



Molecular diversity and patterns of co-occurrence of decapod crustaceans associated with branching corals in the central Red Sea

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Received: 28 November 2023 / Revised: 26 May 2024 / Accepted: 27 June 2024 / Published online: 3 August 2024
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Abstract

Crustaceans are one of the most widespread and speciose groups of marine organisms, fulfilling multiple ecological roles in numerous ecosystems. On coral reefs, many crustacean species form associations with scleractinian corals. Although the Red Sea is considered a biodiversity hotspot, few studies examined the diversity of coral-associated crustacean communities to date. In this study, 460 decapod crustaceans were recovered from 67 coral colonies of the three branching genera *Acropora*, *Pocillopora* and *Stylophora* in the central Saudi Arabian Red Sea. Crabs and shrimps were morphologically identified to the lowest taxonomic level possible, and portions of the mitochondrial COI and 16S rRNA genes were amplified with the objective of assessing their diversity and phylogenetic relationships. Finally, patterns of co-occurrence were evaluated to investigate the presence of species-specific symbiotic epifauna on different host corals. Overall, we recovered four families, five genera, and nine species of Red Sea crabs, nested into 11 molecular clades, and two families, eight genera and 11 species of shrimps, grouped within 12 lineages. Crabs of the species *Trapezia tigrina* were found to be exclusively associated with *Pocillopora* corals, while *Tetralia* crabs and the shrimps *Jocaste japonica* and *Harpilius lutescens* only occurred on *Acropora* colonies, providing evidence that potential loss of host corals due to local and global impacts could lead to consequent shifts in the symbiotic communities on reefs and to the loss of certain associated taxa. This study represents an advancement towards the understanding and molecular characterization of coral-associated benthic communities in the Red Sea and lays the ground for further research assessing the patterns of biodiversity, evolution, and ecological preferences of these organisms in the area.

Keywords Decapoda · Phylogeny · Symbiosis · Coral reefs · Integrative taxonomy

Introduction

Tropical coral reefs are known to be one of the most diverse and productive ecosystems on Earth (Eddy et al. 2018), harbouring a wide variety of organisms and providing habitat, shelter, and food to several species (Wagner et al. 2020). These ecosystems host nearly one quarter of the total marine biodiversity, with estimates of up to millions of species, yet only a part of them is formally described (Knowlton et al. 2010; Stella et al. 2011a; Fisher et al. 2015; Hoeksema 2017). While academic research notoriously focused on estimating hard coral and fish biodiversity patterns, other groups of marine organisms have been largely overlooked (Plaisance et al. 2009; Stella et al. 2011a).

Most coral reef biodiversity is attributed to the cryptofauna, composed of diverse but understudied invertebrate taxa, for which estimates indicate that around 900 species commonly associate with scleractinian corals (Stella et al. 2011a). For instance, it has been shown that symbionts residing on several host corals highly contribute to the overall reef biodiversity (Molodtsova et al. 2016; van der Schoot and Hoeksema 2024). Coral-associated invertebrates can establish a variety of obligate (i.e. one or both organisms entirely depend on the other for their survival) or facultative (i.e. the organisms involved can generally also survive independently or on other substrates) interactions with their hosts (Gittenberger and Gittenberger 2011; Rouzé et al. 2014; Ivanenko et al. 2018; Maggioni et al. 2022). However, the drivers for the establishment and maintenance of such assemblages are yet to be clarified alongside their vulnerability under various local and global threats including climate change (Gates and Ainsworth 2011; Gibson et al.

Communicated by B. W. Hoeksema

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2011; Stella et al. 2022). In particular, the composite architecture of branching corals provides a variety of habitat, food, and refugia for invertebrate epifauna, mostly belonging to the phyla Arthropoda and Mollusca, some of which, in turn, offer their hosts protection from predators and cleaning from sediment, developing mutualistic relationships (e.g. coral guard crabs) (Sheppard et al. 2009; Stella et al. 2011a, 2011b; Enochs and Manzello 2012).

Among decapod crustaceans, diverse faunal assemblages with a wide array of specialisations have been observed to depend on the host coral for feeding and refuge (Abele 1976; Vytopil and Willis 2001), while contributing to maintain coral health (Stewart et al. 2006). For example, species of guard crabs belonging to the genus *Trapezia* Latreille, 1828, are known to protect their host from predators, such as the crown of thorns starfish *Acanthaster planci* (Linnaeus, 1758) (Glynn 1980; Pratchett 2001; McKeon and Moore 2014), while the shrimp *Alpheus lottini* Guerin, 1829, has been observed to defend corals from corallivorous molluscs, such as those ascribed to *Drupella* Thiele, 1925 (McKeon et al. 2012). Moreover, coral-associated decapod crustaceans, such as tetraliid crabs, are known to act as cleaners for their hosts (Stier et al. 2010; Limviriyakul et al. 2016).

In recent years, some initiatives such as the Census of Marine Life (<http://www.coml.org>), the Moorea Biocode Project (<http://bscit.berkeley.edu/biocode>), and the Santo expedition in Vanuatu (<http://www.santo2006.org>) have prioritised the characterization of species using integrated taxonomic approaches. However, research on the epibenthic fauna inhabiting coral reefs in the Saudi Arabian Red Sea is still lagging behind (Edwards and Emberton 1980; Spiridonov and Neumann 2008; Plaisance et al. 2011; Berumen et al. 2013; Britayev et al. 2017). Recently, some studies have focused on the morphology and taxonomy of crabs associated with scleractinians from various regions of the Red Sea (Spiridonov and Neumann 2007; Werding and Hiller 2007; Brösing et al. 2014; Britayev et al. 2017), while other research applied genetic tools to explore invertebrate communities on Automated Reef Monitoring Systems (ARMS) (Al-Rshaidat et al. 2016; Pearman et al. 2018; Carvalho et al. 2019; Villalobos et al. 2022). Nevertheless, studies on coral-associated decapods in the area are still few considering that the region is a recognised marine biodiversity hotspot for multiple groups of metazoans, hosting one of the highest rates of endemism in the world (Briggs 1974; DiBattista et al. 2015; Berumen et al. 2019). Although drivers of evolution of marine organisms in the basin are still debated, the composite geological history of the area, past sea level fluctuations affecting its isolation, and its unique environmental conditions, including extreme temperatures and high levels of salinity, may have influenced the patterns of biodiversity in the Red Sea (DiBattista et al. 2013; Berumen et al. 2019). In this context, the characterization of coral-associated communities is

especially important considering that the increasing habitat loss could lead to changes in the structure of the symbiotic community and, eventually, affect highly specialised organisms (Hoegh-Guldberg et al. 2017).

The aim of this study is to characterize the communities of decapod crustaceans living in between the branching corals *Acropora* Oken, 1815, *Pocillopora verrucosa* (Ellis & Solander, 1786), and *Stylophora pistillata* (Esper, 1792), in the area of the Farasan Banks, Saudi Arabia, in the central Red Sea. We applied an integrated morphological and molecular approach to define the identity and evolutionary relationships of the ectosymbionts (Baeza 2015) that we found living on the tissues of the branching corals. Moreover, we investigated the association patterns of the retrieved crustaceans with the three coral genera to verify if patterns of host specificity and rates of co-occurrence could be detected and to understand whether the potential loss of the hosts could ultimately drive the loss of specific associated taxa, when threatened under a climate change scenario.

