Symbiosis
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Characteristics of the infestation of *Seriatopora* corals by the coral gall crab *Hapalocarcinus marsupialis* Stimpson, 1859 on the great reef of toliara, Madagascar

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Abstract This study describes the association between the obligatory symbiont coral gall crab *Hapalocarcinus marsupialis* and its stony coral hosts *Seriatopora sp*. within the Great Reef of Toliara in Madagascar and attempts to discuss their symbiotic status through comparison with previous studies. These corals are inhabited by crabs living in galls that can be categorised in four distinct morphological stages, where the first one corresponds to a small bud and the last one represents a completely closed gall surrounding the crab inside. Within the reef, 563 colonies of *Seriatopora* species were observed by scuba-diving at ten different stations: 37.8 % of them were infested by *H. marsupialis*, with a total of 763 galls, and with a majority of stage 4 galls. Galls are monopolised by females that can have different morphologies. Females store the sperm in two spermathecae and are fertilised when their morphology and size are similar to males and the gall is not closed. Histological observations coupled with scanning electronic microscopy analyses show that closed galls are made of an external living tissue, a mid skeletal layer and an internal living tissue. The internal living tissue includes polyps similar to the external tissue, some of them being sexually mature. Nitrogen and carbon isotopic signatures confirmed that these crabs are filter-feeders and do not feed on their host. This association perfectly highlights the difficulties to define the symbiotic status of a symbiont if one considers inflexible the three categories of symbiosis commonly defined.

Keywords Coral gall crab · Stony coral · Cryptochiridae · Madagascar

1 Introduction

Coral reefs are considered to be a crucial ecosystem for the biosphere as they allow the development of thousands of different marine species. This is illustrated, for example, by the high potential of symbiotic interactions associating scleractinian corals with various symbionts (Castro 1976). Among them, the genera *Acropora*, *Pocillopora*, *Seriatopora* and *Stylophora* have the most diversified symbiotic fauna (Vytopil and Willis 2011). Symbiotic organisms take advantage of corals to shelter from predators or benefit from a food source (Stella et al. 2011). The branching shapes of these corals can also change the hydrodynamism around the colony (Helmuth et al. 1997) which leads to an increase of the available ecological niches, such as a hypoxic area, a thicker surface boundary layer or a modified flow of organic particles (Vytopil and Willis 2011).

Brachyuran decapods are particularly abundant among branching corals (Patton 1974; Castro 1976) and especially in the Acroporidae and Pocilloporidae families (Abele 1984). Obligate corals' symbiotic crabs generally belong to the families Tetraliidae, Trapeziidae, Xanthidae and Cryptochiridae (Stella et al. 2011), the latter being represented by small and cryptic coral gall crabs currently belonging to 21 genera and 52 species (Davie 2015). Coral gall crabs are

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obligate symbionts inhabiting the skeleton of scleractinian corals by forming a gall or a pit in their host's tissue (Wei et al. 2013). These crustaceans have been known for more than 150 years and many recent studies have been made into their biology and ecology (Jamieson and Tudge 2000; Carricart-Ganivet et al. 2004; Johnsson et al. 2006; Badaro et al. 2012; van der Meij 2012; Mohammed and Yassien 2013; Wei et al. 2013; Vehof et al. 2014; van der Meij 2014; Nogueira et al. 2014), their evolution and phylogeny (Wetzer et al. 2009; van der Meij and Schubart 2014; van der Meij 2015) and their taxonomy (Kropp 1990). The coral hosts act as both protection and a food source for the Cryptochirid crabs. Some species living in shallow depressions or cylindrical pits feed on coral mucus, tissue or trapped organic particles (Kropp 1986; Abelson et al. 1991; Simon-Blecher et al. 1999) while crabs living on galls are filter-feeders (Marshall and Orr 1960; Abelson et al. 1991). Free-living males may move from one colony to another to mate or share a gall with a female (Castro 1976; McCain and Coles 1979; Warner 1977; Vehof et al. 2014). Cryptochirid female crabs remain inside the cavity they inhabit for breeding their entire lives. They have an allometric growth of their abdomen that forms a brood pouch under the cephalothorax. This feature is a synapomorphic character of the Cryptochiridae family that can be also found among female pea crabs (Pinnotheridae, Becker 2010).

Although the obligate character of the symbiosis between coral gall crabs and stony corals is unquestioned, their symbiotic status is not clearly determined as the crabs may be commensals, mutualists or parasites (Kropp 1986; Abelson et al. 1991; Reed et al. 1982; Simon-Blecher et al. 1999; Carricart-Ganivet et al. 2004). While these crabs induce morphological deformations on their coral hosts, they may not have any significant negative effects on their hosts (Rotjan and Lewis 2008).

In this study, a population of the symbiotic coral gall crab *Hapalocarcinus marsupialis* on its coral hosts *Seriatopora* sp. within the Great Reef of Toliara was characterised by considering the following: (i) are the crabs abundant in these locations and (ii) what are the effects of the crabs on their host? The findings, based on histological sections and the symbiotic status of this relationship, will be discussed.

