

The Association of *Ophiothrix lineata* and *Callyspongia vaginalis*: A Brittlestar- Sponge Cleaning Symbiosis?

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With 7 figures

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Abstract. The relationship between a sponge, *Callyspongia vaginalis*, and an associated brittlestar, *Ophiothrix lineata*, was examined for mutualistic symbiotic interaction. Cinematography, feeding experiments, and analyses of stomach contents reveal that *O. lineata* (unlike other *Ophiothrix* species) is a non-selective deposit feeder. Its diet consists of detrital particles adhering to the sponge, which are too large to be utilized by the sponge as food. Thus, the brittlestar cleans the inhalent surface of the sponge as it feeds. Since siltation interferes with sponge pumping-activity, it is suggested that the cleaning behavior of *O. lineata* may enhance the filtration capability of *C. vaginalis*. *In situ* elapsed-time films show that brittlestars expose their arms when they feed, suggesting that they feed only at night because of a need to avoid diurnal predators. Manipulative experiments show that residence in *C. vaginalis* protects *O. lineata* from predatory fish. A

comparison of the incidence of arm regeneration for brittlestars residing on *C. vaginalis*, and on a toxic sponge, *Neofibularia nolitangere*, indicates that factors other than sponge toxicity are involved in protecting sponge-dwelling brittlestars.

Problem

According to WESTINGA & HOETJES (1981, p. 149) the fauna inhabiting sponges is "an ecological community, in which, however, interrelationships are not yet clear." Brittlestars are a common component of that community. Their association with sponges has been documented in the scientific literature (MACGINITIE & MACGINITIE, 1949; PEARSE, 1950; HYMAN, 1955; BACESCU, 1971; RÜTZLER, 1975) and by the popular press (MURPHY, 1980; SEFTON, 1982). In some cases the association is facultative or fortuitous and the brittlestars involved may be found on or off the sponge. The association of *Ophiothrix quinquemaculata* (DELLE CHIAJE) with sponges, for example, has been attributed simply to the climbing behavior of the brittlestar or its reaction to water currents (FEDRA *et al.*, 1976; FEDRA, 1977; STACHOWITSCH, 1980). Unfortunately, the ecology of brittlestars which are facultatively associated with sponges has not been investigated in sufficient detail to accurately characterize the interactions between brittlestar and sponge (PEARSE, 1950; WURZIAN, 1977; WESTINGA & HOETJES, 1981).

In cases where the two taxa are invariably associated there may be a strict symbiosis, with at least the brittlestar benefiting from the association. The brittlestar *Ophiothrix lineata* LYMAN, for example, has been reported as an associate of various sponge species. This study examines the interaction of *O. lineata* with a sponge, *Callyspongia vaginalis* (LAMARCK), to clarify the nature of the symbiosis between the two organisms.

It is possible that sponges offer the brittlestar a refuge from predation. To better understand this potential interaction an additional sponge species was investigated. *Neofibularia nolitangere* (DUCHASSAING & MICHELOTTI) was chosen since it is considerably more toxic than *Callyspongia vaginalis*, and it harbors several of the same brittlestar species as *C. vaginalis*. Toxicity could be evaluated as a factor in protecting sponge-dwelling brittlestars, by comparing the physical condition of brittlestars associated with the two species of sponges.

The diet and mode of feeding of *Ophiothrix lineata* were studied to determine whether it uses the sponge as a source of food. Additional complexities of the association were considered. For example, I indicate below that *Callyspongia vaginalis* may benefit because *O. lineata* clears debris from the incumbent surface of the sponge host and might thereby enhance the filtering efficiency of the host.

