001*V; $r = 0.3198$; $p = 0.2452$; **e**: Ln of abundance of species with uncertain status SUS = 0.5694 + 0.0002*V; $r = 0.4234$; $p = 0.0349$; SUSAN = 2.2087– 6.7116E^{-5}*V; $r = -0.0976$; $p = 0.7294$; **f**: Ln of number of species with uncertain status (SUS): SUSS = 0.6129 + 7.6455E^{-5}*V; $r = 0.2486$; $p = 0.2308$ SUSN = 1.0624 + 6.3374E^{-5}*V; $r = 0.1494$; $p = 0.5951$
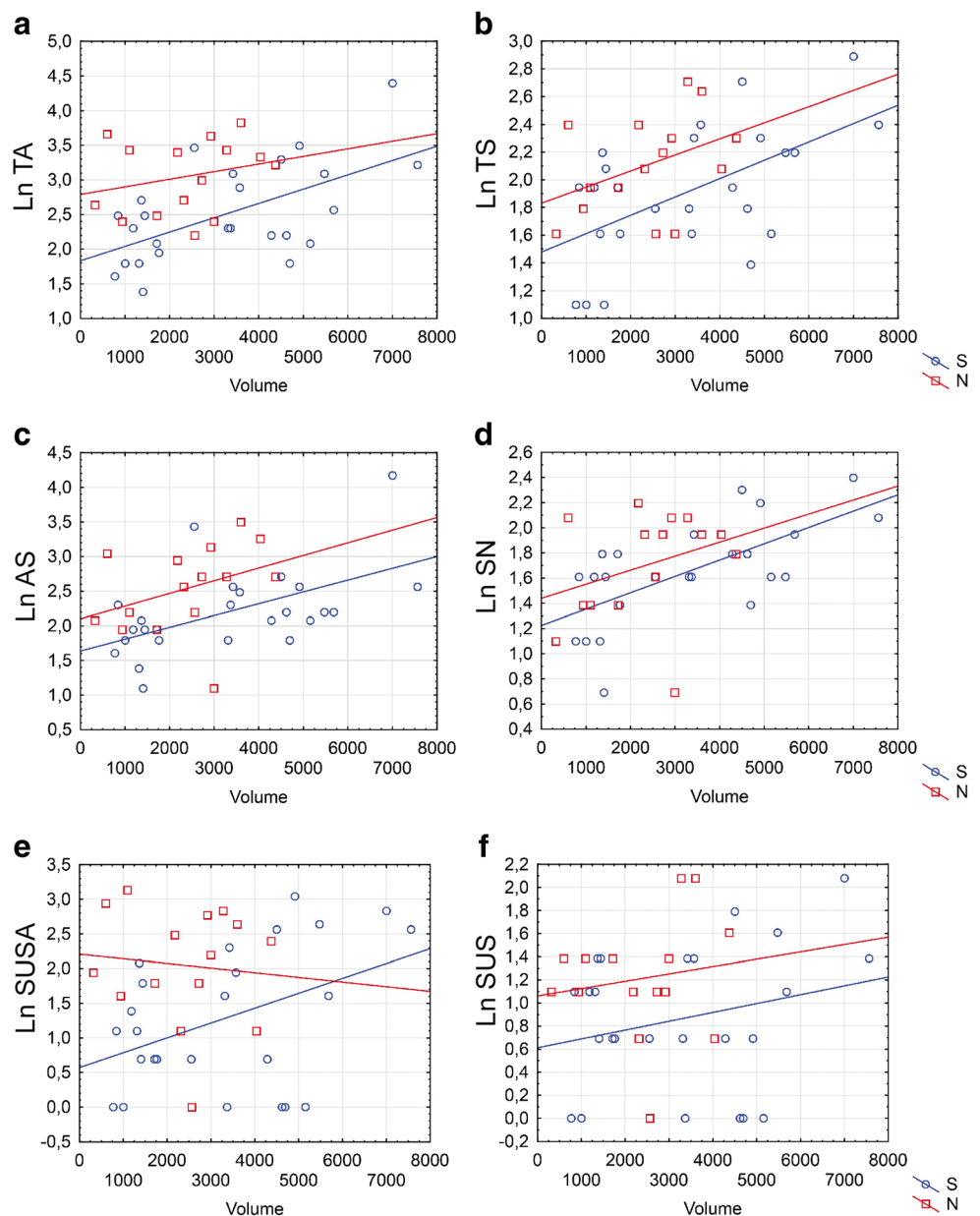
Table 4 Comparison of mean natural logarithm (Ln) of abundance and number of species per coral head between southern and northern areas with colony volume as covariate (results of ANCOVA analysis). The continuous variable is volume of coral heads; categorical variable: southern vs. northern areas (S vs. N)

