Habitat preferences of coral-associated wentletrap snails (Gastropoda: Epitoniidae)

Adriaan Gittenberger^{1,2}, Bert W. Hoeksema^{1,3}

¹ Department of Marine Zoology, Naturalis Biodiversity Center, PO Box 9517, 2300 RA Leiden, The Netherlands

² Institute for Environmental Sciences and Institute for Biology, Leiden University, PO Box 9516, 2300 RA Leiden, The Netherlands

³ E-mail: bert.hoeksema@naturalis.nl

Key words: coral-mollusc associations, Fungiidae, Indo-Pacific, parasitic snails, Scleractinia

Abstract

Examination of about 60,000 scleractinian corals of the families Dendrophylliidae, Euphylliidae and Fungiidae for the presence of associated wentletrap snails (Gastropoda: Epitoniidae) revealed various ectoparasitic life history strategies. Twenty Indo-Pacific wentletrap species were found, which were either host-specific or generalist. Most species were associated with mushroom corals, especially free-living species belonging to the Fungiidae. Snails showed different preferences with regard to their position relative to mushroom corals, the host's size and its substrate. No preferences for depth were found. Infestation rates of mushroom corals in multi-species assemblages were negatively correlated with coral densities, which indicates that epitoniid veliger larvae may actively look for preferential hosts. Indirect proof was found that burrowing shrimps remove any epitoniid that is on or underneath the mushroom coral under which they have their burrow. Fishes like wrasses and damselfishes were seen to eat the snails the moment their host corals were overturned, which suggests that the host corals may provide the snails with protection against predators.

Contents

Introduction	1
Material and methods	3
<i>Fieldwork localities and general methods</i>	3
<i>Sampling</i>	3
<i>Transect studies</i>	3
<i>Measurement of coral sizes</i>	8
<i>Overturned host corals</i>	10
Results	10
<i>Abundance of infestations</i>	10
<i>Associations</i>	11
<i>Coral densities and infestation rates</i>	11
<i>Depth ranges</i>	11
<i>Substrates and attachment</i>	11
<i>Coral sizes</i>	13
<i>Overturned host corals</i>	14
Discussion	17
<i>The trophic role of coral-associated epitoniids</i>	17

<i>Coral densities and depth ranges</i>	18
<i>Substrates</i>	19
<i>Coral sizes and risk of host coral turnover</i>	19
Conclusions and recommendations	20
Acknowledgements	21
References	21

Introduction

In light of the degradation of coral reefs and the potential for coral species extinctions (Carpenter *et al.*, 2008), understanding the biodiversity and ecological complexity of reef communities and their species interdependences is essential (Castro, 1988; Stella *et al.*, 2010, 2011; Hoeksema *et al.*, 2012a). In the present study corals of the scleractinian families Dendrophylliidae, Euphylliidae, and Fungiidae with their associated wentletraps (Gastropoda: Epitoniidae) are used to study such interrelationships.

Epitoniids are generally known to live in association with anthozoans (Cnidaria), such as species of Actinaria (Robertson, 1963, 1966, 1983; Perron, 1978; Schimek, 1986; den Hartog, 1987; Kokshoorn *et al.*, 2007; Hoeksema and Crowther, 2011), Zoantharia (Zahn, 1980; Robertson, 1981) or Scleractinia (Gittenberger and Gittenberger, 2005). Morphological and molecular studies have shown that a large, partly cryptic, adaptive radiation occurred among these epitoniids (Gittenberger *et al.*, 2000; Gittenberger, 2003; Gittenberger and Gittenberger, 2005; Kokshoorn *et al.*, 2007). Their geographical distribution ranges track those of their hosts, with the highest numbers in the Indo-West Pacific, especially in the Coral Triangle (Gittenberger and Gittenberger, 2005).

Although the genetic integrity of epitoniids can be demonstrated by molecular data (Gittenberger *et al.*,

2006; Churchill *et al.*, 2011), shell characters are only partially diagnostic in identifications at species level. In general, life habit and characters of the operculum, the jaw, the radula and the spawn, characterize these conchologically cryptic species much better (Gittenberger and Gittenberger, 2005). These recent findings contradict the hypothesis of Bouchet and Warén (1986: 469) stating that little morphological variation among epitoniids may reflect a low degree of specialization. A fundamental condition for the identification of coral-associated molluscs consists therefore of a good knowledge of the available host coral species (Gittenberger *et al.*, 2000; Kleemann and Hoeksema, 2002; Gittenberger and Gittenberger, 2005, 2011; Hoeksema *et al.*, 2012a).

The snails may use their anthozoan hosts as food source, as protection against predators, or shelter from turbulence. Due to their hidden position, observations of actual feeding epitoniids are scarce (Perron, 1978; den Hartog, 1987; Gofas *et al.*, 2011), but nematocysts in epitoniid gut contents indicate a predatory or parasitic behaviour (Perron, 1978). Apparently, the snails are unaffected by the venom in these nematocysts. Hence, epitoniids are either considered highly specialized micropredators (Robertson, 1970; Hadfield, 1976)

or ectoparasites (Gittenberger, 2003; Gittenberger and Gittenberger, 2005). In the present study, they are considered parasites because they live a long period of their life history on a single host without killing it (see Castro, 1988).

Most coral-associated wentletraps are found with mushroom corals (Fungiidae), which are the main focus of this study. The Fungiidae consist of over 50 species exclusively in the Indo-Pacific (Hoeksema, 1989, 1993a, 1993b, 2009, 2012b; Hoeksema and Dai, 1991; Gittenberger *et al.*, 2011; Benzoni *et al.*, 2012). These corals have a high survival rate during bleaching events (Hoeksema, 1991a; Hoeksema and Matthews, 2011; Hoeksema *et al.*, 2012b), which is also important for the survival of their associated fauna (Hoeksema *et al.*, 2013). Most mushroom corals are free-living in adult phase and can easily be picked up and checked for parasites. Depending on shape, size and weight (Hoeksema, 1988, 1991b), such corals may tumble downward along slopes, be pushed by bottom-dwelling animals, currents and waves, and they may even move themselves (Hubbard, 1972; Jokiel and Cowdin, 1976; Yamashiro and Nishihira, 1995; Plusquellec *et al.*, 1999; Hoeksema and de Voogd, 2012). This mobility may help mushroom corals to

Fig. 1. Research localities in the Indo-West Pacific: 1. Marsha Shagra and Marsa Nakari, c. 350 km S of Hurghada, Egypt; 2. Vilamendhoo Isl., Ari Atoll, Maldives; 3. PhiPhi Isl., Krabi, W Thailand; 4. Okinawa, Rykyu Isl., S Japan; 5. Cebu, Central Philippines; 6. Berau Isl., E Kalimantan, Indonesia; 7. Siladen and Bunaken Isl., N Sulawesi, Indonesia; 8. Togian Isl., Central Sulawesi, Indonesia; 9. Spermonde Archipelago, SW Sulawesi, Indonesia; 10. Bali, Indonesia; 11. Flores, Indonesia; 12. Ambon, Indonesia; 13. Palau; 14. Great Barrier Reef, E Australia.

Fig. 2. Research sites in the southern part of the Spermonde Archipelago, SW Sulawesi, Indonesia, consisting of patch reefs and a barrier reef: 1. Langkai; 2. Kapodasang (shoal); 3. Bone Tambung; 4. Kudingareng Keke; 5. Bone Batang; 6. Samalona; 7. Bone Baku (shoal); 8. Lae-Lae.

disperse and prevent lethal burial in sediment (Abe, 1939; Jokiel and Cowdin, 1976; Hoeksema, 1988; Chadwick-Furman and Loya, 1992; Gilmour, 2002; Bongaerts *et al.*, 2012). It may also be functional in avoiding competition for space (Chadwick, 1988; Hoeksema, 2004; Yamashiro and Nishihira, 1995; Hoeksema and de Voogd, 2012). However, movements by the host may also have implications for the survival of the ectoparasitic snails, which will become exposed to predators when the coral accidentally gets turned upside-down. Despite this risk, mushroom corals appear very much to be a preferred host group for epitoniids among Indo-Pacific Scleractinia (none are known from the Atlantic), which justifies their importance in the present study. In short, this study aims to clarify the ecological differentiation of coral-associated epitoniids, particularly regarding their abundance in relation to host coral densities, depth ranges, substrates, sizes, positions and mobility.

Materials and methods

Fieldwork localities and general methods

Habitat preferences are described for 20 known species of coral-associated epitoniids, most of which are widespread and associated with only one or a restricted number of host species (Gittenberger and Gittenberger, 2005). Approximately 60,000 mushroom corals were searched in 1997 and from 2000 to 2004 for epitoniids during 800 hours of scuba-diving in Egypt (Red Sea), the Maldives (Indian Ocean), western Thailand (Andaman Sea), western Malaysia (South China Sea), southern Japan, Palau (West Pacific), the Philippines, Indonesia and eastern Australia (Fig. 1). In 1997 and 2001, research took place in periods of three and nine months, respectively, in the Spermonde Archipelago off Makassar, SW Sulawesi, Indonesia (Fig. 2). This area (Hoeksema, 1990, 2012a, c) is located in the centre of maximum marine biodiversity (Hoeksema, 2007). Off Makassar the diversity and densities of potential host coral species were higher than at any of the other study localities (Hoeksema, 2012a). Therefore this archipelago was selected for more detailed field studies. Concentrating on mushroom corals, a special effort was made to search all present species within this family for the presence of peitoniid snails. Mushroom corals species that were formally not yet recognized to belong to the Fungiidae (Benzoni *et al.*, 2007, 2012) were not included in the study. Many of these

species live in environments that are usually avoided by divers, *e.g.* at relatively deep (> 25 meter) reef bases or shallow (< 2 meter) slopes and flats, or in areas with strong currents, murky water and sandy bottoms (Hoeksema, 2012a).

Sampling

The snails were collected and conserved in 70% or 95% ethanol for morphological or molecular analyses, respectively. Most associations were photographed in detail with a Sea & Sea SX-1000 SLR camera with a 50 mm macro lens. A white PVC board and a graphite pencil were used underwater to note observations related to the infestations, *i.e.* depth, host species, substrate characteristics, and position of the parasite relative to its host. The fungiid specimens were identified twice, independently by both authors, using photographs and/or specimens. H. Ditlev identified the euphylliids from photographs. The *Tubastraea* species were not identified to species level. The first author identified the epitoniid species. The position of a parasitic snail was recorded as 'buried in sand', 'on the coral host' (Figs 3-4, 8-9), or 'on the substrate underneath the coral' (Figs 5-7). Regarding the size-dependent mushroom coral mobility (Hoeksema, 1988, 1991b, 2004), an upside-down position of the fungiid host (Figs 5-9, 11, 13-14, 16-17) was recorded versus the regular upright orientation (Figs 10, 12). The substrate was characterized as (1) 'flat' for an even bottom of sand, coral or stone, without any crevices (Fig. 12; next to the fungiid coral), as (2) 'burrow' when there was at least one circular burrow (Figs 11, 13-14), possibly made by a crustacean (Fig. 15), or as (3) 'crevices', where crevices occurred but no burrows (Fig. 6).

