Host specificity and coevolution

Chapter 7

Host species, range extensions, and an observation of the mating system of Atlantic shallow-water gall crabs (Decapoda: Cryptochiridae)

Sancia E.T. van der Meij

Abstract

Coral-associated invertebrates dominate the biodiversity of coral reefs. Some of the associations involving symbiotic invertebrates remain unknown or little studied. This holds true even for relatively wellstudied coral reefs, like those in the Caribbean Sea. Coral gall crabs (Cryptochiridae), obligate symbionts of stony corals, form a much-overlooked component of coral reef communities. Most recent studies on the Atlantic members of Cryptochiridae have been conducted off Brazil and little recent data have become available from the Caribbean region. During fieldwork off Curaçao (southern Caribbean Sea), eight new host coral species, belonging to four coral families, were recorded for three cryptochirid species. *Kroppcarcinus siderastreicola* Badaro, Neves, Castro and Johnsson, 2012, previously only known from Brazil, and *Opecarcinus hypostegus* (Shaw and Hopkins, 1977) are new additions to the fauna of Curaçao. Besides the new hosts and geographic range extensions, a free-living male *Troglocarcinus corallicola* Verrill, 1908 was observed visiting a female of the same species lodged in her gall in an *Orbicella annularis* (Ellis and Solander, 1786) colony. This is the first photodocumented record of the 'visiting' mating system in Cryptochiridae.

2014
Bulletin of Marine Science 90: 1001-1010

Introduction

The biodiversity of coral reefs is predominantly composed of invertebrates, many of which live in close association with sponges, molluscs, echinoderms, ascidians, and coelenterates like sea anemones, and soft and stony corals. About 870 invertebrate species are known to be associated with stony corals (Scleractinia) alone, but the extent of these associations is only partially known (Stella *et al*., 2011; Hoeksema *et al*., 2012). Species that live in obligate symbioses with a host depend on it for their survival and, hence, are more vulnerable to extinction (McKinney, 1997). This is a concern in the light of the ongoing degradation of coral reefs, especially given that the coral-associated fauna is relatively unknown. Such associated fauna has not been subject of many surveys, even in relatively well-studied regions like the Caribbean Sea. With the exception of the overview provided by Zlatarski and Martínez-Estalella (1982), most published studies have focused on a particular geographical area, host, or symbiont (Reed *et al*., 1982; Scott 1985, 1987, 1988).

Gall crabs (Cryptochiridae; also known as pit crabs) are obligate symbionts of stony corals (see Castro, 1988) worldwide, but many regions still need to be monitored for their occurrence. Research on Atlantic gall crabs has also been sparse. Kropp and Manning (1987) studied both deep and shallow-water Atlantic cryptochirids and included many new host corals based on museum collections. All published research on Cryptochiridae conducted after 1987 has been carried out in Brazil (Noguiera, 2003; Johnsson *et al*., 2006; Oigman-Pszczol and Creed, 2006; Badaro *et al*., 2012; Noguiera *et al*., 2014), except for one publication from Mexico (Carricart-Ganivet *et al*., 2004). For the three Atlantic species of shallow-water gall crabs recognized to date, a total of 23 host species have been recorded (Kropp and Manning, 1987; Badaro *et al*., 2012). One gall crab species, *Kroppcarcinus siderastreicola* Badaro, Neves, Castro and Johnsson, 2012, is so far only known from Brazil, whereas *Troglocarcinus corallicola* Verrill, 1908 and *Opecarcinus hypostegus* (Shaw and Hopkins, 1977) have amphi-Atlantic distributions (Kropp and Manning, 1987).

The present study focuses on the gall crab fauna off Curaçao, for which previously only one gall crab had been recorded (Kropp and Manning, 1987). The present study uses the 'reversed' approach, which is to investigate the associated fauna from the perspective of the host by collecting specimens from as many coral species as possible.

