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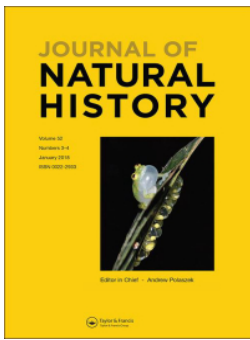
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DNA barcoding, dwelling morphology, and fecundity of the gall-forming shrimp *Paratypton siebenrocki* Balss, 1914 (Caridea: Palaemonidae)

Sancia E. T. van der Meij [iD][a,b], Jessica Bouwmeester [iD][c] and Susanne Bähr [iD][d,e]

aGELIFES, University of Groningen, Groningen, The Netherlands; bMarine Biodiversity Group, Naturalis Biodiversity Center, Leiden, The Netherlands; cSmithsonian Conservation Biology Institute, Smithsonian Institution, Fort Royal, VA, USA; dRed Sea Research Center (RSRC), Biological and Environmental Science and Engineering Division (BESE), King Abdullah University of Science and Technology, Thuwal, Saudi Arabia; eDepartment of Zoological Sciences, Kenyatta University, Nairobi, Kenya

ABSTRACT

Tropical coral reefs offer a wide variety of habitats to countless invertebrate species. Sessile host organisms especially are inhabited by small taxa, of which decapod crustaceans form one of the most diverse communities. Symbiotic palaemonid shrimp species associate with marine invertebrate hosts from multiple phyla, including cnidarians such as stony corals (Scleractinia). The intriguing gall-forming shrimp *Paratypton siebenrocki*, a symbiont of *Acropora* corals in the Indo-Pacific, was collected in the Saudi Arabian Red Sea, Kenya, and the Maldives. Based on morphology *P. siebenrocki* has been considered to be most closely related to the genera *Anapontonia* and *Metapontonia*; however, no clear clustering with either palaemonid genus was observed in a phylogenetic reconstruction based on 16S and COI mtDNA. Here we photo-document the dwellings of *P. siebenrocki* in *Acropora* spp. for the first time, and furthermore we report on the reproductive output of this species. The number of eggs ranged from 345 to 909 (n = 6), and embryo volume differed strongly between early- and late-stage embryos. The carapace length ranged from 2.58 to 4.55 mm for the females and 1.51 to 2.5 mm for the males (n = 5). The number and size of the embryos, combined with their specialised, secluded lifestyle, suggest that *P. siebenrocki* allocates higher energy towards embryo production than free-living confamilials do.

Introduction

Various species are known to dwell in or on scleractinian corals. Fish are perhaps the most well-known taxa inhabiting corals, but they are outnumbered by arthropods – one of the largest groups living in association with corals. Most decapods obligately associated with corals move freely amongst the branches or over the surface of their host, but some species create dwellings in their host (Lai et al. 2009; Horká et al. 2016). The coral-dwelling gall shrimp *Paratypton siebenrocki* Balss (1914) (Palaemonidae) is the only shrimp species

known to induce galls in scleractinian corals that enclose the animal completely. These dwellings are reminiscent of dwellings induced by coral-dwelling gall crabs (Cryptochiridae), especially those of the true gall-forming species *Hapalocarcinus marsupialis* Stimpson, 1859 sensu lato and *Pseudohapalocarcinus ransoni* Fize and Serène, 1956 (Fize and Serène 1957; Bruce 1969; Bähr et al. 2021).

Paratypton siebenrocki is morphologically one of the more unusual palaemonid shrimps, yet there is little documentation in the scientific literature on this remarkable, highly adapted species. Borradaile (1921, p. 3) describes the females of *P. siebenrocki* as 'heavy, clumsy and simplified' and comments on the superficial similarities to the gall crab *H. marsupialis* s.l. in its general outline and build, as well as their adaptations to high reproduction by sacrificing elegance and swift movement. Most of the further literature on *P. siebenrocki* consists of occurrence records and morphological descriptions of single specimens (e.g. Bruce 1969, 1980; Bruce and Trautwein 2007), but in general the species has been rarely observed and collected. This could be attributed to difficulties in spotting the deeply embedded galls *P. siebenrocki* create in their *Acropora* hosts, which we photo-document for the first time.

