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Habitat preferences of 20 Indo-West Pacific wentletrap species (Gastropoda: Epitoniidae) associated with scleractinian corals

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Abstract

By a search of about 60,000 corals for wentletrap infestations, this study revealed several distinctly different epitoniid life strategies in the Indo-West Pacific. The 20 species that were found to be coral-associated were either generalists or specialists. They differed also in their position relative to their hosts, in their substrate preferences and in their host-size preferences. No preferences for depth were found.

Infestation rates are negatively correlated with coral densities, which may indicate that epitoniid veligers can actively find and go to their preferential hosts.

Indirect proof was found that burrowing shrimps with burrows underneath mushroom corals, eat or at least remove any epitoniid that they come across. Fishes, like wrasses and damselfishes, were seen speeding towards epitoniids to eat them, the moment they were exposed artificially.

Contents

Introduction

Wentletraps (Gastropoda: Epitoniidae) in general are permanent ectoparasites or foraging predators that are mostly associated with Actiniaria (Robertson, 1963, 1966, 1983; Perron, 1978; Schimek, 1986; den Hartog, 1987), and less commonly with Zoanthidea (Robertson, 1981; Zahn, 1980) or scleractinian corals (Dendrophylliidae, Euphylliidae, Fungiidae) (A. Gittenberger and E. Gittenberger, 2005). Usually, the exact nature of the various associations is not clear. The snails may use their coelenterate hosts as a food source, for shelter against predators and turbulence, or as a relatively safe spawning site. Due to their hidden position, observations of actual feeding epitoniid snails are scarce (den Hartog, 1987; Perron, 1978), although the presence of nematocysts in their gut contents serves as direct proof for predatory or parasitic behaviour (Perron, 1978). Apparently, the nematocyst venom does not act as a fatal poison for the specialized snails.

The life-cycle of epitoniids starts within an egg-capsule with the development from an undifferentiated egg to a hatching individual, followed by a free-swimming veliger stage, and eventually the settling as a crawling snail (Robertson, 1983, 1994; Bell, 1985; Collin, 2000; A. Gittenberger, 2003). *Epifungium ulu* (Pilsbry, 1921) can go through a complete life-cycle within 36 days (Bell, 1985).

For a good understanding of the biodiversity and ecological complexity of reef communities, species
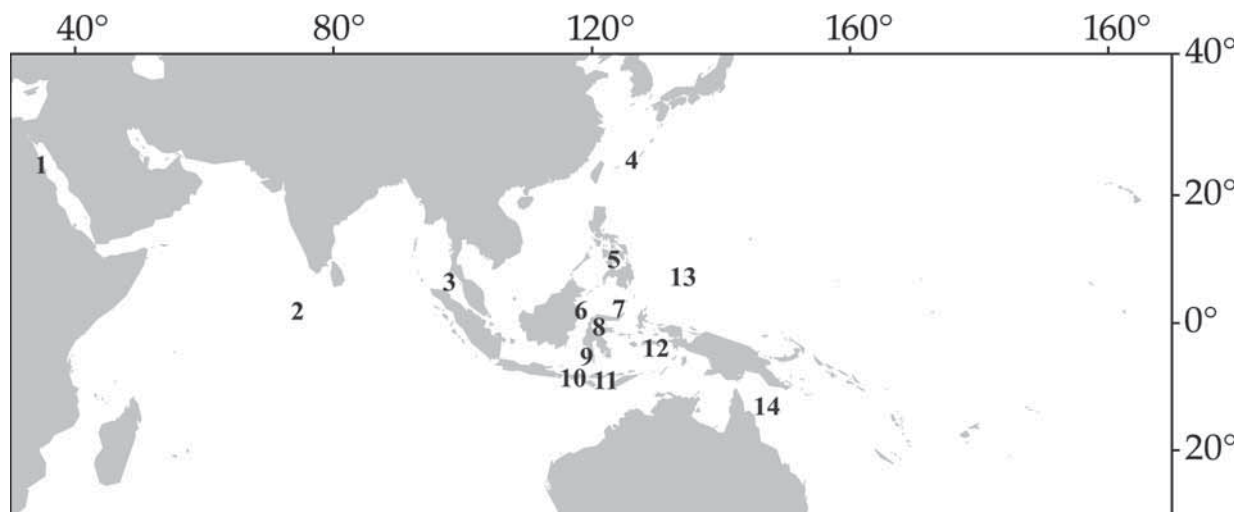
Fig. 1. The Indo-West Pacific region, from the Red Sea to the Hawaiian Archipelago. Research localities are indicated: 1. Marsha Shagra and Marsa Nakari, c. 350 km S of Hurghada, Egypt; 2. Vilamendhoo Island, Ari Atoll, Maldives; 3. PhiPhi Islands, Krabi, Thailand; 4, Okinawa, Rykyu Islands, S Japan; 5. Cebu, Visayas, Central Philippines; 6. Berau Islands, E Kalimantan, Indonesia; 7. Siladen and Bunaken Islands, N Sulawesi, Indonesia; 8. Togian Islands, Central Sulawesi, Indonesia; 9. Spermonde Archipelago, SW Sulawesi, Indonesia; 10. Bali, Indonesia; 11. Flores, Indonesia; 12. Ambon, Indonesia; 13. Palau; 14. Great Barrier Reef, Australia.

interdependencies and their evolutionary histories should be investigated. Hard corals and their parasitic wentletraps are ideal models to study such aspects. Morphological, molecular (A. Gittenberger et al., chapter 8) and ecological studies have shown that a large, partly cryptic, adaptive radiation has taken place among these epitoniids, most of which are highly specialized ecto-parasites (A. Gittenberger et al., 2000; A. Gittenberger, 2003; A. Gittenberger and E. Gittenberger, 2005). Although their identities as separate gene pools can be demonstrated convincingly by molecular data (A. Gittenberger et al., chapter 8), shell shape and sculpture are only partially diagnostic for these gastropod species because of sometimes broadly overlapping character states. In several cases, the habitat and additional morphological characters of the operculum, the jaw, the radula and the spawn, characterize the conchologically cryptic species much better than the more easily accessible shell characters (A. Gittenberger and E. Gittenberger, 2005). These findings contradict the hypothesis of Bouchet and Warén (1986: 469) that a low amount of variation among epitoniids in general may reflect a low degree of specialization. Coral-associated epitoniids are more diverse than previously thought and their cryptic adaptive radiation has remained unnoticed for a long time. Taking recent taxonomic results into account, this

article aims at a better insight in the ecological differentiation of coral-associated epitoniids and their evolutionary history in the Indo-West Pacific.

We focus on the following research questions: [1] Where are the epitoniid snails found, relative to their coral hosts? [2] Is there a relationship between the infestation percentages and the upside down or right side up position of the mushroom corals? [3] Is the substratum on which the coral is found related to the chance of it being infested? [4] Which coral species are associated with particular gastropod parasites? [5] What are the infestation percentages of the coral species populations? [6] Are infestation percentages related to depth? [7] Are infestation percentages, parasite sizes and presence/absence of egg-capsules related to host-sizes? [8] What are natural predators of the epitoniids? [9] What, if any, conchological characters may be linked to the adaptive radiation of the various epitoniid species?

Habitat preferences are described for the 20 species of coral-associated epitoniids that are known, viz. *Epidendrium aureum* A. Gittenberger and E. Gittenberger, 2005; *E. sordidum* A. Gittenberger and E. Gittenberger, 2005; *Epifungium adgranulosa* A. Gittenberger and E. Gittenberger, 2005, *E. adgravis* A. Gittenberger and E. Gittenberger, 2005, *E. adscabra* A. Gittenberger and E. Gittenberger, 2005, *E. hartogi*
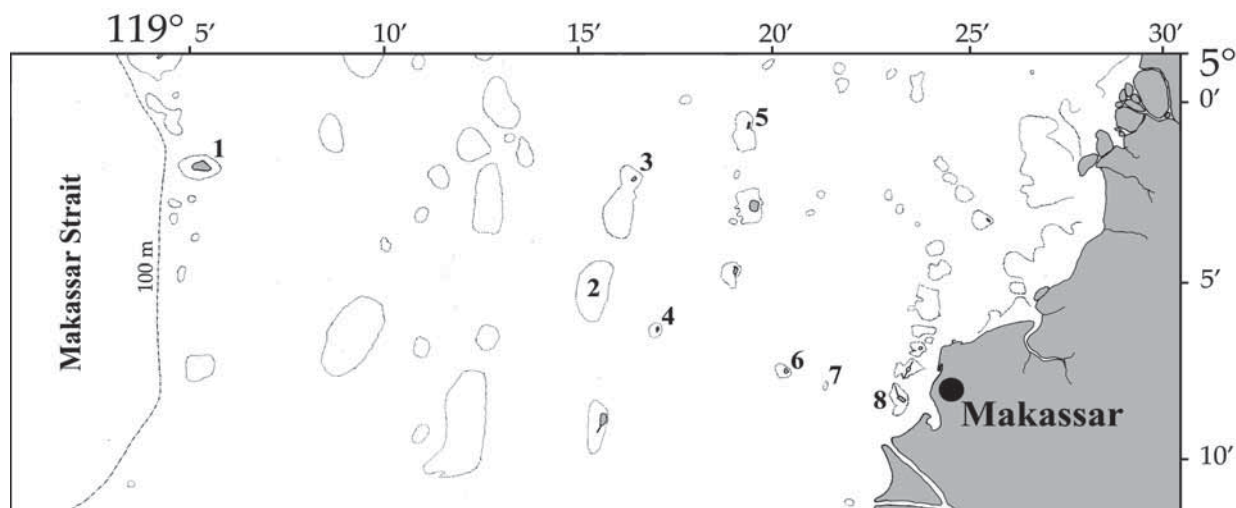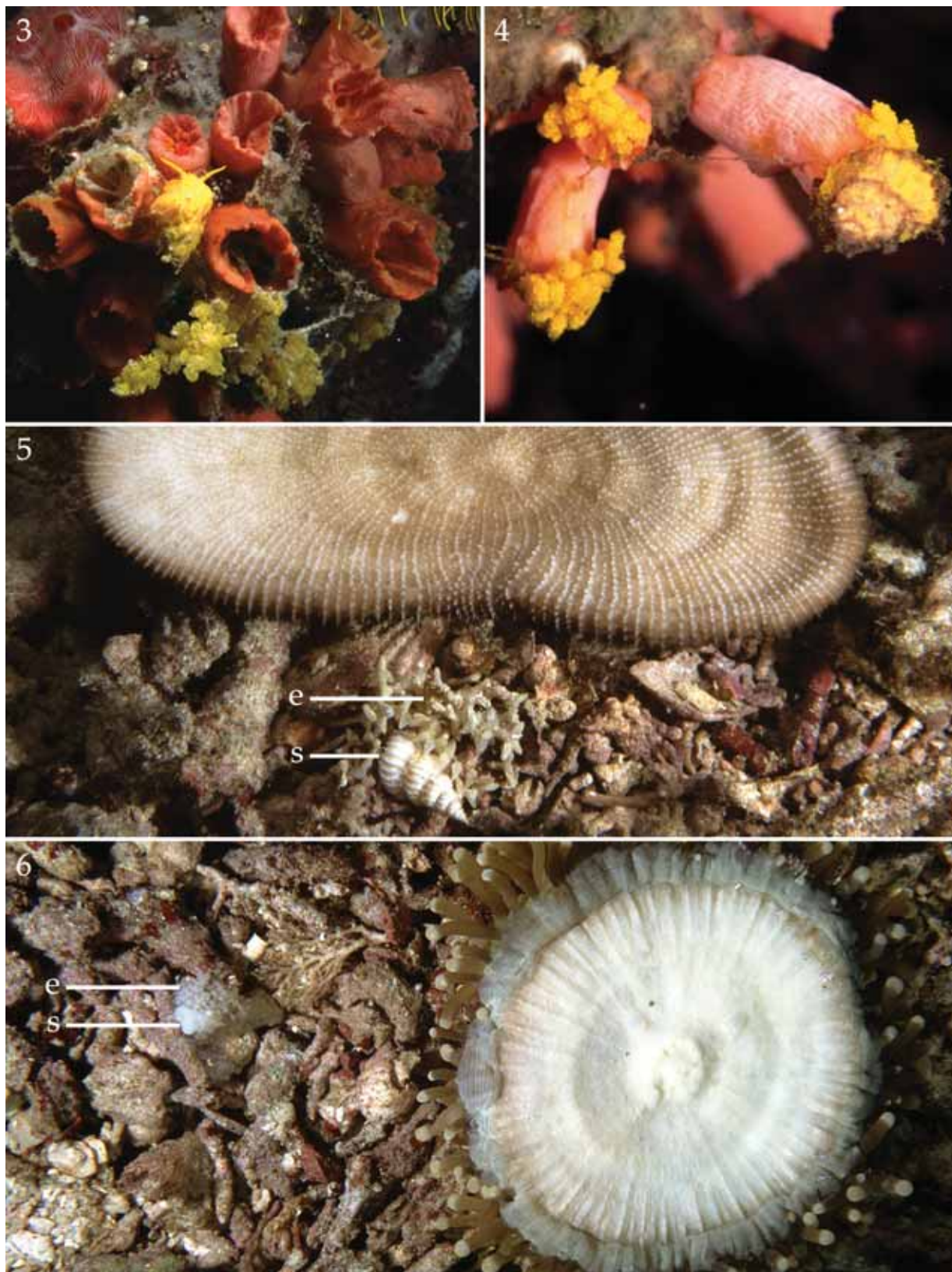
Fig. 2. The southern part of the Spermonde Archipelago, SW Sulawesi, Indonesia, consisting of patch reefs and a barrier reef: Research sites: 1. Langkai Island; 2. Kapodasang (shoal); 3. Bone Tambung Island; 4. Kudingareng Keke Island; 5, Bone Batang Island; 6. Samalona Island; 7, Bone Baku (shoal); 8. Lae-Lae Island.