2 Material and methods

2.1 Sampling

The sampled coral hosts were identified as *Seriatopora hystrix* according to the work of Veron and Pichon (1976). However, recent molecular studies have highlighted the difficulty to properly discriminate species diversity among scleractinian corals, especially for the Pocilloporidae family (Stefani et al. 2011; Keshavmurthy et al. 2013; Pinzon et al. 2013; Warner et al. 2015). Corals from the *Seriatopora* genus have a morphological plasticity which renders difficult the definition of species boundaries based on morphological criteria (Veron and Pichon 1976). For this reason, all the *Seriatopora* individuals where coral gall crabs have been collected are cited here as *Seriatopora* sp. The samplings were done by SCUBA diving at depths of 10–15 m in the shallow reef of Toliara (south-western coast of Madagascar) in November and December 2013. A total of 88 females *Hapalocarcinus marsupialis* were collected using pliers to break off the galls without otherwise damaging the colonies, while 46 males were found free living on the coral hosts. Samples were kept in sea water during the transfer to the laboratory before being fixed in Bouin's solution for 24 h and then stored in 70 % ethanol for histological analysis.

2.2 Crab infestation and transects

Gall formations were divided into four different developmental stages as described by Kotb & Hartnoll (2002; see results). A colony of *Seriatopora* was considered infested when it showed at least one stage 1 gall. Ten stations (Fig. 1) were studied in order to determine the infestation prevalence of the coral gall crabs on their host (number of infested colonies/total number of colonies), and the infestation rate (number of galls on each infested colony). Line transects were carried out by scuba diving and consisted of a surface of 10 m long and 4 m width, in which every *Seriatopora* colony was counted. Transects were made at a constant depth between 10 and

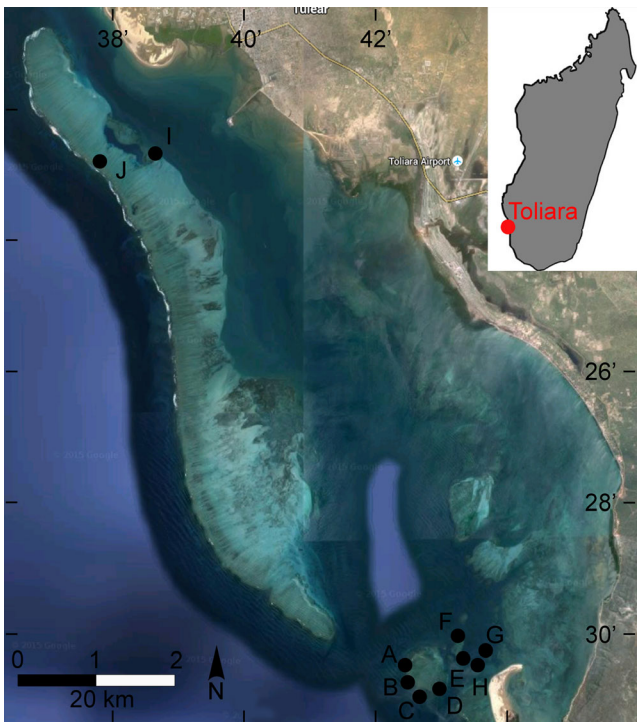

Fig. 1 Areas of the study. Transects performed on the Great Reef of Toliara, Madagascar. Satellite view from Google Maps

15 m depending on the location. (Nosy Tafara reefs including Nosy Arakaivo: station A 23°30′31.4886″S 43°42′35.4846″E, station B 23°30′36.5976″S 43°42′38.016″E, station C 23°30′46.965″S 43°42′46.9188″E and station D 23°30′47.6928″S 43°42′55.0002″E and Nosy Velomitahy: station E 23°30′14.6298″S 43°43′27.822″E and station F 23°30′0.1074″S 43°43′27.4686″E; Belaza reef: station G 23°30′20.4366″S 43°43′53.4252″E and station H 23°30′24.0156″S 43°43′49.7526″E). Stations I and J were located just behind the barrier reef in an area called "Grande Vasque" which is quite protected from tidal currents. The Nosy Tafara reefs are located in the southern channel of the Great Reef in Toliara Bay which is continually subject to tidal currents. Stations A, B, C and D are located in the outer reef of Nosy Arakaivo, and E, F, G and H in small patch reefs in the lagoon. The results were compared with Chi^2 tests and multiple comparisons using the statistical R software.

2.3 Analyses of the coral galls

The coral galls were studied through optical microscopy and scanning electron microscopy in order to see if the crab presence, inducing the gall formation, would affect the coral tissue, the skeleton structures and the gonadal development of the polyps.

Ten coral galls were fixed in 3 % glutaraldehyde buffered by 0.1 M sodium cacodylate and 1.5 % NaCl (pH adjusted to 7.8 with HCl) for 24 h then repeatedly rinsed with the same buffer and increasing ethanol baths (25–50-70). Fragments were then coated with an agarose gel before being decalcified. Agarose blocs were immersed in 10 % citric acid and 10 % formalin solution and changed every day for one week to decalcify. Coral samples were then embedded in paraffin before sectioning. Seven to 10 μm thick sections were made with a Zeiss Microm HM 340E microtome. For general tissue differentiation, coral galls were compared to coral branches without gall crabs and sections were stained with a trichromatic Masson-Goldner light green staining.

