

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

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### 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.

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### 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

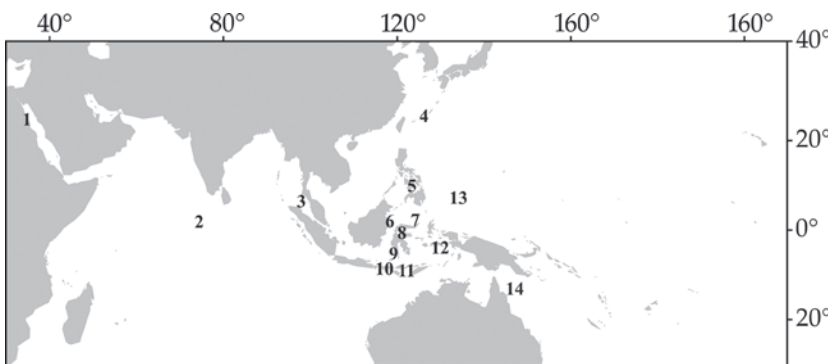


Fig. 1. Research localities in the Indo-West Pacific: 1. Marsha Shagra and Marsa Nakari, c. 350 km S of Hurghada, Egypt; 2. Vilamendhoo Isl., Ari Atoll, Maldives; 3. PhiPhi Isl., Krabi, W Thailand; 4. Okinawa, Rykyu Isl., S Japan; 5. Cebu, Central Philippines; 6. Berau Isl., E Kalimantan, Indonesia; 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.

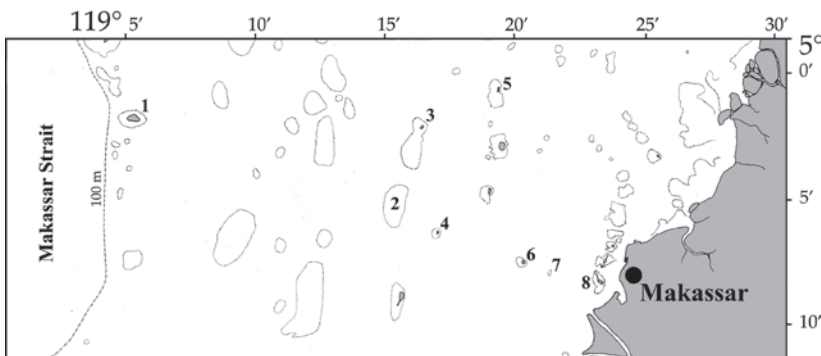


Fig. 2. Research sites in the southern part of the Spermonde Archipelago, SW Sulawesi, Indonesia, consisting of patch reefs and a barrier reef: 1. Langkai; 2. Kapodasang (shoal); 3. Bone Tambung; 4. Kudingareng Keke; 5. Bone Batang; 6. Samalona; 7. Bone Baku (shoal); 8. Lae-Lae.