(A. Gittenberger, 2003), *E. hoeksemai* (A. Gittenberger and Goud, 2000), *E. lochi* (A. Gittenberger and Goud, 2000), *E. marki* A. Gittenberger and E. Gittenberger, 2005, *E. nielsi* A. Gittenberger and E. Gittenberger, 2005, *E. pseudolochi* A. Gittenberger and E. Gittenberger, 2005, *E. pseudotwilae* A. Gittenberger and E. Gittenberger, 2005, *E. twilae* (A. Gittenberger and Goud, 2000), *E. ulu* Pilsbry, 1921, *Epitonium crassicostatum* A. Gittenberger and E. Gittenberger, 2005, *E. graviarmatum* A. Gittenberger and E. Gittenberger, 2005, *Surrepifungium costulatum* (Kiener, 1839), *S. ingridae* (A. Gittenberger and Goud, 2000), *S. oliverioi* (Bonfitto and Sabelli, 2001) and *S. patamakanthini* A. Gittenberger and E. Gittenberger, 2005. Most of these species are associated with only one or a restricted number of coral species and are widespread. Their distributions are similar to those of their hosts, i.e. ranging from the Red Sea or the Maldives, Thailand, Indonesia and Palau to Australia (A. Gittenberger and E. Gittenberger, 2005). Only *S. ingridae* seems to be an exception to this rule. That species is very common in the West Pacific, off the eastern coast of the West Malaysian peninsula, Palau and Sulawesi, but it is not known from anywhere in the Indian Ocean. In contrast, the closely related *S. costulatum*, *S. patamakanthini* and *S. oliverioi* do show more widespread Indo-West Pacific distributions (A. Gittenberger and E. Gittenberger, 2005).

Most coral-associated wentletrap species are found with mushroom corals (Fungiidae), which were the main focus of the present research project. Fungiids have various advantages over other coral groups as model organisms for field studies. The family consists of over 45 species and is abundant throughout the Indo-West Pacific (Hoeksema, 1989b, 1993a, 1993b, 1993d; Hoeksema and Putra, 2002). These corals seem to have a high survival rate during bleaching events (Hoeksema, 1991a), which is also important for the occurrence of associated animals that depend on their survival.

Most mushroom corals are free-living in the adult stage due to their breakage from an early attachment stalk. As a result of the detachment, they may tumble downward along slopes, bottom-dwelling animals may push them, currents and waves may transport them, and they may even move themselves (Hubbard, 1972; Jokiel and Cowdin, 1976; Chadwick, 1988; Chadwick-Furman and Loya, 1992; Yamashiro and Nishihira, 1995; Plusquelllec et al., 1999). This mobility may help mushroom corals to disperse in order to reach favourable habitats, it may prevent burial in soft sediments, and it may have a function in avoiding competition for space (Hoeksema, 1989a, 1993c, 2004; Chadwick, 1988; Chadwick-Furman and Loya, 1992; Yamashiro and Nishihira 1995). The mobility depends on the weight and size of the free-living corals (Hoeksema, 1991b). The mobility of the host may also have implications for the survival of

the ecto-parasitic snails. Movements may cause the parasitic snails occurring underneath to become temporarily more exposed to predators. On the other hand, mobility may also prevent a burial in sediment which would be lethal to both the coral host (Gilmour, 2002a) and its associates. Large corals cannot move easily and offer more surface area for parasites.

These detached corals can easily be handled for the inspection for parasites without causing damage to the corals themselves and their environment.

Material and methods

Fieldwork localities and general methods

About 800 hours scuba-diving were spent underwater by the authors, searching approximately 60,000 stony corals for epitoniids in the Indo-West Pacific, i.e. off Egypt (Red Sea), the Maldives, W Thailand (Andaman Sea), W Malaysia (South China Sea), S Japan, Palau, the Philippines, Indonesia and Australia (fig. 1). Most fieldwork periods lasted one week to a month. 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 is located in the centre of maximum marine biodiversity (Hoeksema, 1993d, 2004a; Hoeksema and Putra, 2002). Off Makassar the coral diversity and densities were higher than at any of the other study localities. Therefore that archipelago was considered the most suitable place for more detailed field studies. Concentrating on free-living mushroom corals, a special effort was made to search all species within this family, including rare or less common ones like the *Fungia* (*Cycloseris*) species, *F.* (*Danafungia*) *fralinae* Nemenzo, 1955, *F.*

Figs 3-6. Habitats of Epitoniidae encountered. 3, *Epidendrium aureum*, snail with egg-capsules on substrate next to dendrophylliid coral host; 4, *Epidendrium sordidum*, shell overgrown with hydroids, together with egg-capsules on dendrophylliid coral host; 5, *Surrepifungium costulatum*, snail with egg-capsules on substrate, revealed by turning the host coral upside down, i.e. a specimen of *Ctenactis echinata*; 6, *Epifungium hoeksemai*, snail with egg-capsules on substratum, revealed by turning the host coral upside down, i.e. a specimen of *Heliofungia actiniformis*. 3-4, Ari Atoll, Maldives; 5-6, SW Sulawesi, Indonesia. Abbreviations: e, egg-capsules; s, snail.

(*Verrillofungia*) *spinifer* Claereboudt and Hoeksema, 1987, *Heliofungia actiniformis* (Quoy and Gaimard, 1833), *Sandalolitha dentata* Quelch, 1884, *Halomitra clavator* Hoeksema, 1989, and *Zoopilus echinata* Dana, 1846. Most of these species live in environments that are usually avoided by divers, e.g. at relatively deep (up to 45 meter) or shallow (< 2 meter) slopes and flats, in areas with strong currents or murky water, or on sandy bottoms.

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, substratum characteristics, and position of the parasite relative to its host. The fungiids were identified twice, independently by both authors, after photographs and/or specimens. Dr. H. Ditlev identified the euphylliids from photographs. The dendrophylliids (*Tubastrea* and *Dendrophyllia* species) were not identified to species level. The first author identified the epitoniid species. The position of a parasite was recorded as 'buried in sand' (no illustration), '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, 1989a, 1991b, 2004b), an upside down position of the fungiid host (figs 5-9, 11, 13-14, 16-17) was recorded opposite the more regular orientation (figs 10, 12), since the former position may minimize the survival of snails because of their exposure to predators. The substratum was characterized as (1) 'flat' for an even bottom of sand, coral or stone, without any holes or crevices (fig. 12; to the right of the fungiid coral), as (2) 'burrow' when there was at least one circular burrow (figs 11, 13-14), possibly made by a crustacean (e.g. fig. 15), or as (3) 'holes' where holes and crevices occurred but no burrows (fig. 6).

Transect studies

In the Spermonde Archipelago (fig. 2; locality 9 in fig. 1) mushroom corals were searched for epitoniids

along horizontal transects at 3, 6, 9, 12, 15 and 18 m depth. This was done at seven sites on five coral reefs, at various distances from the coastline, i.e. at W Lae-Lae Island, W Bone Baku reef, E Samalona Island, W Samalona Island, E Kudingareng Keke Island, W Kudingareng Keke Island and NW Langkai Island, respectively (fig. 2). A transect line was marked by a measuring tape, attached to the bottom at 3, 6, 9, 12, 15 and 18 m depth. Mushroom 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 observed along the first 100 m, the transect length was extended to reach this number. For each transect and site fungiid densities and infestation percentages were calculated. The infestation percentages were plotted against the fungiid densities. To get an indication of mushroom coral species composition for each locality and depth, about 4500 fungiids were identified and counted along the transects. Based on the resulting species compositions and the total number of corals in the transects, an approximate number of specimens that was searched for each fungiid species was calculated. These approximate numbers were used to calculate the infestation percentages for the most common epitoniid species, i.e. *Epifungium ulu*, *E. pseudotwilae* and *E. twilae*.

Measuring coral-sizes

During the three-months fieldwork period in 1997 in the Spermonde Archipelago, the size of all infested corals was measured. This was done by comparing these with the outlines of surfaces of 10, 25, 50, 100, 150, 200 and 300 cm², drawn on boards, after which the specimens were recorded as belonging to one of those size-classes. To fit all fungiid shapes, five boards were made for corals varying from round to elongated, i.e. with length/width indexes of 1, 1.5, 2,

Figs 7-9. Habitats of Epitoniidae encountered (continued). 7, *Epifungium nielsi*, snail with egg-capsules on substratum, revealed by overturning the host coral, i.e. *Fungia paumotensis*; 8, *Epifungium pseudolochi*, snail with egg-capsules on coral, revealed by overturning the host, i.e. *Fungia costulata*; 9, *Epifungium twilae*, snail with egg-capsules on coral, revealed by overturning the host, i.e. *Herpolitha limax*. 7, Ari Atoll, Maldives; 8, Marsa Nakari, 350 km S of Hurghada, Egypt; 9, SW Sulawesi, Indonesia.

3 and 4. Off W Kudingareng Keke Island, the surface size of all specimens of *Fungia* (*Verrillofungia*) *concinna*, *F.* (*V.*) *repanda* and *Herpolitha limax* at 3-18 m depth, was measured to get an indication of the size distributions within their populations. These three species were chosen because they were abundant at all locations and the most common hosts of the abundant epitoniids *Epifungium ulu* and *E. twilae*. The null-hypothesis, infestations by *E. ulu* and *E. twilae* are not related to coral-size, was tested with Chi-square against three alternative hypotheses, i.e. [1] coral-size influences the probability of being infested; [2] host-size is positively correlated with parasite-size; [3] host-size is positively correlated with the percentage of cases of infestation with egg-capsules present.
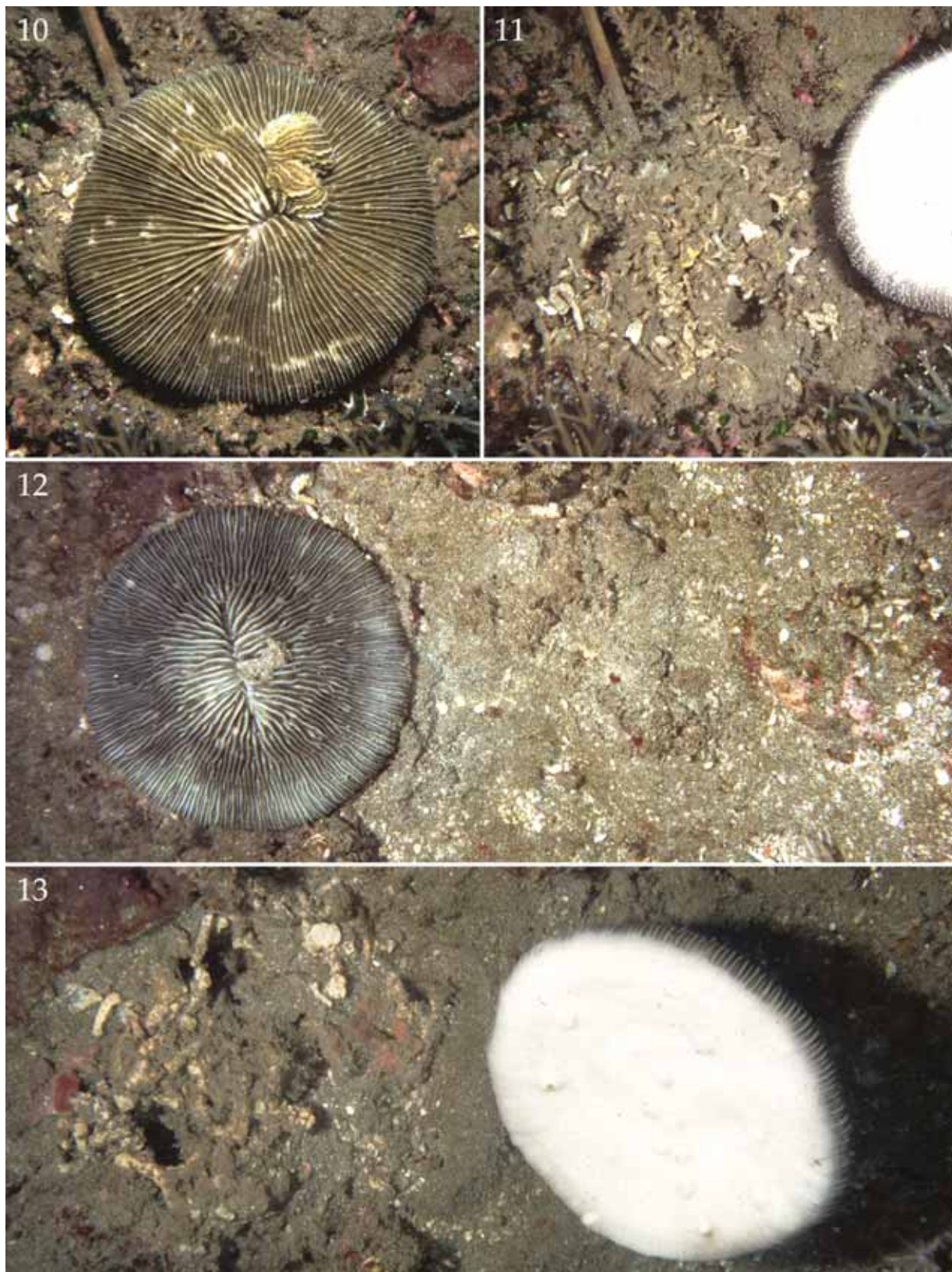
Turned over hosts and epitoniid predators

