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Distributions over reefs and shelves

Chapter 13

Cross-shelf distribution patterns of gall crabs in the Makassar Strait (SW Sulawesi, Indonesia)

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Abstract

Coral reef cryptofauna forms an important component of tropical marine biodiversity, consisting primarily of invertebrates dwelling in and on corals and other sessile organisms. Distribution patterns of associated organisms are, however, poorly understood. During fieldwork on reefs in the Spermonde archipelago, the cross-shelf distribution patterns of gall crabs (Cryptochiridae) associated with mushroom corals (Fungiidae) were studied from near-shore to offshore over the 40 km wide Spermonde Shelf. Occurrence rates of crabs was measured in four parallel shelf zones along the shore with the use of belt quadrats at 5 m depth intervals over the reef bottom down to a maximum of 40 m. Four gall crab species were encountered, of which *Fungicola syzygia* was the most abundant and inhabited the widest range of mushroom coral hosts. The primary factor determining gall crab distributions was host coral availability. Host shifts were observed when the preferred host was absent in certain shelf zones or at certain depths. The mid- and outer shelf reefs had the highest occurrence rates of gall crabs, while those near-shore had lower occurrence rates. Highest occurrence rates of gall crabs were observed from 5 to 15 m depth, and mostly at 10 m depth.

Manuscript under review

Introduction

Coral-associated organisms contribute highly to the species richness of coral reefs, especially in the Coral Triangle, where the highest concentrations of coral host species can be found (Hoeksema, 2007). Nonetheless, such associated faunas are relatively understudied, possibly because many symbionts that seek shelter in their host are 'cryptic' owing to their small size, camouflage, or endosymbiotic lifestyle (e.g. Scott, 1987; Bickford *et al*., 2007). The size of the coral host may be important for the composition of the associated fauna (Schiemer *et al*., 2009; Carvalho *et al*., 2014). The nature of such associations is often uncertain, implying that they can be either commensals or parasites (Castro, 1988; Buhl-Mortensen and Mortensen, 2004).

Reef habitats support abundant and diverse assemblages of small crustaceans; a large portion of the more than 500 (out of nearly 2,000) brachyuran crab species dwelling on Indo-Pacific coral reefs live in close association with scleractinian corals (Serène, 1972). This includes both motile species such as copepods and amphipods, as well as (mostly) sessile species such as *Paguritta* hermit crabs (Paguridae) and gall crabs (Cryptochiridae). The associations between corals and crustaceans range from facultative arrangements to obligate dependencies (Stella *et al*., 2011; Hoeksema *et al*., 2012).

Gall crabs are obligate associates of stony corals, living in enclosed galls or pits in their coral hosts. Although cryptochirids have been known to science for over 150 years, little is known about their ecology and biology. They are common inhabitants of coral reefs, but easily overlooked because they are small and reside inside holes (Hoeksema and van der Meij, 2013). According to the last taxonomic revision of Indo-Pacific gall crabs (Kropp, 1990a), two species are known to live in association with Fungiidae corals: *Fungicola fagei* (Fize and Serène, 1956) and *F. utinomi* (Fize and Serène, 1956). Hoeksema *et al*. (2012) reported on a *Dacryomaia* species as a third cryptochirid species associated with Fungiidae, and van der Meij and Hoeksema (2013) reported on an undescribed species, closely related to *F. fagei*, which is now described as *F. syzygia* van der Meij, 2015.

Literature on distribution patterns of coral-associated organisms is scarce (Preston and Doherty, 1994; Oigman-Pszczol and Creed, 2006; Gittenberger and Hoeksema, 2013; van der Meij and Hoeksema, 2013). The presence of coral-associated organisms evidently depends on host availability, which may be related to various environmental factors, such as distance offshore, exposure to winds, and depth (Cleary *et al*., 2005; Hoeksema, 2012a, b). It is not entirely understood how these environmental factors interact with occurrence rates (Gittenberger and Hoeksema, 2013; van der Meij and Hoeksema, 2013), with the possible exception of sedimentation. Sediment is expected to hinder gall crabs and other endosymbiotic invertebrates because it may clog their burrows (Kramarsky-Winter *et al*., 1995), whereas the host itself may be well equipped to shed sediments (Bongaerts *et al*., 2012; Erftemeijer *et al*., 2012).

