

# Ecology of the *Leptoconchus* spp. (Gastropoda, Coralliophilidae) infesting Fungiidae (Anthozoa, Madreporaria)

by Claude MASSIN

## Abstract

Underwater surveys of 27,000 mushroom corals (Fungiidae) at Papua New Guinea (Laing Island, Madang and Motupore), Singapore, the Maldives (Ari Atoll and South Male Atoll), the Red Sea (Hurghada), Indonesia (Makassar, Sulawesi) and examination of 1,000 fungiids from museum collections (mainly National Museum of Natural History, Leiden) have shown that 36 coral species were infested by several species of Coralliophilidae belonging to the genus *Leptoconchus*. The rate of infestation of the mushroom coral assemblage varied from 0 to 7%. The two most infested Fungiidae were *Fungia (Fungia) fungites* and *F. (Verrillofungia) repanda*. At the east side of Laing Island, *F. (F.) fungites* reached an infestation rate of 19%, the highest value ever recorded.

The rate of infestation was positively correlated with hydrodynamics and negatively with turbidity. It was, however, not correlated with the density of the fungiid assemblage.

Infestation was maximum in shallow water (1-5 m); nearly no *Leptoconchus* spp. were found deeper than 20 m. Place of settlement of the mollusc (coral centre or edge), opening of the burrow (oral/aboral side of the coral) and deformation of coral skeleton varied according to the coral species infested. These variations seemed specifically related to the different *Leptoconchus* species rather than the infested host species.

**Key-words:** Fungiidae, *Leptoconchus*, Coralliophilidae, ecology, parasitism, coral-host relationships.

## Résumé

L'étude *in situ* de 27.000 Fungiidae en Papouasie Nouvelle-Guinée (Laing Island, Madang et Motupore), à Singapour, aux îles Maldives (Ari Atoll et South Male Atoll), en Mer Rouge (Hurghada), en Indonésie (Makassar, Sulawesi) et l'examen de Fungiidae provenant de collections muséologiques (principalement du National Museum of Natural History, Leiden) montrent que 36 espèces sont parasitées par plusieurs espèces de Coralliophilidae appartenant au genre *Leptoconchus*. Le taux d'infestation des populations de Fungiidae étudiées varie de 0 à 7%. Les deux espèces de Fungiidae les plus parasitées sont *Fungia (Fungia) fungites* et *F. (Verrillofungia) repanda*. Sur le côté Est de l'île de Laing, 19% des *F. (F.) fungites* sont parasités, ce qui représente le plus fort taux jamais observé.

L'intensité du parasitisme est positivement corrélée avec l'agitation hydrodynamique et négativement avec la turbidité. En revanche, elle ne présente pas de relation avec la densité de population des Fungiidae.

Contribution n° 355 of the Léopold III Biological Station, Laing Island.

Le parasitisme est maximum en eau peu profonde (1-5 m); il est rare de trouver des *Leptoconchus* spp. à plus de 20 m de profondeur. L'emplacement où la larve du mollusque se fixe (partie centrale ou périphérique du corail), l'ouverture de la loge (face orale ou aborale du corail) et la déformation du squelette du corail varient en fonction de l'espèce de Fungiidae. Ces variations semblent spécifiquement liées aux différentes espèces de *Leptoconchus* plutôt qu'à l'espèce hôte infestée.

**Mots-clefs:** Fungiidae, *Leptoconchus*, Coralliophilidae, écologie, parasitisme, relations corail-hôte.

## Introduction

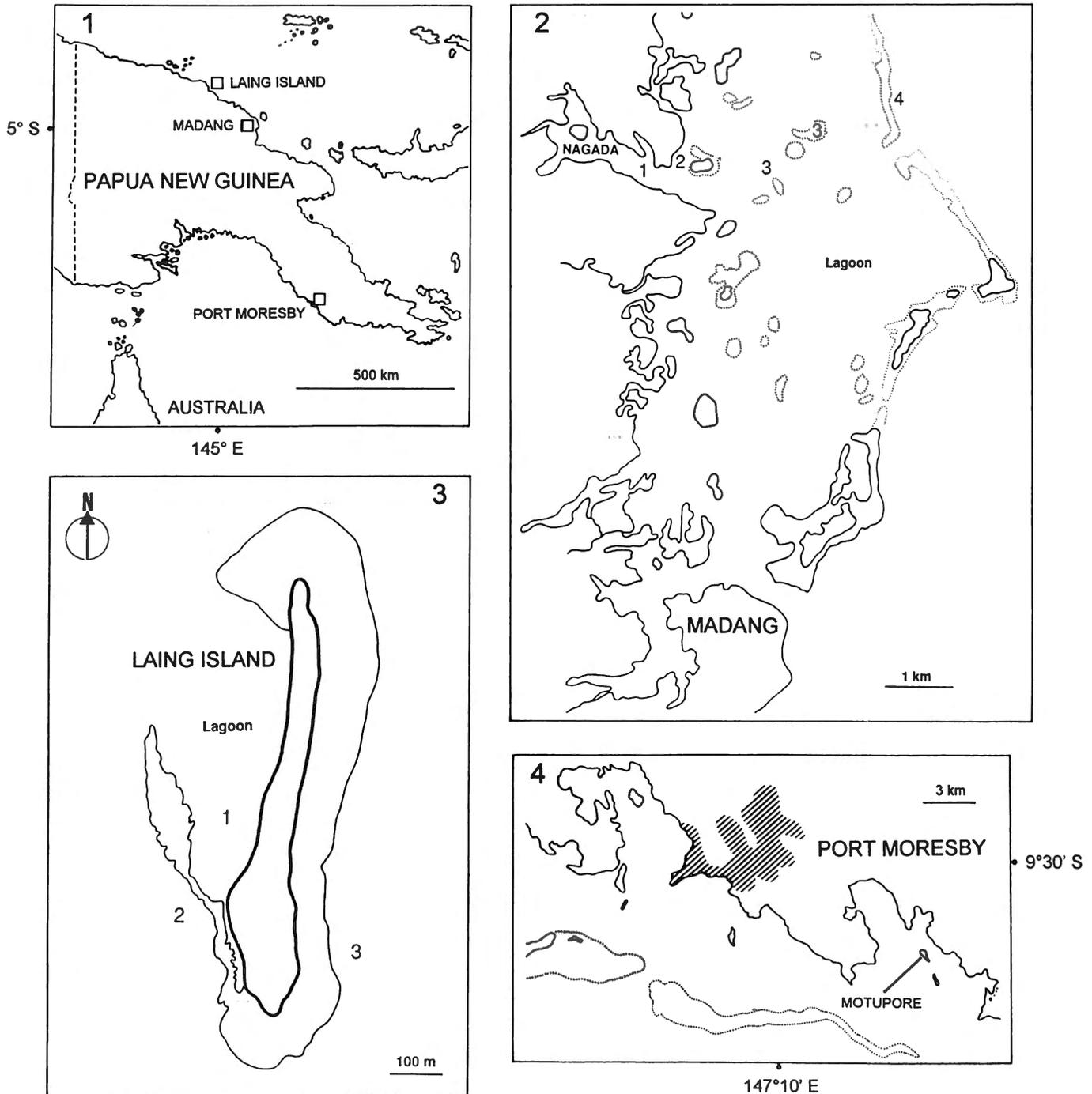
Indo-pacific corals can be infested by many mollusc species (ROBERTSON, 1970) among which the boring Coralliophilidae (Gastropoda). They represent inconspicuous animals that infest mainly corals belonging to the families Fungiidae and Faviidae (MASSIN, 1989). So far, there is little information on their biology and ecological requirements.

Taxonomic studies of the Fungiidae (HOEKSEMA, 1989a, b, 1990, 1993a, b; HOEKSEMA & CHANG-FENG DAI, 1991) and studies on their ecology and distribution (CLAEREBOUDT, 1989; KOH & CHOU, 1989; HOEKSEMA, 1990, 1991a, b, 1992; HOEKSEMA & MOKA, 1989; CHADWICK-FURMAN & LOYA, 1992) stimulated the study on the biology and ecology of *Leptoconchus* species infesting these corals.

## Material and methods

The fungiids were observed and collected by SCUBA diving between 0 and 30 m depth at Laing Island, Hansa Bay, Madang Province (fig. 3), off of Madang, Madang Province (fig. 2), and at Motupore Island Research Station, Central Province (fig. 4), all three in Papua New Guinea (fig. 1); at Singapore (fig. 6); at the Ari Atoll and South Male Atoll, the Maldives (fig. 5), at Hurghada, Red Sea, Egypt (fig. 7) and off Makassar, Sulawesi, Indonesia (figs 8-9). The fungiids collections of the National Museum of Natural History (Leiden, the Netherlands), the Museum of the National University of Singapore (Singapore) and the Royal Belgian Institute of Natural Sciences (Brussels, Belgium) were examined for infested Fungiidae.

Most of the infested Fungiidae were measured (diameter or



Figs 1-4. – Papua New Guinea. 1. General view; 2. Madang reefs (Madang Province); 3. Laing Island, Hansa Bay (Madang Province); 4. Motupore (Central Province).

length/width) and photographed. The distance between the opening of the siphon and the mouth or the centre of the coral was measured. Random cumulative curves of settlement were established (fig. 10). Curve A was calculated from the centre of a circle or an ellipse and curve B was calculated from the median of a rectangle. Curve A was compared with cumulative curve of settlement of *Leptoconchus* living in circular Fungiidae with burrow opening at both oral and aboral sides and of *Leptoconchus* living in elliptical Fungiidae with burrow opening at the aboral side. Curve B was compared

with cumulative curves of settlement of *Leptoconchus* living in elliptical Fungiidae with a very long mouth slit and with the burrow opening at the oral side.

For most of the infested fungiids, coral thickness was measured at the centre and on the edge. This height, including septal and coastal teeth, was measured at the level of the most exsert septae (primary septae). The ratio shell height/shell width (H/W) of the *Leptoconchus* specimens was calculated for the females. Shells are defined as globose when  $H/W \geq 0.8$  and lenticular when  $H/W \leq 0.7$ .

