

**PARASITES AND BIOTIC DISEASES IN FIELD AND CULTIVATED SEA CUCUMBERS**

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**ABSTRACT**

Amongst echinoderms, the Holothuroidea represents the class that is the most infested by parasites. Parasites of holothuroids are Bacteria, Protozoa and Metazoa. There are about 150 species of metazoans which parasitize holothuroids. Most of them are turbellarians, gastropods, copepods, crabs or fishes. The main body compartments suffering of the infestations are the digestive system and the coelom. The diseases induced by metazoan parasites are mostly structural: they create galls at the surface of the epidermis, pierce the respiratory tree or dig into the body wall down to the coelom. Most metazoans that live in the digestive system do not induce obvious diseases and their relationship with their hosts is probably close to commensalism. Most Protozoa that parasitize holothuroids are sporozoans. They occur mainly in the coelom and/or the haemal system, one species having been reported infesting the gonads. Even in heavily infested hosts, the signs of disease induced by sporozoans are low: at most, host haemal lacuna is occluded by trophozoites or cysts are formed into the coelomic epithelium.

The most pathogen agents reported from cultured sea cucumbers are Bacteria. Cultivated holothuroids may suffer from a bacterial disease, called skin ulceration disease, that affects their body wall. In particular, juvenile *Holothuria scabra* reared in the Aqua-Lab hatchery of Toliara, Madagascar, suffered from such a disease that caused death within three days. The first sign of the infection is a white spot that appears on the integument of individuals, close to the cloacal aperture. The spot extends quickly onto the whole integument leading to the death of individuals. The lesions consist in a zone where the epidermis is totally destroyed and where collagen fibres and ossicles are exposed to the external medium. This zone is surrounded by a border line where degrading epidermis is mixed with connective tissue. Lesions include three bacterial morphotypes: rod-shaped bacteria, rough ovoid bacteria, and smooth ovoid bacteria. Three species of bacteria have also been put in evidence in the white spot lesions thanks to biomolecular analyses (DGGE and sequencing): *Vibrio* sp., *Bacteroides* sp., and an  $\alpha$ -Proteobacterium.

**Keywords:** Parasitoses; Bacteria; Holothuroidea

**INTRODUCTION**

Many organisms are reported to infest echinoderms, especially holothuroids. Holothuroid associates are either commensals or parasites. The first are harmless for the hosts: they often live at the surface of holothuroids that act as protective substrates against eventual predators. For the second, holothuroids also represent biotic substrates where they can live but yet serve sometimes as a source of food and/or as a source of developmental stimuli without which they cannot complete their life cycle. Parasites are always harmful for their hosts and they induce diseases that are non lethal most of the time but that

can cause the host's death in a few cases. According to a review on echinoderm diseases (Jangoux 1990), more than one third of echinoderm parasites live in or on holothuroids. No bacteria had been recorded at that time and only protozoan and ten metazoan taxa of high rank in the Linnean hierarchy were known to infest holothuroids. According to Jangoux (1990), most parasitic animals were Platyhelminthes (39 turbellarian species and 3 flukes), then Mollusca (33 gastropods and 4 bivalves), Arthropoda (one tardigrade, 22 copepods, 8 crabs and 2 pycnogonids), Pisces (9 carapids), Bryozoa (4 species), Annelida (2 polychaetes) and finally Porifera, Cnidaria, Entoprocta (1 species each) and Nematoda (undetermined number of species).

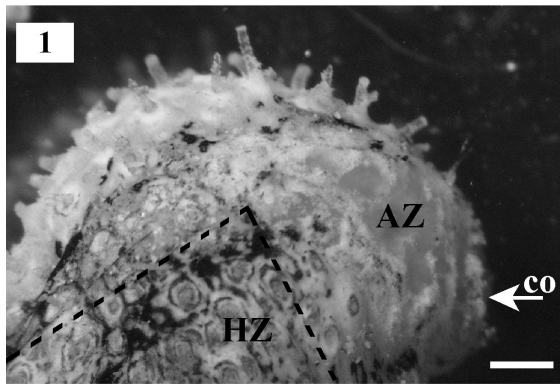
The present report aims at synthesising the main parasites and biotic diseases of sea cucumbers and includes the recent studies on the subject since the work of Jangoux (1990). It particularly emphasises new bacterial parasites and the disease that they induce.

## BACTERIA

Almost nothing is known about bacterial parasites and diseases in holothuroids. Morgan (2000) reported that a broodstock of *Holothuria scabra* from Bribie Island (Australia) suffered from a bacterial disease. The infection provoked the loss of epidermal pigmentation associated with the presence of huge amount of viscous mucus. The lesions first arose around the mouth and/or cloacal opening of animals and then spread on both sides of the individuals before possibly encompassing the whole body. If infected animals were not eliminated from the broodstock, up to 95% of the reared individuals died (Morgan, 2000). According to this author, *Vibrio harveyi* was the predominant bacterium in the lesions of affected holothuroids. Becker (2002) reported on a disease, called the skin ulceration disease, affecting juvenile *H. scabra* reared in the hatchery of Toliara, Madagascar. Microscopic and biomolecular techniques (denaturing gradient gel electrophoresis and sequencing) together with bacterial cultures and infection assays were used to characterise the disease and to investigate the microbial communities of the lesions.