To examine which factors may control gall crab occurrences, a good knowledge of the host species and their distributions is conditional. Ideally, the research should be undertaken in an area where clear environmental gradients can be discerned that affect both the host species and the associated organisms. This area should also be species-rich regarding host assemblages and associated fauna in order to distinguish the effects of host preference and inter-specific competition among the crabs.

In this paper the focus is on the cross-shelf distribution patterns of gall crab species associated with mushroom corals (Fungiidae) in the Spermonde archipelago in SW Sulawesi (Indonesia), which is situated in the Coral Triangle. A total of 37 fungiid species has been observed in this archipelago, some of which show wide cross-shelf distribution ranges (Hoeksema, 2012a, b).

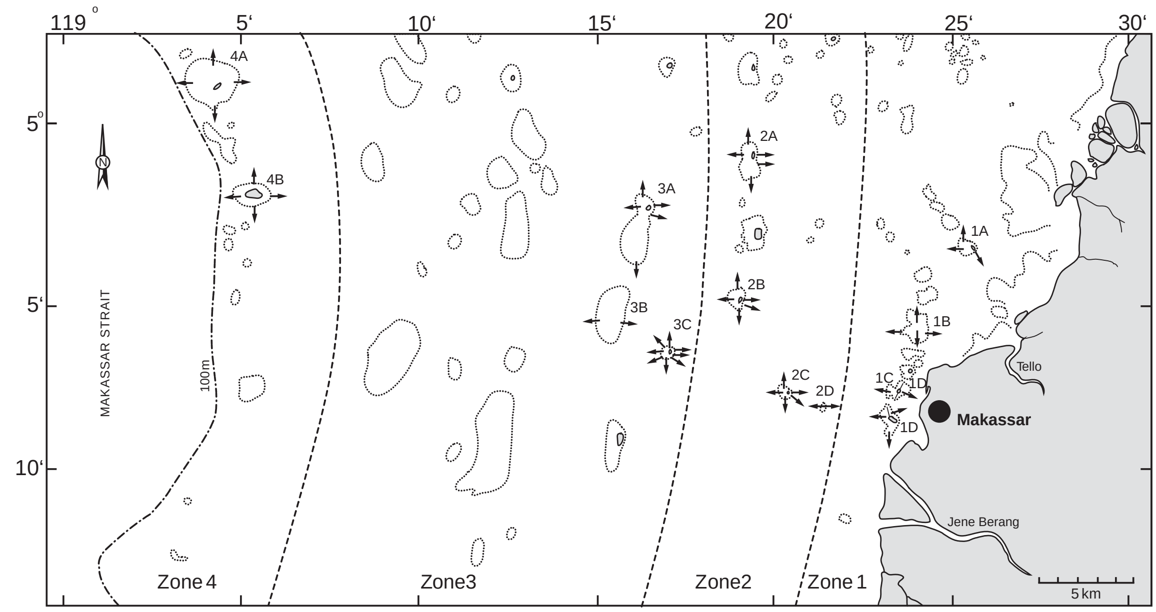

Fig. 1. Map of the Spermonde archipelago, showing zone I-IV.

Most fungiid species are free-living (Hoeksema, 1989; Gittenberger *et al.*, 2011) and may co-exist in dense multi-species aggregations within their depth range overlaps (Hoeksema, 2012a, b; Hoeksema and Benzoni, 2013). Because of these ecological traits, mushroom corals and their associates can easily be counted and used in quantitative comparative studies using quadrats over reef transects dealing with co-occurrence in both host species assemblages and their associated fauna.

Material and methods

The fieldwork was carried out in the Spermonde archipelago, off SW Sulawesi in 1994 (Fig. 1). The Spermonde Archipelago is situated on a well-documented carbonate coastal shelf, approximately 40 km across, with several environmental influences that vary along on-to-offshore gradients (Cornils *et al.*, 2010; Hoeksema, 2012a; Sawall *et al.*, 2013; references therein). These influences are related to sewage seepage and pollution from the city of Makassar and to fluvial discharge with land-eroded sediments and sewage from the mouths of the nearby Jene Berang river to the south and smaller rivers to the north. Makassar city, the capital of South Sulawesi province, is a major port with a population of over one million inhabitants (Hoeksema, 2012a, b; references therein).