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

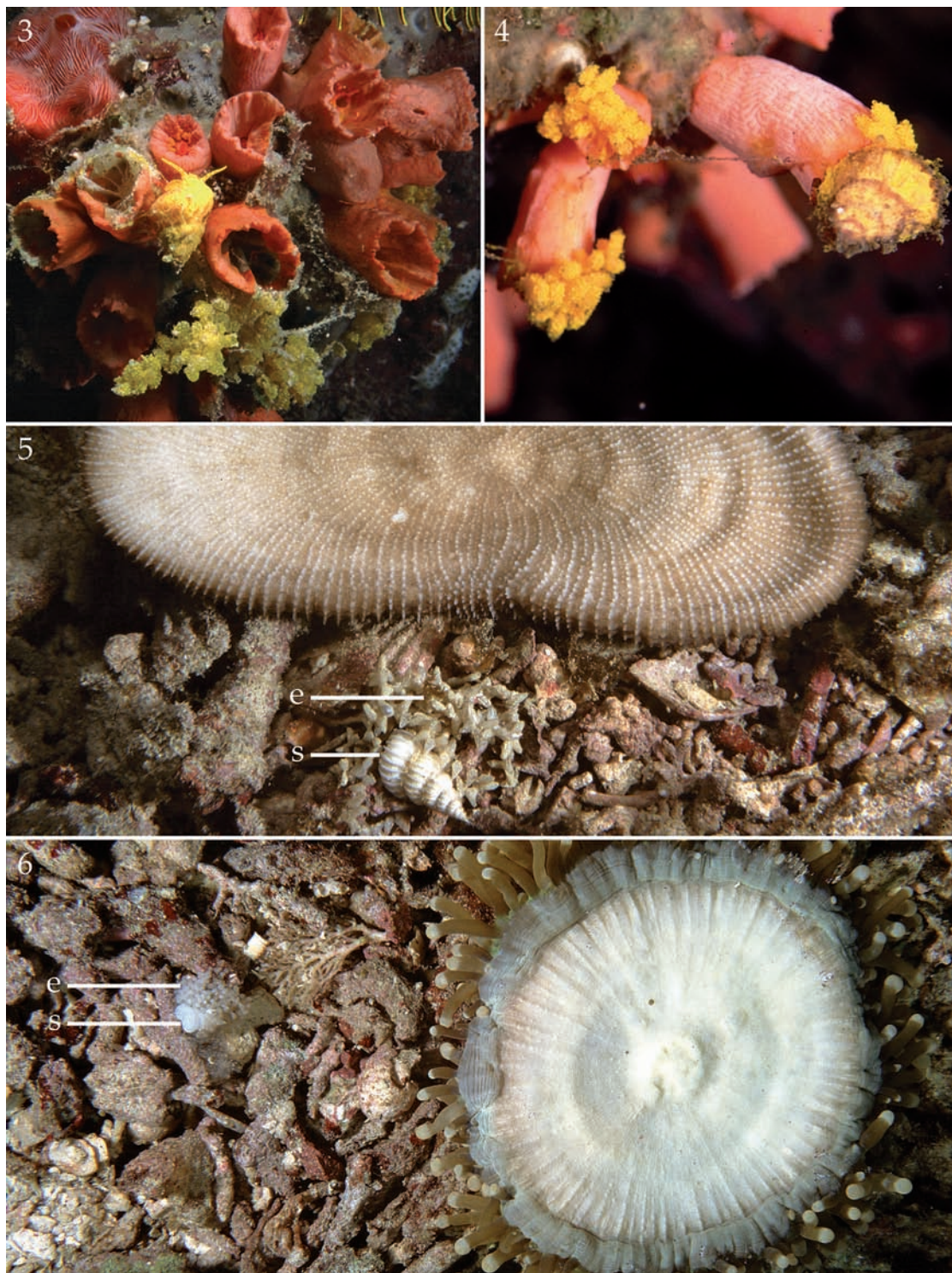
species live in environments that are usually avoided by divers, *e.g.* at relatively deep (> 25 meter) reef bases or shallow (< 2 meter) slopes and flats, or in areas with strong currents, murky water and sandy bottoms (Hoeksema, 2012a).