Balss (1914) described *P. siebenrocki* in the monospecific genus *Paratypton* and commented that the species 'without any doubt belongs to the Pontoniiden, but with unknown affinities'. A year later, Balss (1915, p. 83) superficially compared the species with the genus *Typton* Costa, 1844, but did not provide further placement details. Bruce (1969) considered the species to be most closely related to *Anapontonia* Bruce, 1966 and *Metapontonia* Bruce, 1967 rather than to *Typton*, whereas Bruce (1980) discussed a resemblance with the genus *Veleronia* Holthuis, 1951. The subfamily Pontoniinae is currently no longer recognised (De Grave et al. 2015). In this study we assess the position of *P. siebenrocki* for the first time in a phylogenetic context based on COI and 16S mtDNA.

Lastly, Borradaile (1921) commented on the large, arching abdominal pleura enclosing a large 'brood pouch' in *P. siebenrocki*. Symbiotic decapod crustaceans inhabiting sheltered habitats can allocate more energy towards embryo production and often have higher reproductive output than free-living species (e.g. Hines 1992; Azofeifa-Solano et al. 2014; van der Meij et al. 2018; Bähr et al. 2021). Here we report on various reproductive traits of *P. siebenrocki*, including embryo counts and brood mass volume for six ovigerous females, and compare the data with reproductive strategies in other symbiotic palaemonid shrimps.

Material and methods

A male–female species pair of *P. siebenrocki* (Figure 1a, b) was collected from the coral *Acropora arabensis* Hodgson and Carpenter, 1995 during a research cruise in the Saudi Arabian Red Sea. The specimens were collected on 9 March 2013, from 2 metres depth at Mahama, Farasan Islands, Saudi Arabia (16.581°N 42.116°E), and are deposited in the Crustacea collections of Naturalis Biodiversity Center in Leiden, The Netherlands, under accession number RMNH.Crus.D.54440. Furthermore, various specimens were collected in *Acropora* coral nurseries in the Wasini Channel, Shimoni, in Kenya in November–December 2019 (4.650°S 39.387°E), and in March 2022 a male specimen was collected from 12 metres depth at Velassaru reef, South Malé Atoll, in the Maldives (4.120°N 73.412°E). Lastly, two specimens were collected from *Acropora* sp. at Merulina reef (23.507°N
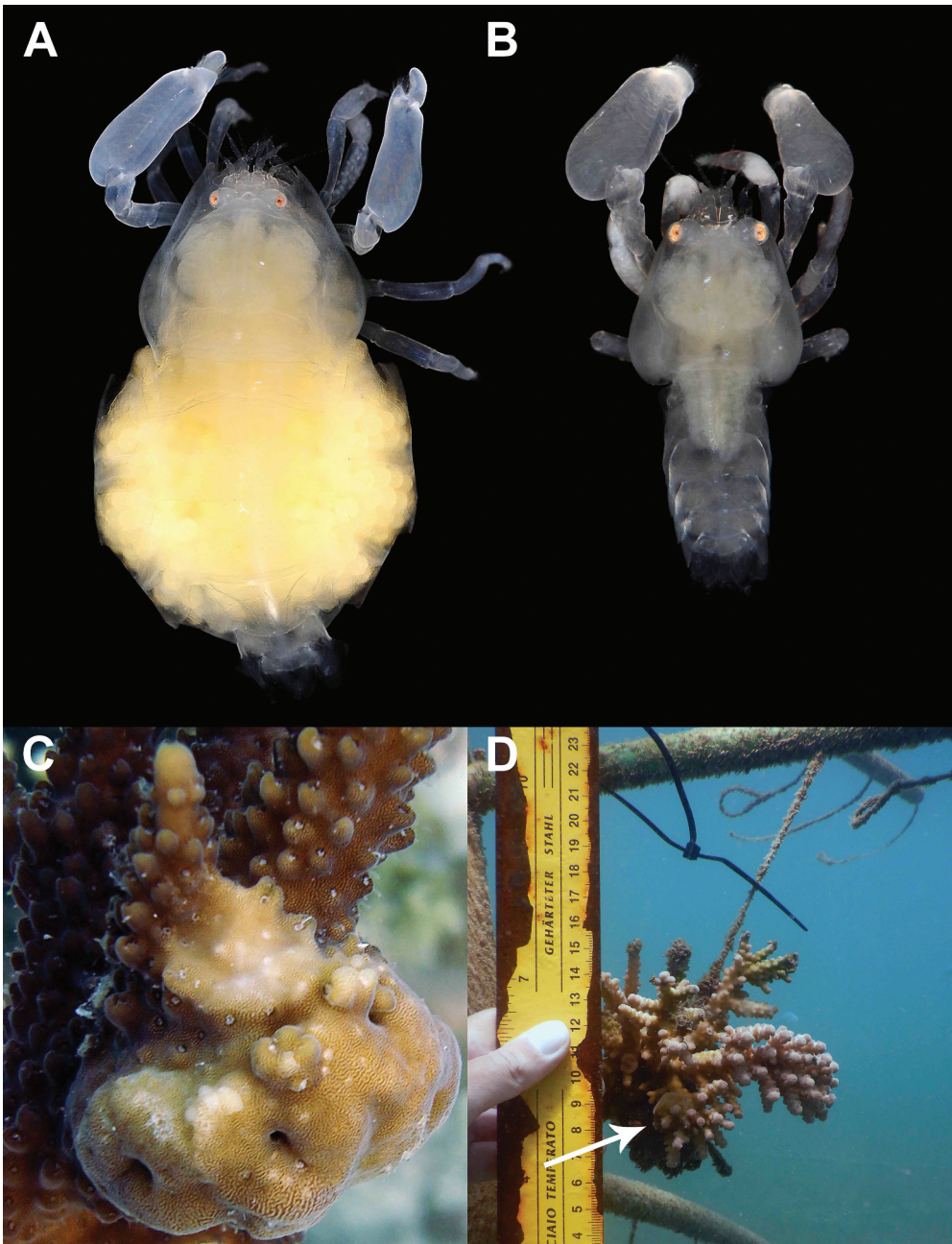
Figure 1. *Ex situ* images of *Paratypton siebenrocki* (RMNH.Crus.D.54440): (A) ovigerous female and (B) male. Dwelling morphology of *P. siebenrocki*. (C) Dwelling in *Acropora arabensis* from Farasan Islands (Red Sea) with ventilation pores, host of the specimens shown in a and b; and (D) *Acropora* cf. *verweyi* fragment in REEFolution nursery in Kenya, arrow indicates dwelling. Photos (a, b) by Arthur Anker, (c) by Jessica Bouwmeester, (d) by Susanne Bähr.