The reefs are arranged in rows parallel to the coast line, which is reflected in their distribution in four shelf zones (Fig. 2). The reefs are rich in coral species, which is related to the various reef environments (Umbgrove, 1930; Moll, 1983; Best *et al.*, 1989). The distribution of mushroom corals off SW Sulawesi varies with: 1) the arrangement of reefs along cross-shelf gradients, from onshore to offshore, 2) the circum-reef variation in wind exposure and subsequent wave action, and 3) the depth range, from the shallow reef flat down to the reef slope and the sandy bottom of the reef base below (Hoeksema, 2012a, b).

A total of 11 reefs divided over four zones were surveyed (Figs 1-2). Data collection consisted of two parts. Firstly, mushroom corals were collected at various depths (down to 40 m) in four shelf zones parallel to the shoreline as a preliminary inventory of crab-infested mushroom coral species. Secondly, belt quadrats of 50 x $2m^2$ at isobaths across depth gradients in the transects sites (at 1, 5,

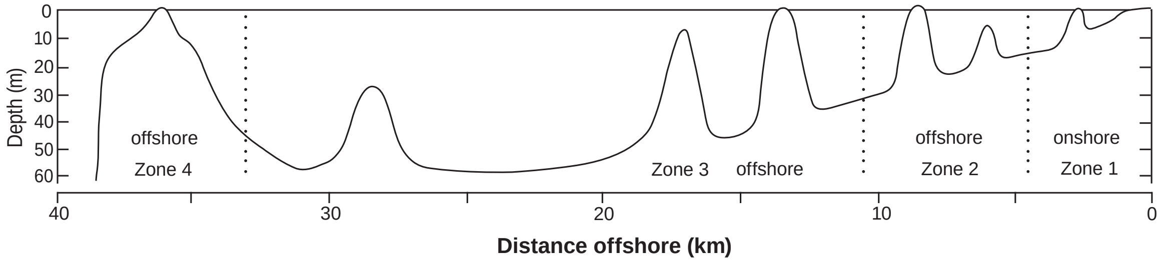

Fig. 2. Schematic cross-section of the central Spermonde Shelf from the Makassar Strait to the mainland (after Hoeksema, 2012a).

10, 15, 20 and 25 m) were monitored for mushroom corals containing gall crabs at 27 sites. In each quadrat an area of 100 m^2 was searched for gall crab species, except in zone 4 at a depth of 5 meters where this was 50 m^2. Transect work was predominantly carried out on the wave-exposed west sides of the reefs, as mushroom coral species are most abundant here (Fig. 1, Table 1).

For the identification of the host corals, a taxonomic revision of the Fungiidae (Hoeksema, 1989) was used, combined with a classification based on a molecular phylogeny reconstruction (Gittenberger *et al*., 2011). The corals were split with a hammer and chisel and the gall crab was extracted for identification. All gall crab samples were eventually stored in 70% ethanol and deposited in the collections of Naturalis in Leiden (collection coded as RMNH.Crus.D). Gall crab identifications and associations are based on literature (Fize and Serène, 1957; Takeda and Tamura, 1979; Kropp, 1990a; Hoeksema *et al*., 2012; van der Meij and Hoeksema, 2013; van der Meij, 2015a). The gall crab-host associations reported in Hoeksema *et al*. (2012) were largely derived from this survey. *Dacryomaia* sp. is possibly new to science, which is currently being studied by the first author (see also Paulay *et al*., 2003).

Results

The percentage of corals inhabited by gall crabs was highest on Samalona reef in zone II (Fig. 1, Table 2). Barang Caddi (zone II), Bone Tambung and Kudingareng Keke (both zone III) also had

Table 1. List of 11 reefs in four reef zones on the Spermonde Shelf with the position of 27 transects (Fig 1), maximum depth (m) are provided.

