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# Clownfish hosting anemones (Anthozoa, Actiniaria) of the Red Sea: new associations and distributions, historical misidentifications, and morphological variability

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## Abstract

**Background:** The Red Sea contains thousands of kilometers of fringing reef systems inhabited by clownfish and sea anemones, yet there is no consensus regarding the diversity of host anemone species that inhabit this region. We sought to clarify a historical record and recent literature sources that disagree on the diversity of host anemone species in the Red Sea, which contains one endemic anemonefish, *Amphiprion bicinctus* Rüppell 1830.

**Results:** We conducted 73 surveys spanning ~ 1600 km of coastline from the northern Saudi Arabian Red Sea to the Gulf of Aden and encountered seven species of host anemones, six of which hosted *A. bicinctus*. We revise the list of symbionts for *A. bicinctus* to include *Stichodactyla haddoni* (Saville-Kent, 1893) and *Stichodactyla mertensii* Brandt, 1835 which were both observed in multiple regions. We describe Red Sea phenotypic variability in *Heteractis crispa* (Hemprich & Ehrenberg in Ehrenberg, 1834) and *Heteractis aurora* (Quoy & Gaimard, 1833), which may indicate that these species hybridize in this region. We did not encounter *Stichodactyla gigantea* (Forsskål, 1775), although the Red Sea is the type locality for this species. Further, a thorough review of peer-reviewed literature, occurrence records, and misidentified basis of record reports dating back to the early twentieth century indicate that it is unlikely that *S. gigantea* occurs in the Red Sea.

**Conclusions:** In sum, we present a new guide for the host anemones of the Red Sea, revise the host specificity of *A. bicinctus*, and question whether *S. gigantea* occurs in the central and western Indian Ocean.

**Keywords:** Marine ecology, Amphiprionae, Stichodactylidae, Saudi Arabia, Indian Ocean

## Background

The symbiosis between clownfishes (Amphiprionae) and their host sea anemones (Actiniidae, Stichodactylidae, and Thalassianthidae) is an iconic example of mutualism in the ocean. Many studies investigate the interactions between these hosts and occupants to not only understand

the evolution and ecology of this relationship, but also broadly test fundamental questions regarding symbiosis (Marcionetti et al. 2019; Roux et al. 2019). As such, correctly characterizing the specificity of anemonefish to different hosts (i.e., which symbiont anemonefish naturally pair with members of the ten host anemone species) and the distributions of both host anemone and anemonefish is critically important in understanding the evolutionary processes that have given rise to these relationships and their biogeography (Camp et al. 2016). Additionally, as host sea anemones constitute critical habitat for a range of

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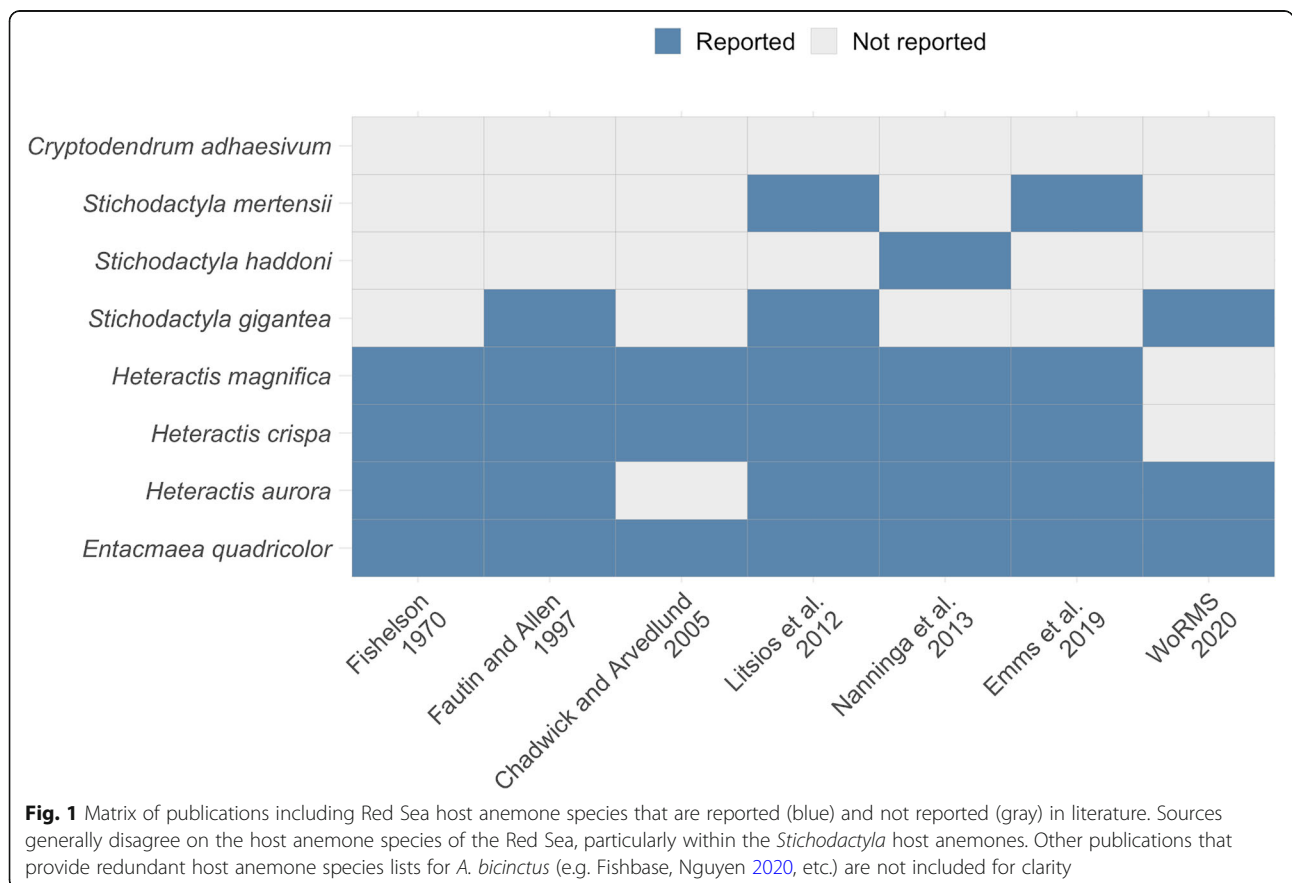
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fishes and invertebrates, changes in their distributions are important for multiple species on several trophic levels (Randall and Fautin 2002; Arvedlund et al. 2006). While clownfish host specificity, distributions, and symbiosis have been thoroughly investigated using clownfish and sea anemone species from many tropical regions of the world (e.g. Richardson et al. 1997; Srinivasan et al. 1999; Camp et al. 2016; Titus et al. 2020), comparatively little work on the subject has been conducted in the Red Sea (but see, e.g., Chadwick and Arvedlund 2005, Huebner et al. 2012, Nanninga et al. 2014).

The Red Sea contains over 2000 km of fringing reef habitat, but is only inhabited by one species of anemonefish, *Amphiprion bicinctus* Rüppell 1830, which ranges from the Gulf of Aqaba in the north to the Gulf of Aden in the south. More than 50% of all publications from the Red Sea come from the northern Gulf of Aqaba or Sinai Peninsula, but this region constitutes less than 2% of the total area of the Red Sea (Berumen et al. 2013). The comparatively smaller collection of publications directly investigating Red Sea anemones is even more biased towards this region: ~80% of research on this topic was conducted in the Sinai Peninsula (based on ISI Web of Knowledge review, Section 2.3). While *A. bicinctus* has

been the subject of recent studies (Brolund et al. 2004, Nanninga et al. 2014, Howell et al. 2016, Casas et al. 2018), published information on the diversity and distribution of its host sea anemones is largely conflicting and inconsistent. Studies from the Red Sea and Gulf of Aden typically list three to five host species for *A. bicinctus*: *Entacmaea quadricolor* (Leuckart in Rüppell & Leuckart, 1828), *Heteractis aurora* (Quoy & Gaimard, 1833), *Heteractis crispera* (Hemprich & Ehrenberg in Ehrenberg, 1834), *Heteractis magnifica* (Quoy & Gaimard, 1833), *Stichodactyla mertensii* (Brandt, 1835), and *Stichodactyla gigantea* (Forsskål, 1775) (Red Sea host combinations from Fishelson 1970, Fautin and Allen, 1992, Nanninga et al. 2014, Emms et al. 2020; Fig. 1).

