

Parasitism, commensalism or mutualism? The case of Scyphozoa (Coronatae) and horny sponges

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ABSTRACT: The relationship between the scyphozoan *Nausitoë punctata* and the horny sponges *Cacospongia scalaris*, *Dysidea avara* and *D. fragilis* was analyzed. Evidence was found for utilization of the thecae of *N. punctata* as a substitute for skeletal fibres. Consequently some metabolic costs associated with skeleton-building may be reduced for the sponge. Further potential benefits for the scyphozoan, e.g. protection against predation and mechanical disturbance, and trophic advantages, are discussed. This association is suggested to be non-parasitic and mutualistic, and widely distributed among 6 orders and 8 families of the Demospongiae which occur throughout the Northwestern Mediterranean.

INTRODUCTION

Mutualistic associations between organisms are thought to play an important role in structuring marine communities (Vance 1978). Such relationships contribute, along with competition, predation and physical disturbance, to increased complexity and diversity in certain benthic ecosystems (Osman & Haugsness 1981). They have been traditionally considered to be more widespread in tropical than in temperate zones as a result of environmental stability (Futuyma 1973, May 1973) and biotic pressure (high levels of predation and competition) (Addicot 1984).

Sponges are reported to be one of the benthic invertebrate groups that most frequently host other benthic invertebrates (Santucci 1922, Pearse 1932, 1950, Arndt 1933, Fishelson 1966, Long 1968, Pansini 1970, Sube 1970, Bacescu 1971, Sarà & Vacelet 1973, Frith 1976, Ruetzler 1976, Uebelacker 1977, Peattie & Hoare 1981). They are microcosms in which different levels of interaction between host and colonizer may be present. The high number of inhabitants of some of the sponges studied (up to 200 specimens of the polychaete *Syllis spongicola* per cm² of sponge; Bacescu 1971) made them worthy of being described as 'living hotels' (Pearse 1950). Quantitative comparisons of sponge dwellers with inhabitants of the surrounding substrata showed that certain sponges are very efficient ecological niches (Ruetzler 1976) and, in some cases, behave as ecological islands (Uebelacker 1977).

Generally, these associations are considered to be

harmless relationships in which organisms occupy the interstitial spaces of the sponge without causing any noticeable damage to its structure (mere inquilinism). Nonetheless, some cases of true mutualism have been reported (Bloom 1975, Forester 1979). When morphological or cytological alterations of the sponge became evident, the association has been conventionally considered parasitism without analysing the balance of costs versus possible benefits for both partners (Connes et al. 1971). Thus, the invasion of sponges by the scyphozoan *Nausitoë punctata* Kölliker 1853 (Syn.: *Stephanoscyphus mirabilis* Allman 1874, *Spongicola fistularis* Shultze 1877), could be considered a case of parasitism on the basis of the surface morphological changes of inhabited sponges and because it also disturbs their functional orifices. In addition, the polyp growth, although apparently limited (Werner 1979), and the continuous generation of new polyps by branching does not enable the sponge to recover and kill the invader, in contrast to the situation described for other colonizers with limited growth like the cirripedian *Acasta spongites* Poli (Ruetzler 1976). Moreover, new planules arising from the scyphomedusae, resulting from annual polyp strobilation (Werner 1979) can occupy new functional orifices in successive generations.

In light of the above, one could reasonably suppose that, if no benefits were obtained by the sponge, invasion by the scyphozoan would probably cause considerable damage, ending in the death of the sponge. However, long-term observations of such highly

infested sponges casts some doubt upon the parasitic nature of the association, since they remained alive and grew for years (present study). Furthermore, if *Nausitoë punctata* is a parasite, the sponge's reaction would tend toward its isolation (Connes 1968, Sube 1970, Connes et al. 1971, Uriz 1983) whereas if not, some interaction between the 2 partners could be expected.

The question that arose from these observations was whether infested sponges were in a regressive state as a consequence of a parasitic relationship or, on the contrary, were in some way benefitting from the presence of the scyphozoan. If some benefits for the scyphozoan were also found, this association could be considered a facultative mutualism (Boucher et al. 1982, Addicot 1984).