Material and methods

Between 16 October and 9 November, 2013, fieldwork was conducted around Curaçao (Dutch Caribbean, Leeward Islands) in the southern Caribbean Sea. A total of 23 localities were visited, 22 on the leeward side and one on the windward side of the island. Cryptochirids were sampled from a wide range of corals to a maximum depth of 40 m. After in situ photography, crabs were collected from their coral hosts and taken to the CARMABI research station for further processing. All cryptochirids were photographed in vivo with a digital SLR camera with 50/60 mm macro lens, and subsequently fixed in 80% ethanol. The crab specimens were stored in the scientific collections of Naturalis Biodiversity Center in Leiden, the Netherlands. Identifications of cryptochirids were based on Kropp and Manning (1987) and Badaro *et al*. (2012), whereas coral identifications were based on Wells (1973), Zlatarski and Martínez-Estalella (1982), Humann and DeLoach (2002), Coralpedia (http://coralpedia.bio.warwick.ac.uk), and the reference collections of Naturalis Biodiversity Center. Coral nomenclature was updated following Budd *et al*. (2012).

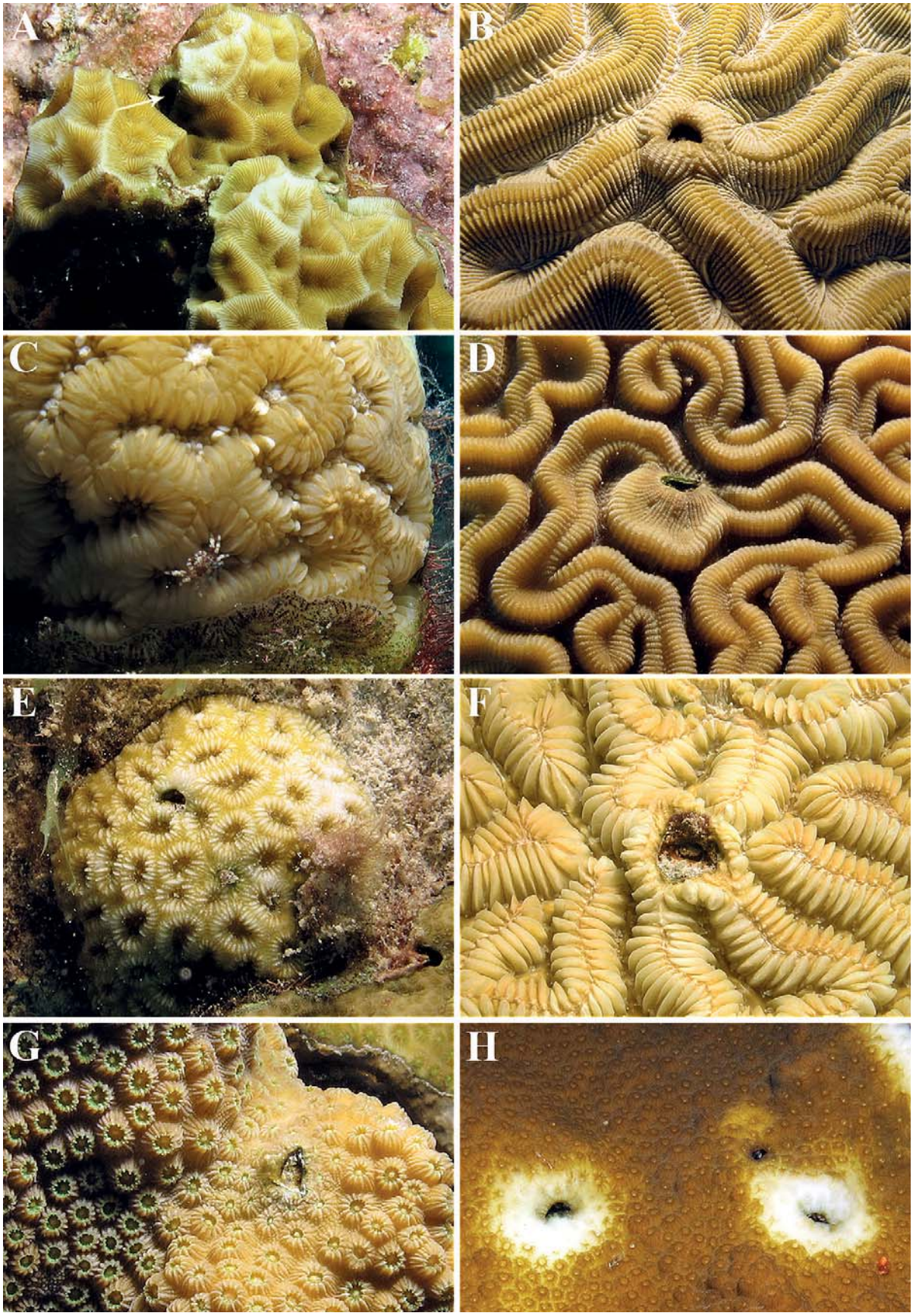

Fig. 1. Gall crab dwellings in the newly reported coral hosts. **A**, *Agaricia humilis*; **B**, *Colpophyllia natans*; **C**, *Dendrogyra cylindrus* (free-living male); **D**, *Diploria labyrinthiformis*; **E**, *Favia fragum*; **F**, *Meandrina meandrites*; **G**, *Orbicella faveolata*; **H**, *Orbicella franksi*. For the associated gall crab species, see Table 1.

Table 1. Overview of the reef coral species hosting shallow-water Atlantic cryptochirids. Names of coral species indicated **in bold** represent new host records. Tcor = *Troglocarcinus corallicola* Verrill, 1908, Ohyp = *Opecarcinus hypostegus* (Shaw and Hopkins, 1977), Ksid = *Kroppcarcinus siderastreicola* Badaro *et al*., 2012.

Coral family/species	Crab	Present study	References earlier records	Remarks
Agariciidae				
Agaricia agaricites (Linnaeus, 1758)	Ohyp	*n* = 5	Kropp and Manning, 1987, Scott, 1987	