Materials and methods

Sampling and morphological identification

Sampling for the present study took place in May 2017 at 13 reef sites in the area of the Farasan Banks, Saudi Arabia, central Red Sea (Fig. 1a, b). A total of 67 branching coral colonies, about 20 cm in diameter, belonging to *Acropora* spp. ($n=21$), *P. verrucosa* ($n=18$), and *S. pistillata* ($n=28$), were collected by SCUBA diving between 1 and 30 m depth. Before sampling, each coral colony was covered with a plastic zip-lock bag to minimise the loss of associated ectosymbionts. Coral colonies were photographed underwater using a Canon Powershot G15 digital camera in an Ikelite underwater housing and collected using hammer and chisel. The coral colonies were then sorted aboard the research vessel MV Dream Master (Saudi Arabia), identified based on the physical sample and the in situ pictures, and inspected to retrieve ectosymbiotic taxa. Decapod crustaceans were then extracted from the colonies, placed in falcon tubes, labelled, and preserved in 97% ethanol for further analyses.

Crabs and shrimps were morphologically identified at King Abdullah University of Science and Technology (KAUST, Thuwal, Saudi Arabia), where each specimen was separated from the others, photographed under a stereomicroscope, and labelled prior to storage in 95% ethanol. Decapod crustaceans were identified to the lowest possible taxonomic level based on diagnostic morphological traits (e.g. Galil 1987; Castro 1997; Castro et al. 2004; McKeon and Moore 2014; Castro 2015; Rouzé et al. 2017) and by consulting expert taxonomists. Specimens are stored at KAUST.

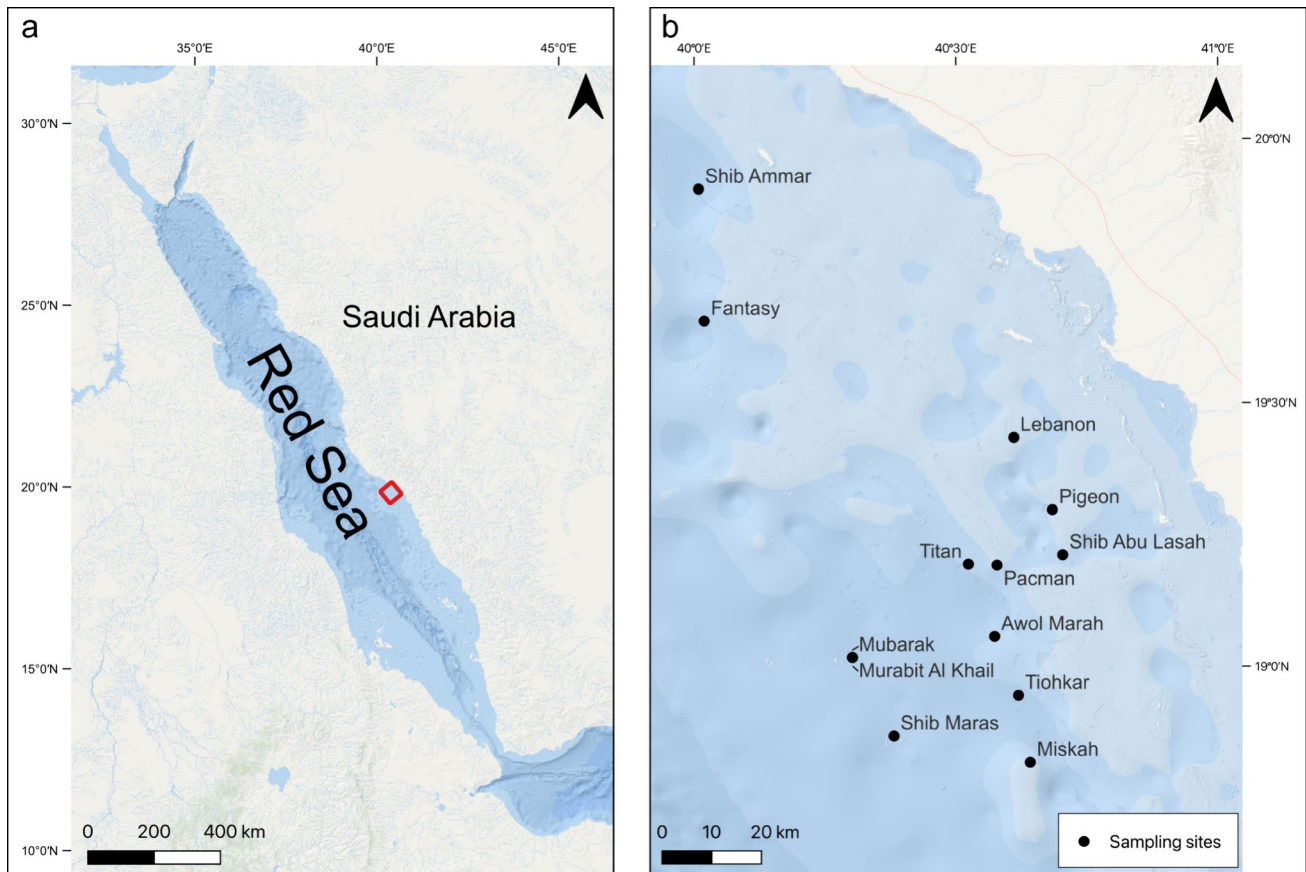


Fig. 1 Maps of the study area: **a** the Red Sea with the location of the study area; **b** the position of the 13 sampling sites in the Farasan Banks, Saudi Arabian central Red Sea. The maps were created with QGIS v.3.32.2 and contains ESRI Ocean data

DNA extraction, amplification, and sequencing

Total genomic DNA was extracted from all collected symbionts. The last pereopod of each specimen was sub-sampled from each individual crab and shrimp for DNA extraction using a Dneasy® Blood and Tissue kit (Qiagen Inc., Hilden, Germany) according to the manufacturer's protocol. Extracted DNA quantity and quality were assessed using a NanoDrop® 2000c spectrophotometer (Thermo Fisher Scientific, Waltham, MA, USA).

Two regions were amplified using polymerase chain reactions (PCRs). A portion of the cytochrome *c* oxidase subunit I gene (COI) was amplified using the primers LCO1490 (5' – GGT CAA CAA ATC ATA AAG ATA TTG G – 3') and HCO2198 (5' – TGA TTT TTT GGT CAC CCT GAA GTT TA – 3') (Folmer et al. 1994) and a portion of the 16S rRNA gene (16S) using the primers 16H10 (5' – AAT CCT TTC GTA CTA AA – 3') (Schubart 2009) and 16L2 (5' – TGC CTG TTT ATC AAA AAC AT – 3') (Schubart et al. 2000). Reactions were performed in a final volume of 15 µL obtained with 1.2 µL of DNA, 1.5 µL of each primer (10 µM), 3.3 µL of H₂O, and 7.5 µL of 2× Multiplex PCR Master Mix (Qiagen, Hilden, Germany). The following temperature conditions were

used for the amplification of COI: 95 °C for 15 min, followed by 30 cycles of 94 °C for 30 s, 46 °C for 1 min, and 72 °C for 1 min, followed by a final extension at 72 °C for 7 min. The temperature profile used for the amplification of 16S was as following: 95 °C for 15 min, followed by 39 cycles of 95 °C for 5 s, 47 °C for 1 min, and 72 °C for 1 min, followed by a final extension at 72 °C for 10 min.

All PCR products were purified adding 2 µL Illustra™ ExoProStar™ (Global Life Sciences Solutions Operations UK Ltd, Buckinghamshire, UK) to 5 µL of amplified DNA in a final volume of 7 µL followed by incubation for 15 min at 37 °C and for 15 min at 80 °C. COI and 16S purified products were sequenced in both forward and reverse directions using an ABI 3730x1 DNA analyser (Applied Biosystems, Waltham, MA, USA) at KAUST BioSciences Core Laboratories (Thuwal, Saudi Arabia).

