



SHORT REPORT



## Siphonophora of the Gulf of Aqaba (Red Sea) and their associations with crustaceans

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### ABSTRACT

Numerous studies have been carried out on marine taxa of the Gulf of Aqaba region, but few have concentrated on gelatinous zooplankton. Here, a new collection of pelagic hydrozoan siphonophore species is described from a study made during December 2013, whilst snorkelling along the Israeli coast of the Gulf of Aqaba to a depth of 5 m. Ten species were identified, including two species present in both post-larval and adult life stages. Four species are first records for the Gulf, and almost all the specimens collected were found to be associated with one or more hyperiid amphipod crustaceans or phyllosoma lobster larvae. Two of these crustacean species (*Thamneus rostratus* and *Phronima colletti*) are first records for the Red Sea region, a third (*Parascelus edwardsi*) was previously observed in this area, but not in the associations here recorded, and a fourth (*Palinurellus wieneckii*) is found to have undergone a northward extension of its distributional range. Moreover, our observation of *P. wieneckii* phyllosoma larvae attached to colonies of *Agalma okenii* constitutes the first evidence of palinurid (spiny lobster) association with siphonophores. The siphonophore taxa found in this study and those from previous studies are tabulated, and species richness discussed in relation to species lists published from other recent tropical studies worldwide. The hyperiid amphipod taxa identified are also tabulated and discussed in relation to the nature and possible means of invasion of gelatinous host siphonophores by crustaceans.

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## Introduction

Siphonophores are a cosmopolitan group of pelagic hydrozoans, distributed throughout all oceans of the world (Mapstone 2014), that play an important role in the food-web dynamics (Guerrero et al. 2016). They are limited primarily by latitude, depth, water temperature and hydrological processes (Lo et al. 2014; Mapstone 2014). In tropical seas, species richness can be high, with 55 siphonophore species recorded from the surface waters around Taiwan in the South China Sea (Lo et al. 2012), 82 species reported from all depths in the Gulf of Mexico (Pugh & Gasca 2009), 61 known from the Mediterranean Sea (Bouillon et al. 2004) and 89 species found from all depth horizons in the Indian Ocean (Daniel 1985). In contrast, only 25 siphonophore species have so far been reported from the Red Sea (Totton 1954), with only six species coming from the Gulf of Aqaba (Vaissière & Seguin 1982). This is perhaps surprising since both the Gulf and the Red Sea are deep (with maximum depths of 1500–1800 m), but their waters are oligotrophic with a nearly isothermal water column below a shallow

wind-mixed surface layer, due to their desert settings, low freshwater inputs and lack of through-flow of oceanic water (from the Gulf of Aden) (Richter & Abu-Hilal 2006). In the Gulf of Aqaba, considered a miniature 1:10 replica of the Red Sea proper, winter-mixing may extend down to 800 m, depending on heat flux the previous winter, and lead to a marked plankton bloom in spring (reviewed in Richter & Abu-Hilal 2006) which can sometimes occur earlier, during the winter months, as encountered in this study.

Siphonophores have long been recognized as hosts to various organisms. The range of such associations extends from dinoflagellates (*Stylodinium gastrophilum* Cachon, Cachon & Bouquaeux, 1965) (Cachon et al. 1969) to vertebrates (*Caristius* sp.) (Janssen et al. 1989). However, the most common organisms inhabiting siphonophores appear to be hyperiid amphipods (Harbison et al. 1977). These exclusively pelagic crustaceans are often host specific, with members of families Paraphronimidae, Lycaeopsidae, Pronoidae, Parascelidae and Platyscelidae being typically associated with siphonophores and having developed many adaptations to

such relationships (Harbison et al. 1977; Laval 1980). These can include mouthpart modifications (Dittrich 1992), conglobation (Laval 1980) and acquisition of host body colour (Gasca & Haddock 2016). The only other crustacean taxa so far recorded in association with siphonophores are phyllosoma larvae of slipper lobsters (Scyllaridae) (see Ates et al. 2007).