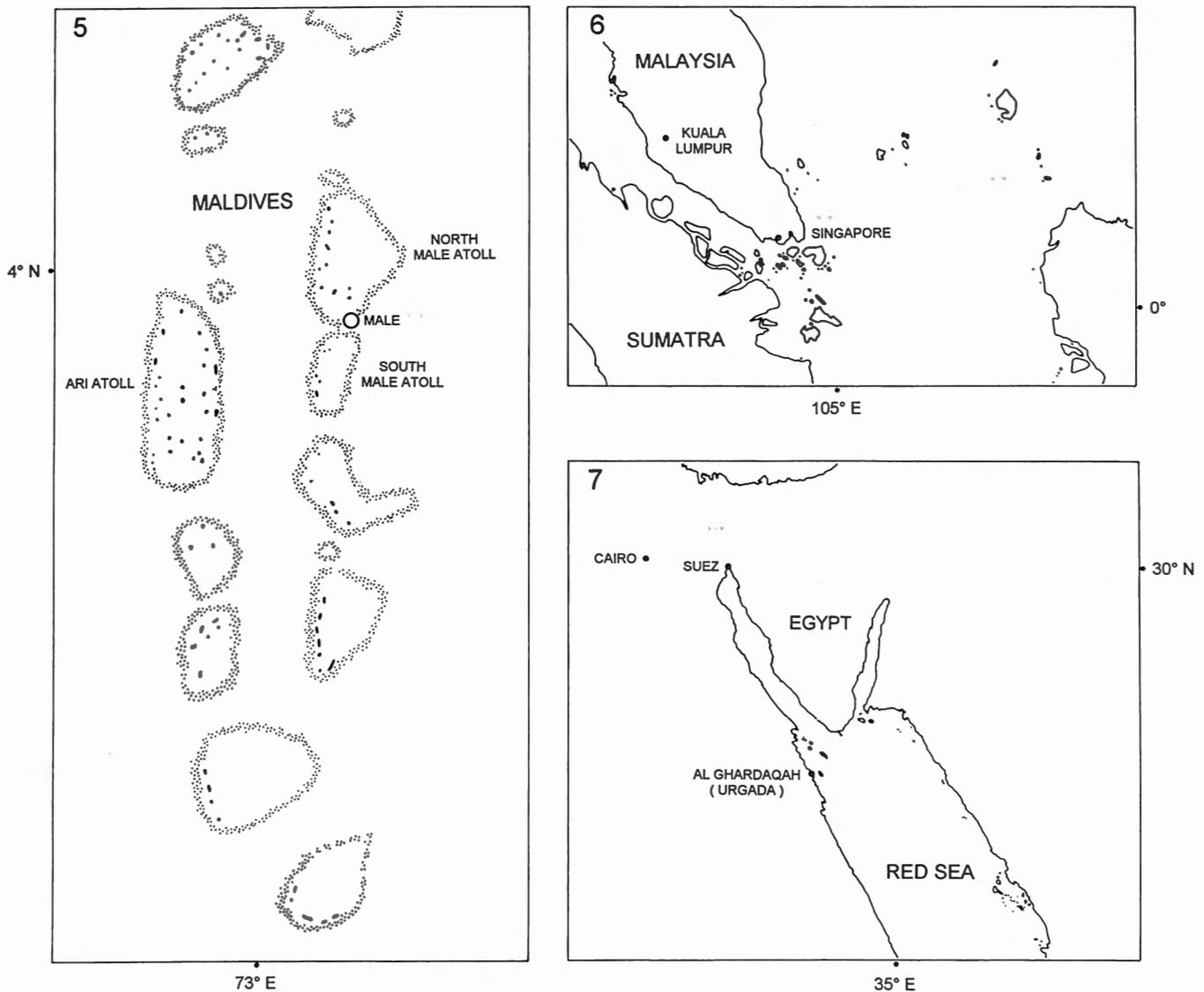


Fig. 5. – The Maldives. • Fig. 6. – Singapore. • Fig. 7. – Hurgada (Egypt, Red Sea).

Each infested fungiid was broken by cracking it with pincers. The molluscs were extracted from their hole, then counted, anaesthetized with 4%  $MgCl_2$  for a few hours and fixed in 10% buffered formalin. Later on, they were preserved in 70% buffered alcohol.

Population density of mushroom coral assemblages were measured by counting the fungiids larger than 50 mm in diameter, present on surface of 25 X 2 or 50 X 2 m at different depths: 2-4 or 2-5 m and 4-7 or 5-10 m according to the profile of the studied site. Together, the most common corals were identified underwater and the presence or absence of *Leptoconchus* specimens was noted. Prospected sites were selected on protected, semi-protected and exposed areas.

About forty infested *Fungia* specimens (mainly *Fungia (Fungia) fungites* and a few *F. scutaria*, *F. paumotensis* and *Halomitra pileus*) have been observed *in situ* in a protected area (zone 1, fig. 3) day and night to notice the activity of the tentacles of the *Fungia* and of the siphons of the *Leptoconchus*. Siphons were observed extended (well visible

above coral surface), contracted (still visible but at level with the coral surface) and withdrawn (no longer visible).

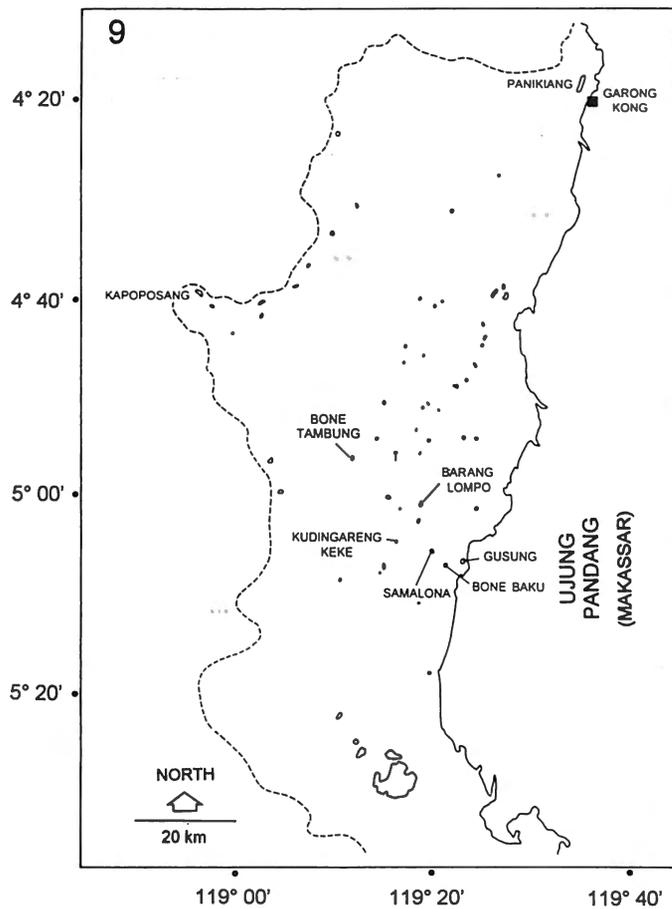
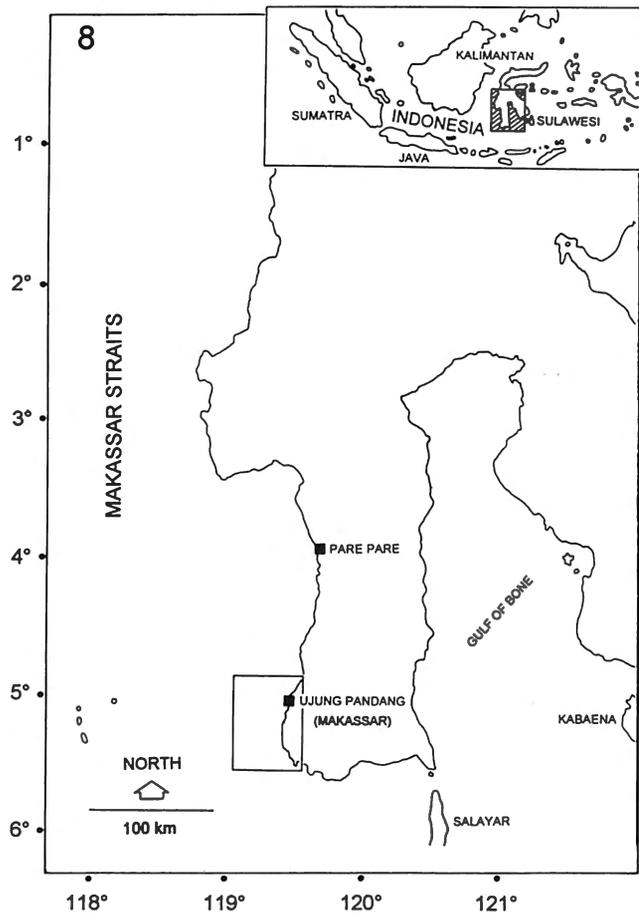
## Results

### GENERAL DISTRIBUTION OF INFESTED FUNGIIDS AND RATE OF INFESTATION

A total of 28,000 mushroom coral individuals (Fungiidae) were examined (27,000 in the field and 1,000 in museum collections). Of the 43 known species in this family, 7 had, up to now, not been found infested by *Leptoconchus* species (table 1). Four of the non infested fungiids belonged to the genera *Podabacia*, *Lithophyllon* and *Cantharellus*, which included only fixed fungiids. Three others i.e. *Fungia (Cycloseris) hexagonalis*, *F. (Pleuractis) taiwanensis* and *Halomitra clavator* are rare species generally characteristic of soft, sandy or muddy bottoms.

Table 1. List of fungiids observed and/or collected + data of literature. A: opening of *Leptoconchus* burrow at aboral side of coral; F: record from field collected material; IND: Indonesia; L: record from literature; M: record from museum collections; MAL: Maldives; nbr: number of infested corals observed; NCAL: New Caledonia; O: opening of *Leptoconchus* burrow at oral side of coral; PNG: Papua New Guinea; RS: Red Sea; SEY: Seychelles; TAW: Taiwan; 1: HOEKSEMA & ACHITUV 1993; 2: ZIBROWIUS & ARNAUD 1994; 3: HOEKSEMA 1993a; 4: HOEKSEMA 1993b; 5: VERON 1990.

Coral species	origin	infest.	Oral/Aboral	nbr	locality
<i>Fungia (Cycloseris) sinensis</i>	L <sup>1</sup>	+	O	6	IND
<i>Fungia (Cycloseris) fragilis</i>	M+F	+	O	3	IND+PNG
<i>Fungia (Cycloseris) hexagonalis</i>	M	-	/	0	IND
<i>Fungia (Cycloseris) distorta</i>	M	+	O	1	IND
<i>Fungia (Cycloseris) cyclolites</i>	M	+	O	1	IND
<i>Fungia (Cycloseris) vaughani</i>	M	+	O	4	IND
<i>Fungia (Cycloseris) sommervillei</i>	M+L <sup>2</sup>	+	O	2	IND+SEY
<i>Fungia (Cycloseris) costulata</i>	F	+	O	5	PNG+IND
<i>Fungia (Cycloseris) tenuis</i>	F	+	O	6	PNG
<i>Cantharellus doederleini</i>	M	-	/	0	RS
<i>Cantharellus noumeae</i>	M	-	/	0	NCAL
<i>Cantharellus jebbi</i>	L <sup>3</sup>	+	O	1	PNG
<i>Fungia (Wellsofungia) granulosa</i>	F	+	O	18	PNG+IND
<i>Fungia (Pleuractis) mollucensis</i>	M+F	+	O	13	IND
<i>Fungia (Pleuractis) gravis</i>	M+F	+	A	6	IND+PNG
<i>Fungia (Pleuractis) paumotensis</i>	F	+	O	35	PNG+IND
<i>Fungia (Pleuractis) taiwanensis</i>	M	-	/	0	TAW
<i>Fungia (Pleuractis) seychellensis</i>	L <sup>4</sup>	+	A	1	SEY
<i>Fungia (Verrillofungia) scabra</i>	M	+	A	3	IND
<i>Fungia (Verrillofungia) spinifer</i>	F	+	A	2	PNG
<i>Fungia (Verrillofungia) concinna</i>	F	+	A	16	PNG/IND
<i>Fungia (Verrillofungia) repanda</i>	F	+	A	58	PNG+MAL+IND
<i>Fungia (Lobactis) scutaria</i>	F	+	O	20	PNG
<i>Herpolitha limax</i>	F	+	A	15	PNG/IND
<i>Polyphyllia talpina</i>	F	+	O	7	PNG+IND
<i>Polyphyllia novaehiberniae</i>	F	+	O	4	PNG
<i>Heliofungia actiniformis</i>	M+F	+	A	23	IND+PNG
<i>Fungia (Danafungia) fralinae</i>	M+F	+	A	2	IND
<i>Fungia (Danafungia) horrida</i>	M+F	+	A	18	PNG+RS+IND
<i>Fungia (Danafungia) scruposa</i>	F	+	O	37	PNG+MAL+IND
<i>Fungia (Fungia) fungites</i>	F	+	O	301	PNG+MAL+IND
<i>Halomitra pileus</i>	F	+	O	18	PNG+MAL+IND
<i>Halomitra clavator</i>	M	-	/	0	IND
<i>Ctenactis albitentaculata</i>	F	+	A	6	PNG
<i>Ctenactis crassa</i>	F	+	A	7	PNG+IND
<i>Ctenactis echinata</i>	F	+	A	7	PNG
<i>Sandalotitha robusta</i>	F	+	A	3	PNG
<i>Sandalotitha dentata</i>	M+F	+	A	2	IND+PNG
<i>Zoopilus echinatus</i>	M+F	+	O	2	IND+PNG
<i>Podabacia motuporensis</i>	L <sup>5</sup>	-	/	0	PNG
<i>Podabacia crustacea</i>	F	+	O	3	PNG
<i>Lithophyllon mokai</i>	M	-	/	0	IND
<i>Lithophyllon undulatum</i>	M+F	+	A	1	IND



Figs 8-9. – Indonesia. 8. Spermonde Archipelago (Sulawesi); 9. Reefs off Makassar (Sulawesi).