38.079°E) during a cruise near Yanbu in the Red Sea in October 2022 (Supplementary Figure S1). The specimens from the Maldives and Yanbu cruise are currently stored at the King Abdullah University of Science and Technology (KAUST) in Thuwal, Saudi Arabia.

A few eggs from the specimen collected from Mahama, Farasan Islands, in the Red Sea (RMNH.Crus.D.54440) were used for molecular analyses. Sequences were obtained from the mitochondrial cytochrome c oxidase subunit I (COI, partially) and 16S genes (LCO1490 and HCO2198, Folmer et al. 1994, p. 16L2 and 16H10; Schubart 2009), using the protocol in van der Meij (2015), and were used to infer phylogenetic relationships between the examined taxa. Attempts to obtain Histone h3 nuclear gene sequence data failed. For the phylogenetic analyses a subset of the dataset of Horká et al. (2016) was used, with the addition of *Anapontonia denticauda* Bruce, 1966 (16S: MH286364) and *Metapontonia fungiacola* Bruce, 1967 (COI: KX245152, 16S: KX169192). *Chlorotocella gracilis* Balss (1914) was used as an outgroup based on Horká et al. (2016). The new sequences are deposited in GenBank under numbers OP415638 and OP418251, and GenBank information for all other species can be retrieved from Horká et al. (2016). All species names were updated using the World Register of Marine Species (WoRMS) database (WoRMS Editorial Board 2022).