Information on the host carpet anemones (*Stichodactyla* spp.) is particularly contentious in the Red Sea. Studies identify contradictory combinations of carpet anemone species in the region, databases produce occurrence records that contradict published ranges and distributions, and some authors refer to the same species of host anemone in multiple studies by alternate names. This confusion is likely a result of similar morphologies and a changing taxonomic nomenclature through time between the three carpet



anemones: *Stichodactyla haddoni* (Saville-Kent, 1893), *S. mertensii*, and *S. gigantea*.

*Stichodactyla gigantea* was the first carpet anemone described in the Red Sea, by Forsskål in 1775 (as *Priapus giganteus*). This species was subsequently listed as a Red Sea inhabitant in publications over the next 200 years (Gohar 1948, Schlichter 1968, Allen 1972, Litsios et al. 2012). *Stichodactyla haddoni* and *S. mertensii* are not typically listed in older publications from the Red Sea, but several recent studies list various combinations of these species in the region (Nanninga et al. 2013, Gatins, Saenz-Agudelo, Scott and Berumen, 2018, Emms et al. 2020). Between 1900 and 1980 there were numerous instances of one host carpet anemone species being described by another species' name. For example, Allen uses the name *Stoichactis gigantea* to refer to *Stichodactyla mertensii* in multiple publications (Allen 1972, 1973, 1975a, 1975b, 1978). Dunn (1981), who produced the seminal work on host sea anemone distributions and anemonefish pairings, subsequently cites Allen (1972) when discussing the Red Sea distribution of the carpet anemones: "*Stichodactyla mertensii* is not host for *Amphiprion bicinctus* in the Red Sea as indicated by Allen; rather, *S. gigantea* is." This is just one example of many taxonomic contradictions present in this group over the last 150 years which have persisted to the present, resulting in numerous published identification errors in the region. Further, incomplete host anemone descriptions in Red Sea field guides exacerbate identification problems. For example, Lieske et al. (2004) list *S. gigantea*, *E. quadricolor*, *H. aurora*, *H. crispa*, and *H. magnifica* as hosts for *A. bicinctus*, contradicting other recent authors. Additionally, Lieske and Myers do not mention *S. gigantea* as a Red Sea species at all in the sea anemone section of their field guide, adding further confusion. Taken together, these contradictions in a range of sources underscore the need for the clarification of Red Sea host anemone species.

To determine the species of host sea anemones and clarify their anemonefish associations in the Red Sea and eastern Gulf of Aden we conducted visual surveys of host anemones. Using these surveys as a baseline, we then reevaluated previous reports from the literature, identifying likely misidentifications in the historical basis of record reports and host anemone occurrence records. We further reviewed anemone and anemonefish occurrence records from two databases: the Ocean Biogeographic Information System (OBIS) and the citizen science database iNaturalist, in order to identify current trends in host anemone distributions. In sum, we collectively present a new guide to the host sea anemones of the Red Sea, revise the host specificity of the Red Sea clownfish, and note characteristics of the Red Sea host anemone species observed on surveys.

## Results

### Host anemone species encountered in the Red Sea and Gulf of Aden

During the 73 surveys (Methods 5.1) along the eastern Red Sea coastline, we identified seven species of host sea anemones at variable depths of 1 to 25 m: *Stichodactyla mertensii*, *Stichodactyla haddoni*, *Heteractis magnifica*, *Heteractis crispa*, *Heteractis aurora*, *Entacmaea quadricolor*, and *Cryptodendrum adhaesivum* (Tables 1 and 2; Figs. 2, 3 and 4). Of these species, all but *C. adhaesivum* were observed hosting *A. bicinctus* in situ (interviews with Egyptian dive operators provide anecdotal evidence of *A. bicinctus* in association with *C. adhaesivum*, but this was not confirmed by our surveys). Table 1 identifies the anemone species observed, their substrate, habitat, and depth profile, and the region they were observed in.

### Identifying characteristics of Red Sea and Gulf of Aden host anemones

#### *Stichodactyla mertensii*

*Stichodactyla mertensii* (Figs. 2b and 3a, b) was encountered in all surveyed regions of the Red Sea and Gulf of Aden, in reef slope and patch reef habitats from 1.3 to 21 m depth, adhered in cavities within the reef rock structure. Specimens of this species observed in the Red Sea and Gulf of Aden were tan, pale yellow or brown, with short to medium length marginal oral disc tentacles (6–12 mm) and brightly colored verrucae which sometimes adhere to sand or reef rock (and help hold the oral disc open) and extend to the underside of the oral disc. This species is often large, exceeding 80 cm in some cases. *Stichodactyla mertensii* tends to have longer tentacles around the mouth, often three to five times as long as tentacles around the margins of the disc, and a flat oral disc.

#### *Stichodactyla haddoni*

*Stichodactyla haddoni* (Figs. 2c and 3c, d) was encountered in the southern and central Saudi Arabian regions, in the sand amongst patch reef habitats from 9 to 13 m depth. Red Sea *S. haddoni* individuals encountered on surveys (and from other personal observations) were pale, whitish to tan, with stripes around the margins of the oral disc. In other regions, such as Papua New Guinea, this species is often green, green-yellow or other colors; these colors were never observed in the Red Sea. The lack of prominent verrucae in this species is unique amongst host carpet anemones. *Stichodactyla haddoni*'s tentacle morphology differs from the other *Stichodactyla* species; *S. haddoni* possesses relatively short (4–8 mm), even length, narrow-stalked tentacles, which are more adhesive than those of *S. mertensii*. When disturbed, *S. haddoni* can completely retract into the sand, unlike *S. gigantea* and *S. mertensii*.

**Table 1** Sea anemone species occurrence record data for anemones observed on coral reef surveys in the Red Sea and Gulf of Aden. Surveys were divided into four region categories: Northern Saudi Arabia, Central Saudi Arabia, Southern Saudi Arabia, and Djibouti. Typical habitat type, depth range, and substrate type of anemone occurrences by species are included

Anemone Species	Region Observed	Habitat Type	Depth Range	Substrate type
<i>Stichodactyla mertensii</i>	All regions	Reef slope and patch reef	1.3 to 21 m	Rock
<i>Stichodactyla haddoni</i>	Southern and Central Saudi Arabia	Patch reefs	9 to 13 m	Sand
<i>Heteractis magnifica</i>	All regions	Reef slope and patch reef	1 to 25 m	Rock
<i>Heteractis crispa</i>	All regions	Reef slope and patch reef	6 to 23 m	Sand/rock margin
<i>Heteractis aurora</i>	Southern Saudi Arabia	Patch reef habitats	9 to 20 m	Sand/rock margin
<i>Entacmaea quadricolor</i>	All regions	Reef slope and patch reef	3 to 25 m	Rock
<i>Cryptodendrum adhaesivum</i>	Central Saudi Arabia	Reef slope and patch reef	1 to 9 m	Sand/rock margin

***Heteractis magnifica***

*Heteractis magnifica* (Fig. 2d) was encountered in all surveyed regions of the Red Sea and Gulf of Aden, in reef slope and patch reef habitats from 1 to 25 m depth, usually on exposed reef rock. Fully-expanded tentacles of this species are long (up to 75 mm) and rounded or slightly bulbous, often with brightly colored tips. Tentacle colors may be bright yellow, shades of green, tan, or reddish-brown, and column colors typically range from bright reds to purples. The entire column and pedal disc of this species is visible on healthy individuals, unlike in other species. In the Saudi Arabian Red Sea and Gulf of Aden, column colors are usually red to reddish-brown. Verrucae are inconspicuous on this species and do not attach to sand. When disturbed, this species retracts its tentacles into the column, forming a distinctive ball shape.