MATERIAL AND METHODS

Sponges inhabited by the scyphozoan *Nausitoë punctata* were monitored for 2 yr at 1 to 6 mo intervals on rocky semi-dark substrata between 8 and 30 m depth in the littoral zone of Blanes (Northwestern Mediterranean, Iberian Peninsula). The percentage of infested sponges was calculated in a restricted uniform area of about 200 m². From January to May 1991, a total of 150 infested and non-infested specimens of the horny sponges *Cacospongia scalaris* Schmidt, *Dysidea avara* (Schmidt) and *Dysidea fragilis* (Montagu) were collected by SCUBA, and placed in an open-system aquarium with seawater pumped directly from the sea, for further examination. Some specimens were transferred to small closed-system aquaria in order to observe the production of scyphomedusae and to study the growth of the sponge skeleton after killing the scyphozoan.

Specimens carefully cleaned of accompanying fauna, flora and substratum were weighed after being drained for 20 s. Sponge wet weight was calculated by subtracting from the entire specimen weight (i.e. sponge plus scyphozoan) a value obtained by multiplying the number of polyps of scyphozoans present by the mean wet weight of a representative polyp (0.01 ± 0.004 g) (mean of 50 polyps). The weight of small rocks and calcareous debris attached to the sponges, which became evident when the cell material of the specimens was eliminated, was also subtracted.

Microscopical observations and measurements (conule number, polyp number, length of the scyphozotheca protruding from the sponge) were made with a Wild M8 stereomicroscope, following 3 d of specimen adaptation to aquarium conditions. They were conducted without removing the specimens from seawater to avoid contraction or damage due to handling. A 1 cm

square frame was placed on the sponge surface, and the number of polyps inside this frame counted under a stereomicroscope. The process was repeated throughout the whole sponge surface of every specimen of each species, carefully preventing overlap between squares.

Optic and SEM observations of the sponge skeleton and horny thecae of the scyphozoan were carried out on specimens whose organic matrix was previously removed by decay in seawater. Skeletal parts fixed in 4% formalin were dehydrated by immersion in a graded series of ethanol, subjected to the critical point, coated with gold palladium in a sputtering E-5000 and observed through a Hitachi scanning electron microscope.

The skeleton dry weight of the sponge was obtained after dehydration at 90 °C to constant weight. The dry weight of the scyphothecae present in each specimen was subtracted from the sponge-scyphozoan dry weight. This value was estimated by multiplying the mean dry weight of a representative theca (calculated from 50 individuals) by the number of thecae present in a given individual.

The relationship between the number of primary fibres reaching the sponge surface (conules) and the number of polyps of the Scyphozoa, and that between the sponge skeleton weight and the number of polyps, per sponge biomass unit, were described using regression analyses ('Microstat' by Ecosoft, Inc., 1978-85).

Since an increase in the habitual amount of fouling could indicate a deficient health state in benthic sessile organisms (pers. obs.), comparisons of the presence (*G*-test for an $R \times C$ contingency table) and abundance in percent cover (Student's *t*-test) of fouling, between infested and non-infested sponges (Sokal & Rohlf 1979), were performed in order to obtain complementary information on the health state of the infested sponges. Estimates of sponge surface area covered by epibionts were derived from projecting the sponge image, through a camera clara, onto a 'Genius' digitizer linked to the computer by the program HiPad2 (modified version of the original design by K. Foreman of the Woods Hole Oceanographic Institution).

RESULTS

In the studied area, sponge species inhabited by scyphozoans were numerous with horny sponges (Order Dictyoceratida and Dendroceratida) being the most frequently colonized (Table 1). The scyphozoan infesting the sponges was a colonial, branched form belonging, on the basis of morphological characteristics of the polyp and medusa, to the species *Nausitoë punctata* Kölliker (Werner 1970, Chapman & Werner 1972).

Table 1 Relative frequency in which sponge species host Scyphozoa in the studied area

Order	Species	Relative frequency range
Dictyoceratida	<i>Spongia officinalis</i>	< 1 %
	<i>Ircinia oros</i>	< 1 %
	<i>Cacospongia scalaris</i>	21–50 %
	<i>Cacospongia mollior</i>	1–10 %
Dendroceratida	<i>Dysidea avara</i> ^a	11–20 %
	<i>Dysidea fragilis</i> ^a	21–50 %
	<i>Pleraplysilla spinifera</i>	< 1 %
Verongida	<i>Aplysina aerophoba</i>	< 1 %
Poecilosclerida	<i>Crambe crambe</i>	1–10 %
	<i>Phorbas tenacior</i>	21–50 %
Petrosida	<i>Petrosia ficiformis</i>	< 1 %
Halichondrida	<i>Hemimycale columella</i>	1–10 %