Agaricia fragilis Dana, 1846	Ohyp	*n* = 1	Shaw and Hopkins 1977, Kropp and Manning, 1987	
Agaricia grahamae Wells, 1973	Ohyp	*n* = 1	Kropp and Manning, 1987, Scott, 1987	
Agaricia humilis Verrill, 1901	Ohyp	*n* = 1		New host for *O. hypostegus*.
Agaricia lamarcki Milne-Edwards and Haime, 1851	Ohyp	*n* = 11	Kropp and Manning, 1987, Scott, 1987	
Astrocoeniidae				
Stephanocoenia intersepta (Lamarck, 1816)	Tcor	—	Scott, 1985	As *S. michellini* by Scott (1985), considered a j.s. of *S. intersepta* (see Zlatarski and Martínez-Estalella, 1982). There is no material available to check if this record should possibly be attributed to *K. siderastreicola*.
S. intersepta	Ksid	*n* = 4		First record outside of Brazil, new host for *K. siderastreicola*.
Caryophylliidae				
Polycyathus sp.	Tcor	—	Kropp and Manning, 1987	
Meandrinidae				
? *Dendrogyra cylindrus* Ehrenberg, 1834	Tcor	*n* = 1		This is a tentative new host record. One male was collected from a *D. cylindrus* colony, but no dwelling was found (see Fig. 1).
Dichocoenia stokesii Milne-Edwards and Haime, 1848	Tcor	*n* = 2	Verrill, 1908, Shaw and Hopkins, 1977	As *Dichocoenia* sp. by Verrill (1908) and Shaw and Hopkins (1977).
Meandrina meandrites (Linnaeus, 1758)	Tcor	*n* = 7		New host for *T. corallicola*.
Merulinidae				
Orbicella annularis (Ellis and Solander, 1786)	Tcor	*n* = 2	Scott, 1985, 1987, Kropp and Manning, 1987	
Orbicella faveolata (Ellis and Solander, 1786)	Tcor	*n* = 3		New host for *T. corallicola*.
Orbicella franksi (Gregory, 1895)	Tcor	*n* = 4		New host for *T. corallicola*.
Montastraeidae				
Montastraea cavernosa (Linnaeus, 1766)	Tcor	*n* = 4	Scott, 1985, Kropp and Manning, 1987	
Mussidae				
Colpophyllia natans (Houttuyn, 1772)	Tcor	*n* = 6		New host for *T. corallicola*.
Diploria labyrinthiformis (Linnaeus, 1758)	Tcor	*n* = 5		New host for *T. corallicola*.
Favia fragum (Esper, 1795)	Tcor	*n* = 2		New host for *T. corallicola*.
Favia gravida Verrill, 1868	Tcor	—	Kropp and Manning, 1987	*Favia gravida*'s distribution range includes Brazil and the eastern Atlantic (Laborel, 1969, 1974).