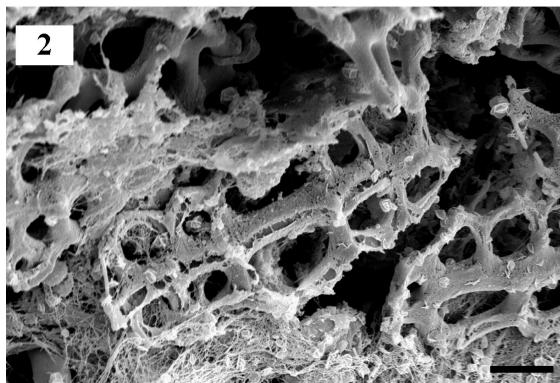
The skin ulceration disease, that affects the body wall of juvenile *Holothuria scabra* at Toliara, appeared for the first time in September 2000 and broke out in February 2001, May 2001, February 2002 and July 2002. The infection extended very quickly in the aquaria, being highly contagious: in February 2001, the skin ulceration disease reached a peak and affected two third of the juveniles two days after its appearance. The disease was also highly virulent causing death three days after detection of the first symptoms.

The first obvious sign of the disease was the appearance of little, white, rounded spots of *ca.* 1 mm in diameter corresponding to areas where the epidermis was destroyed. The white colour of the lesions is due to the exposure of the connective tissue that follows the destruction of the cuticle, the epidermis and the upper part of the connective tissue. Yet, the mesothelium, the muscles and the internal organs remained unaffected. The first white spots always appeared close to the cloacal opening and this was quickly followed by the outbreak of other spots similar in size, shape and colour in the posterior half of the individuals. The rest of the body remained healthy and the behaviour of diseased and healthy holothuroids was unchanged except that the former did not seem to burrow anymore. Twenty-four hours later, white spots spread and joined together to form a large, posterior lesion which covered about a fifth of the body surface (Fig. 1). Podia inside this lesion were totally destroyed. Other spots then appeared on the anterior part of the body and ossicles became visible externally, some of them separating from the integument. Forty-eight hours later, more than a half of the body surface was affected. Juveniles were much less active and became almost translucent, their internal organs being seen through the body wall. Three days after the beginning of the disease, the whole body surface was affected. Dead individuals were reduced to pellets of tissues heavily infested by microorganisms.

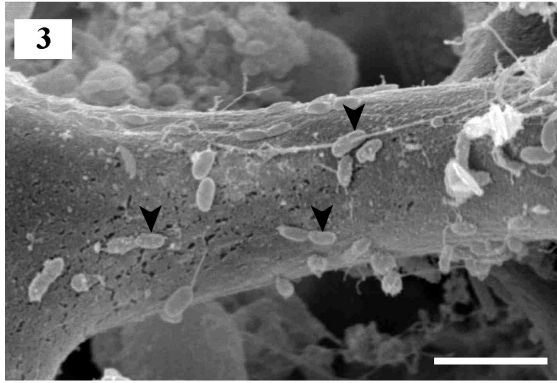


**Figure 1.** Juvenile of *Holothuria scabra* affected by the skin ulceration disease (O.M.). AZ: affected zone; CO: cloacal orifice; HZ : healthy zone. Scale bar = 100  $\mu\text{m}$

With the use of scanning electron microscopy, two different zones of the body surface may be observed in the white spot lesions of diseased holothuroids: (1) the affected zone, colonised by microorganisms, where the epidermis and cuticle is totally destroyed and where a disorganised connective tissue is exposed to the medium and (2) a borderline of a few tens of micrometers wide where the surface is colonised by microorganisms and where patches of degrading epidermis are mixed with degrading, exposed connective tissue. In the affected zone, collagen fibres are running in all directions, breaking off from each other and ossicles, some of them being highly degraded, are exposed to the external medium (Fig. 2). Three bacterial morphotypes are observed in these two zones: rod-shaped bacteria, rough ovoid bacteria and smooth ovoid bacteria. The last were observed degrading holothuroid ossicles (Fig. 3).



**Figure 2.** S.E.M. views of a lesion of a *Holothuria scabra* juvenile affected by the skin ulceration disease showing degraded ossicles in the affected zone and smooth ovoid bacteria on an ossicle, respectively. Scale bars = 10  $\mu\text{m}$ .



**Figure 3.** S.E.M. views of a lesion of a *Holothuria scabra* juvenile affected by the skin ulceration disease showing smooth ovoid bacteria on a degrading ossicle. Scale bars = 5  $\mu$ m.

The biomolecular techniques identified three species of bacteria in the lesions. The first, *Vibrio* sp., has been isolated in bacterial cultures of sea cucumber lesions and identified by DNA sequencing. The two other bacteria, *Bacteroides* sp. and an  $\alpha$ -Proteobacterium, have been detected by the denaturing gradient gel electrophoresis method. From the three bacteria, *Vibrio* sp. is the best candidate as the etiological agent of the skin ulceration disease. It is indeed close to *Vibrio harveyi* and *V. alginolyticus*, two well-known pathogenic bacteria. *Vibrio harveyi* is responsible of numerous infections to both vertebrates and invertebrates.