### *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*

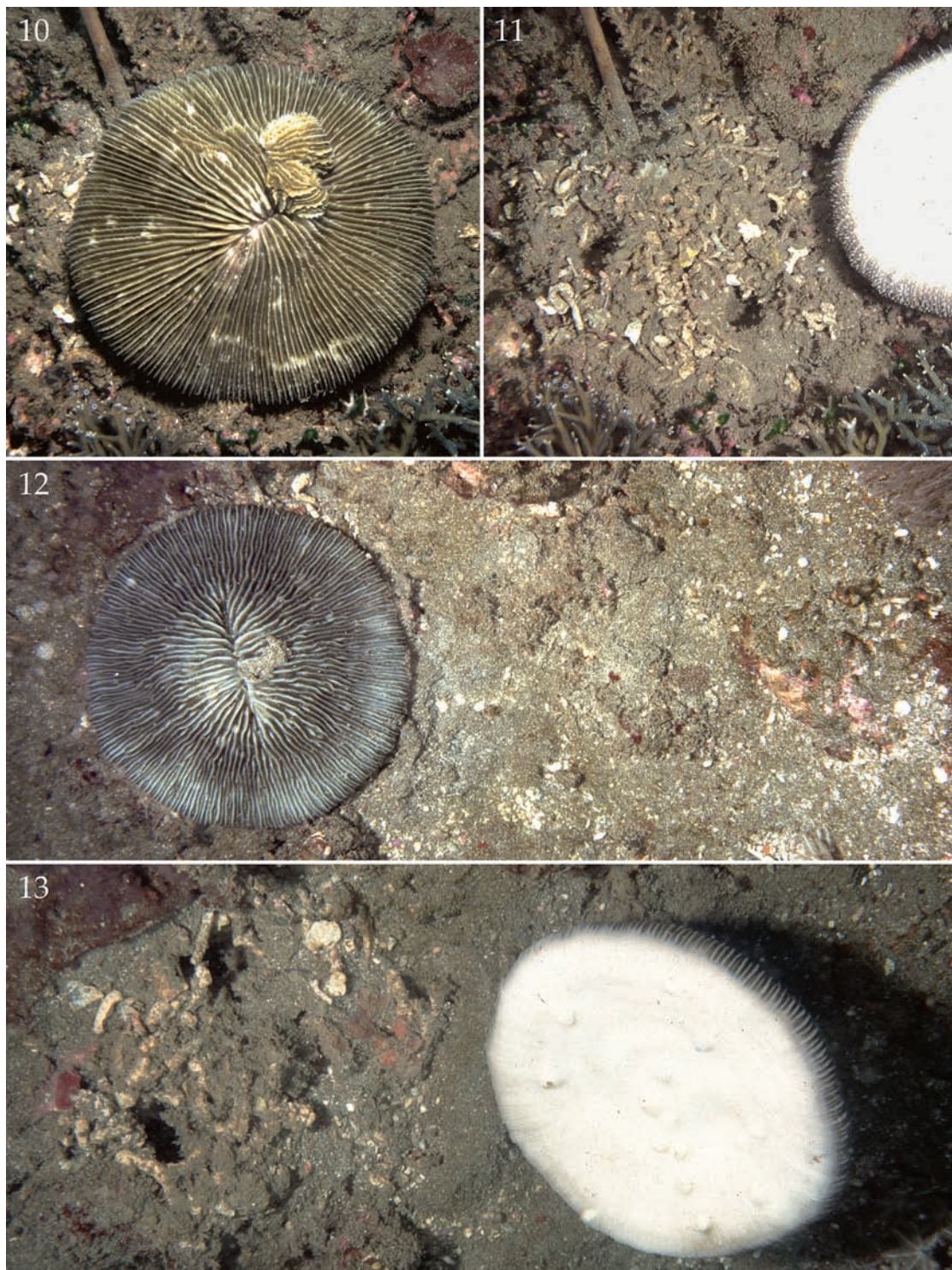
In the Spermonde Archipelago (Fig. 2; locality 9 in Fig. 1) mushroom corals were surveyed in belt transects. This was done at seven sites on five coral reefs that vary in mushroom coral fauna, depending on their distance from the coastline (see Hoeksema, 2012a): W Lae-Lae, W Bone Baku, E Samalona, W 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.





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 cm<sup>2</sup>, 24 quadrants of 30×30 cm<sup>2</sup>, 24 quadrants of 20×35 cm<sup>2</sup> and 24 quadrants of 25×40 cm<sup>2</sup>, 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 cm<sup>2</sup>) were put in upright position in the 22×25 cm<sup>2</sup> quadrants. In addition, 24 corals of *Lithophyllon repanda* (size class 100-150 cm<sup>2</sup>) were placed in 30×30 cm<sup>2</sup> quadrants, 24 *Herpolitha limax* corals (size class 100-200 cm<sup>2</sup>) were placed in 20×35 cm<sup>2</sup> quadrants, and 24 *H. limax* specimens (size class

200-300 cm<sup>2</sup>) were placed in 25×40 cm<sup>2</sup> 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.*  $\leq 10$  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

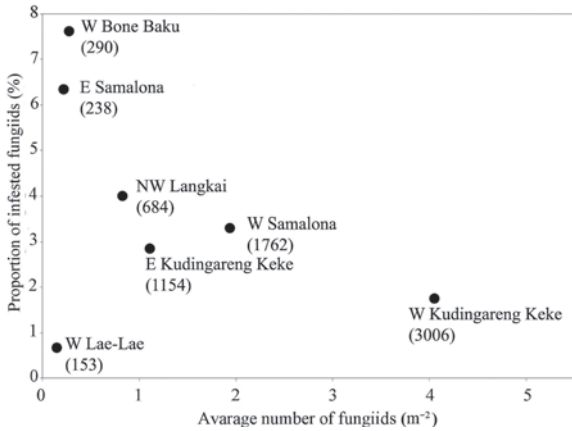


Fig. 18. Infestation rates of mushroom corals (%) plotted against mushroom coral density in the Spermonde Archipelago, SW Sulawesi, Indonesia; n values are indicated (in brackets).