The coral skeleton was also observed by scanning electron microscopy to see if any modification was induced by the crab. The skeleton was obtained through a 24 h bath of 10 % sodium hypochlorite, to eliminate living tissues, before being metallised with a JEOL JFC-1100E Ion Sputter and observed with a JEOL JSM 6100 scanning electron microscope.

2.4 Coral gall crab development

Before being embedded and prepared for histology as explained above for coral galls, the sizes of crab cephalothoraxes were measured to determine if there was a correlation between the crab size and its maturity. Cephalothoraxes were measured with the ImageJ software (Rasband 1997) from the top of the rostrum to the cephalothorax basis for the Carapace Length (CL), and between the lateral extremities for the Carapace Width (CW) for all the females. On the 88 females, 24 of them showed a brood. All the eggs from 10 randomly chosen females were counted with a binocular magnifier and their diameter measured with the same software. Females were considered sexually mature when vitellogenic oocytes were present in their ovaries, while they were considered fertilised when sperm was observed in their spermathecae.

2.5 Coral gall crab feeding mode

The feeding habit of *Hapalocarcinus marsupialis* was investigated with the measurements of δ15N and δ13C isotopic compositions of crab tissues. For that purpose, tissues of 11 females (entire individuals) and of three potential food sources were investigated (coral tissues, suspended organic matter and incrusting algae found at the basis of coral colonies). Tissues of 10 coral colonies of *Seriatopora* sp. that inhabited the crabs, 4 filtrates (0.2 μm) of 5 l each of sea water collected in the vicinity of corals and tissues of 3 unidentified incrusting algae were collected and analysed following the method explained in details in Caulier et al. (2014). In brief, samples were oven-dried at 60 °C for 48 h before being crushed into powder and acidified with 37 % fuming HCl in a jar for 48 h in order to remove skeleton carbonates that do not come from the diet. Isotopic ratios and elemental content measurements were performed with a mass spectrometer (VG Optima, Isoprime, UK) coupled to a CNS elemental analyser (Carlo Erba, Italy) for combustion and automated analysis. Nitrogen and carbon contents are expressed in percent relative to dry weight. Isotopic ratios are presented as δ values (‰), expressed relative to the VPDB (Vienna Peedee Belemnite) standard for carbon and to atmospheric N2 for nitrogen. Reference materials were IAEA-N1 (δ15N = + ± 0.04 ‰) and IAEA CH-6 (sucrose) (δ13C = −10.95 ± 0.11 ‰). Non parametric statistical Mann-Withney and Kruskal-Wallis tests were used to compare the isotopic signatures.

3 Results

3.1 Gall structure and development

During the gall formation, four distinct stages were observed at the coral branch extremity (Fig. 2). The first one corresponds to a little bud at the top of the branch, measuring a few millimetres in size; the second one presents two little valves up to 1 cm in height with the beginning

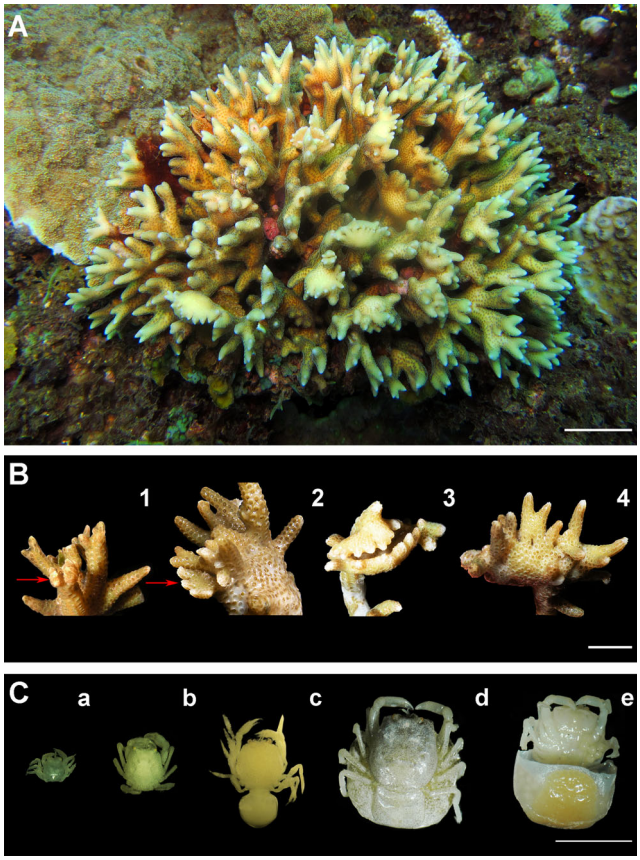

Fig. 2 The coral host and its symbiotic crabs **a** Colony of *Seriatopora* sp. showing several galls at different developmental stages (scale bar: 5 cm) **b** Developmental stages of a gall induced by the coral gall crab (scale bar: 1 cm) **c** Adult male (a) and females (b-e) at different developmental stages (b, c, d in dorsal view, e in ventral view) of the coral gall crab *H. marsupialis* (scale bar: 5 mm)

of a curving shape; the third one is higher than 1 cm and is characterised by two big valves but is not closed, forming a large cavity for the crab; and the fourth stage represents the completely closed gall confining the symbiotic crab inside and measuring more than 3 cm. When the gall is closed, there are always small holes all around the gall closure, opening to the outside.

