

REVIEW

Diseases of Echinodermata. IV. Structural abnormalities and general considerations on biotic diseases

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ABSTRACT: Reported structural abnormalities mostly concern the echinoid test; these are not uncommon and indicate great plasticity of the echinoids. More than 400 animal agents have been reported from echinoderms. Most external agents either have processes that penetrate the body wall or live in cysts or galls on or in the body wall; intradigestive agents usually occur free in the digestive cavity; internal agents are mostly intracoelomic and live either free in the coelomic cavity or attached to the coelomic wall. Host reactions to invading organisms are either inflammatory-like reactions (i.e. intratissular migration of some coelomocytes towards the site of infection), connective-tissue reactions (i.e. formation of a thick fibrous sheet isolating the agent from the host's connective tissue) or coelomocyte reactions (i.e. endocytosis of microorganisms or walling off of animal agents entering the host's coelomic cavity). All known mass mortalities due to biotic disease agents are caused by microorganisms. With very few exceptions, animal agents do not kill their echinoderm host: most of them are well tolerated and do not appear to result in major consequences for the hosts concerned. Echinozoa (Holothuroidea and Echinoidea) and Asterozoa (Asteroidea and Ophiuroidea) exhibit a different degree of sensitivity to animal pathogens, the asterozoans' defensive mechanisms being apparently more efficient than those of echinozoans. Echinoderms play a key role in many benthic communities and their diseases – especially lethal or castrating diseases – should have major effects on the biological environment (this has been demonstrated in a few cases of disease-related mass mortalities). Echinoids and ophiuroids represent a prominent part of the diet of many fishes; their role as vector of fish diseases caused by trematodes or nematodes requires investigation.

INTRODUCTION

The present paper is the last of a series of 4 that review the diseases of Echinodermata. The different groups of disease agents (i.e. microorganisms, protists, and metazoans) were surveyed in detail in Parts I to III (Jangoux 1987a, b, c). Part IV will first review the structural abnormalities and presumed neoplasia presented by the echinoderms; it will then consider the location, effect and ecological consequence of biotic agents as well as the reaction and sensitivity of echinoderms to pathogens.

STRUCTURAL ABNORMALITIES AND NEOPLASIA

Test abnormalities have been reported for many species of regular and irregular echinoids especially by Koehler (1922, 1924), Chadwick (1924), Jackson (1927), Brattström (1946), Chesher (1969), Moore (1974), Hinegardner (1975) and Allain (1978). These abnormalities involve mainly non-pentamerous individuals; or those with a pinched or bifurcated ambulacrum, a depressed or distorted test, a depressed apex, or a depigmented epiderm (for illustrations see e.g. Koehler

1922, Moore 1974). Test abnormalities may have different causes: external injuries, genetic malformations, critical environmental conditions, or biotic or nutritional diseases. That test abnormalities may be caused by malnutrition was emphasized by Koehler (1922). While Moore (1974) considered they resulted mainly from metabolic upset, Hinegardner (1975) attributed the loss of pentamerous symmetry in laboratory-reared echinoids to as yet undetermined genetic factors. Whatever the cause, that these abnormalities are not uncommon indicates great plasticity of the echinoids. Conspicuous test deformations in echinoids living in polluted areas (Dafni 1980, 1983) suggest that many of the abnormalities reported may be induced by particular environmental conditions (see also Allain 1978).

Body shape abnormalities (e.g. abnormal arm number in normally pentamerous species) were reported also for asteroids. According to Hotchkiss (1979), these abnormalities appear to be generally the consequence of regeneration following predator injury. Watts et al. (1983), however, present evidence that ray-number abnormalities in asteroids can be caused by high salinities during early development.