Material and Methods

1. Location

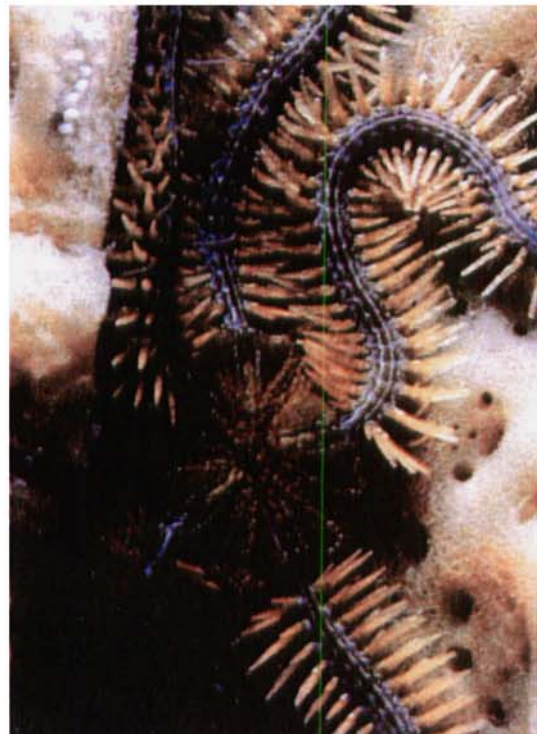
The study site was a cut in the Belize Barrier Reef to the south of Carrie Bow Cay (RÜTZLER & MACINTYRE, 1982, p. 11, for location). The area is about 5 m deep, predominantly a sandy bottom with scattered coral heads, sponges, gorgonian colonies, and patches of seagrass. It is subjected to strong tidal and wind-driven currents that can dramatically alter the turbidity of the water in the cut.

Fig. 1 (right). At night, the arms of the brittlestar, *Ophiothrix lineata*, are extended along the outer walls of the sponge, *Callyspongia vaginalis*. Polyps of the epizoic zoanthid, *Parazoanthus parasiticus* (DURCHASSAING & MICHELOTTI) are evident on the largest sponge tube.



Fig. 2 (bottom). At night, the distal portion of the arms of *Ophiothrix lineata* protrude from the osculum of *Callyspongia vaginalis*. As the brittlestar's arms slowly sweep across the inhalent surface of the sponge its attenuate tube-feet and long, slender arm-spines collect the detrital particles on which it feeds.

Fig. 3 (right hand bottom). A tube of *Callyspongia vaginalis* torn open during the day to reveal a specimen of *Ophiothrix lineata*. The brittlestar's disc is covered by fields of low, rough granules alternating with large, bare radial shields. The lines from which the species name derives are visible along the dorsal surface of the arms.



2. Elapsed-time cinematography

A tube sponge, *Callyspongia vaginalis*, with a resident population of the brittlestar, *Ophiothrix lineata*, was filmed *in situ* for three days using an underwater strobe and a 16 mm elapsed-time movie camera set for exposures at 20 sec intervals (equipment described in detail by EDGERTON *et al.*, 1968). A buoyant plastic float, used as a current meter, was tethered near the base of the colony inside the picture area. The angle of the float line indicated approximate current speed (HENDLER, 1982 a), however, only relative fluctuations in current speed are considered in this paper.

During filming, the intensity of ambient illumination was monitored continuously with a photometer (United Detector Technology, Inc. 40 X Opto-meter) and a potentiometric strip chart recorder. The photometer sensor was shielded with an uncalibrated diffuser and mounted on an unshaded sector of the laboratory roof on Carrie Bow Cay.

3. Behavioral analyses

Using the time-lapse film, the movements of the brittlestars and the rates of sediment clearance from the surface of the sponge were analysed with a stop-motion 16-mm projector (L-W International 224-A MK VI Photo-Optical Data Analyser). Brittlestar activity was measured by enumerating the brittlestar arms visible on the outer (inhalant) surface of the sponge at appropriate intervals (Figs. 1, 2, 3).

To evaluate the rate at which adhering material was removed from the surface of the sponge, the sponge was dusted with fine sediment before the nocturnal cycle of brittlestar activity and then filmed. Frames of the film were projected and traced on graph paper, and the area covered by sediment in each frame was estimated by counting graph paper squares. The clearance rates were calculated separately for portions of the sponge that were reached by the brittlestar arms and for portions unaffected by the movements of the brittlestars. These results contrast the rate of clearance effected by the brittlestar with the rate of clearance attributable to gravity and water movement.

To clarify whether brittlestars merely dislodged particles from the surface of the sponge or actually could ingest them, the following experiment was performed. A mixture of brine shrimp eggs, and chopped fish scales and mucus was applied to the surface of a sponge. The eggs measured 0.47 ± 0.03 mm ($\bar{x} \pm$ s. d.) diameter. After 15 min, the sponge tubes were quickly torn open (Fig. 3), the brittlestars were removed, and while still underwater they were put into a plastic bag that was injected with concentrated formaldehyde solution. This treatment ensured that the stomach contents were quickly preserved and that the brittlestars did not regurgitate. After transferring the preserved samples to alcohol, the gut contents were removed from the brittlestar discs and examined for the presence of brine shrimp eggs.