Molecular data analyses

Forward and reverse sequences were assembled and edited using Geneious® v.2021.2.2 (Biomatters Ltd., Auckland, New Zealand). Previously deposited sequences available

on public databases (GenBank and BOLD) (Ratnasingham and Hebert 2007) were included to the newly produced dataset. Multiple sequence alignments were performed using MAFFT v.7.490 (Kato and Standley 2013) with the E-INS-I option. Alignments were manually inspected and edited using AliView v.1.28 (Larsson 2014). Newly obtained sequences were deposited in GenBank database (Accession numbers: Online Resource 1).

Phylogenetic trees were inferred using maximum likelihood (ML) with RAxML v.2 (Stamatakis 2014) and Bayesian inference (BI) with MrBayes v.3.2.6 (Ronquist et al. 2012) on the CIPRES server (Miller et al. 2010). Prior to running phylogenetic analyses, appropriate evolutionary models were selected using jModelTest2 (Darriba et al. 2012) on the CIPRES server (Miller et al. 2010), resulting in the model GTR + I + G for COI and GTR + G for 16S. Maximum likelihood analyses were performed using default parameters and 1000 bootstrap replicates. For Bayesian analyses, two independent runs for four Markov chains were conducted for 10 million generations, with trees sampled every 1000th generation, and burn-in was set to 25%. Inter- and intraspecific genetic distances were calculated using MEGA v.11 with 1000 bootstrap replicates (Tamura et al. 2021. See Online Resource 2).

Statistical analyses

The occurrence of decapod crustaceans on their host corals and the patterns of association between different species of crabs and shrimps were assessed through correlation analyses performed using the R package *corrplot* (Wei and Simko 2021). Graphs were designed using the R packages *ggplot2* (Wickham 2016), *corrplot* (Wei and Simko 2021) and *ggpubr* (Kassambara 2023). All statistical analyses were performed using Rstudio v.4.2.2 (R Core Team 2022).

Results

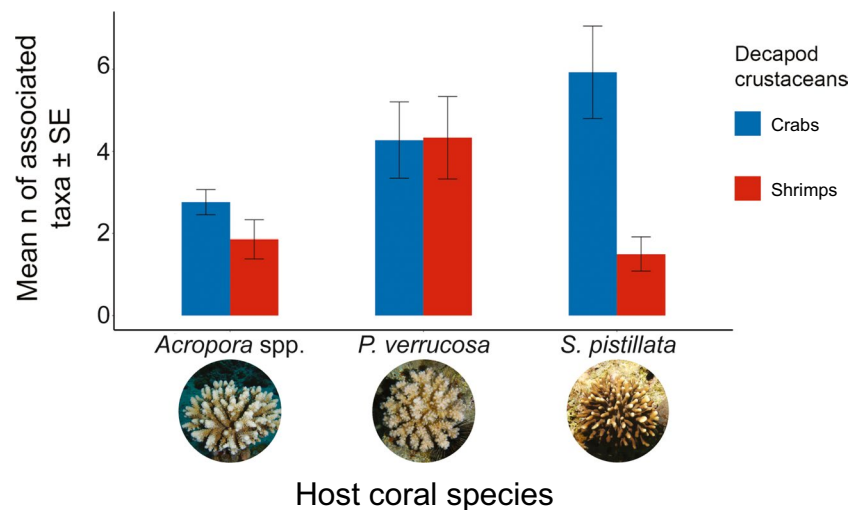
Morphological diversity and identification of coral-associated decapods

A total of 66 coral colonies out of the 67 collected were inhabited by decapod crustacean symbionts. A total number of 460 decapod crustacean individuals, including 301 crabs and 159 shrimps, was retrieved, representing six families, 14 genera, and 23 morphospecies (Online Resource 1). The total number of decapod crustaceans (crabs and shrimps) residing within each coral colony ranged from 2 to 11 in *Acropora* spp. colonies (mean = 4.6 ± 2.4 standard error SE), from 0 to 26 in *P. verrucosa* colonies (mean = 8.6 ± 7.5 SE), and from 1 to 25 in *S. pistillata* colonies (mean = 7.4 ± 6.7 SE) (Fig. 2).

Most of the specimens collected were morphologically identified to species level, while poorly preserved samples were only identified to genus level. Morphological analyses revealed that the collected symbiotic crabs could be ascribed to the three families: Trapeziidae Miers, 1886, Tetraliidae Castro, Ng and Ahyong, 2004, and Xanthidae MacLeay, 1838. Crabs belonging to the family Trapeziidae included the four morphospecies: *Trapezia bidentata* (Forskål, 1775), *Trapezia cymodoce* (Herbst, 1801), *Trapezia guttata* Rüppell, 1830, and *Trapezia tigrina* Eydoux and Souleyet, 1842. Representatives of the family Tetraliidae belonged to the three different morphospecies *Tetralia cavimana* Heller, 1860, *Tetralia glaberima* (Herbst, 1790), and *Tetralia nigrolineata* Serène & Pham, 1957. Non-strictly coral-symbiotic crabs (i.e. taxa that can also be free-living independently of the host coral) included representatives of the family Xanthidae, namely *Luniella spinipes* (Heller, 1860) and *Actaea* spp., and of the family Pilumnidae Samouelle, 1819, namely the genus *Pilumnus* Leach, 1816.

The symbiotic shrimps collected belonged to two families: Alpheidae Rafinesque, 1815, and Palaemonidae

Fig. 2 Decapod crustaceans and their host corals: mean numbers of crabs and shrimps associated with taxa of branching corals sampled for the present study. Error bars indicate the standard error (\pm SE)



Rafinesque, 1815. The family Alpheidae was mostly represented by the species *Alpheus lottini* Guérin, 1829, and the genus *Synalpheus* Spence Bate, 1888. Shrimps belonging to the family Palaemonidae included the species *Harpiliopsis depressa* (Simpson, 1860) and *Periclimenes madreporae* (Bruce, 1969) and the genera *Jocaste* Holthuis, 1952, *Exoclimenella* Bruce, 1995, and *Harpilius* Dana, 1852.

Alignments and sequence data

For the crabs, we successfully amplified 150 COI sequences and 148 16S sequences. Newly obtained sequences were combined with 107 COI and 64 16S sequences previously deposited in GenBank and BOLD (Online Resource 1). The COI alignment comprised 528 bp, including 248 conserved and 280 variable sites, while the 16S a total of 503 bp, with 211 conserved and 283 variable sites. For the shrimps, we obtained 104 COI and 78 16S sequences. Newly generated sequences were combined with 43 and 26 sequences from GenBank for COI and 16S, respectively (Online Resource 1). The COI alignment comprised 640 bp, with 312 conserved and 328 variable sites, while the 16S alignment was composed of 505 bp, including 186 conserved and 307 variable sites. For the remaining 131 specimens, either they did not successfully amplify with any of the two markers or the obtained sequences were not readable.

Phylogenetic analyses

Both ML and BI phylogenetic reconstructions resolved the same major clades for both crabs and shrimps. However, the BI trees provided a better resolution of the phylogenetic hypotheses presented. Hence, we reported the BI topologies (Figs. 3 and 4), including BI posterior probabilities and ML bootstrap values at nodes.