Isophyllia sinuosa (Ellis and Solander, 1786)	Tcor	—	Scott, 1985, Kropp and Manning, 1987	
Manicina areolata (Linnaeus, 1758)	Tcor	*n* = 2	Rathbun, 1937, Utinomi, 1944, Shaw and Hopkins, 1977, Scott, 1985, Kropp and Manning, 1987, Carricart-Ganivet, 2004	As *Meandra areolata* by Rathbun (1937), as *Meandra areolata* and *Meandrea areolata* var. *hispida* by Utinomi (1944).
Mussa angulosa (Pallas, 1766)	Tcor	*n* = 2	Shaw and Hopkins, 1977	
Mussismilia hispida (Verrill, 1901)	Tcor	—	Utinomi, 1944, Coelho, 1966 in Kropp and Manning, 1987	*As Mussa (Isophyllia) dipsacea, Mussa (Symphyllia) hispida*, and *Mussa Harrttii* var. *conferta* by Utinomi (1944), as *M. hispida tenuisepta* by Coelho (1966). Genus endemic for Brazil.
M. hispida	? Ohyp	—	Noguiera, 2003	*Opecarcinus hypostegus* has only been recorded from *M. hispida* by Noguiera (2003). Because no other records exist, I tentatively include it here.
Mycetophyllia sp.	Tcor	—	Kropp and Manning, 1987	
Pseudodiploria clivosa (Ellis and Solander, 1786)	Tcor	*n* = 3	Verrill, 1908, Scott, 1985	As *Meandra clivosa* by Verrill (1908), as *Diploria clivosa* by Scott (1985).
Pseudodiploria strigosa (Dana, 1846)	Tcor	*n* = 4	Scott, 1985, Kropp and Manning, 1987	As *Diploria strigosa* by Scott (1985) and Kropp and Manning (1987).
Scolymia lacera (Pallas, 1766)	Tcor	—	Shaw and Hopkins, 1977, Martínez-Estalella, 1982	
Oculinidae				
Oculina sp.	Tcor	—	Kropp and Manning, 1987	
Oculina varicosa Lesueur, 1821	Tcor	—	Scotto and Gore, 1981	
Sclerhelia hirtella (Pallas, 1766)	Tcor	—	Kropp and Manning, 1987, den Hartog, 1989	
Siderastreidae				
Siderastrea siderea (Ellis and Solander, 1786)	Tcor	—	Kropp and Manning, 1987	
S. siderea	Ohyp	—	Scott, 1985, 1987	
S. siderea	Ksid	*n* = 8		First record outside of Brazil, new host for *K. siderastreicola*.
Siderastrea stellata (Verrill, 1868)	Tcor / Ohyp	—	Johnsson *et al.*, 2006	
S. stellata	Ksid	—	Noguiera *et al*., 2014	Records from Bahia State: Tinharé-Boipeba Archipel, Todosos-Santos Bay, and the North Shore.
Siderastrea sp.	Ksid	—	Badaro *et al*., 2012	Described from Guarajuba (type locality) and Praia do Forte (Brazil) in northern Bahia State.