	SS	MS	F	p
Ln of abundance				
Volume	4.24292	4.24292	13.2461	**0.0008**
S vs N	4.42970	4.42970	13.8292	**0.0007**
Ln of species number				
Volume	1.99257	1.99257	14.4110	**0.0005**
S vs N	0.85253	0.85253	6.1659	**0.0177**
Ln of symbionts abundance				
Volume	3.52254	3.52254	11.5288	**0.0016**
S vs N	2.16164	2.16164	7.0748	**0.0115**
Ln of symbionts species number				
Volume	1.91868	1.91868	15.5406	**0.0003**
S vs N	0.20924	0.20924	1.6947	0.2010
Ln of SUS abundance				
Volume	3.16887	3.16887	3.67701	0.0629
S vs N	7.44835	7.44835	8.64274	**0.0056**
Ln of SUS species number				
Volume	0.64922	0.649221	1.94223	0.1717
S vs N	1.51785	1.517850	4.54086	**0.0398**

Statistically significant results are marked in **bold**

the explained percentage of variability in these cases is moderate, ranging from 45 to 67%.

Our results agree with those observations of Austin et al. (1980), Black and Prince (1983) and Edwards and Emberton (1980), but particularly with Abele and Patton (1976) for Panamá, as they employed the same method to measure colony volumes. Our data coincided with those for Panamá in terms of total species number and abundance (Table 3), revealed similar correlation coefficients and showed lower regression coefficients (Table 3), probably reflecting higher diversity and abundance of SUS reported in Panamá (Abele 1976).

Black and Prince (1983) and Edwards and Emberton (1980) measured the volume of branches or inter-branchial space (as available living space) and found positive correlations with the number of species and individuals. These correlations agree with increase in living space providing new microhabitats and, thus, allow additional symbionts to colonize the coral. This may be important for the most strongly competitive symbionts (Vannini 1985; Huber 1987). Particularly, direct competition seems to prevent the presence of more than one large heterosexual pair of *Trapezia* per colony (Abele and Patton 1976; Edwards and Emberton 1980; present study), while smaller species such as *T. digitalis* (Edwards and Emberton 1980; present study) and juveniles of other species may co-occur. Co-occurrence appears to be facilitated in colonies with greater volumes, although the

Table 5 Taxa contributing to the 90% of the differences between the quantitative compositions of *Pocillopora*-associated communities in the southern (S) and northern (N) areas according to the SIMPER analysis