^a Species included in the order Dendroceratida according to Boury-Esnault et al. 1990

In the horny sponges studied, each conule (surface protrusion) represents the apex of a primary skeletal fibre, the main structural support built by the sponge to grow upwards (Fig. 1). The aquiferous system of the horny sponges is organized in such a way that many inhalant orifices, corresponding to several inhalant cavities, surround a conule (Fig. 2B). The sponge ectosome of the infested specimens rose up around the polyps in the same way as it did on the tips of the primary fibres in non-infested specimens. In all 3 sponge species, the polyps of the scyphozoan were surrounded by inhalant orifices, as the conules were in non-infested specimens. In each case, their tentacles were pointed directly against the inhalant flow (Fig. 2A).

A 2 to 3 mm wide zone devoid of any sponge fibre was present underneath the sponge ectosome of the most infested specimens of both species of *Dysidea*, the thecae of *Nausitoë punctata* being the only stiff structure supporting the sponge tissues in this zone (Figs. 1B & 2D). When *N. punctata* died, as was the case after 2 mo of maintenance in aquaria without any food supply, the sponges grew over the thecae of the scyphozoan and new primary fibres quickly formed, starting from the thecae and building new conules at the sponge surface (Fig. 1C).

Primary fibres were absent from specimens of *Dysidea avara* with 10 or more polyps cm^{-2} and from those of *D. fragilis* with more than 19 polyps cm^{-2} (Fig. 2D). In contrast, they were always present in *Cacospongia scalaris* (Fig. 2C), even in the most infested specimens, since the number of polyps cm^{-2} was always less than the species-specific number of conules cm^{-2} (Table 2). The species-specific mean distance

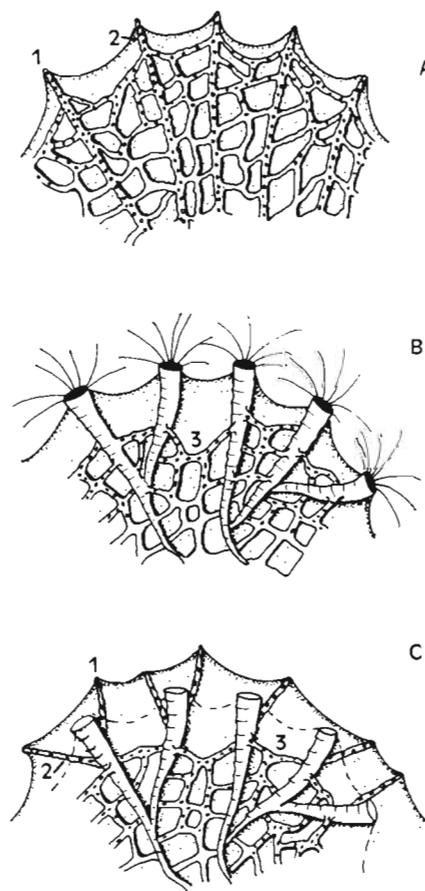


Fig. 1 *Dysidea avara*. Schematic representation of the skeleton: (A) Specimen without *Nausitoë punctata*; (B) specimen with live polyps of *N. punctata*; (C) the same specimen as in (B) after killing the scyphozoan. (1) Surface conules; (2) primary (main) fibres; (3) secondary fibres

between conules (Table 2) was maintained in infested specimens with some or all conules replaced by polyps.

Primary fibres of *Dysidea fragilis*, *D. avara* and *C. scalaris* and secondary fibres of *Dysidea* spp. are filled with foreign material consisting of sponge spicules, calcareous debris or sand (Vacelet 1959). In the case of *D. avara* and *D. fragilis*, primary and secondary fibres were difficult to differentiate in infested specimens because primary fibres were short and tortuous. Moreover, they sometimes joined 2 scyphozoan thecae similarly to secondary fibres (Fig. 3C). In any case, the scarce primary fibres were notably shorter than those of non-infested specimens. Evidence of a solid linkage of sponge fibres to the horny thecae of the scyphozoan was obtained from the scanning electron microscope observations for the 3 sponges. No zone of inhibition between the attached fibre and the horny tube was distinguishable, both forming a unique solid structure as a result of joint growth (Fig. 3).