In this paper we give an account of siphonophore species collected whilst snorkelling in the Gulf of Aqaba, discussing their diversity in terms of their global distribution, and providing novel records of crustaceans associated with these hydrozoans.

## Material and methods

The samples for this project were collected whilst snorkelling in Israel's coastal zone of the Gulf of Aqaba at the beginning of December 2013. Specimens were taken by divers in two locations: near Eilat town centre, and close to the Interuniversity Institute for Marine Science in Eilat (IUI). In both cases, specimens were collected up to 30 m from the shore down to a depth of 5 m. Each time a siphonophore was spotted, it was first checked visually for the presence of associated crustaceans and then both the specimen and its associated crustaceans were captured in a plastic container. After preliminary *in vivo* analyses, all samples were fixed in 4% borax-buffered formaldehyde in seawater and packed for shipping.

Identification of siphonophores followed the most current revisions and species descriptions including Carré (1979), Pugh (1998), Pugh & Baxter (2014) and Pugh (2016). These, together with additional works (Totton 1954; Daniel 1973; Vaissière & Seguin 1982; Seguin 1984), were used to discuss species distribution ranges. Siphonophore specimens were also subjected to detailed morphological examination to detect changes occurring in their tissues as a result of their association with crustaceans.

Amphipods were identified using keys, together with comments on species morphology and synonymies by several authors (Spandl 1924; Laval 1970; Bowman & Gruner 1973; Vinogradov et al. 1982; Shih 1991; Zeidler 1992). Slides of taxonomically important amphipod appendages were sent to Wolfgang Zeidler (Adelaide, Australia) for confirmation of species attributions. Species identification and determination of developmental stage of the phyllosoma larvae were based on works by Michel (1970) and Prasad et al. (1975).

## Results

Ten species of siphonophores were identified from among the specimens collected, including four which

are new records for the Gulf of Aqaba (Table I). In all, over 90 siphonophore colonies were examined, and species identified included the three calycophorans *Chelophyes appendiculata* (Eschscholtz, 1829), *Mugilaea atlantica* Cunningham, 1892 and *Sulculeolaria quadrivalvis* de Blainville, 1830, and the seven physonects *Agalma elegans* (Sars, 1846) and *A. okenii* Eschscholtz, 1825 together with their *Athorybia* and *Crystallomia* post-larval forms, *Athorybia rosacea* (Forskål, 1775), *Cordagalma ordinatum* (Haeckel, 1888), *Forskalia tholoides* Haeckel, 1888, *Halistemma rubrum* (Vogt, 1852) and *Frillagalma vityazi* (Daniel, 1966).

All associated crustacean taxa were also identified, and their infection ratios estimated, with c. 80% of colonies being infected with amphipods (Table II). Stage X phyllosoma larvae of the spiny lobster *Palinurellus wienckii* (de Man, 1881) were also found, including a specimen of a larva 15 mm long attached to a single colony of *A. okenii*, and a second 16 mm long holding two relatively small *A. okenii* specimens in separate pereopods.

Most amphipods (excluding *Phronima colletti* Bovalius, 1887) were found feeding on siphonophore tissue, as indicated by tissue damage directly adjacent to each crustacean. Crustaceans were also observed buried deep within the mesoglea of nectophores of *A. okenii*, lateral to the nectosac. Signs of additional tissue damage, presumably from feeding, were also noted in specimens of *A. okenii* associated with the phyllosoma larvae.

## Discussion

In this study more species of Siphonophora have been found in the Gulf of Aqaba than previously known, despite the simplicity of the collection method. Also, larval stages have been identified for the first time in two physonects, *Agalma elegans* and *Agalma okenii*, indicating that these species must have been reproducing in the Gulf of Aqaba during the study period. These gelatinous species must play an important role in food web dynamics during plankton blooms in the Gulf, and are probably feeding on a range of hard-bodied planktonic prey from copepods to sergestid shrimps (if present in the Gulf) and perhaps even fish larvae (Biggs 1977; Purcell 1981).