The crab sequences analysed fell within a total of 33 clades in the COI phylogenetic hypotheses and within 21 molecular clades in the 16S reconstruction. In particular, for the COI, crabs associated with coral colonies from the Red Sea were included in seven molecular clades (clade III, clade V, clade VII, clade XI, clade XVII, clade XXVI, clade XXVIII) and for the 16S within 11 different molecular clades (clade III, clade V, clade VII, clade XI, clade XVII, clade XXVI, clade XXVIII, clade XXXIII, clade XXXVI, clade XXXVII, clade XXXVIII). In the COI reconstruction, the genus *Trapezia* nested into four clades, clade III (*T. guttata*), clade V (*T. bidentata*), clade VII (*T. tigrina*), and clade XI (*T. cymodoce*) (Fig. 3a). These four clades included sequences from different locations (Red Sea and Reunion Island for *T. guttata* (clade III), Red Sea and New Caledonia for *T. cymodoce* (clade XI), Red Sea, French Polynesia, and Mexico for *T. tigrina* (clade VII)). In the 16S reconstruction instead, representatives of the genus *Trapezia* clustered into six molecular clades,

namely clade III (*T. guttata*), clade V (*T. bidentata* L1), clade XXXVII (*T. bidentata* L2), clade VII (*T. tigrina*), clade XI (*T. cymodoce*), and clade XXXVIII (*Trapezia* sp.) (Fig. 3b). Five of these six clades also included sequences from different locations (Red Sea, New Caledonia, and Reunion Island for *T. guttata* (clade III), Red Sea and Reunion Island for *T. bidentata* L1 (clade V), New Caledonia and Palmyra Atoll for *T. bidentata* L2 (clade XXXVII), and Red Sea and Philippines for *T. tigrina* (clade VII)). One clade (clade XXXVIII (*Trapezia* sp.)) only included sequences from the Red Sea. Thus, the 16S reconstruction allowed to distinguish two lineages of *T. bidentata* (L1 (clade V) and L2 (clade XXXVII)), which instead clustered into a single clade in the COI reconstruction (clade V), and to further report an additional lineage of *Trapezia* sp. (clade XXXVIII), which grouped two specimens from our Red Sea dataset which sequences were not readable when amplified with the COI marker. With regard to the genus *Tetralia*, morphological analyses revealed the presence of three morphospecies among our samples, namely *T. cavimana*, *T. glaberrima*, and *T. nigrolineata*. Yet, all the Red Sea material fell within the same molecular clade (clade XVII) in both the COI and the 16S trees independently of the morphology. The COI reconstruction revealed two additional clades for this genus, grouping previously deposited sequences from New Caledonia and Papua New Guinea, which were not available for the 16S marker, namely clade XVIII (*T. ocucaerulea*) and clade XIX (*Trapezia* sp.), respectively (Fig. 3b). Finally, non-symbiotic crabs from the Red Sea fell within two clades in the COI phylogenetic tree (Fig. 3a), clade XXVI (*Luniella spinipes*) and clade XXVIII (*Actaea* sp.), and within four clades in the 16S reconstruction (Fig. 3b), namely, clade XXVI (*Luniella spinipes*), clade XXVIII (*Actaea* sp.), clade XXXIII (*Pilumnus* sp.), and clade XXXVI (*Pilumnus* sp.).

When considering shrimps sequences, the COI analyses revealed the presence of 32 molecular clades, while the 16S reconstruction identified 20 molecular clades. The material from the Red Sea examined for the present study fell within 12 molecular clades (clade I, clade IV, clade VIII, clade XI, clade XII, clade XIV, clade XVI, clade XVII, clade XIX, clade XXI, clade XXIII, clade XXIV) when amplified with the COI marker and within eight molecular clades (clade I, clade VIII, clade XI, clade XII, clade XVII, clade XXIII, clade XXIV, clade XXXIV) when considering the 16S phylogeny reconstructions. Species of the genus *Alpheus* fell within three clades based on the COI locus, namely clade I (*A. lottini*) (clade A sensu Williams et al. (2002) and Van Wormhoudt et al. (2019)), clade IV (*Alpheus bucephalus* Coutière, 1905), and clade VIII (*Alpheus bucephaloides* Nobili, 1905) (Fig. 4a). However, the genus *Alpheus* was only represented by two clades from the Red Sea in the tree inferred from 16S: clade I (*A. lottini*) and clade VIII (*A. bucephaloides*) (Fig. 4b). In both phylogeny reconstructions, two clades included representatives of the genus *Synalpheus*, namely clade XXIII (*Synalpheus triunguiculatus*

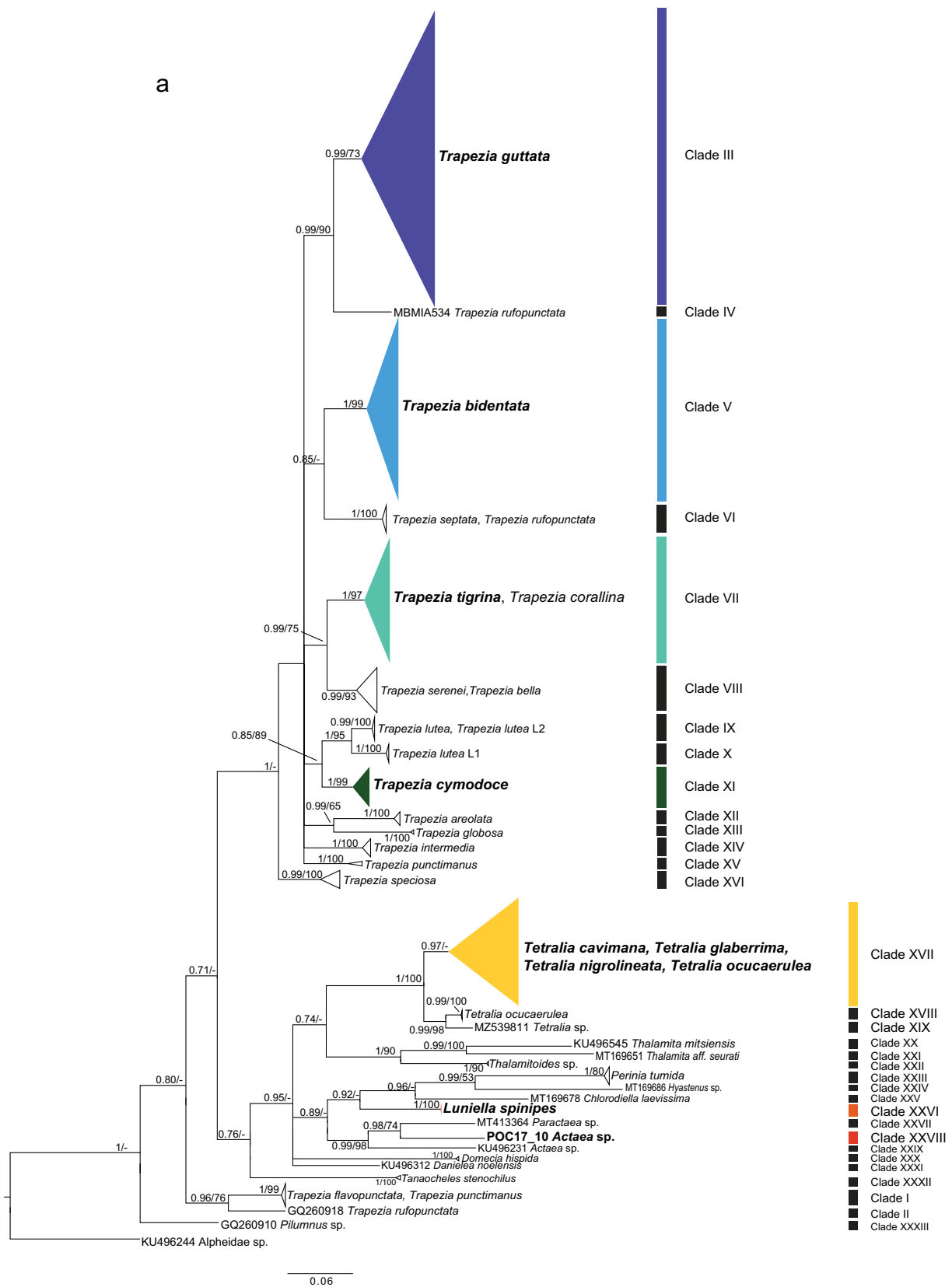


Fig. 3 Bayesian inference phylogenetic reconstruction of the symbiotic crabs in association with branching corals of the genera *Acropora*, *Pocillopora*, and *Stylophora* sampled in the Central Red Sea based on two molecular markers: **a** COI (*Alpheus lottini* was selected

as outgroup) and **b** 16S (*Alpheidae* sp. was chosen as outgroup). Node values correspond to Bayesian posterior probability (≥ 0.7) and maximum likelihood bootstrap values ($\geq 70\%$). Taxa for which new sequences were obtained in this study are in bold