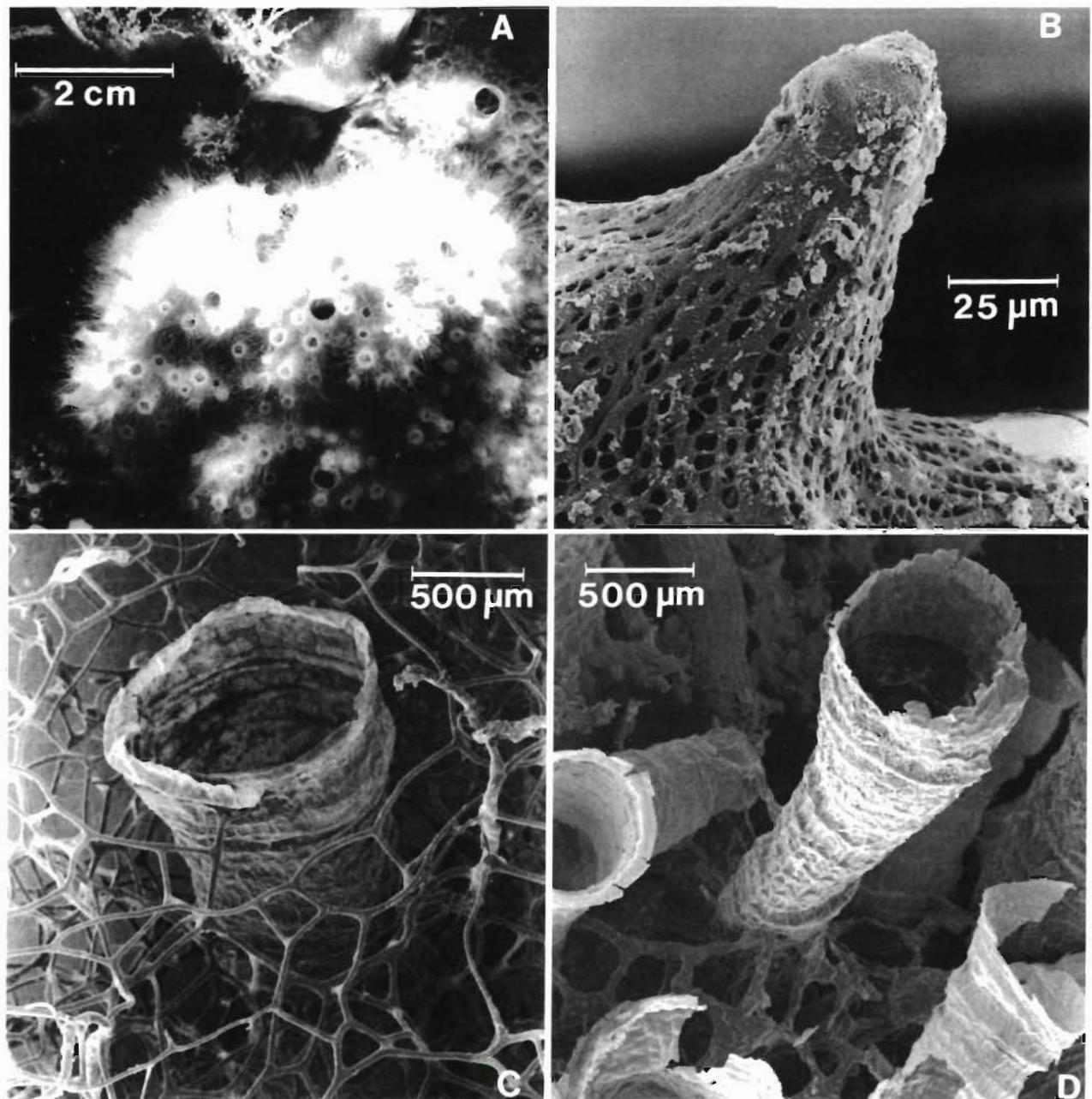


Fig. 2. (A) *Dysidea fragilis*. A heavily infested specimen. (B) Surface of a horny sponge showing the ostia distribution around a conule. (C) Theca of *Nausitoë punctata* surrounded by mainly secondary but also primary fibres of *Cacospongia scalaris*. (D) Thecae of *N. punctata* attached to the skeletal net of *D. fragilis*

Table 2. *Cacospongia scalaris*, *Dysidea avara* and *D. fragilis*. Number of surface conules per cm² and distance between conules in non-infested specimens