Shelf zone	Reef	Transect direction with maximum depth (m)						
		N	NW	W	SW	S	SE	E
Zone I	Lae-Lae	-	-	10	-	-	-	10
	Lae-Lae Keke	-	-	10	-	-	-	10
Zone II	Barang Caddi	-	-	25	-	25	20	-
	Barang Lompo	-	25	25	-	-	-	-
	Bone Baku	-	-	20	-	-	-	-
	Samalona	20	-	25	-	25	20	25
Zone III	Badi	-	-	40	-	-	-	-
	Bone Tambung	35	35	35	-	-	-	-
	Kudingareng Keke	-	30	30	-	35	25	25
	Lumu Lumu	-	-	40	-	-	-	-
Zone IV	Langkai	5	-	15	-	-	-	-

Table 2. Cross-shelf distribution in the Spermonde archipelago. Coral presence/absence data and zonations I-IV after Hoeksema (2012a). All Fungiidae identifications updated after Gittenberger et al. (2011). Abbreviations of localities: B = Badi; BB = Bone Baku; BC = Barang Caddi; BL = Barang Lompo; BT = Bone Tambung; KK = Kudingareng Keke; LA = Langkai: LL = Lae Lae; LLK = Lae Lae Keke; LU = Lumu Lumu; S = Samalona. Symbols: ♦ = species inhabited by *Dacryomaia* sp.; ▲ = species inhabited by *Fungicola fagei*; ● = species inhabited by *F. syzygia* ■ = species inhabited by *F. utinomi*; ○ = species present, not inhabited by gall crab; - = coral species absent; ? = no species presence/absence data available.

	I		II				III				IV	
Coral host	LLK	LL	BB	S	BL	BC	KK	B	BT	LU	LA	%
Ctenactis albitentaculata Hoeksema, 1989	-	-	-	○	?	○	○	?	○	?	○	0
C. crassa (Dana, 1846)	-	-	○	○	?	○	○	?	○	?	○	0
C. echinata (Pallas, 1766)	○	○	○	■	?	○	○	?	○	?	○	13
Cycloseris costulata (Ortmann, 1889)	○	○	○	○	●	●	●♦	?	○	●	○	40
C. cyclolites (de Lamarck, 1816)	-	-	○	○	?	-	○	?	○	?	-	0
C. distorta (Michelin, 1842)	-	-	-	-	?	-	○	?	-	?	-	0
C. fragilis (Alcock, 1893)	-	-	●	○	?	○	○	?	●	?	-	40
C. mokai (Hoeksema, 1989)	-	-	○	○	?	○	○	?	○	?	○	0
C. sinensis (Milne Edwards and Haime, 1851)	-	-	-	○	?	○	○	?	○	?	○	0
C. somervillei (Gardiner, 1909)	-	-	-	○	?	○	○	?	○	?	-	0
C. tenuis (Dana, 1846)	-	-	○	●	?	○	○	?	○	?	○	17
C. vaughani (Boschma, 1923)	-	-	-	○	?	-	○	?	○	?	-	0
Danafungia horrida (Dana, 1846)	○	○	○	■	?	○	○	?	○	?	○	13
D. scruposa (Klunzinger, 1879)	○	○	○	○	?	○	○	○	○	?	○	0
Fungia fungites (Linnaeus, 1758)	○	○	○	○	?	○	○	?	■	?	○	13
Halomitra pileus (Linnaeus, 1758)	-	-	○	■	?	○	○	?	■	?	○	33
Heliofungia actiniformis (Quoy and Gaimard, 1833)	○	○	○	○	?	○	○	?	○	?	○	0
H. fralinae (Nemenzo, 1955)	-	-	-	○	?	○	○	?	○	?	○	0
Herpolitha limax (Esper, 1797)	○	○	○	○	?	■	○	?	○	?	●	13
Lithophyllon concinna (Verrill, 1864)	○	○	○	○	■	■	■	?	○	■	○	40
L. repanda (Dana, 1846)	○	○	■	■	■	■	●■	■	■	■	■	82
L. scabra (Döderlein, 1901)	○	○	○	●■♦	♦	○	♦	?	♦	?	○	44
L. spinifer (Claereboudt and Hoeksema, 1987)	-	-	-	-	?	-	-	?	-	?	-	0
L. undulatum Rehberg, 1892	-	-	-	○	♦	♦	♦	♦	♦	?	-	83
Lobactis scutaria (de Lamarck, 1801)	-	-	○	○	?	○	○	?	○	?	○	0
Pleuractis granulosa (Klunzinger, 1879)	-	-	○	●♦	●	●♦	●♦	●	●♦	●♦	●	89
P. gravis (Nemenzo, 1955)	○	-	○	○	?	○	○	?	○	?	○	0
P. moluccensis (van der Horst, 1919)	○	○	○	●	●	●	●	●	●	●	○	64
P. paumotensis (Stutchbury, 1833)	●	○	●	●	●	●	●	●	●	●	●	91
Podabacia crustacea (Pallas, 1766)	○	○	-	▲	?	○	○	?	○	?	-	17
Polyphyllia talpina (Lamarck, 1801)	○	○	○	○	?	○	○	?	○	?	○	0
Sandolitha dentata Quelch, 1884	-	-	-	○	?	○	○	?	○	?	-	0
S. robusta (Quelch, 1886)	○	○	○	○	?	○	■	?	○	■	▲	33
Zoopilus echinatus Dana, 1846	-	-	-	-	?	-	○	?	○	?	-	0
% inhabited	6	0	13	32	-	28	27	-	28	-	21	