Transect studies

In the Spermonde Archipelago (Fig. 2; locality 9 in Fig. 1) mushroom corals were surveyed in belt transects. This was done at seven sites on five coral reefs that vary in mushroom coral fauna, depending on their distance from the coastline (see Hoeksema, 2012a): W Lae-Lae, W Bone Baku, E Samalona, W Samalona, E Kudingareng Keke, W Kudingareng Keke, and NW Langkai (Fig. 2). At each site horizontal transects, marked by a 50 m long measuring tape, were searched at 3, 6, 9, 12, 15 and 18 m depth (see Hoeksema, 2012a). This method allows the recording of sufficient abundance data on host and parasites in contrast to the roving diving technique, which only gives incidence data

Figs 3-6. Habitats of coral-dwelling Epitoniidae. 3, *Epidendrium aureum* snail with spawn on substrate next to its dendrophylliid host (*Tubastraea* sp.); 4, *Epidendrium sordidum* shell overgrown by hydroids, with spawn on dendrophylliid host (*Tubastraea* sp.); 5, *Surrepifungium costulatum* snail with spawn on coarse sand under host (*Ctenactis echinata*); 6, *Epifungium hoeksemai* snail with spawn on coarse sand under host (*Heliofungia actiniformis*). Locations: 3-4, Ari Atoll, Maldives; 5-6, SW Sulawesi, Indonesia. Abbreviations: s=snail, sp=spawn.

Figs 7-9. Habitats of Epitoniidae (continued); snails with spawns on sandy substrate under fungiid host. 7, *Epifungium nielsi* under a *Pleuractis paumotensis* (Ari Atoll, Maldives); 8, *Epifungium pseudolochi* under a *Cycloseris costulata* (Marsa Nakari, 350 km S of Hurghada, Egypt); 9, *Epifungium twilae* under *Herpolitha limax* (SW Sulawesi, Indonesia).

Figs 10-13. Habitats of Epitoniidae (continued); sediment with two burrows under free-living mushroom corals, SW Sulawesi, Indonesia. 10-11, *Lithophyllon repanda*, in situ (10) and removed (11) to show two circular burrows; 12-13, *Pleuractis granulosa*, in situ (12) and removed (13) to show two circular burrows.

Figs 14-17. Possible predators of epitoniids in Indonesia. 14, *Fungia fungites* removed to show a circular burrow; 15, a shrimp, *Alpheus frontalis*, under a free-living *Ctenactis echinata*; 16, a wrasse, *Halichoeres melanurus*, monitoring an overturned fungiid; 17, a damselfish, *Plectroglyphidodon lacrymatus*, monitoring an overturned fungiid. Locations: 14, Bali; 15-17, SW Sulawesi.

Table 1. Epitoniid species and their fungiid host species recorded at various Indo-West Pacific localities.

Epitoniid snail	Fungiid host species																															
	<i>Cycloseris costulata</i>	<i>Cycloseris distorta</i>	<i>Cycloseris fragilis</i>	<i>Cycloseris sinensis</i>	<i>Cycloseris somervillei</i>	<i>Cycloseris tenuis</i>	<i>Cycloseris vaughani</i>	<i>Pleuractis granulosa</i>	<i>Pleuractis</i> sp. 1	<i>Pleuractis gravis</i>	<i>Pleuractis mollucensis</i>	<i>Pleuractis paumotensis</i>	<i>Lithophyllon scabra</i>	<i>Lithophyllon concinna</i>	<i>Lithophyllon repanda</i>	<i>Lithophyllon spinifer</i>	<i>Danafungia horrida</i>	<i>Danafungia scruposa</i>	<i>Lobactis scutaria</i>	<i>Fungia fungites</i>	<i>Halomitra pileus</i>	<i>Heliofungia actiniformis</i>	<i>Ctenactis albitentaculata</i>	<i>Ctenactis crassa</i>	<i>Ctenactis echinata</i>	<i>Herpolitha limax</i>	<i>Sandalolitha robusta</i>	<i>Sandalolitha dentata</i>	<i>Podabacia crustacea</i>	<i>Zoopilus echinatus</i>		
<i>Epifungium</i>																																
<i>E. pseudolochi</i>	x																															
<i>E. lochi</i>	x	x	x	x	x	x	x																									
<i>E. adgranulosa</i>								x																								
<i>E. marki</i>									x																							
<i>E. adgravis</i>										x																						
<i>E. nielsi</i>											x	x																				
<i>E. adscabra</i>													x																			
<i>E. ulu</i>														x	x	x	x	x	x	x	x	x				x	x	x				
<i>E. hoeksemai</i>																					x											
<i>E. twilae</i>																									x	x						
<i>E. pseudotwilae</i>																												x	x	x	x	
<i>Epitonium</i>																																
<i>E. crassicostatum</i>	x																															
<i>E. graviarmatum</i>							x																									
<i>Surrepifungium</i>																																
<i>S. costulatum</i>																								x	x	x	x	x	x			
<i>S. ingridae</i>														x							x			x	x			x				
<i>S. oliverioi</i>														x							x						x	x				
<i>S. patamakanthini</i>													x	x		x				x		x		x	x			x				

(Hoeksema and Koh, 2009). The corals were counted within a distance of one meter at both sides along the tape guided by a 1 m long aluminium rod. When less than 100 corals were found along the first 100 m, the transect length was extended to reach this number. Fungiid densities and infestation rates based on presence/absence data were calculated for each transect and site. The number of snails per host coral was not considered important because they were occurring as single individuals or in clusters of snails of varying size, usually together with spawn (egg capsules sensu Robertson, 1994). The infestation rates were plotted against the fungiid densities. About 4,500 fungiids were identified to species level to get an indication of the species composition along the transect. Based on these species compositions and the total number of corals in the transects, the approximate number of specimens that was searched for each fungiid species

was calculated. These numbers were used to calculate the infestation rates for the most common epitoniid species.

Measurement of coral sizes

Infested corals in the Spermonde Archipelago were divided and recorded in eight size classes measured in occupied substrate area (<10, 10-25, 25-50, 50-100, 100-150, 150-200, 200-300, and >300 cm²), by placing them on plastic boards with the outlines of coral surfaces of 10, 25, 50, 100, 150, 200 and 300 cm² drawn on them. To fit variable fungiid contour shapes, boards were made for corals varying from circular to oval and elongated with length/width ratios of 1, 1.5, 2, 3 and 4, respectively.

In order to compare the size of infested vs. non-infested corals, specimens were selected of the most

Fungiid host species	n	Epitoniid		
		<i>E. ulu</i>	<i>E. pseudotwilae</i>	<i>E. twilae</i>
<i>Danafungia horrida</i>	280	0.7	0.0	0.0
<i>Danafungia scruposa</i>	401	1.0	0.0	0.0
<i>Fungia fungites</i>	759	1.5	0.0	0.0
<i>Lobactis scutaria</i>	125	1.6	0.0	0.0
<i>Lithophyllon concinna</i>	791	3.7	0.0	0.0
<i>Lithophyllon repanda</i>	2098	2.2	0.0	0.0
<i>Ctenactis echinata</i>	415	0.2	0.0	1.0
<i>Herpolitha limax</i>	393	0.0	0.0	6.6
<i>Sandalolitha robusta</i>	173	0.0	4.1	0.0
<i>Zoopilus echinatus</i>	136	0.0	7.4	0.0

Table 2. Infestation rate (%) of fungiid populations by three *Epifungium* species (SW Sulawesi).

Epitoniid species	Position relative to host			Depth (m)
	buried	on sand	on coral	
<i>Epidendrium</i>				
<i>E. aureum</i>		x	x	2-28
<i>E. sordidum</i>		x	x	3-35
<i>Epifungium</i>				
<i>E. adgranulosa</i>		x	x	3-18
<i>E. adgravis</i>		x	x	3-30
<i>E. hoeksemai</i>	x	x	x	1-20
<i>E. lochi</i>		x	x	3-27
<i>E. nielsi</i>		x	x	4-36
<i>E. ulu</i>		x	x	1-35
<i>E. adscabra</i>			x	3-18
<i>E. hartogi</i>			x	9-18
<i>E. marki</i>			x	15-28
<i>E. pseudolochi</i>			x	20-30
<i>E. pseudotwilae</i>			x	4-25
<i>E. twilae</i>			x	5-38
<i>Epitonium</i>				
<i>E. crassicostatum</i>	?	?	?	9
<i>E. graviarmatum</i>	?	?	?	35
<i>Surrepifungium</i>				
<i>S. costulatum</i>	x	x		3-18
<i>S. ingridae</i>	x	x		1-26
<i>S. oliverioi</i>	x	x		4-38
<i>S. patamakanthini</i>	x	x		5-18

Table 3. Depth range and position of epitoniid snails relative to the coral host recorded at various Indo-West Pacific localities: buried in sandy substratum underneath, living on sand underneath or on coral surface.

abundant host species (Hoeksema, 1990), *i.e.* *Lithophyllon concinna* (Verrill, 1864), *L. repanda* (Dana, 1846), and *Herpolitha limax* (Esper, 1797), which were the most frequently infested by the most common epitoniids, *i.e.* *Epifungium ulu* Pilsbry, 1921, and *E. twilae* (Gittenberger and Goud, 2000 in Gittenberger *et al.*, 2000). The size classes of the corals were recorded at 3-18 m depth at W Kudingareng Keke, regardless

of their infestation rate. The null-hypothesis that infestations by *E. ulu* and *E. twilae* are not related to coral-size, was tested by Chi-square against three alternative hypotheses, *i.e.* [1] coral size influences the probability of being infested, [2] host size is positively correlated with epitoniid shell size, and/or [3] host size is positively correlated with the percentage of infestations with epitoniid spawns.

Overtured host corals

Free-living fungiids are known to occasionally get overturned (Hoeksema, 1988, 2004). To investigate how this may affect epitoniid snails underneath the corals, 16 fungiid host corals of various species with snails and/or spawns of *Epifungium ulu* were carefully turned upside-down at 6–12 m depth on the reef slope NW of Langkai. After two hours and after two days the numbers of epitoniids and spawns were counted that were still present. Because the time available to find as many infected corals as possible was limited and the identity of the hosts was not relevant for the experiment, there was no preference with regard to host species.

In addition, two host corals with snails and spawns of *Epifungium ulu* and one with snails and spawns of *E. twilae* were placed upside-down, next to each other on the reef slope of W Kudingareng Keke. The specimens were observed from a distance of about 3 meters for 30 minutes to check whether any animals would predate on them.

It has been hypothesized that the overturning of a fungiid coral from an upright position to upside-down and back to upright, depends upon its size and form (Hoeksema, 1988). The rate at which this may happen was studied experimentally in the Spermonde Archipelago, using populations of 12 species, varying in shape from circular, viz. *Danafungia horrida* (Dana, 1846), *D. scruposa* (Klunzinger, 1879), *Fungia fungites* (Linnaeus, 1758), *Lithophyllon concinna* (Verrill, 1864), *L. repanda* (Dana, 1846), and *L. scabra* (Döderlein, 1901), and oval, viz. *Lobactis scutaria* (Lamarck, 1801), *Pleuractis gravis* (Nemenzo, 1955) and *P. paumotensis* (Stutchbury, 1833), to elongated, viz. *Ctenactis echinata* (Pallas, 1766), *Herpolitha limax* (Esper, 1797) and *Polyphyllia talpina* (Lamarck, 1801). With a waterproof pen, 360 quadrants of 22×25 cm², 24 quadrants of 30×30 cm², 24 quadrants of 20×35 cm² and 24 quadrants of 25×40 cm², were drawn and numbered on two orange, plastic cover cloths, which were fastened with pegs at a depth of 18 m on a slope of approximately 15° at W Kudingareng Keke reef. For each of the 12 species, 24 specimens (size class 25–100 cm²) were put in upright position in the 22×25 cm² quadrants. In addition, 24 corals of *Lithophyllon repanda* (size class 100–150 cm²) were placed in 30×30 cm² quadrants, 24 *Herpolitha limax* corals (size class 100–200 cm²) were placed in 20×35 cm² quadrants, and 24 *H. limax* specimens (size class

200–300 cm²) were placed in 25×40 cm² quadrants. The corals that had turned themselves over within three and within ten days were recorded. The experiment was repeated with all corals in upside-down position at the start. After four hours and after two days it was recorded how many had returned to an upright position.