Species	Conule no. cm ⁻²				Distance between conules (mm)	
	Min.	Max.	Mean	SD	Mean	SD
<i>C. scalaris</i>	15	24	18.3	3.2	1.0	0.4
<i>D. avara</i>	8	12	10.1	1.4	4.3	0.6
<i>D. fragilis</i>	29	37	31.6	2.4	1.0	0.1

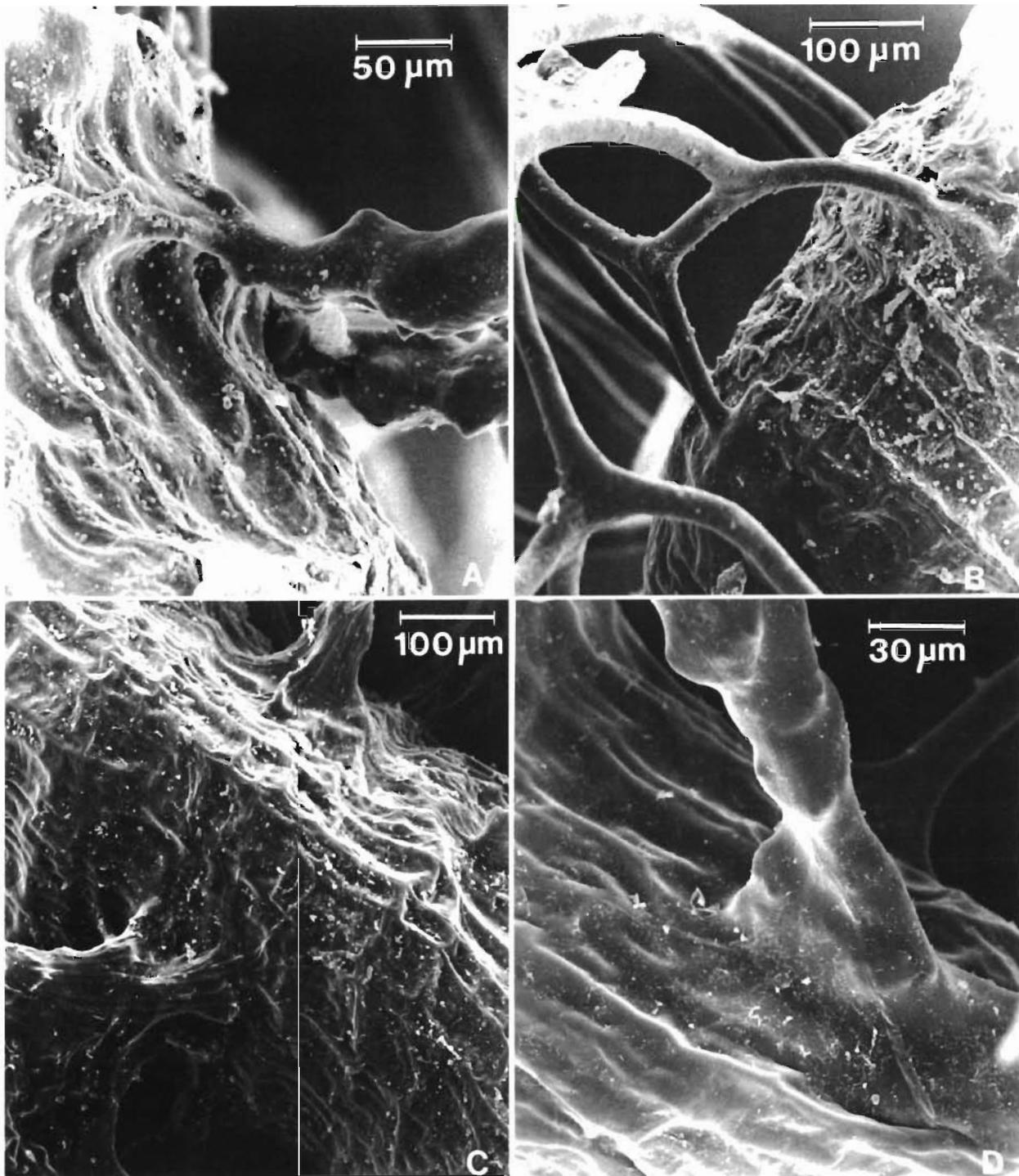


Fig. 3. Evidence of solid linkage between sponge fibres and the horny thecae of *Nausitoë punctata*: (A) Primary fibre of *Cacospongia scalaris*; (B) secondary fibres of *C. scalaris*; (C) primary fibres of *Dysidea fragilis*; (D) secondary fibres of *D. avara*