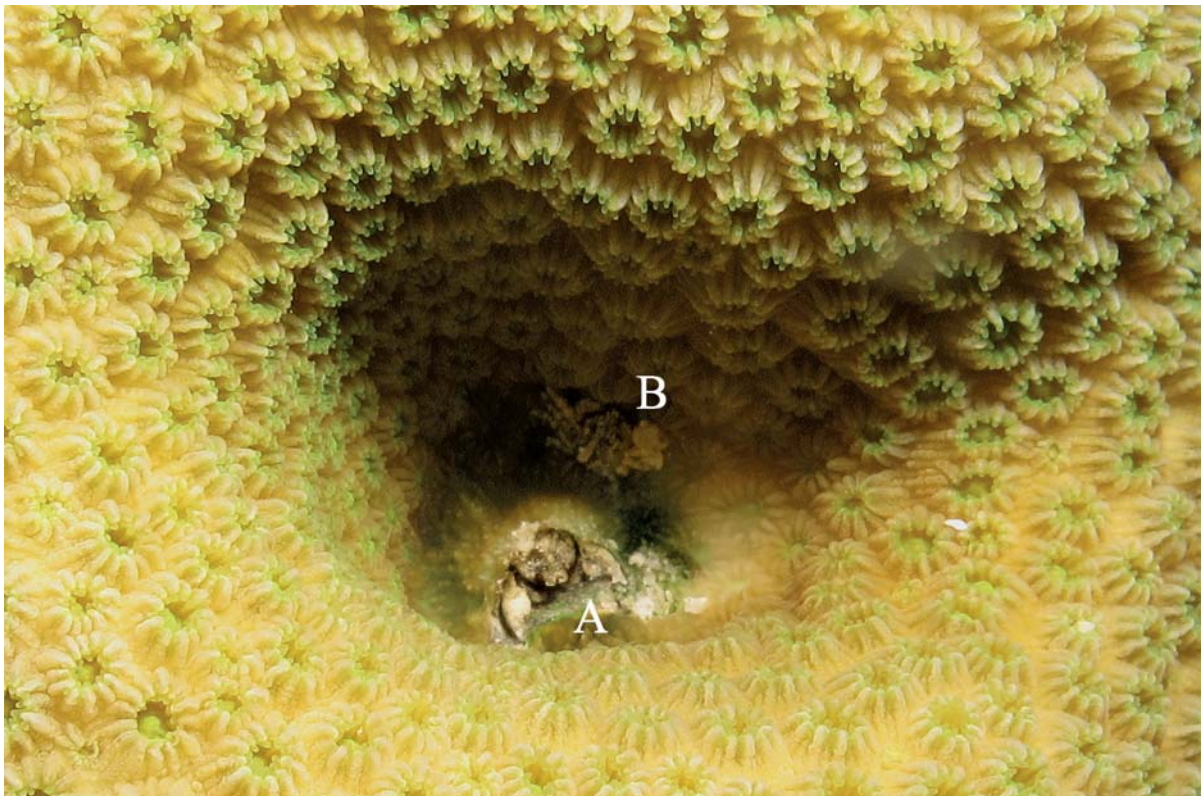

Fig. 2. A female *Troglocarcinus corallicola*. **A**, in her lodge inside a colony of the coral *Orbicella annularis*, with a free-living male; **B**, residing closely.

Results

In total, 21 coral species were recorded hosting three cryptochirid species off Curaçao. Eight of these 21 coral species represent new records as cryptochirid hosts (Fig. 1A-H). With an additional 10 host records based on literature, the number of Atlantic host coral species for gall crabs is now 31 (Table 1). The majority of the coral species housing gall crabs belong to the coral families Agariciidae and Mussidae, the latter being the Atlantic coral family with most species. *Favia fragum* (see Table 1 for species authorities), *Manicina areolata*, and *Mussa angulosa* were only recorded in low densities, yet they were found inhabited by cryptochirids on two different occasions. Some common coral species (e.g. *Colpophyllia natans* and *Meandrina meandrites*) were frequently found inhabited by gall crabs. *Mycetophyllia* sp. was previously recorded as a host in Kropp and Manning (1987), but despite extensive searches, no cryptochirid was found associated with *Mycetophyllia* off Curaçao.

Kroppcarcinus siderastreicola is recorded here outside of Brazil for the first time, with *Siderastrea siderea* and *Stephanocoenia intersepta* as new hosts. *Opecarcinus hypostegus*, representing a new record for Curaçao, was found in association with five *Agaricia* species, of which *Agaricia humilis* is a new record. The agariciid *Helioseris cucullata* was encountered on a few reefs, but was not found inhabited by cryptochirids. *Troglocarcinus corallicola* was associated with a wide range of hosts, but did not occur in association with Agariciidae (Table 1).

Male 'visiting' female gall crab

During a dive in Slangenbaai (Snake Bay) a male *T. corallicola* was observed residing close to the dwelling of a female (Fig. 2A-B). The female was partially extended from her lodge, an

uncommon sight for cryptochirids. The male was observed for approximately 5 min during which he did not move. This immobility could have been caused by the presence of the diver and/ or the flashes of the camera strobe. In the present study, cryptochirid males were collected mainly from their own dwelling on a host coral, with the exception of this record of *T. corallicola* from *Orbicella annularis*, a free-living male *T. corallicola* from *Dendrogyra cylindrus* and a free-living male *T. corallicola* from *Pseudodiploria clivosa* (Table 1).