The percentage of specimens in overturned position under natural conditions was recorded for the 23 most common fungiid species in the Spermonde Archipelago on the basis of at least 100 randomly checked specimens per species.

Results

Abundance of infestations

About 1.5% of all examined mushroom corals (n=60,000) appeared infested by epitoniids that belonged to the following 20 species (see Gittenberger and Gittenberger, 2005): *Surrepifungium costulatum* (Kiener, 1839) (n=103 infested hosts), *S. ingridae* (Gittenberger and Goud, 2000) (n=43), *S. Oliverioi* (Bonfitto and Sabelli, 2001) (n=10), *S. patamakanthini* Gittenberger and Gittenberger, 2005 (n=27), *Epidendrium aureum* Gittenberger and Gittenberger, 2005 (n=52), *E. sordidum* Gittenberger and Gittenberger, 2005 (n=22), *Epifungium adgranulosa* Gittenberger and Gittenberger, 2005 (n=20), *E. adgravis* Gittenberger and Gittenberger, 2005 (n=38), *E. hoeksemai* (Gittenberger and Goud, 2000) (n=34), *E. lochi* (Gittenberger and Goud, 2000) (n=36), *E. nielsi* Gittenberger and Gittenberger, 2005 (n=83), *E. ulu* Pilsbry, 1921 (n=191), *E. adscabra* Gittenberger and Gittenberger, 2005 (n=22), *E. hartogi* (Gittenberger, 2003) (n=10), *E. marki* Gittenberger and Gittenberger, 2005 (n=4), *E. pseudolochi* Gittenberger and Gittenberger, 2005 (n=5), *E. pseudotwilae* Gittenberger and Gittenberger, 2005 (n=68), *E. twilae* (Gittenberger and Goud, 2000) (n=98), *Epitonium crassico-statum* Gittenberger and Gittenberger, 2005 (n=1), and *E. graviarmatum* Gittenberger and Gittenberger, 2005 (n=1). The 870 recorded infestations involved 1,657 snails, on average about two per coral while 283 (32.5%) of the hosts also had epitoniid spawns. Approximately 2,500 free-living fungiids were found in an upside-down position and only one of these had only spawns without any snail. Along the transects off SW Sulawesi, 3.7% of all corals (n=7,219) were found to be infested by epitoniids.

Associations

Thirty fungiid species were found to host wentletrap snails (Table 1). Two abundant mushroom coral species with >1000 specimens inspected were never found associated with wentletraps, *i.e.* *Polyphyllia talpina* (Lamarck, 1801) and *Heliofungia fralinae* (Nemenzo, 1955). Occasionally snails belonging to the species *Epifungium ulu*, *E. hoeksemai*, *E. twilae* and *E. pseudotwilae* were found co-habiting a single host coral with snails of the species *Surrepifungium costulatum*, *S. ingridae*, *S. oliverioi* and *S. patamakanthini*, in which case the first was always attached to the coral and the latter occurred on or inside the sediment underneath.

The infestation rates shown by the most common epitoniids in the Spermonde Archipelago varied per host species, with maxima of 3.7% on *Lithophyllon concinna* by *Epifungium ulu*, 7.4% by *E. pseudotwilae* on *Zoopilus echinatus* Dana, 1846, and 6.6% by *E. twilae* on *Herpolitha limax* (Table 2).

Five *Epifungium* species are host-specific (Table 1), whereas the five other ones have at least two hosts. On the other hand, 24 fungiids are host for only one *Epifungium*, whereas only five mushroom coral species are a habitat for more than one *Epifungium* (Table 1). These do not necessarily compete for space, since the relatively small *Cycloseris costulata* hosts two *Epifungium* species, but in allopatry: *E. pseudolochi* in the Red Sea and *E. lochi* from the Maldives to Palau (Gittenberger and Gittenberger, 2005). The two most generalistic species within the genus *Epifungium* are *E. lochi* and *E. ulu* but the first only inhabits seven closely related free-living *Cycloseris* species, while *E. ulu* lives with eight fungiid host species that are less closely related (Table 1). *E. hoeksemai* is associated with two remotely related host coral species, *i.e.* *Fungia fungites* and *Heliofungia actiniformis*. Its habitat preferences are unusual, since it is the only epitoniid that was variably found buried in the sand, on the substrate, or on the coral's surface (Table 3).

Epifungium hartogi was commonly observed in association with two euphylliid coral species, *Plerogyra diabolotus* Ditlev, 2003, and *P. simplex* Rehberg, 1892, but not with *Plerogyra sinuosa* (Dana, 1846), even though this was by far the most common euphylliid at most localities. *Epidendrium aureum* and *E. sordidum* occurred both sympatrically and syntopically in mixed populations directly next to or on the dendrophylliid *Tubastraea* sp. (Gittenberger and Gittenberger, 2005: Figs 58–59).

Coral densities and infestation rates

Infestation rates varied significantly between sites ($X^2=63.4$, $p<0.001$; Fig. 18) and transects ($X^2=21.7$, $p<0.025$; Fig. 19). At nearly all sites, with the exception of W Lae-Lae, the coral densities and the infestation percentages were negatively correlated ($r=-0.43$, $p<0.001$). When the W Lae-Lae record is excluded the correlation becomes even stronger ($r=-0.80$, $p<0.001$). A similar strong negative correlation ($r=-0.98$, $p<0.001$), was found for the coral densities and the percentages of infestation by *Epifungium ulu* at E and W Kudingareng Keke. Only data from Kudingareng Keke were used in the analysis, because only there large numbers of corals ($n>100$) could be searched in all transects. These findings are supported by observations in Egypt, the Maldives, Thailand and Palau, where infestation rates of over 50% were repeatedly found at sites with very low coral densities, *i.e.* ≤ 10 corals / dive. At sampled sites where over 100 corals were found, infestation percentages never exceeded 5%.

Depth ranges

No correlation between infestation rate and depth was found for *Epifungium ulu* within a depth range of 1–35 m (Fig. 19, Table 3). Specimens of *E. lochi*, *E. adgravis*, *E. marki* and *E. pseudolochi* usually occur deeper than those of other species (Table 3) because of the depth preference of their host corals (Table 1). On the relatively rare occasions that these host species were found in shallower water, the associated epitoniids were also present, but because of their low densities no depth-related correlation could be calculated for these species. The only indication of a depth preference was found for *E. twilae*. None of its 107 infested host corals in the Maldives, Thailand and Indonesia was found deeper than 24 m, where the potential hosts *Ctenactis crassa* (Dana, 1846), *C. echinata* (Pallas, 1766) and *Herpolitha limax* (Esper, 1797) were rare, whereas all four lots of epitoniids in the Red Sea were found at 30–38 m depth (*e.g.* *E. twilae* in Table 3). *Ctenactis* was absent here, but *H. limax* was common at 6–45 m depth with 0% infestation by *E. twilae* ($n=50$) at 6–30 m depth and 33% infestation ($n=12$) at 30–45 m, although the maximum depth with *E. twilae* here was 38 m (Table 3).

Substrates and attachment

Mushroom corals in the Spermonde Archipelago on flat substrates and those above crevices or burrows

Fig. 18. Infestation rates of mushroom corals (%) plotted against mushroom coral density in the Spermonde Archipelago, SW Sulawesi, Indonesia; n values are indicated (in brackets).

Fig. 20. Percentages of fungiid corals on three substrate types in the Spermonde Archipelago: on flat sediment (n=362), on sediment with circular burrows (n=329) or with crevices (n=1,620); each of which were infested by *Surrepifungium costulatum* (n=3), *S. ingridae* (n=5), *Epifungium adgranulosa* (n=1), *E. adgravis* (n=2), *E. adscabra* (n=9), *E. hoeksemai* (n=4), *E. lochi* (n=4), *E. nielsi* (n=9), *E. pseudotwilae* (n=5), *E. twilae* (n=7) and *E. ulu* (n=47).

show different infestation rates (Fig. 20). Corals on flat substrate showed significantly higher infestation rates ($X^2=14.9$, $p<0.001$), whereas those above a burrow were the least likely infested ($X^2=14.8$, $p<0.001$). Snails of *Epifungium adgranulosa*, *E. adgravis*, *E. hoeksemai*, *E. lochi*, *E. nielsi* and *E. ulu*, were found on both the substrate and on the underside of their fungiid host (Table 3). *E. ulu* specimens underneath hosts dwelling on a flat bottom (n=26) were encountered more frequently attached to the host (96%) than

Fig. 19. Infestation rates of mushroom corals by *Epifungium ulu* (%) plotted against mushroom coral density along transects at 6, 9, 12 and 15 m depth on the east (squares) and west (dots) side of Kudingareng Keke Island, SW Sulawesi, Indonesia (see Fig. 2). Total n=3,671 corals; a minimum number of 172 corals per transect. Transect depths are indicated next to the data points.

Fig. 21. Percentages of fungiid corals at W Lae-Lae (n=184), W Bone Baku (n=289), E Kudingareng Keke (n=1,154) and Langkai (n=84), on flat sediment (white), sand with burrows (grey) or sediment with burrows (black).

lying on top of the substrate ($X^2=22.2$, $p<0.001$), whereas regarding those on a substrate with crevices (n=66) no significant preference was found for either ($X^2=1.2$, $p=0.3$) with 44% attached to the coral. Shells and spawn were usually attached to the substrate by mucus threads. These threads were noted to be extremely elastic and strong enough to pull specimens back to their hosts over distances up to 50 cm.

The proportions of corals lying on either a flat bottom, a burrow or crevices vary significantly between

Fig. 22. Numbers of specimens of *Lithophyllon concinna* in the size classes 10-25, 25-50, 50-100, 100-150, 150-200 and 200-300 cm² observed as infested by *Epifungium ulu* in the Spermonde Archipelago (see Fig. 2), next to the expected numbers when infestations are random, based on the coral size distribution of *L. concinna* specimens off W Kudingareng Keke, Spermonde Archipelago (n=63).

SW Sulawesi sites (Fig. 21; $X^2=412.4$, $p<0.001$). Although the number of corals on a flat substrate remained similar, a burrow was observed more frequently at localities closer to the coast and a substrate with crevices was most common further offshore.