Fig. 3 (continued) b

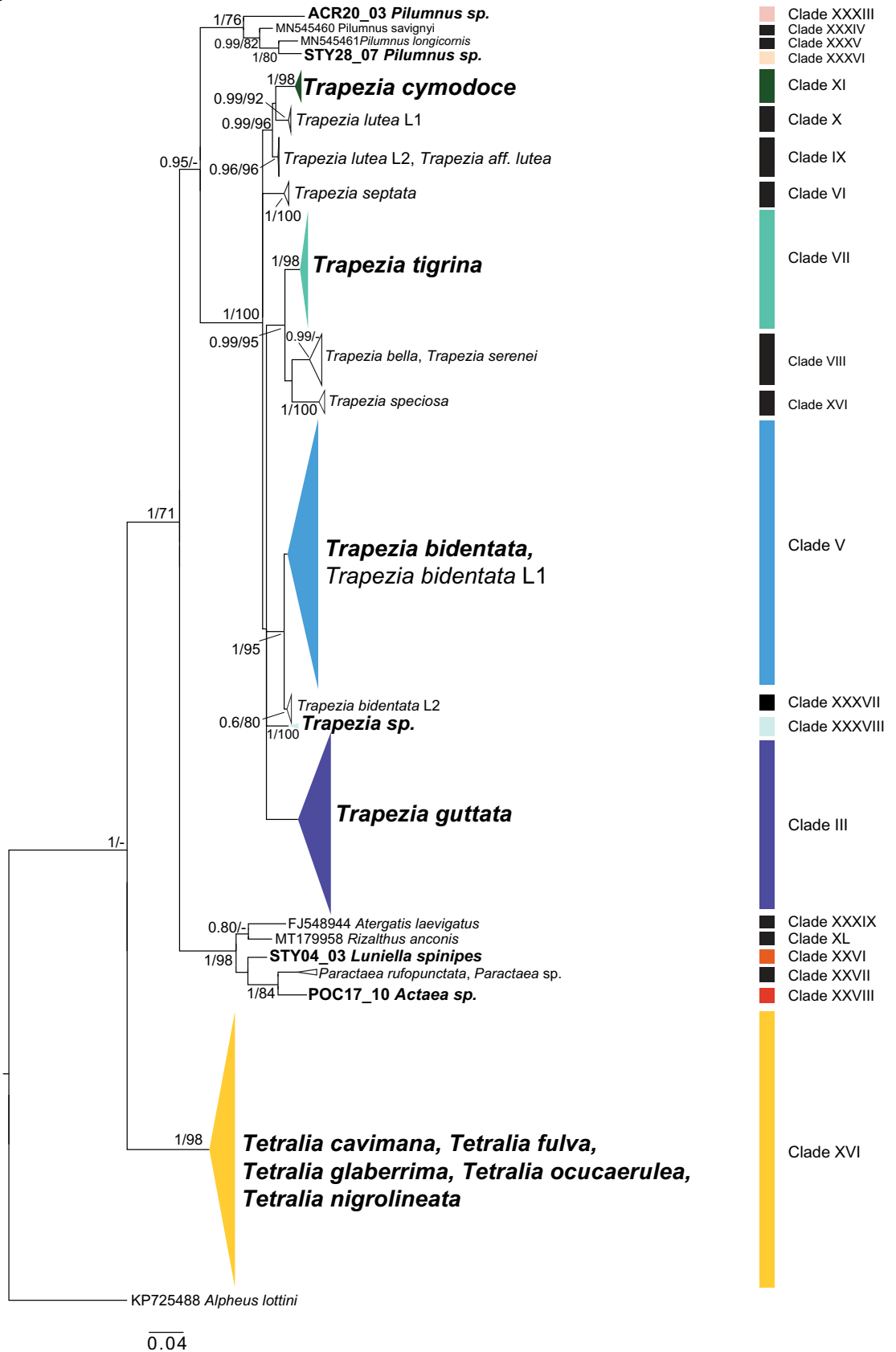


Fig. 4 Bayesian inference phylogenetic reconstruction of the symbiotic shrimps in association with branching corals of the genera *Acropora*, *Pocillopora*, and *Stylophora* sampled in the Central Red Sea based on two molecular markers: **a** COI (*Trapezia cymodoce* was selected as outgroup) **b** 16S (*Trapezia cymodoce* was chosen as outgroup). Node values correspond to Bayesian posterior probability (≥ 0.7) and maximum likelihood bootstrap values ($\geq 70\%$). Taxa for which new sequences were obtained in this study are in bold