Scanning electron microscopy images show no difference between the skeleton of a branch belonging to an uninhabited coral and the one of the gall valves (Fig. 3). However, different shapes of the polyp columella can be seen on the coral valves: it can either be smooth and cylindrical or shapeless (Fig. 3).

No modifications of the polyp tissues were observed on the coral sections. There were polyps located on the inner surface of the galls as well as the outer surfaces (Fig. 4). In Fig. 4a, the two valves (lv and rv) are visible and polyps are present on the outer surface. The empty space between the two valves represents the location where the female crab lived. Polyps are also present at the base of the gall, and both the valve polyps and the base can be mature, showing well-developed male and female gonads (fg and mg, Fig. 4). The female gonad is clearly visible due to the presence of the vitellogenic oocyte, while the male gonad shows spermatozoids (Fig. 6).

3.2 Crab infestation

The crab *Hapalocarcinus marsupialis* was found on *Seriatopora* species and *Pocillopora sp*. Only *Seriatopora* sp. was focused on. A total of 563 colonies were observed: 213 of them were infested by at least one gall. A total of 763 galls were recorded which corresponded to an infestation rate ranging between 1 and 27 galls in a single colony. The percentage of inhabited corals was at its maximum at station B (57.10 %), which is located on the outer reef, even though here the number of colonies was the lowest. The lowest percentage of inhabited corals was at stations H and F (15.50 % and 16.70 % respectively, Fig. 5) with the lowest number of galls (23 and 5 respectively). These two stations are located in a channel between the Nosy Araikavo reef and the coast. The maximum number of coral galls was observed at station D, with 187 galls for 37 coral hosts (Table 1). Considering all the stations, the prevalence of crab infestation reached 37.8 % and the stage 4 gall was the most abundant with 319 observations. The numbers of stage 1, 2 and 3 galls were 134, 177 and 133 respectively. There is no correlation between the total number of inhabited corals on a station and the infestation rate (Pearson's correlation $r = 0.46$; p-value >0.05). The eight stations located on the Nosy Tafara reefs can be put into two groups: the West Side including stations A, B, C and D, on the outer reef Nosy Arakaivo, and the East Side, including stations E, F, G and H, in the channel between the reef and the coast. The number of colonies was nearly equal between the west side and the east side (219 and 207 colonies respectively) but the infestation rates were significantly different: 47 % of the corals were inhabited on the west side and 26.6 % on the east side (chi-squared =5.69, $p < 0.05$). Consequently, there were more galls observed on the west side ($n = 262$) than the east side ($n = 167$, chi-squared =21.04, p-value <0.05), while the stage 4 gall was the most represented with 203 galls observed for the west side and 56 for the east side. Table 1 summarises the dataset for each station. There was no linear correlation between the number of infested corals and the average number of galls on a single colony at each station (Pearson's correlation, $p = 0.46$) Table 2.

3.3 Female coral gall crabs maturity

Females with a cephalothorax measuring less than 2.575 cm long had a similar morphology to the males. Bigger females had a hypertrophied abdomen forming a

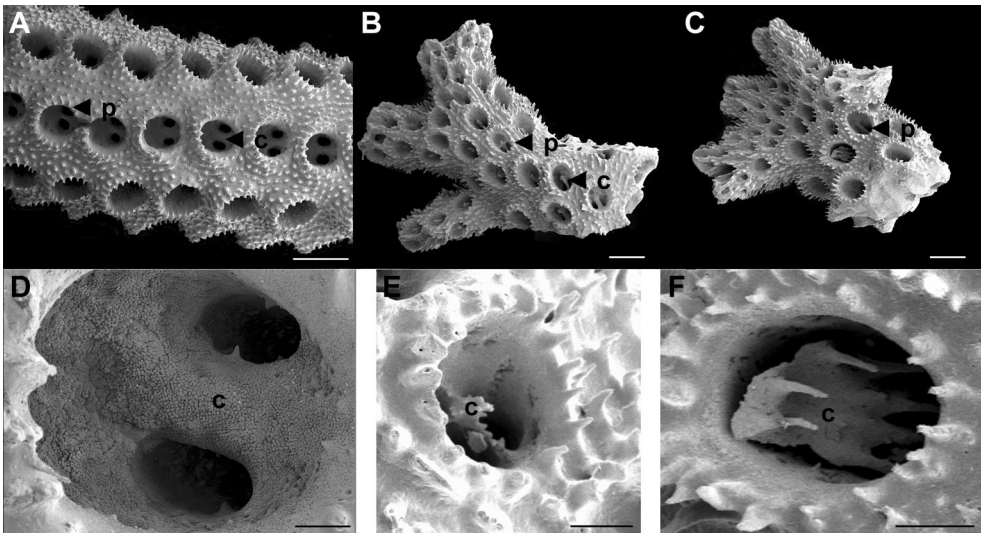

Fig. 3 Scanning electron microscopy of the coral skeleton and detailed views of the columella **a** Healthy branch of a coral colony (scale bar: 1 mm) **b** External surface of the stage 1 gall (scale bar: 1 mm) **c** Internal surface of the stage 1 gall (scale bar 1 mm) **d** Columella of a polyp located on a healthy branch (scale bar: 100 μm) **e** Columella of a polyp located on the external surface of a stage 1 gall (scale bar: 250 μm) **f** Columella of a polyp located on the internal surface of a stage 1 gall (scale bar: 250 μm). c: columellae, p: polyp