***Heteractis crispa***

*Heteractis crispa* (Figs. 2e and 4) was encountered in all surveyed regions of the Red Sea and Gulf of Aden, in

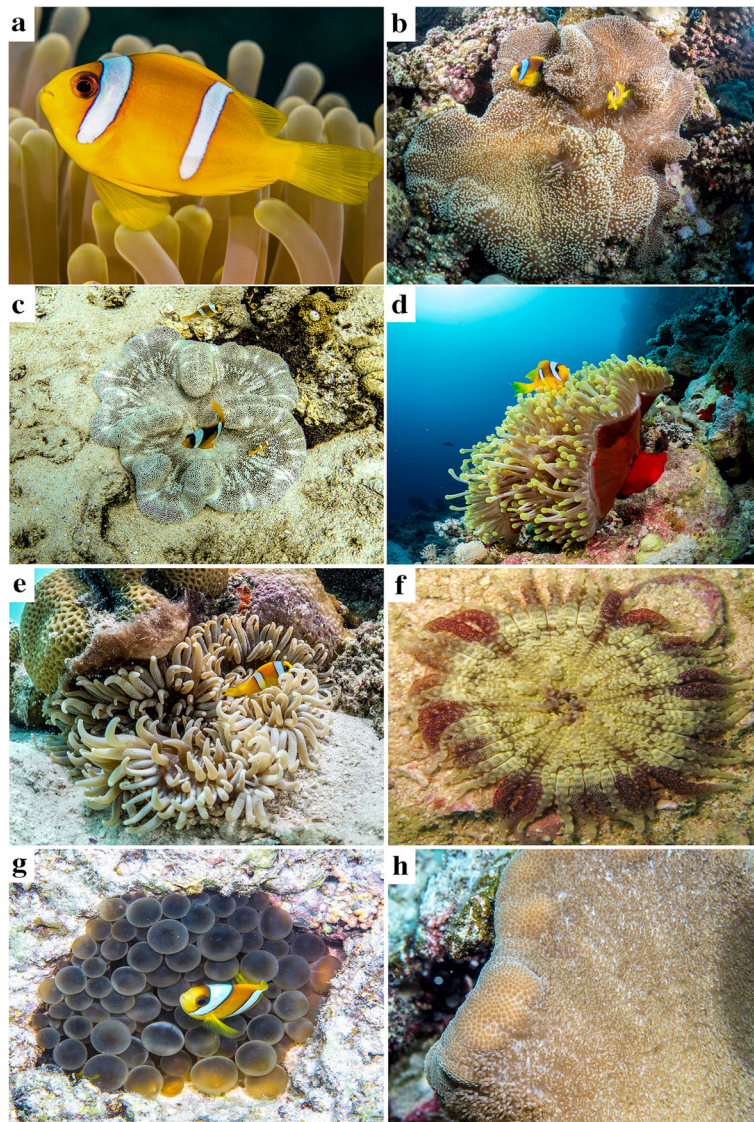
reef slope and patch reef habitats, usually at the base of rocks with the foot buried in sand at the rock/sand margin. This species was found at depths ranging from 6 to 23 m. This species has characteristically leathery, often curled, tentacles. Tentacles of this species also taper slightly to a point, unlike the rounded or bulbous morphology of other common Red Sea species such as *H. magnifica* and *E. quadricolor*. Colors range from white and light purple to tan or yellow. The column is typically gray and leathery, with conspicuous, starkly contrasting adhesive verrucae, usually adhered to sediment.

***Heteractis aurora***

*Heteractis aurora* (Figs. 2f and 4) was encountered in the southern region of Saudi Arabia, in patch reef habitats at depths from 9 to 20 m, at the sand/rock margin. This species has brown, grey, or purple tentacles, and its oral disc is usually the same color as its tentacles. Tentacles of *H. aurora* are shorter than those of *H. crispa*, are banded by white lines, and often have swellings which

**Table 2** Host sea anemone species total counts, for individuals observed on coral reef surveys in three regions of the Saudi Arabian Red Sea and Djibouti. Numbers indicate the total number of individuals seen in roving visual surveys by scuba divers within each region. Total number of surveys in each region are indicated in the last row

Host anemone species	Northern Saudi Arabia	Central Saudi Arabia	Southern Saudi Arabia	Djibouti	Total
<i>Stichodactyla mertensii</i>	3	29	12	6	50
<i>Stichodactyla haddoni</i>	0	2	2	0	4
<i>Stichodactyla gigantea</i>	0	0	0	0	0
<i>Heteractis magnifica</i>	1	84	17	1	103
<i>Heteractis crispa</i>	1	13	2	1	17
<i>Heteractis aurora</i>	0	0	2	0	2
<i>Entacmaea quadricolor</i>	13	46	23	4	86
<i>Cryptodendrum adhaesivum</i>	0	2	0	0	2
<i>Heteractis malu</i>	0	0	0	0	0
<i>Macroactyla doreensis</i>	0	0	0	0	0
<b>Total</b>	<b>18</b>	<b>176</b>	<b>58</b>	<b>12</b>	<b>264</b>
<b>No. Surveys</b>	<b>11</b>	<b>20</b>	<b>29</b>	<b>13</b>	<b>73</b>



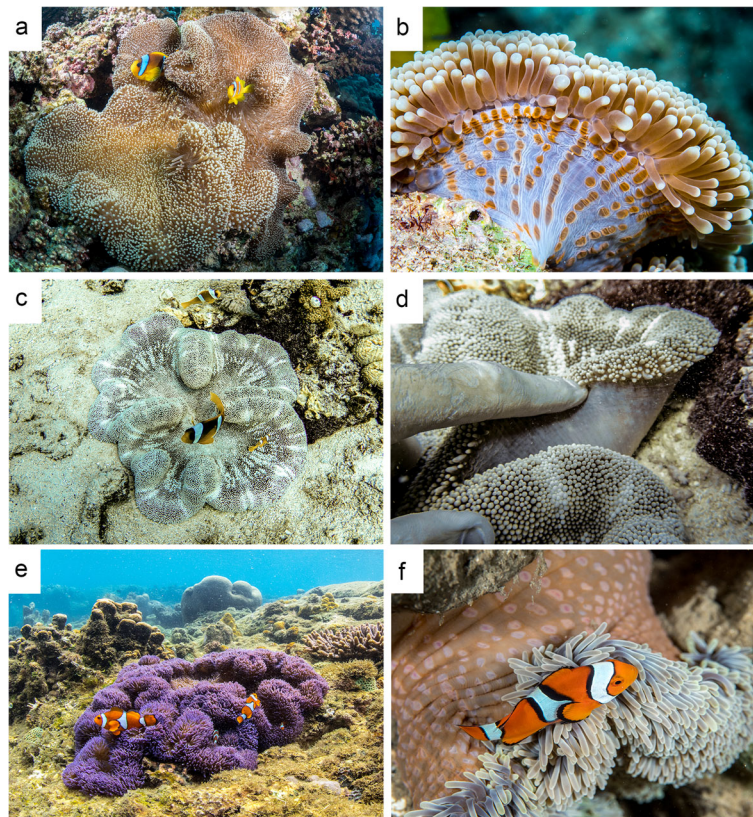
**Fig. 2** Representative photographs of sea anemone species that were observed hosting *Amphiprion bicinctus* (a) during in situ surveys conducted along the Saudi Arabian coast of the Red Sea and in the eastern Gulf of Aden (Djibouti). b: *Stichodactyla mertensii*; c: *Stichodactyla haddoni*; d: *Heteractis magnifica*; e: *Heteractis crispa*; f: *Heteractis aurora*; g: *Entacmaea quadricolor*. *Cryptodendrum adhaesivum* (h) was observed on surveys but not with *A. bicinctus* symbionts. (Photos by Morgan Bennett-Smith and Francesca Benzoni)

resemble strings of beads. Verrucae on the column of this species are lighter in color and extend from the oral disc downward to mid-column. The lower column is often red or orange. Red Sea *H. aurora* demonstrated a distinct morphological gradient, with some individuals closely resembling *H. crispa* (Fig. 4). From our surveys, and personal observations on other dives, *H. aurora* in the Red Sea possess highly variable tentacle morphology, with some features that appear similar to *H. crispa* (Fig. 4a). Red Sea *H. aurora* morphologies spanned the *H. crispa*–*H. aurora* spectrum, and included individual anemones with smooth but striated tentacles (Fig. 4b), individuals with tentacles that are ridged and banded,

but have smooth tentacle tips (Fig. 4c), to individuals that have semi-beaded tentacles (Fig. 4d) and that look most similar to *H. aurora* anemones from other localities that have the “classic” fully beaded tentacle morphology (Fig. 4e).