The alignment of the protein-coding gene COI was translated to amino acids to check for stop codons, but none were present. The substitution saturation for COI was tested in DAMBE v. 7.0.13 (Xia 2018) using the index proposed by Xia et al. (2003). The third codon position was found to be saturated and excluded from the subsequent analyses. The concatenated dataset was aligned using MAFFT on the GUIDANCE2 server (Sela et al. 2015); the alignment score was 0.994554. Unreliable columns, with a score below 0.93, were removed from the dataset. The best-fit nucleotide substitution model for the COI and 16S datasets was $GTR + I + G$, based in ModelFinder (Kalyaanamoorthy et al., 2017) under the Akaike information criterion. An Maximum Likelihood (ML) analysis based on the concatenated dataset was conducted with IQ-TREE (Nguyen et al. 2015) for 10,000 ultrafast bootstraps (Minh et al. 2013). Bayesian inferences coupled with Markov chain Monte Carlo techniques (six chains) were run for 7,000,000 generations in MrBayes 3.2.5 (Ronquist et al. 2012), with a sample tree saved every 100 generations and the burn-in set to 25%. Likelihood scores stabilised at a value of 0.003050, and chain convergence was visually inspected in Tracer v. 1.7.1 (Rambaut et al. 2018). Consensus trees were visualised in FigTree v. 1.4.0 (Rambaut, 2009). Lastly, we compared our COI sequence data with two *P. siebenrocki* sequences available from the Moorea Biocode project (accession codes BMOO-03607/8), to test for evolutionary divergence (p-distance) between the Red Sea and Moorea.

In the REEFolution *Acropora* coral nursery in Kenya, *Acropora* fragments grow in floating nursery trees until they are large enough to be outplanted to the reef. Unhealthy-looking fragments are used to feed *Acanthaster* starfish kept in enclosures for feeding experiments. In November–December 2019 the last author observed five dwellings in the coral nursery, and collected the *P. siebenrocki* shrimps for egg counts and carapace length measurements before feeding the remainder of the coral fragments to the starfish. No attempts were made to check or count all available nursery coral fragments for dwellings. A total of six ovigerous females and five males were available for embryo counts and brood volume measurements; embryo stages are based on Zimmermann et al. (2015). No

facilities were available in Kenya for further measurements or deposition of these specimens. The graph and box plot were created in R Studio v. 4.1.0 (R Core Team 2021).

Results

Dwelling morphology

All known host records of *P. siebenrocki* belong to the coral genus *Acropora*. The following records are available in the literature: *A. hyacinthus* (Dana, 1846), *A. millepora* (Ehrenberg, 1834, as *Acropora squamosa* (Brook, 1892)), *A. mossambica* Riegl, 1995, *A. palmerae* Wells, 1954, *A. polystoma* (Brook, 1891, as *A. massawensis* von Marenzeller, 1907), *A. squarrosa* (Ehrenberg, 1834), *A. tubicinaria* (Dana, 1846; taxon inquirendum), and *A. valida* (Dana, 1846, as *A. variabilis* (Klunzinger, 1879)) (Bruce 1969, 1980; Bruce and Trautwein 2007). In addition, there is a record of a juvenile *P. siebenrocki* specimen collected from *Pocillopora eydouxi* (Bruce 1980, p. 245); however, on p. 243 of the same publication the host is identified as *A. variabilis* (= *A. valida*). In Bruce's review of coral-associated shrimps only *Acropora* is listed as a host of *P. siebenrocki*, hence we consider the record from *P. eydouxi* a possible *lapsus calami* and not a true association (Bruce 1998). The herein reported association with *Acropora arabensis* Hodgson and Carpenter, 1995 (Figure 1c) and *A*. cf. *verweyi* Veron and Wallace, 1984 are new host records for *P. siebenrocki*. It is, however, important to note that morphological, *in situ* identification of *Acropora* is highly problematic; there are ongoing efforts for phylogenomic resolution of the Acroporidae to help elucidate the challenging systematics of this coral family (see e.g. Cowman et al. 2020).

The specimen from the Farasan Islands (Red Sea) inhabited a colony of *Acropora arabensis*. Midway along a branch a clear protrusion was visible with at least three, but likely more, ventilation pores (Figure 1c). Separate chambers, as described by Bruce (1969), were not observed but they could have been damaged when opening the dwelling. The galls of the Kenya specimen were observed at either the base or the mid-part of the fragments grown in the nursery (Figure 1d). The number of ventilation pores seemed to vary between three and five per chamber, but separation of the chambers was not clearly visible. Interestingly, the inside of two of the sampled galls were partially pink to dark brown in colour. A male specimen of *P. siebenrocki* was sampled from *Acropora* sp. in the Maldives from a gall with slightly separated chambers. Lastly, the samples from Merulina reef (near Yanbu) in the Red Sea were sampled from a dwelling located at a joint formed by two separate branches (Supplementary Figure S1c, d). The opened dwelling shows five ventilation pores (Supplementary Figure S1a, b).