The constituents of the natural diet of *Ophiothrix lineata* were determined for 90 specimens from 14 *Callyspongia vaginalis* sampled during the afternoon and for 71 specimens from 11 sponges sampled at night. The specimens were preserved in the same manner as those in the brine shrimp ingestion experiment. Stomach contents from each specimen were rinsed into a vial. When particles in the vials settled, all the samples were scrutinized. The quantity of material in each sample was rated on a scale from 1 to 3, based on the relative volume of material in the sample.

After gently agitating the sample vial, a subsample of the gut contents from each individual was removed with a wide bore pipette and placed on a well slide beneath a coverslip. A single, randomly chosen microscope field at $100\times$ magnification was traced using a camera lucida, and the longest axis of each particle in the field was measured from the drawing. The frequency distributions of particles in the stomachs of brittlestars sampled during the day and of those sampled at night were calculated (for 0.05 mm size categories) as a percentage of the total number of particles measured.

The naturally occurring accumulation of particles on the outer surface of *Callyspongia vaginalis* was sampled for comparison with the brittlestar stomach contents. An underwater suction device (CLARK, 1971), fitted with a $54\ \mu\text{m}$ mesh screen over the exhaust valve, was used to capture material clinging to the incurrent wall of the sponge. Collections were made in the afternoon from 20 sponge colonies, and the settled particles in the sample were analysed microscopically and statistically using the same technique applied to the stomach contents.

4. Size and distribution of brittlestars

The populations of brittlestars on 12 specimens of *Callyspongia vaginalis* and 6 specimens of *Neofibularia nolitangere* were removed underwater. For *C. vaginalis*, every brittlestar visible on the outer wall of the sponge was collected first. Then, the tubes of the sponge colony were opened and the brittlestars within were placed in a separate container. Because of the complex structure of *N. nolitangere*, the brittlestars collected from the outside and inside of each colony were combined.

The specimens collected in the field were anaesthetized and preserved in alcohol in the laboratory. After identifying each brittlestar to species, the disc diameters and maximum arm lengths were measured with calipers, ruler, or ocular micrometer. In addition, the arms of each specimen were examined for signs of autotomy or breakage and regeneration. A regeneration index (RI) was calculated as the fraction of regenerating arms divided by the number of arms examined, multiplied by 100. Arms broken during sampling were disregarded since they could not be critically examined for signs of regeneration.

5. Predation

The degree of protection afforded the brittlestars by *Callyspongia vaginalis* was evaluated in 10 experiments, as follows. A sponge was selected for the experiment with a resident population of *Ophiothrix lineata*. Eleven specimens of *O. lineata* were removed from another sponge. Five of those brittlestars were placed on the sand at the base of the experimental sponge, and five were placed on the outer wall of the experimental sponge. Finally, one specimen was crushed to attract predators. Attacks by fish that damaged brittlestars beneath, on, and inside the experimental sponge were tallied separately. To determine the percentage of survival after 5 min, the number of *O. lineata* remaining on and beneath the sponge were counted. The experimental sponges were not examined to determine the number of resident brittlestars in the sponge tubes, because specimens inside the sponge were never attacked.

A related series of 10 experiments was carried out, by placing crushed specimens of *O. lineata* inside 3 to 5 tubes of a sponge and then an additional crushed specimen on the sand at the base of the sponge. Predatory fish attracted to the area were observed to determine whether they would pursue and attack injured brittlestars inside the sponge.

Results

1. Distribution of brittlestars

Different suites of brittlestar species are found on *Callyspongia vaginalis* and *Neofibularia nolitangere*. Fig. 4 shows that 6 species of brittlestars are associated with the two sponges. However, *Ophiothrix lineata* and *O. oerstedii* LÜTKEN are restricted to *C. vaginalis*, while *Ophiactis quinqueradialis* LJUNGMAN is restricted to *N. nolitangere*.