Free-living fungiid corals are known to occasionally turn around (see e.g. Hoeksema, 2004b). To investigate how this overturning may affect epitoniid snails that live hidden underneath the corals, 16 hosts with snails and/or egg-capsules of *Epifungium ulu* were carefully turned upside down NW of Langkai Island (for site, see fig. 2), preventing accidental detachment of the parasites. After two hours and after two days the numbers of epitoniids and egg-capsule clutches that were still on their hosts were counted.

Two corals with snails and egg-capsules of *Epifungium ulu* and one with snails and egg-capsules of *E. twilae* were placed upside down, next to each other, off W Kudingareng Keke Island (for site, see fig. 2). The specimens were observed from a distance of about 3 meters for 30 minutes to check which animals would attack them. These epitoniid species were selected since their shells are similar in height but not in width, i.e. shells of *E. twilae* are relatively much broader (fig. 9; A. Gittenberger and E. Gittenberger, 2005). Snails with broader shells might be more difficult to grasp depending on the size of the mouths of the potential predator fishes. Additionally, all animals that were seen eating or attacking epitoniids at any time during one of the field surveys were recorded and photo-graphed whenever possible.

It has been hypothesized that the overturning of a fungiid coral from an upright position to upside down and back again, depends upon its size and form (Hoeksema, 1989a). 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. *Fungia* (*D.*) *horrida*, *F.* (*D.*) *scruposa*, *F.* (*F.*) *fungites*, *F.* (*V.*) *concinna*, *F.* (*V.*) *repanda* and *F.* (*V.*) *scabra*, and oval, viz. *F.* (*L.*) *scutaria*, *F.* (*P.*) *gravis* and *F.* (*P.*) *paumotensis*, to elongated, viz. *Ctenactis echinata*, *Herpolitha limax* and *Polyphyllia talpina*.

With a waterproof pen, 360 squares of 22×25 cm, 24 squares of 30×30 cm, 24 squares of 20×35 cm and 24 squares of 25×40 cm, were drawn and numbered on two orange, plastic cloths, which were fastened with pegs to the sea-bottom, at a depth of 18 m, on a slope of on average 15º, at W Kudingareng Keke Island (see fig. 2). For each of the 12 species, 24 specimens (size-class 25-100 cm²) were put in upright position in the 22×25 cm squares. Additionally, 24 corals of *Fungia* (*Verrillofungia*) *repanda* (size-class 100-150 cm²) were placed in 30×30 cm squares, 24 *Herpolitha limax* corals (size-class 100-200 cm²) in 20×35 cm squares, and 24 *H. limax* specimens (size-class 200-300 cm²) in 25×40 cm squares. The corals that proved to have turned after three and after ten days were scored. The experiment was repeated with all corals in upside down position at the start and after four hours and after two days it was recorded how many had turned back. Then the corals were temporarily taken from the water in buckets to measure the length/width ratio and wet weight, after which they were returned to the reef.

More than 100 specimens of each of the 23 most common fungiid species in the Spermonde Archipelago were checked to calculate the percentages of the coral populations that are lying upside down under natural conditions.

Results

General results

About 1.5% of all mushroom corals that were searched (n=60,000) was found with epitoniids.

Figs 10-13. Burrow substrata, SW Sulawesi, Indonesia. 10-11, *Fungia repanda*; 10, in situ; 11, overturned, i.e. revealing two circular burrows; 12-13, *Fungia granulosa*; 12, in situ; 13, overturned, i.e. revealing two circular burrows.

Among the various species the number of infestations varied from a single one to 103. For each of the 20 epitoniid species the number is indicated between brackets: *Surrepifungium costulatum* (103), *S. ingridae* (43), *S. oliverioi* (10) and *S. patamakanthini* (27), *Epidendrium aureum* (52), *E. sordidum* (22), *Epifungium adgranulosa* (20), *E. adgravis* (38), *E. hoeksemai* (34), *E. lochi* (36), *E. nielsi* (83), *E. ulu* (191), *E. adscabra* (22), *E. hartogi* (10), *E. marki* (4), *E. pseudolochi* (5), *E. pseudotwilae* (68), *E. twilae* (98), *Epitonium crassicostatum* (1) and *E. graviarmatum* (1). Of the 870 observed cases of infestation, 283 (32.5%) included egg-capsules. In total 1657 epitoniid specimens were collected, that is on average about two snails per host. Of the c. 2,500 fungiids found upside down, only one was infested and that by epitoniid egg-capsules only. In the transects off SW Sulawesi, 3.7% of all corals (n=7219) were found in association with an epitoniid species, viz. *Epifungium adgranulosa*, *E. adscabra*, *E. hoeksemai*, *E. lochi*, *E. marki*, *E. nielsi*, *E. pseudotwilae*, *E. twilae*, *E. ulu*, *Surrepifungium costulatum*, *S. ingridae* or *S. patamakanthini*.

Coral species and their hosted wentletraps

For the associations that were found per species, see table 1. When a single host coral was found associated with both an *Epifungium* and a *Surrepifungium* wentletrap species, the *Epifungium* was always on the coral while the *Surrepifungium* was on the substratum underneath or had burrowed inside the sediment.

The infestation percentages of the mushroom coral populations in the Spermonde Archipelago, by *Epifungium ulu*, *E. pseudotwilae* and *E. twilae*, are indicated in table 2. Throughout the Indo-West Pacific, *E. ulu* was found to have infested seven, two, one and six corals of *Ctenactis echinata*, *Halomitra pileus*, *Herpolitha limax* and *Sandalolitha robusta*, respectively, while about 8,000, 2,000, 5,000 and 2,000 specimens of these host species were searched. This indicates that the infestation percentages are in general less than 0.3%. The *Halomitra* and *Sandalolitha* infestations were found in Indonesia and Palau, while the *Ctenactis* hosts were predominantly found in Egypt (Red Sea), Indonesia and Palau. The *Herpolitha* infestation was recorded in

Table 1. Epitoniid species and their associated fungiid host species. Abbreviations: FCcos, *Fungia* (*Cycloseris*) *costulata*; FCdis, *F.* (*C.*) *distorta*; FCfra, *F.* (*C.*) *fragiles*; Fcsin, *F.* (*C.*) *sinensis*; FCsom, *F.* (*C.*) *somervillei*; FCten, *F.* (*C.*) *tenuis*; FCvau, *F.* (*C.*) *vaughani*; FWgra, *F.* (*Wellsofungia*) *granulosa*; FPspA, *F.* (*Pleuractis*) sp. A; FPgra, *F.* (*P.*) *gravis*; FPmol, *F.* (*P.*) *mollucensis*; FPpau, *F.* (*P.*) *paumotensis*; FVsca, *F.* (*Verrillofungia*) *scabra*; FVcon, *F.* (*V.*) *concinna*; FVrep, *F.* (*V.*) *repanda*; FVspi, *F.* (*V.*) *spinifer*; FDhor, *F.* (*Danafungia*) *horrida*; FDscr, *F.* (*D.*) *scruposa*; FLscu, *F.* (*Lobactis*) *scutaria*; FFfun, *F.* (*Fungia*) *fungites*; Hpile, *Halomitra pileus*; Hacti, *Heliofungia actiniformis*; Calbi, *Ctenactis albitentaculata*; Ccras, *C. crassa*; Cechi, *C. echinata*; Hlima, *Herpolitha limax*; Srobu, *Sandalolitha robusta*; Sdent, *S. dentata*; Pcrus, *Podabacia crustacea*; Zechi, *Zoopilus echinatus*.

Epitoniid species	FCcos	FCdis	FCfra	FCsin	FCsom	FCten	FCvau	FWgra	FPspA	FPgra	FPmol	FPpau	FVsca	FVcon	FVrep	FVspi	FDhor	FDscr	FLscr	FFfun	Hpile	Hacti	Calbi	Ccras	Cechi	Hlima	Srobu	Sdent	Pcrus	Zechi
Epifungium:																														
pseudolochi	X																													
lochi	X	X	X	X	X	X	X																							
adgranulosa								X																						
marki									X																					
adgravis										X																				
nielsi											X	X																		
adscabra													X																	
ulu														X	X	X	X	X	X	X	X			X	X	X				
hoeksemai																					X		X							
twilae																								X	X	X				
pseudotwilae																											X	X	X	X
Epitonium:																														
crassicostatum	X																													
graviarmatum					X																									
Surrepifungium:																														
costulatum																							X	X	X	X	X	X		
ingridae														X				X					X	X	X		X			
oliverioi														X				X										X	X	
patamakanthini														X	X		X		X					X	X		X			

Indonesia. A special effort was made to find as many epitoniid species as possible, for each locality, during the time that was available. Because most *Fungia* species are associated with only one epitoniid species, whereas most *Ctenactis*, *Halomitra*, *Herpolitha*, and *Sandalolitha* species have several associates,

Figs 14-17. Possible predators of epitoniids in Indonesia. 14, *Fungia fungites*, overturned, revealing a circular burrow; 15, *Alpheus frontalis*, from underneath fungiid, i.e. a specimen of *Ctenactis echinata;* 16, a wrasse, *Halichoeres melanurus*, checking out overturned fungiids; 17, a damselfish, *Plectroglyphidodon lacrymatus*, checking out an overturned fungiid. 14, Bali; 15-17, SW Sulawesi.

specimens of the latter group of coral genera were searched more intensively at all localities, except for the Spermonde Archipelago where fungiids were randomly searched, independent of species.