#### *Entacmaea quadricolor*

*Entacmaea quadricolor* (Fig. 2g) was encountered in all surveyed regions of the Red Sea and Gulf of Aden, in reef slope and patch reef habitats from 3 to 25 m, with the foot of the animal attached to cavities deep in the reef rock structure. This species’ tentacles and oral disc range from red or green, to brown or tan and come in



**Fig. 3** Carpet anemone species that were observed hosting *Amphiprion bicinctus* (a, c) during in situ surveys in the Red Sea with identifying characteristics of the column and tentacles shown (b, d). a, b: *Stichodactyla mertensii*. c, d: *Stichodactyla haddoni*. e, f: *Stichodactyla gigantea* hosting *Amphiprion percula* in Papua New Guinea. Column verrucae help to distinguish between carpet species; *S. haddoni* differs from both *S. gigantea* and *S. mertensii* in having no discernable verrucae, while *S. mertensii* is distinguishable from *S. gigantea* by its bulbed tentacle tips (compared to tapered) and verrucae which lengthen into lines and ultimately into streaks on the pedal disc (*S. gigantea* verrucae remain more circular and do not persist to the pedal disc). *Stichodactyla gigantea* was not encountered on any surveys in the Red Sea, and is only shown here to illustrate the differences in morphology (photos by Morgan Bennett-Smith)

two morphologies: bulbed and elongated. Bulbous tentacles have swollen tips, forming round or oval bulbs to a maximum diameter of ~ 15 mm. Elongated, blunt-ended tentacles can reach 80-100 mm in length and more closely resemble those of *H. magnifica*. Verrucae are absent in this species. On Red Sea reefs, *E. quadricolor* is often observed in areas of low wave exposure with its pedal disc inserted into holes in the reef rock. When disturbed, *E. quadricolor* can disappear fully from view by withdrawing into the reef structure.

#### *Cryptodendrum adhaesivum*

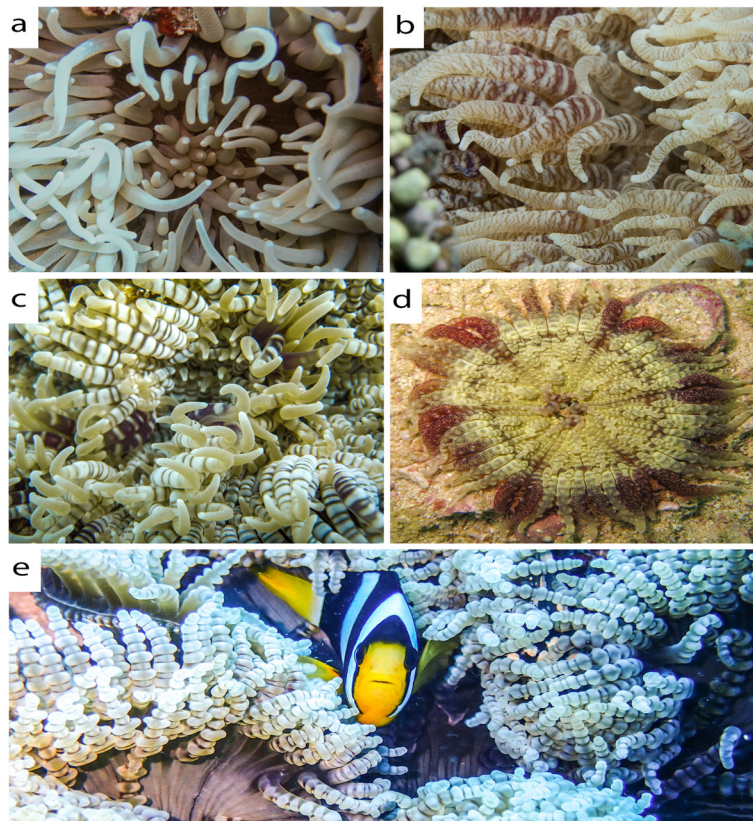
*Cryptodendrum adhaesivum* (Klunzinger, 1877, Fig. 2h) was observed in the central Saudi Arabian region without anemonefish symbionts, in reef slope and patch reef habitats from depths of 1 to 9 m. In the Red Sea, this species was found on sand at the base of reef rock. Outside of the Red Sea, it is only known to associate with one anemonefish, *Amphiprion clarkii*. This species possesses short, sticky tentacles, which can vary in color from the tips to the base. The mouth of this species is

often a different color from the tentacles. Tentacles around the mouth branch into five or more projections, outer tentacles are simple and bulbous, and its oral disc is usually flat when expanded. This is the only species with a starkly contrasting tentacle morphology from the mouth to the oral disc margins.

#### Review of historical Red Sea carpet anemone occurrence records

We downloaded occurrence records from two databases: the Ocean Biogeographic Information System (OBIS) and iNaturalist (Methods 5.4). Search results from OBIS returned several occurrence records of *S. gigantea* in the Red Sea, but zero records of *S. mertensii* in the same region. However, verified results from iNaturalist indicate the opposite: photograph uploads from iNaturalist users, for which we confirmed the accuracy of anemone identifications, document *S. mertensii* but not *S. gigantea* in the Red Sea (Fig. 5a).

Further, anemonefish occurrence records indicate that none of the anemonefish species that associate with *S.*



**Fig. 4** Morphological gradient observed between *Heteractis crisper* (a) and *Heteractis aurora* (e). Panels b, c, and d illustrate intermediate phenotypes in the Red Sea. Tentacles of individuals more closely resembling *H. crisper* were smooth, but occasionally lined by pigment; individuals more closely resembling *H. aurora* possessed tentacles which were broken into characteristic “beads”, in varying degrees. a: Gulf of Aqaba, Red Sea; b: Farasan Banks, Red Sea; c: Gulf of Aqaba, Red Sea; d: Farasan Banks, Red Sea; e: Maldives, Arabian Sea (photos by Morgan Bennett-Smith, Francesca Benzoni and Benjamin Titus)

*gigantea* (*Amphiprion akindynos*, *Amphiprion ocellaris*, *Amphiprion percula*, *Amphiprion perideraion*, and *Amphiprion rubrocinctus*) occur in either the Red Sea or the Indian Ocean (Fig. 5b, left), but *S. mertensii* symbionts (*Amphiprion akallopisos*, *Amphiprion allardi*, *Amphiprion akindynos*, *A. bicinctus*, *Amphiprion chrysogaster*, *Amphiprion chrysopterus*, *Amphiprion fuscaudatus*, *Amphiprion latifasciatus*, *Amphiprion tricinctus*, *Amphiprion ocellaris*) are distributed throughout the Pacific and Indian Oceans (Fig. 5b, right). There are recent reports of *S. gigantea* and two symbionts (*A. ocellaris* and *A. akindynos*) in the Andaman Sea, but not west of this region (Ragunathan et al. 2014). *Amphiprion clarkii* can associate with all ten global host anemone species and even soft coral (Arvedlund and Takemura 2005) and has been documented in different parts of the Indian Ocean, but we excluded this species from Fig. 5 because *A. clarkii* does not typically inhabit *S. gigantea* (Den Hartog 1997). We also found no documentation of this association in the Indian Ocean, where *A. clarkii*'s current distribution is likely a recent range expansion (Litsios et al. 2014). Taken together, verifiable host anemone and anemonefish occurrence