Table 3. Number of commonly inhabited fungiid coral individuals present per zone and transect depth (number of inhabited corals between brackets in **bold**). % indicates the occurrence rate. In zone I no reef was present below 10 m depth, in zone IV no reefs were present below 15 m (indicated by -).

crab species	zone	1 m		5 m		10 m		15 m		20 m		25 m	
coral species		n	%	n	%	n	%	n	%	n	%	n	%
	Dacryomaia sp.												
Pleuractis granulosa	I	0	0	0	0	0	0	-	-	-	-	-	-
	II	0	0	1(0)	0	28(0)	0	16(0)	0	1(0)	0	0	0
	III	0	0	5(0)	0	87(**1**)	0	80(0)	0	3(0)	0	5(0)	0
	IV	0	0	0	0	3(0)	0	1(0)	0	-	-	-	-
Lithophyllon scabra	I	2(0)	0	3(0)	0	0	0	-	-	-	-	-	-
	II	0	0	5(0)	0	10(0)	0	3(0)	0	0	0	0	0
	III	0	0	4(0)	0	20(0)	0	11(0)	0	0	0	0	0
	IV	1(0)	0	0	0	0	0	0	0	-	-	-	-
L. undulatum	I	0	0	0	0	0	0	-	-	-	-	-	-
	II	0	0	1(0)	0	1(0)	0	2(0)	0	0	0	0	0
	III	0	0	4(0)	0	7(0)	0	5(0)	0	1(0)	0	0	0
	IV	0	0	0	0	1(0)	0	0	0	-	-	-	-
	Fungicola fagei												
Sandalolitha robusta	I	2(0)	0	4(0)	0	0	0	-	-	-	-	-	-
	II	0	0	15(0)	0	16(0)	0	11(0)	0	0	0	0	0
	III	0	0	15(0)	0	26(0)	0	3(0)	0	0	0	0	0
	IV	0	0	5(**1**)	20	1(0)	0	0	0	-	-	-	-
	F. syzygia												
Cycloseris costulata	I	0	0	3(0)	0	2(0)	0	-	-	-	-	-	-
	II	0	0	4(0)	0	56(**1**)	1.8	47(**1**)	2.1	1(0)	0	0	0
	III	0	0	6(0)	0	99(0)	0	129(0)	0	16(0)	0	18(0)	0
	IV	0	0	0	0	0	0	0	0	-	-	-	-
Pleuractis granulosa	I	0	0	0	0	0	0	-	-	-	-	-	-
	II	0	0	1(0)	0	28(**2**)	7.1	16(**1**)	6.3	1(0)	0	0	0
	III	0	0	5(0)	0	87(**6**)	6.9	80(0)	0	3(0)	0	5(0)	0
	IV	0	0	0	0	3(0)	0	1(0)	0	-	-	-	-
P. moluccensis	I	0	0	30	0	8(0)	0	-	-	-	-	-	-
	II	0	0	0	0	50(**2**)	4.0	56(**1**)	1.8	8(0)	0	1(0)	0
	III	0	0	0	0	0	0	14(0)	0	1(**1**)	100	14(**1**)	7.1
	IV	0	0	0	0	0	0	0	0	-	-	-	-
P. paumotensis	I	27(0)	0	20(0)	0	0	0	-	-	-	-	-	-
	II	1(0)	0	43(**2**)	4.7	95(**9**)	9.5	46(**4**)	8.7	2(0)	0	0	0
	III	0	0	67(**3**)	4.8	109(**9**)	8.3	27(**4**)	14.8	1(0)	0	0	0
	IV	0	0	26(0)	0	4(0)	0	0	0	-	-	-	-
	F. utinomi												
Halomitra pileus	I	0	0	0	0	0	0	-	-	-	-	-	-
	II	0	0	1(0)	0	2(0)	0	4(0)	0	0	0	0	0
	III	0	0	5(0)	0	12(0)	0	4(0)	0	0	0	0	0
	IV	0	0	5(0)	0	1(0)	0	0	0	-	-	-	-