In total 31 species of free-living fungiid species were found at the research locations (fig. 1), i.e. *Fungia* (*Cycloseris*) *costulata*, *F.* (*C.*) *distorta*, *F.* (*C.*) *fragilis*, *F.* (*C.*) *sinensis*, *F.* (*C.*) *somervillei*, *F.* (*C.*) *tenuis*, *F.* (*C.*) *vaughani*, *F.* (*Wellsofungia*) *granulosa*, *F.* (*Pleuractis*) sp. A, *F.* (*P.*) *gravis*, *F.* (*P.*) *moluccensis*, *F.* (*P.*) *paumotensis*, *F.* (*Verrillofungia*) *scabra*, *F.* (*V.*) *concinna*, *F.* (*V.*) *repanda*, *F.* (*V.*) *spinifer*, *F.* (*Dana-fungia*) *horrida*, *F.* (*D.*) *scruposa*, *F.* (*Lobactis*)
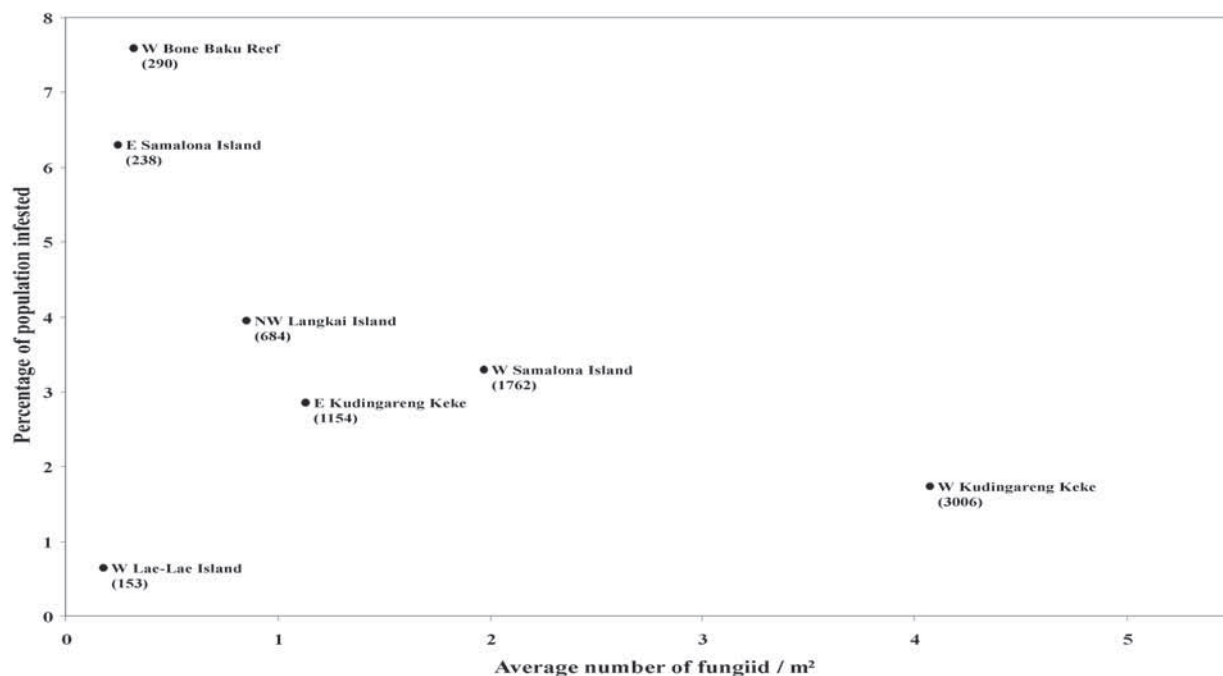
Fig. 18. Mushroom coral densities of the coral reef localities in the Spermonde Archipelago, SW Sulawesi, Indonesia, plotted against epitoniid infestation percentages. Sites (fig. 2) and n-values are indicated next to data points
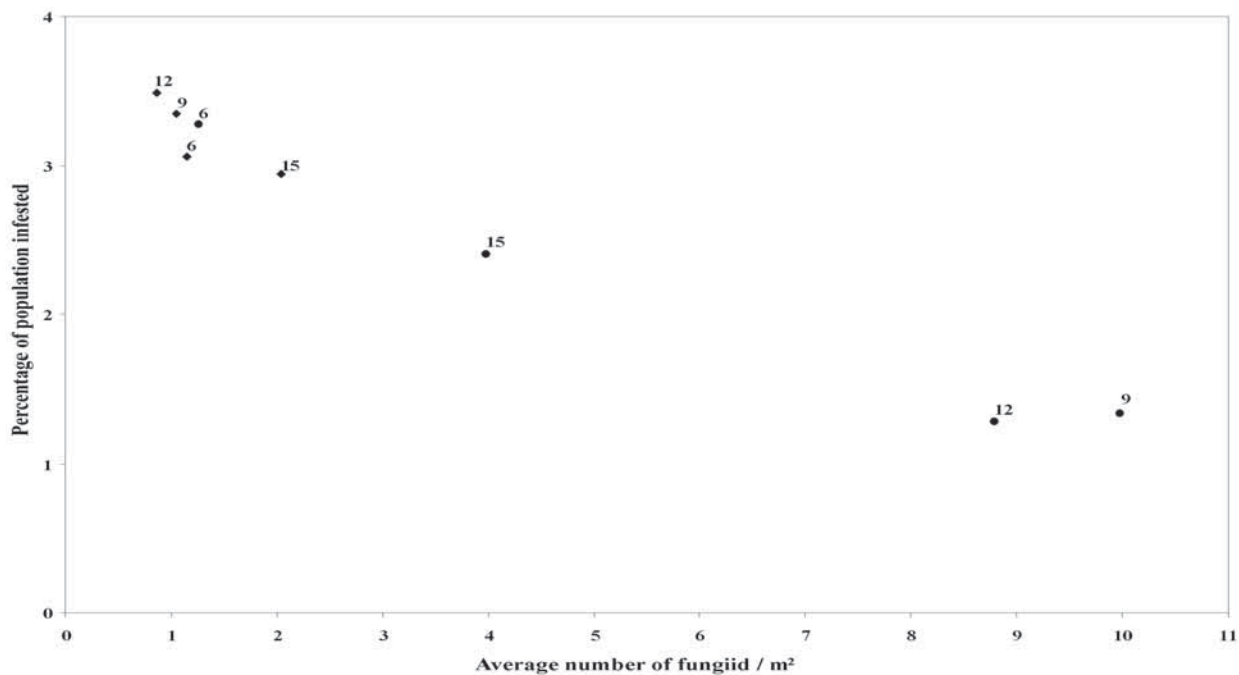

Fig. 19. Mushroom coral densities at 6, 9, 12 and 15 m depth transects on the east (diamonds) and west (circles) side of Kudingareng Keke Island, Spermonde Archipelago, SW Sulawesi, Indonesia (fig. 2), plotted against infestation percentages by *Epifungium ulu*. Total n = 3671 corals; a minimum number of 172 corals per transect. Transect depth is indicated next to the data points.

scutaria, *F.* (*Fungia*) *fungites*, *Halomitra pileus*, *Heliofungia actiniformis*, *Ctenactis albitentaculata*, *C. crassa*, *C. echinata*, *Herpolitha limax*, *Sandalolitha dentata*, *S. robusta*, *Zoopilus echinatus*, *Polyphyllia talpina* and *Fungia* (*Danafungia*) *fralinae*. Only *P. talpina* and *F.* (*D.*) *fralinae*, were never found in associations with wentletraps, even though over 1000 specimens of each of these species were inspected. Only two of the three euphylliid species that were investigated, i.e. *Plerogyra diabolotus* Ditlev, 2003, and *P. simplex* Rehberg, 1892, were found in association with an epitoniid species, i.e. *Epifungium hartogi* (A. Gittenberger, 2003). *Plerogyra sinuosa* (Dana, 1846), by far the most common euphylliid at most localities, was never found to be infested. At most places where dendrophylliid corals were found in association with epitoniids, i.e. in the Maldives, the Philippines, Palau and Indonesia, *Epidendrium aureum* and *E. sordidum* occurred both sympatrically and syntopically, directly next to or on the corals, in mixed populations, infesting the same specimens (A. Gittenberger and E. Gittenberger, 2005: figs 58-59).

Coral densities and infestation percentages

The relative numbers of infestations vary significantly over localities (X^2=63.4, p<0.001) and transects (X^2=21.7, p<0.025). At nearly all sites, with the exception of W Lae-Lae Island (fig. 18), the coral densities and the infestation percentages of the

fungiid populations are negatively correlated, i.e. r = -0.43. When the W Lae-Lae Island record is excluded the correlation becomes stronger, i.e. r = -0.80. A similar negative correlation, i.e. r = -0.98, was found for the coral densities and the percentages of infestation by *Epifungium ulu* along the transects (fig. 19) off E and W Kudingareng Keke Island. Only these transects were used in this analysis, because only there more than a hundred corals could be searched in the four transects, at 6, 9, 12 and 15 m depth, respectively. These findings are in agreement with observations made in Egypt, the Maldives, Thailand and Palau. In those areas, infestation percentages of over 50% were repeatedly found at sites where only 10 mushroom corals or less could be found during a dive, so that we may conclude that the fungiid density was very low there. Dives with over 100 records of inspected corals never yielded infestation percentages higher than 5%.

Depths

No correlations between infestation percentages and depths were found in the transect study (fig. 19). In general, at all investigated Indo-West Pacific localities no epitoniid species shows a preference for depth as such. Species like *Epifungium lochi*, *E. adgravis*, *E. marki* and *E. pseudolochi*, usually occur deeper than others, but in those cases the coral hosts have a preference for greater depth. When their hosts were occasionally found in shallower water, the epitoniids

Table 2. Infestation percentages of fungiid populations in the Spermonde Archipelago, SW Sulawesi, Indonesia, by *Epifungium ulu*, *E. pseudotwilae* and *E. twilae*.

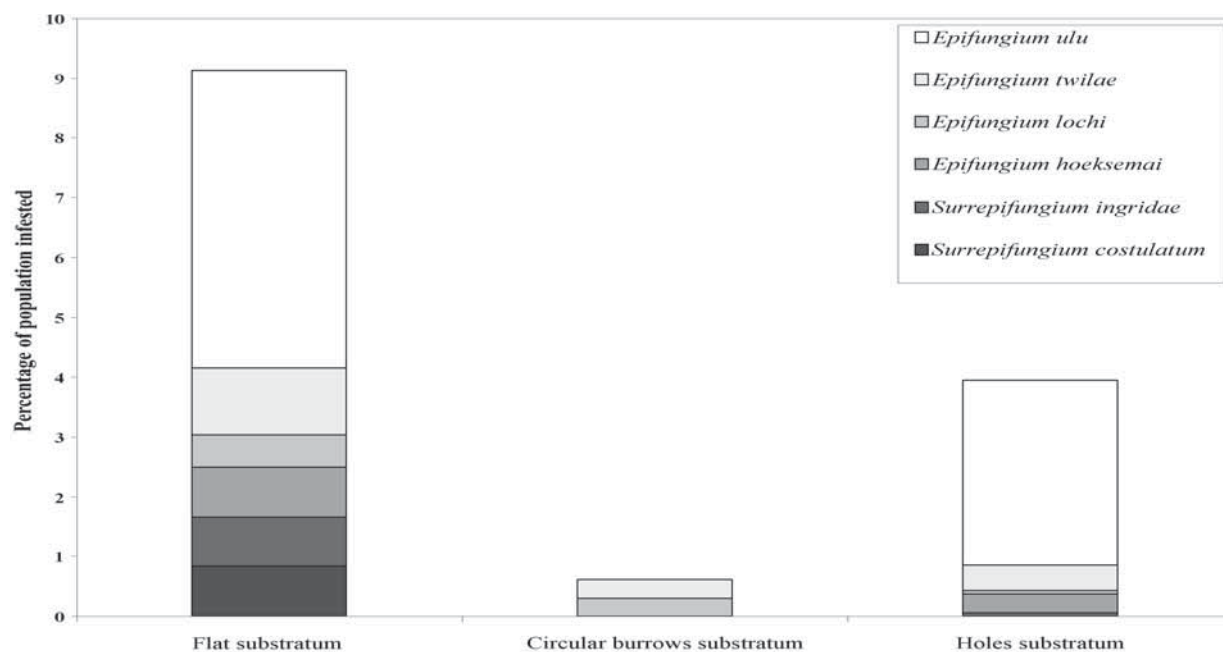| Epitoniids / Fungiids	*Epifungium ulu*	*Epifungium pseudotwilae*	*Epifungium twilae*
Fungia (*D.*) horrida (n = 280)	0.71 %	0.00 %	0.00 %
Fungia (*D.*) *scruposa* (n = 401)	1.00 %	0.00 %	0.00 %
Fungia (*F.*) *fungites* (n = 759)	1.45 %	0.00 %	0.00 %
Fungia (*L.*) *scutaria* (n = 125)	1.60 %	0.00 %	0.00 %
Fungia (*V.*) *concinna* (n = 791)	3.67 %	0.00 %	0.00 %
Fungia (*V.*) *repanda* (n = 2098)	2.24 %	0.00 %	0.00 %
Ctenactis echinata (n = 415)	0.24 %	0.00 %	0.96 %
Herpolitha limax (n = 393)	0.00 %	0.00 %	6.62 %
Sandalolitha robusta (n = 173)	0.00 %	4.05 %	0.00 %
Zoopilus echinatus (n = 136)	0.00 %	7.35 %	0.00 %