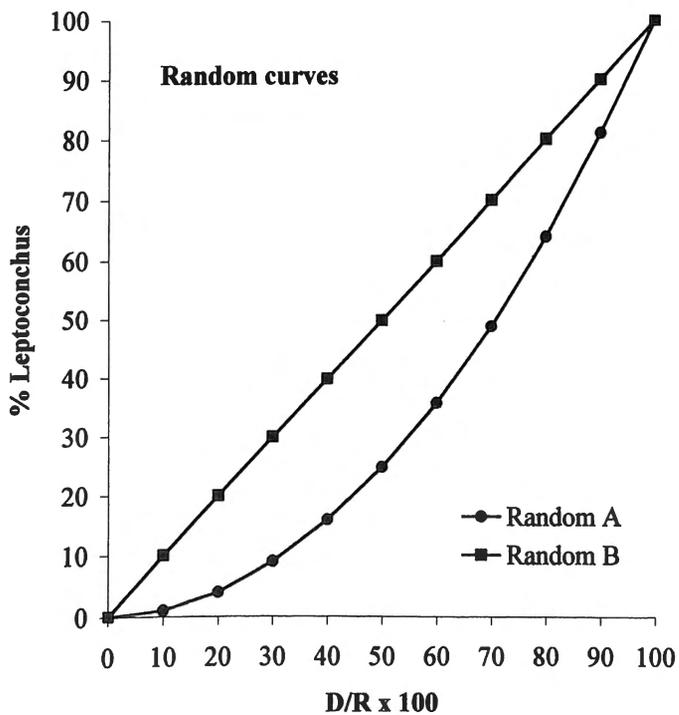


Fig. 10. – Random cumulative curves of settlement. A: calculated from center of a circle or an ellipsoid; B: calculated from median of a rectangle. D: shorter distance from mouth of coral to opening of burrow of the mollusc. R: radius (curve A) or 1/2 width (curve B) of coral.

The most infested species were, by decreasing order, *Fungia (Fungia) fungites*, *F. (Verrillofungia) repanda*, *F. (Pleuractis) paumotensis*, and *F. (Danafungia) scruposa* (table 1). However, variations occurred and some coral species heavily infested at one locality were free of *Leptoconchus* at another locality (table 2)

The two most prospected sites in Papua New Guinea were Laing Island and Madang (figs 11, 12). At Madang reefs,

Table 2. Number of infested specimens/total number of infested fungiids collected x 100 for the ten most infested fungiids species according to table 1. PNG: Papua New Guinea; IND: Indonesia.

Coral species	PNG	IND
<i>Fungia (Fungia) fungites</i>	39.3	15.0
<i>Fungia (Verrillofungia) repanda</i>	12.9	5.0
<i>Fungia (Pleuractis) paumotensis</i>	2.5	25.0
<i>Fungia (Danafungia) scruposa</i>	6.2	12.0
<i>Heliofungia actiniformis</i>	4.0	8.0
<i>Fungia (Lobactis) scutaria</i>	5.0	/
<i>Fungia (Wellsofungia) granulosa</i>	2.5	8.0
<i>Fungia (Danafungia) horrida</i>	2.0	2.0
<i>Halomitra pileus</i>	3.2	1.0
<i>Fungia (Verrillofungia) concinna</i>	3.5	3.0

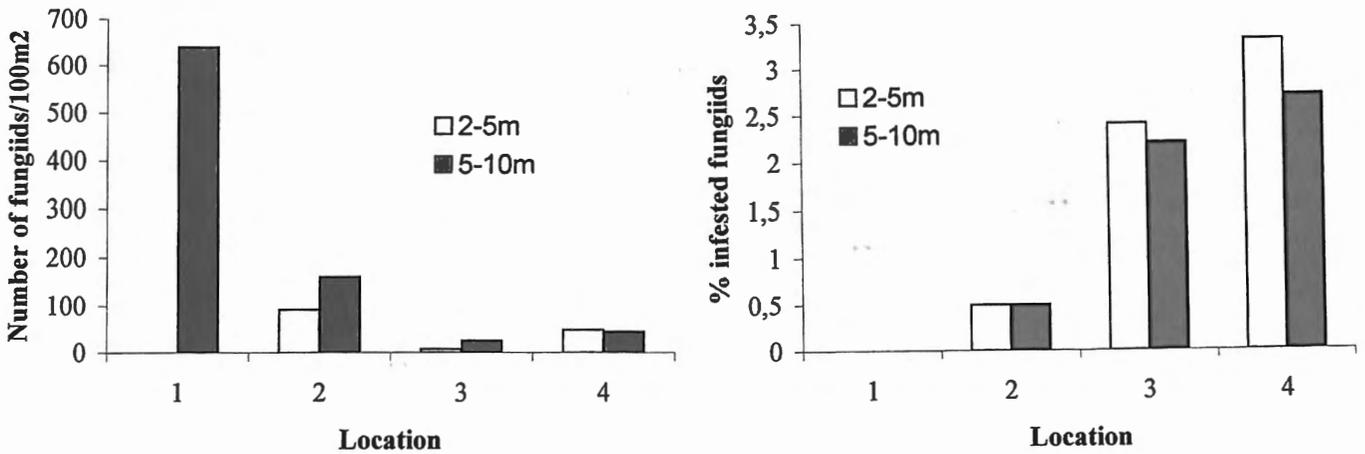


Fig. 11. – Number of fungiids/100 m<sup>2</sup> and rate of infestation versus different localities through Madang's Reef (Papua New Guinea).

(fig. 11) there was a clear decrease in the number of Fungiidae/100 m<sup>2</sup> and an increase in the rate of infestation when sampling from the Mangrove (protected area: point 1, fig. 2) to the barrier reef (exposed area: point 4, fig. 2). *Fungia (Fungia) fungites* represented 8% of the fungiid assemblage in the mangrove area and 36% on the barrier reef. Figure 11 shows also that on the barrier reef, depth (2-5m versus 5-10m) had no influence on the number of fungiids/100 m<sup>2</sup>. Moreover, the mangrove which corresponded to very turbid waters, lacked any *Leptoconchus*.

At Laing Island (fig. 3), which is similar to a barrier reef, the density of Fungiidae was always higher between 4-7 m than between 2-4 m depth in exposed (point 3, fig. 3) and semi-protected areas (point 1, fig. 3). In contrast, the infestation rate was similar or higher between 2-4 m than between 4-7 m depth. At the exposed side of Laing Island, *Fungia (Fungia) fungites* reached an infestation rate of 19%, the highest value ever recorded. The number of fungiids/100 m<sup>2</sup> between 0 and 10 m depth varied from 0 to 640 with an average of 161 (Madang + Laing Island).

Table 3. Number of fungiid species infested (A) and number of specimens infested (B) at several coral reefs in the Spermonde Archipelago (fig. 9).

A	Localities	B	Localities
0	Panikiang	0	Panikiang
1	Lae-Lae	1	Lae-Lae
2	Gusung	2	Gusung
5	Barang Lompo	12	Barang Lompo
7	Barang Caddi	13	Bone Tambung
8	Bone Tambung	18	Barang Caddi
12	Samalona	25	Samalona
12	Kudigareng Keke	32	Kudigareng Keke

At Makassar, reefs close to the coast as Panikiang, Lae-Lae or Gusung (fig. 9), with turbid to very turbid waters, were nearly free of *Leptoconchus*. In offshore direction, the number of infested fungiids increased and the further away

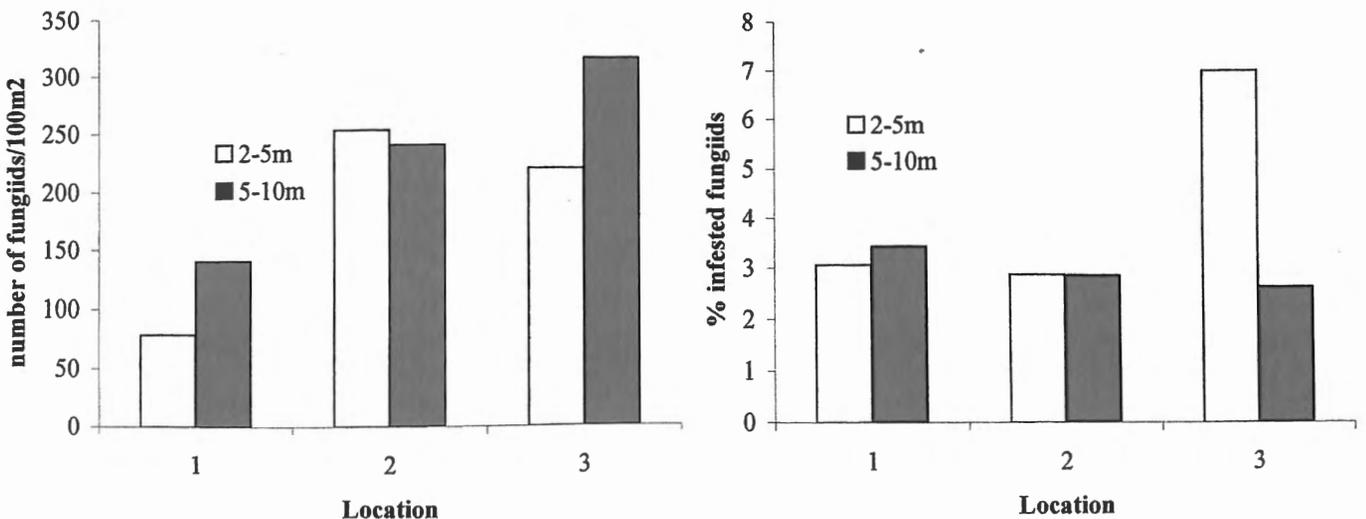


Fig. 12. – Number of fungiids/100 m<sup>2</sup> and rate of infestation versus different localities around Laing Island (Hansa Bay, Papua New Guinea).

from the coast, the more infested the fungiid assemblage (table 3). However, the rate of infestation of the fungiid assemblage for the whole area was still very low: 0 to 0.02%. At Makassar, the three most infested species were, by decreasing order, *Fungia (Pleuractis) paumotensis*, *F. (Fungia) fungites* and *F. (Pleuractis) moluccensis*.

The most heavily infested fungiids were found at Papua New Guinea (North Coast) and Indonesia (Sulawesi). In these areas, up to now, 35 fungiid species, representing 85 % of the species present, were infested by *Leptoconchus* spp. Around the Maldives and at the Red Sea (Hurghada) only four and one fungiid species, respectively, were observed infested by *Leptoconchus* spp. No *Leptoconchus* spp. were observed in Fungiidae around the reefs close to Singapore, where the reefs are situated in muddy water.