Discussion

Previously only one published record was available for the gall crab fauna of Curaçao; LB Holthuis collected *Troglocarcinus corallicola* in 1957 from unknown coral hosts in Piscadera Baai (Piscadera Bay, record in Kropp and Manning, 1987). This record was also the only available record from the southern Caribbean Sea. The results of the present study increase the gall crab fauna of Curaçao from one to three species, and it now has the highest number of recorded cryptochirid-coral associations. *Opecarcinus hypostegus* and *T. corallicola* were already known from various localities in the Caribbean region, but the recently described *K. siderastreicola* was so far only known from off Bahia State, Brazil (Badaro *et al*., 2012; Noguiera *et al*., 2014). *Kroppcarcinus siderastreicola* is now also documented from the Caribbean Sea. It is possible that *K. siderastreicola* also occurs in the central Atlantic Ocean, like *T. corallicola* and *O. hypostegus*, because its host coral genus *Siderastrea* has a distribution range that includes western off Africa (Laborel, 1974; Neves *et al*., 2010; Nunes *et al*., 2011). *Siderastrea siderea* is now recorded to host *K. siderastreicola*, a new host for the species. This coral species was previously considered restricted to the Caribbean Sea, but was recently recorded off Brazil (Neves *et al*., 2010).

Eight new coral hosts were recorded for gall crabs, which increases the number of Atlantic host coral species from 23 to 31 (Table 1). The new host records include common coral species like *Colpohyllia natans, Diploria labyrinthiformis*, and *Meandrina meandrites*, all of which are inhabited by *T. corallicola*, a generalist that occurs in association with a wide variety of Atlantic coral species (Verrill, 1908; Kropp and Manning, 1987). *Opecarcinus hypostegus* is associated with Atlantic species of the coral families Agariciidae (Kropp and Manning, 1987, present study) and Siderastreidae (Scott, 1985, 1987; Johnsson *et al*., 2006), whereas *K. siderastreicola* is now known from Siderastreidae and the astrocoeniid *S. intersepta*. Consistent with previous collections, no gall crabs were encountered in corals belonging to the families Acroporidae and Poritidae (Kropp and Manning, 1987; Kropp, 1990a).

One of the newly recorded hosts, *Dendrogyra cylindrus*, is possibly not a true host of cryptochirids. A male *T. corallicola* was found on the surface of a colony, among the coral tentacles, but no dwelling was found. No other gall crabs were found on *D. cylindrus* colonies despite further searching. This single observation, also based on the fact that there are no other records of gall crabs associated with long-tentacled coral species, may reflect the wanderlust of a free-living male.

The observation of a free-living male *T. corallicola* close to the lodged female in an *Orbicella annularis* colony is consistent with Asakura (2009), who, based on anecdotal evidence and observations (see McCain and Coles, 1979; and references in Asakura, 2009), used the term 'visiting' for the mating system in which cryptochirid males 'visit' females inhabiting separate galls or pits. Baeza and Thiel (2007) used the term 'visiting' or 'pure-search polygynandry of sedentary females,' and Guinot *et al*. (2013) used 'visiting' for the mating system in which males of symbiotic species of crabs move from host to host in search of potential female mates. Baeza and Thiel (2007) presume that a 'pure-search polygynandry of sedentary females' evolves when

hosts are extremely small, which is (mostly) not the case in cryptochirids. Asakura (2009) specifically mentioned *T. corallicola*: '… the male crab normally resides outside the gall, which was constructed by the female, and is thought to visit the gall of the female for mating.' The fact that almost all other males were collected from their own dwelling, as well as the close proximity to the female, suggests that this male was indeed 'visiting.' This is the first photodocumented observation of this mating system in cryptochirids.

Acknowledgements

The fieldwork was funded by KNAW (Schure-Beijerinck-Poppingfonds) and the TREUB maatschappij (Society for the Advancement of Research in the Tropics), and supported by the CARMABI Research Station and DiveVersity Curaçao. Two reviewers provided constructive comments on an earlier version of this manuscript.