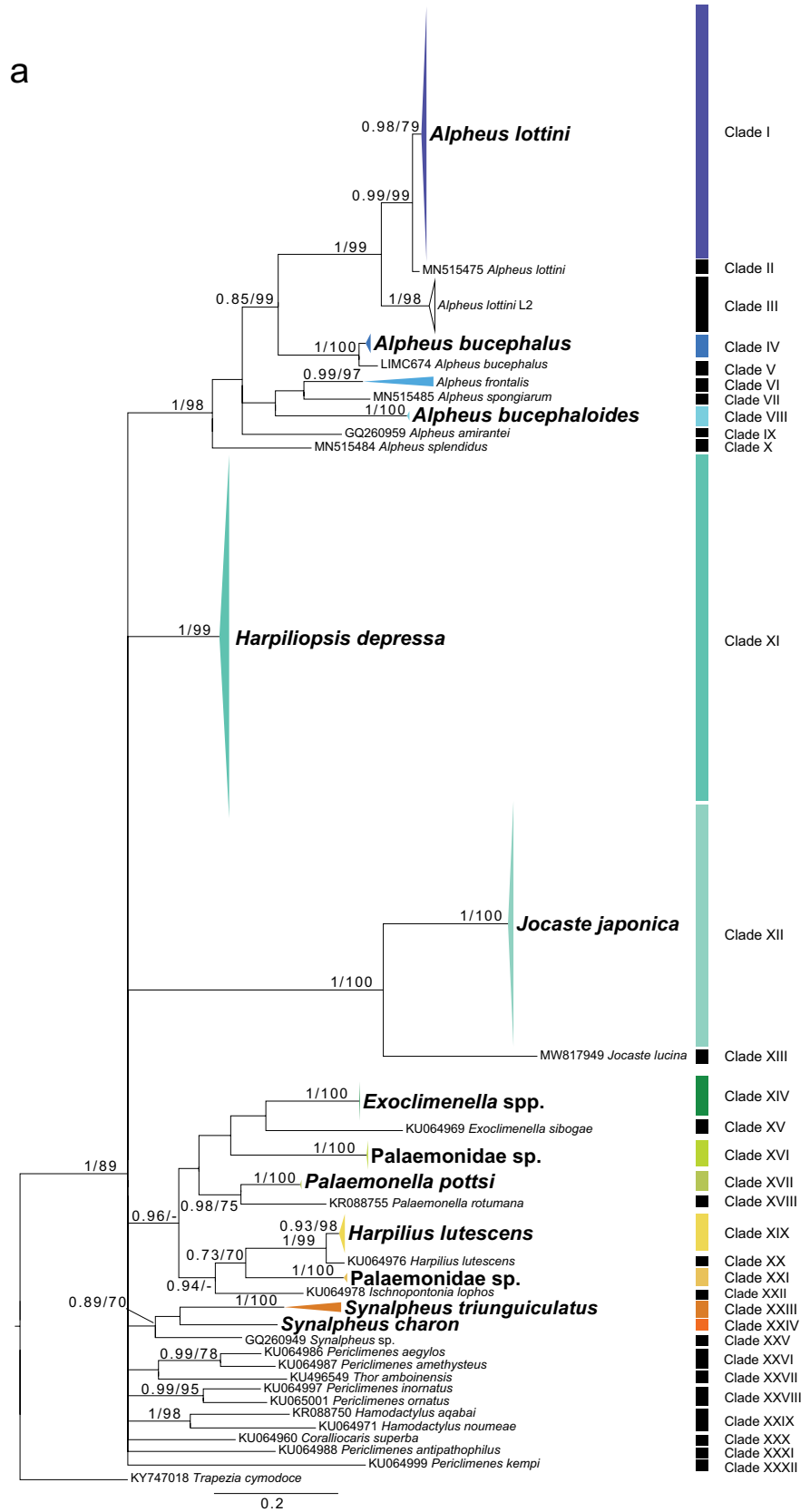
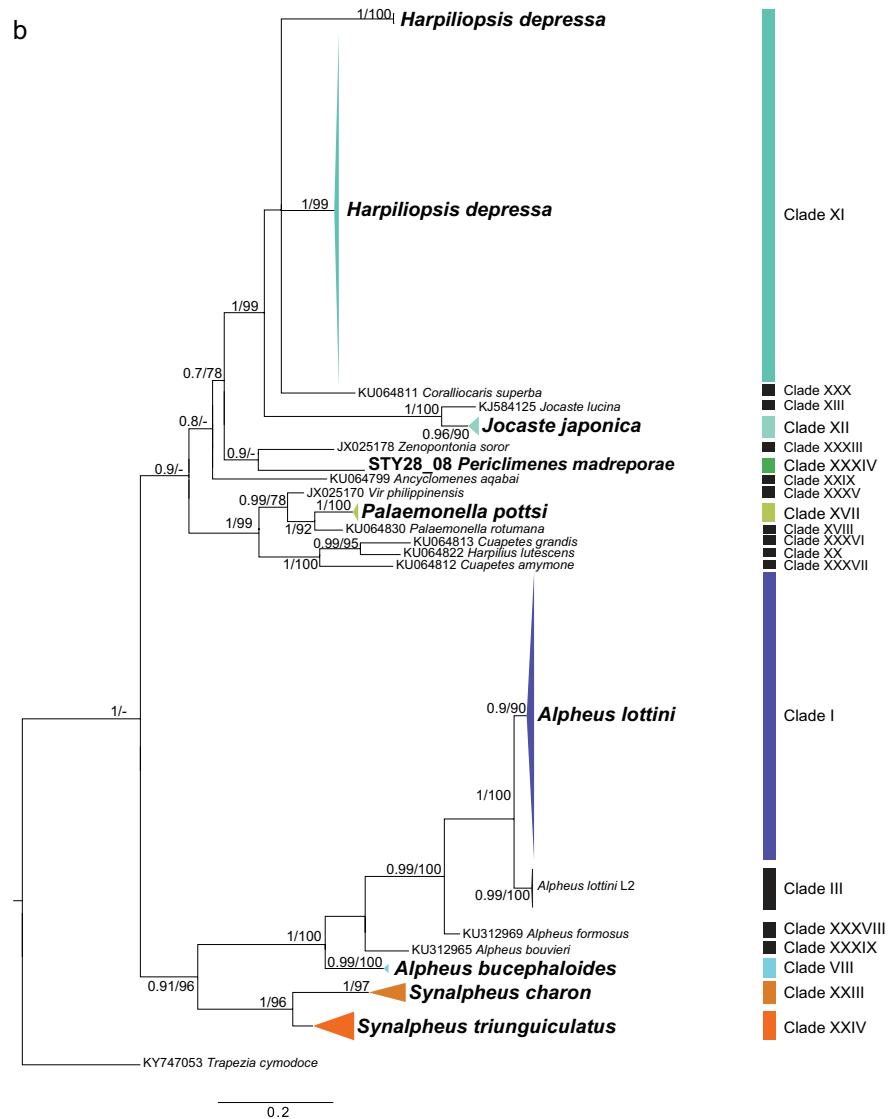


Fig. 4 (continued)



(Paulson, 1875)) and clade XXIV (*Synalpheus charon* (Heller, 1861)) (Fig. 4a, b). Although the genera and species of shrimps retrieved in this study belonged to two families, namely Alpheidae and Palaemonidae, the phylogenetic relationships between the two families could not be further clarified by the molecular analyses performed for this study (Fig. 4; Online Resource 4). Moreover, both COI and 16S phylogenetic analyses revealed three additional molecular clades of symbiotic shrimps from the Red Sea material, namely clade XI (*Harpiliopsis depressa*), clade XII (*Jocaste japonica*) (Ortmann, 1890), and clade XVII (*Palaemonella pottsii*) (Borradaile, 1915) (Fig. 4a, b). Finally, while the COI trees identified one molecular clade for the species *Harpilius lutescens* (clade XIX), one clade for the genus *Exoclimenella* (clade XIV), and two clades of the genus *Periclimenes* (clade XVI and XXI) (Fig. 4a), the 16S phylogeny reconstructions only revealed one clade for the species *P. madreporae* (clade XXXIV) (Fig. 4b).

Composition and species co-occurrence of decapod ectosymbiont communities

Crabs belonging to the species *T. guttata* mainly occurred within *S. pistillata* colonies (98%; $n = 136$), while *T. tigrina* was observed to be exclusively associated with *P. verrucosa* (100%; $n = 21$) (Fig. 5a). *Trapezia bidentata* and *T. cymodoce* were observed to be associated with both *P. verrucosa* (80% and 17%, respectively) and *S. pistillata* (20% and 83%, respectively) corals (Fig. 5a). Crabs belonging to the genus *Tetralia* were solely associated with *Acropora* colonies (100%) (Fig. 5a). *Alpheus* shrimps and *Harpiliopsis depressa* were commonly associated with both *P. verrucosa* (53% and 72%, respectively) and *S. pistillata* (47% and 28%, respectively) (Fig. 5a). The shrimps *J. japonica* and *Harpilius lutescens* were exclusively found on *Acropora* colonies (100%) (Fig. 5a). Lastly, representatives of