### PROTOZOA

Ciliates living in the digestive tract and in the respiratory trees of holothuroids have been reported by Barel and Kramer (1977). Holothuroids are otherwise mainly infested by members of five gregarine genera (13 described species) - *Cystobia*, *Diplodina*, *Goniospora*, *Lithocystis* and *Urospora* - and one species of coccidia (*i.e.*, *Ixoreis psychropotae*). Deposit-feeding holothuroids are very sensitive to gregarine infestations. Kroll and Jangoux (1989), for example, observed that 90% of the 50 *Holothuria tubulosa* collected in the bed of *Posidonia* at Castello (Ischia Island, Italy) were infested by gregarines. The high infestations of holothuroids by gregarines can be explained by the fact that echinoderms may infest themselves simply by swallowing sediment that contains mature sporocysts. The life cycle of gregarines is complex and includes six developmental stages - sporocysts, sporozoites, trophozoites, gamontes, gametocysts, and sporogonia - that are all observed within the holothuroids. Once in the digestive system, sporocysts are broken down and sporozoites are liberated owing to the physico-chemical properties of the digestive fluid (Jangoux 1990). Generally, they penetrate cells of the digestive system and migrate into the haemal system or the coelom. A more or less prolonged stay in the host's haemal system is necessary for a few species, probably for most of them, but the described species are often known only from one stage that infested a specific host's body part. Trophozoites and subsequent stages are extracellular and found in the haemal lacuna, attached to the coelomic epithelium or embedded into coelomic brown bodies. The escape of gregarines from the hosts is unknown though it is generally accepted that they leave holothuroids through evisceration or at the host's death. Recently, Doignon *et al.* (2003) observed that the coelomic content (brown bodies and parasites) of *Holothuria tubulosa* is purged seasonally, a phenomenon that could exist in other species. To explain this coelomic purge, the main hypothesis was that it would be an indirect result of the host's spawning as it occurs at that time: to discharge their gametes, holothuroids raise their body, adhere on the substratum by their posterior end and then contract muscles. This behaviour would cause an overpressure in the peri-cloacal end of the animal and consequently the expulsion of the coelomic fluids through the coelo-cloacal ducts, carrying the coelomic contents, brown bodies and parasites, away to the environment.

Diseases induced by protozoans to holothuroids are reduced to small internal wounds and no lethality due to gregarines has been described in literature. Growth of the *Cystobia* trophozoites progressively occludes the host's haemal lacuna, and a particular haemal outgrowth is formed like a bell-clapper protruding into the coelomic cavity; the clapper represents the so-called "stalked gregarine" that is formed by an evagination of the underlying haemal lacuna whose distal end encloses an enlarged trophozoite or a cyst (Jangoux 1990). One species, *Diplodina gonadipertha*, infests the gonads of *Cucumaria frondosa* and could partially destroy the gonads (Djakonov 1923). The single species of Coccidia, *Iroxeis psychropotae*, lives in the gut-associated haemal system of deep sea holothuroids (Massin *et al.*, 1978).

## METAZOA

### Platyhelminthes

Jangoux (1990) has found 5 Acoela, 34 Umagillidae (Rhabdocoela) and 3 Trematoda infesting holothuroids. Five umagillids have been described since his review (Table 1). The acoels are found mostly in the digestive tract of holothuroids, one species has been observed in the coelom and another one in the respiratory trees. Umagillids infest either the coelom or the digestive tract. Snyder (1980) could determine neither beneficial nor detrimental effects due to the occurrence of gut-associated umagillids. He concluded that these symbionts should be considered simply commensals. In contrast, Shinn (1981) reported that the gut-associated umagillids always compete with their host for nutrients and thus may exert adverse effects. He noted that all the umagillids studied by him ingest intestinal host tissue and he considered that they parasite their hosts to varying degrees. Whether they are living in the gut or in the coelom, they breed in the hosts and release egg capsules. Egg capsules are defecated in gut-associated umagillids or are accumulated in the holothuroid body cavity in coelom-associated umagillids. Coelomic umagillids swim in the host's body cavity and they are thought to ingest host's coelomic fluid together with coelomocytes (Shinn 1983) or to feed on coelom-associated organisms such as ciliates (Jennings 1980).

**Table 1.** New species of Platyhelminthes infesting holothuroids that have been described since Jangoux(1990)'s review.

<b>Turbellaria</b>	<b>Host</b>	<b>Geographical area</b>	<b>Source</b>
<b>Umagillidae</b>			
<i>Anoplodium heronensis</i>	<i>Stichopus</i> sp.	Great Barrer Reef	Canon (1990)
<i>Anoplodium leighi</i>	<i>Stichopus</i> sp.	New Zealand	Canon (1990)
<i>Paranotothrix</i> sp.	various holothuroids	Seychelles	Martens and De Clerck (1994)
<i>Anoplodium</i> sp.	<i>Stichopus variegatus</i> <i>Actinopyga miliaris</i>	Seychelles	Martens and De Clerck (1994)
<i>Wahlia westbladi</i>	<i>Stichopus mollis</i>	Australia	Jondelius (1996)

Infestations by umagillids can be very high. The 27 individuals of *Telenota anax*, *Holothuria fuscogilva*, *H. coluber* and *Actinopyga mauritiana* collected in Hansa Bay (Papua New Guinea) were all infested by gut-associated umagillids and some of them by more than 200 flatworms (Eeckhaut, pers. obs.). Doignon *et al.* (2003) studied the infestation of *H. tubulosa* by the coelom-associated umagillid *Anoplodium parasita*. They observed that 26 holothuroids out of the 202 collected at Banyuls-sur-mer (France) were infested by 1 to 6 adult *A. parasita*. The infestation of the holothuroids by the turbellarian egg capsules was very important: 128 out of the 202 holothuroids inspected contained at least 6 and up to 10,000 egg capsules (mean of 1,433). Quite uniform throughout the year, the number of egg capsules found in the coelom as well as the number of holothuroids infested by egg capsules fall drastically in July. Interestingly, this period is the one where the gonads of holothuroids

were fully developed. Doignon *et al.* (2003) suggested that the release of the egg capsules could be made through coelo-rectal ducts and would be an indirect result of the host spawning.