A review of early literature by Wellings (1969) does not reveal any definite case of neoplasia among echinoderms. According to Sparks (1972) the only possible neoplasms recorded in echinoderms are the tumor-like epidermal lesions reported by Fontaine (1969) in the ophiuroid *Ophiocoma nigra*. Ophiuroid tumors consist of densely packed cells (mostly melanocytes and spherulocytes with light-brown granules); they lack connective tissue elements. These tumors may grow. Late-stage lesions are roughly divided into cortical and medullary regions, the latter having undifferentiated and fibroblast-like cells. According to Sparks (1972) tumors of *O. nigra* are apparent neoplasms and present evidence of metastases. However, similar kinds of 'tumors', i.e. clots of densely packed cells with brownish pigmented granules, frequently occur within echinoderm tissues. These clots are often located either in the hemal system or within epithelial tissues. Possibly, they correspond to unwanted material, mostly degenerating coelomocytes, in the process of being eliminated. As for the tumor observed by Smith et al. (1973) in the intestine of *Holothuria leucopilota*, the reviewer believes it to be simply an unusual outgrowth of the ventral hemal vessel of the holothuroid gut.

GENERAL CONSIDERATIONS ON BIOTIC DISEASES

As discussed in Part I (Jangoux 1987a), I have

adopted the definition of parasites proposed by Kinne (1980, p. 19) and used it in a very broad sense, considering disease agents (parasites *sensu lato*) to represent any kind of a harmful associate which affects, if even slightly, the echinoderm's tissues or internal fluids (i.e. coelomic and hemal fluids). I consequently considered all external and internal associates whose detrimental effects were demonstrated or documented, as well as intradigestive symbiotes that act or may potentially act as parasites. The latter still require critical investigation as to their role – neutral or detrimental – in relation to the echinoderm's life, i.e. its ecological potential and health status.

Immune defense mechanisms of echinoderms have been studied mostly during the past 10 yr. Cellular defense mechanisms act through phagocytic coelomocytes whose ability to phagocytose and/or to wall off the unwanted material entering the echinoderm body cavities is well known (Smith 1981, Bang 1982, Karp & Coffaro 1982, Dybas & Fankboner 1986). Cell-types similar to coelomocytes have been seen also in experimentally altered echinoderm body walls (pathological alteration or reaction to allografts: Höbaus 1980, Karp & Coffaro 1982, Gilles & Pearse 1986, Maes et al. 1986). These cells massively invade the altered areas producing an inflammatory-like reaction. Moreover, coelomic fluids of echinoderms possess naturally-occurring humoral factors such as hemolysin and hemagglutinin (Ryoyama 1973, 1974; see also Bang 1982) as well as bactericidal substances (Wardlaw & Unkles 1978, Service & Wardlaw 1984, 1985). All this demonstrates that echinoderms are well armed to

Animal agents associated with echinoderms are summarized in Table 1. More than one-third of these agents live on or in holothuroids (Fig. 1). Crinoids, regular echinoids and asteroids harbor a rather similar number of harmful associates. As for irregular echinoids, agents mostly infest spatangoids (18 species), the remaining species affecting clypeasteroids. Gastropods, turbellarians and copepods comprise the most numerous agents affecting the phylum Echinodermata. However, myzostomids, ascothoracids and sporozoans are also well represented. Holothuroids appear to provide a most suitable substrate for parasites of many kinds, except for myzostomids and ascothoracids. These latter 2 groups infest specifically crinoids or asteroids. Detailed information on each species of disease agents (its taxonomical position and relations with the host) are given in this review Parts I to III (Jangoux 1987a, b, c). Although a great deal of echinoderm parasites have been known for many years, definite information on the biotic diseases of echinoderms is still rare. Interestingly, echinoderms – while rather intensively parasitized – never act as parasites themselves.