large pouch, the marsupium, under the cephalothorax (Fig. 1). A total of 59 females with a fully developed abdomen were observed, 24 of them incubated a brood in their pouch, and they were always inside completely closed galls. The other females were collected in open galls and had no brood. The number of eggs ranged between 148 and 565 in a single brood for the 10 randomly chosen females. The mean egg diameter was about 0.492 ± 0.014 mm and there was no difference between the egg sizes from either the same brood or different broods (p = 0.1; ANOVA). Histological sections showed three distinct maturity stages according to the female morphology. Immature females with a similar aspect to the males had no vitellogenic oocytes and empty spermathecae (Fig. 6). Females with a completely developed marsupium were always fertilised and had the spermathecae filled with spermatozoids, but they showed immature oocytes or vitellogenic oocytes (Fig. 6). Immature females (1.9 ± 0.5 cm length, 1.9 ± 0.6 cm width) were always smaller than females with the

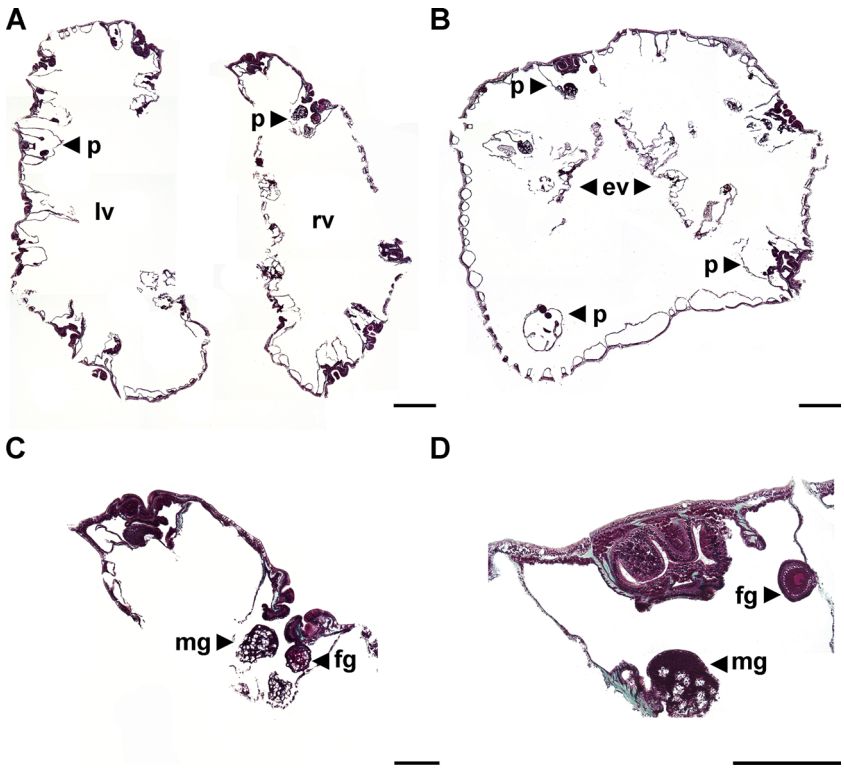

Fig. 4 Coral gall histology **a** Transverse section through the two valves of a stage 2 gall (scale bar: 500 μm) **b** Transverse section through the basis of the gall showing the end of the internal surfaces of the valves (scale bar: 500 μm) **c** Transverse section of a polyp located on the external surface of the right valve (scale bar: 100 μm) **d** Transverse section of a polyp located on the branch surface (scale bar: 100 μm) ev: end of the valves, fg: female gonad, lv: left valve, mg: male gonad, p: polyp, rv: right valve