Taxon	Av. dissim.	Contrib. %	Cumulative %	Mean abund. S	Mean abund. N
Polychaeta	12.12	17.07	17.07	2.96	4.27
Periclimenes madreporae	10	14.09	31.16	0.72	3.93
Amphipoda	5.842	8.226	39.38	0.36	2.47
Trapezia bidentata	5.676	7.992	47.37	2.04	3
Harpiliopsis depressa	4.436	6.246	53.62	1.96	1.07
Alpheus lottinii	3.079	4.335	57.96	1.4	1.2
Trapezia tigrina	2.935	4.132	62.09	0.76	0.533
Trapezia digitalis	2.864	4.033	66.12	0.32	1
Ophiocoma sp.	2.56	3.604	69.72	0.6	0.667
Hapalocarcinus marsupialis	2.368	3.334	73.06	1	0.2
Domecia hispida	2.309	3.252	76.31	0.64	0.733
Trapezia guttata	1.932	2.72	79.03	0.12	0.933
Alpheus sp.	1.704	2.4	81.43	0.08	0.467
Gastropoda gen.sp.	1.559	2.195	83.62	0.16	0.467
Palaemonella rotumana	1.345	1.893	85.52	0.12	0.333
Brachyura megalopae	1.244	1.751	87.27	0.08	0.333
Yemenicaris trullicauda	1.047	1.475	88.74	0.24	0.133
Alpheidae juv	0.9586	1.35	90.09	0.36	0.133
Trapezia_cymodoce	0.8954	1.261	91.35	0.28	0

Av. dissim average dissimilarity, *Contrib.* contribution, *Cumulative* cumulative contribution, *abund.* abundance

moderate percentages of explained variability (Fig. 7) certainly indicate that factors like branch morphology or the presence of dead tissue may also contribute to explaining this variability in number and abundance of coral-associated species.

Measuring the volume of fragmented colonies or their inter-branch space (e.g., Black and Prince 1983; Edwards and Emberton 1980) probably represents a better approach to the real living space within a colony. However, our approach was easy to apply and the obtained volumes according to Austin et al. (1980), were significantly correlated with that of the inter-branchial space. Multivariate infracommunity analyses could also allow us to assess the impact of factors other than colony volume. However, they necessarily require large samples, which may not always be available in multi-purpose surveys such as the one framing our study. This way, univariate methods of infracommunity comparisons considering colony volume as a factor (e.g., our ANCOVA approach) are revealed to be useful enough.

Sub-regional variability

The species composition in the two studied areas of the Arabian Red Sea coast is not as variable as that between areas studied in Panamá (Abele 1976) and Australia (Black and Prince 1983). In fact, there was no clear spatial or bathymetric grouping of the infracommunities associated with *Pocillopora*, neither in terms of diversity nor in abundance (Electronic supplement 3). Nevertheless, we observed that the species composition and diversity were slightly higher in the southern than in the northern area. The composition of symbionts was similar, while that for all species differed mainly due to SUS having low prevalence. However, at least two symbiotic species, *T. cymodoce* and *Coralliophila* sp., also contributed to this variability, as they were relatively common in the southern area and absent in the northern. *Trapezia cymodoce* is common in very shallow, often intertidal Red Sea coral habitats where *T. bidentata*, the most common species of our survey, has not been previously reported (Klunzinger 1913; Galil 1987; Neumann and Spiridonov 1999; authors observations in RSS 2012–2013). Accordingly, the presence of *T. cymodoce* in the southern area may be partly explained by the greater number of samples collected, which included many shallow locations (Electronic supplements 1–2). The RSS collections indicate that *Harpiliopsis depressa* in Pocillopora-associated infracommunities may be also replaced by its congener *H. beaupresii* (Audoin, 1826;) in other localities of the Red Sea (Ďuriš 2017).

A higher variability in diversity at the same, or even at lower, spatial scale than that analyzed in our study occurred for the decapod fauna associated with *P. damicornis* in Panamá and Australia (Abele 1976; Black and Prince 1983). There, the sub-regional differences were driven by stable vs.

greatly variable environmental conditions (Abele 1976). Therefore, we suggest that the relatively low variability in species diversity of the communities associated with *P. verrucosa* at the two studied Red Sea areas corresponds to the relatively homogenous environmental characteristics along the northwestern Arabian coast. The only difference in oeanographical conditions, at least in the studied area, was a gradual northward decrease in temperature (Bruckner et al. 2012).