Dysidea fragilis exhibited the highest levels of infestation (30 polyps cm^{-2}) followed by *D. avara* and *Cacospongia scalaris* (11 polyps cm^{-2}) (Fig. 4). A significant negative correlation was found between the conule number (number of primary fibres reaching the surface) and the number of polyps of *Nausitoë punctata* per cm^2 of sponge surface. A linear regression was obtained for *C. scalaris* and *D. avara* ($r^2 = 0.87$, $p < 0.001$ in both cases) while an exponential line best described the relationship of *D. fragilis* ($r^2 = 0.93$, $p < 0.001$) (Fig. 4). A strong negative correlation was also found for the 3 sponge species between the skeletal sponge weight and the number of polyps of *N. punctata*, per sponge biomass unit. A logarithmic regression ($r^2 = 0.83$, $p < 0.001$) was obtained for *C. scalaris* while a power model gave the best fit for *D. avara* ($r^2 = 0.83$, $p < 0.001$) and *D. fragilis* ($r^2 = 0.88$, $p < 0.001$) (Fig. 5).

In all the sponges under study, oscula were conspicuous and clearly differentiable from ostia. *Nausitoë punctata* occupied inhalant orifices and may have formed

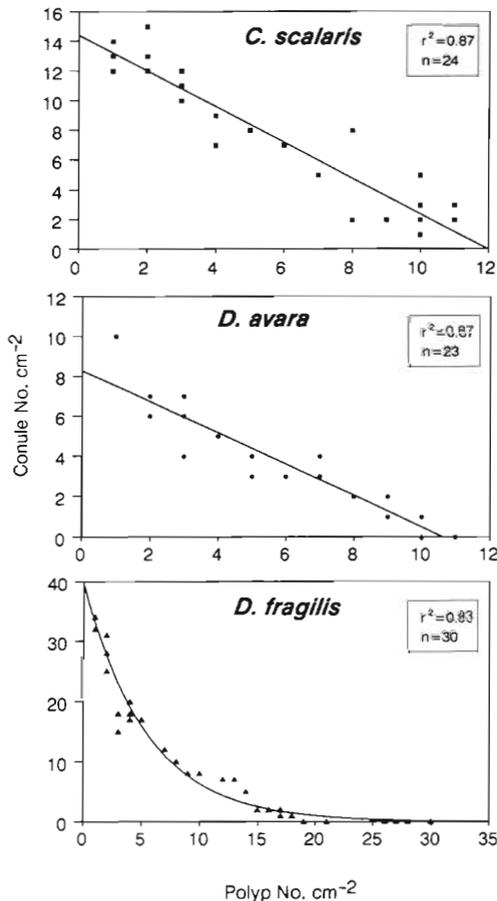


Fig. 4. *Cacospongia scalaris*, *Dysidea avara* and *D. fragilis*. Relationships between the number of surface conules and the number of polyps of *Nausitoë punctata* per cm^2 of sponge

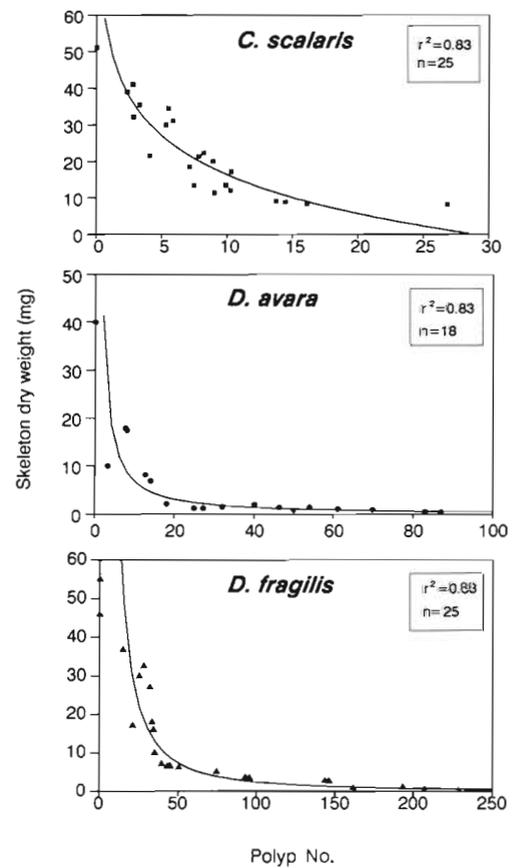


Fig. 5. *Cacospongia scalaris*, *Dysidea avara* and *D. fragilis*. Relationships between skeleton dry weight and number of polyps per sponge biomass unit

new ones. However, individuals never actually occupied oscula (Fig. 2A). There was even a 3 to 7 mm wide zone of 'oscular influence', devoid of scyphozoans.