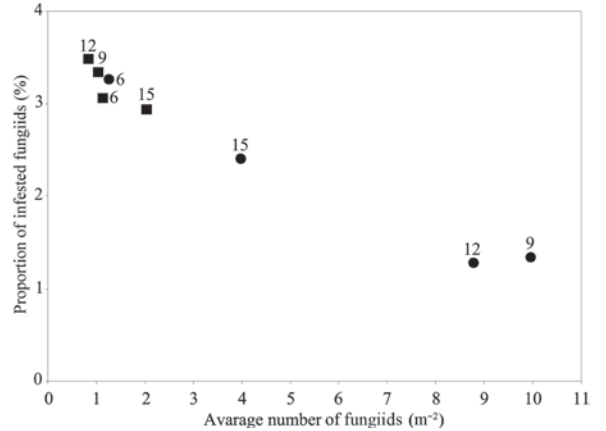


Fig. 19. Infestation rates of mushroom corals by *Epifungium ulu* (%) plotted against mushroom coral density along transects at 6, 9, 12 and 15 m depth on the east (squares) and west (dots) side of Kudingareng Keke Island, SW Sulawesi, Indonesia (see Fig. 2). Total n=3,671 corals; a minimum number of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

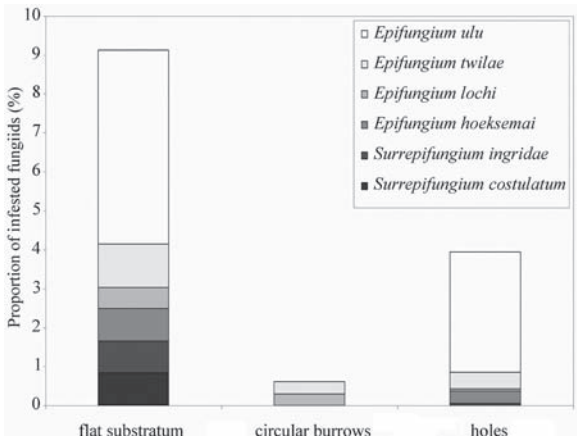


Fig. 20. Percentages of fungiid corals on three substrate types in the Spermonde Archipelago: on flat sediment (n=362), on sediment with circular burrows (n=329) or with crevices (n=1,620); each of which were infested by *Surrepifungium costulatum* (n=3), *S. ingridae* (n=5), *Epifungium adgranulosa* (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).

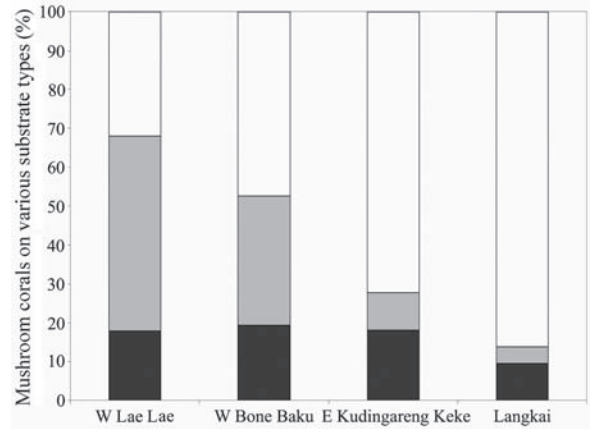


Fig. 21. Percentages of fungiid corals at W Lae-Lae (n=184), W Bone Baku (n=289), E Kudingareng Keke (n=1,154) and Langkai (n=84), on flat sediment (white), sand with burrows (grey) or sediment with burrows (black).

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

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 spawns 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

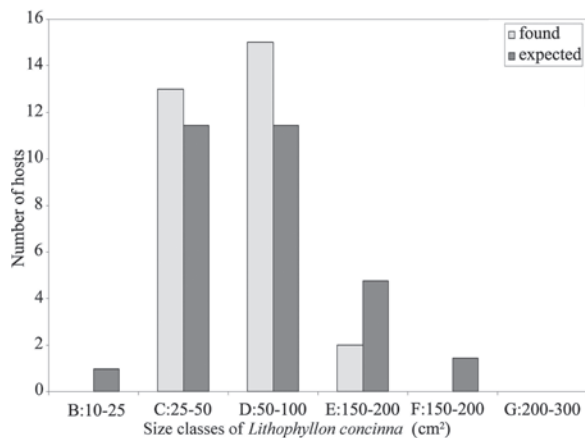


Fig. 22. Numbers of specimens of *Lithophyllon concinna* in the size classes 10-25, 25-50, 50-100, 100-150, 150-200 and 200-300 cm<sup>2</sup> observed as infested by *Epifungium ulu* in the Spermonde Archipelago (see Fig. 2), next to the expected numbers when infestations are random, based on the coral 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*