The physonect *Frillagalma vityazi* is a first record for the Gulf of Aqaba, and, although primarily a mesopelagic species, it has also been found at all depths from the surface to 2000 m elsewhere worldwide (Pugh 1998). It is typically a warm water species, and must have entered the Gulf over the shallow sill at the Strait of Tiran, and also previously entered the Red

**Table I.** Species list of Gulf of Aqaba siphonophores from the present research together with data from previous studies (Totton 1954; Alvarino 1974; Vaissière & Seguin 1982; Seguin 1984). X, species recorded; (X), species presumably present in samples; o, new records in present research.

	Totton 1954	Alvarino 1974	Vaissière & Seguin 1982	Seguin 1984	Present research
<b>Calycophorae</b>					
<i>Abylopsis eschscholtzii</i> (Huxley, 1859)		x			
<i>A. tetragona</i> (Otto, 1823)	x	x	x	x	
<i>Amphicaryon</i> sp.	x				
<i>Chelophyes appendiculata</i> (Eschscholtz, 1829)		x			x
<i>C. contorta</i> (Lens & van Riemsdijk, 1908)		x	x	x	
<i>Diphyes dispar</i> Chamisso & Eysenhardt, 1821		x		x	
<i>Enneagonum hyalinum</i> Quoy & Gaimard, 1827		x			
<i>Eudoxoides mitra</i> (Huxley, 1859)		x			
<i>Lensia hotspur</i> Totton, 1941	x				
<i>L. meteori</i> (Leloup, 1934)	x				
<i>L. subtilis</i> (Chun, 1886)	x	x		x	
<i>L. subtiloides</i> (Lens & van Riemsdijk, 1908)	x	x			
<i>Muggiaea atlantica</i> Cunningham, 1892	x				x
<i>Sulculeolaria chuni</i> (Lens & van Riemsdijk, 1908)	x	x		x	
<i>S. quadrivalvis</i> de Blainville, 1830	x	x	x	x	x
<b>Physonectae</b>					
<i>Agalma elegans</i> (Sars, 1846)	(x)	x			x
<i>Athorybia</i> post-larvae					o
<i>A. okenii</i> (Eschscholtz, 1825)	x	x	x	x	x
<i>Crystallomia</i> post-larvae	(x)				o
<i>Athorybia rosacea</i> (Forsskål, 1775)	x	x			x
<i>Cordagalma ordinatum</i> (Haeckel, 1888)	x	x		x	x
<i>Forskalia</i> sp.	x				
<i>Forskalia tholoides</i> Haeckel, 1888					o
<i>Frillagalma vityazi</i> Daniel, 1966					o
<i>Halistemma cupulifera</i> Lens & van Riemsdijk, 1908	x <sup>a</sup>				
<i>H. rubrum</i> (Vogt, 1852)	(x)				
<i>H. transliratum</i> Pugh & Youngbluth, 1988	x <sup>a</sup>				x

<sup>a</sup>Although Totton (1954) did not identify his specimens as either *Halistemma transliratum* or *H. cupulifera*, Pugh & Baxter (2014) suggested that these species were present in his samples, based on Totton's drawings.

Sea over the shallow sill at Bab el Mandeb, from the Gulf of Aden. It is unlikely to have arrived in this region via the Suez Canal, as postulated for some other siphonophore species by Alvarino (1974), since there are no records for *F. vityazi* from the Mediterranean Sea (Mapstone 2009).