At all SW Sulawesi sites (Fig. 1) mushroom corals above burrows did not host any epitoniids with only two exceptions. Burrows seemed to be more common in the sand underneath mushroom corals than in the sand around them. Gobies (Gobiidae) and goby shrimps (Alpheidae) were occasionally seen hiding underneath mushroom corals that revealed one or two burrows after being turned over. Individuals of two burrowing shrimp species were observed to push the mushroom coral quickly over the sand when it was blocking their escape routes: a specimen of *Alpheus frontalis* H. Milne Edwards, 1837 (Caridea: Alpheidae; Fig. 15) underneath *Ctenactis echinata* at Palau and a specimen of *Axiopsis* sp. (Thalassinidea: Axiidae) underneath a *Herpolitha limax* coral in the Spermonde Archipelago, Indonesia.

Coral sizes

At the west side of Kudingareng Keke reef (SW Sulawesi), the infestation of *Lithophyllon concinna* (n=63) and *L. repanda* (n=84) by *Epifungium ulu* was examined in relation to the host's size and similarly for *Herpolitha limax* (n=153) infested by *E. twilae*

Fig. 23. Numbers of specimens of *Lithophyllon repanda* in the size classes 10-25, 25-50, 50-100, 100-150, 150-200, 200-300 and >300 cm² observed as infested by *Epifungium ulu* in the Spermonde Archipelago (see Fig. 2), next to the expected numbers when infestations are random, based on the coral size distribution of *L. repanda* specimens off W Kudingareng Keke, Spermonde Archipelago (n=84).

Fig. 24. Numbers of specimens of *Herpolitha limax* in the size classes 10-25 cm², 25-50 cm², 50-100 cm², 100-150 cm², 150-200 cm², 200-300 cm² and >300 cm² observed as infested by *Epifungium twilae* in the Spermonde Archipelago (see Fig. 2), next to the expected numbers when infestations are random, based on the coral size distribution of *Herpolitha limax* specimens off W Kudingareng Keke, Spermonde Archipelago (n=153).

(Figs 22-24). *E. ulu* specimens were significantly more abundant underneath large specimens of *Lithophyllon repanda* (Fig. 23; $X^2=14.4$, $p<0.001$) than would be expected randomly, whereas they were found less frequently under larger *Lithophyllon concinna* corals than at random, but this difference is not significant (Fig. 22; $X^2=1.8$, $p=0.20$). *E. twilae*

Fig. 25. The maximum shell lengths found in *Epifungium ulu* samples (n=146) and their distributions in the size classes 0-25 cm² (n=13), 25-100 cm² (n=103) and >100 cm² (n=30) of their coral hosts, in the Spermonde Archipelago, Indonesia.

Fig. 26. The maximum shell lengths found in *Epifungium twilae* samples (n=46) and their distributions in the size classes 0-25 (n=17), 25-100 (n=14) and >100 cm² (n=15) of their coral hosts in the Spermonde Archipelago, Indonesia.

specimens occurred significantly more frequently underneath larger hosts (Fig. 24; $X^2=4.7$, $p<0.05$). Larger corals are significantly more frequently infested by relatively large specimens of both *E. ulu* (Fig. 25; $X^2=11.2$, $p<0.025$) and *E. twilae* (Fig. 26; $X^2=67.1$, $p<0.001$). Underneath larger host corals, spawns of both *E. ulu* (Table 4; $X^2=4.7$, $p<0.05$) and *E. twilae* (Table 4; $X^2=10.3$, $p<0.05$) were found significantly more frequently than would be expected by chance.

Overtured host corals

No mushroom coral in overtured position ($n \sim 2,000$) was observed to be infested by epitoniids. One single overtured coral was observed with epitoniid spawns of unknown identity. Fig. 28 illustrates the fate of 28 epitoniids and seven spawns that were initially attached to 16 coral hosts. During the overturning experiment, some snails were immediately

Epitoniids	Host coral size class					
	10-50 cm ²		50-150 cm ²		>150 cm ²	
<i>E. ulu</i>	%	n	%	n	%	n
with spawn	26	16	42	35	60	6
without spawn	74	46	58	48	40	4
<i>E. twilae</i>	%	n	%	n	%	n
with spawn	17	3	29	4	65	11
without spawn	83	15	71	10	35	6

Table 4. Size distributions of *Epifungium ulu* and *E. twilae* samples with or without spawn on corals in the size classes 0-50 cm², 50-150 cm² and >150 cm² (SW Sulawesi).

Table 5. Overturning experiment at SW Sulawesi. Data are based on 24 specimens per species in each size class. Species ranking by number of overturned corals in size class 25-100 cm².

Fungiid species	Size class (cm ²)	Average length / width	Average weight (g)	Number of overturned corals (n = 24) after 2 days
<i>Polyphyllia talpina</i>	25-100	3.6	142	20
<i>Herpolitha limax</i>	25-100	2.2	127	11
	100-200	3.1	302	11
	> 200	3.4	754	1
<i>Lobactis scutaria</i>	25-100	1.6	135	9
<i>Pleuractis gravis</i>	25-100	1.6	251	7
<i>Pleuractis paumotensis</i>	25-100	1.7	131	5
<i>Lithophyllon repanda</i>	25-100	1.1	127	5
	100-150	1.1	326	0
<i>Ctenactis echinata</i>	25-100	2.2	94	4
<i>Danafungia scruposa</i>	25-100	1.1	127	3
<i>Lithophyllon scabra</i>	25-100	1.1	75	3
<i>Lithophyllon concinna</i>	25-100	1.2	110	1
<i>Danafungia horrida</i>	25-100	1.0	163	1
<i>Fungia fungites</i>	25-100	1.1	93	0

pulled from their hosts by currents or by fish, such as Labridae (e.g. *Halichoeres melanurus* (Bleeker, 1851) Fig. 16)) and Pomacentridae (e.g. *Plectroglyphidodon lacrymatus* (Quoy and Gaimard, 1825) (Fig. 17)). One of two corals that were still hosting epitoniids after two days, had returned to an upright position, whereas the other was situated inside a crevice, away from currents.

In the experiment in which three hosts were turned upside-down, i.e. two corals of *Lithophyllon repanda*, each with two specimens and spawns of *Epifungium ulu* and one coral of *Herpolitha limax* with two *E. twilae* snails, all *E. ulu* were eaten or removed within 30 minutes by wrasses and damselfishes, while the *E. twilae* snails survived.

No significant differences in righting rate were found among the mushroom corals in the overturning experiment, since only three of the 360 fungiids (12

species × 24 specimens + 3 larger size classes × 24 specimens) had turned over (upside-down) within 10 days. Among mushroom coral species significant differences in numbers of individuals had regained an upward position within two days ($X^2=58.3$, $p<0.001$; Table 5). Corals of elongate species such as *Polyphyllia talpina*, *Herpolitha limax* and *Lobactis scutaria* showed much higher frequencies of righting than round corals, although almost all corals of the largest and heaviest size classes of *H. limax* and *Lithophyllon repanda* remained upside-down (Table 5). In SW Sulawesi, 1,109 out of 26,277 fungiids (4.2%), were observed in upside-down position under natural conditions. These percentages differed significantly among species (Fig. 28; $X^2=202.1$, $p<0.001$). Corals of oval and round polystomatous species such as *Sandalolitha robusta* (Quelch, 1886) and *Halomitra pileus* (Linnaeus, 1758), were most frequently found in

Fig. 27. Numbers of snails and spawns of *Epifungium ulu* that remained on the underside of the host corals after overturning; after two hours and after two days, off W Langkai (see Fig. 2).

Fig. 28. Percentages of fungiid populations observed in overturned position in the Spermonde Archipelago (Fig. 2); n values are indicated per species.

upside-down position (Fig. 28). Of all fungiids, *Heliofungia actiniformis* was most frequently found in upright position (Fig. 28). This species is well known for its righting capacity (Abe, 1939).

Discussion

The trophic role of coral-associated epitoniids

Unlike Bouchet and Warén (1985), we consider winkletrap snails to be highly specialised parasites because they exploit their hosts as habitat and food source for a relatively long time during their short life, even though their hosts are not clearly harmed, whereas predators can be distinguished by their momentary association with a prey and the rapid and destructive consumption of whole individuals or large fragments (Castro, 1988). Epitoniids on corals live indeed a much shorter life than their hosts and remain constantly in contact with them, or very close, like buried in the sediment underneath. In contrast to short-lived epitoniids that stick to a single host individual during their entire life, predatory *Drupella* species (Johnson and Cumming, 1995; Claremont *et al.*, 2011) are known to have a life span of several years (Black and Johnson, 1994), during which they are able to kill many corals while occurring in small groups or large aggregations (Turner, 1994; Cumming, 1999; Morton and Blackmore, 2009; Hoeksema *et al.*, 2013). The ecological strategy of epitoniids is more similar to that of ovulid snails on Octocorallia and Antipatharia (Schiaparelli *et al.*, 2005; Reijnen *et al.*, 2010) and *Pedicularia* snails on stylasterid corals (Goud and Hoeksema, 2001; Braga-Henriques *et al.*, 2011) in which the hosts become at most partly eaten over a long time period by a few parasites but not entirely consumed in a short time by a single large predator or a pack of smaller ones.

A fundamental condition for the identification of coral-associated molluscs consists of a good knowledge of the available host coral species (*e.g.* Gittenberger and Gittenberger, 2005; Hoeksema *et al.*, 2012a), as also demonstrated for the endoparasitic gastropod genus *Leptoconchus* Rüppell, 1834 (Coralliophilidae) (Hoeksema and Gittenberger, 2008; Gittenberger and Gittenberger, 2011), and coral-boring mussels (Mytilidae) of the genera *Fungiacava* Goreau *et al.*, 1968, and *Leiosolenus* Carpenter, 1856 (Hoeksema and Kleemann, 2002; Kleemann and Hoeksema, 2002; Owada and Hoeksema, 2011).

All common free-living fungiid species were found in association with epitoniids except for *Heliofungia fralinae* and *Polyphyllia talpina* (Table 1). These two species can be distinguished from most other fungiids because of their relatively long tentacles, although the fungiid with the longest tentacles, *Heliofungia actiniformis* (Quoy and Gaimard, 1833), was found in association with two species, *i.e.* *Epifungium hoeksemai* and *Surrepifungium patamakanthini*. It remains unclear why *H. fralinae* and *P. talpina* have not been found infested even though more than 1,000 specimens of each were examined. When the entirely recorded associated fauna of mushroom corals is taken into account, *H. fralinae* appears to have no known associate at all, whereas *P. talpina* has a record of seven associated species as compared to at least 21 recorded for *H. actiniformis* (Bos, 2012; Hoeksema *et al.*, 2012a). Therefore, the absence of epitoniids on *H. fralinae* is not unique and may perhaps be related to toxins excreted by this particular species as a defense mechanism in interspecific coral interactions (Sheppard, 1979; Thomason and Brown, 1986; Abelson and Loya, 1999).

In the present study, some *Epifungium* and *Surrepifungium* species are considered specialists by being associated with a monophyletic group of host corals or just a single host species, whereas others are generalists by having associations with various coral species that are distantly related (Gittenberger *et al.*, 2011). Hence, the four burying *Surrepifungium* species, *viz.* *S. costulatum*, *S. ingridae*, *S. oliverioi* and *S. patamakanthini*, are all considered generalists. They resemble mostly epitoniid species that live buried in the sediment underneath sea-anemones (Kokshoorn *et al.*, 2007). Because they live hidden in the sand underneath their host corals it is difficult to observe their feeding behaviour *in situ*. Maybe the snails extend their proboscis towards the coral tissue while remaining protected in the substrate underneath as in the sea-anemone-associated *Epitonium clathrus* (Linnaeus, 1758) and *E. clathratulum* (Kamacher, 1798) which may extend their proboscis to up to three times the shell-length towards the stem or the tentacles of the host (Perron, 1978: 65; Robertson, 1983: 4; den Hartog, 1987: 105; Gofas *et al.*, 2011: 211).