Populations of certain brittlestars show different characteristics on the two sponges studied. There are differences in the mean size of the *Ophiothrix angulata* (SAY) and *O. suensoni* LÜTKEN on the two species of sponges (Fig. 4). For both brittlestar species the mean disc diameter of specimens on *Neofibularia* is significantly greater than for specimens on *Callyspongia* (*O. angulata*, $t = 72.52$, $n = 130$, $P < 0.001$; *O. suensoni*, $t = 19.45$, $n = 142$, $P < 0.001$).

The differences in the mean sizes of *O. lineata* inside and outside *Callyspongia vaginalis* is more striking, with larger specimens inside, and is also statistically significant ($t = 16.34$, $n = 154$, $P < 0.001$) (Fig. 4). *O. angulata* shows the

same trend ($t = 2.40$, $n = 103$, $P < 0.02$), as does *O. suenisoni* ($t = 5.46$, $n = 75$, $P < 0.001$) (Fig. 4). The data for *O. oerstedii* are inadequate to test for such a difference in mean disc diameter.

2. Circadian rhythm

A specimen of *Callyspongia vaginalis* was filmed for three days and the patterns shown in the three films were quite similar. The results of the film taken on 19 April, 1982 are shown in Fig. 5. The activity of the brittlestar arms outside the sponge (Figs. 1, 2), begins at dusk and diminishes in the morning. The peak intensity of activity occurs between about 1900 and 2400 h, during darkness. Because there was moonlight during the filming period, photometer values for illumination were recorded at night. There is no evident correlation between the intensity of nocturnal illumination and the activity of brittlestars (Fig. 5). Neither is there an obvious correlation between the strength of the current (generally travelling in surges moving less than 5 cm s^{-1}) and the activity of the brittlestars (Fig. 5).

3. Feeding activity

The nocturnal behavior of *Ophiothrix lineata* consists of moving its arms like a pendulum, very slowly sweeping across the surface of the sponge (Figs. 1, 2).

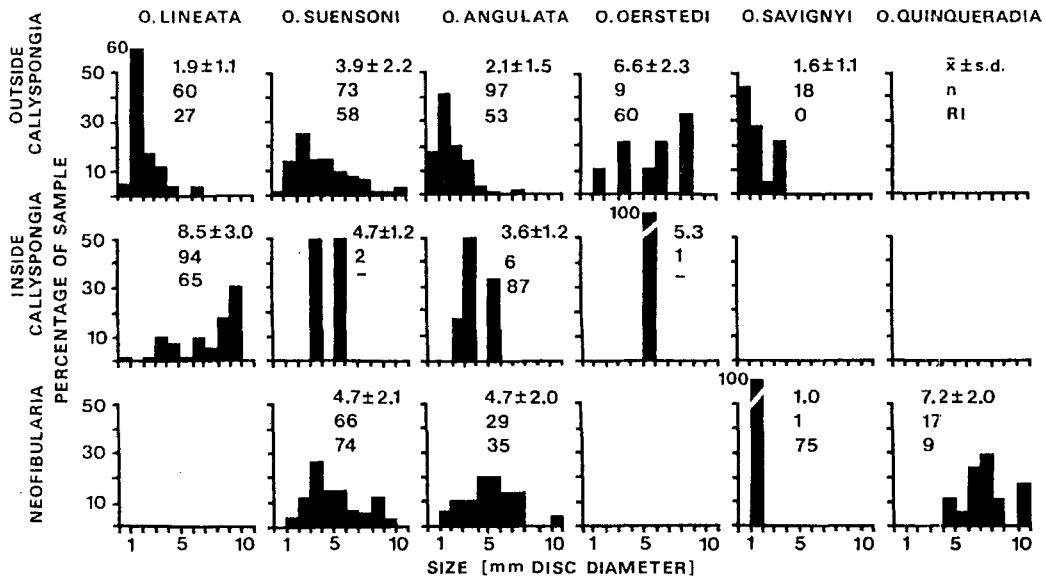


Fig. 4. Size-frequency distributions of brittlestars (*Ophiothrix lineata*, *O. suenisoni*, *O. angulata*, *O. oerstedii*, *Ophiactis savignyi* (M. & T.), and *O. quinqueradina*) collected from the outside and inside surfaces of *Callyspongia vaginalis*, and from *Neofibularia nolitangere*. The disc diameter (mean and s. d.), number of specimens, and regeneration index are indicated for each sample of brittlestars.