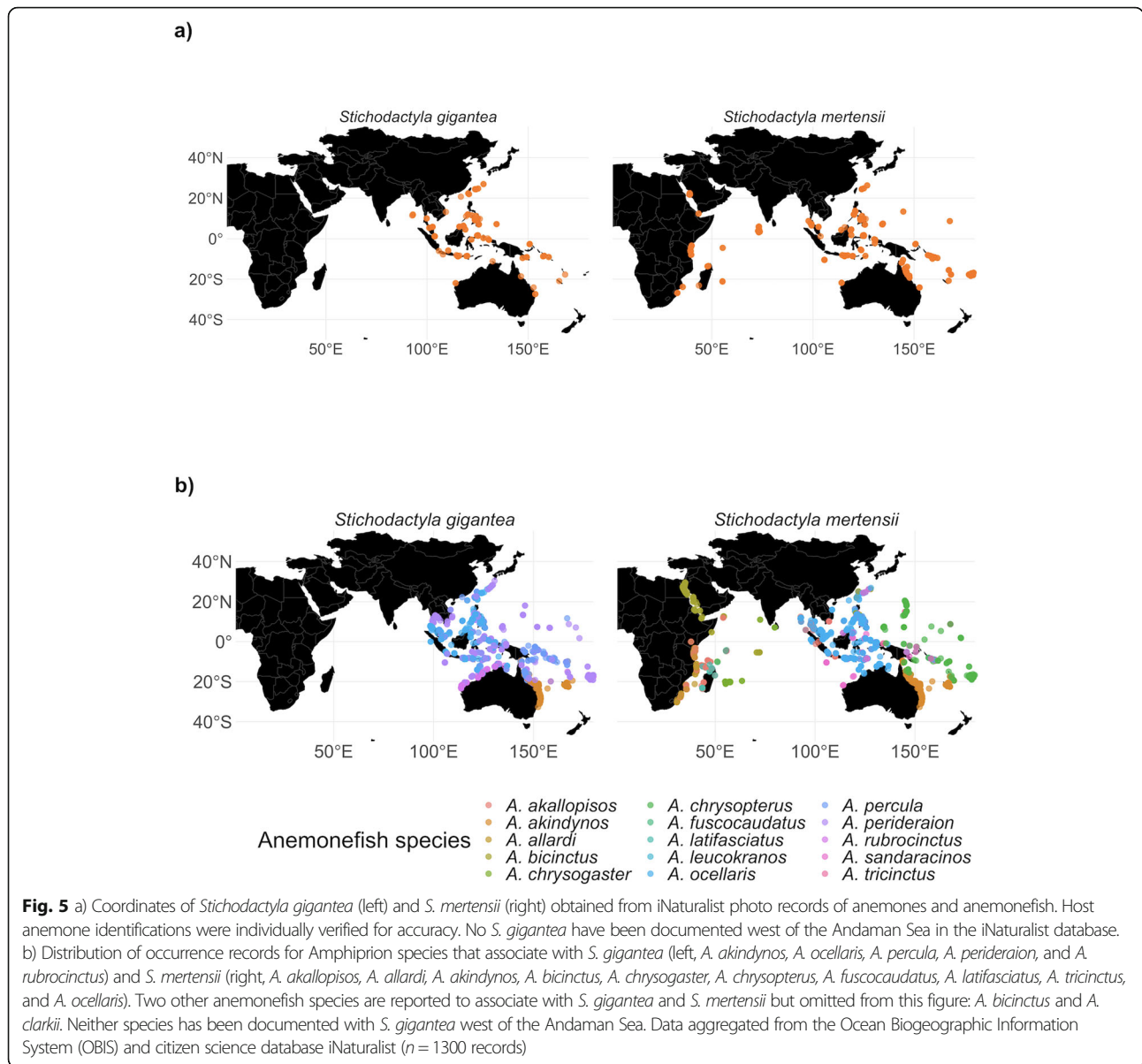
records from iNaturalist indicate that *S. gigantea* and its anemonefish symbionts do not occur in the Red Sea and are also absent from the Western Indian Ocean. Based on these findings, we propose revised Indian Ocean distributions and anemonefish associations for all host sea anemones within the Stichodactylidae family (Fig. 6).

## Discussion

### Red Sea host anemones

This study presents a multisource list that now includes eight host sea anemones in the Red Sea, seven of which have been described hosting *A. bicinctus*, and one (*Cryptodendrum adhaesivum*) that has been documented and suggested as a host (Dunn 1981, Chadwick and Arvedlund 2005, Emms et al. 2020) but was not confirmed as such in our surveys. Seven of the eight host anemones were directly observed in our visual surveys: *Heteractis crisper*, *Heteractis aurora*, *Entacmaea quadricolor*, *Heteractis magnifica*, *Cryptodendrum adhaesivum*, *Stichodactyla mertensii*, and *Stichodactyla haddoni*.

Our documentation of symbiosis between *S. mertensii* and *S. haddoni* with *A. bicinctus* resolves conflicting



reports of their distribution along the coast of Saudi Arabia. Anecdotal reports (e.g., dive shop operators) from the Egyptian coast suggest *C. adhaesivum* may host *A. bicinctus* in some areas, but this symbiosis has not been documented in the literature nor in our survey effort – *C. adhaesivum* that we found in Saudi Arabia only harbored *Dascyllus trimaculatus* (Rüppell, 1829). Our results considerably revise the host anemone distributions and diversity in the Red Sea.

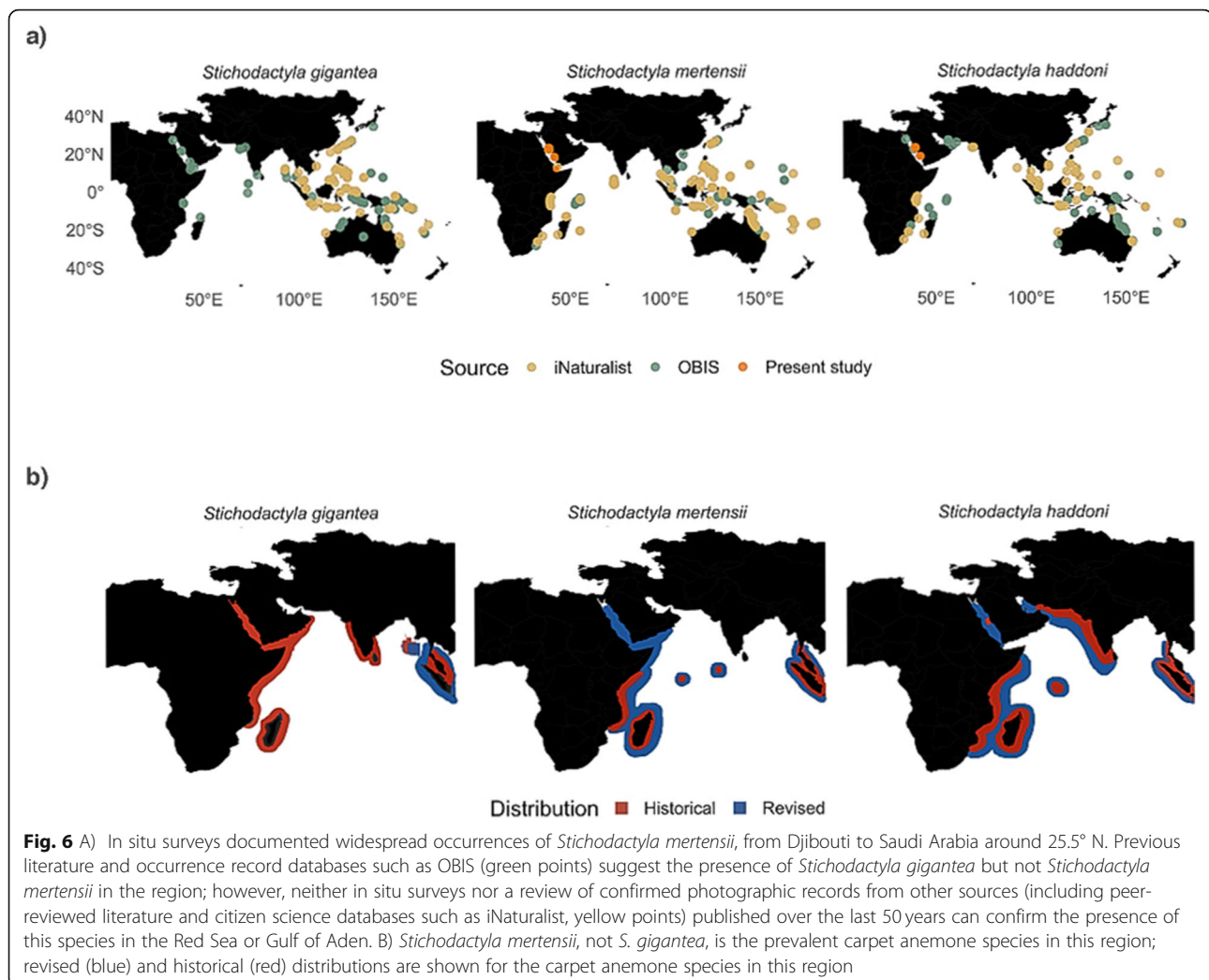
However, one purported Red Sea anemone species, *S. gigantea*, was not observed in our surveys, with or without fish symbionts. Further, we found no records containing photos or preserved specimens from the Red Sea in either the literature or databases reviewed. This calls into question previous reports of this species occurring

in the Red Sea and other nearby localities, and warrants further discussion, particularly in light of widespread observations of a similar looking species, *S. mertensii*, and the potential for misidentification among all host carpet anemone species.