All the genera and subgenera of Fungiidae were infested by *Leptoconchus* spp. which makes the Fungiidae the most infested coral family.

THE POSITION AND THE NUMBER OF *LEPTOCONCHUS* IN THE CORAL

The place of settlement on a fungiid and the number of *Leptoconchus* in a fungiid varied greatly depending on the coral species. These differences were obvious mainly between species that had the opening of the burrow either at the oral side or at the aboral side of the fungiid.

Opening of *Leptoconchus* burrows at the oral side of monostomatous fungiids

Sixteen monostomatous infested fungiids had the opening of the *Leptoconchus* burrow at the oral side i.e. *Fungia (Cycloseris) sinensis*, *F. (C.) fragilis*, *F. (C.) distorta*, *F. (C.) cyclolites*, *F. (C.) vaughani*, *F. (C.) sommervillei*, *F. (C.) costulata*, *F. (C.) tenuis*, *Cantharellus jebbi*, *F. (Wellsofungia) granulosa*, *F. (Pleuractis) mollucensis*, *F. (P.)*

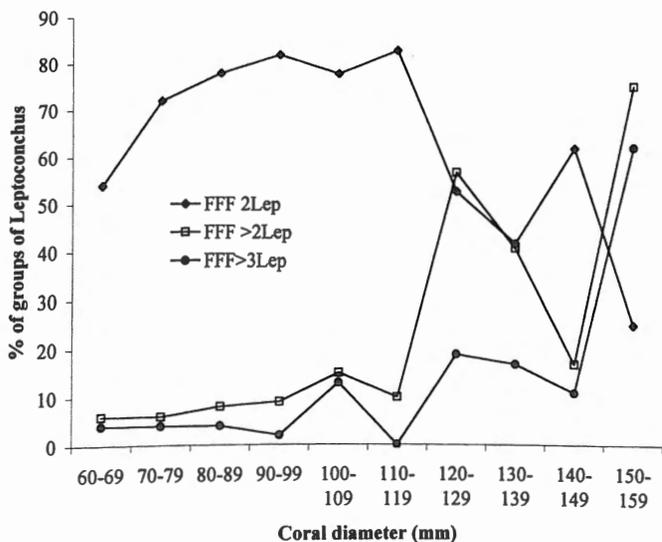


Fig. 13. – Number of *Leptoconchus* individuals present versus coral diameter: *Fungia (Fungia) fungites*.

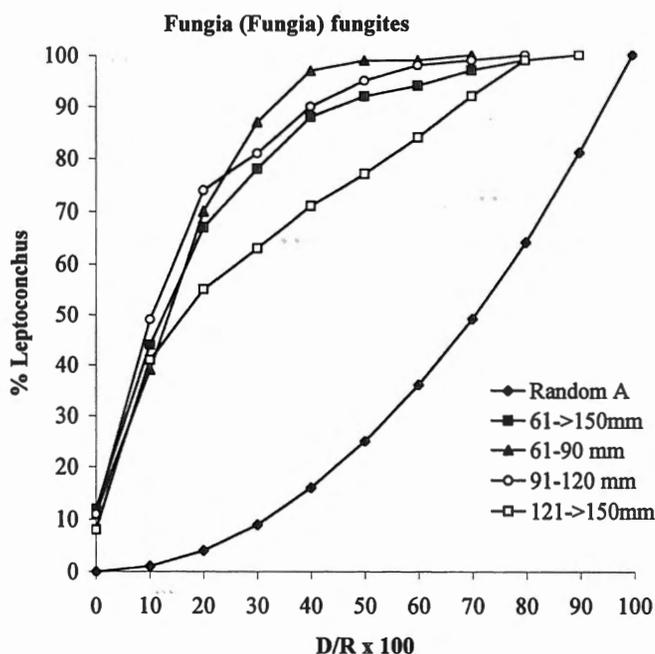


Fig. 14. – Cumulative curves of settlement of *Leptoconchus* individuals infesting *Fungia (Fungia) fungites*.

*paumotensis*, *F. (Lobactis) scutaria*, *F. (Danafungia) scruposa*, and *F. (F.) fungites*.

Small *Fungia (Fungia) fungites* (<60 mm in diameter) were never infested. In corals ranging from 60 to 120 mm in diameter, there were nearly always 2 *Leptoconchus* individuals per coral (81% of the observations) whereas more than 2 or 3 *Leptoconchus* individuals in a single coral were exceptional (<10% of the observations) (fig. 13). In large corals (>120 mm in diameter), 2 *Leptoconchus* snails, per coral were less frequent than in small corals (<60% of the observations), whereas the observations dealing with more than 2 or 3 *Leptoconchus* specimens in a single coral were more abundant (>40%) (fig. 13). Six *Leptoconchus* individuals (three well separated pairs) per *F. (F.) fungites* was the maximum observed.

The cumulative curve of settlement of *Leptoconchus* infesting *F. (F.) fungites* (fig. 14) clearly shows that the molluscs were concentrated near the mouth opening: 90% of the *Leptoconchus* specimens were near the coral mouth on a surface representing 50% of the coral surface. The smaller the coral, the more concentrated were the *Leptoconchus* individuals near the coral mouth (fig. 14). These observations were valid for *F. (F.) fungites* populations from the Maldives and Papua New Guinea.

Measurements of *F. (F.) fungites* corals show that their thickness varied with increasing size. Up to 120 mm in diameter, the peripheral thickness increased slowly whereas the central thickness remained nearly constant (fig. 15). Beyond 120 mm in diameter, the thickness increment was restricted to the central part of the corals whereas the edge remained constant (fig. 15).

The *Leptoconchus* specimens infesting *Fungia (Danafungia) scruposa* and *F. (Lobactis) scutaria* presented very similar

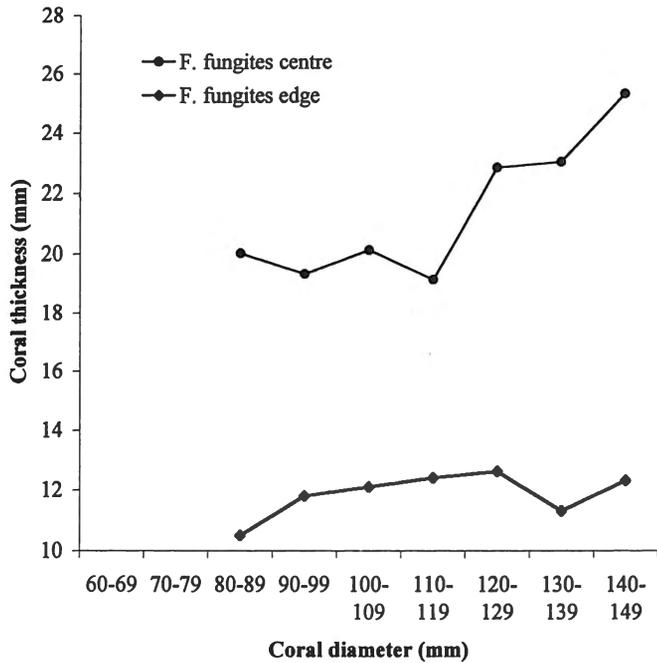


Fig. 15. - Coral thickness versus coral diameter: *Fungia (Fungia) fungites*.

settlement curves (fig. 16): 95% of the molluscs were concentrated near the coral mouth on a surface representing 10% of the coral surface. Inside *F. (D.) scruposa*, up to 80% of the molluscs had the siphon in the mouth opening. Moreover, the number of *Leptoconchus* snails infesting a coral was restricted to one or two (88 and 79% of the observations for *F. (D.) scruposa* and *F. (L.) scutaria*, respectively).

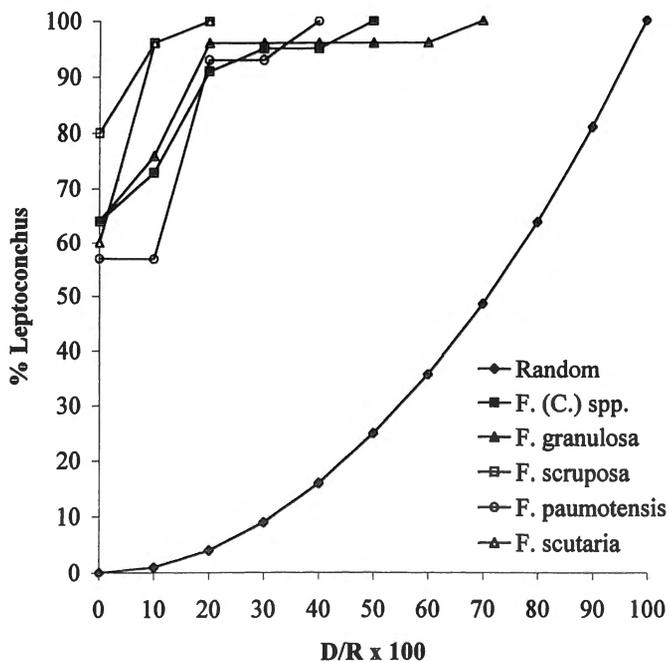


Fig. 16. - Cumulative curves of settlement of *Leptoconchus* individuals infesting *Fungia (Wellsofungia) granulosa*, *F. (Pleuractis) paumotensis*, *F. (Cycloseris) spp.*, *F. (Danafungia) scruposa* and *F. (Lobactis) scutaria*.

The *Leptoconchus* specimens infesting *Fungia (Wellsofungia) granulosa*, *F. (Pleuractis) paumotensis* and all the *F. (Cycloseris) spp.* presented very similar cumulative curves of settlement (fig. 16). The *Leptoconchus* specimens were somewhat less concentrated near the coral mouth than those of *F. (D.) scruposa* and *F. (L.) scutaria*.

The single infested specimen of *Cantharellus jebbi* had the opening of the mollusc burrow close to the mouth and resembled the settlement pattern of the *Fungia (Cycloseris) spp.*

In all the monostomatous fungiids with the *Leptoconchus* opening at the oral side, there was generally no or only a weak deformation of the coral skeleton (figs 17a, b, e, 18a). Only occasionally strong deformations, with sometimes formation of secondary mouths (figs 17c, d, f ; 18b, c), were observed. Eighty to 90% of the *Leptoconchus* individuals infesting the monostomatous fungiids with the opening at the oral side were single or occurs in pairs. Clusters of 3 *Leptoconchus* specimens represented more or less 10% of the observations and 4 *Leptoconchus* snails or more together were exceptional. Moreover, the shell of *Leptoconchus* was always globose.

Tentacles of *Fungia (F.) fungites*, *F. (Lobactis) scutaria* and *F. (Pleuractis) paumotensis* came out around 6 p.m. at sunset. At 9 p.m. they were all fully extended. At 6 a.m. nearly all the tentacles of the *Fungia* spp. were withdrawn. During day time, 20% of the *Leptoconchus* siphon were completely withdrawn (fig. 19). This value decreased at sunset to reach its lowest value (5%) at 3 a.m. Between 6 p.m. and 6 a.m. siphons were particularly visible, 75% being in full extension (fig. 19). Around midnight the percentage of extended siphons already decreased (fig. 19). During day and night dives, proboscides of the *Leptoconchus* spp. were never observed protruding through the opening of the burrow.