The flukes *Himasthla leptosoma* and *zoogonoides viviparus* infest the body wall, at the base of the buccal tentacles of *Leptosynapta* spp. The first species has also been observed in the brown bodies (Cuénot 1892, 1912; Jangoux 1990). A third species, *Tetrarhynchus holothuriae* would occur in the body wall of *Molpadia* sp. (Shipley 1903). Holothuroids are probably intermediate hosts for flukes. Sea birds are the definite hosts of *Himasthla leptosoma*.

### **Annelida**

The most recent review on symbiotic polychaetes is the one of Martin and Britayev (1998). They have found 18 polychaete species commensal of holothuroids and one parasite. The parasite, *Ophryotrocha puerilis*, occurs in the coelomic cavity of *Ocnus planci* from Napoli (Monticelli 1892; Barel & Kramer 1977; Jangoux 1990). Ganapati and Rhadakrishna (1962) noted that 50% of the holothuroids *Molpadia* sp. were infested by the small hesionid *Ancistrocyllis* sp. either in the digestive tract or respiratory trees. Commensal polychaetes are simply attached by their parapodia to the surface of holothuroids and are considered totally harmless for their hosts. Britayev and Lyskin (2002), however, recently demonstrated that *Gastrolepia clavigera*, the commonest Indo-Pacific polychaete associated to holothuroids, partially eats the host's integument. Holothuroid spicules represented up to 75% of the polychaete's gut content. These results suggest that symbiotic polychaetes currently considered as commensals could be true parasites.

### **Mollusca**

Four Bivalvia and 33 Gastropoda are known to infest holothuroids (Jangoux 1990). Bivalves live in the cloaca or inhabit small pouches dug into the digestive wall of synaptid holothuroids (Jangoux 1990). Gastropods are free on the body surface or induced galls on it; they are also found in the respiratory tree, the digestive tract or the coelom. Ectoparasitic gastropods feed on host's tissues or fluids using their proboscis which penetrates more or less deeply into the holothuroid body wall or crosses it to reach the coelomic cavity or the haemal system (Jangoux 1990). Intradigestive symbionts enter the digestive tract in order to feed by puncturing the digestive wall (Jangoux 1990). A special case of intradigestive symbiosis is the one developed by *Megadenus cantharelloides* which attaches to the digestive wall of *Stichopus chloronotus* with its proboscis reaching the host's body wall in order to feed on dermal tissue (Humphreys & Lützen 1972). With the exception of *Gasterosiphon deimatis* which feed on haemal fluid (Koehler & Vaney 1903), intracoelomic gastropods are believed to derive their energy from the host's coelomic fluid by direct absorption of nutrients through their body wall (Jangoux 1990).

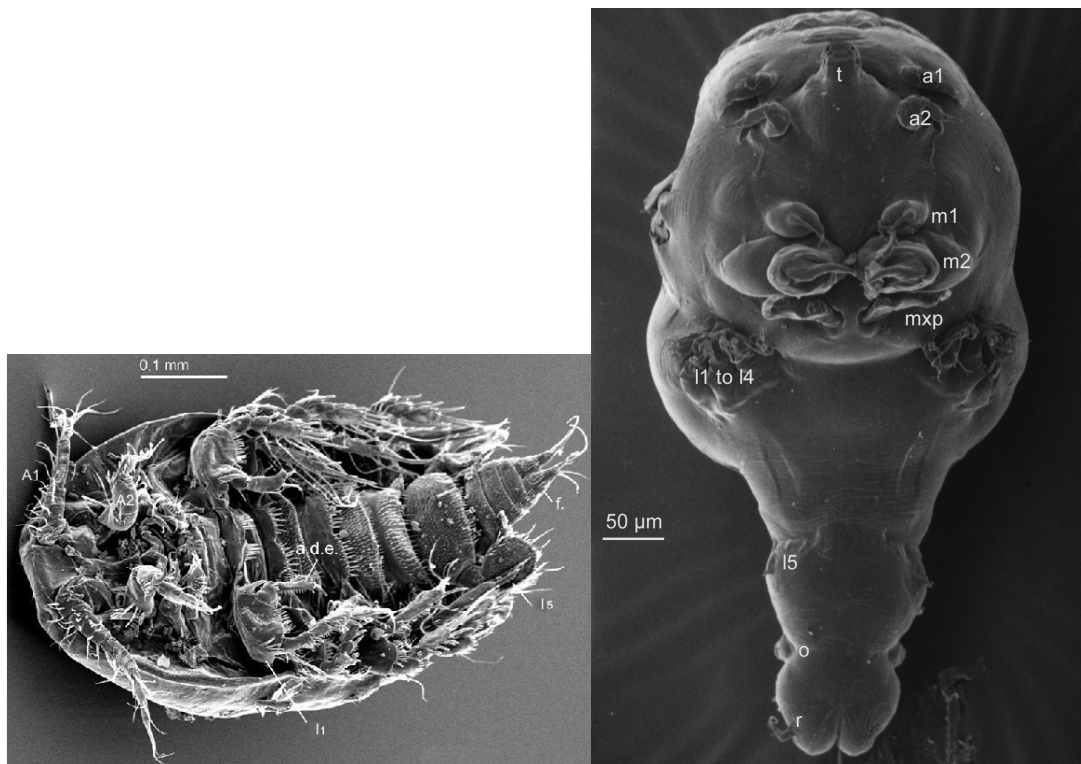
Harmful effects of parasitic gastropods are not restricted to their feeding activities but they may produce attachment lesions involving host reactions and induction of galls. It is also reported that the intracoelomic *Entocolax* spp. may castrate their hosts (Heding and Mandahl-Barth 1938). So far, there is no data indicating that parasitic eulimids can seriously affect the holothuroid cycle and the ecological consequences of this parasitism may be quite limited for the holothuroid populations involved (Jangoux 1990).