#### Red Sea and Indian Ocean *Stichodactyla* species

In contrast to most literature sources, observations of *S. mertensii* along the Saudi Arabian coastline indicate that the known range of this species should be expanded significantly northward to include the Red Sea. The next closest observation, according to OBIS, is approximately 2000 km south near Madagascar (OBIS 2020). Other sources cite East Africa as the northwestern boundary of its range (Fautin and Allen, 1992). Given the broad





distance covered by recent observations of this species along the Saudi Arabian coastline, *S. mertensii* has likely been present in the Red Sea for several decades or longer, which is particularly interesting given the complete absence of the commonly reported carpet anemone species in the region, *S. gigantea*, on surveyed reefs. Our initial review found only eight Red Sea records of *S. gigantea*, all from one database (Fautin 2013), and none with associated photographs or specimens. Further, of those eight records, three report the “original scientific name” as *Actinia (Isacmaea) gigantea*. According to WoRMS, *Isacmaea gigantea* Hemprich & Ehrenberg has been synonymized with *Stichodactyla gigantea* (Daly and Fautin 2020a, 2020b); however, *Actinia (Isacmaea) gigantea* (Forsskål) has been synonymized with *Stichodactyla haddoni* (Daly and Fautin 2020a, 2020b). To further confuse the matter, the “original scientific author” listed in the database is neither Hemprich & Ehrenber nor Forsskål, but Saville-Kent, who described *S. haddoni*.

The nomenclature of *S. mertensii* and *S. gigantea* in the Red Sea is also conflicting and the physical appearances of *S. mertensii*, *S. gigantea*, and *S. haddoni* are all relatively similar, which may have led to published misidentifications in the Red Sea among these species. In Dunn’s seminal guide to anemonefishes and their distributions (Dunn 1981), there are two records of *S. gigantea* in association with *A. bicinctus* in the Red Sea: “Das Zusammenleben von Riffanemonen und Anemonfischen” (Schlichter 1968) and “Commensalism between fish and anemone” (Gohar 1948). Schlichter 1968 reports *S. gigantea* (identified as *Discosoma giganteum*, now synonymized with *S. gigantea*, Fautin 2013) from the Egyptian coastline, near Hurghada, and identifies the species based solely on the physical description of a “fleshy mouth and very short tentacles” (Schlichter 1968). No other descriptive information is provided, and the only photographs in Schlichter’s publication are of *H. crispata*. On its own, this description is at most inconclusive, however, the author goes on to describe the behavior of

the anemones in question: “...when the anemones were touched a little more forcefully, they pulled back abruptly into the ground, and only a gentle depression in the sand indicated where they were to be found.” This behavior is an identifying characteristic of *S. haddoni*, which can and does retract completely into the sand, but is not reported as an identifying characteristic of *S. gigantea* (Fenner 2016, personal observations).

We have been unable to find any other conclusive records of *S. gigantea* in the Red Sea literature spanning the last 100 years, and the type specimen collected from the Red Sea (Forsskål, 1775) was lost from the Coelenterates Collection at the Universitetets Zoologiske Museum in Copenhagen. Dunn (1981) reports, “Much of Forsskål’s (1775) original description, while accurate, is not diagnostic, but the extreme adhesiveness of the tentacles which may result in tearing the animal apart permits firm identification of his description with this species”. Adhesiveness is a relatively subjective and variable characteristic (e.g., *S. mertensii* and *S. haddoni* are both generally “adhesive”, and both *S. haddoni* and *S. gigantea* tentacles can tear off when touched); based on confirmed current survey data, review of past reports and misidentifications, and Forsskål’s incomplete description, we consider it likely that misidentifications between these carpet anemone species go back to the type specimen from the Red Sea. It is, however, important to reiterate that we were not able to conduct surveys on the Egyptian coastline as part of this study. Instead, we re-examined past records and anemone photographs from this region. As such, we cannot completely rule out that *S. gigantea* may occur on the western coastline of the Red Sea in low abundance, and that historical identifications were correct. If this is the case, then the abundance of this species in the area has substantially declined, for unknown reasons.

Rigorous systematic and taxonomic revision will be required to formally disentangle the conflicting species descriptions within *Stichodactyla*, but we call into question Forsskål as the taxonomic authority of *S. gigantea*. Rather, based on our anemone surveys throughout the Red Sea and updated distributions from global databases, we hypothesize that the identity of Forsskål’s anemone description is most likely what is currently recognized as *S. haddoni*.

As a clownfish host, recent literature generally does not report *S. haddoni* as hosting *A. bicinctus* in the Red Sea (e.g., Emms et al. 2020). However, our surveys confirmed the association between these two species. As *S. haddoni* was found in both the southern and central Red Sea regions (and has possibly been observed in other Red Sea regions as indicated by OBIS misidentifications and non-scientific reports from Egypt), populations of this species may be widespread (albeit not very abundant) in the Red Sea. It is also possible that survey

efforts in the region may have failed to thoroughly canvas suitable *S. haddoni* habitats; some reports indicate this species prefers sandy-bottom habitats in waters as deep as 40 m, and often far from heavily surveyed reef habitats (Attaran-Fariman and Javid 2015). During our surveys, this species typically occurred in sandy habitats from 9 to 13 m depth. The depth limitations of our surveys, however, limit our ability to comment on deeper distributions.

Similar to the previous discussion of *S. mertensii* and *S. gigantea*, *S. haddoni* and *S. gigantea* also look superficially similar. It is therefore possible that anemones identified as *S. gigantea* in this region were indeed *S. haddoni*, as discussed above in reference to Schlichter’s incorrect identifications. Conversely, other studies from the Red Sea likely incorrectly identified *S. mertensii* as *S. haddoni*, including one publication that listed 357 *S. haddoni* individuals in the Saudi Arabian Red Sea (Hobbs et al. 2013). *Stichodactyla mertensii* was considerably more abundant across all surveyed regions along the entire coastline of Saudi Arabia; unverifiable (no photographs or specimens) studies that report *S. haddoni* or *S. gigantea* in abundance on surveys in this region, and do not report *S. mertensii*, are likely incorrect in their identifications. Further, in other Indian Ocean regions, including South Africa, both *S. mertensii* and *S. haddoni* have been recently reported on surveys (Acuña and Griffiths 2004; Laird and Griffiths 2016); *S. gigantea* has not been reported.

In summary, the widespread documentation of *S. mertensii* from our surveys in the Saudi Arabian Red Sea and literature review results have three possible explanations: i) *S. mertensii* has experienced a recent range expansion into the Red Sea through the Gulf of Aden, ii) *S. mertensii* has been historically present in the Red Sea but not documented, or iii) host carpet anemone species in the Red Sea have been historically misidentified as *S. gigantea*. We consider the third scenario to be most likely. The large distance covered by recent observations (almost 2000 km of coastline) suggests that this species is not new in the Red Sea, ruling out a recent range expansion. As carpet anemone and clownfish pairs are highly visible, charismatic partnerships on coral reefs, we also find it unlikely that *S. mertensii* has been historically overlooked by studies in the Red Sea, especially in more frequently-visited reefs such as those in Egypt. In addition to our study’s documentation on the eastern coastline, recent photographs and unpublished citizen science records from Egypt and Sudan indicate *S. mertensii* is widely distributed on the western coastline of the Red Sea. Thus, it is likely that the conflicting nomenclature and similarity in morphological characteristics among carpet anemone species resulted in their historical misidentifications in the Red Sea. Determining the

absence of a species in a large region is much more difficult than determining the presence of that same species; however, we consider it likely that *S. gigantea* is at least ecologically irrelevant in the Red Sea, and likely not present at all.