Table 1. Number of species of animal agents living with echinoderms. Only identified and documented agents are considered (detrimental effects demonstrated or probable). (Original)

Hosts	Agents																				Total	
	Sporozoa	Protozoa ²	Porifera	Cnidaria	Mesozoa	Turbellaria	Trematoda	Nematoda	Entoprocta	Polychaeta	Myzostomida	Gastropoda	Bivalvia	Tardigrada	Copepoda	Thoracida	Ascothoracida	Malacostraca	Arthropoda ²	Bryozoa		Pisces
Crinoidea	1	1	-	4	-	4	2	-	1	-	19	7	-	-	2	10	2	2	-	6	-	61
Holothuroidea	15	-	1	1	-	39	3	-	1	2	-	34	3	1	22	-	-	10	2	4	7	145
Echinoidea (Regularia)	-	3	-	1	-	14	7	3	-	-	-	24	-	-	11	6	-	5	2	-	-	76
Echinoidea (Irregularia)	7	-	-	-	-	6	-	-	-	-	-	-	1	1	-	2	2	10	-	-	-	29
Asteroidea	-	1	-	1	-	6	-	2	-	-	2	19	-	-	3	-	25	1	2	-	3	65
Ophiuroidea	-	-	1	1	1	1	4	1	1	1	3	6	-	-	16	-	6	-	1	-	-	43
Total	23	5	2	8	1	70	16	6	3	3	24	90	4	2	54	18	35	28	7	10	10	

¹ Non-sporozoan protozoans
² Miscellaneous arthropod groups (acarions, pycnogonida, insects)

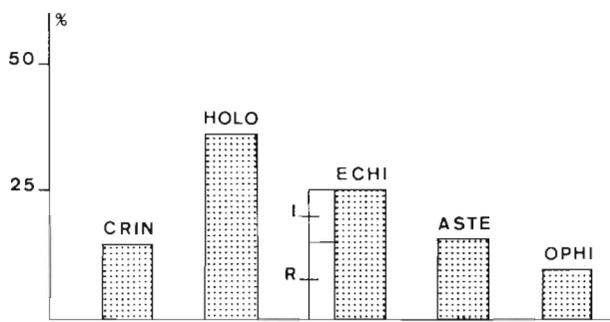


Fig. 1. Relative percentage of animal agent species living in each of the echinoderm groups indicated. CRIN: Crinoidea; HOLO: Holothuroidea; ECHI: Echinoidea (I: irregular; R: regular); ASTE: Asteroidea; OPHI: Ophiuroidea. Original

Location and effects of animal agents

A classification according to host sites of harmful associates (on or in echinoderms) is presented in Table 2 (see also Fig. 2). Agents mostly inhabit 3 different sites: body wall, digestive cavity, and coelomic cavity. This corresponds to an external (A), intradigestive (B) or internal (C) location.

External agents (A-agents)

Among external agents (A1 to A3-agents; Table 2), A1-agents mostly occur on holothuroids and echinoids. They comprise strictly ectoparasitic species such as, for example, eulimid gastropods and pinnotherid crabs

infesting the external body surface. A1-agents presumably include many more species than considered here. This is because most unattached associates, while often said to be ectoparasitic, have received only taxonomical attention.

A2-agents can firmly attach themselves to the host's external body surface in spite of the presence of a cutaneous epithelium. Such associates have rarely been observed on asteroids and irregular echinoids; they have been reported only casually on holothuroids, regular echinoids and ophiuroids. However, crinoids appear to be rather sensitive to A2-agents. Possibly, crinoid sensitivity to these agents results from a weak defensive capacity of their epidermal barrier.

A3-agents are by far the most common external echinoderm associates. Although they all live, in one way or another, within the echinoderms' body wall, they show conspicuous differences in their feeding habits. Several A3-agents feed independently of their host. They may be, for instance, suspension-feeders simply sheltering in galls or cysts (i.e. most of the harmful myzostomids). Independent feeding also occurs in a few gastropods and copepods causing galls in echinoid spines or body wall. This could also be the case in some organisms inhabiting ophiuroid branchial bursae. However, most A3-agents feed at the expense of their host, either by ingesting body-wall tissues or by sucking up internal fluids. Body-wall feeders are mainly gallicole gastropods, such as asteroid-associated *Stilifer* spp. A few copepods also feed in this manner (e.g. *Scottomyzon gibberum*). External fluid-feeders are also mainly gastropod molluscs. Several species use their proboscis to penetrate the body wall