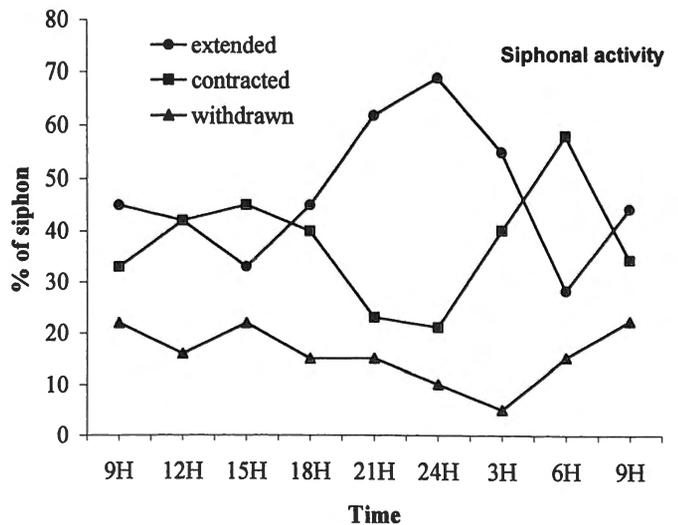


Fig. 19. - Siphonal activity.

#### Opening of *Leptoconchus* burrows at the oral side of polystomatous fungiids

Five polystomatous infested fungiid species had the *Leptoconchus* opening at the oral side, i.e. *Halomitra pileus*, *Polyphyllia talpina*, *P. novaehiberniae*, *Zoopilus echinatus*

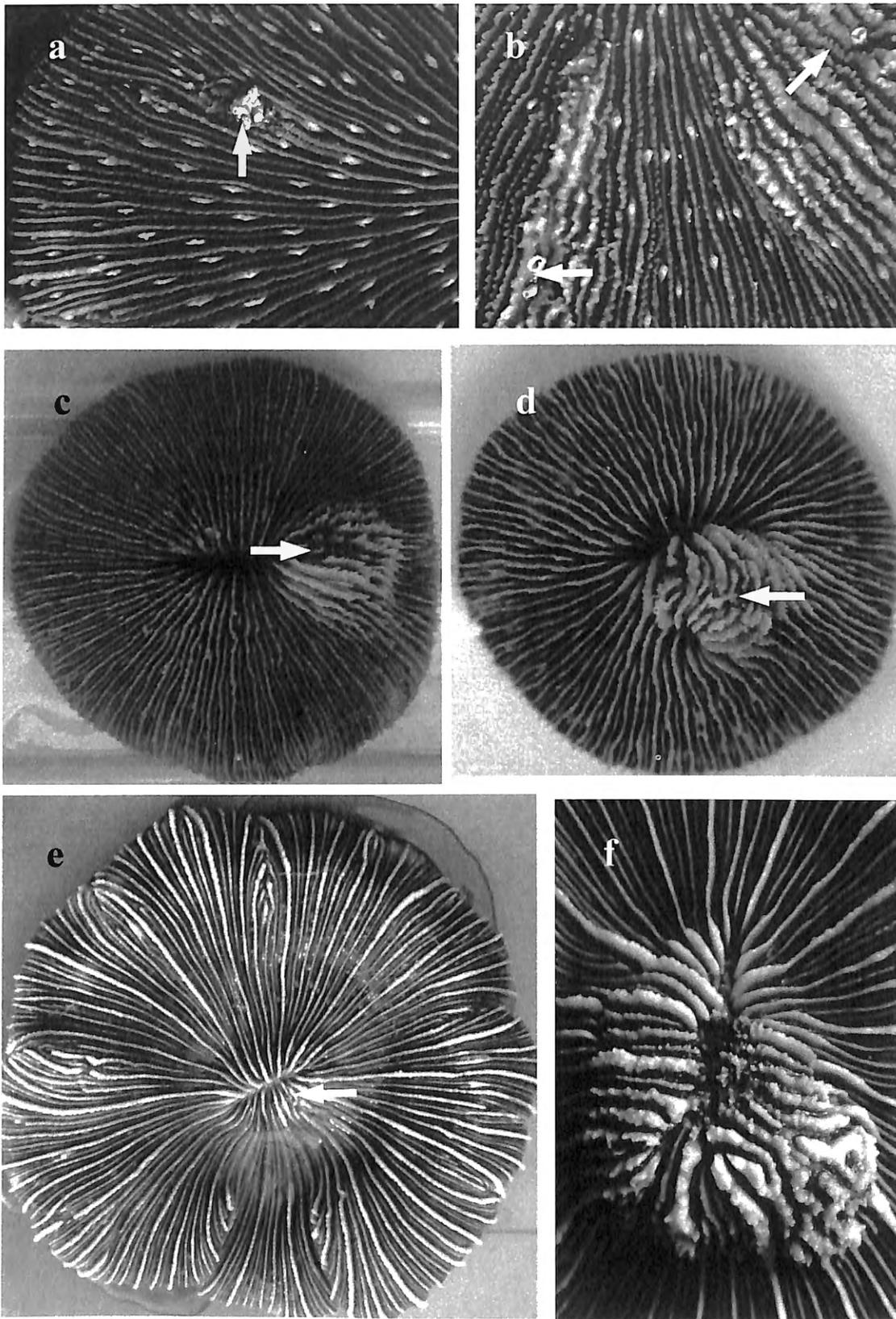


Fig. 17. – a: oral side of *Fungia* (*Fungia*) *fungites* without deformation of coral skeleton. Arrow indicates a pair of siphons of *Leptoconchus* specimens; b: oral side of *F.* (*F.*) *fungites* without deformation of coral skeleton. Arrows indicate siphons of *Leptoconchus* specimens; c & d: oral side of *F.* (*F.*) *fungites* with deformation of coral skeleton. Arrows indicate opening of *Leptoconchus* burrows; e: oral side of *Fungia* (*Danafungia*) *scruposa* without deformation of coral skeleton. Arrow indicates opening of a *Leptoconchus* burrow; f: close up of oral side (central part) of a *F.* (*D.*) *scruposa* with strong deformation of coral skeleton around the mouth.

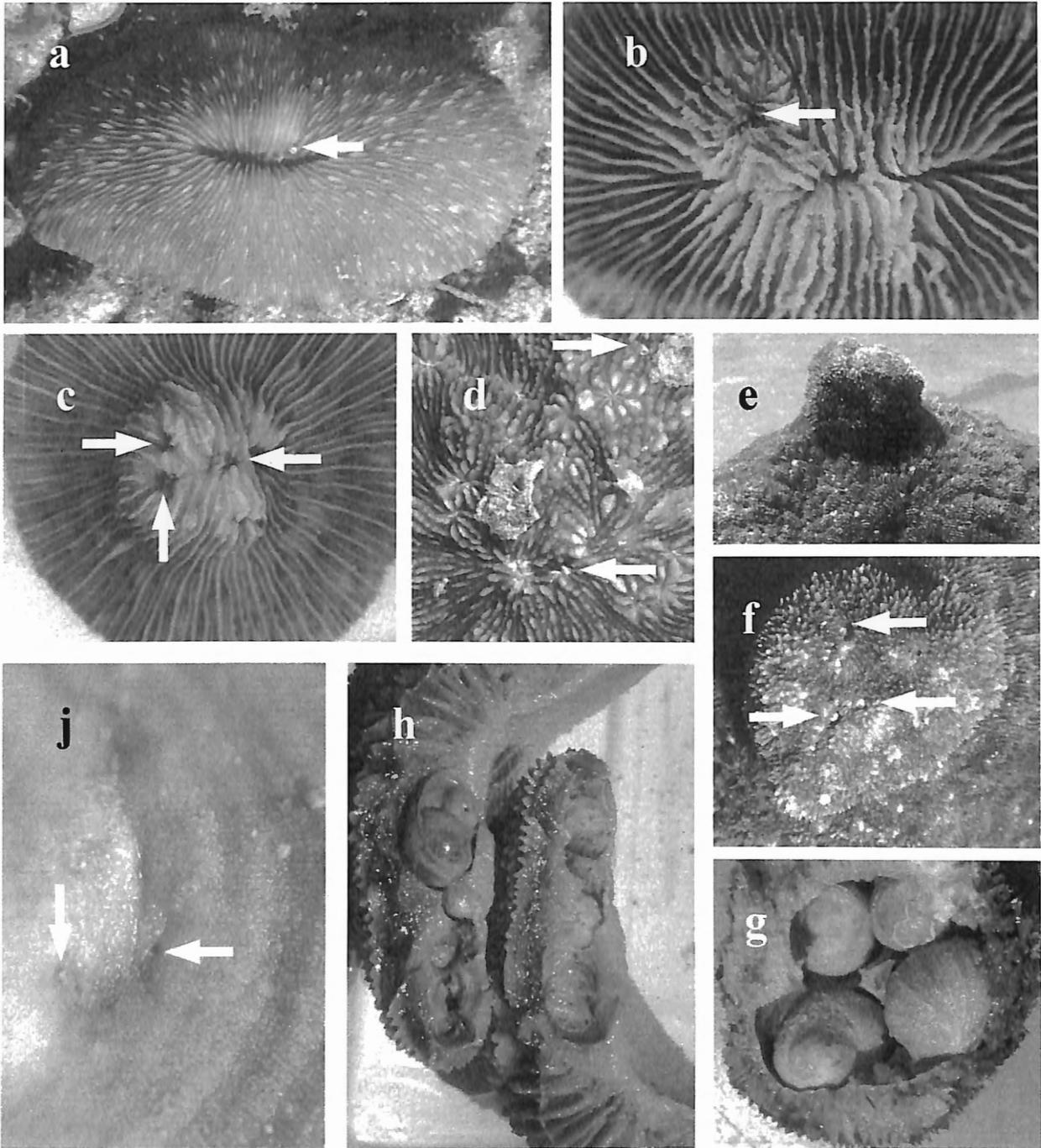


Fig 18. – a: oral side of *Fungia (Lobactis) scutaria* without deformation of coral skeleton. Arrow indicates siphon of a *Leptoconchus* specimen; b: oral side of *Fungia (Pleuractis) paumotensis* with strong deformation of coral skeleton. Arrow indicates opening of a *Leptoconchus* burrow; c: oral side of *Fungia (Wellsofungia) granulosa* with strong deformation of coral skeleton. Arrows indicate opening of *Leptoconchus* burrows; d: oral side of *Halomitra pileus* without deformation of coral skeleton. Arrows indicate siphons of *Leptoconchus* specimens; e & f: gall formed on the oral side of *Holomitra pileus*. Arrows indicate siphons of *Leptoconchus* specimens; g: inside gall showing a cluster of globose *Leptoconchus* individuals; h: *Heliofungia actiniformis* split and showing inside a cluster of lenticular *Leptoconchus* specimens. No deformation of coral skeleton is visible; j: aboral side of *Ctenactis crassa* without deformation of coral skeleton. Arrows indicate openings of a *Leptoconchus* burrow.

and *Podabacia crustacea*. Except *H. pileus*, few of them were found infested (table 1) and cumulative curves of infestation could not be established.

*Leptoconchus* infesting *H. pileus* presented a cumulative curve of settlement close to the *Leptoconchus* infesting *F. (F.) fungites* (fig. 20): 95% of the settlement occurred on 50% of the coral surface starting from the centre.

The polystomatous fungiids infested with the *Leptoconchus* opening at the oral side generally presented a low (*Zoopilus echinatus*, *Podabacia crustacea*) or a strong (*Polyphyllia* spp.) deformation of the coral skeleton. The shells of the *Leptoconchus* specimens infesting those corals were lenticular. Sometimes, as for *Halomitra pileus*, there was formation of a gall (fig. 18e-f) containing a cluster of globose *Leptoconchus* (fig. 18g).