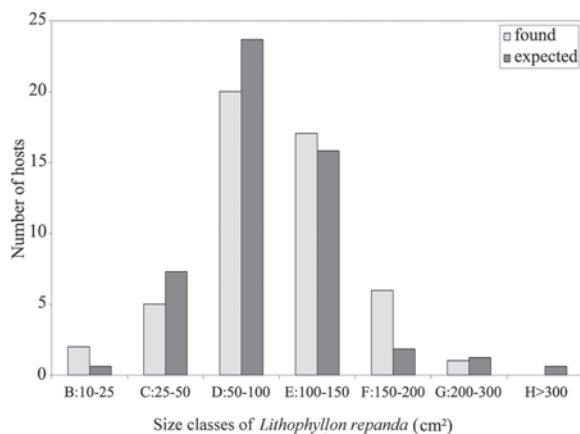


Fig. 23. Numbers of specimens of *Lithophyllon repanda* in the size classes 10-25, 25-50, 50-100, 100-150, 150-200, 200-300 and >300 cm<sup>2</sup> observed as infested by *Epifungium ulu* in the Spermonde Archipelago (see Fig. 2), next to the expected numbers when infestations are random, based on the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

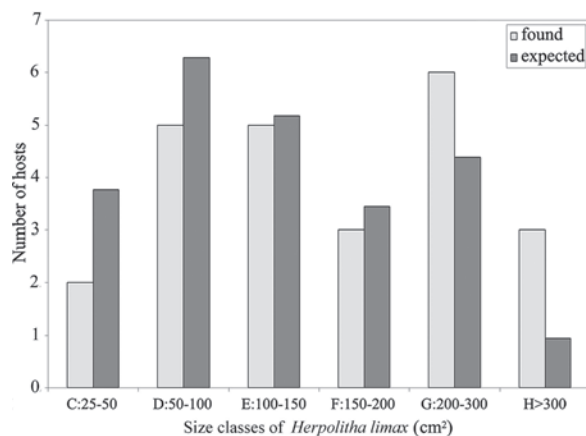


Fig. 24. Numbers of specimens of *Herpolitha limax* in the size classes 10-25 cm<sup>2</sup>, 25-50 cm<sup>2</sup>, 50-100 cm<sup>2</sup>, 100-150 cm<sup>2</sup>, 150-200 cm<sup>2</sup>, 200-300 cm<sup>2</sup> and >300 cm<sup>2</sup> observed as infested by *Epifungium twilae* in the Spermonde Archipelago (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*

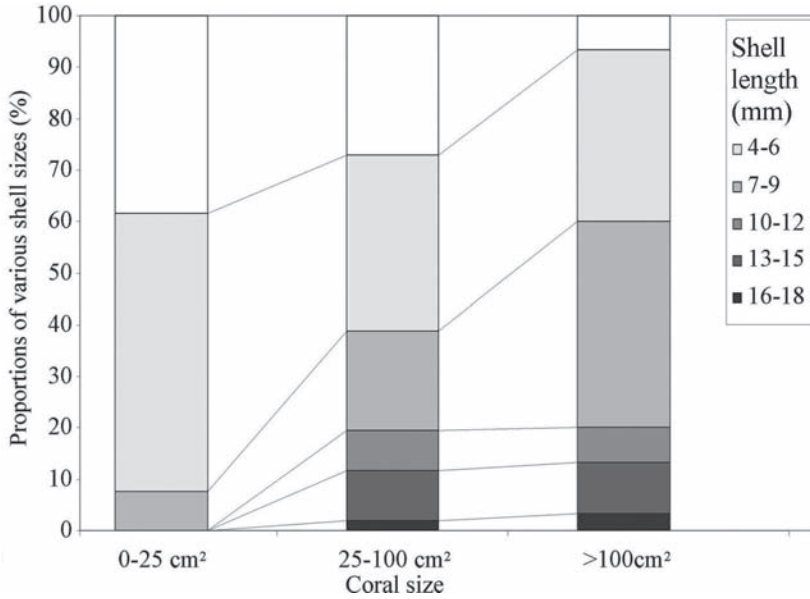


Fig. 25. The maximum shell lengths found in *Epifungium ulu* samples (n=146) and their distributions in the size classes 0-25 cm<sup>2</sup> (n=13), 25-100 cm<sup>2</sup> (n=103) and >100 cm<sup>2</sup> (n=30) of their coral hosts, in the Spermonde Archipelago, Indonesia.