Some differences in the mean length of the thecae protruding from the sponge were found among the 3 sponge species (Fig. 6A). The thecae protruded much more in the case of *Cacospongia scalaris* ($\bar{x} = 1.8$ mm; $SD = 0.43$) than in *Dysidea avara* ($\bar{x} = 1.1$ mm; $SD = 0.24$) and *D. fragilis* ($\bar{x} = 0.1$; $SD = 0.02$). The maximum length of the polyps of *Nausitoë punctata* living in the sponges under study was 10 mm ($\bar{x} = 7.6$, $SD = 1.9$ mm) in *C. scalaris*, 11 mm ($\bar{x} = 7.8$, $SD = 2.4$ mm) in *D. avara* and 13 mm ($\bar{x} = 9.6$, $SD = 3.4$ mm) in *D. fragilis* ($n = 50$ polyps).

No significant dependence (G-test) was found between the presence of *Nausitoë punctata* and that of fouling in any of the sponge species studied (Fig. 6B). Nevertheless, the total area fouled was significantly greater in infested than in non-infested specimens of *Cacospongia scalaris* ($p < 0.05$; t -test). Due to the interaction of this sponge with the cirripede *Acasta spongites* (a species, always present, which also plugs the sponge's functional orifices) and *N. punctata*, it was

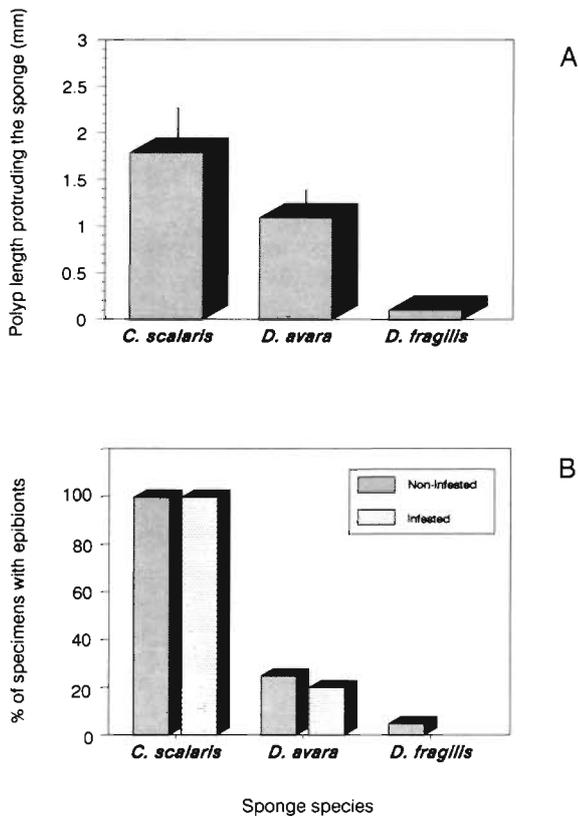


Fig. 6. (A) *Nausitoë punctata*. Mean length of tubes protruding from sponges (+1 SD). (B) Presence of other epibionts in sponges infested and non-infested by *N. punctata*

not possible to evaluate the sole influence of *N. punctata* in the sponge cover by epibionts.

DISCUSSION

Possible benefits versus costs for the scyphozoan

That some advantages are gained by the Scyphozoa from this association can be deduced from the fact that all specimens were associated with sponges in the study area. Moreover, the greater mean length of polyp thecae of individuals inhabiting sponges (9.6, 7.8 and 7.6 mm, in *Dysidea fragilis*, *D. avara* and *Cacospongia scalaris*, respectively), than that of free polyps (mean 6.8 mm) (Werner 1970), may also be an indication of some trophic advantage for *Nausitoë punctata* dwelling in sponges.