If *Epifungium* and *Surrepifungium* species share a single host together (Table 1), the *Epifungium* is found on the coral itself while the *Surrepifungium* occurs on or in the substrate underneath. *Epifungium* snails are in general closer to their food, but they are also constantly within reach of the corals' nematocysts. They

may be able to resist these nematocysts, which might explain why *Epifungium* species have more specialized host associations than *Surrepifungium* species. Likewise, commensal shrimp and fish species are also known to cohabitate single mushroom coral individuals, either living on different parts of the host or sharing similar places, especially in between tentacles of *Heliofungia actiniformis* (Hoeksema and Fransen, 2011; Bos, 2012).

Epifungium hartogi is the only *Epifungium* species that is associated with euphylliid corals. The snails are hidden deep inside the mouth cavity (the stomach) of their host (Gittenberger, 2003). They may only leave their shelter for spawning and are hard to detect. Other epitoniids may be hidden in similar habitats, although only few are known to live as endoparasites. Zahn (1980: 132) illustrates an epitoniid that hides in the cavity of a zoanthid belonging to the genus *Sphenopus* Steenstrup, 1856. This genus is unique among zoanthids because its species are free-living on sand or semi-buried (Reimer *et al.*, 2012). It is unclear whether its epitoniid associate is most closely related to burying wentletraps or epizoid species. Although many genera and species of Epitoniidae have been described (Gofas, 2012), the description of many is only based on the morphology of empty shells, while their host and mode of life remains unknown.

In general, sister species do not occur sympatrically and syntopically, but the sister taxa *Epidendrium aureum* and *E. sordidum* (for phylogenetic positions, see Gittenberger *et al.*, 2006) are found in the same area on the same host species, *Tubastraea* sp., without any obvious niche differentiation as reflected by dissimilar life history strategies or radulas (Gittenberger and Gittenberger, 2005). However, *E. sordidum* is the only known epitoniid species with shells that are completely overgrown by other organisms, like hydroids, forams and vermetids (Fig. 4). They are therefore better camouflaged and more difficult to spot than the bright yellow *E. aureum* (Fig. 3). This kind of co-occurrence among sister taxa is not unique among gastropods, as recently shown for two ovulid snails (Lorenz and Meilaun, 2011), and may either indicate sympatric or allopatric speciation. Possible mechanisms for sympatric speciation in gastropods may be related to differentiation in ecological traits (Krug, 2011). Other records of sister taxa with much overlap in distribution patterns concern several pairs of mushroom coral species in the Spermonde Archipelago (Hoeksema, 2012c).

Unlike endolithic molluscs (Hoeksema and Kleemann, 2002; Kleemann and Hoeksema, 2002; Mas-

sin, 1989, 2000; Massin and Dupont, 2003; Gittenberger and Gittenberger, 2011; Owada and Hoeksema, 2011) ectoparasitic epitoniids do not inflict serious visible damage to their host corals, as for instance seen in infestations by flatworms (Hoeksema and Farenzena, 2012). The mucus layer secreted by mushroom corals may be a means to protect their soft tissue against damage and is believed to be nutritious for other animals (Krupp, 1982, 1984, 1985; Drollet *et al.*, 1993). Mushroom corals are successful in regenerating and repairing their tissue (Chadwick and Loya, 1990; Kramarsky-Winter and Loya, 1996; Chadwick-Furman *et al.*, 2000). Owing to their fragmentation and their regenerative capacity and survival, some mushroom corals are even capable of forming large aggregations (Chadwick and Loya, 1990; Yamashiro and Nishihira, 1998; Gilmour, 2002, 2004; Hoeksema, 2004; Hoeksema and Gittenberger, 2010; Hoeksema and Waheed, 2011; Hoeksema and Yeemin, 2011). Hence, infestations by epitoniids may slightly harm mushroom corals and is not likely to have any lethal effect.

Coral densities and depth ranges

The infestation percentages by *Epifungium ulu* in the transects at 6, 9, 12 and 15 m depth on the reef slopes of W and E Kudingareng Keke, are independent of depth and negatively correlated with coral density (Fig. 19). Among the seven reefs that were studied in SW Sulawesi, only Lae-Lae had an exceptionally low infestation rate given the number of potential host corals. The mushroom corals on this reef belong to relatively few species that show high densities at shallow depths (Hoeksema, 2012a). The water around this nearshore reef is usually murky and the shallow sea floor contains much silt because of its close proximity to the mouth of the Jeneberang River (Fig. 2). Epitoniids are not exceptional among invertebrate benthic species by showing low species numbers and low densities on nearshore reefs on the Spermonde Shelf (Cleary *et al.*, 2005; Becking *et al.*, 2006; de Voogd *et al.*, 2006; Hoeksema and Crowther, 2011). Similar patterns have been observed off Jakarta, where both molluscs and corals showed a decline in species richness on nearshore reefs as a result of terrigenous impact (van der Meij *et al.*, 2009, 2010). Although mushroom corals are well capable of sediment-shedding (Bongaerts *et al.*, 2012; Erfte-meijer *et al.*, 2012), their associated fauna may be less resistant to sedimentation (van der Meij and Hoeksema, 2013).

The free-living fungiids on nearshore reefs in the Spermonde Archipelago occurred relatively more frequently on substrates with burrows than at the other localities (Fig. 21), which may also restrict their infestation rates (see *Substrates*). A negative correlation between coral density and number of infested individuals supports the hypothesis that epitoniid veliger larvae become evenly dispersed over coral reefs and depths. They can actually actively search for a suitable host by means of chemotaxis (Salo, 1977; Perron, 1978; Bell, 1985). This explains the relatively high infestation rates when few suitable fungiid hosts are present. Exceptions are reef sites that are dominated by mushroom coral species that appear to be immune to epitoniids, such as *Heliofungia fralinae* (see Hoeksema, 2004).

The use of chemotaxis may also explain how epitoniid species maintain their host specificity, although mushroom corals have been observed to form large and dense multi-species assemblages in various Indo-West Pacific localities, including the Red Sea (Pichon, 1974; Claereboudt, 1988; Goffredo and Chadwick-Furman, 2000; Latypov, 2007; Elahi, 2008; Hoeksema and Koh, 2009; Hoeksema and Matthews, 2011; Hoeksema, 2012a; Hoeksema *et al.*, 2012b). Only in case of a potential shortage of preferred host corals it may be more advantageous for wentletrap species to switch from one host species to another, as also observed in corallivorous *Drupella* snails (Hoeksema *et al.*, 2013).

Coral-associated epitoniids do not show a clear preference for a specific depth range (*e.g.* Fig. 19, Table 3). The only exception is an *Epifungium twilae* population in the Red Sea, where infestations were only recorded at > 29 m depth, even though potential hosts also occurred at shallower depths. This may be related to an unusually heavy rainfall in the year prior to the fieldwork, which formed several freshwater lakes in the desert, one of which drained towards the coast covering the research site with dirt and sand. Visibility remained only good at greater depths. Indirect evidence for epitoniids avoiding murky water was also found on Lae-Lae in the Spermonde Archipelago (see *Coral densities and depth ranges*), where infestation rates were much lower than on offshore reefs (Figs 18, 21).

Substrates

A significantly higher number of epitoniids was found on corals living on flat substrates than on sediment with burrows in them (Fig. 20). In the latter case they can more easily be reached by predators from below. This might also explain why in such cases most *Epi-*

fungium ulu snails are observed on the substrate (Fig. 6) instead of on the coral's surface. Alternatively, when the underground is flat, the snails are found significantly more frequently attached to the coral itself. Most of the burrows found underneath mushroom corals (Figs 11, 13-14) were probably made by shrimps, like *Alpheus frontalis* (Fig. 15) and *Axiopsis* sp., and by goby shrimps and burrow-dwelling gobies. These shrimps and gobies may remove and eat epitoniids that lived above the burrowing. *Surrepifungium* snails bury into the sand for protection and are never found on the coral surface, in contrast to most *Epifungium* species, with the exception of *E. hoeksemai* (Table 3).

Coral sizes and risk of host coral turnover

Coral size matters in relation to infestations by epitoniids, which inhabit their hosts for only a limited time. For instance, the life history of *Epifungium ulu* (Bell, 1985), which includes eggs, a planktonic veliger stage, and the settling as a benthic snail has been observed to be completed within 36 days (Robertson, 1983, 1994; Bell, 1985; Collin, 2000; Gittenberger, 2003). However, variation in protoconch size and whorls number among epitoniids (Gittenberger and Gittenberger, 2005), suggests that the duration of the planktonic larval stage may be different in other species.

The presence of *Epifungium ulu* and *E. twilae* snails with their spawns, is clearly related to host size since [1] the snails are more frequently found underneath larger hosts (Figs 23-24), [2] larger snails are more often observed with larger hosts (Figs 25-26) and [3] individual snails are more frequently observed with spawns underneath the largest hosts (Table 4). These results can be explained by a combination of factors. Most importantly, since larger corals are usually older, they have been exposed to possible infestation for a longer period of time. A coral may be host for several generations of snails, although it is unknown whether these are successive generations, *i.e.* whether veligers settle on the same host as their parents.

Moreover, larger host corals are heavier than smaller ones and can be overturned less easily, thus preventing exposure of the snails to potential predators. The preference of epitoniids for larger hosts may also be related to the convex (domed) shape of large free-living mushroom corals (Hoeksema and Moka, 1989; Hoeksema, 1993c), leaving more living space for epitoniids in between the coral disc and the substrate. This is especially relevant for snails that do not bury into the sand, like most *Epifungium* species (Table 3),

or species that have broad shells (height/width ratios 1.0–1.2), like *E. pseudotwilae* and *E. twilae* (Fig. 9). These wentletraps are found on fungiids that may become relatively large, like those belonging to *Ctenactis*, *Herpolitha*, *Podabacia*, *Sandalolitha* and *Zoopilus* (Table 1; Hoeksema 1989, 1991b). These polystomatous coral species have their mouths more or less evenly distributed over their upper surface, which allows them to become large (Hoeksema, 1991b). Because of their convex shape not all mouths are in direct contact with the substrate. Hence, large specimens may not right themselves easily and because of their high number of mouths, their upside-down position perhaps does not entirely prevent food intake, which may enable them to survive for long periods.

Epitoniids with more slender shells (height/width ratio >2.0) like *Epifungium adgranulosa*, *E. adscabra*, *E. marki*, *E. nielsi* (Fig. 7), *E. lochi* (Fig. 8) and *E. pseudolochi*, are associated either with small fungiids belonging to free-living *Cycloseris* species, *Lithophyllon scabra*, *Pleuractis granulosa* (Fig. 12), or oval *Pleuractis* species that can be slightly convex (Fig. 7).