### **Arthropoda**

Twelve pinnotherid crabs are associated with holothuroids. Most live in the respiratory trees or the posterior part of the digestive tract. One, *Pinnotheres decanus*, is rarely found in the coelomic cavity. *Lissocarcinus orbicularis*, the commonest Indo-Pacific crab associated with holothuroids, is often found walking at the host's body surface. Presumably, holothuroid-associated crabs do not feed on host tissues, and most of them do not cause any detrimental effects, except to slightly wound the wall of

respiratory trees or cloaca (Jangoux 1990). A notable exception to this rule is the pea crab *Pinnotheres halingi* which causes a significant atrophy of the right respiratory tree (Hamel *et al.*, 1999).

At least eighty-five cases of association between holothuroids and copepods have been described to date. The symbiotic copepods belong to four classes (Harpacticoida, Cyclopoida, Poecilostomatoida and Siphonostomatoida), and the holothuroid hosts to more than twenty genera. But still, there is little information regarding the relations between hosts and symbionts (see, e.g., Humes 1980). Most associations reported essentially describe the localisation of the symbionts in regards to the host and the presence/absence of conspicuous characteristics that would be induced by the symbiont presence (Jangoux 1990). In the majority of these associations (*ca.* 60%), copepods are defined as external symbionts, with a rather unclear definition of their relations with the holothuroid host. Since Jangoux (1990)'s review, only the work of Gomes da Silva (2001) focused on the biology of symbiotic copepods, *i.e.* the poecilostome *Synaptiphilus luteus* (Fig. 4) and the siphonostome *Allantogynus delamarei* (Fig. 5). The first has never been reported as free living and shows a wide range of host tolerance (weak specificity). Its hosts are the northern Atlantic synaptid holothuroids *Labidoplax digitata*, *Leptosynapta inhaerens*, *L. gallienei* and *L. bergensis* (Bocquet 1952, Bocquet & Stock 1957, Humes 1980). Gomes da Silva (2001) performed population studies on *S. luteus* and showed that, if females are encountered throughout the year on their hosts, infestation by males occurs seasonally, the males and females being only present simultaneously on the hosts for a restricted mating period. Gomes da Silva (2001) also studied the coelomocyte reaction induced by *Allantogynus delamarei* in the body cavity of the Mediterranean aspidochirot holothuroids *H. tubulosa* and *H. poli*. The parasite shows many peculiarities, no male is known, only the females and three larval stages are described (Changeux 1958). The female shows a highly modified morphology, she secretes an incubating envelope in which she continuously secretes ovigerous sacs each containing two embryos. The female and her ovigerous sacs are embedded in this incubating envelope, from which only the buccal tube protrudes to puncture the mesothelium of the host's coelomic cavity.



**Figures 4 and 5.** Ventral views of a female *Synaptiphilus luteus* and of a female *Allantogynus delamarei*, respectively. a1: antennula, a2: antenna, ade: distal endopodite article, m1: maxillula, m2: maxilla, mxp: maxillipede, o: laying orifice, l1 to l4: leg 1 to leg 4, l5: leg 5, r: caudal ramus, t: buccal tube.

## Pisces

Although some pearlfish (Carapidae, Ophidiiformes) are free-living, this family includes fishes that are able to live in association with different invertebrates. The origin of “pearlfish” would be the discovery of dead carapid fishes, paralysed and completely covered by nacreous substance in an oyster shell (Ballard 1991). However, the majority of the species belonging to the Carapini tribe (*Carapus* spp. and *Encheliophis* spp.) are usually found in the respiratory trees or in the coelomic cavity of holothuroids or in the coelomic cavity of asteroids.

Pearlfishes associated with sea cucumbers are listed in Table 2. Although the fishes are able to enter in different host species, they often show a preference to a specific one (Trott & Trott 1972, Gustato *et al.* 1979). *C. boraborensis*, *C. homei*, *C. mourlani* and *E. gracilis* can live in the same host species and are found in the same waters, but they usually do not inhabit the same host individual (Smith 1964, Trott 1981, Shen & Yeh 1987, Vandenspiegel & Jangoux 1989, Markle & Olney 1990). If it exists, a system of sea cucumber recognition is not yet correctly highlighted. These fishes are able to produce sounds (Parmentier *et al.* 2003). Sounds are not likely to be used by the fish to identify the presence of another fish in the holothuroid before penetration but are produced in the presence of congeneric individuals, inside holothuroids (Parmentier *et al.* 2003). Pearlfish sound emissions could be a communication system that is used in a place where the visibility is strongly reduced and where chemical communications may be masked by the host.