The major sub-regional variability in community structure of the associates with *P. verrucosa* along the NW Saudi Arabian coast concerned the covariation in number of SUS species and individuals with colony volume, which were higher in the northern than in the southern area. As most symbionts of *Pocillopora* are facultative (= SUS in our study), the differences in the diversity of the associated communities may reflect the differences in habitat diversity of the surrounding reef (Black and Prince 1983), a hypothesis indirectly supported by our data. Sample size was larger in the southern than in the northern area, but the habitat variability was apparently lower, as most samples were from relatively shallow reefs at stations 1 and 12. Furthermore, the southern localities were, overall, more exposed than the northern ones. These factors affected SUS, but probably have little impact on the core symbiotic assemblage, which was driven by the specific coral environment, as well as by biotic interactions inside the colony.

The higher number of SUS and the absence of correlation between species intensity and abundance for SUS in the northern area may also be explained by the presence of colonies with partial tissue necrosis (authors qualitative personal observations) that were absent in the southern area. Increasing area of dead tissues facilitate corals colonization by free-living organisms (Stella et al. 2010), such as the small polychaetes and amphipods present in the northern area and absent in the southern one. Therefore, we suggest that the proportion of living tissue is an important predictor of the abundance of colony inhabitants for the Red Sea *P. verrucosa*, a trend also observed in the communities associated with *P. damicornis* and *Acropora nasuta* (Stella et al. 2010).

Geographical variations in species diversity and composition in pocilloporid-associated communities

The species diversity in the Indo-Pacific pocilloporid-associated communities ranged from 36 species found off the Arabian coast to 127 from Oahu (Hawaii), which is the highest symbiont diversity reported worldwide for a single host species in a given area, among corals (Stella et al. 2011b), but also among sponges and crinoids (Britayev and Mekhova 2011; Klitgaard 1998; Ribeiro et al. 2003). In contrast, the symbionts' diversity is much lower and less variable (Table 6), ranging from 9 species in Panamá (eastern coast of

Table 6 Comparison of biodiversity of communities associated with pocilloporid corals throughout the Indo-Pacific and Tropical Eastern Pacific based on the present study and the literature data

Area and host species	Sample size (colonies number)	Total species number	Number of decapods species	Number of symbiont species obligatory/ facultative/uncertain status	Reference
Red Sea coast of Saudi Arabia (PV)[a]	40	36	25	12/3 /20	Present study
Sudanese Red Sea (SP)[b]	155	49	47	8/7/32	Edwards and Emberton 1980
Coast of Panama (PV)	35	61	55	7/2/52	Abele and Patton 1976
Lizard Island, Great Barrier Reef (PD)	50	102	37	15/4/83	Stella et al. 2010
Heron Island, Great Barrier Reef (PD)	70+	107	70	15/3/83	Patton 1966, 1974, Austin et al. 1980 summarized
Oahu, Hawaii	18	127	Unknown	11/1?/115	Coles 1980
Rottnest Islands (Australia, 32°S)	54	67	34	8/3/56	Black and Prince 1983
Point Quobba (Australia, 24°30′)	12	45	32	10/3/32	Black and Prince 1983

PV Pocillopora verrucosa, *PD P. damicornis*, *PM P. meandrina*, *SP Stylophora pistillata*

[a] all associated species included

[b] crustaceans only included

the Pacific Ocean) to 19 at Lizard Island (central part of the Great Barrier Reef) and being similar, or even lower, to that found in other host taxa. For example, the polychaetes *Chaetopterus* spp. harbor 3–4 specialized symbiotic species, the sponge *Hyattella intestinalis* harbors 13 and the unstalked crinoid *Comaster nobilis* (Carpenter, 1884) harbors 20 species (Britayev et al. 2017; MacDonald et al. 2006; Britayev and Mekhova 2011). Unexpectedly, the northern Saudi Arabia coast shows one of the highest symbiont diversities within the Indo-Pacific region, 15, which is nearly the same number as recorded in association with another pocilloporid, *Stylophora pistillata*, at the Sudanese coast of the Red Sea (but decapods only, Table 6). This trend confirms the overall view of the Red Sea as a hot spot for faunal diversity (Sheppard et al. 1992; DiBattista et al. 2016).