The Gulf of Aqaba, with its relatively high temperature and salinity levels, represents a good example of an unwelcoming ecosystem (Alvarino 1974). Moreover, the presence of a deep outflow from the Gulf, over the shallow sill at Bab el Mandeb, appears to successfully exclude most deep sea planktonic species (Totton 1954). Despite this, the present study has recorded 10 siphonophore taxa in the Gulf, a few less than Alvarino (1974), but more than Vaissière & Seguin (1982) and

Seguin (1984) (Table I). This number is also lower than the 25 species identified in the Red Sea by Totton (1954), but is to be expected due to the limiting physical barrier of the Bab el Mandeb sill. Thus, species richness in the Gulf is low for a tropical habitat, especially when compared with the species richness of Siphonophora in the Indian Ocean overall, and also the richness demonstrated in recent studies on siphonophore assemblages from the South China Sea and the Gulf of Mexico, as noted above.

The distribution of all siphonophore species encountered here is cosmopolitan. The polygastric stages of *Chelophyes appendiculata* and *A. elegans* appear to be the most common siphonophores worldwide (Mapstone 2009), although the record for

**Table II.** Recorded species of amphipods with their locality in the host organisms.

Host species	Associated organisms			
	Species	Life stage	No.	Locality in host
<i>Agalma elegans</i> (Sars, 1846)	<i>Parascelus edwardsi</i> Claus, 1879	juveniles (1–2 mm)	14	N, B
	<i>Phronima colletti</i> Bovallius, 1887	male (4 mm)	1	N
<i>Agalma okenii</i> Eschscholtz, 1825	<i>Parascelus edwardsi</i> Claus, 1879	juveniles (2–3 mm)	21	N, B
		adult male (5 mm)	1	N, B
<i>Crystallomia</i> post-larvae	<i>Parascelus edwardsi</i> Claus, 1879	juveniles (2–3 mm)	32	N, B
	<i>Thamneus rostratus</i> (Bovallius, 1887)	juvenile (2.5 mm)	1	N, B
<i>Athorybia rosacea</i> (Forsskål, 1775)	<i>Parascelus edwardsi</i> Claus, 1879	juveniles (2–3 mm)	12	B
<i>Forskalia tholoides</i> Haeckel, 1888	<i>Parascelus edwardsi</i> Claus, 1879	juveniles (1–2 mm)	17	N

Note: The table includes only the siphonophore species on which amphipods were found. No., number of collected specimens; N, nectophore; B, bract.

*C. appendiculata* from the Gulf of Aqaba is only the second so far published from the Red Sea region (Table I). *Muggiaea atlantica*, *A. okenii*, *Athorybia rosacea*, *Cordagalma ordinatum* and *Forskalia tholoides* are also all cosmopolitan, though in general confined to the epipelagic zone of warm and temperate waters worldwide (Carré 1968; Kirkpatrick & Pugh 1984; Mapstone 2009; Minemizu et al. 2015). *Sulculeolaria quadri-valvis* has been observed in the Atlantic, Indian and Pacific Oceans, as well as in enclosed basins such as the Mediterranean Sea (Carré 1979), and is also mainly epipelagic (Carré 1979; Mapstone 2009). Like *F. vityazi*, it has an affinity for warmer waters, although occasional records also exist from deeper oceanic regions (Casanova 1972; Mapstone 2009).

Records for amphipods are more common worldwide than those for siphonophores, making any shifts in distribution easier to trace. Hitherto, in the Red Sea, 34 species of hyperiids have been identified (Spandl 1924; Bowman & McGuinness 1982; Vinogradov et al. 1982), as given in Table II. These include *Parascelus edwardsi* (under the junior synonym *Parascelus typhoides* Claus, 1879), which is a common species and widely distributed in tropical and subtropical seas (Hurley 1955; Brusca 1981; Bowman & McGuinness 1982; Vinogradov et al. 1982; Zeidler 1992). Also, *P. edwardsi* (especially juveniles) has previously been observed living in association with many hydrozoans, including the siphonophores *A. okenii*, *Bathypphysa sibogae* Lens & van Riemsdijk, 1908, *Diphyes dispar* Chamisso & Eysenhardt, 1821 and *F. tholoides* (Biggs & Harbison 1976; Harbison et al. 1977; Laval 1980, under the junior synonym *Thyropus edwardsi*). Unsurprisingly, *P. edwardsi* was also found in *A. okenii* (both adult and larval stages) and in *F. tholoides* in this study, and two new host species recorded for this amphipod include *A. elegans* and *A. rosacea*.