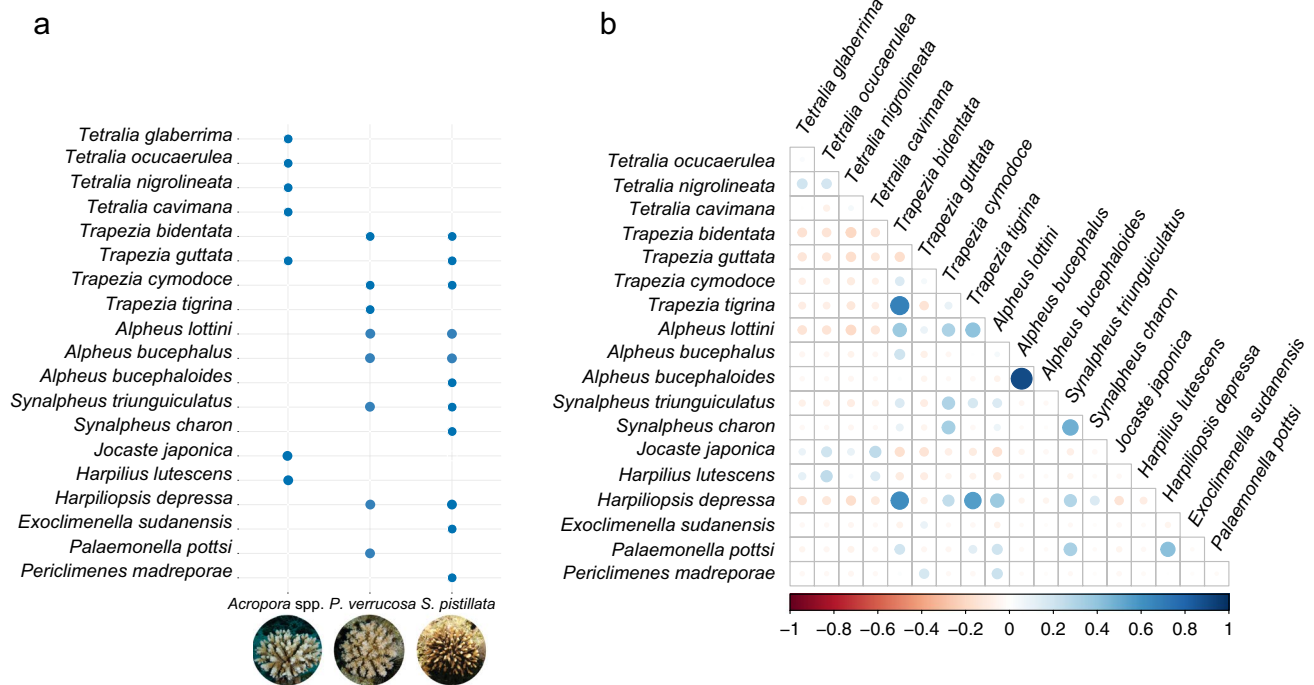


Fig. 5 **a** Presence-absence matrix showing the occurrence of the 460 collected decapod crustaceans ectosymbionts with the three different branching host coral taxa. **b** Correlation plot showing the co-occurrence of decapod crustaceans ectosymbionts. In the bottom bar, “1” indicates a positive linear correlation between the two species considered, thus the presence of the two species of decapod crustaceans at the same time within the same host coral; “0” and “-1” indicate

no linear correlation and negative linear correlation between two species, respectively, hence suggesting that the two associated crustaceans never occur with the same host coral. Colour depth and size of the circles indicate the strength of the correlation. Decapods that were only identified to genus level or not recognised as symbionts of the branching scleractinian corals considered were excluded from the correlation analysis

the genera *Cuapetes* Clark, 1919, and *Periclimenes* Costa, 1844, which are not commonly known as *Acropora* symbionts (Stella et al. 2011a; Horká et al. 2016; Frolová et al. 2022), were also retrieved from the sampled *Acropora* colonies.

When investigating the co-occurrence of different species of decapod crustaceans within the same coral colonies, a correlation analyses showed a strong and significant correlation ($p \leq 0.001$) in the presence of *T. bidentata* with *T. tigrina* ($r = 0.67$) and *Harpiliopsis depressa* ($r = 0.62$), *T. tigrina* with *A. lottini* ($r = 0.4$) and *H. depressa* ($r = 0.55$), *A. bucephalus* with *A. bucephaloides* ($r = 0.89$), *H. depressa* with *P. pottsi* ($r = 0.41$), and *S. triunguiculatus* with *S. charon* ($r = 0.48$) (Fig. 5b; Online Resource 3). A significant positive correlation ($p \leq 0.01$) was also found when considering the presence of *A. lottini* with *T. bidentata* ($r = 0.36$), *T. cymodoce* ($r = 0.31$), and *H. depressa* ($r = 0.36$), *T. cymodoce* with *S. charon* ($r = 0.33$), and *P. pottsi* with *S. triunguiculatus* ($r = 0.32$) (Fig. 5b; Online Resource 3). Other species pairs, although sporadically observed together, did not show any significant correlation in their co-occurrence within the hosts (Fig. 5b; Online Resource 3).

Discussion

Decapod crustaceans represent most of the coral-associated fauna reported in the literature (Alonso-Domínguez et al. 2022). Although limited research is available on crustacean presence and abundance in the Red Sea and to our knowledge the association of Decapoda with branching corals in this region was not previously investigated through a molecular approach, the species occurrence observed in the present study is consistent with findings reported from different areas of the world (Rouzé et al. 2017; Pisapia et al. 2020). When analysing the biodiversity of decapod crustaceans associated with *P. verrucosa*, our findings confirmed those of Britayev et al. (2017), who observed the presence of four species of the crab genus *Trapezia* (*T. bidentata*, *T. tigrina*, *T. guttata*, *T. cymodoce*) and of three shrimps (*A. lottini*, *H. depressa*, and *P. madreporae*) along the northern Saudi Arabian coast of the Red Sea. Moreover, along the Sudanese coastline of the Red Sea, Edwards and Emberton (1980) reported the occurrence of the crab *T. guttata* and the shrimps *A. bucephaloides*, *S. charon*, and *H. depressa* as symbionts of *S. pistillata* colonies, which is in line with the patterns of ectosymbiont occurrence observed in the

present study. Our results were also in agreement with those of Pisapia et al. (2020), who reported *Trapezia* species to be the most abundant taxa with the coral family Pocilloporidae Gray, 1840 in Moorea, French Polynesia. Trapeziidae crabs observed in our study were similar to those reported by Rouzé et al. (2017) from New Caledonia, highlighting the presence of the species *T. guttata* (clade I), *T. bidentata* (clade V), *T. tigrina* (clade VII), and *T. cymodoce* (clade XI). Our specimens of the shrimp species *A. lottini* were all included within the lineage of *A. lottini* L1, described by Rouzé et al. (2017) from New Caledonia and Reunion Island. Although a second lineage of *A. lottini* was previously observed in New Caledonia and the Pacific Ocean (*A. lottini* L2, *sensu* Rouzé et al. (2017); clade B *sensu* Knowlton and Weigt (1997) and Van Wormhoudt et al. (2019)), none of our specimens appeared to be related to such lineage. This suggests that the *A. lottini* L1 lineage may be a widespread taxon distributed from the Red Sea to the Pacific Ocean, while the *A. lottini* L2 lineage may have a narrower geographic distribution. However, due to a lack of enough comparative material encompassing all biogeographical regions, the divergence of Red Sea lineages could not be ascertained. In future studies, next-generation sequencing approaches (e.g. the target enrichment of Ultra Conserved Elements and Exons) (Wolfe et al. 2019) could elucidate species boundaries and the actual geographical distribution of the different lineages in the Indo-Pacific region.

When looking at different host coral species, we observed variation in the composition of the decapod crustacean communities. While, on average, *P. verrucosa* coral colonies had a comparable number of associated crabs and shrimps individuals, the latter represented a smaller portion of symbiotic individuals in comparison to *Acropora* corals and less than half of the observations considering *S. pistillata* hosts (Fig. 2). Both alpheid shrimps and trapeziid crabs are recognised to be highly dependent on their hosts, showing species-specific patterns of association with the corals (Vytopil and Willis 2001; Stella et al. 2010), as well as a high territoriality and species-specific ecological traits (Lassig 1977; Rouzé et al. 2017). Accordingly, our study showed associations between *Alpheus* and *Trapezia* species and pocilloporid corals, in particular considering the snapping shrimp *A. lottini* and the crabs *T. tigrina*, *T. cymodoce*, and *T. bidentata*. The specific association between the lineage of *A. lottini* (L1) and *T. cymodoce* was also reported by Rouzé et al. (2017) from New Caledonia, suggesting that this shrimp species may provide a beneficial contribution to *T. cymodoce* by cleaning their chelipeds (Lassig 1977). The presence of both trapeziid crabs and alpheid shrimps on *Pocillopora* colonies was also observed by Huber (1987) and Castro (1996), highlighting their success in excluding other crustacean taxa with similar demands from their ecological niches, which could explain the species-specificity of their occurrence (Chomitz et al.