The obligate symbionts associated with the Sudanese colonies of *S. pistillata* were less diverse than the Arabian ones (Table 6), while the facultative symbionts were more diverse and included six species absent from the Arabian coast. The two locations shared the presence of the decapods *Domecia hispida* and, probably, *Calcinus* sp. (in which the Arabian species probably belongs to one of the three reported from Sudan).

The core group of obligate symbionts were formed by species of *Trapezia* both in the Sudanese and the Saudi Arabian coasts, all five species being already reported from the Red Sea (Galil 1987; Castro et al. 2004). The differences between the two faunas were, thus, related with the alpheid and palaemonid shrimps. The alpheid *Synalpheus charon* (Heller, 1861) dominated at the Sudanese coast, but was absent in Saudi Arabia, where it was replaced by *A. lottini*. The

latter was also present, but less frequently, in shallow water *Stylophora*-associated communities from Sudan, where it was reported as *Alpheus sublucanus* (Forskål, 1775; Edwards and Emberton 1980), a synonymy of *A. lottini* according to the Opinion 1367 of the International Commission of Zoological Nomenclature (Banner and Banner 1981). In turn, the palaemonids *Periclimenes madreporae, Harpilius* cf. *consobrinus* and *Yemenicaris trullicauda* were only present off the Arabian coast.

On the other hand, the community associated with *Pocillopora* in the Saudi Arabian Red Sea showed a surprising similarity to that from the Australian Great Barrier Reef, which shared five crabs (*T. bidentata, T. digitalis, T. cymodoce, T. guttata* and *Domecia hispida*), and three shrimps (*Alpheus lottini, Harpiliopsis depressa* and *Periclimenes madreporae*). Accordingly, we hypothesize that the marked similarity in the species composition of pocilloporid-associated communities along the Red Sea is largely determined by the characteristics of the host species (*Pocillopora* and *Stylophora*) rather than by distance between sampling areas (Sudan vs. Saudi Arabia), which is particularly emphasized by the fact that the two long-distant locations, the Red Sea and the Eastern Australian coast, may share 50% of the associated species.

Taxonomic composition of pocilloporid-associated communities

In this section, we will focus on the core group of the pocilloporid-associated community, the symbionts. There are about 83 invertebrate species, excluding copepods and

Fig. 8 Comparison of the taxonomic composition of the symbiotic communities in the Saudi Arabian Red Sea (present study), Australia (Heron Island, Patton 1966, 1974 and Lizard Island, Stella et al. 2010), and all over the world's oceans (Allen and Erdmann 2012; Stella et al. 2011b)
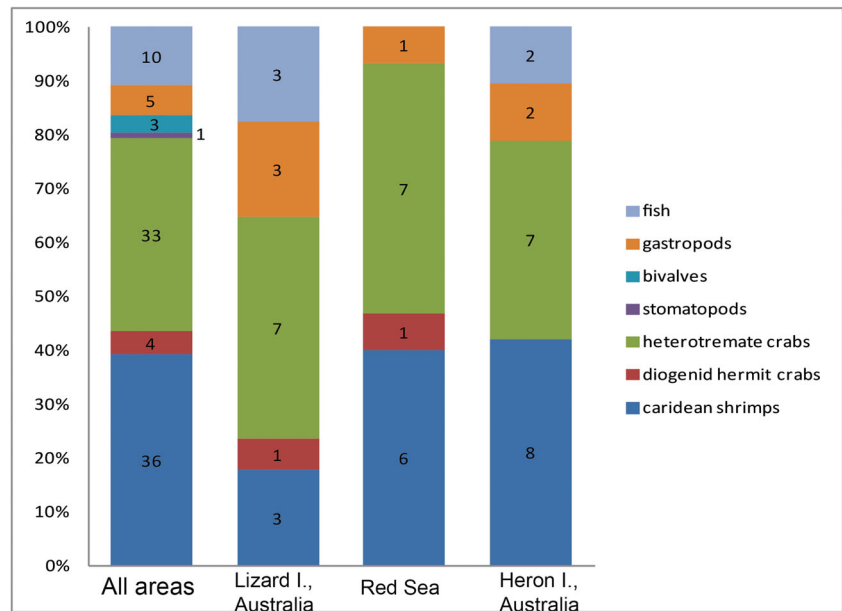
sponges (i.e., caridean shrimps, diogenid hermit crabs, heterotremate crabs, stomatopods, bivalves, gastropods) and no less than 10 fish species, living as obligate and facultative symbionts in association with pocilloporid corals all over the world's ocean (Allen and Erdmann 2012; Stella et al. 2011b). However, more than 70% are shrimps and crabs (Fig. 8). The diversity of the Arabian community represents less than 16%, and lacks several relevant groups like fish, bivalves and stomatopods. Nevertheless, the two most diverse groups, shrimps and crabs, are present in both areas (Fig. 8).