Epitoniids are hardly ever found underneath fungiids that are turned upside-down or on top of their host in upright position, although many mushroom coral surveys were performed (e.g. Hoeksema, 1991a; 1993, 2012a, Hoeksema and Moka, 1989; Hoeksema and Koh, 2009; Hoeksema and Matthews, 2011; Waheed and Hoeksema, 2013). Wentletraps may become removed from their host within hours or days after the coral disc has been turned over (Fig. 27) and are either eaten by fishes (Figs 16–17) or removed by currents. They were also not found on neighbouring corals. The spawns may remain somewhat longer (Fig. 27) because they are attached to the host by several mucus threads instead of only one or two that hold the snails themselves (Gittenberger and Gittenberger, 2005). The righting ability differed significantly among various fungiid species (Table 5), as well as the relative frequency of specimens found in overturned position (Fig. 28). Hosts that do not easily overturn are less risky as hosts for wentletraps, but no preference for such species was found (Table 1).

Epifungium pseudotwilae and *E. twilae* are associated with relatively large mushroom coral species, e.g. those belonging to *Ctenactis*, *Herpolitha*, *Sandalolitha*, and *Zoopilus* (Hoeksema, 1989, 1991b). Wrasses, damselfish and gobies are more frequently found underneath such large corals than small corals and may therefore be more threatening to *E. pseudotwilae* and *E. twilae* than to other *Epifungium* species. Their wide

conical shells are noticeably broader than those of the other *Epifungium* species (Gittenberger and Gittenberger, 2005). Small fishes with narrow mouths that can reach the underside of the coral discs may not be able to grasp the shell of these species. The shells of both species are very similar in shape although they are not sister taxa (Gittenberger *et al.*, 2006), which may reflect a convergent evolution as a result of a selective preference for longer shells by predatory fish. This hypothesis is supported by the exposure experiment in which damselfishes and wrasses only ate the slender specimens of *Epifungium ulu*, without attacking the relatively broad *E. twilae* shells.

Conclusions and recommendations

Twenty wentletrap snails (Epitoniidae) in the present study are known to be parasites of scleractinian corals: 17 species are associated with mushroom corals (Fungiidae), two *Epidendrium* species with dendrophylliid corals and one *Epifungium* species with two *Plerogyra* species (Euphylliidae) (Gittenberger and Gittenberger, 2005). Among the 17 snails associated with Fungiidae, 11 *Epifungium* spp. dwell on the host coral's under surface, four *Surrepifungium* spp. live buried in sediment underneath the host coral, and two *Epitonium* spp. have an unknown life style because they have only been found as empty shells in the proximity of mushroom corals. The species not associated with mushroom corals were found outside or inside in the host's polyps. Six *Epifungium* spp. on mushroom corals have been recorded with a single host species, like both *Epitonium* spp., while none of the *Surrepifungium* spp. are host-specific. Except for one occasion, no coral-associated wentletrap species showed a particular depth preference. Infestation rates were negatively correlated with coral densities, which indicates that epitoniid veliger larvae may actively look for preferential hosts. Holes underneath hosts appeared to have a restrictive influence on the occurrence of the associated snails. Malacovorous fishes consumed snails the moment their host corals were overturned, which suggests that the hosts normally provide the snails with protection against predators. Future evolutionary studies will deal with how snail-host associations relate to a molecular phylogeny reconstruction of the Epitoniidae (Gittenberger *et al.*, in prep). Other research may focus on how numbers, sizes, the presence of spawns and sex of the snails varies among coral hosts and how these correspond with host size and the

time of the year, which ideally could be carried out with the most common host and snail species, *i.e. Epi-fungium ulu* and *E. twilae*.

Acknowledgements

We are grateful to Prof. Dr. Edmund Gittenberger (Leiden) and Dr. David G. Reid (London) for critically discussing an early draft of the manuscript. Dr. Merijn Bos, Dr. Pat Colin, Ms. Lori Colin, Ms. Rachel Collin, Mr. Hans Ditlev, Dr. Mark Erdmann, Mr. Jeroen Goud, Mr. Victor de Grund, Dr. Bas Kokshoorn, Mr. Somnuk Patamakanthin, Mr. Somwang Patamakanthin, Mr. Niels Schrieken, and Dr. Nicole J. de Voogd are thanked for their help in providing information and material. Dr. Charles H.J.M. Fransen (Leiden) is thanked for the identification of the burrowing crustaceans. We are also grateful to Prof. Dr. Alfian Noor (Hasanuddin University, Makassar) for his support in Makassar. This research project was supported by WOTRO (grant nr. W 82-249) with additional funding by the Schure-Beijerinck-Popping Fonds (KNAW), the Alida Buitendijkfonds (Leiden University and Naturalis Biodiversity Center), and the Jan Joost ter Pelkewijkfonds (Leiden University and Naturalis Biodiversity Center). The research in Indonesia was generously sponsored by the Indonesian Institute of Sciences (LIPI). We want to thank two anonymous reviewers for their constructive comments on the final manuscript.

References

- Abe N. 1939. Migration and righting reaction of the coral *Fungia actiniformis* var. *palawensis* Döderlein. *Palao Tropical Biological Station Studies* 4: 671-694.
- Abelson A, Loya Y. 1999. Interspecific aggression among stony corals in Eilat, Red Sea: a hierarchy of aggression ability and related parameters. *Bulletin of Marine Science* 65: 851-860.
- Becking LE, Cleary FR, de Voogd NJ, Renema W, De Beer M, Van Soest RWM, Hoeksema BW. 2006. Betadiversity of tropical marine assemblages in the Spermonde Archipelago, Indonesia. *Marine Ecology* 27: 76-88.
- Bell JL. 1985. Larval growth and metamorphosis of a proso-branch gastropod associated with a solitary coral. *Proceedings of the 5th International Coral Reef Congress* 5: 159-164.
- Benzoni F, Stefani F, Stolarski J, Pichon M, Mitta G, Galli P. 2007. Debating phylogenetic relationships of the scleractinian *Psammocora*: molecular and morphological evidences. *Contributions to Zoology* 76: 35-54.
- Benzoni F, Arrigoni R, Stefani F, Reijnen BT, Montano S, Hoeksema BW. 2012. Phylogenetic position and taxonomy of *Cycloseris explanulata* and *C. wellsii* (Scleractinia: Fungiidae): Lost mushroom corals find their way home. *Contributions to Zoology* 81: 125-146.
- Black R, Johnson MS. 1994. Growth rates in outbreak populations of the corallivorous gastropod *Drupella cornus* (Röding 1798) at Ningaloo Reef, Western Australia. *Coral Reefs* 13: 145-150.
- Bleeker P. 1851. Bijdrage tot de kennis der ichthyologische fauna van de Banda-eilanden. *Natuurkundig Tijdschrift voor Nederlandsch-Indië* 2: 225-261.
- Bonfitto A, Sabelli B. 2001. *Epitonium (Asperiscala?) oliverioi*, a new species of Epitoniidae (Gastropoda) from Madagascar. *Journal of Molluscan Studies* 67: 269-274.
- Bongaerts P, Hoeksema BW, Hay KB, Hoegh-Guldberg O. 2012. Mushroom corals overcome live burial through pulsed inflation. *Coral Reefs* 31: 399.
- Bos AR. 2012. Symbiotic fishes (Gobiidae and Labridae) of the mushroom coral *Heliofungia actiniformis* (Scleractinia; Fungiidae). *Coral Reefs* 31: 133.
- Bouchet P, Warén A. 1986. Revision of the Northeast Atlantic bathyal and abyssal Acrididae, Eulimidae, Epitoniidae (Mollusca: Gastropoda). *Bollettino Malacologico*, Suppl. 2: 299-576.
- Braga-Henriques A, Carreiro-Silva M, Porteiro FM, de Matos V, Sampaio Í, Ocaña O, Ávila SP. 2011. The association between a deep-sea gastropod *Pedicularia sicula* (Caenogastropoda: Pediculariidae) and its coral host *Errina dabneyi* (Hydrozoa: Stylasteridae) in the Azores. *ICES Journal of Marine Science* 68: 399-407.
- Carpenter KE, Abrar M, Aeby G, et al. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321: 560-563.
- Carpenter PP. 1856. Monograph of the shells collected by T. Nuttall, Esq. On the Californian coast, in the years 1834-5. *Proceedings of the Zoological Society of London*. 1856: 209-229.
- Castro A. 1988. Animal symbioses in coral reef communities: a review. *Symbiosis* 5: 161-184.
- Chadwick NE. 1988. Competition and locomotion in a free-living fungiid coral. *Journal of Experimental Marine Biology and Ecology* 133: 189-200.
- Chadwick NE, Loya Y. 1990. Regeneration after experimental breakage in the solitary reef coral *Fungia granulosa* Klunzinger, 1879. *Journal of Experimental Marine Biology and Ecology* 142: 221-234.
- Chadwick-Furman NE, Loya Y. 1992. Migration, habitat use, and competition among mobile corals (Scleractinia: Fungiidae) in the Gulf of Eilat, Red Sea. *Marine Biology* 114: 617-623.
- Chadwick-Furman NE, Goffredo S, Loya Y. 2000. Growth and population dynamic model of the reef coral *Fungia granulosa* Klunzinger, 1879 at Eilat, northern Red Sea. *Journal of Experimental Marine Biology and Ecology* 249: 199-218.
- Churchill CKC, Ó Foighil D, Strong EE, Gittenberger A. 2011. Females floated first in bubble-rafting snails. *Current Biology* 21: R802-803.
- Claereboudt M. 1988. Spatial distribution of fungiid coral population on exposed and sheltered reef slopes in Papua New Guinea. *Proceedings of the 6th International Coral Reef Symposium, Townsville, Australia* 2: 715-720.
- Claremont M, Reid DG, Williams ST. 2011. Evolution of coral-livory in the gastropod genus *Drupella*. *Coral Reefs* 30: 977-990.
- Cleary DFR, Becking LE, de Voogd NJ, Renema W, De Beer M, Van Soest RWM, Hoeksema BW. 2005. Variation in the diversity and composition of benthic taxa as a function of distance offshore, depth and exposure in the Spermonde Archipelago, Indonesia. *Estuarine Coastal and Shelf Science* 65: 557-570.
- Collin R. 2000. Development and anatomy of *Nitidiscala tincta* (Carpenter, 1865) (Gastropoda: Epitoniidae). *Veliger* 43: 302-312.