Fig. 20. Percentages of fungiid corals lying on either evenly flat sediment (n = 362), on circular burrows (n = 329) or on holes (n = 1620) substratum that 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).
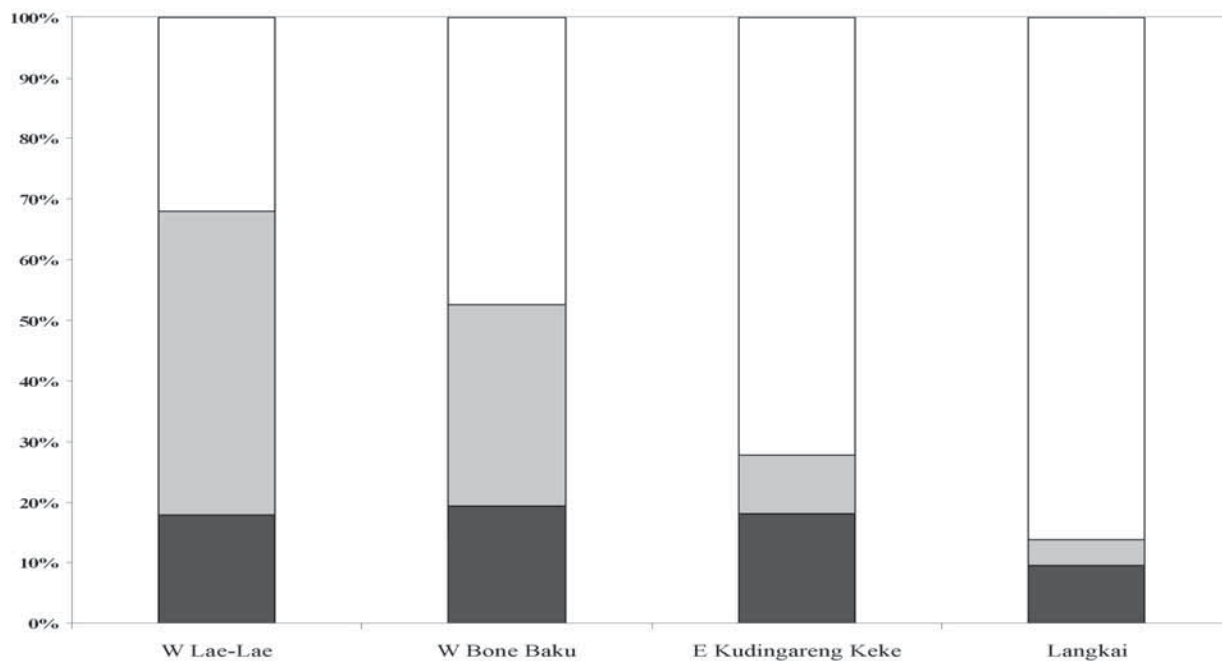

Fig. 21. Percentages of fungiids at the sites W Lae-Lae (n = 184), W Bone Baku (n = 289), E Kudingareng Keke (n = 1154) and Langkai (n = 684), either lying on flat sediment (white), substrata with burrows (grey) or with holes (black).

were usually found there as well. The only exception that is known concerns some populations of *E. twilae* from the Red Sea. None of the 107 samples of that species found in the Maldives, Thailand and Indonesia, came from more than 24 m depth, but the four samples from the Red Sea were found at 30, 35, 35 and 40 m, respectively. The absence of *E. twilae* deeper than 24 m in the Maldives, Thailand and Indonesia, may be related to the fact that specimens of the preferred host species, i.e. *Ctenactis crassa*, *C. echinata* and *Herpolitha limax*, were rare at those depths. At the Red Sea locality, *Ctenactis* species were not present, but *H. limax* was common at 6-45 m depth. Although > 50 specimens of *H. limax* from

less than 30 meter of depth were inspected, none of these was found to be infested, whereas 4 of the 12 specimens that were found deeper hosted *E. twilae*.

Substrata

The structure of the substratum has implications for the occurrence of corals and their infestation by epitoniids. Figure 20 shows the infestation percentages of corals found on flat, holes and burrow substrata, respectively, in the Spermonde Archipelago. Corals that lie on a flat substratum have significantly the highest chance of being infested (X^2=14.9, p<0.001), whereas corals that are found on a burrow substratum significantly have the lowest chance of acting as a host (X^2=14.8, p<0.001). Specimens of some epitoniid species, i.e. *Epifungium adgranulosa*, *E. adgravis*, *E. hoeksemai*, *E. lochi*, *E. nielsi* and *E. ulu*, can be found both on the substratum and on the underside of their fungiid host (table 3). When there is a flat substratum below its host, *Epifungium ulu* is found significantly more often attached to the coral (n=25) than lying on the substratum (n=1)(X^2=22.2, p<0.001). When a substratum with holes is present, no significant preference is found (X^2=1.2, p=0.3), although relatively more specimens (n=37) are found on the substratum than on the coral itself (n=29).

The relative numbers of corals lying on either a flat, a burrow or a holes substratum vary significantly between localities off SW Sulawesi (fig. 21; X^2=412.4, p<0.001). Although the number of corals on a flat substratum remains similar, a burrow substratum is found more often at localities closer to the coast and a holes substratum is found more often away from the coast.

At all Indo-West Pacific localities investigated (fig. 1) mushroom corals were found also on burrow substrata, but except for two cases of infestation in the Spermonde Archipelago, they did not host any epitoniids in such a habitat. Burrows are found more often underneath mushroom corals than around them, which suggests that their occurrence is correlated.

Occasionally gobies (Gobiidae) and goby-shrimps (Alpheidae) were seen hyding away underneath mushroom corals that, after being turned over, revealed one or two burrows. Two shrimp species that are known to live in burrows were found associated with gobies. The shrimps were caught be pushing the

Table 3. Depth range and positions of epitoniid shells relative to the coral host.

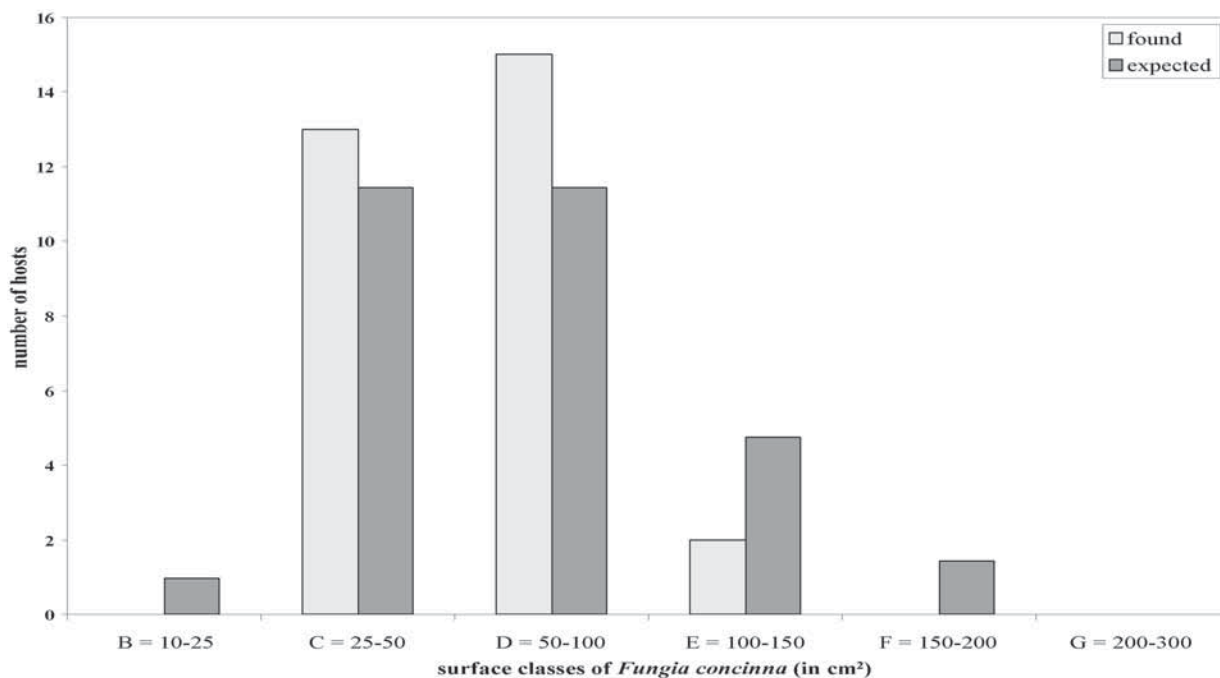| Epitoniid species	Position relative to the host			Depth (meter)
	Buried in substratum	On substratum	On coral	
Epidendrium:				
aureum		X	X	2-28
sordidum		X	X	3-35
Epifungium:				
adgranulosa		X	X	3-18
adgravis		X	X	3-30
hoeksemai	X	X	X	1-20
lochi		X	X	3-27
nielsi		X	X	4-36
ulu		X	X	1-35
adscabra			X	3-18
hartogi			X	9-18
marki			X	15-28
pseudolochi			X	20-30
pseudotwilae			X	4-25
twilae			X	5-38
Epitonium:				
crassicostatum	?	?	?	9
graviarmatum	?	?	?	35
Surrepifungium:				
costulatum	X	X		3-18
ingridae	X	X		1-26
oliverioi	X	X		4-38
patamakanthini	X	X		5-18

Fig. 22. Number of specimens of *Fungia concinna* in the size classes 10-25, 25-50, 50-100, 100-150, 150-200 and 200-300 cm^2 that was found infested by *Epifungium ulu* in the Spermonde Archipelago, SW Sulawesi, Indonesia (see fig. 2), next to the number that is expected when infestations are random, based on the coral size distribution of *Fungia concinna* specimens off W Kudingareng Keke, Spermonde Archipelago (n = 63).
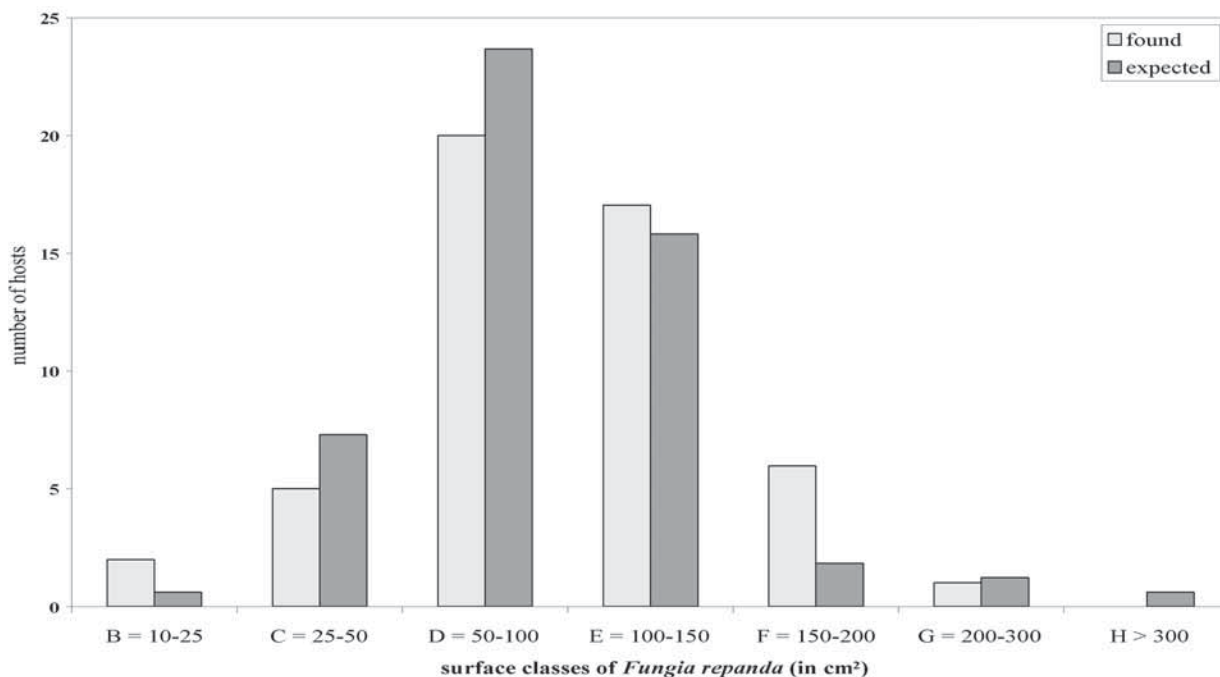