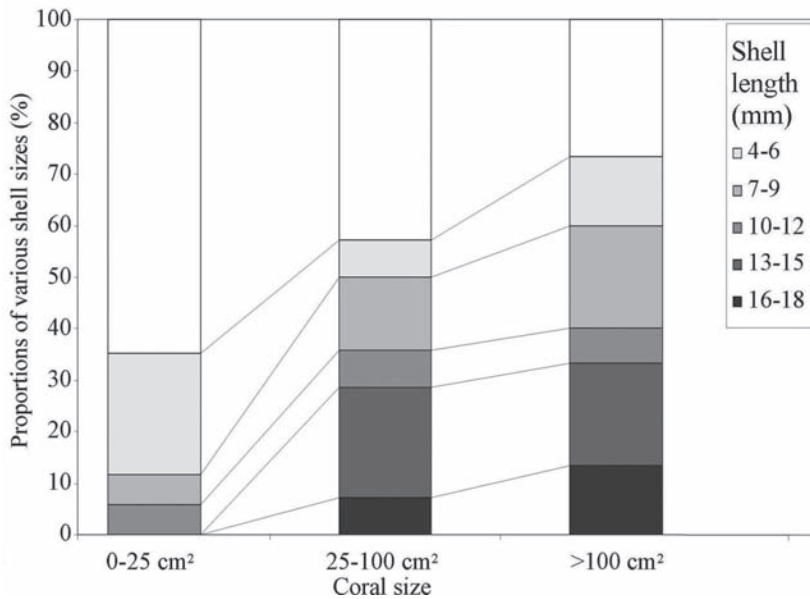


Fig. 26. The maximum shell lengths found in *Epifungium twilae* samples (n=46) and their distributions in the size classes 0-25 (n=17), 25-100 (n=14) and >100 cm<sup>2</sup> (n=15) of their coral hosts in the Spermonde Archipelago, Indonesia.

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.

*Overturned host corals*

No mushroom coral in overturned position (n = ~2,000) was observed to be infested by epitoniids. One single overturned 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 <sup>2</sup>		50-150 cm <sup>2</sup>		>150 cm <sup>2</sup>	
<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 cm<sup>2</sup>, 50-150 cm<sup>2</sup> and >150 cm<sup>2</sup> (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 cm<sup>2</sup>.

Fungiid species	Size class (cm <sup>2</sup> )	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>Pleuroactis gravis</i>	25-100	1.6	251	7
<i>Pleuroactis 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

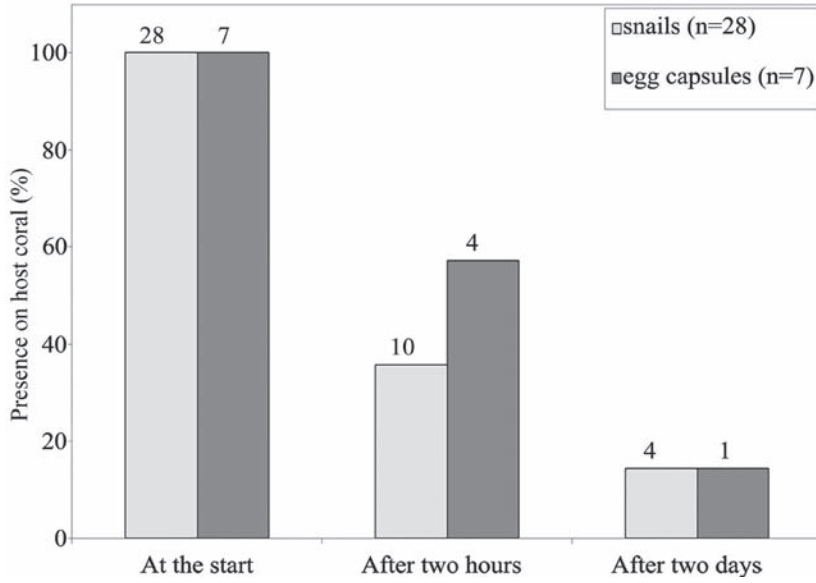


Fig. 27. Numbers of snails and spawns of *Epifungium ulu* that remained on the underside of the host corals after overturning; after two hours and after two days, off W Langkai (see Fig. 2).