The most likely benefits of this relationship for the scyphozoan are: (1) protection against physical disturbances, as the sponge strengthens the scyphozoan colony by integrating its own skeleton with the scyphotheca of *Nausitoë punctata*, (2) trophic advantages, as inhalant flow carries out small organic partic-

les susceptible to capture by the tentacles of the scyphozoan. (The positioning of the polyp tentacles against a slow flow, as in the inhalant flow created by the sponge, has been shown in other cnidarians to be optimal for capturing particles; Patterson 1991); and (3) chemical defence against potential predators, as the 3 sponges examined exhibit toxicity (Amade et al. 1987, Uriz et al. in press). The scyphozoan will have had to develop resistance against the sponge's chemical defences in order to make this association successful. Nevertheless, these adaptative processes are common in epibionts, symbionts and predators of toxic species (Hay et al. 1988, Hoppe 1988, Paul & Van Alstyne 1988, Hay et al. 1989, Uriz et al. in press).

Other more hypothetical advantages such as habitat for recruitment (settlement and fixation) could also be considered, since planules may be attracted towards a suitable substratum (sponge) either by chemical cues or by a mechanical response to the inhalant current produced by the sponge (up to 1 cm s⁻¹ in aquarium specimens).

No costs derived from this association for the Scyphozoa are evident from this typological study, although some costs would be expected from any mutualistic relationship if mutualism is considered to derive from antagonistic interactions (Thompson 1988). These might be better investigated at the population level. The restriction of the distribution of *Nausitoë punctata* to that of its sponge host could be considered a potential cost.

Possible benefits versus costs for the sponge

The most likely benefits obtained by the sponge are linked to the use of the horny thecae of the scyphozoan as skeletal fibres. Sponges do not identify the theca of *Nausitoë punctata* as a parasite, since they do not isolate it, but as a primary fibre or suitable substratum, since mainly secondary but also primary fibres were found fused to it. This could represent a significant metabolic saving, because the skeleton appropriates a considerable portion of metabolic sponge effort (McClintock 1987, Desqueyroux-Faundez 1990).

Another role of the primary fibres may be to provide support to sponge cells carrying sandy particles from the sponge surface along the fibres (Teragawa 1986). This could also be performed by the thecae of the Scyphozoa, as they provide the necessary membrane tension to the sponge ectosome, similar to the tips of the primary fibres in non-infested specimens. The tubes of *Nausitoë punctata* also provide support for the sponge tissues and help for the organization of the aquiferous system. The 3-dimensional growth acquired by the sponges without the necessity of building pri-

mary fibres is advantageous to the sponge growth thanks to a more efficient pumping of water (Vogel 1977). On the other hand, the scyphozoan cleans the water surrounding the sponge of large particles likely to foul the ostia. Its movements may also cause microturbulence, increasing the residence time of the small particles, and, consequently, the probability of being carried into the sponge via currents.

The plugging of the ostia by *Nausitoë punctata* does not seem to cause severe damage to the sponge. Reorganization of the aquiferous system would appear to be the main cost to the sponge derived from this association. Some orifices of the inhalant region remain functional and additional ostia can be easily formed due to the ectosome tension of these sponges (Teragawa 1990). Consequently, water inflow can be offset without excessive additional costs through both remaining and new-formed orifices.

The differences in the mean length of the thecae protruding from the 3 sponge species could be ascribed to different levels of coupling in growth rates between the scyphozoan and the sponge.

The healthy state of sponges of the genus *Dysidea* is supported by the epibiosis data since a benthic organism in a 'regressive' state is characterized by a significant increase in its fouled surface. In the 3 sponges studied, the presence of fouling was significantly independent of the presence of *Nausitoë punctata*. Only in *Cacospongia scalaris*, was the total coverage by epibionts significantly greater in infested individuals. In this case the association seems to be slightly negative for the sponge. The length in which the polyps of *N. punctata* protrude from this species, higher than that in the species of *Dysidea*, supports this assumption. Nevertheless, the simultaneous association of *C. scalaris* with another specific partner (*Acasta spongites*) surely influences the outcome of its interaction with the scyphozoan, since correlated outcomes are frequent in multiple associations (Thompson 1988). It would be desirable to investigate the influence of *N. punctata* on specimens free of the cirripede, but this would also be unrealistic, since no specimens without *A. spongites* occur in the area under study.

As shown in coral communities (Glynn 1976), a system that appeared to be parasitic seems on closer inspection, to reveal mutualistic interactions. However a more thorough experimental approach would be necessary to confirm the mutualistic nature of this association. Experiments should be focused on substratum preferences (sponge versus others) of the planulae (scyphozoan) during the settlement process, differential growth rates of sponges and scyphozoans living with and without each other, under the same environmental conditions, and predation pressure on scyphozoans inside and outside sponges.

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