- Cumming RL. 1999. Predation on reef-building corals: multi-scale variation in the density of three corallivorous gastropods, *Drupella* spp. *Coral Reefs* 18: 147-157.
- Dana JD. 1846. *United States Exploring Expedition during the years 1838-1842. Zoophytes* 7. Lea and Blanchard, Philadelphia.
- Ditlev H. 2003. New scleractinian corals (Cnidaria: Anthozoa) from Sabah, North Borneo. Description of one new genus and eight new species, with notes on their taxonomy and ecology. *Zoologische Mededelingen, Leiden* 77: 193-219.
- Döderlein L. 1901. Die Korallengattung *Fungia*. *Zoologischer Anzeiger* 24: 351-360.
- Drollet JH, Glaziou P, Martin PMV. 1993. A study of mucus from the solitary coral *Fungia* fungites (Scleractinia: Fungiidae) in relation to photobiological UV adaptation. *Marine Biology* 115: 263-266.
- Elahi R. 2008. Effects of aggregation and species identity on the growth and behavior of mushroom corals. *Coral Reefs* 27: 881-885.
- Ertfemeijer PLA, Riegl B, Hoeksema BW, Todd PA. 2012. Environmental impacts of dredging and other sediment disturbances on corals: a review. *Marine Pollution Bulletin* 64: 1737-1765.
- Esper EJC. 1797. Die Planzenthier. Fortsetzungen 1 (1797): 1-230. Abbildungen I: Madrepora pls. 1-87. Raspischen Buchhandlung, Nurnberg.
- Gilmour JP. 2002. Acute sedimentation causes size-specific mortality and asexual budding in the mushroom coral, *Fungia fungites*. *Marine and Freshwater Research* 53: 805-812.
- Gilmour JP. 2004. Asexual budding in Fungioid corals. *Coral Reefs* 23: 595.
- Gittenberger A. 2003. The wentletrap *Epitonium hartogi* spec. nov. (Gastropoda: Epitoniidae), associated with bubble coral species, *Plerogyra* spec. (Scleractinia: Euphylliidae), off Indonesia and Thailand. *Zoologische Verhandelingen, Leiden* 345: 139-150.
- Gittenberger A, Gittenberger E. 2005. A hitherto unnoticed adaptive radiation: epitoniid species (Gastropoda: Epitoniidae) associated with corals (Scleractinia). *Contributions to Zoology* 74: 125-203.
- Gittenberger A, Gittenberger E. 2011. Cryptic, adaptive radiation of parasitic snails: sibling species of *Leptoconchus* (Gastropoda: Coralliophilidae) in corals. *Organisms, Diversity and Evolution* 11: 21-41.
- Gittenberger A, Goud J, Gittenberger E. 2000. *Epitonium* (Gastropoda: Epitoniidae) associated with mushroom corals (Scleractinia: Fungiidae) from Sulawesi, Indonesia, with the description of four new species. *The Nautilus* 114: 1-13.
- Gittenberger A, Kokshoorn E, Gittenberger E. 2006. A molecular phylogeny of Epitoniidae (Mollusca: Gastropoda), focusing on the species associated with corals. Pp. 207-213 in: Gittenberger A: *The evolutionary history of parasitic gastropods and their coral hosts in the Indo-Pacific*. PhD thesis, Leiden University.
- Gittenberger A, Reijnen BT, Hoeksema BW. 2011. A molecularly based phylogeny reconstruction of mushroom corals (Scleractinia: Fungiidae) with taxonomic consequences and evolutionary implications for life history traits. *Contributions to Zoology* 80: 107-132.
- Gofas S. 2012. Epitoniidae. Accessed through: World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=132> on 2012-11-11
- Gofas S, Moreno D, Salas C. 2011. Moluscos marinos de Andaluía: una guía para su identificación. Vol. I. Servicio de Publicaciones e Intercambio Científico, Universidad de Málaga.
- Goffredo S, Chadwick-Furman NE. 2000. Abundance and distribution of mushroom corals (Scleractinia: Fungiidae) on a coral reef at Eilat, northern Red Sea. *Bulletin of Marine Science* 66: 241-245.
- Goreau TF, Goreau NI, Neumann Y. 1968. *Fungiacava eilatis* n. gen., n. sp. (Bivalvia, Mytilidae), a boring bivalve commensal in reef corals. *American Zoologist* 8: 799.
- Goud J, Hoeksema BW. 2001. *Pedicularia vanderlandi* spec. nov. (Gastropoda: Ovulidae), a symbiotic snail on the hydrocoral *Distichopora vervoorti* Cairns & Hoeksema, 1998 (Hydrozoa: Stylasteridae) from Bali, Indonesia. *Zoologische Verhandelingen, Leiden* 334: 77-97.
- Hadfield MG. 1976. Molluscs associated with living tropical corals. *Micronesica* 12: 133-148.
- Hartog JC den. 1987. Observations of the wentletrap *Epitonium clathratulum* (Kamacher, 1797) (Prosobranchia, Epitoniidae) and the sea anemone *Bunodosoma biscayensis* (Fischer, 1874) (Actiniaria, Actiniidae). *Basteria* 51: 95-108.
- Hoeksema BW. 1988. Mobility of free living fungioid corals (Scleractinia), a dispersion mechanism and survival strategy in dynamic reef habitats. *Proceedings 6th International Coral Reef Symposium* 2: 715-720.
- Hoeksema BW. 1989. Taxonomy, phylogeny and biogeography of mushroom corals (Scleractinia: Fungiidae). *Zoologische Verhandelingen, Leiden* 254: 1-295.
- Hoeksema BW. 1990. Systematics and ecology of mushroom corals (Scleractinia: Fungiidae). PhD Thesis, Leiden University.
- Hoeksema BW. 1991a. Control of bleaching in mushroom coral populations (Scleractinia: Fungiidae) in the Java Sea: stress tolerance and interference by life history strategy. *Marine Ecology Progress Series* 74: 225-237.
- Hoeksema BW. 1991b. Evolution of body size in mushroom corals (Scleractinia: Fungiidae) and its ecomorphological consequences. *Netherlands Journal of Zoology* 41: 122-139.
- Hoeksema BW. 1993a. Mushroom corals (Scleractinia: Fungiidae) of Madang Lagoon, northern Papua New Guinea: an annotated checklist with the description of *Cantharellus jebbi* spec. nov. *Zoologische Mededelingen, Leiden* 67: 1-19.
- Hoeksema BW. 1993b. Historical biogeography of *Fungia* (*Pleuraetis*) spp. (Scleractinia: Fungiidae), including a new species from the Seychelles. *Zoologische Mededelingen, Leiden* 67: 639-654.
- Hoeksema BW. 1993c. Phenotypic corallum variability in Recent mobile reef corals. *Courier Forschungsinstitut Senckenberg* 164: 263-272.
- Hoeksema BW. 2004. Impact of budding on free-living corals at East Kalimantan, Indonesia. *Coral Reefs* 23: 492.
- Hoeksema BW. 2007. Delineation of the Indo-Malayan centre of maximum marine biodiversity: The coral triangle. Pp. 117-178 in: Renema W., ed., *Biogeography, time and place: distributions, barriers and islands*. Springer, Dordrecht.
- Hoeksema BW. 2009. Attached mushroom corals (Scleractinia: Fungiidae) in sediment-stressed reef conditions at Singa-

- pore, including a new species and a new record. *Raffles Bulletin of Zoology* Suppl. 22: 81-90.
- Hoeksema BW. 2012a. Distribution patterns of mushroom corals (Scleractinia: Fungiidae) across the Spermonde Shelf, South Sulawesi. *Raffles Bulletin of Zoology* 60: 183-212.
- Hoeksema BW. 2012b. Mushroom corals (Scleractinia: Fungiidae) of Espiritu Santo (Vanuatu, West Pacific) with the description of a new species. *Zoosystema* 34: 429-443.
- Hoeksema BW. 2012c. Evolutionary trends in onshore-offshore distribution patterns of mushroom coral species (Scleractinia: Fungiidae). *Contributions to Zoology* 81: 199-221.
- Hoeksema BW, Crowther AL. 2011. Masquerade, mimicry and crypsis of the polymorphic sea anemone *Phyllodiscus semoni* and its aggregations in South Sulawesi. *Contributions to Zoology* 80: 251-268.
- Hoeksema BW, Dai CF. 1991. Scleractinia of Taiwan. II Family Fungiidae (with the description of a new species). *Bulletin Zoological Institute, Academia Sinica, Taipei* 30: 201-226.
- Hoeksema BW, Farenzena ZT. 2012. Tissue loss in corals infested by acoelomorph flatworms (*Waminoa* sp.). *Coral Reefs* 31: 869.
- Hoeksema BW, Fransen CHJM. 2011. Space partitioning by symbiotic shrimp species cohabitating in the mushroom coral *Heliofungia actiniformis* at Semporna, eastern Sabah. *Coral Reefs* 30: 519.
- Hoeksema BW, Gittenberger A. 2008. Records of some marine parasitic molluscs from Nha Trang, Vietnam. *Basteria* 72: 129-133.
- Hoeksema BW, Gittenberger A. 2010. High densities of mushroom coral fragments at West Halmahera, Indonesia. *Coral Reefs* 29: 691.
- Hoeksema BW, Kleemann K. 2002. New records of *Fungiacaeva eilatensis* Goreau et al., 1968 (Bivalvia: Mytilidae) boring in Indonesian mushroom corals (Scleractinia: Fungiidae). *Basteria* 66: 25-30.
- Hoeksema BW, Koh EGL. 2009. Depauperation of the mushroom coral fauna (Fungiidae) of Singapore (1860s-2006) in changing reef conditions. *Raffles Bulletin of Zoology* Suppl. 22: 91-101.
- Hoeksema BW, Matthews JL. 2011. Contrasting bleaching patterns in mushroom coral assemblages at Koh Tao, Gulf of Thailand. *Coral Reefs* 30: 95.
- Hoeksema BW, Moka W. 1989. Species assemblages and phenotypes of mushroom corals (Fungiidae) related to coral reef habitats in the Flores Sea. *Netherlands Journal of Sea Research* 23: 149-160.
- Hoeksema BW, de Voogd NJ. 2012. On the run: free-living mushroom corals avoiding interaction with sponges. *Coral Reefs* 31: 455-459.
- Hoeksema BW, Waheed Z. 2011. Initial phase of autotomy in fragmenting *Cycloseris* corals at Semporna, eastern Sabah, Malaysia. *Coral Reefs* 30: 1087.
- Hoeksema BW, Yeemin T. 2011. Late detachment conceals serial budding by the free-living coral *Fungia fungites* in the Inner Gulf of Thailand. *Coral Reefs* 30: 975.
- Hoeksema BW, van der Meij SET, Fransen CHJM. 2012a. The mushroom coral as a habitat. *Journal of the Marine Biological Association of the United Kingdom* 92: 647-633.
- Hoeksema BW, Matthews JL, Yeemin T. 2012b. The 2010 coral bleaching event and its impact on the mushroom coral fauna of Koh Tao, Western Gulf of Thailand. *Phuket Marine Biological Center Research Bulletin* 71: 71-81.
- Hoeksema BW, Scott C, True JD. 2013. Dietary shift in coral-livorous *Drupella* snails following a major bleaching event at Koh Tao, Gulf of Thailand. *Coral Reefs* doi: [10.1007/s00338-012-1005-x](https://doi.org/10.1007/s00338-012-1005-x).
- Hubbard JAEB. 1972. *Diaseris distorta*, an "acrobatic" coral. *Nature* 236: 457-459.
- Johnson MS, Cumming RL. 1995. Genetic distinctness of three widespread and morphologically variable species of *Drupella* (Gastropoda, Muricidae). *Coral Reefs* 14: 71-78.
- Jokiel PL, Cowdin HP. 1976. Hydromechanical adaptation in the solitary free-living coral *Fungia scutaria*. *Nature* 262: 212-213.
- Kanmacher F. 1798. Second edition of Adams J, Essays on the microscope : containing a practical description of the most improved microscopes; a general history of insects, their transformations, peculiar habits, and oeconomy : an account of the various species, and singular properties, of the hydrae and vorticellae: a description of three hundred and eighty-three animalcula : with a concise catalogue of interesting objects: a view of the organization of timber, and the configuration of salts, when under the microscope. Dillon and Keating, London.
- Kiener LC. 1839. Genre *Scalaire*. Pp. 1-22, Pls 1-7 in: *Species general et iconographie des coquilles vivantes comprenant la collection du Muséum d'histoire naturelle de Paris : la collection Lamarck, celle du prince Masséna (appartenant maintenant à M.B. Delessert) et les découvertes récentes des voyageurs*. Rousseau and Baillière, Paris.
- Kleemann K, Hoeksema BW. 2002. *Lithophaga* (Bivalvia: Mytilidae), including a new species, boring in mushroom corals (Scleractinia: Fungiidae) at South Sulawesi, Indonesia. *Basteria* 66: 11-24.
- Klunzinger CB. 1879. *Die Korallenthiere des Rothen Meeres* 3. Gutmann, Berlin.
- Kokshoorn B, Goud J, Gittenberger E, Gittenberger A. 2007. Epitoniid parasites (Gastropoda, Prosobranchia, Epitonidae) and their host sea anemones (Cnidaria, Actiniaria, Ceriantharia) in the Spermonde archipelago, Sulawesi, Indonesia. *Basteria* 71: 33-56.
- Kramarsky-Winter E, Loya Y. 1996. Regeneration versus budding in fungiid corals: a trade-off. *Marine Ecology Progress Series* 134: 179-185.
- Krug PJ. 2011. Patterns of speciation in marine gastropods: A review of the phylogenetic evidence for localized radiations in the sea. *American Malacological Bulletin* 29: 169-186.
- Krupp DA. 1982. The composition of the mucus from the mushroom coral *Fungia scutaria*. *Proceedings 4th International Coral Reef Symposium, Manila* 2: 9-73.
- Krupp DA. 1984. Mucus production by corals exposed during an extreme low tide. *Pacific Science* 38: 1-11.
- Krupp DA. 1985. An immunochemical study of the mucus from the solitary coral *Fungia scutaria* (Scleractinia, Fungiidae). *Bulletin of Marine Science* 35: 163-175.
- Lamarck JBPA de M de. 1801. *Système des animaux sans vertèbres*. Deterville, Paris.
- Latypov YY. 2007. Free-living scleractinian corals on reefs of the Seychelles Islands. *Russian Journal of Marine Biology* 33: 222-226.