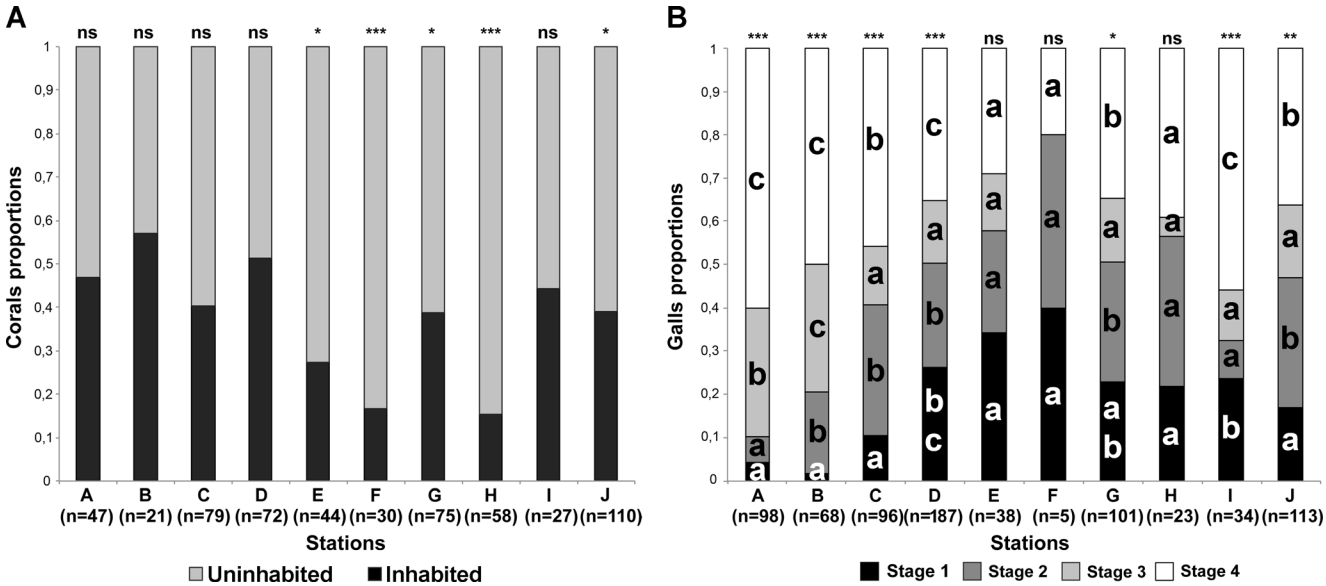

Fig. 5 Characteristics of the infestation by the coral gall crab on the Great Reef of Toliara **a** Comparison of the infestation rate between each station (uninhabited corals versus inhabited corals) **b** Comparison of the proportions of each infestation stage for each station. For both figures, the stars above the bars represent the statistical significance of the Chi-squared tests for the multiple comparisons. The letters refer to the multiple comparisons test between each developmental stage for one station (chi-square tests). ns: non-significant *: significant $p < 0.05$ **: very significant $p < 0.01$ ***: highly significant $p < 0.001$

marsupium (3.5 ± 0.4 cm length, 3.7 ± 0.4 cm width). According to these samples, females of less than 2.3 cm in length were immature and their marsupium was not fully developed. Yet, females were mature from 2.5 cm and had both spermathecae filled with spermatozoids and vitellogenic oocytes (Figs. 6 and 7).

4 Discussion

A recent molecular study demonstrates that a complex of cryptic species occurs inside the coral gall crab family Cryptochiridae (van der Meij 2015). For example, the crab *Fungicola fagei* was formerly considered as a single species until van der Meij (2015) discovered a complex of cryptic species in which the new crab *F. syzigia* share different fungiid coral hosts, and have very subtle morphological differences with *F. fagei*. Since such genetic differences are found inside cryptochirid crabs, it is not unlikely that the coral gall crab *Hapalocarcinus marsupialis*, always regarded as a single species in this study, may also refer to a complex of cryptic species.

On the Great Reef of Toliara, *H. marsupialis* was found on 37.80 % of the 563 colonies of *Seriatopora* species observed. The prevalence of the infestation on Toliara reached similar values to that observed in the Red Sea, where 37.1 % of 101

Table 1 Number of infested and healthy corals recorded on each station with the number of the different developmental stages observed St 1 to 4: stage of the galls

	Corals observed			Prevalence (%)	Galls observed					Mean galls/coral
Station	Healthy	Infested	Total		St1	St2	St3	St4	Total	
A	25	22	47	46.80	4	6	29	59	98	4.45
B	9	12	21	57.10	1	13	20	34	68	5.67
C	47	32	79	40.50	10	29	13	44	96	3.00
D	35	37	72	51.40	49	45	27	66	187	5.05
E	32	12	44	27.30	13	9	5	11	38	3.16
F	25	5	30	16.70	2	2	0	1	5	1.00
G	46	29	75	38.70	23	28	15	35	101	3.48
H	49	9	58	15.50	5	8	1	9	23	2.55
I	15	12	27	44.40	8	3	4	19	34	2.83
J	67	43	110	39.10	19	34	19	41	113	2.63
Total	350	213	563	37.80	134	177	133	319	763	3.38

Table 2 Mean values of $\delta^{15}N$ and $\delta^{13}C$ (± SD) of the coral gall crab *H. marsupialis* and its potential food sources

Specimens	Number tested	Mean isotopic ratio measurement	
		δ15N	δ13C
H. marsupialis	11	−18.05 (±0.40)	5.64 (±0.48)
S. hystrix	10	−20.08 (±0.81)	2.64 (±0.28)
Filtrates	3	−17.64 (±1.10)	3.38 (±0.94)
Algae	3	−11.39 (±3.31)	3.108 (±0.73)

colonies of *Stylophora pistillata* (Pocilloporidae) were infested with a maximum of 14 galls on a single colony (Mohammed and Yassien 2013). This is more than previous studies into pit crabs inhabiting non-branching corals (Simon-Blecher and Achituv 1997; Van der Meij and Hoeksema 2013; Nogueira et al. 2014), which is probably due to a smaller suitable surface for crabs. The host specificity of *Seriatopora* species was also found on the Queensland reefs in Australia, where *H. marsupialis* lived on every species of the Pocilloporidae family but were particularly abundant on *S. hystrix* (Patton 1966). Such selectivity has been suggested to optimize survival and reproductive success (Orians and Wittenberger 1991; Pulliam and Danielson 1991).