Fig. 23. Number of specimens of *Fungia repanda* in the size classes 10-25, 25-50, 50-100, 100-150, 150-200, 200-300 and >300 cm^2 that was found infested by *Epifungium ulu* in the Spermonde Archipelago, SW Sulawesi, Indonesia (see fig. 2), next to the number that is expected when infestations are random, based on the coral size distribution of *Fungia repanda* specimens off W Kudingareng Keke, Spermonde Archipelago (n = 84).
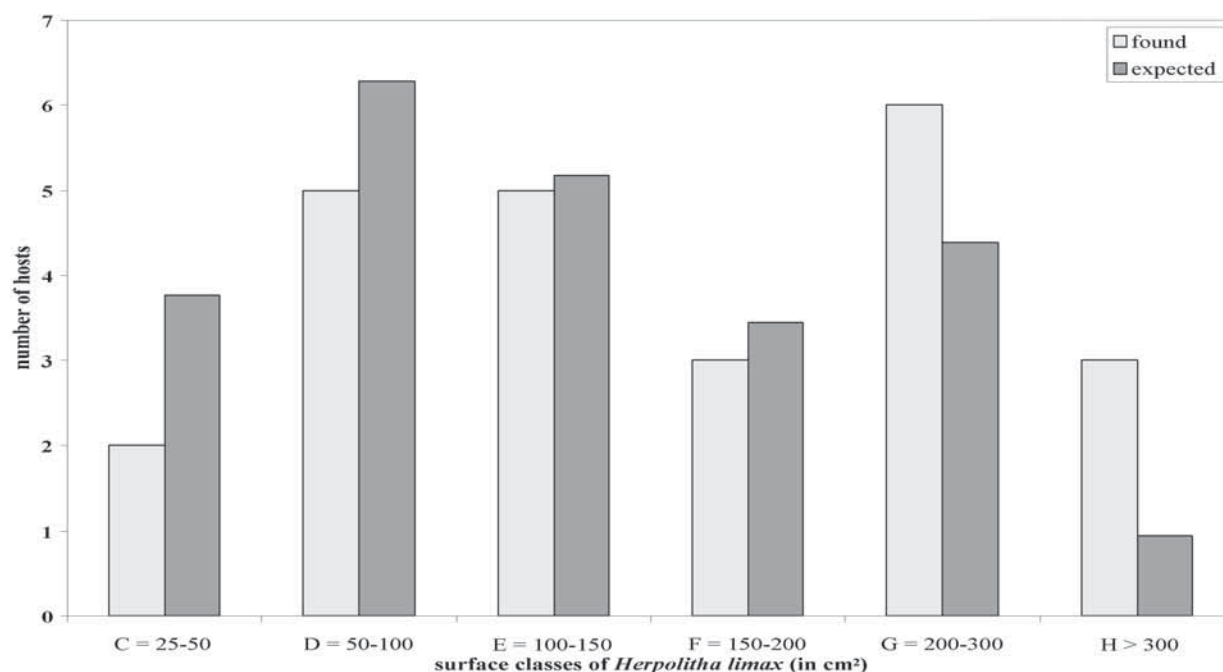
Fig. 24. Number of specimens of *Herpolitha limax* in the size classes 10-25, 25-50, 50-100, 100-150, 150-200, 200-300 and >300 cm² that was found infested by *Epifungium twilae* in the Spermonde Archipelago, SW Sulawesi, Indonesia (see fig. 2), next to the number that is expected when infestations are random, based on the coral size distribution of *Herpolitha limax* specimens off W Kudingareng Keke, Spermonde Archipelago (n = 153).

mushroom-coral quickly over the sand, blocking their escape routes. This concerned *Alpheus frontalis* H. Milne Edwards, 1837 (Caridea: Alpheidae; fig. 15), found underneath *Ctenactis echinata* at Palau, and *Axiopsis* sp. (Thalassinidea: Axiidae) found underneath *Herpolitha limax* off SW Sulawesi.

Both the shells and the egg-capsules are usually attached to the substrate by one or two, or by numerous mucus threads. By coincidence it turned out that these threads may be elastic and strong enough to pull some of the collected specimens out of the collection tube,

back to their habitat over distances of up to about 50 cm. This unforeseen experiment made clear that the snails may be strongly connected to the substratum

Coral-sizes

At W Kudingareng Keke Island, 63, 84 and 153 specimens of *Fungia* (*Verrillofungia*) *concinna*, *F.* (*V.*) *repanda* and *Herpolitha limax*, respectively, were collected to study the size distributions within

Table 4. The size distributions of *Epifungium ulu* and *Epifungium twilae* samples with egg-capsules versus samples without egg-capsules (grey), found on corals in the size classes 0-50 cm², 50-150 cm² and >150 cm² in the Spermonde Archipelago, SW Sulawesi, Indonesia.

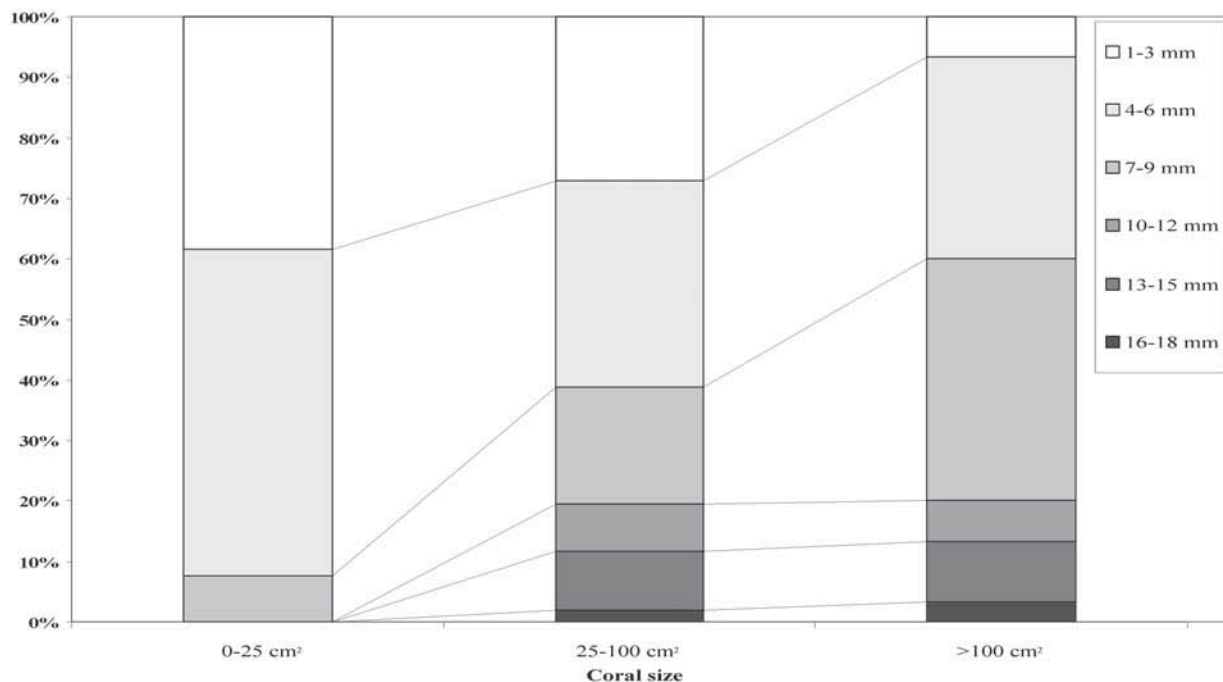| Coral size class:	10-50 cm²		50-150 cm²		>150 cm²	
Epifungium ulu samples	percentage	N	percentage	N	percentage	N
with egg-capsules	26%	16	42%	35	60%	6
without egg-capsules	74%	46	58%	48	40%	4
Epifungium twilae samples	percentage	N	percentage	N	percentage	N
with egg-capsules	17%	3	29%	4	65%	11
without egg-capsules	83%	15	71%	10	35%	6

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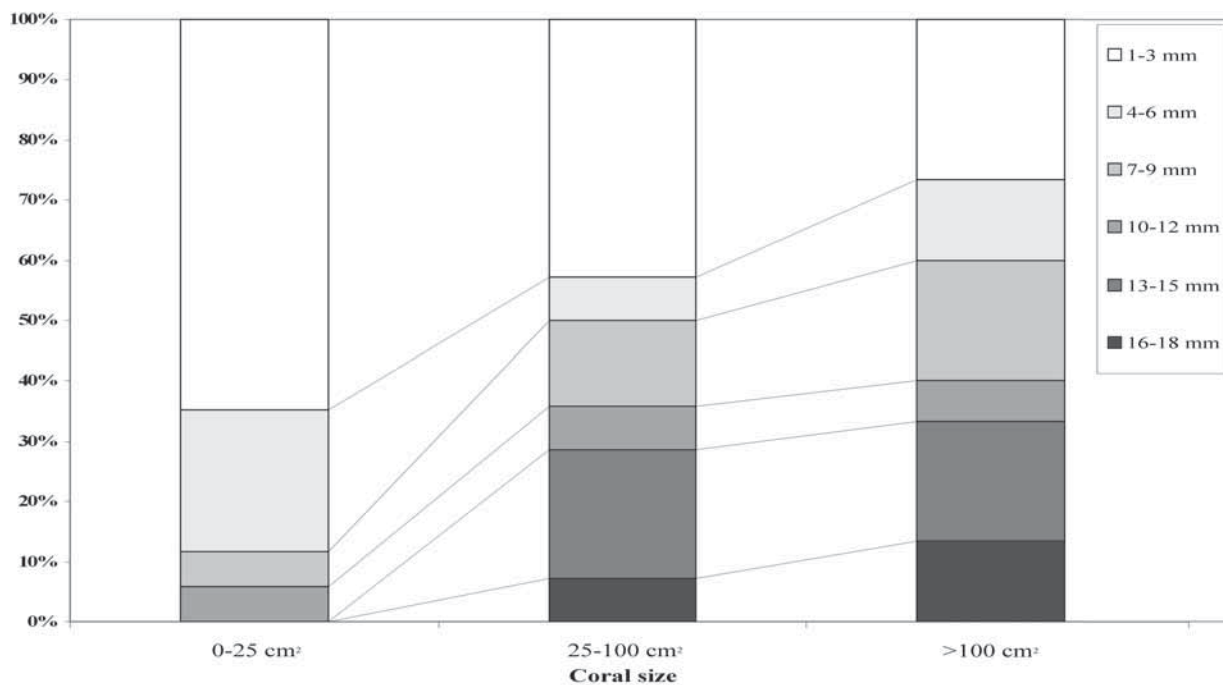

Fig. 26. The maximum shell heights found in *Epifungium twilae* samples (n= 46) and their distribution in the size classes 0-25 (n = 17), 25-100 (n = 14) and >100 cm² (n = 15) of their coral hosts in the Spermonde Archipelago, SW Sulawesi, Indonesia.

populations (figs 22-24) and the infestations by *Epifungium ulu* (figs 22-23) and *E. twilae* (fig. 24) in various size classes. *Epifungium ulu* specimens were found significantly more often underneath relatively large specimens of *Fungia repanda* (fig. 23; X^2=14.4, p<0.001). *Epifungium ulu* specimens were found less than expected on larger *Fungia concinna* corals, but this difference is not significant (fig. 22; X^2=1.8, p=0.20). *Epifungium twilae* specimens were found significantly more often with larger hosts (fig. 24; X^2=4.7, p<0.05). Furthermore, larger corals are infested significantly more frequently by relatively large specimens of *E. ulu* (fig. 25; X^2=11.2, p<0.025) and *E. twilae* (fig. 26; X^2=67.1, p<0.001). Under larger host corals, specimens of *Epifungium ulu* (table 4; X^2=4.7, p<0.05) and *E. twilae* (table 4; X^2=10.3, p<0.05) are found significantly more often with egg-capsules than without.

Turned over hosts and epitoniid predators

Only a single coral among c. 2000 that were found in upside down position was infested by epitoniid egg-capsules and none with one or more snails. Figure 27 illustrates the fate of 28 epitoniids and 7 clutches of egg-capsules that were initially attached to 16 coral hosts. The coral discs were placed upside down and checked after two hours and once again after two days. While turning the corals, some snails were immediately pulled from their hosts by the currents or by fish, mainly Labridae [e.g. fig. 16: *Halichoeres melanurus* (Bleeker, 1851)] and Poma-centridae [e.g. fig. 17: *Plectroglyphidodon lacrymatus* (Quoy and Gaimard, 1825)]. One of the two corals that still hosted epitoniids after two days had returned to an upright position, whereas the other coral was lying somewhat hidden in a hole, out of the current.

In the experiment in which three hosts were laid upside down, i.e. two with specimens and egg-capsules of *Epifungium ulu* and one with *E. twilae*, all *Epifungium ulu* were eaten or removed within 30 minutes by wrasses and damselfishes, while *E. twilae* survived.