cont. Table 3

crab species	zone	1 m		5 m		10 m		15 m		20 m		25 m	
coral species		n	%	n	%	n	%	n	%	n	%	n	%
Lithophyllon concinna	I	0	0	0	0	0	0	-	-	-	-	-	-
	II	0	0	26(0)	0	56(0)	0	45(0)	0	2(0)	0	0	0
	III	1(0)	0	51(0)	0	234(0)	0	62(0)	0	1(0)	0	2(0)	0
	IV	0	0	78(0)	0	4(0)	0	0	0	-	-	-	-
L. repanda	I	1(0)	0	0	0	0	0	-	-	-	-	-	-
	II	2(0)	0	98(**1**)	1.0	126(**2**)	1.6	64(0)	0	2(0)	0	0	0
	III	11(0)	0	428(**6**)	1.4	628(**4**)	0.6	180(0)	0	2(0)	0	3(0)	0
	IV	0	0	474(**1**)	0.2	52(0)	0	2(0)	0	-	-	-	-
Sandalolitha robusta	I	2(0)	0	4(0)	0	0	0	-	-	-	-	-	-
	II	0	0	15(0)	0	16(0)	0	11(0)	0	0	0	0	0
	III	0	0	15(**1**)	6.7	26(0)	0	3(0)	0	0	0	0	0
	IV	0	0	5(0)	0	1(0)	0	0	0	-	-	-	-
Infested corals per depth		50(0)	-	1462 (**15**)	-	1865 (**36**)	-	923 (**11**)	-	45 (**1**)	-	30 (**1**)	-

high rates of corals inhabited by gall crabs, followed closely by Langkai (zone IV). Despite the abundant presence of mushroom corals, gall crabs were absent in the onshore zone I, as well as at 1 m depth in the other three zones.

Fungicola syzygia was the most abundant gall crab species inhabiting Fungiidae over the whole shelf area, despite its near-absence close to the shore line. This species was only encountered once on an on-shore reef (outside transects), but was found abundantly on the mid-shelf reefs in zones II and III (Tables 2-3). The single specimen in zone I was found in a coral of *Pleuractis paumotensis*. This mushroom coral species hosted *F. syzygia* across the whole shelf, including the most offshore reefs. It also showed its highest abundance near-shore, and was common elsewhere on the shelf (Hoeksema, 2012a). *Pleuractis granulosa, P. moluccensis* and *P. paumotensis* were regularly found inhabited on reefs in zone II-IV, just like *Cycloseris costulata*. This latter species was inhabited by both *F. syzygia* and *Dacryomaia* sp. *Fungicola utinomi* was observed inhabiting *Lithophyllon repanda* on all reefs in zones II-IV, and also frequently observed in *L. concinna* on the same reefs. *Dacryomaia* sp. inhabited *Lithophyllon scabra*, *L. undulatum* and *P. granulosa* in zones II-III. *Fungicola fagei* was only observed on two reefs, inhabiting the phylogenetically closely related species *Podabacia crustacea* and *Sandalolitha robusta* (Table 2).