Our study shows that the infestation rate is different between the locations: corals from the west part of Nosy Tafara reef are more infested by crabs than the eastern part. The establishment of *H. marsupialis* on the western sites is older (i.e. has the highest proportion of closed galls) than the eastern sites. These observations are probably the result of hydrodynamic and environmental effects that could influence larval dispersion and settlement. The Nosy Tafara reefs divide the south of Toliara into two parts: the west side is strongly exposed to swells and tides while the east side is more set back and protected (Pichon 1978). Moreover, larvae do not seem to choose where to settle based on the numbers of adult crabs. This can be assumed as there is no correlation between the number of infested corals at a station and the average number of galls on a single colony. Furthermore, a maximum of 27 galls were observed per coral. In comparison, authors of other studies into pit crabs found a maximum of 4 crabs per coral with a more widespread occurrence of 1 or 2 symbionts (Simon-Blecher and Achituv 1997; Nogueira et al. 2014). While an intraspecific competition is expected in cryptochirid crabs (Nogueira et al. 2014), it is not the case for *H. marsupialis*. This could be explained by the the branching shape of the coral hosts that provide more possibilities to settle alone on the top of a branch without competing with conspecifics (Vytopil and Willis 2011). These groupings of crabs on the same coral host may also provide significant advantages for both males and females to reproduce, as males are free-living and look for sedentary females (Vehof et al. 2014).

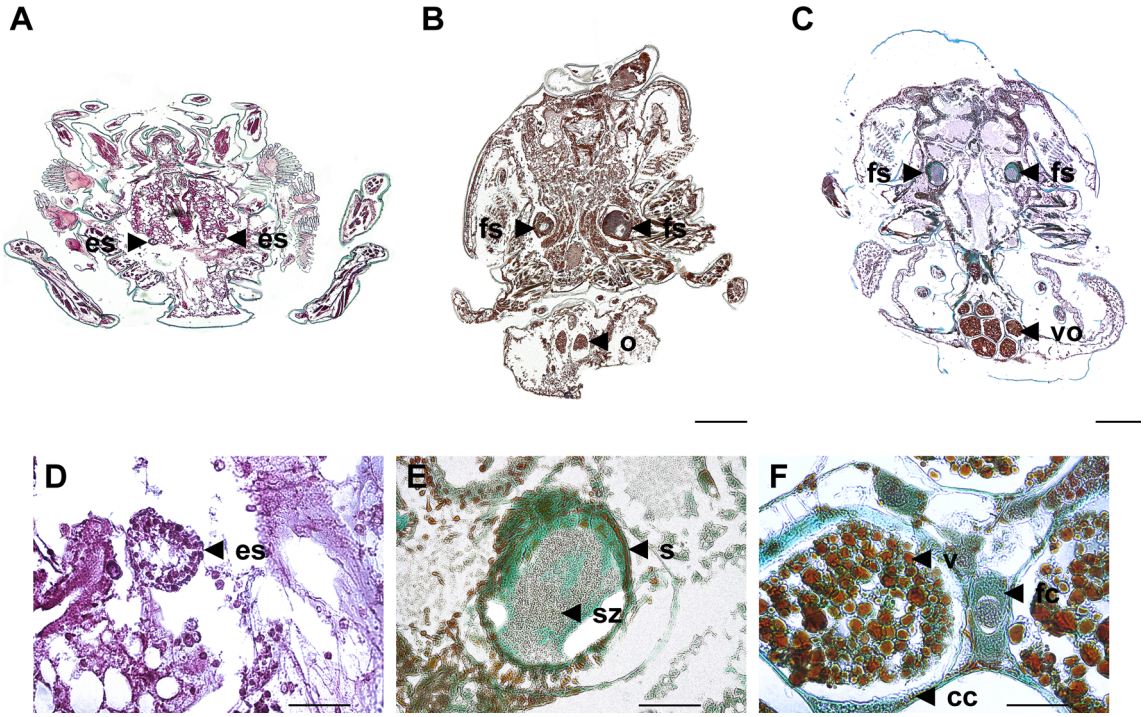

Fig. 6 Gonadal developmental stage of female crabs **a** Section through an immature female crab (scale bar: 500 μm) **b** Fertilized female crab showing its spermathecae full of spermatozoids (scale bar: 500 μm) **c** Mature and fertilized female crab showing full spermathecae and vitellogenic oocytes (scale bar: 500 μm) **d** Detailed view of an empty spermathecae (scale bar: 100 μm) **e** Detailed view of a spermathecae filled with spermatozoids (scale bar: 50 μm) **f** Detailed view of a vitellogenic oocyte (scale bar: 50 μm). cc: conjonctive capsule, es: empty spermathecae, fc: follicular cell, fs: full spermathecae, o: oocytes, s: spermathecae, sz: spermatozoids, v: vitellus, vo: vitellogenic oocytes