2023). Moreover, the co-occurrence of alpheid shrimps with other *Trapezia* species was reported by Stier et al. (2012), confirming the synergistic effects of multiple ectosymbionts occurring on branching corals (Billick and Case 1994; McKeon et al. 2012). Interestingly, Hoeksema and Franssen (2011) found that various shrimps species belonging to Palaemonidae and Thoridae Kingsley, 1878, co-occurred in the scleractinian *Heliofungia actiniformis* (Quoy and Gaimard, 1833) by living in different parts of the coral host, an aspect that unfortunately we did not investigate during our underwater sampling. As such, species of crabs and shrimps may co-occur on coral colonies to combine their defensive strategies and enhance the chances of survival of their hosts against predators (e.g. corallivorous starfish and gastropods) (McKeon et al. 2012). While their co-occurrence did not appear to be significantly correlated, *Tetralia* crabs were observed to share their habitat within *Acropora* colonies with the palaemonid shrimps *H. lutescens* and *J. japonica*, possibly due to their common substrate preference (Limviriyakul et al. 2016). Rouzé et al. (2017) also highlighted that the strength of the interactions between crabs and shrimps species may vary depending on their geographical locality. Hence, such behaviours and patterns of symbiont associations should be further investigated in the Red Sea and the wider Indo-Pacific region, to better elucidate their interactions.

The patterns of association of decapod crustaceans highlighted in our study are particularly significant not only when looking at the interactions between crustacean taxa but also when analysing the occurrence of symbionts with the hosts. While the data here reported refer to a single sampling effort, coral-associated fauna may be subject to temporal variation (Alvarado and Vargas-Castillo 2012), and further sampling could be needed to test whether the decapod community composition associated with branching corals changes through time and under particular conditions (e.g. seasonality). Although the coral colonies collected for this study were not bleached, nor presented evidence of partial mortality, sampling was performed after the 2015–2016 bleaching event, which affected coral reefs globally and in the Red Sea (Monroe et al. 2018), and could have impacted the associated benthic communities as well (Britayev et al. 2023).

The association of certain crustacean species (e.g. the genus *Tetralia* and the species *Trapezia tigrina*, *Jocaste japonica*, and *Harpilius lutescens*) with specific corals takes on relevance considering the current status of coral reef ecosystems. The challenges coral reefs are facing in a scenario of climate change (Hoegh-Guldberg et al. 2017; Hughes et al. 2018a), ocean acidification (Pandolfi et al. 2011; Andersson and Gledhill 2012), and anthropogenic stressors (Burke et al. 2011; Hughes et al. 2018b) could in fact have implications not only on the host corals, but also on the associated benthic communities, threatening their biodiversity (Hoeksema 2017). Accordingly, the loss of significant coral taxa could lead to

habitat depletion for obligate symbionts and shifts in the structure of reef ecosystems and communities, eventually leading to the extinction of highly specialised symbionts occurring within a limited range of hosts. For instance, Stella et al. (2011b) demonstrated that bleaching of *Pocillopora damicornis* (Linnaeus, 1758) colonies in Lizard Island, Australia, negatively affected the occurrence of the obligate symbionts *T. cymodoce* crabs, significantly lowering their density and fecundity within a few weeks.

As the frequency of marine heatwaves and bleaching events has increased in the Red Sea (Genevier et al. 2019), leading to mortality of branching corals, according to our results, this could lead to the loss of habitat availability for associated decapod crustaceans and consequent decrease in the occurrence and abundance of host-specific genera (Britayev et al. 2023). While Furby et al. (2013) reported the families Acroporidae Verrill, 1901, and Pocilloporidae to be the most abundant coral genera in shallow-water reefs of the central Saudi Arabian Red Sea, they found 33% of the *Acropora* colonies to be affected by the 2010 bleaching event, compared to 19% of the *Pocillopora* coverage. For instance, the higher susceptibility documented for acroporids during major bleaching events in the central Red Sea (Furby et al. 2013; Monroe et al. 2018) could lead to a loss of *Tetralia* crabs and of shrimps of the species *J. japonica* and *H. lutescens*, which in our study were solely observed in association with *Acropora* colonies (Fig. 5). Considering that Robitzch et al. (2015) found a single population of *P. verrucosa* in our study area, mortality of these corals could negatively affect trapeziid crabs and alpheid shrimps living in between their branches, as shown by our results (Fig. 5). Such loss of associated organisms would ultimately affect their functional roles (e.g. cleaning and protection of the hosts), thus leading to cascade effects negatively influencing entire reef ecosystems. Nevertheless, patterns of ectosymbiont assemblages and occurrence in different study areas could align or shift depending on the evolutionary lineage of the host corals, even considering single species (Rouzé et al. 2017), thus leading to different scenarios in areas beyond the Red Sea.

Conclusions

The present study represents an example towards the understanding of the diversity of decapod crustaceans associated with branching corals in the central Red Sea and serves as a baseline for further research on the molecular diversity of decapod crustaceans, as well as providing a reference barcoding dataset for future studies applying methodologies such as ARMS and environmental DNA (eDNA). Since investigating the occurrence and

abundance of marine organisms is fundamental to assess their patterns of biodiversity and evolution (Bowen et al. 2013), as well as their patterns of co-occurrence, this study provided insights into the potential loss of decapod crustaceans associated with branching corals in the context of bleaching and host mortality, highlighting how the loss of certain coral taxa in the Red Sea could lead to the extinction of highly specialized symbionts.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12526-024-01457-1>.

Acknowledgements This research was completed in accordance with the policies and procedures at KAUST (King Abdullah University of Science and Technology). Permissions relevant for KAUST to undertake the research have been obtained from the relevant governmental agencies in the Kingdom of Saudi Arabia. Authors wish to thank the captain and crew of the MV Dream Master, the KAUST Coastal and Marine Resources Core Laboratory, and AK Gusti (KAUST) for field-work logistics in the Red Sea. Additionally, we wish to thank three anonymous reviewers for their valuable comments as well as the journal editor for handling the submission and providing useful comments that helped improving the quality of the manuscript.

Funding This study was supported by KAUST (baseline research funds to ML Berumen and F Benzoni). LM was supported by additional funding from the KAUST Visiting Student Research Program.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical approval No animal testing was performed during this study. This study was conducted in compliance with all relevant policies and procedures of King Abdullah University of Science and Technology (KAUST).

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements. The study is compliant with CBD and Nagoya protocols.

Data availability Data generated and/or analysed during the current study are included in this published article and its supplementary information files. Sequences obtained in this study were deposited in GenBank database (OR857734-OR857835; OR857584-OR857733; OR852973-OR853050; OR852824-OR852972); accession numbers are available as Online Resource of the present manuscript.

Author contribution LM: Formal analysis; investigation; data curation; writing, original draft; writing, review and editing; visualization. TIT: Conceptualization; methodology; validation; investigation; data curation; writing, original draft; writing, review and editing; supervision; project administration. RA: Conceptualization; investigation; sampling; data collection; writing, review and editing; supervision. DM: Conceptualization, investigation, sampling. MT: Sampling. AA: Validation, investigation. RL: Validation, investigation. MP: Sampling. MLB: Resources, funding acquisition. FB: Methodology; resources; writing, review and editing; supervision; project administration; funding acquisition. All authors have read and agreed to the published version of the manuscript.

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