**Table 2.** Fishes associated with echinoderms (Parmentier, 2003). (\*) most common host (indicated when known); A : asteroid; B: bivalve; H : holothuroid

Carapidae		Hôte	Auteur
<i>Carapus acus</i>	H	<i>Stichopus regalis</i> (*)	Arnold (1953, 1957), Gustato <i>et al.</i> (1979), Vitturi & Catalano (1988), Kloss & Pfeiffer (2000)
	H	<i>Holothuria tubulosa</i> (*)	Arnold (1953, 1956, 1957), Gustato <i>et al.</i> (1979), Vitturi & Catalano (1988), Kloss & Pfeiffer (2000)
	H	<i>Holothuria poli</i>	Arnold (1956, 1957)
	H	<i>Holothuria helleri</i>	Arnold (1956, 1957)
	H	<i>Holothuria sanctori</i>	Arnold (1956)
<i>Carapus bermudensis</i>	H	<i>Actinopyga agassizi</i> (*)	Arnold (1956), Smith & Tyler (1969), Van Meter & Ache (1974), Trott (1970), Smith <i>et al.</i> (1981), Tyler <i>et al.</i> (1992)
	H	<i>Isiostichopus badionatus</i>	Smith and Tyler (1969)
	H	<i>Astichopus multifidus</i>	Trott (1970)
	H	<i>Holothuria glaberrima</i>	Trott (1970)
	H	<i>Holothuria princeps</i>	Dawson (1971)
	H	<i>Holothuria lentiginosa</i>	Miller & Pawson (1979), Valentine & Goeke (1983), Smith & Tyler (1969), Trott (1970), Tyler <i>et al.</i> (1992)
<i>Carapus mourlani</i>	H	<i>Culcita novaeguineae</i>	Mortensen (1923), Petit (1934), Schultz (1960), Smith (1964), Trott (1970), Trott & Trott (1972), Meyer-Rochow (1977, 1979), Meyer-Rochow & Tiang (1978), Machida (1989)
	A	<i>Pentaceros hawaiiensis</i>	Markle & Olney (1990)
	A	<i>Choriaster granulatus</i>	Markle & Olney (1990)
	A	<i>Acanthaster planci</i>	Cheney (1973), Machida (1989)
	H	<i>Stichopus variegatus</i>	Markle & Olney (1990)
	H	<i>Stichopus chloronotus</i>	Markle & Olney (1990)
	H	<i>Bohadschia argus</i>	Trott (1970), Meyer-Rochow (1977), Machida (1989), Markle & Olney (1990)
	H	<i>Actinopyga mauritania</i>	Markle & Olney (1990)
<i>Carapus homei</i>	H	<i>Bohadschia argus</i> (*)	Smith (1964), Branch (1969), Trott (1970), Vandenspiegel & Jangoux (1989), Markle & Olney (1990)
	H	<i>Stichopus chloronotus</i> (*)	Smith (1964), Branch (1969), Trott (1970), Trott & Garth (1970), Trott & Trott (1972), Seymour & McCosker (1974), Markle & Olney (1990)



H	<i>Stichopus variegatus</i>	Trott (1970), Meyer-Rochow (1977)
H	<i>Thelenota ananas</i>	Markle & Olney (1990)
H	<i>Actinopyga echinites</i>	Markle & Olney (1990)
H	<i>Holothuria ocellata</i>	VandenSpiegel & Jangoux (1989)
A	<i>Culcita schmideliana</i>	Hipeau-Jacquotte (1967), Jangoux (1974)
A	<i>Mithrodia fisheri</i>	Jangoux (1974)
B	<i>Pteria lotorium</i>	Mahadevan (1959)

Carapidae	Hôte	Auteur	
<i>Carapus boraborensis</i>	H	<i>Thelenota ananas</i>	Smith (1964), Trott (1970), Meyer-Rochow (1977), VandenSpiegel & Jangoux (1989), Markle & Olney (1990)
	H	<i>Bohadschia argus</i>	Smith (1964), Markle & Olney (1990), VandenSpiegel & Jangoux (1989)
	H	<i>Stichopus chloronotus</i>	Markle & Olney (1990)
	H	<i>Pearsonothuria graeffei</i>	VandenSpiegel & Jangoux (1989)
	H	<i>Thelenota anax</i>	Ballard (1991) – Parmentier <i>et al.</i> (2002)
<i>Encheliophis sagamianus</i>	H	<i>Holothuria mertensiothuria</i>	Tanaka (1908), Arnold (1956)
	A	<i>Certonardoia semiregularis</i>	Yosii (1928)
	A	<i>Nardoia semiregularis</i>	Arnold (1956)
<i>Encheliophis vermicularis</i>	H	<i>Holothuria kefersteinii</i>	Trott (1970)
	H	<i>Holothuria leucospilota</i>	Murdy & Cowan (1980), Masuda <i>et al.</i> (1984)
	H	<i>Holothuria lubrica</i>	Steinbeck & Ricketts (1941)
	H	<i>Thelenota ananas</i>	Markle & Olney (1990)
	H	<i>Holothuria atra</i>	Schultz (1960)
	H	<i>Holothuria scabra</i>	Murdy & Cowan (1980)
<i>Encheliophis gracilis</i>	H	<i>Holothuria scabra</i>	Arnold (1956)
	H	<i>Thelenota ananas</i>	Shen & Yeh (1987), Markle & Olney (1990)
	H	<i>Holothuria atra</i>	Strasburg (1961), Schultz (1960)
	H	<i>Actinopyga crassa</i>	Markle & Olney (1990)
	H	<i>Bohadschia vitiensis</i>	Markle & Olney (1990)
	H	<i>Bohadschia argus</i>	Smith (1964), Trott (1970), Machida (1989), Markle & Olney (1990)
	H	<i>Stichopus chloronotus</i>	Smith (1964)
	H	<i>Holothuria chilensis</i>	Trott (1970)
	H	<i>Stichopus sp.</i>	Markle & Olney (1990)
	A	<i>Culcita discoidea</i>	Arnold (1956)
	A	<i>Culcita novaeguineae</i>	Branch (1969), Trott (1970)
<i>Encheliophis chardewalli</i>	H	<i>Actinopyga mauritania</i>	Parmentier (2003)