Table 2. Classification of animal agents affecting echinoderms according to location. (Original)

Hosts	External			Intradigestive		Internal		
	A1	A2	A3	B1	B2	C1	C2	C3
Crinoidea	–	23	28	6	–	7	1	1
Holothuroidea	8	7	10	43	11	53	12	2
Echinoidea (Regularia)	6	8	24	29	7	12	–	6
Echinoidea (Irregularia)	3	10	–	6	–	9	–	–
Asteroidea	3	1	21	4	1	35	–	1
Ophiuroidea	1	6	24	2	1	4	–	6
Total	21	55	107	90	20	120	13	16
	A agents: 283			B agents: 110		C agents: 149		

A1-agents live free or simply cling to outer host-body surface
A2-agents attach to outer host-body surface (viz. epithelium-covered body surface)
A3-agents have processes that permanently penetrate or cross the body wall, or live in cysts or galls on or in the body wall (including spines), or live permanently in naturally-occurring ectodermal invaginations (viz. genital bursae of ophiuroids)
B1-agents live free in digestive cavity
B2-agents attach to or bury in the digestive wall
C1-agents inhabit coelomic cavity or ambulacral system (live free, or attached to coelomic wall, or embedded in mesenteries)
C2-agents live in hemal system
C3-agents live in gonads

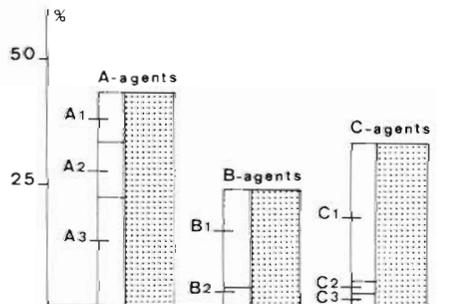


Fig. 2. Relative percentage of each category of echinoderm-infesting animal agents; for explanations see Table 2. (Original)

in order to suck up coelomic, ambulacral, or hemal fluid (*Euchineulima* spp., *Thyca* spp., *Pisolaria brychius*, respectively). It has been suggested that the proboscis of parasitic eulimid gastropods would secrete particular material that brings about a rapid loosening of connective tissue of the echinoderm body wall, thereby facilitating penetration of the host's integument (Smith 1984). Ectoparasitic gastropods sucking up hemal fluid occur mostly in holothuroids whose hemal fluid has a high energy content. Possibly, a similar feeding habit has been developed by other ectoparasitic gastropods infesting crinoids (e.g. *Balcis devians* and *Melanella comatulicola*) and asteroids (*Thyca* spp.). The proboscises of these gastropods have been seen to be inserted into the host's coelomic or radial canals which are closely associated with a well-developed hemal lacuna.

Coelomic-fluid feeders appear to be a rather paradoxical adaptation, since the coelomic fluid is not particularly energy-rich. Such a feeding habit implies that the agents feed on coelomocytes or 'browse' on internal tissues, however this is poorly documented for A3-agents. Can ingestion of coelomocytes alone meet the energy requirements of the parasites? If so, such infestation should be rather harmless since echinoderms produce new coelomocytes almost continuously. Finally, many A3-agents of ophiuroids, especially crustaceans, inhabit the genital bursae of their host. Genital bursae are easily accessible and well sheltered. Moreover, gonads open into the bursae which means a potential supply of energy-rich material. Yet this does not imply that bursal-inhabiting associates necessarily feed on the host's gonads.

Detrimental effects of external agents are not restricted to their feeding. Some induce conspicuous modifications of the host's skeleton. There are 3 kinds of such modifications: (1) hypertrophy of skeletal ossicles (caused for example by gallicole myzostomids and spine-inhabiting gastropods or copepods); (2) development of supernumerary skeletal ossicles (e.g. around subcutaneous cysts of some crinoid-infesting myzostomids; around cysts of some copepods living in ophiuroid genital bursae); (3) inhibition of the development of skeletal ossicles (such as that caused by the asteroid-associated gastropod *Parvioris equestris*). Skeletal modifications have also been reported for diseases caused by microorganisms, i.e. the bald-sea-urchin disease (see Jangoux 1987a). A3-agents may

also cause dermal outgrowths, mostly in gastropods and copepods.