The most frequently inhabited coral species were *Lithophyllon repanda*, *L. undulatum*, *Pleuractis granulosa* and *P. paumotensis*, which housed three out of the four known gall crabs inhabiting fungiids. *Fungicola fagei*, encountered on only two Spermonde reefs, is associated with fungiids belonging to the genera *Podabacia* and *Sandalolitha*, which were observed in all zones.

Occurrence rates

In most fungiid host corals, gall crabs reside in pits between the septae with a narrow opening for water circulation. However, crab species associated with free-living corals of *Lithophyllon repanda* reside in gall-like structures with overhangs near the coral mouth. However, such overhangs can also be observed in pits of *Dacryomaia* sp. in corals of the attached *L. undulatum*.

Occurrence rates can be obtained based on transect data (Table 3). For example, in zone II at 5 m depth, *F. syzygia* inhabited two out of 43 available *Pleuractis paumotensis* corals, resulting in an occurrence rate of 4.7%. At 10 and 15 m depth, the respective occurrence rates for the same coral host were 9.5% and 8.7%, respectively.

If outliers are ignored (*F. fagei* infesting one out of five *S. robusta* corals and *F. syzygia* inhabiting a single available *P. moluccensis* coral), the occurrence rates range between 0.2 and 14.8 %. Data for *Dacryomaia* sp. and *F. fagei* is scarce, relating to a lower abundance in comparison to *F. syzygia* and *F. utinomi*. Of the latter two, *F. syzygia* has a higher overall abundance in its respective hosts than *F. utinomi* (Table 3).

Depth distributions

Data on the depth distribution of gall crabs were obtained from belt quadrats of 50 × 2m^2 along depth gradients (1, 5, 10, 15, 20 and 25 m; Table 3). Only results concerning the preferred coral host species of the gall crabs during the research efforts are mentioned here (Table 2; Hoeksema *et al*., 2012; van der Meij and Hoeksema, 2013).

No inhabited fungiid species were observed in the belt transects of zone I, as well as in all the 1-m depth belt quadrats. Most gall crabs were found at 10 m depth, where also the highest density of host corals was found. The depth with the highest concentrations of fungiids increased with distance from the coast (except for Langkai in zone IV).

Fungicola syzygia was present at depths with high densities of available host coral species. The highest occurrence rates were found in zones II and III at 10 and 15 m depth in its preferred host *Pleuractis paumotensis,* which was also present in zone IV, but to a lesser extent (Table 3). Its sister species *P. moluccensis* (see Gittenberger *et al*., 2011) prefers greater depths (> 15 m), where it hosts *F. syzygia*. *Fungicola fagei* was only observed in zone IV, where it inhabited one out of the five observed *Sandalolitha robusta* individuals. Zones II and III had many available host corals belonging to the genera *Podabacia* and *Sandalolitha*, but these were not inhabited by gall crabs. *Fungicola utinomi* was only found at 5 and 10 m depth in zones II and III, where its preferred host species *Lithophyllon repanda* also showed its highest abundance. The occurrence rates are much lower than for *F. syzygia*. Only one specimen of *Dacryomaia* sp. was found at 10 m depth in a colony of *Pleuractis granulosa* (zone III).

Discussion

The distribution of mushroom corals on the Spermonde shelf varies with: 1) the distance of reefs offshore, 2) the circum-reef variation in exposure to wave action, and 3) the depth range (Hoeksema, 2012a, b). Mushroom corals of the mid-shelf reefs Barang Caddi, Samalona, Bone Tambung, and Kudingareng Keke (zones II and III) show the highest occurrence rates (> 30%). These four mid-shelf reefs are more remote from terrigenous impact than reefs in the near-shore zone I, and also less affected by *Halimeda* dust, upwelling and wave impact as on the offshore reefs of zone IV (Hoeksema, 2012a).