Systematic position and biogeography

Blasting of the COI barcode of *Paratypton siebenrocki* in the National Center for Biotechnology Information (NCBI) database, with the records limited to Palaemonidae, revealed no close match. *Conchodytes monodactylus* Holthuis, 1952 was closest, with a percentage identity of 83.7%. A phylogenetic reconstruction based on 62 samples (plus outgroup), a subset of Horká et al. (2016), did not show support for clustering of

Figure 2. Phylogeny reconstruction based on 16S and COI mtDNA. *Paratypton siebenrocki* (in bold) does not show a clear clustering with *Anapontonia* or *Metapontonia* in this reduced dataset from Horká et al. (2016). Topology is based on Maximum Likelihood (ML) analyses, support values are ML (UFBoot) on the left and Bayesian Inference (BI) on the right. Only values ≥ 90 are shown; – represents a value below this threshold.

P. siebenrocki with a specific species or clade (Figure 2). Our phylogenetic reconstruction is similar in overall topology to those of Horká et al. (2016), although it lacks the support values for the various clades – likely because of missing nuclear genetic data.

Table 1. Reproductive traits (median ± 95% CI) of gravid *Paratypton siebenrocki* females collected in Kenya.

	Carapace length (mm)	Embryos (n)	Embryo volume (mm^3)	Brood mass volume (mm^3)
All females	3.52	548	0.26	154.64
(n = 6)	(3.14–4.14)	(362–834)	(0.21–0.33)	(145.92–167.41)
Females with early-stage embryos	4.29	759	0.197	150
(n = 3)	(2.58–4.55)	(345–909)	(0.18–0.24)	(81.4–160)
Females with late-stage embryos	3.33	515	0.34	170
(n = 3)	(3.07–3.70)	(378–582)	(0.29–0.38)	(145–176)

Paratypton siebenrocki has been recorded from eastern Africa through to French Polynesia (Bruce and Trautwein 2007, Figure 1). Balss (1914) reported *P. siebenrocki* from the Egyptian Red Sea (Senafir, Koseir and Mersa Sheikh in Egypt [in Balss (1915) the locality Mersa Sheikh is absent, and instead Sherm Sheikh is mentioned], and it was already reported from Kenya by Bruce and Trautwein (2007). Here we record the species from South Malé Atoll in the Maldives for the first time. The Moorea Biocode Project (French Polynesia) contains two sequences of *P. siebenrocki* (BMOO-3607/8). The p-distance between the Red Sea and Moorea sequences is 14.1% (SE ± 1.3); however, translation of the sequences to amino acid data revealed only three polymorphisms.

Reproduction

Six ovigerous females were collected in the coral nurseries in Kenya; three females had early-stage embryos, and three had late-stage embryos. The average embryo number dropped from 759 to 515 between early and late stages; however, the total brood mass volume remained roughly the same (150 mm^3 vs 170 mm^3). The females carrying the early-stage embryos were larger than those carrying the late-stage embryos (Table 1). Larger females were capable of carrying larger numbers of eggs than smaller females (Figure 3a), and embryo volume (mm^3) strongly differs between early- and late-stage embryos (Figure 3b). Five males were collected with carapace lengths ranging from 1.51 to 2.5 mm.
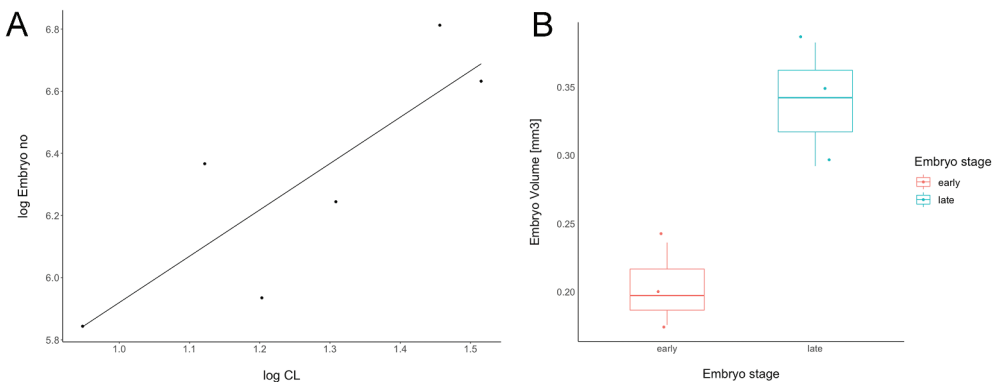
Figure 3. (a) Log egg number vs log carapace length (CL) in *Paratypton siebenrocki*; (b) box plot showing the egg volume of early and late stage embryos.