- Linnaeus C. 1758. *Systema Naturae. Regnum Animale*. Laurentii Salvii, Holmiae, Stockholm.
- Lorenz F, Melaun, C. 2011. A new species of *Simnia* from England (Caenogastropoda: Ovulidae). *Molluscan Research* 31: 167-175.
- Massin C. 1989. Boring Coralliophilidae (Mollusca, Gastropoda): coral host relationship. *Proceedings of the 6th International Coral Reef Symposium* 3: 177-184.
- Massin C. 2000. Ecology of the *Leptoconchus* spp. (Gastropoda, Coralliophilidae) infesting Fungiidae (Anthozoa, Madreporaria). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie* 70: 235-252.
- Massin C, Dupont S. 2003. Study on the *Leptoconchus* (Gastropoda, Coralliophilidae) infesting Fungiidae (Anthozoa: Scleractinia): 1. Presence of nine Operational taxonomic units (OTUs) based on anatomical and ecological characters. *Belgian Journal of Zoology* 133: 123-128.
- Meij SET van der, Hoeksema BW. 2013. Distribution of gall crabs inhabiting mushroom corals on Semporna reefs, Malaysia. *Marine Biodiversity* doi: [10.1007/s12526-012-0135-2](https://doi.org/10.1007/s12526-012-0135-2)
- Meij SET van der, Moolenbeek RG, Hoeksema BW. 2009. Decline of the Jakarta Bay molluscan fauna linked to human impact. *Marine Pollution Bulletin* 59: 101-107.
- Meij SET van der, Suharsono, Hoeksema BW. 2010. Long-term changes in coral assemblages under natural and anthropogenic stress in Jakarta Bay (1920-2005). *Marine Pollution Bulletin* 60: 1442-1454.
- Milne Edwards H. 1837. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux, II. Librairie de Roret, Paris.
- Morton B, Blackmore G. 2009. Seasonal variations in the density of and corallivory by *Drupella rugosa* and *Cronia margariticola* (Caenogastropoda: Muricidae) from the coastal waters of Hong Kong: 'plagues' or 'aggregations'. *Journal of the Marine Biological Association of the United Kingdom* 89: 147-159.
- Nemzeno F. 1955. Systematic studies on Philippine shallow-water scleractinians I. Suborder Fungiida. *Natural and Applied Science Bulletin* 15: 3-84, pls. 1-14.
- Owada M, Hoeksema BW. 2011. Molecular phylogeny and shell microstructure of *Fungiacava eilatensis* Goreau et al., 1968, boring into mushroom corals (Scleractinia: Fungiidae), in relation to other mussels (Bivalvia: Mytilidae). *Contributions to Zoology* 80: 169-178.
- Pallas PS. 1766. *Elenchus Zoophytorum*. Van Cleef, Hagae-Comitum.
- Perron F. 1978. The habitat and feeding behavior of the wentletrap *Epitonium greenlandicum*. *Malacologia* 17: 63-72.
- Pichon M. 1974. Free living scleractinian coral communities in the coral reefs of Madagascar. *Proceedings of the 2nd International Coral Reef Symposium, Brisbane* 2: 173-181.
- Pilsbry HA. 1921. Marine mollusks of Hawaii. *Proceedings of the Academy of Natural Sciences of Philadelphia* 72: 360-382.
- Plusquellec Y, Webb G, Hoeksema BW. 1999. Automobility in Tabulata, Rugosa, and Extant scleractinian analogues: stratigraphic and paleogeographic distribution of Paleozoic mobile corals. *Journal of Palaeontology* 73: 985-1001.
- Quelch JJ. 1886. Report on the reef-corals collected by H.M.S. Challenger during the years 1873-76. *Report on the Scientific Results of the Voyage of H.M.S. Challenger, Zoology* 16 (3): 1-203, pls. 1-12.
- Quoy JRC, Gaimard P. 1825. Description des Poissons. Chapter IX. In: Freycinet L de, Voyage autour du Monde..exécuté sur les corvettes de L. M. "L'Uranie" et "La Physicienne," pendant les années 1817, 1818, 1819 et 1820. Paris. Description des Poissons. Chapter IX. In: Freycinet, L. de, Voyage autour du Monde, pp. 329-616, Atlas pls. 43-65.
- Quoy JRC, Gaimard P. 1833. *Voyage de Découvertes de l'Astrolabe Exécuté par Ordre du Roi, Pendant les Années 1826-1827-1828-1829, sous le Commandement de M.J. Dumont D'Urville*. J. Tastu, Paris.
- Rehberg H. 1892. Neue und wenig bekannte Korallen. *Abhandlungen Naturwissenschaftlichen Verein Hamburg* 12: 1-50, pls. 1-4.
- Reimer JD, Lin M, Fujii T, Lane DJW, Hoeksema BW. 2012. The phylogenetic position of the solitary zoanthid genus *Sphenopus* (Cnidaria: Hexacorallia). *Contributions to Zoology* 81: 43-54.
- Reijnen BT, Hoeksema BW, Gittenberger E. 2010. Host specificity and phylogenetic relationships among Atlantic Ovulidae (Mollusca: Gastropoda). *Contributions to Zoology* 79: 69-78.
- Robertson R. 1963. Wentletraps (Epitoniidae) feeding on sea anemones and corals. *Proceedings of the Malacological Society of London* 35: 51-63.
- Robertson R. 1966. Coelenterate-associated prosobranch gastropods. *American Malacological Union Annual Reports* 1965: 6-8.
- Robertson R. 1970. Review of the predators and parasites of stony corals with special reference to symbiotic prosobranch gastropods. *Pacific Science* 24: 43-54.
- Robertson R. 1981. *Epitonium millecostatum* and *Coralliophila clathrata*: Two prosobranch gastropods symbiotic with Indo-Pacific *Palythoa* (Coelenterata: Zoanthidae). *Pacific Science* 34: 1-17.
- Robertson R. 1983. Observations on the life history of the wentletrap *Epitonium albidum* in the West Indies. *American Malacological Union Bulletin* 1: 1-12.
- Robertson R. 1994. Wentletrap egg capsules and veligers: what they are and how to see and study them. *American Conchologist* 22: 5-6.
- Rüppell E. 1834. Description of a new genus of pectinibranchiated gasteropodous Mollusca (*Leptoconchus*). *Proceedings of the Zoological Society of London* 2: 105-106.
- Salo S. 1977. Observations on feeding, chemoreception and toxins in two species of *Epitonium*. *Veliger* 20: 168-172.
- Schiaparelli S, Barucca M, Olmo E, Boyer M, Canapa A. 2005. Phylogenetic relationships within Ovulidae (Gastropoda: Cypraeoidea) based on molecular data from the 16S rRNA gene. *Marine Biology* 147: 411-420.
- Schimek RL. 1986. A diet that stings; sea anemones as food for snails. *Shells and Sea Life* 18(11): 173-175.
- Sheppard CRC. 1979. Interspecific aggression between reef corals with reference to their distribution. *Marine Ecology Progress Series* 1: 237-247.
- Steenstrup JJS. 1856. *Sphenopus marsupialis* (Gmelin). Saerskilt Aftryk. Af det Kongelige danske Videnskabernes Selskabs Forhandler.
- Stella JS, Jones GP, Pratchett MS. 2010. Variation in the structure of epifaunal invertebrate assemblages among coral hosts. *Coral Reefs* 29: 957- 973.

- Stella JS, Pratchett MS, Hutchings PA, Jones GP. 2011. Coral-associated invertebrates: diversity, ecological importance and vulnerability to disturbance. *Oceanography and Marine Biology: An Annual Review* 49: 43-104.
- Stutchbury S. 1833. An account of the mode of growth of young corals of the genus *Fungia*. *Transactions of the Linnean Society of London* 16: 493-497.
- Thomason JC, Brown BE. 1986. The cnidom: an index of aggressive proficiency in scleractinian corals. *Coral Reefs* 5: 93-101.
- Turner SJ. 1994. The biology and population outbreaks of the corallivorous gastropod *Drupella* on Indo-Pacific reefs. *Oceanography and Marine Biology: An Annual Review* 32: 461-530.
- Verrill AE. 1864. List of the polyps and corals sent by the Museum of Comparative Zoology to other institutions in exchange, with annotations. *Bulletin of the Museum of Comparative Zoology* 1: 29-60.
- Voogd NJ de, Cleary DFR, Hoeksema BW, Noor A, Van Soest RWM. 2006. Sponge betadiversity in the Spermonde Archipelago, Indonesia. *Marine Ecology Progress Series* 309: 131-142.
- Waheed Z, Hoeksema BW. 2013. A tale of two winds: species richness patterns of reef corals around the Semporna peninsula, Malaysia. *Marine Biodiversity*. doi: [10.1007/s12526-012-0130-7](https://doi.org/10.1007/s12526-012-0130-7)
- Yamashiro H, Nishihira M. 1995. Phototaxis in Fungiidae corals (Scleractinia). *Marine Biology* 124: 461-465.
- Yamashiro H, Nishihira M. 1998. Experimental study of growth and asexual reproduction in *Diaseris distorta* (Michelin, 1843), a free-living fungiid coral. *Journal of Experimental Marine Biology and Ecology* 225: 253-267.
- Zahn LP. 1980. *Living together in the sea*. TFH Publications, Neptune.

Received: 21 May 2012

Revised and accepted: 17 December 2012

Published online: 29 January 2013

Editor: R.W.M. van Soest