#### ***Heteractis crispa*/*Heteractis aurora* morphological variability**

Recent work that has used molecular techniques to resolve host anemone phylogenies (e.g. Titus et al. 2019) has indicated that *Heteractis crispa* and *Heteractis aurora* are closely related, and may be sister taxa. In the Red Sea, we observed a morphological gradient between these two species, with many anemones exhibiting overlapping phenotypes in Saudi Arabia (Fig. 4). In other parts of the western Indian Ocean, specimens have been observed and photographed by citizen science contributors that appear to illustrate morphological characteristics of these two species within the same individual. Neither species was particularly abundant at our survey localities, and these low population densities, combined with the morphological gradient we observed, may hint at ongoing hybridization. Future studies integrating genomic and morphological techniques are necessary to further disentangle whether these species hybridize, or if both *H. crispa* and *H. aurora* simply exhibit a wide degree of phenotypic variability (as seen in *E. quadricolor*).

#### ***Amphiprion bicinctus*: generalist anemonefish**

The host specificity of different clownfish species varies widely, from specialists (one associated host anemone, e.g., *Amphiprion frenatus*) to generalists (ten associated host anemones, e.g., *Amphiprion clarkii*). Some sources (e.g., WoRMS, FishBase) list as few as three species of host anemones for *A. bicinctus*, which is around the average host specificity for all 28 extant species of anemonefish. Based on this study, *A. bicinctus* is one of the most generalist clownfish: only *Amphiprion clarkii* has been documented in symbiosis with more host anemones. One other species, *Amphiprion akindynos*, is known to associate with seven host anemones, which is in the range of *A. bicinctus*' host specificity--depending on two inconclusive anemone associations for *A. bicinctus* (*C. adhaesivum* and *S. gigantea*), the Red Sea clownfish is either the second or third most generalist clownfish species. *Amphiprion bicinctus*' ability to use a diverse array of sea anemone microhabitats may be crucial in helping it adapt to future changing cnidarian communities in the Red Sea.

#### **Conclusions**

The proposed distributions and Red Sea clownfish associations for the host sea anemone species in Saudi Arabia provide current information for studies that

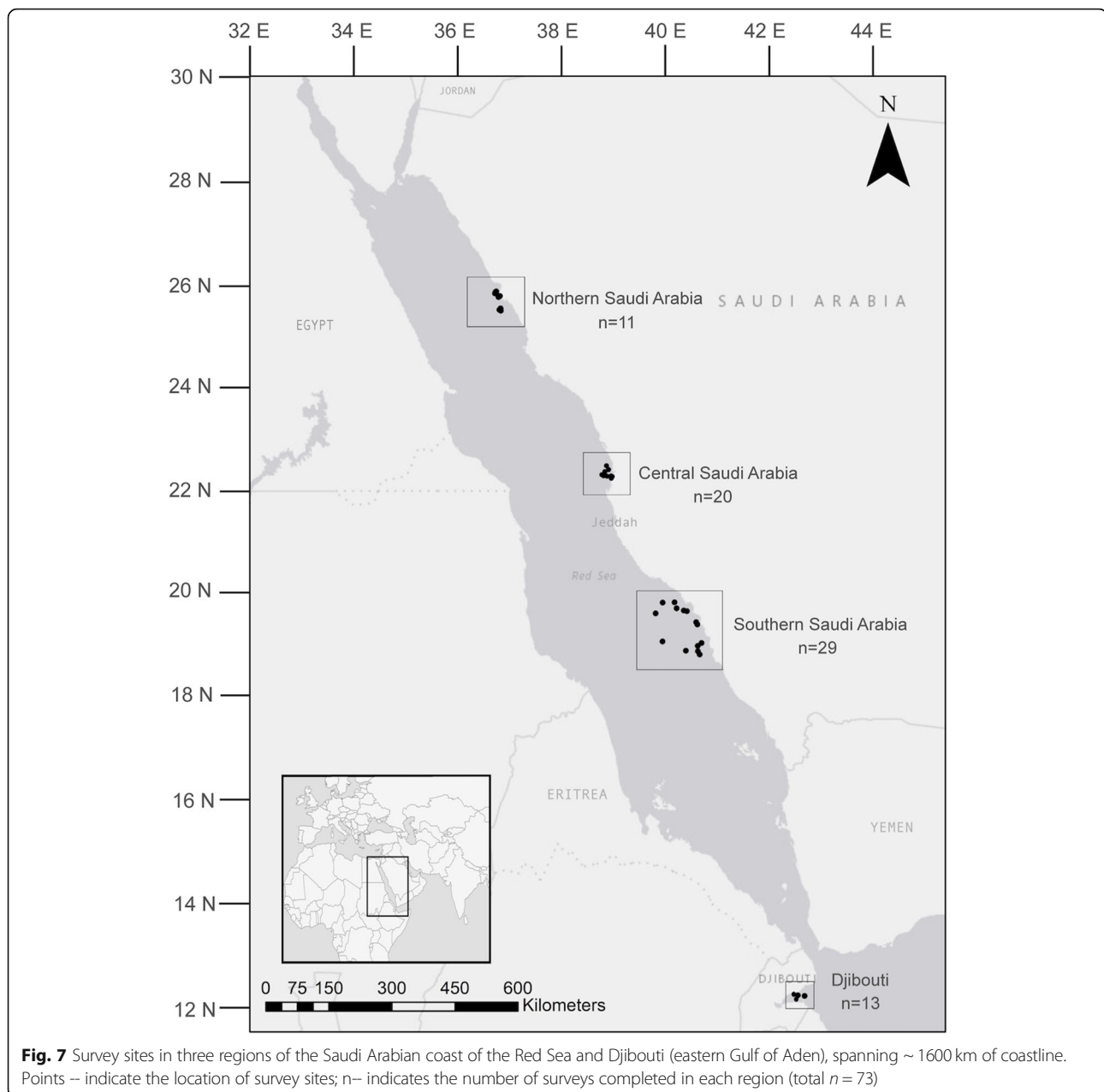
use these species as models and may help us better predict the impacts of changes in cnidarian communities on Red Sea coral reefs, which despite its reputation as a thermal refugium, is warming faster than other global oceans (Chaidez et al. 2017). Many zooxanthellate cnidarians, including tropical sea anemones, are increasingly threatened by rising sea temperatures and subsequent bleaching events (Hobbs et al. 2013). In the case of symbiotic fauna that are specialized in microhabitat usage, climatic disturbance may have severe consequences for both symbiotic partners (Pratchett et al. 2012). This study is a valuable baseline that will allow the evaluation of coral reef communities through time (e.g. species composition changes), especially in light of increasing bleaching events that affect host sea anemones. This work will also provide a baseline for researchers to monitor the impacts of ongoing, large-scale coastal development projects on a taxonomic group common to coral reefs of the eastern Red Sea.

#### **Methods**

##### **Field surveys**

To evaluate the diversity of host anemone species in the eastern Red Sea and the Gulf of Aden, we conducted 73 visual survey dives across reefs in the southern, central, and northern regions of the Saudi Arabian coastline of the Red Sea and one region in Djibouti (Fig. 7, Additional file 1 Appendix Table 1). Roving transects were conducted by survey teams of 2–3 scuba divers for ~60-min periods (at an estimated rate of ~0.75 m per second) at maximum depths of 25 m, and all anemones encountered were identified and photographed. Most anemones were photographed with an Olympus OMD EM1 Mark II camera inside a Nauticam underwater housing with Sea and Sea YSD2-J strobes. Other photographs were taken on Canon G7X cameras inside Meikon underwater housings or a Canon 5DIV inside a Nauticam underwater housing.