Discussion

Dwelling morphology

Paratypton siebenrocki is obligately associated with a variety of species in the coral genus *Acropora*, including branching and corymbose colonies. Bruce (1969) provided a description of the dwelling of *P. siebenrocki*, and mentions that the only external indication of the presence of *P. siebenrocki* is a general disturbance of the regularity of the adjacent corallites. At four localities (Farasan Islands and reefs near Yanbu in the Red Sea, Kenya, and Maldives) samples were retrieved from *Acropora* and the host corals showed a clear swelling at the base or at the mid-part of a side branch (Figure 1c, d). However, the samples from Merulina reef (near Yanbu, Red Sea) show how highly cryptic some of the dwellings of *P. siebenrocki* can be (Supplementary Figure S1c–e); this observation is possibly more in line with the dwelling from which Bruce (1969) obtained his specimens. Bruce (1969, p. 179) furthermore commented:

> On opening the cysts the females were found to occupy the larger chamber in a head-down position. The male occupied the smaller upper chamber. When removed from the cyst the female was found to be very sluggish and almost unable to swim. The male was active and swam readily.

Similarly, we also observed the females to barely move (hindered by their large egg masses), while the males were very mobile. We were not able to confirm the position of females and males residing in clearly separated chambers as described by Bruce (1969), which could be due to damage while opening the dwellings. Whereas Bruce (1969) did not comment on any colouration inside the galls, we observed two of the galls in Kenya to be partially pink and dark brown inside – the reason for which is unclear. The dwellings from Merulina reef (near Yanbu, Red Sea) did not show any colouration inside the galls; for the other samples, dwelling colouration was not recorded.

To date, only a small number of *P. siebenrocki* specimens are available for study in natural history collections, despite the species' wide distribution range from the Red Sea to the Pacific Ocean (Bruce and Trautwein 2007). There is no information on the density or population size of this species; however, several authors report finding only one or two specimens in substantial collections of coral-associated decapods from a particular location (e.g. Patton 1966; Bruce 1980; Nomura et al. 1996). Interestingly, *P. siebenrocki* appears rather abundant in the coral nursery in Kenya, where multiple dwellings were encountered in *Acropora* fragments. While snorkelling on a nearby natural reef, multiple dwellings were observed in *Acropora* cf. *verweyi*, suggesting that these reefs could be the source of the *P. siebenrocki* population in the coral nursery. When placed in the nurseries the *Acropora* fragments are roughly finger-sized and thus presumably too small to already contain dwellings, hence shrimp larvae most likely settled on the fragments in the nurseries. A recent study shows that coral nurseries can support a diverse community of mobile epifauna (Wee et al. 2019). Our observations of *P. siebenrocki* in the Kenyan REEFolution nurseries highlight that these nurseries can also support populations of rarely reported immobile endofauna.

Based on its highly specialised habitat, *P. siebenrocki* has been considered to be a nano-plankton feeder (Borradaile 1921; Bruce 1969). The latter author suggests that the male's pleopods are specialised for the production of water currents, on which

the male and female can feed. Similarly, the gall-forming crab *H. marsupialis* s.l. – which inhabits comparable (semi-)closed dwellings in Pocilloporidae corals – is considered a suspension feeder by some authors (Potts 1915; Terrana et al. 2016, but see Kropp 1986). A preliminary study on the trophic position of symbiotic Palaemonidae associated with various host phyla indicated the presence of two ecological groupings: one group where the species largely consume the same food sources as their hosts (commensal/mutualistic) and the other where the shrimps derive much of their carbon intake from their host taxa (obligate/facultative parasites) (De Grave et al. 2021). Most scleractinian corals are both auto- and heterotrophs, with heterotrophy accounting for 15–35% of daily metabolic requirements in healthy corals (Houlbrèque and Ferrier-Pagès 2009). Perhaps a third ecological grouping is present, where the food source neither (or only partially) corresponds to that of their host, nor includes feeding on the host.