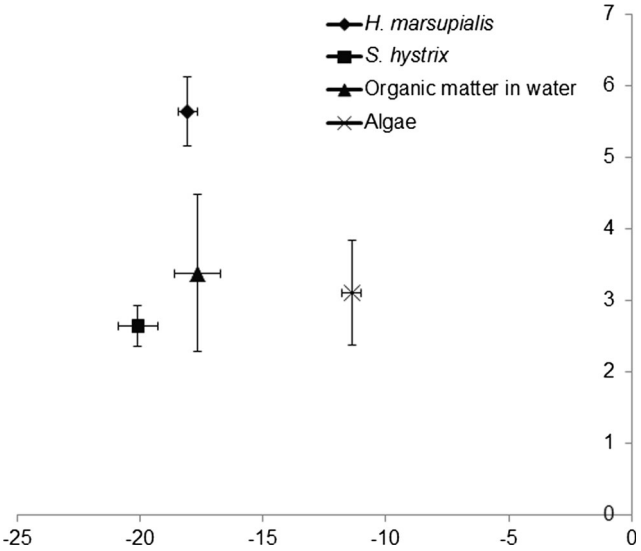

Fig. 7 Average values (±S.D.) of $\delta^{15}N$ and $\delta^{13}C$ for the crabs and their potential food sources: coral hosts, algae and organic matter in water

The diet of the coral gall crab *H. marsupialis* has been discussed many times in the past, and a lot of different feeding habits have been assigned to this species (Stimpson 1859, Henderson 1906, Potts 1915, Patton 1976, Kropp 1986). Our results based on carbon and nitrogen isotopic signatures show that *H. marsupialis* is mainly a suspension-feeder as they capture organic particles from the water flow, the morphology and hydrodynamism of the galls probably favouring particles trapping and availability (Abelson et al. 1991). Since heavier particles may settle inside galls (Abelson et al. 1991) and Kropp (1986) observed crabs gathering mucus at the coral surface, it is plausible that there are multiple feeding strategies in the Cryptochiridae family.

Histological analyses show that immature females that live in unclosed galls are fertilized when their shape is still similar to males, i.e. when they have not a marsupium. Females grow in parallel to the gall development and only females with the marsupium completely developed lie inside closed galls. After the gall closes, the female produces eight or more egg batches within the following 10 months (Kotb and Hartnoll 2002). Mating could be a stimulus accelerating the female growth and allowing the abdomen to have its final morphology. The latter forms a large marsupium under the cephalothorax where eggs are brooded. The female body size is limited by the gall cavity and this is the principal determinant of reproductive output in addition to the body cavity that limits brood size in brachyuran crabs (Hines 1982). Because the females are relatively small, the development of a marsupium allows them to brood a high number of eggs that are protected against coral cnidocytes. The mean egg size of 0.492 mm for *H. marsupialis* is relatively high related to the body size that reach up to 25 mm in carapace length. In comparison, the blue crab *Callinectes sapidus* produce eggs with a diameter of only 0.252 mm while its body size reach up to 180 mm in carapace length (Hines 1986; Hines et al. 1987). According to Hines (1982), this large size corresponds to a short larval development and a higher recruitment size increasing the settlement efficiency.

Survival of females are thus strongly dependant of their hosts, as immature females are never found inside closed galls and fertilized females are never found outside them. This spectacular synchronisation between the life cycle of the symbiont and the abnormal growth of the coral host branches brings the matter on the symbiotic status of the coral gall crab *H. marsupialis*; are they parasites, commensals or mutualists? Those three categories are defined in accordance with their effects on the hosts, which are respectively negative, neutral or positive (Kinne 1980). Many examples, however, highlight that the boundaries between those statuses are not rigid and that the symbiotic interactions are much more correctly illustrated by a symbiotic continuum (Parmentier and Michel 2013). In this continuum, the sum of the interactions between a symbiont and its host defines the status of the symbiosis, which is variable depending on the life cycle of both host and symbiont or the environmental conditions. Cryptochirid crabs may have a negative impact on their coral hosts by (i) reducing their growth by feeding on coral tissues (Simon-Blecher et al. 1999) or due to abnormal growth of the skeleton (Simon-Blecher and Achituv 1997); (ii) leading to the death of polyps due to the crab settlement and (iii) favouring algal and fungal growth in and around the pit which leads to an energy loss for the coral (Simon-Blecher et al. 1999). On the other hand, cryptochirid crabs may have a positive impact on their coral hosts by bringing nutrients and organic matter to coral polyps in being active filter feeders. If these crabs are considered parasites because they bore into the skeletons of their hosts, Mokady et al. 1998 relativized this phenomenon among boring bivalves suggesting that the benefit provided through nutrient enrichment may significantly outweight the cost of localized structural damage. At the level of *Seriatopora* populations, the impact of *H. marsupialis* is negligible: corals in low infested or highly infested sites do not show any sign of disease. At the level of colonies, the main negative impact of *H. marsupialis* is the abnormal skeletal development forcing corals to spend energy to create the galls. However, at the level of individuals, histological analyses show that polyps into the galls are normal and sexually functional. Feeding habits of *H. marsupialis* do not match with a parasitic association as they feed on organic particles brought by the water flow. While they can gather mucus from the host surface to eat trapped particles, it may not represent a metabolic drain (Carricart-Ganivet et al. 2004; Badaro et al. 2012). The two last observations would indicate that the symbiosis is

at least neutral for the hosts. In conclusion, this marine association perfectly illustrates that the placement of the coral gall crab in a symbiosis category is not applicable and that, instead, the use of the symbiotic continuum is the best way to characterise it.

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