Echinoderm ectoparasites do not castrate their host, except for some forms of Ascothoracida which live in the genital bursae of ophiuroid. These, however, do not cause typical castration – none of them is said to feed on gonadal tissues – but are considered to inhibit both gonadal growth and germinal development. The bursal-inhabiting copepod *Amphiurophilus amphiuræ*, which infests the brooding ophiuroid *Amphipholis squamata*, presumably suppresses incubating embryos by diverting part of their food supply without affecting the host's gonads.

Intradigestive agents (B-agents)

Agents inhabiting the digestive system of echinoderms (B1 and B2-agents; see Table 2) mainly infest holothuroids and regular echinoids. While most B1-agents are turbellarian worms, a few gastropods and copepods also live freely in the digestive cavity. Presumed detrimental effects of these associates are poorly documented. However, some of them exhibit a typical parasitic behavior by feeding on digestive host epithelium. In contrast, B2-agents, while living within the digestive wall and producing conspicuous deformations, seem to be rather independent from host tissues as far as feeding is concerned. Thus gut-associated crabs of echinoids ingest primarily the food pellets of the host. Similarly, bivalve molluscs inhabiting gut outgrowths are basically suspension feeders. A detrimental effect on host nutrition might of course occur. This depends greatly on the location of the associates, those living in the holothuroid cloaca or echinoid anal tube being supposedly harmless. B2-agents feeding at the expense of host structures are almost exclusively gastropod molluscs. They generally do not feed on digestive tissues; in most species the proboscis penetrates hemal lacunae, gonads or the body wall.

Internal agents (C-agents)

Internal agents (C1 to C3-agents; Table 2) live either within the coelom, the hemal system or the gonads of the host. Echinoderms harbor a highly diverse intracoelomic fauna (C1-agents): sporozoans, turbellarians, aberrant gastropods, copepods, ascothoracids and fishes are not uncommon in their body cavities. Turbellarians and copepods are the main free-living C1-agents. Their feeding habits require special attention by researchers. Only Changeux (1961) reported intracoelomic copepods 'browsing' on holothuroid mesothelium. The assumption of Jennings & Metrick

(1968) that intracoelomic turbellarians feed essentially on intracoelomic ciliates, although not impossible, appears improbable (so far, intracoelomic turbellarians have been recorded much more often than intracoelomic ciliates). Other free-living C1-agents are fishes and motile stages of sporozoans, viz, trophozoites and gamonts. These latter are almost exclusively found in the coelom of spatangoid echinoids. (Trophozoites and gamonts of sporozoans of holothuroids inhabit primarily hemal lacunae.) Presumably they feed via direct intramembranous absorption of nutrients from the coelomic fluid. Fishes either behave as strict parasites in ingesting the host's gonads or respiratory trees, or they only shelter in the echinoderm coelom and prey upon shrimp and other free-living crustaceans they catch outside.

A second category of C1-agents are simply floating or deposited in the host's body cavity, i.e. sporozoan cysts and most ascothoracids. Intrategumentary absorption of coelomic nutrients has usually been suggested as the feeding method of intracoelomic ascothoracids. Wagin (1976), however, concluded that they feed mostly on coelomocytes.

The last category of C1-agents includes organisms attached to the coelomic wall and hanging into the body cavity: spatangoid ascothoracids and aberrant gastropods from holothuroids (*Enteroxenos* and allied genera). The body wall of the latter is always surrounded by a host-produced envelope consisting of an inner connective tissue layer and an outer mesothelial layer. As indicated by Jangoux (1987b, p. 227) hemal lacunae within the host's envelope would facilitate parasite nutrition. In the absence of hemal lacunae – an absence which would be worth demonstrating – intrategumentary nutrition from the coelomic fluid must be assumed. The only intracoelomic gastropod that is definitely a hemal-fluid feeder, *Gasterosiphon deimatis*, has been recorded in the body cavity of a deep-sea holothuroid.