In general, predation by fishes varies strongly over time and place. Some fishes had to be scared away before turning over a fungiid. Otherwise, they would most probably have speeded forward to snatch any epitoniids revealed. Small, slender fishes like wrasses were often encountered hiding below large fungiids, like convex corals of *Herpolitha*, *Sandalolitha* and *Ctenactis*. A substratum with holes or an irregular substratum is usually present in these cases, creating an entrance for the fishes under the coral margin. If a flat substratum is present and the coral is not convex but also flat, there is not enough room for a fish to get below it.

No significant differences were found between the corals in the turn-over rate experiment, because only 3 of the 360 fungiids, i.e. 360 = (12 species × 24 specimens) + (3 larger size-classes × 24 specimens), had turned over within the 10 days of the experiment. The number of specimens that had regained an upward position within 2 days after being turned over at the start, did differ significantly between the twelve species (X^2=58.3, p<0.001), viz. *Fungia* (*Danafungia*) *horrida*, *F.* (*D.*) *scruposa*, *F.* (*Fungia*) *fungites*, *F.* (*Verrillofungia*) *concinna*, *F.* (*V.*) *repanda*, *F.* (*V.*) *scabra*, *F.* (*Lobactis*) *scutaria*, *F.* (*Pleuractis*) *gravis*, *F.* (*P.*) *paumotensis*, *Ctenactis echinata*, *Herpolitha limax* and *Polyphylia talpina*, and the size classes of *F.* (*V.*) *repanda* and *H. limax*. The turn back ratios are shown in table 5.

In the Spermonde Archipelago, 1,109 out of 26,277 fungiids, i.e. 4.2%, were observed as upside down under natural conditions. These percentages differ significantly between the species (fig. 28; X^2=202.1, p<0.001).

Discussion and conclusions

Coral species and their hosted wentletraps

Epifungium and *Surrepifungium* species are here referred to as either specialists or generalists, dependent on being associated with only one or a monophyletic group of host species, versus an association with some distantly related hosts (coral phylogeny based on molecular data: A. Gittenberger et al., chapter 8). After these definitions, most *Epifungium* species, i.e. *E. adgranulosa*, *E. adgravis*, *E. adscabra*, *E. hartogi*, *E. lochi*, *E. marki*, *E. nielsi*, *E. pseudolochi*, *E. pseudotwilae* and *E. twilae*, are to be called specialists (table 1). The hosts of *E. pseudotwilae*, i.e. *Sandalolitha*, *Podabacia* and *Zoopilus* species, and the hosts of *E. twilae*, i.e. *Herpolitha* and *Ctenactis* species, do
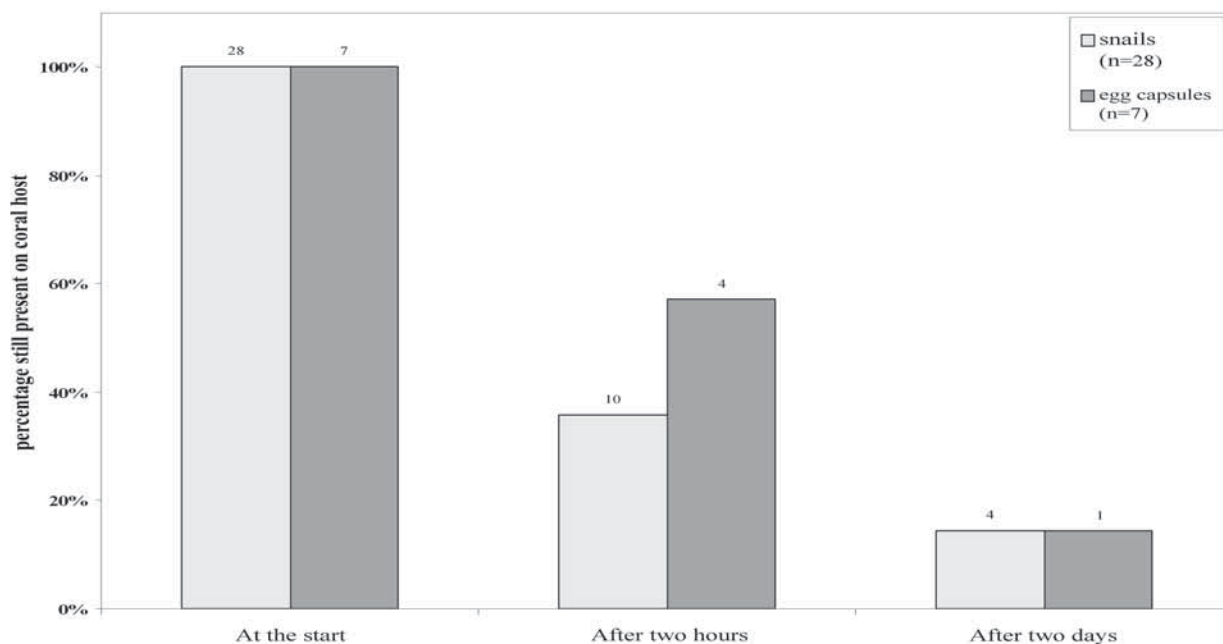
Fig. 27. The numbers of shells and egg-capsule clutches of *Epifungium ulu* that remained on the underside of the host corals even though they were overturned; after two hours and after two days, off W Langkai, Spermonde Archipelago, SW Sulawesi, Indonesia (see fig. 2).

not form two clades in the Fungiidae phylogeny reconstruction based on morphology by Hoeksema (1989b). However, anticipating the publication of a revised, molecular phylogeny reconstruction of the Fungiidae, we consider *E. pseudotwilae* and *E. twilae* specialists (A. Gittenberger et al., chapter 3).

All fungiid species, except *Fungia* (*Cycloseris*) *costulata*, are associated with only one *Epifungium* specialist (table 1). The two species that have specialized on *F.* (*C.*) *costulata* may have been able to do so because of their allopatry, since *Epifungium pseudolochi* is restricted to the Red Sea, while *E. lochi* is found in the Indo-West Pacific, from the Maldives, Indonesia, Australia to Palau (A. Gittenberger and E. Gittenberger, 2005).

Epifungium hartogi is exceptional in being the only *Epifungium* species that is associated with euphylliid corals. The snails are hidden deep inside the mouth cavity (the stomach) of their host (A. Gittenberger, 2003), which has been illustrated before for a zoanthid-associated wentletrap species (Zann, 1980: 132, upper fig.). Because the snails are invisible then from outside and since they may only need to leave their shelter for spawning, many more epitoniids living in similar habitats where they are easily overlooked might await discovery.

The four *Surrepifungium* species, viz. *S. costulatum*, *S. ingridae*, *S. oliverioi* and *S. patamakanthini*, and the two *Epifungium* species, viz. *E. hoeksemai* and *E. ulu*, may be considered generalists. *Surrepifungium* species and *E. hoeksemai* resemble most epitoniids associated with sea-anemones, and differ from other coral-associated species by their ability to bury themselves into the sand. The feeding behaviour of the *Surrepifungium* species has not yet been observed. Maybe the snails extend their proboscis towards the coral tissue while remaining protected against the nematocysts on the substrate underneath. A similar behaviour has been observed in sea-anemone-associated epitoniids like *Epitonium clathratulum* (Kanmacher, 1797); these snails may extend their proboscis to up to three times the shell-length towards the stem or the tentacles of their host (e.g. Perron, 1978: 65; Robertson, 1983: 4; den Hartog, 1987: 105).

Occasionally an *Epifungium* species may share its host with an epitoniid of the genus *Surrepifungium* (table 1). If so, the *Epifungium* is found on the coral itself while the *Surrepifungium* occurs on or in the substratum underneath. In *Surrepifungium* the snails are never found on their hosts, opposite to what is

usually observed in *Epifungium*. In the latter case the snails are closest to their food but constantly within reach of the particular coral species' nematocysts. The *Epifungium* species have to be adapted to more extreme environments, which might explain why they are more strictly specialized to their hosts than the *Surrepifungium* species.

The habitat preferences of *Epifungium hoeksemai* are unusual for coral-associated epitoniids. These snails differ from other coral-associated epitoniids in being able to bury in the sand, or crawl on the substratum below their hosts, or over the coral's surface (table 3). *Epifungium hoeksemai* further differs from the other generalists in being associated with only two host species, i.e. *Fungia (F.) fungites* and *Heliofungia actiniformis*, instead of at least four and usually more than six (table 1). These two coral species differ conspicuously, both morphologically (Hoeksema, 1989b) and genetically (A. Gittenberger et al., chapter 3). *Fungia (F.) fungites* is exceptional among the 21 *Fungia* species that are known to be associated with epitoniids in that it may be found with two *Epifungium* species. All the other *Fungia* species, except for *F. (C.) costulata*, are known to be associated with only a single wentle-

trap species (table 1). The second host of *E. hoeksemai*, i.e. *H. actiniformis*, is unusual by its fleshy tentacles (fig. 6) that are at least ten times longer than those of other fungiids. *Heliofungia actiniformis*, *Fungia (Danafungia) fralinae* (see Hoeksema, 2004b) and *Polyphyllia talpina* have the longest tentacles among the fungiids. The latter two species are the only free-living mushroom coral species that were never found associated with epitoniids, even though more than 1000 specimens of each were searched. Only tentacle length distinguishes them as a couple from the other fungiids. However, the association between *E. hoeksemai* and *H. actiniformis* contradicts the hypothesis that relatively long tentacles in general prevent wentletraps from settling on a particular fungiid.

Even though *Epifungium ulu* does infest *Ctenactis*, *Halomitra*, *Herpolitha* and *Sandalolitha* populations, with population infestation percentages of less than 0.3%, there seems to be a preference for *Fungia* species that are not associated with any other *Epifungium*, with the exception of *E. hoeksemai* (table 1). This is at least suggested by the infestation percentages of 0.7-3.7% of the populations of such *Fungia* species in the Spermonde Archipelago (table

Table 5. Results of turn back rate experiment off W Kudingareng Keke, SW Sulawesi, Indonesia. All data are based on 24 specimens for each species and size class. The fungiid species are ordered by the turn back rate of 24 specimens in the size class 25-100 cm².

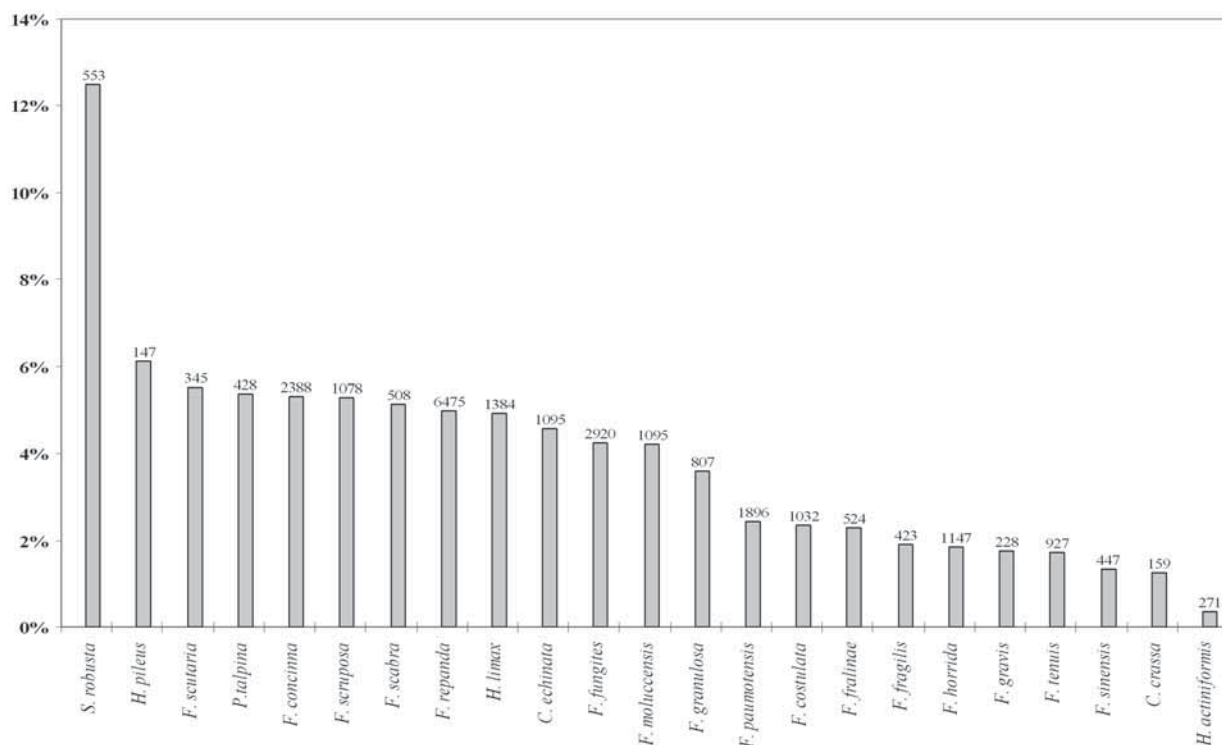| fungiid species:	Coral size-class (cm²)	Average of length / width	Average weight (gram)	Number of corals (n = 24) that turned back after 2 days
Polyphyllia talpina	25-100	3.6	142	20
Herpolitha limax	25-100 100-200 >200	2.2 3.1 3.4	127 302 754	11 11 1
Fungia scutaria	25-100	1.6	135	9
Fungia gravis	25-100	1.6	251	7
Fungia paumotensis	25-100	1.7	131	5
Fungia repanda	25-100 100-150	1.1 1.1	127 326	5 0
Ctenactis echinata	25-100	2.2	94	4
Fungia scruposa	25-100	1.1	127	3
Fungia scabra	25-100	1.1	75	3
Fungia concinna	25-100	1.2	110	1
Fungia horrida	25-100	1.0	163	1
Fungia fungites	25-100	1.1	93	0

Fig. 28. Percentages of fungiid species populations that were observed in upside down position in the Spermonde Archipelago, SW Sulawesi, Indonesia. The n-values are indicated above the columns.