Systematic position and biogeography

Paratypton siebenrocki has a wide distribution range from the Red Sea and Eastern Africa through to French Polynesia (Bruce and Trautwein 2007). COI sequence data shows 14% divergence between a specimen from the Red Sea and a specimen from Moorea, at both ends of its distribution range, yet this only translates to three different amino acids. Coincidentally, Borradaile (1921) had a specimen from Pago Pago in American Samoa in the Pacific Ocean, which he could compare with Balss' specimens from Kosseir in the Red Sea, and from Jaluit, Marshall Islands. Minor morphological differences in the length of the antennal flagella and the exposure of the eye segment in dorsal view were observed, but all specimens were deemed to belong to the same species (Borradaile 1921).

No clear clustering of *P. siebenrocki* with other (symbiotic) palaemonids is observed in our phylogenetic reconstruction (Figure 2; UltraFast Bootstrap approximation (UFboot) and Bayesian Inference (BI) values ≥ 95 are considered supported). The species clusters with low support with various Atlantic species, a result that is difficult to explain and – based on the low support values – should be disregarded. Moreover, for some species discussed by Bruce as possibly closely related to *Paratypton*, e.g. *Veleronia*, no genetic data is currently available. Nonetheless, based on the currently available genetic data a close relationship with *A. denticauda* or *M. fungiacola*, as suggested by Bruce (1969), seems unlikely. *Anapontonia denticauda* clusters with full support with *Ischnopontonia lophos* (Barnard, 1962), whereas *M. fungiacola* clusters with *Pliopontonia furtiva* Bruce, 1973. The overall clustering at the species/genus level in our phylogenetic reconstruction is in agreement with Horká et al. (2016), with the exception of a lack of resolution for the main clades, likely because nuclear markers are lacking in our dataset. Further research is needed to pinpoint the systematic position of *P. siebenrocki* amongst the Palaemonidae, possibly using multiple markers or a different genetic approach.

Reproduction

The maximum reported number of embryos reported in a study on the reproductive output of symbiotic palaemonid shrimps is 605 (van der Meij et al. 2018). The

P. siebenrocki females in this study carried between 345 and 909 embryos (Table 1). Bruce (1969) reported 1278 embryos from a single ovigerous female.

In the Atlantic species *Periclimenes rathbunae* Schmitt, 1924, embryo mortality of 24% between early and late embryo stages was reported (Azofeifa-Solano et al. 2014). de Moraes et al. (2017) report 16.6% embryo loss in *Periclimenes paivai* Chace, 1969, whereas van der Meij et al. (2018) report no embryo loss in *Cristimenes commensalis* (Borradaile, 1921) and *Pontoniopsis comanthi* Borradaile, 1915. The latter authors speculated that the lack of observed loss could be related to the more enclosed and thus protected ecospace of *C. commensalis* and *P. comanthi*; however, that would not explain why *P. siebenrocki* – inhabiting a highly protected ecospace – appears to show embryo loss between egg stages (Table 1). Our sample size of six ovigerous females is too small to draw any real conclusions, but it is striking that the brood mass volume remains more or less constant between egg stages. Hence we speculate that a brood mass volume of 150–170 mm^3 might be the upper limit of what *P. siebenrocki* females can carry.

Embryo volume (mm^3) of *P. siebenrocki* is tenfold higher than those reported from other symbiotic Palaemonidae (van der Meij et al. 2018, table 2), with early-stage embryos being of much smaller size than late-stage eggs (Table 1; Figure 3b). The unusually large embryos, when compared to other symbiotic palaemonids (Table 1; van der Meij et al. 2018), are often linked to abbreviated larval development (Strathmann 1977; Bruce and Trautwein 2007). Moreover, fecundity is closely related to female size (Corey and Reid 1991; Azofeifa-Solano et al. 2014), which also appears to be the case in *P. siebenrocki* (Figure 3a). Although reproductive output – a value used to compare the fraction of the total energy budget diverted to reproduction – could not be calculated, it is apparent that *P. siebenrocki* can allocate a lot of energy towards reproduction based on the size and number of its embryos, which is in line with other symbiotic decapods inhabiting a sheltered habitat.

Disclosure statement

No potential conflict of interest was reported by the authors.

ORCID

Sancia E. T. van der Meij 🔸 http://orcid.org/0000-0002-3759-8945
Jessica Bouwmeester 🔸 http://orcid.org/0000-0002-9221-537X
Susanne Bähr 🔸 http://orcid.org/0000-0002-6834-4120

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