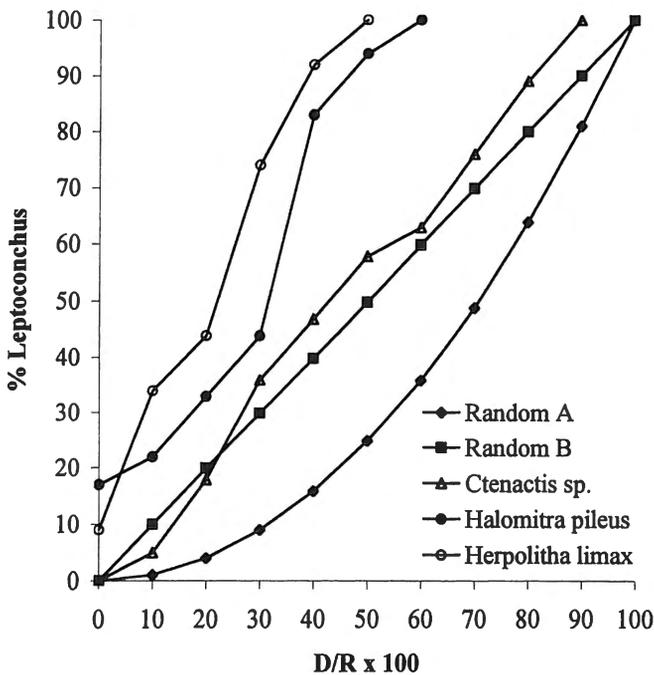


Fig. 20. — Cumulative curves of settlement of *Leptoconchus* individuals infesting *Ctenactis* spp., *Halomitra pileus* and *Herpolitha limax*.

*Opening of Leptoconchus burrows at the aboral side of monostomatous fungiids*

Twelve monostomatous infested fungiids had the *Leptoconchus* opening at the aboral side, i.e. *Fungia (Pleuractis) gravis*, *F. (P.) seychellensis*, *F. (Verrillofungia) repanda*, *F. (V.) concinna*, *F. (V.) spinifer*, *F. (V.) scabra*, *Heliofungia actiniformis*, *F. (Danafungia) fralinae*, *F. (D.) horrida*, *Ctenactis albitentaculata*, *C. echinata*, and *C. crassa*<sup>1</sup>.

1. *C. crassa* is a polystomatous fungiid. However, all the mouths resulted of intrastomodeal budding inside the axial groove. I consider this subdivision of the mouth not important for the settlement of a *Leptoconchus*. Consequently, in the present work, *C. crassa* will be dealt with the monostomatous fungiids.

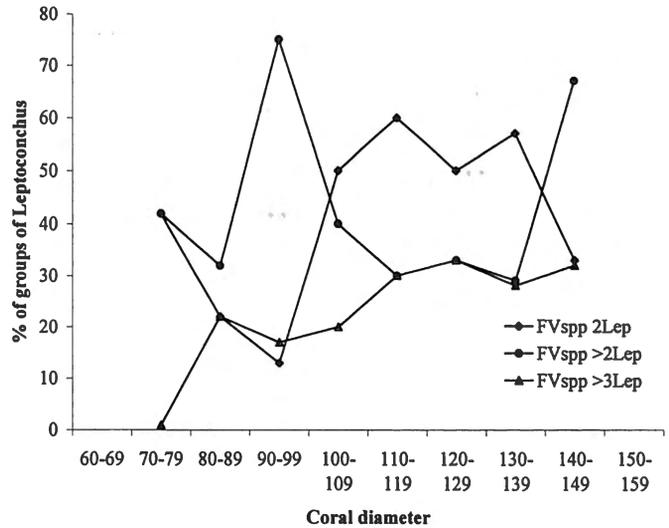


Fig. 21. — Number of *Leptoconchus* specimens present versus coral diameter: *Fungia (Verrillofungia)* spp.

The number of *Leptoconchus* specimens in *Fungia (Verrillofungia) repanda* and *F. (V.) concinna* populations was poorly correlated with the coral diameter (fig. 21). Two *Leptoconchus* specimens per coral represented only 42 % of the observations, whereas more than 2 or 3 *Leptoconchus* specimens in a single coral represented 40 % of the observations. The situation was the same for *Heliofungia actiniformis* in which up to ten *Leptoconchus* snails, forming a cluster, were observed in a single coral (fig. 18h).

The *Leptoconchus* individuals infesting *F. (V.) repanda*, *F. (V.) concinna*, *H. actiniformis*, and *F. (P.) gravis* presented very similar curves of settlement (fig. 22), which were close

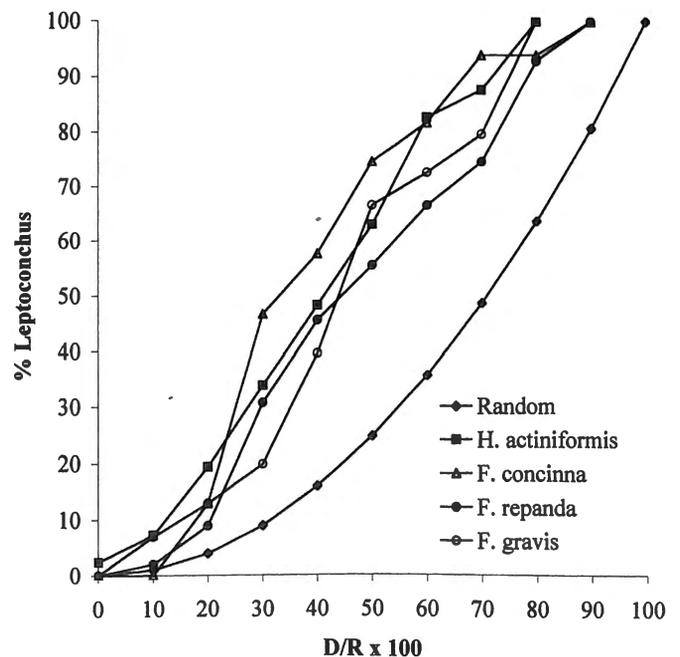


Fig. 22. — Cumulative curves of settlement of *Leptoconchus* individuals infesting *Heliofungia actiniformis*, *Fungia (Verrillofungia) concinna*, *F. (V.) repanda* and *F. (Pleuractis) gravis*.

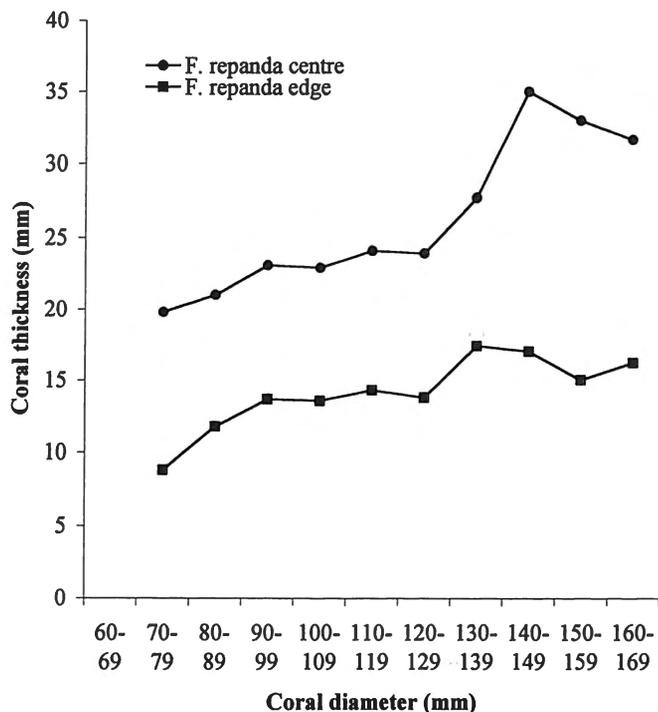


Fig. 23. – Coral thickness versus coral diameter: *Fungia (Verrillofungia) repanda*.

to a “B” random F. curve. The *Leptoconchus* individuals infesting *Ctenactis* spp. had a curve of settlement (fig. 20) very close to an “A” random curve.

For the *Leptoconchus* infesting the species *F. (V.) spinifer*, *F. (V.) scabra*, *F. (D.) fralinae*, *F. (D.) horrida*, and *F. (P.) seychellensis* data were too scarce to establish cumulative curves of settlement.

Measurements of *F. (V.) repanda* thickness were reported in figure 23. Up to 120 mm in diameter, the peripheral thickness increased faster than the central thickness. Beyond 120 mm in diameter, the thickness increment was much faster near the centre than at the periphery.

All the *Fungia (Verrillofungia)* species, the two above mentioned species of *F. (Danafungia)*, *Heliofungia actiniformis* and the *Ctenactis* spp. that were infested by *Leptoconchus* specimens had no deformation of the skeleton (figs 18j, 24a-c, f) or only a weak one (fig. 24d-e). This deformation was mainly visible on the aboral side resulting in the lost of the alignment of the aboral costal spines (fig. 24e). The shell of the *Leptoconchus* snails infesting *F. (P.) gravis*, *Ctenactis* spp. and *H. actiniformis* were globose whereas the shells of the ones infesting *F. (V.)* spp. and *F. (D.) horrida* were lenticular.

#### Opening of the *Leptoconchus* burrows at the aboral side of polystomatous fungiids

Four polystomatous fungiids that were infested, i.e. *Herpolitha limax*, *Sandalolitha robusta*, *S. dentata* and *Lithophyllon undulatum*, had the opening of the burrow of the *Leptoconchus* specimens at the aboral side.

The *Leptoconchus* individuals infesting *H. limax* presented a

cumulative curve of settlement (fig. 20) very similar to the one of those infesting *H. pileus* (fig. 20) and clearly distinct from a random curve. No cumulative curves of settlement could be established for the *Leptoconchus* infesting the two *Sandalolitha* species and *Lithophyllon undulatum* because of the scarcity of the observation (table 1).

In all the polystomatous fungiids mentioned above, one or two *Leptoconchus* specimens were present per specimen in 82% of the observations. If more *Leptoconchus* specimens occurred in a single coral, they occurred in pairs or isolated. Only once a cluster of 3 *Leptoconchus* individuals was observed.

The presence of *Leptoconchus* individuals did not induce a deformation of the skeleton (thickening) for *Sandalolitha robusta* and *S. dentata* (figs 24g, 25a) but did so for *H. limax* (fig 25b). For the latter, 73% of the specimens infested presented a strong deformation of the septa and a thickening of the coral (fig. 25b). The deformation was always at the oral side. At the aboral side the deformation was weak (fig. 25c) or absent (fig. 25e). The shells of the *Leptoconchus* infesting *H. limax* were globose and those infesting *Sandalolitha* spp. were lenticular.

#### SHELL HEIGHT VERSUS CORAL THICKNESS

From table 4 it appeared that there was a relationship between  $H_{\square}/T_c$  ( $H_{\square}$ : height of shell of  $\square$  *Leptoconchus*;  $T_c$ : thickness of the coral near the center) and the presence/absence of a deformation of the coral skeleton. All the studied corals (except *Fungia (Pleuraetis) gravis*) could be divided among 3 categories:

- 1)  $H_{\square}/T_c \times 100 < 60$ : coral deformation appeared in 0-30% of the observations,
- 2)  $60 < H_{\square}/T_c \times 100 < 70$ : coral deformation appeared in 30-55% of the observations,
- 3)  $H_{\square}/T_c \times 100 > 70$ : coral deformation appeared in 92-100% of the observations.

The third category included all the thin corals as *Polyphyllia* spp., *Halomitra pileus*, *Podabacia crustacea* and *Zoopilus echinatus*.

*F. (P.) gravis* corals that did not fit in these categories presented frequent deformation of the coral skeleton even when it was infested by small *Leptoconchus* ( $H_{\square}/T_c \times 100 = 43 \pm 7$ ;  $n=7$ ).