The near-shore reefs in zone I contain fewer fungiid species than those in zones II – IV because they are the most influenced by sediments, river discharge, sewage and harbour activities, and also because the surrounding sea floor is shallow, which implies that the depth ranges of onshore reefs offer less available space for some mushroom coral habitats than those on the deeper offshore reefs (Hoeksema, 2012a, b). Evidently, low host coral availability offers less potential habitat for gall crabs. Nevertheless, the percentage of crab-inhabited corals is also lower on near-shore reefs than in the other zones. Van der Meij and Hoeksema (2013) showed that reefs in the

Semporna area that were under influence of natural or anthropogenic disturbances had lower occurrence rates of gall crabs. Stress has a negative effects on coral assemblages and hence on their associated cryptofauna (Risk *et al*., 2001; van der Meij *et al*., 2010). Similarly, Preston and Doherty (1990, 1994) showed that coral-dwelling crustacea on the Great Barrier Reef had a maximum abundance on the mid-shelf reefs, and that their total abundance was significantly lower on the inner shelf reefs.

Occurrence rates

Van der Meij and Hoeksema (2013) discussed various studies on occurrence rates in gall crabs, and show that low occurrence rates are possibly linked to natural and anthropogenic stress. Apart from this study, only one study (in Brazil) used belt quadrats to determine occurrence rates, with occurrence rates ranging between 17 and 21% (Oigman-Pszczol and Creed, 2006). However, the quadrats were haphazardly placed in areas where at least one of the studied coral species occurred, whereas the in the present study they were placed over the reef at depth intervals regardless of the presence of fungiid corals. This might explain the higher observed occurrence rates in the Brazilian study, in addition to differences caused by the discrepancy in coral fauna composition.

The present study shows much variation in occurrence rates among crab species and within species among preferred host corals. The most abundant corals are not necessarily the most commonly inhabited (Scott, 1987; Norton and Carpenter, 1998), which is related to the host preference of the gall crabs (van der Meij and Hoeksema, 2013: Table 1). So far, it is unclear why the crabs show specific host preferences. For mushroom corals such preferences are also known from several wentletrap snails (Epitoniidae) and parasitic *Leptoconchus* snails (Gittenberger and Gittenberger, 2011; Gittenberger and Hoeksema, 2013) and some commensal shrimp species (Hoeksema *et al*., 2012). In comparison, some species of boring mussels (Mytilidae) living inside fungiid corals may have a much broader host spectrum (Owada and Hoeksema, 2011), while information on host-specific composition of crypobenthic fish fauna is hardly available for fungiids (Bos, 2012; Hoeksema *et al*., 2012) and other corals (Schiemer *et al*., 2009; Reijnen *et al*., 2011; Duchene *et al*., 2013; Tornabene *et al*., 2013). Preference for a particular host may be advantageous when many potential hosts are abundantly available. Moreover, host corals may produce bioactive compounds influencing settlement of gall crab larvae in some species. No direct cause may be present when host preferences have been derived from ancestral associated species in which the association was more advantageous than in descendant species.

Depth distributions

Depth, so far, does not seem to be a limiting factor for gall crabs, which inhabit their fungiid hosts in wide depth ranges. The maximum depth record for gall crabs in this study was 32 m (in *Pleuractis granulosa* during a reconnaissance survey on the sandy reef base of Pulau Badi), while there are also shallow records of 1 m depth (host *P. granulosa*, Papua New Guinea, Institut Royal des Sciences Naturelles de Belgique (IRNSB) coll. nr. 26862/84-46). Mushroom corals at greater depths are usually dwelling on sand (Hoeksema, 2012a), but this does not appear to affect the presence of crabs as long as their hosts are also able to survive in sandy habitats.

Several fungiid species show a downward shift in depth range with increasing distance offshore (Table 3; Hoeksema, 2012a). At depths outside the preferred depth ranges of the preferred host coral, gall crabs appear to shift to the second-preferred host coral. *Fungicola syzygia* shifts from *Pleuractis paumotensis* to *P. moluccensis* at depths > 15 m. On the other hand, *Fungicola utinomi* in *L. repanda* was predominantly observed at 5 and 10 m depth, despite the host's occurrence at 15 m depth. This indicates that the depth ranges of gall crabs are not necessarily strictly related to those of their hosts and that some gall crab species might show more restricted depth ranges than others regardless of their host coral.

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