C2-agents spend most of their life cycle in the host's hemal lacunae. So far, this group comprises only holothuroid-infesting sporozoans.

Animal agents parasitizing echinoderm gonads (C3-agents) are not very numerous. They include species of protozoans, mesozoan, trematodes, nematodes and myzostomids. Most of them feed directly on gonadal tissues.

While internal agents often castrate their host, the method of castration may differ considerably. Classical castration occurs with agents feeding directly on germinal tissues, e.g. gonad-infesting ciliates of asteroids and gonad-infesting myzostomids of ophiuroids. Less drastic castration may be caused by encysted organisms invading the gonad and supposedly blocking the passage of hormonal substances needed by

echinoderms for gametogenesis (Pearse & Timm 1971). The 'passive castration' (Wagin 1946) induced by some intracoelomic and intrabursal associates is of great interest. It should be more properly termed 'competitive castration' as it appears to result from nutritional competition between associate(s) and host's gonads. It causes either slight or total regression of the gonads, depending on the number of agents, and is presumably reversible when the agents are dislodged from their host. Competitive castration may be inferred for Mesozoa and some intracoelomic gastropods inhabiting holothuroids (e.g. *Entocolax schwanwitschi* and *Paedophorus dicoelobius*) as well as for intracoelomic ascothoracids of spatangoids (*Ulophysema* spp.).

Infestation routes, host reactions and virulence

Infestation of echinoderms by internal agents takes place mainly through body openings (i.e. mouth, anus, gonopores; also branchial bursae of ophiuroids), or through thin areas of the body-wall (e.g. tube feet, respiratory papulae). Intracoelomic copepods of *Holothuria* spp. enter the host's body cavity by penetrating the anterior part of its gut. A similar behavior prevails in most sporozoans inhabiting deposit-feeding echinoderms. Cloaca and respiratory trees of holothuroids also allow the passage of infesting stages of internal agents (i.e. some sporozoans, turbellarians, and fishes). Larvae of most intracoelomic gastropods of holothuroids (*Enteroxenos* and allied genera) also enter the host's body cavity through the digestive wall or, more rarely, through the body wall. These gastropods, however, live never totally free in the coelom; they are always surrounded by an envelope produced by the hosts (this envelope is continuous with the outer tissues of the host's digestive tract or body wall). Infesting larvae of asteroid-associated ascothoracids may enter their host through respiratory papulae, as do some intracoelomic copepods. Larvae of ascothoracids living in spatangoids enter the host through the genital pores. No report has come to the reviewer's attention that refer to the routes taken by nematodes and digenic trematodes which enter the internal tissues or body cavities of echinoderms.

There are 3 kinds of host reactions counteracting invading organisms: (1) inflammatory-like reactions; (2) connective-tissue reactions; (3) coelomocyte reactions. Inflammatory-like reactions occur mostly in diseases caused by microorganisms and algae (see Jangoux 1987a) or upon cutaneous wound repair (e.g. Menton & Eisen 1973). Basically these reactions consist of a migration of red spherule cells and phagocytic cells towards the site of infection (Johnson & Chapman 1970,

Johnson 1971, Maes et al. 1986). These cells are of coelomic origin. According to Johnson (1971; see also Service & Wardlaw 1984), red spherule cells would act as a 'general disinfectant'. Their presence in or close to a wounded or infested area prevents penetration or settlement of unwanted organisms. In holothuroids and echinoids red spherule cells always occur in every tissue or organ, although they are generally present in rather low densities. This cell type has not been reported in pathologically altered body areas of asteroids or ophiuroids.