In most cases, there is only one fish per host. However, specimens of *Encheliophis* (*E. gracilis*, *E. vermicularis* and *E. sagamianus*) were reported to be sexually paired in various holothuroids (Murdy & Cowan 1980, Trott 1981). More than two specimens of *C. homei*, *C. mourlani* and *C. bermudensis* can be observed in a same host (Aronson & Mosher 1951, Meyer-Rochow 1977, Trott & Trott 1972, Smith *et al.* 1981). Meyer-Rochow (1977) holds the record with fifteen *C. mourlani* in a specimen of *Bohadschia argus*. Although no data were reported in the literature, the presence of sexual pairs suggests that sea cucumbers serve also as breeding sites. Sea cucumbers also act as developmental stimulators for some carapid larvae. In *Carapus* and *Encheliophis* species, the penetration inside a sea cucumber is followed by heavy transformations during which the fish length is reduced by 60%.

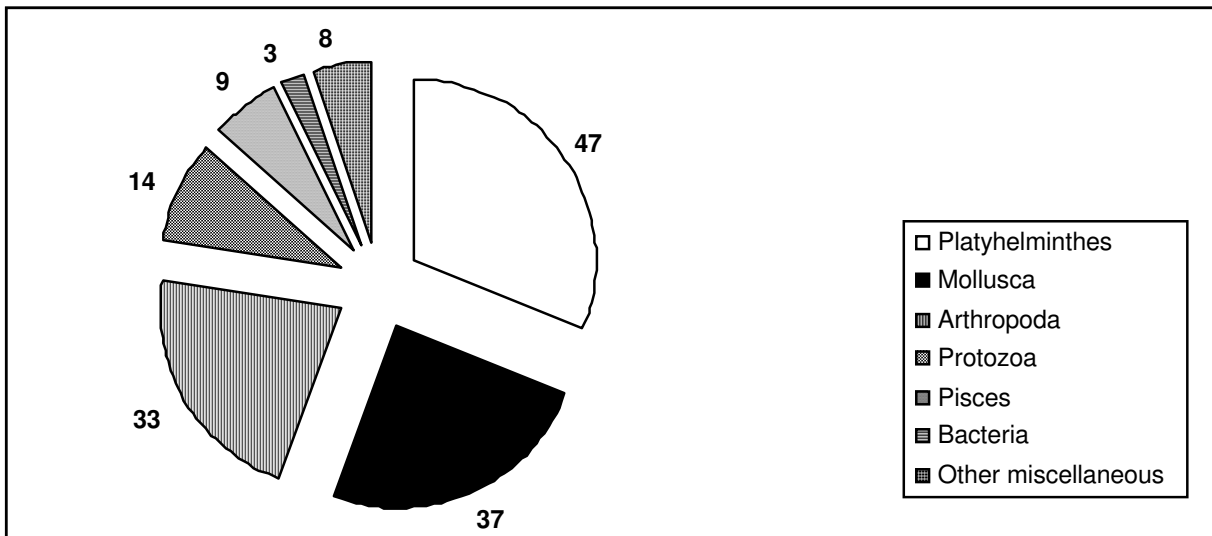
The stomach contents (Trott, 1970; Murdy & Cowan, 1980; VandenSpiegel & Jangoux, 1989) and the musculo-skeletal descriptions of the buccal and pharyngeal jaws (Parmentier *et al.* 1999, 2000a, 2000b) have suggested different kinds of symbiosis depending on the species. Various authors have suggested that *Carapus* adults could be parasites (Arnold, 1953; Gustato, 1976; Trott, 1981) while others consider them as commensals, using their hosts as shelters and leaving them to hunt small preys

such as annelids, crustaceans (shrimp, decapod, amphipod) and small fishes (Trott, 1970; Meyer-Rochow, 1979; VandenSpiegel & Jangoux, 1989; Parmentier *et al.*, 2000a,b). They can also be cannibals, feeding on other carapids within their host (Parmentier, pers. obs.). On contrast, *Encheliophis* species are true parasite, feeding on the internal tissues of their host, mainly the gonads (Smith, 1964; Trott, 1970; Trott & Trott, 1972; Murdy & Cowan, 1980; Trott, 1981).