Also presented here is the first record for *Thamneus rostratus* (Bovallius, 1887) in the Red Sea region. This hyperiid amphipod species is widely distributed in warm waters globally, but is far less common than *P. edwardsi*. *Thamneus rostratus* was found living in an unidentified medusa by Dana (1853, as *Daira debilis*) and later by Stephensen (1925). As *Thamneus platyrhynchus* (Stebbing, 1888), it was later found in *Pelagia noctiluca* (Forsskal, 1775) by Harbison et al. (1977), and more recently it was recorded in two hydro-medusae, *Aequorea coerulescens* (Brandt, 1835) and *Solmissus incisa* (Fewkes, 1886), for the first time (Gasca & Haddock 2004; Gasca et al. 2007, respectively). In the present study, juvenile specimens were observed inhabiting the nectophores of a relatively small siphonophore (the post-larval stage of *A. okenii*). Judging

from the damage to the nectosac musculature, specimens of both *P. edwardsi* and *T. rostratus* had entered the mesoglea of the nectophores directly via the nectosac rather than through the body tissues. The presence of amphipod exuviae nested within cnidarian tissue corroborates previous assumptions that some crustaceans can spend a significant part of their lifetime within the mesoglea of gelatinous hosts (Gasca et al. 2007).

Another hyperiid recorded in this study was *Phronima colletti*, a species widely distributed in the temperate and tropical waters of all oceans (Vinogradov et al. 1982; Shih 1991; Zeidler 1992). However, numerous records for this species have been misidentified, according to Shih (1991). Hitherto *P. colletti* has not been found in the Red Sea, nor has it been recorded in association with siphonophores.

Phyllosoma larvae of slipper lobsters (Scyllaridae) have frequently been found associating with cnidarians, but only few studies document their associations with siphonophores (see Ates et al. 2007). In published observations, phyllosoma larvae typically use cnidarians either for transport and/or as a food source. However, Ates et al. (2007) found a phyllosoma larva that was possibly seeking protection from predators inside a siphonophore colony. Interestingly, no such association between spiny lobsters (Palinuridae) and siphonophores were ever recorded, though based on palinurid phyllosoma gut content analyses they were expected to occur (e.g. Suzuki et al. 2006). Therefore, our records of *Palinurellus wieneckii* phyllosoma larvae attached to *A. okenii* colonies constitute the first direct observations of palinurid lobster larvae associations with siphonophores, and further evidence that they are feeding on these hydrozoans. The present record of *P. wieneckii* also demonstrates a northward extension of distributional range of this crustacean in the Red Sea, previously only recorded off the Arabian coast (Holthuis 1991).

Siphonophores appear to be valuable target hosts for crustaceans. With their long colonies, they offer plenty of living/hiding spaces. Siphonophores are also well known for their efficiency as predators (Purcell 1980) and relatively high protein content (Wang et al. 2014), thus granting their kleptoparasites (amphipods) and predators (amphipods and phyllosoma larvae) food in abundance. It is not surprising therefore, that most of the colonies encountered in this study had associated crustaceans, allowing documentation of a broad range of amphipod placements 'inside-colonies', from clinging to the surface of gelatinous tissues to living deeply buried within the mesoglea. Vader (1980), although working on benthic sea anemones,



provided an interesting review of the host specificity and different levels of cnidarian–amphipod interactions and adaptations. An equivalent study dealing with pelagic animals would be highly desirable in the future if more associations, with associated detailed morphological examinations, could be discovered.

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