Connective-tissue reactions counteract organisms which tend to stay within the connective tissue layer. A thick fibrous sheet is formed which surrounds and thus isolates the foreign organisms from the host's tissue. Such reactions are not an uncommon defense mechanism against sporozoans cysts, trematode metacercariae or invading nematodes. They also counteract some animal agents, such as copepods and ascothoracids, that infest either the genital bursae of ophiuroids or the coelomic cavity of holothuroids.

Coelomocyte reactions counteract agents entering the host's coelomic cavity. Generally, they are inconspicuous reactions resulting in phagocytosis or completely walling off the foreign organism. A massive and very particular coelomocyte reaction is initiated by motile stages of spatangoid intracoelomic gregarines; each participating coelomocyte becomes pointed, the parasite taking on the appearance of a minute pin cushion.

It was generally not yet possible to evaluate agent virulence, except in the case of microorganisms or algae. They produce conspicuous pathological alterations which often kill the host. All known mass mortalities of echinoderms due to biotic disease agents are caused by microorganisms. So far, no animal agent has been reported to kill the host, except for a few small ectoparasitic crabs living on some echinoids. Diseases caused by animal agents become obvious only if they result in particular changes in the echinoderm's body shape. As a rule, internal damage is not detectable from the outside, and echinoderms appear perfectly healthy even when massively infested (e.g. by some sporozoans or mesozoans).

Relative sensitivity of echinoderms to animal pathogens

The 'pathogenic index' for each echinoderm group has been tentatively estimated (Table 3). Although rather approximate, the indexes reveal that Echinozoa and Asterozoa exhibit a very different degree of sensitivity to animal pathogens. It is not possible to explain this difference on the grounds of morphological, ethological or ecological considerations. The reviewer supposes that

Table 3. Pathogenic indexes of echinoderm classes. (Original)

Hosts	Estimated no. of recent host species	No. of species of animal agents	Pathogenic index*
Crinozoa	700	60	8.6
Echinozoa	2000	240	12.0
Holothuroidea	1100	141	12.8
Echinoidea	900	99	11.0
Asterozoa	3800	109	2.9
Asteroidea	1800	66	3.7
Ophiuroidea	2000	43	2.2

* (No. of species of animal agents / no. of echinoderm species) × 100

it results basically from physiological properties and implies that the asterozoans' defensive mechanisms are more efficient than those of echinozoans.

ECOLOGICAL CONSEQUENCES OF ECHINODERM DISEASES

Echinodermata constitute a large and highly distinctive group of marine invertebrates. World-wide, they are found from the shoreline to the deepest ocean trenches. As bottom-dwellers they have colonized all marine benthic biotopes and, characteristically, tend to occur in dense populations. Clearly, the ecological radiation of the Echinodermata has been considerable and they can be considered a major macrobenthic animal group. Many littoral echinoderms greatly affect the bioeconomics of both hard- and soft-bottom communities. For instance, they are frequently top predators in their community (e.g. many asteroids) or controlling agents of seagrass or kelp beds (e.g. numerous regular echinoids). Some species have tentatively been classified as 'key species', i.e. species which by size or number, mode of life, or activity can functionally dominate a community. Moreover, echinoids and ophiuroids form part of the diet of many fishes and macroinvertebrates, such as crustaceans. Although the ecological consequences of echinoderm diseases have not been studied nor considered – except for a few cases of spectacular and virulent diseases caused by microorganisms – these diseases should have prominent effects on the biological environment.

The ultimate ecological consequence of diseases caused by microorganisms in echinoderm populations is a reduction or even elimination of the populations concerned. In contrast, most diseases caused by animal agents do not appear to result in major consequences for the echinoderms concerned and are well tolerated. One may consider each echinoderm, especially the

holothuroids, as an animal substrate on/in which various other organisms live, either permanently or temporarily. Together, the echinoderm and its associates form a usually well-balanced biological complex. Some animal agents, however, may castrate echinoderms and consequently affect the renewal and long-term stability of the population concerned. Quantitative estimations of the effect of castrating agents have never been made. Of course, the effects will depend on infestation rates. Ecological effects of other non-castrating agents are almost impossible to assess at the population level. We can only imagine that, when numerous, agents such as arm-infesting myzostomids, bursal-inhabiting copepods or coelom-sheltered fishes would 'weaken' their host population.