When shell height represented more than 70% of the coral thickness, deformation was always present. At the level of the deformation the ratio  $H_{\square}/T_c \times 100$  was  $50.7 \pm 9$  ( $n=10$ ). For the corals without deformation the ratio  $H_{\square}/T_c \times 100$  was  $51.0 \pm 7$  ( $n=7$ ).

#### Discussion

Data collected from different localities were difficult to compare because of the great discrepancy in the number of observations. At areas where a few dives were performed (Red Sea, Singapore), only the presence or absence of infested fungiids could be ascertained. Most of the graphs were based on observations from Papua New Guinea and from the Maldives.

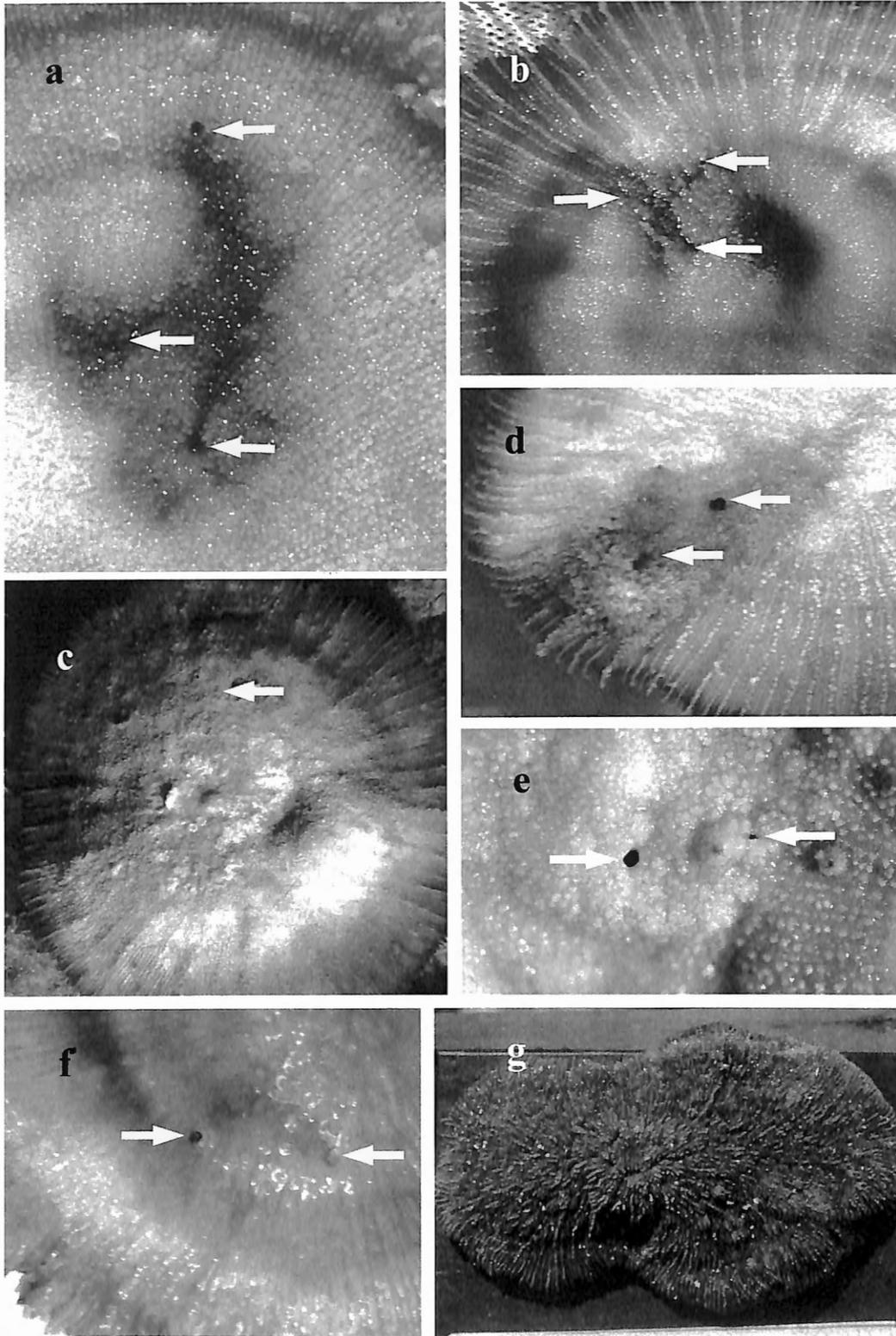


Fig. 24. – a: aboral side of *Ctenactis echinata* without deformation of coral skeleton. Arrows indicate openings of *Leptoconchus* burrows; b: aboral side of *Fungia (Verrillfungia) concinna* with slight deformation of coral skeleton. Arrows indicate opening of *Leptoconchus* burrows; c: aboral side of *F. (V.) concinna* without deformation of coral skeleton. Arrow indicates opening of a *Leptoconchus* burrow; d: aboral side of *Fungia (Verrillfungia) repanda* with slight deformation of coral skeleton. Arrows indicate opening of *Leptoconchus* burrows; e: aboral side of *Ctenactis echinata* with slight deformation of coral skeleton. Arrows indicate opening of *Leptoconchus* burrows; f: aboral side of *Heliofungia actiniformis* without deformation of coral skeleton. Arrows indicate opening of *Leptoconchus* burrows; g: oral side of *Sandalolitha robusta* without deformation of coral skeleton.

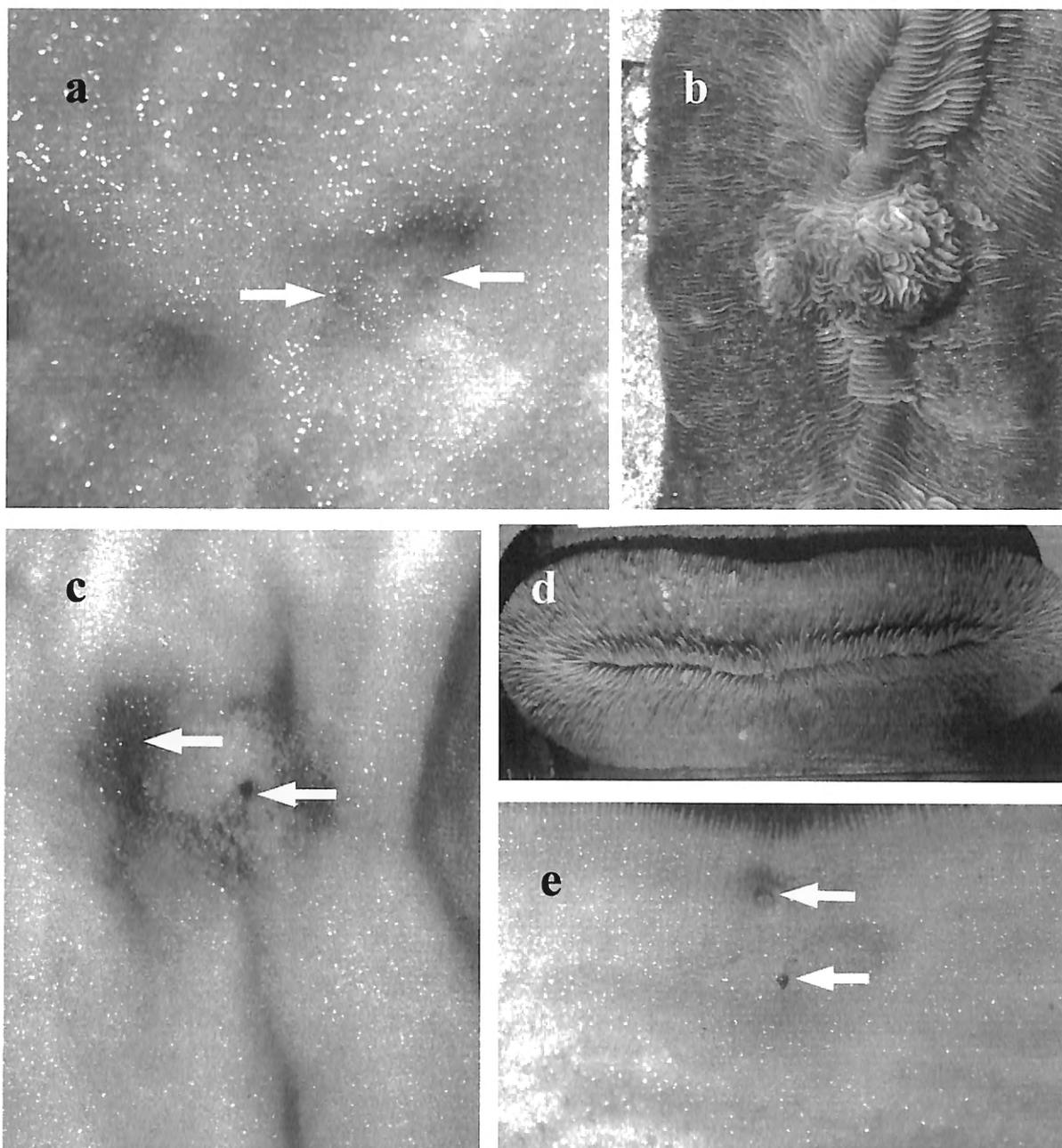


Fig. 25. – a: aboral side of *Sandalolitha robusta* (specimen of figure 24g) without deformation of coral skeleton. Arrows indicate opening of *Leptoconchus* burrows; b & c: oral and aboral side of *Herpolitha limax* with strong deformation of coral skeleton. Arrows indicate opening of *Leptoconchus* burrows; d & e: oral and aboral side of *H. limax* without deformation of coral skeleton. Arrows indicate opening of *Leptoconchus* burrows.

The infestation rate was not correlated with the density of the fungiid assemblage. This was observed at different localities, such as the North Coast of Papua New Guinea and the Spermonde Archipelago (Sulawesi, Indonesia). Both areas have a very high population density [161 fungiids/100 m<sup>2</sup> (present study) and 106 fungiids/100 m<sup>2</sup> (HOEKSEMA, 1990)] but showed quite different infestation rates (0-7% versus 0-0.02%).

At the species level, the same discrepancies were observed between Papua New Guinea and Sulawesi. At Papua New Guinea, *Fungia (Fungia) fungites* was the species most heav-

ily infested (39.3% of the fungiids infested) while *Fungia (Pleuractis) paumotensis* was only ranked at the 11<sup>th</sup> place with 2.5% of the fungiids infested. At Sulawesi, *F. (P.) paumotensis*, with 25% of infestation rate, was the fungiid most infested. The same was shown by *Fungia (Verrillofungia) repanda*: 12.9% of the fungiids infested in Papua New Guinea versus 5% in the Spermonde Archipelago. This was not correlated to local abundance of the species because *F. (F.) fungites*, *F. (V.) repanda* and *F. (P.) paumotensis* were the three most abundant species at both Papua New Guinea (CLAERBOUDT, 1989) and the

Table 4. H♀ : shell height of *Leptoconchus*; Tc: thickness of coral skeleton at centre; Te : thickness of coral skeleton at edge; Def: height of deformation of coral skeleton; D/O: number of corals with deformation versus total number of corals observed.