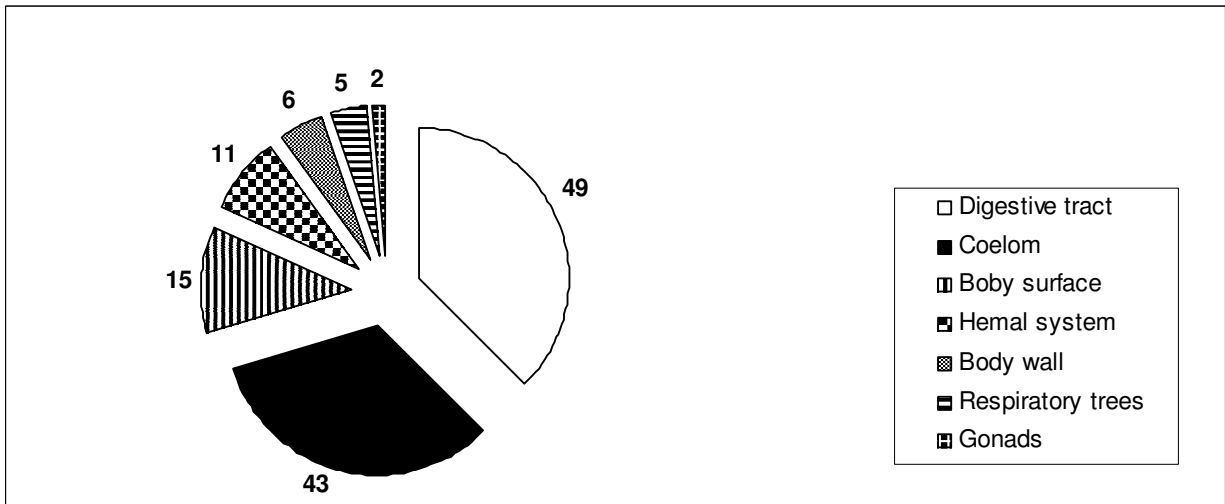
Some individuals can be frequently found in the general cavity of holothuroids, implying a perforation of the respiratory tree or the stomach. This kind of injury, also done when the fish leaves its host, should be negligible as pearlfishes do not always infest the same host. However in a heavily infested population, chances that a given host is infested regularly increase; hence repeated loss of coelomic fluid and successive wound repairs have to be considered (Jangoux, 1990). On the other hand, Cuvierian tubules are never exuded and holothuroid eviscerations seem never caused at the time of pearlfish entry.

**GENERAL CONSIDERATIONS**

Platyhelminthes, Mollusca and Arthropoda are the taxa that include the highest numbers of holothuroid parasites but low attention has been devoted to holothuroid-associated gregarines and it is very probable that the number of infesting species recorded in the future will be higher than that of metazoan taxa (Fig. 6). The digestive tract (including the cloaca) is the body compartment that is the most infested (Fig. 7) and gut-associated parasites are flatworms, molluscs and crustaceans. Most of them are living free in the digestive tract, gliding on the digestive wall. The symbiotic relations that they develop with the holothuroids are still not well firmly established and their parasitic status relies more on suggestions than on true experiments or valuable observations. The coelom of holothuroids is also well infested and other flatworms, molluscs and crustaceans are living in there but also protozoan gregarines and carapid fishes. Other body compartments - the haemal system, ambulacral system, respiratory trees, gonads and body wall - are less affected by parasites. The body wall, in particular, is mainly affected by gastropods.



**Figure 6.** Number of species per taxon infesting holothuroids.



**Figure 7.** Location of the parasites in the holothuroid body. When a parasite infested two body compartments, both have been included in the graph.

Infestation of holothuroids by internal parasites takes place mainly through body openings (mouth and cloacal aperture). Intracoelomic organisms reach the coelom in passing through the digestive wall. Intracoelomic copepods enter the coelom by penetrating the anterior part of the gut, larvae of most intracoelomic gastropods enter the coelom through the digestive wall and carapid fishes pierce the cloacal wall (Jangoux 1990). Holothuroid reactions to parasites are of three types: (1) inflammatory-like reactions; (2) connective tissue reactions and (3) coelomocyte reaction (Jangoux 1990). Inflammatory-like reactions consist in the migration of defensive cells (red spherules and coelomocytes) to the site of infection and occur mainly in diseases caused by microorganisms. Connective tissue reactions counteract organisms such as gastropods that tend to stay within the connective tissue layer. Coelomocyte reactions are directed towards intracoelomic parasites and result in the phagocytosis or the walling off of foreign organisms.

All the protozoans and metazoans parasites currently described in scientific literature are not lethal for wild or cultured adult holothuroids. They are thus of no economic importance and their presence in or on adult holothuroids should not alarm the sea cucumber industrial stockbreeders. However, it should be emphasised that the high density of holothuroid populations in cultures could favour overinfestations by parasites and could influence some important parameters in farming such as the growth speed of individuals or the reproductive abilities of breeders. Most alarming are the infections of sea cucumber juveniles by bacteria that can eradicate nearly all individuals of cultured populations in a few days. Parameters that cause the apparition of bacterial diseases are poorly known and we suppose that an increase in temperature and/or a too high density of individuals in aquaria can favour the infection of individuals. The best way to avoid such bacterial disease is to check constantly the health of juveniles and to eliminate sick individuals. Juveniles that are not too infected can recover by treating them with a faint formalin solution in salt water for a few minutes.

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