Comparison between local pocilloporid-associated faunas is complicated by the fact that most publications reported on the decapod crustacean component only (e.g., Abele 1979; Abele and Patton 1976; Coles 1980; Edwards and Emberton 1980; Patton 1966), with some groups being probably underestimated due to identification difficulties (e.g., palaemonid shrimps). Accordingly, only two local areas from the Great Barrier Reef, Heron and Lizard Islands (Patton 1966, 1974 and Stella et al. 2010, respectively), are appropriate for comparison with our data (Fig. 8). They both differ from Saudi Arabia in the presence of fish. The Heron Island and Saudi Arabia communities are similar in having two main, nearly equal in size symbiont groups, shrimps and crabs that comprise about 80% of all species. In contrast, a high proportion of crabs and a low proportion of shrimps characterized the community associated with *Pocillopora* at Lizard Island.

Conclusions

This study reports on the diversity of the community associated with the colonies of the coral *Pocillopora verrucosa* at the NW coast of Saudi Arabia in the Red Sea. The number of obligate and facultative symbiotic species (15) was very close to that expected by the Chao 2 model. This indicates that 40 coral colonies may be regarded as a representative sample to make a valid inventory of *Pocillopora* symbionts' diversity in this particular area. The subregional comparison revealed differences between the southern and northern areas, which had only 52.8% of the total species in common. However, this variability is mostly attributed to the SUS. The community structure varied mainly in number of species and individuals, this being generally higher in the northern area. Our results support that the variability in pocilloporid-associated communities depends mainly on SUS (which reflects differences in species and habitat diversity of the surrounding reef), while the community core consisting of obligate symbionts is more conservative. The total species diversity of pocilloporid-associated communities across the Indo-Pacific and the Tropical East Pacific widely varies owing to the SUS number, while the diversity of true symbionts is much lower and less variable. The number of symbiotic species found in the Saudi Arabian coast of the northern Red Sea is among the highest in the Indo-Pacific.

The community associated with *Pocillopora* in the Saudi Arabian Red Sea showed a surprising similarity to that from the Australian Great Barrier Reef. Accordingly, we hypothesized that the similarity in species composition of pocilloporid-associated communities is largely determined by hosts characteristics rather than by the distance between sampling areas. An alternative hypothesis explaining the similarity between such remote regions is the possible existence of cryptic endemic coral-associated species in the Red Sea, which may certainly be expected taking into account the high

endemism level of the Red Sea biota (Sheppard et al. 1992; DiBattista et al. 2016). This latter hypothesis appears to be supported by the finding of endemic cryptic species in the Red Sea gall crabs (Cryptochiridae) living in symbiosis with various corals (van der Meij 2015). Whether cryptic endemic species are also present among pocilloporid symbionts or not needs to be addressed in future studies.

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