Coral	H♀ (mm)	Tc (mm)	Te (mm)	H♀ x 100/Te	H♀ x 100/Tc	H♀ x 100/Def.	D/O
<i>Fungia (Cycloseris) spp</i>	6.1±1.6 (n=10)	12.7±2.9 (n= 9)	6.5±1.3 (n= 9)	94±16 (n=12)	50±10 (n=12)	/	1/12
<i>F. (Wellsofungia) granulosa</i>	5.9±1.5 (n=11)	15.4±5.7 (n=13)	9.6±3.7 (n=13)	79±15 (n=10)	49± 8 (n=10)	/	0/10
<i>F. (Pleuractis) gravis</i>	9.3±2.3 (n= 7)	21.1±2.9 (n= 5)	14.2±3.7 (n= 5)	61±9 (n= 7)	43± 7 (n= 7)	34± 7 (n= 5)	5/7
<i>F. (Pleuractis) paumotensis</i>	14.4±2.7 (n= 6)	22.9±4.5 (n= 9)	15.4±2.6 (n= 9)	96±15 (n= 6)	63±11 (n= 6)	50±12 (n= 3)	3/6
<i>F. (Verrillofungia) spinifer</i>	5.7±1.5 (n= 7)	/	/	68±12 (n= 7)	24± 5 (n= 7)	/	0/7
<i>F. (Verrillofungia) concinna</i>	11.4±3.1 (n=12)	17.7±6.5 (n=10)	11.2±2.4 (n=10)	94±21 (n=11)	64±19 (n=11)	65±15 (n= 6)	6/11
<i>F. (Verrillofungia) repanda</i>	9.3±2.4 (n=58)	24.5±5.1 (n=52)	14.1±3.1 (n=52)	68±18 (n=56)	38±10 (n=56)	39± 6 (n= 8)	8/56
<i>F. (Lobactis) scutaria</i>	11.6±2.7 (n=19)	20.9±4.4 (n=17)	11.5±2.5 (n=17)	104±17 (n=17)	58± 9 (n=17)	/	0/17
<i>Herpolitha limax</i>	13.8±3.6 (n=14)	22.3±3.9 (n=11)	12.9±3.1 (n=13)	113±24 (n=13)	64±16 (n=10)	55± 5 (n= 5)	5/13
<i>Polyphyllia spp.</i>	8.2±2.2 (n=12)	10.8±2.8 (n=10)	8.2±2.4 (n=10)	90±12 (n=12)	70±10 (n=12)	47± 6 (n=11)	11/12
<i>Polyphyllia talpina</i>	9.3±2.2 (n= 7)	11.8±3.0 (n= 6)	9.0±2.5 (n= 6)	/	/	/	/
<i>Polyphyllia novaehiberniae</i>	6.6±0.7 (n= 5)	9.3±1.5 (n= 4)	6.9±1.5 (n= 4)	/	/	/	/
<i>Heliofungia actiniformis</i>	14.4±3.7 (n=19)	27.4±3.6 (n=12)	19.0±2.1 (n=12)	70±17 (n=18)	50±12 (n=18)	/	2/18
<i>Fungia (Danafungia) horrida</i>	7.2±1.5 (n= 7)	19.5±4.9 (n= 7)	11.6±3.6 (n= 7)	67±17 (n= 7)	38± 4 (n= 7)	/	2/7
<i>F. (Danafungia) scruposa</i>	14.4±3.4 (n=30)	23.9±6.7 (n=26)	12.0±2.9 (n=27)	119±32 (n=30)	58±12 (n=30)	54± 9 (n= 9)	9/30
<i>F. (Fungia) fungites</i>	12.8±2.4 (n=265)	22.3±3.7 (n=71)	11.7±1.8 (n=69)	115±22 (n=79)	59±11 (n=82)	58± 7 (n=14)	14/82
<i>Halomitra pileus</i>	13.5±4.6 (n=29)	18.6±2.9 (n=11)	10.4±0.6 (n= 6)	137±28 (n= 8)	74±21 (n=25)	46± 7 (n=15)	25/25
<i>Ctenactis spp</i>	13.1±3.0 (n=12)	26.5±3.6 (n=10)	16.5±1.5 (n=10)	86±18 (n=21)	53±10 (n=20)	/	2/21
<i>C. echinata</i>	18.9±2.4 (n= 7)	31.7±2.7 (n= 6)	18.8±1.7 (n= 6)	101±14 (n= 7)	61±12 (n= 6)	/	2/6
<i>C. crassa</i>	12.9±3.5 (n= 8)	26.5±4.3 (n= 6)	16.9±1.5 (n= 6)	/	/	/	/
<i>C. albitentaculata</i>	13.6±1.7 (n= 4)	26.5±2.3 (n= 4)	15.9±1.4 (n= 4)	/	/	/	/
<i>Podabacia crustacea</i>	7.2±1.1 (n= 5)	/	/	211±16 (n= 4)	95±27 (n=5)	58± 5 (n= 3)	5/5

Spermonde Archipelago (HOEKSEMA & MOKA, 1989; HOEKSEMA, 1990). Local differences in fungiids infested were already observed in other molluscs, such as the mytilid *Fungiacava eilatensis* (see GOREAU *et al.*, 1969). Within a fungiid species, some populations seemed to be more "sensitive" to parasites than others.

Going from a mangrove area to a barrier reef (with increasing distance from the shore) there is an increase in hydrodynamics (wave exposure) and a decrease in turbidity (TOMASCIK *et al.*, 1997). The rate of infestation was positively correlated with hydrodynamics and negatively with turbidity (fig. 11). Mangrove areas in front of Madang (Papua New Guinea), shelf zones close to the coast at the Spermonde Archipelago (Sulawesi), reefs close to Singapore, and deep (>20m) muddy environments which were all characterized by turbid waters had never, or exceptionally, been observed with infested fungiids. Obviously, turbid waters were not favourable to *Leptoconchus* settling and/or development.

Cumulative curves of settlement showed that there was a great difference in the distribution on the coral surface between the *Leptoconchus* individuals with an oral burrow opening and those with an aboral one (at least for monostomatous fungiids).

*Leptoconchus* with an oral burrow opening were not settling randomly on the coral. They were always concentrated close to the mouth slit, occupying maximum 50% of the coral surface (starting from the center). For most of them, (*Fungia* (*Danafungia*) *scruposa*, *F. (Lobactis) scutaria*, *F. (Wellsofungia) granulosa*, *F. (Pleuractis) paumotensis*, and *F. (Cycloseris) spp.*), the opening of the *Leptoconchus* burrows was located very close to the mouth slit if not in the mouth slit itself (figs 17e, 18a) as it is the case with the mytilid *Fungiacava eilatensis* (GOREAU *et al.*, 1969). Only *F. (F.) fungites* presented openings of *Leptoconchus* burrows more widespread on its oral surface. The smaller the corals, the closer to the mouth slit were the positions of the *Leptoconchus* burrows (fig. 14). Moreover, there was also a clear relationship between the number of *Leptoconchus* specimens present in a coral and the coral size, 120 mm across being a hinge diameter above which more *Leptoconchus* specimens were present (fig. 13). This phenomenon was probably linked to the growth of the coral thickness: beyond 120 mm across the thickness near the center of the coral increased significantly (fig. 15), allowing more *Leptoconchus* individuals to establish. The thickness at the edge of the coral remained nearly constant (fig. 15) and most probably never reached the value that would allow the full growth of the *Leptoconchus* shells.

For the *Leptoconchus* spp. with the burrow opening at the oral side of the coral, the prominent extension of the siphons at night suggested an increase in the respiratory function and hence of the mollusc metabolism. Since their movements in the burrow must be very limited, the increasing night activities could be related to feeding activities. With a proboscis that never protrudes from the coral surface, the *Leptoconchus* specimens are unable to browse the polyps as do many free living Coralliophilidae (see WARDS, 1965; ROBERTSON, 1970; OTT & LEWIS, 1973; BRAWLEY & ADEY, 1982; GUZMAN, 1988; PAGE, 1988; HAYES, 1990; BRUCKNER *et al.*, 1997). The *Leptoconchus* individuals have to feed on the

fungiid's food into the coelenteron and/or on zooxanthellae as do the mytilid *Fungiacava eilatensis* (GOREAU *et al.*, 1970).

For the *Leptoconchus* snails with the burrow opening at the oral side of polystomatous fungiids, which induce a strong deformation of the coral skeleton (gall), the location of the burrow should be random. Here the thickness of the coral is no longer a limiting factor and the mouths of the coral are no longer centrally located. Nevertheless, location of the *Leptoconchus* specimens in *Halomitra pileus* was not random; since they remained relatively close to the coral center (fig. 20). No explanation is available for this kind of distribution.

The *Leptoconchus* specimens with the burrow opening at the aboral side of monostomatous fungiids were more widespread on the coral surface and coral thickness seemed not to be a limiting factor. No relationships were observed between shell forms and coral thickness. Moreover, neither globose nor lenticular shells induced a prominent deformation of the coral skeleton.

For the *Leptoconchus* specimens with the burrow opening at the aboral side of polystomatous fungiids there seemed to be a relationship between the shell form (globose/lenticular) and the presence/absence of a deformation of the coral skeleton. Furthermore, the *Leptoconchus* infesting *Herpolitha limax*, even if a coral deformation (thickening) occurred, were concentrated near the center, where the coral thickness was nearly twice as at the edge.

With or without deformation of the coral skeleton and whatever the coral, *Leptoconchus* specimens occupied half of the available total coral thickness. This represents nearly the entire coral thickness that can be occupied. More or less 40% of the total coral thickness is represented by the spines of the costae and by the septa of lower orders that are exert (HOEKSEMA 1990: fig. 39). The 60% that can be occupied by *Leptoconchus* specimens corresponded to the height of the compound synapticulae located in between the septa.

Presence/absence of a deformation of the coral skeleton was not linked to the location of the *Leptoconchus* snails (see cumulative curves of settlement) in the coral. Corals like *Fungia* (*W.*) *granulosa*, *F. (L.) scutaria*, *F. (D.) scruposa* with molluscs highly concentrated near the mouth opening (fig. 16) or corals like *F. (V.) repanda*, *Heliofungia actiniformis*, *Ctenactis* spp. with molluscs randomly distributed (figs 20, 22) were evenly present in categories 1 ( $H_{\square}/T_c \times 100 < 60$ ) and 2 ( $60 < H_{\square}/T_c \times 100 < 70$ ) deduced from table 4.

Shell shape of *Leptoconchus* individuals (globose or lenticular) was not necessarily linked to the coral thickness nor to the fact that the burrow opening was at the oral or aboral side of the coral. Globose shells were found in thin corals (*Halomitra pileus*) whereas lenticular shells were found in thick corals (*Fungia* (*V.*) *repanda*, *F. (D.) horrida*, *Sandalolitha robusta*). Lenticular shells had the burrow opening as well at the oral side (*Zoopilus echinatus*, *Polyphyllia* spp.) as at the aboral side (*F. (V.) spp.*, *F. (D.) horrida*, *Sandalolitha robusta*) of the coral.

The most heavily infested Fungiidae were living together in the same habitat and were supposed to have the same ecological requirements. Consequently, openings of *Leptoconchus* burrows at oral/aboral side are not linked to a

special habitat but rather would depend on *Leptoconchus* species. Shell shape, and shell distribution in the coral seem also to be linked to the *Leptoconchus* species and not to the coral species. All these criteria can be used in the taxonomy of the *Leptoconchus*.

They are most welcome since *Leptoconchus* shells present very few characters to distinguish them one from each other. According to the present observations, several species belonging to the genus *Leptoconchus* infest the family Fungiidae and not a single species as first believed (BOUILLON *et al.*, 1983). The *Leptoconchus* species found in Fungiidae by BOUILLON *et al.* (1983) was identified as *Leptoconchus peronii* (LAMARCK, 1818) (= *L. striatus* RÜPPELL, 1835). However, studies on coral/mollusc specificity (MASSIN, 1983, 1989, 1990) and general shell shapes are not in agreement with this early identification. The taxonomy of *Leptoconchus* species infesting Fungiidae will be dealt in a separate paper.

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