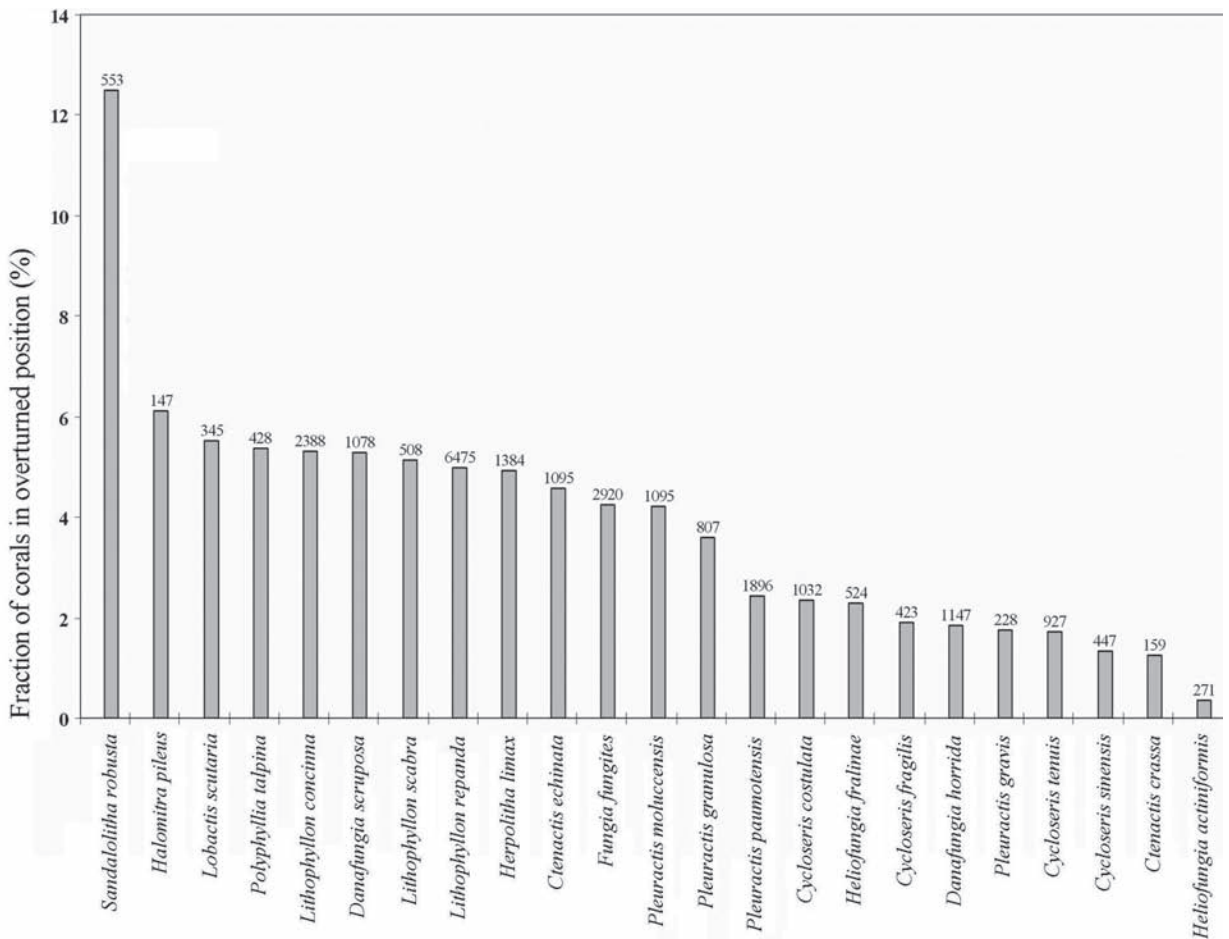


Fig. 28. Percentages of fungiid populations observed in overturned position in the Spermonde Archipelago (Fig. 2); n values are indicated per species.



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 wentletrap 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 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 Franssen, 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 epizoic 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*.

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