The tip of the arm moves at a mean rate of 3.14 ± 1.96 cm/min. Only 1.6% of the 2,566 arms counted during film analysis were lifted off the incurrent wall of *Callyspongia*; most arms remain in contact with the sponge (Fig. 5).

When the outside of a sponge was dusted with sediment, the moving arms of the brittlestars cleared a swath through the film of sediment clinging to the sponge. Fig. 6 illustrates the fraction of the surface of the sponge cleared at intervals after the brittlestars began feeding in the evening. The sediment on the sponge disappears in step with the emergence of brittlestar arms and increasing brittlestar activity (Fig. 6). Comparing the portion of the sponge brushed by the moving brittlestar arms with that area outside the reach of the brittlestars, clearly the portion of the sponge affected by the brittlestars loses silt more rapidly than the remainder of the sponge (Fig. 6).

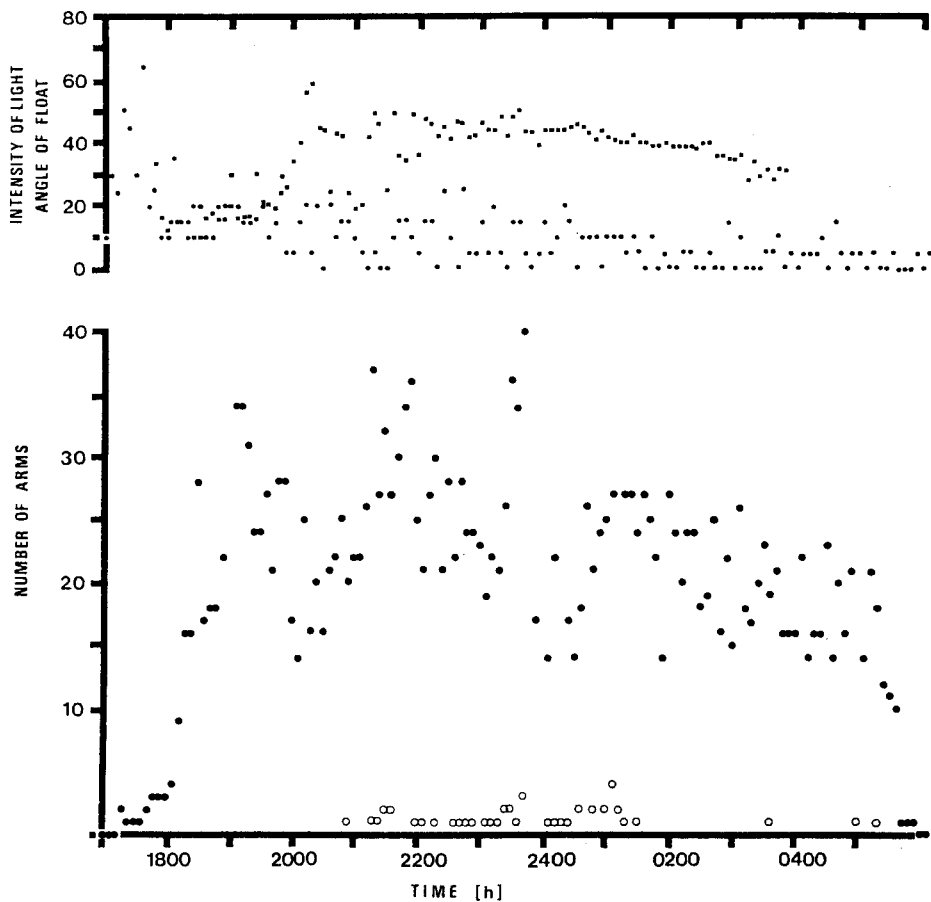


Fig. 5. Fluctuations of the intensity of activity of *Ophiothrix lineata* on *Callyspongia vaginalis*, expressed as the number of brittlestar arms visible on the outside surface of a sponge (large solid circles) in an elapsed-time film. Also shown are: the numbers of arms lifted off the surface of the sponge (open circles), the relative light intensity (squares), and the angle of the current-meter float (small circles).