Effects of echinoderm diseases on echinoderms' predators mostly concern echinoderms affected by biotic communicable diseases, i.e. those caused by digenic trematodes or by nematodes (see Jangoux 1987b). Since numerous echinoids and ophiuroids represent a prominent part of the diet of many fishes, the role of echinoderms as vectors of fish diseases requires investigation.

Littoral echinoderms are frequently top predators in their community (many paxilloid and forcipulatid asteroids; for review see Menge 1982), or controlling agents of seagrass or kelp beds (numerous regular echinoids; for review see Lawrence & Sammarco 1982, Harrold & Pearse 1987). Experimental or natural removal of these predators or controlling agents produces major environmental changes (e.g. Paine 1971, Estes et al. 1978, respectively). Catastrophic decline of predatory echinoderms caused by disease was noted only by Dungan et al. (1982) in the asteroid *Heliaster kubinji*; these authors, however, did not consider impacts on the biological environment. Mass mortalities by diseased *Strongylocentrotus franciscanus* were followed by rapid expansion of 4 species of brown algae (Pearse & Hines 1979). Subsequent competition among algal species was severe, and within 1 yr only 1 algal species inhabited the area. Another lethal disease that affects the echinoid *Paracentrotus lividus* was studied by Boudouresque et al. (1981) who established that the decrease in echinoid density promoted an explosive growth of epiphytes on leaves of the seagrass *Posidonia oceanica*.

Widespread disease-related mass mortalities of *Strongylocentrotus droebachiensis* occurred from 1981 along the coast of Nova Scotia, Canada (Miller & Colodey 1983, Scheibling 1984). *S. droebachiensis* is the dominant herbivore of the kelp beds of Nova Scotia (e.g. Mann 1982); mass mortalities of the echinoids was expected to result in colonization by subtidal macroalgae followed by an increase of benthic primary production (Miller & Colodey 1983). Moore & Miller (1983)

reported that in areas where *S. droebachiensis* was absent for 1 yr the percentage algal cover was 2 to 14 times higher than in areas with echinoids. In the absence of echinoids, macroalgae expanded to deeper and more sheltered locations: the kelp *Laminaria longicruris* gained a dominant status and fleshy seaweeds developed in the subtidal (Moore & Miller 1983, Miller 1985, Johnson & Mann 1986). According to Scheibling (1984) and Scheibling & Stephenson (1984), mass mortalities of *S. droebachiensis* would play a key role in determining the structure and stability of the rocky subtidal ecosystem off Nova Scotia, by controlling the abundance of the dominant herbivore.

The echinoid *Diadema antillarum* – the principal herbivore and the most effective bioeroder of the Caribbean region (e.g. Bak et al. 1984, Liddell & Ohlhorst 1986) – suffered a widespread and conspicuous mass mortality resulting in a drastic reduction of the population densities to 1 to 7% of their previous level (Lessios et al. 1984; see also Jangoux 1987a). Mass mortality was caused by a virulent biotic disease (Bak et al. 1984, Hughes et al. 1985). Elimination of *D. antillarum* from most Caribbean reefs resulted in a significant increase of fleshy and filamentous algae as well as of some macroalgae (Hughes et al. 1985, de Ruyter van Steveninck & Bak 1986, de Ruyter van Steveninck & Breeman 1987). This increase was achieved at the expense of other benthic organisms such as corals, crustose corallines and clonid sponges whose settlement has been considerably reduced (de Ruyter van Steveninck & Bak 1986, Liddell & Ohlhorst 1986). Investigators generally believe the situation is irreversible and will fundamentally affect the Caribbean reef ecosystem unless the populations of *D. antillarum* are restored or those of other herbivores take over the role of the diadematids.

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