2). At none of the fieldwork localities (fig. 1) in the Indo-Pacific, any indication was found for local, divergent preferences of *E. ulu*. *Halomitra* and *Sandalolitha* infestations were rarely found in both Indonesia and Palau, and the *Ctenactis* infestations are rare in Egypt (Red Sea), Indonesia and Palau. The infestation percentages of *Fungia* populations seem to be much higher at all fieldwork localities.

The host preferences of *Epitonium crassicostatum* and *E. graviarmatum* cannot be indicated because both species are known from one empty shell only, found with *Fungia* (*Cycloseris*) *costulata* and *F.* (*C.*) *vaughani*, respectively.

In general, sister species do not occur sympatrically and syntopically, but *Epidendrium aureum* and *E. sordidum* are found together on the same host species without any obvious niche differentiation. There may be differences however, since *Epidendrium sordidum* is the only epitoniid species with shells that are usually completely overgrown by other organisms, like hydroids (fig. 4), forams and vermetids (A. Gittenberger and E. Gittenberger, 2005), during

their lifetime. As a consequence, these snails are better camouflaged and possibly somewhat better protected against predators, as compared to *Epidendrium aureum* (fig. 3). The life-strategies of these two species seem to be very similar in all other aspects and a realistic mechanism that might have triggered sympatric speciation cannot be indicated.

Trophic aspect of mollusc-coral relationship

Unlike endoparasitic molluscs of the families Coralliophilidae and Mytilidae (Bouillon et al., 1980; Massin, 1989, 1992; Hoeksema and Achituv, 1993; Hoeksema and Kleemann, 2002; Kleemann and Hoeksema, 2002; Massin and Dupont, 2003), the ectoparasitic epitoniids do not appear to inflict serious visible damage to their coral hosts. The thick layer of mucus secreted by most mushroom corals may be defensive and in itself is believed to have high food quality (Krupp, 1982, 1984, 1985; Chadwick, 1988). Mushroom corals are very successful in regenerating

and repairing their tissue (Chadwick and Loya, 1990; Kramarsky-Winter and Loya, 1996; Chadwick-Furman et al., 2000). Fragmented mushroom corals are also known for their regenerative capacity and survival, which may result in large areas covered by these free-living corals (Hoeksema, 1989b; Chadwick and Loya, 1990; Littler et al., 1997; Yamashiro and Nishihira, 1998). Just before they die, adult polyps may even generate complete new buds from their soft tissue (Gilmour, 2002a, 2002b, 2004a, 2004b; Hoeksema, 1989b, 2004b; Kramarsky-Winter and Loya, 1996, 1998). Hence, infestations by epitoniids may slightly harm individual fungiids, but is not likely to have any lethal effect on mushroom coral populations. There are also no indications that infested mobile mushroom corals may actively turn themselves upside down to expose their parasites for removal by potential predators.

Coral densities

Low epitoniid infestation percentages in relatively high fungiid densities were observed in Egypt (Red Sea), the Maldives, Thailand, Indonesia and Palau. The infestation percentages by *Epifungium ulu* in the transects at 6, 9, 12 and 15 m off W and E Kudingareng Keke Island, are independent of depth and also negatively correlated with coral density (fig. 19). Among the seven reefs that were studied in the Spermonde Archipelago, only the Lae-Lae Island had an exceptionally low infestation percentage in combination with its number of potential coral hosts, diverging from the general trend. The relatively low number of infestations in this case may be caused by the fact that the water at Lae-Lae Island is murky because of its position close to the land, the city Makassar, and a river outlet (fig. 2). The fungiids here were also lying relatively more often on substrata with burrows than at the other localities (fig. 21) and fungiids with burrows underneath are almost never infested (fig. 20).

The negative correlation between coral density and infestation percentage supports the hypothesis that before settlement, a certain number of veligers are evenly dispersed over coral reefs and depths. Apart from that it has to be accepted that the veligers can actively go for a suitable host. Host species recognition by chemotaxis was already described for epitoniids

by Bell (1985), Perron (1978) and Salo (1977). It explains the relatively high infestation percentages when few suitable fungiid hosts are present. Exceptional are those reef areas that are covered almost entirely by corals of a single fungiid species that is immune to epitoniids, e.g. *Fungia (Danafungia) fralinae* (see Hoeksema, 2004b).

Depth ranges

In general coral-associated epitoniids do not show any preference for depth (e.g. fig. 19). The species that are usually found in deep waters, like *Epifungium lochi*, are related to corals, like *Fungia (Cycloseris)* species, with a preference for those depths. The only exception to this rule is an *Epifungium twilae* population in the Red Sea, off Marsa Nakari, Egypt. Infestations (n=4) only occurred deeper than 29 meters, even though suitable hosts were present at all depths. This may be related to the unusually heavy rainfall in the year previous to the fieldwork, which formed some freshwater lakes in the desert. One of these lakes formed a small canal towards the coast, flowing into the sea at the fieldwork locality, with much dirt and sand, which made the shallow water very murky for several months. The visibility remained good only at greater depths (local dive guides, pers. comm.). Indirect evidence for epitoniids disliking murky waters was also found off Lae-Lae Island in the Spermonde Archipelago (see fig. 2), where infestation percentages were much lower than expected (fig. 18).

Substrata

A significantly higher number of epitoniids was found on corals living on flat substrata than on those from a substratum with holes (fig. 20). This may be explained by the fact that in the latter case potential predators, like fish, can reach below a fungiid disc, making use of such holes, as was observed in the field repeatedly. This might also explain why in *Epifungium ulu* most snails are observed on the substratum (like *Epifungium hoeksemai* in fig. 6) instead of on the coral's surface when there are holes below the coral. Under those conditions the snails might be more easily overlooked by fish. Alternatively, when the underground is flat, the snails are found

significantly more often on the coral itself.

Snails of *Surrepifungium* species are never found on the coral's surface. In contrast to *Epifungium* species, except for *E. hoeksemai*, they may bury themselves into the sand (table 3), to be protected against potential threads like fishes and currents.

Most of the burrows that were found under mushroom corals (figs 11, 13-14) are probably made by shrimps, like the ones that were caught, i.e. *Alpheus frontalis* (fig. 15) and *Axiopsis* sp., and the goby-shrimps and gobies that were seen below fungiids in the field. These shrimps or gobies may remove and eat any epitoniid that tries to settle above its home, i.e. the burrow. This may explain why a significantly low number of epitoniid snails was found with fungiids lying on substrata containing burrows.

Coral-sizes

Coral-size matters in relation to infestation with epitoniid snails. The presence of *Epifungium ulu* and *E. twilae*, with their egg-capsules, is clearly related to host-size since [1] the snails are more frequently found underneath larger than smaller hosts (figs 23-24), [2] larger snails are more often observed with larger hosts (figs 25-26) and [3] epitoniids are relatively more often found together with egg-capsules underneath larger hosts (table 4). These results can be explained by a combination of factors.

Larger host-corals are heavier than smaller ones and will be overturned less easily. Consequently, they constitute a more stable environment for snails that cannot survive on upside down mushroom corals. Since larger usually also means older, the largest corals have been the longest period of time exposed to infestation. An individual coral may be a host for years and maybe generations of snail parasites. In fact, up to 20 snails, with a large variety of shell-heights, indicative of different generations, have been found on a single coral. It remains to be investigated whether these are successive generations, i.e. whether some veligers stay and settle below their parents' coral, not leaving their place of birth.

The preference of epitoniids for larger hosts may also be related to the convex (domed) shape of some free-living mushroom corals, leaving more living space for epitoniids in between the disc and the substratum. This is especially relevant for snails that cannot bury into the sand, i.e. most *Epifungium* species (table 3), or have broad shells (height/width 1.0-1.2), i.e. *Epifungium pseudotwilae* and *E. twilae* (fig. 9; A. Gittenberger and E. Gittenberger, 2005). These wentletraps are only found associated with fungiids that are or can become relatively large, i.e. species of *Ctenactis*, *Herpolitha*, *Podabacia*, *Sandalolitha* and *Zoopilus* (see Hoeksema, 1989b, 1991b). Epitoniids with more slender shells (height/width >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, i.e. *Fungia* (*Cycloseris*) species, *F.* (*Wellsofungia*) *granulosa* (fig. 12), or *F.* (*Verrillofungia*) *scabra*, or with fungiids that have oval discs which are not or rarely convex, e.g. the *Fungia* (*Pleuractis*) species (fig. 7).

Epifungium hoeksemai (fig. 6) and *E. ulu*, the only two generalists in *Epifungium*, have moderately broad-conical to slender-conical shells with H/W indexes of 1.6-2.4 and 1.7-3.3, respectively (A. Gittenberger and E. Gittenberger, 2005: figs 70-73, 75-76). In *E. hoeksemai* the snails may bury into the substrate; maybe they do so when the space under a host is limited. This behaviour is not known from any other *Epifungium* species. Most of the coral hosts of *E. hoeksemai* and *E. ulu* have discs that are at least slightly convex, i.e. *Ctenactis echinata*, *Fungia* (*Danafungia*) species, *F.* (*Lobactis*) *scutaria*, *F.* (*Fungia*) *fungites*, *Halomitra pileus*, *Heliofungia actiniformis*, *Herpolitha limax* and *Sandalolitha robusta*.

Turned over hosts and epitoniid predators

Epitoniids are hardly ever found on fungiids that lie upside down. Usually the wentletraps are removed from their host within hours or days after the coral disc has been turned over (fig. 27). Snails that become abruptly exposed to the open water will either be eaten by fishes (figs 16-17) or be removed from their food-source and shelter by the water turbulence. Maybe the latter alternative was underscored during the fieldwork, because corals were always turned upside down carefully. Under natural conditions the coral discs will be turned around much more abruptly, by the then relatively strong currents. The egg-capsules may 'survive' somewhat longer than the

snails because their clutches are attached to the substrate by many mucus threads instead of only one or two that hold the shells of the snails themselves.

The frequencies of overturning differ conspicuously between the various fungiid species (table 5), as do the numbers of specimens lying upside down under natural conditions (fig. 28). It may be assumed that being associated with hosts that do not easily turn over enhances the survival rate for the wentletraps, but a preference of epitoniids for the most 'stable' host species was not noticed.

Epifungium pseudotwilae and *E. twilae* are associated with fungiids that may be relatively large, e.g. *Ctenactis*, *Herpolitha*, *Sandalolitha* and *Zoopilus* species. Wrasses, damselfish and gobies are more frequently found below such large corals and may therefore be more threatening to *E. pseudotwilae* and *E. twilae* than to the other *Epifungium* species. According to molecular data (A. Gittenberger et al., chapter 8), despite their conchological similarity, *E. pseudotwilae* and *E. twilae* are not sister species. Their shells are conspicuously broader than those of the other *Epifungium* species, which have far more slender shells (A. Gittenberger and E. Gittenberger, 2005). The broadly conical shell shape in both *E. pseudotwilae* and *E. twilae* might have originated by parallel evolution, resulting from a selection pressure by fish predators. Small fishes that may reach the underside of the coral discs may not be able to get hold of the broad *E. pseudotwilae* and *E. twilae*, simply because their mouths are too small. This hypothesis is supported by the observation that damselfishes and wrasses only ate the slender specimens of *Epifungium ulu*, without attacking the relatively broad, large *E. twilae*.

Acknowledgements

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