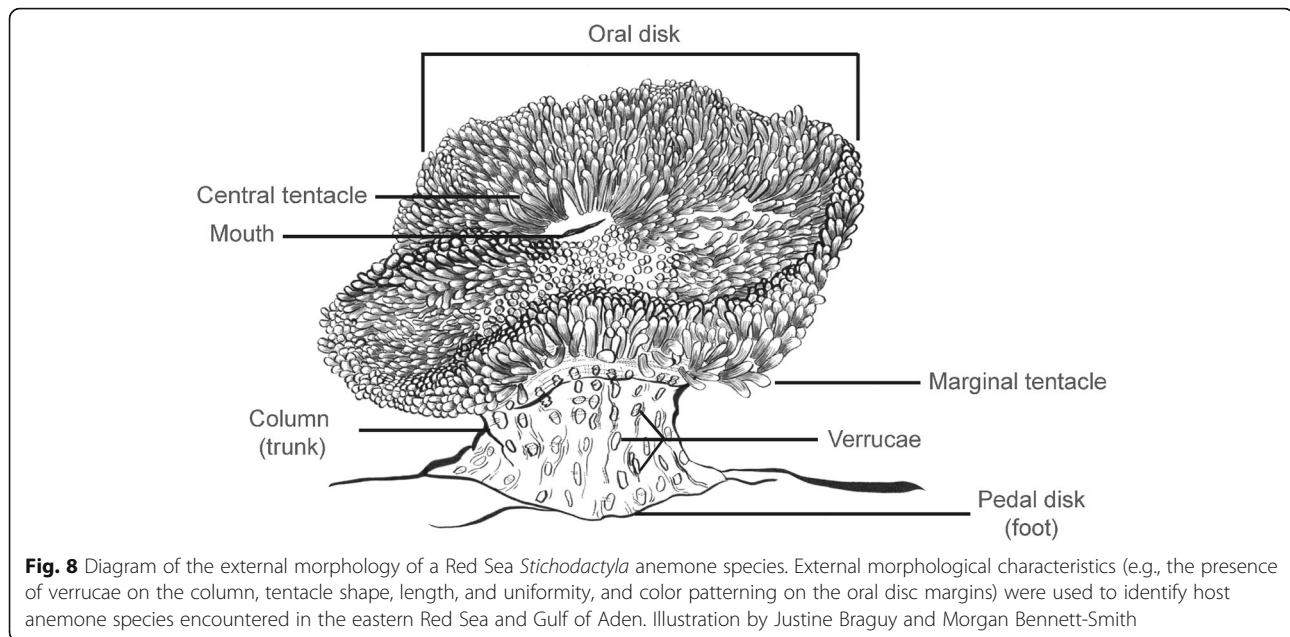
In the northern Saudi Arabian region, surveys were conducted at 11 sites in the Al Wajh lagoon region in February 2020. Surveyed reef coordinates spanned from 25.8845° N 36.5862° E to 25.5734° N 36.6936° E. In the central Saudi Arabian region, surveys were conducted at 20 sites near Thuwal, Saudi Arabia, from June–December 2019. Surveyed reef coordinates spanned from 22.5078° N 38.9503° E to 22.2614° N 39.0525° E. In the southern Saudi Arabian region, surveys were conducted at 29 sites in the Farasan Banks in February 2019 and January–February 2020. Surveyed reef coordinates spanned from 19.7895° N 40.1456° E to 19.7933° N 40.3990° E. In Djibouti (Gulf of Aden), surveys were conducted at 13 sites in February–March 2020. Surveyed reef coordinates spanned from 11.9723° N to 43.3331° E to 11.5933° N 42.8510° E.



### Morphological identifications

To identify sea anemone species in the field, external morphological characteristics (Fig. 8) were recorded and dichotomous keys were used to determine species identifications (Dunn 1981, Fautin and Allen 1992). Several important morphological characteristics that were used in identifying host anemones in the field include: the size and shape of the oral disc (flat, undulating, balled around the tentacles); the size, shape, color, and prevalence of verrucae (warty projections on the column) towards the pedal disc; the size, shape, density and uniformity of tentacles throughout the oral disc; the color patterning on the margins of the oral disc; the

substratum in which the pedal disc was anchored (sand, rockwork, or rubble); and the coloration and appearance of the mouth. All anemones encountered were photographed to confirm identifications. Representative specimens of each species (three individuals per species) were collected at local inshore reefs and transferred alive to the laboratory, where they were kept in flow-through aquaria at the King Abdullah University of Science and Technology (KAUST). These specimens allowed careful examination of structures difficult to assess in the field, such as the prevalence of verrucae towards the pedal disc. Lab specimens were used to confirm field identifications and photographs.



### Literature review

To review the purported number of host anemone species in the Red Sea, we queried the Ocean Biogeographic Information System (OBIS) for published observational records of clownfish-hosting sea anemones in the Red Sea. Taxon ID 1360 (Actiniaria) was used to search for Red Sea records using database geographic layer areas collectively covering the Red Sea: 40033, 10,248, 10,249, 121, 63, and 34,264. Records for each of the 10 global sea anemone host species (*Heteractis magnifica*, *Heteractis aurora*, *Heteractis crista*, *Heteractis malu* [Haddon & Shackleton, 1893], *Stichodactyla mertensii*, *Stichodactyla haddoni*, *Stichodactyla gigantea*, *Entacmaea quadricolor*, *Macrodactyla doreensis* [Quoy & Gaimard, 1833], and *Cryptodendrum adhaesivum*) were compiled. Further, an ISI Web of Knowledge review was conducted for other publications that may not have directly produced in situ database records. This was done using the Web of Science Core Collection, using search terms “Red Sea”, “giant sea anemones”, “host sea anemones”, “Actiniaria”, and “*Amphiprion bicinctus*”. We reviewed the Red Sea basis of record material detailed by the most-referenced source of host anemone associations (Dunn 1981) for one species in question, *S. gigantea*. We also reviewed and manually verified occurrence records for *Amphiprion bicinctus* and the ten global host anemone species from the citizen science database iNaturalist, creating a data set of ~15,000 occurrence records of anemonefish and host anemones between the two databases.

### Occurrence record analysis

To further evaluate the distributions and associations of the host *Stichodactyla* species and their symbionts, we

visualized a) occurrence records of the carpet anemones and b) occurrence records of carpet anemone anemonefish symbionts, in the Indian and Indo-Pacific Oceans. Data preprocessing and visual analysis were performed in R version 3.6 (R Core Team 2020; R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria URL <https://www.R-project.org/> and RStudio Team 2016; RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL <http://www.rstudio.com/>). Data was manually cleaned to remove erroneous points, including coordinates on land, duplicate entries, and entries without species-level identification. We also verified all photographs of host anemone identifications in the research-grade iNaturalist occurrence entries that were used (iNaturalist, accessed Feb. 2020), to ensure accurate identifications. Individual latitude and longitude coordinates of occurrence records from OBIS and iNaturalist (Methods 5.1) were plotted using the R packages ‘ggplot’ (Wickham 2016), ‘sf’ (Pebesma 2018), and ‘geosphere’ (Hijmans et al. 2011).

### Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s41200-021-00216-6>.

**Additional file 1: Appendix Table 1.** Sampling site coordinates with number of anemones encountered in northern, central, and southern Saudi Arabia and Djibouti.

### Acknowledgements

We would like to thank two scientists who helped early in this project but have since passed away before publication: Dr. Nanette Chadwick for her help early on with Red Sea anemone guidance, and Dr. Daphne Fautin for advice and survey suggestions. We thank them for their help, and for all of their great work in marine science over the last 50 years. Thank you to Dr.

Alison Green for photographs of host anemones from Djibouti, to Prof. Francesca Benzoni for photos from the Farasan Banks and advice. Thank you to Claire Shellem for comments on the manuscript, and all other members of the Reef Ecology Lab who participated in field work: Shannon Brown, Lucy Fitzgerald, Alex Kattan, and Micaela Justo. KAUST's Coastal and Marine Resources Core Lab staff provided assistance in the field. Thank you to Larisa Morales for help with RStudio. This work was supported by the King Abdullah University of Science and Technology (baseline funding to MLB).

#### Authors' contributions

MBS and JEM conceived and designed the research objectives. MBS and JEM conducted field surveys. BMT provided expert identifications. MBS analyzed the data. MBS, JEM, and BMT wrote the manuscript. MLB edited the manuscript. All authors read and approved the final manuscript.

#### Funding

This study was funded by KAUST baseline research funds to MLB. Support for BMT was provided by a National Science Foundation grant (DEB-1934274).

#### Availability of data and materials

The datasets and code generated during and/or analysed during the current study are available from the corresponding author on request.

#### Declarations

##### Ethics approval and consent to participate

No animal testing was performed during this study. Surveys and sampling were conducted in accordance with regulations of the King Abdullah University of Science and Technology's Institutional Animal Care and Use Committee under approved protocols 18IACUC13 and 19IACUC09. All necessary permits for sampling and observational field studies have been obtained by the authors from the relevant authorities and are mentioned in the acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

##### Competing interests

The authors declare that they have no competing interests.

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Received: 17 April 2021 Accepted: 11 October 2021

Published online: 25 November 2021

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