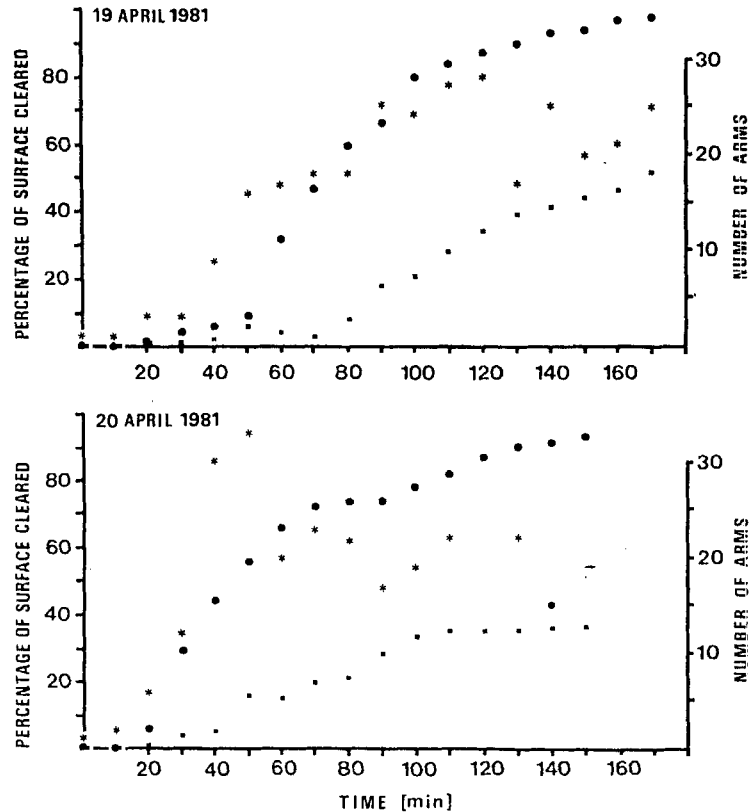


Fig. 6. The rate of clearance of sediment from the surface of a specimen of *Callyspongia vaginalis* dusted with silt, measured from elapsed-time films for two nights. The rate of clearance on portions of the sponge reached by *Ophiothrix lineata* (circles) is contrasted with clearance rate for the area not swept by brittlestar arms (squares). The number of *O. lineata* arms visible on the sponge (asterisks) is directly proportional to the intensity of brittlestar activity.

An experiment utilizing brine-shrimp eggs was performed to determine whether the particles removed from the surface of *Callyspongia vaginalis* are merely brushed off the sponge or could be ingested by the brittlestars. Of 14 *Ophiothrix lineata* exposed to the brine-shrimp egg mixture during two night dives, 7 individuals ingested brine-shrimp eggs. Four specimens of *O. lineata* were exposed to the mixture during the day, and no brine-shrimp eggs were found in their stomachs. These data are too few to warrant formal statistical comparison of night versus day behavior. In the stomach contents of 12 specimens collected at night, there was naturally occurring food material, the remaining 2 specimens had empty stomachs. In contrast, 1 specimen from the day sample contained naturally occurring food and 3 lacked food. These data are consistent with the cinematographic record of greater feeding activity at night and the results, discussed below, of an analysis of naturally occurring stomach contents.

It was rarely possible to discern identifiable particles amongst the material sampled in stomach contents and material sampled from sponges. The samples consisted largely of unidentifiable debris. Some chitinous parts, diatoms, bits of plant tissue, and sponge spicules regularly appeared in small numbers. Foraminifera, fragments of filamentous algae and strands of blue-green algae, copèpods, ostracod fragments, gorgonian spicules, and tiny gastropods were occasionally or rarely detected in the stomach contents and from the sponge wall. In addition, fragments of thecate hydroids were collected from the surface of the sponge.

To determine whether the brittlestars selectively removed material from the surface of the sponge, the size frequency distributions of particles from the sponge surface and from the stomach content samples were compared (Fig. 7). The same range of particle sizes occurs on the sponge and in the brittlestar stomachs from night and day collections. Pairwise in the three samples, the proportions of particles in different size categories are not significantly different ($\chi^2 = 1.0067$ with d.f. = 10, $P = 0.9995$). This result suggests that the brittlestars do not remove material selectively, at least according to particle size. One has to consider that the size spectrum in the stomach may have been influenced by agglutination or breakdown of particles by the brittlestar and the technique of removing particles from the sponge. However, the similarity of the size-frequency distributions from the three groups is striking.

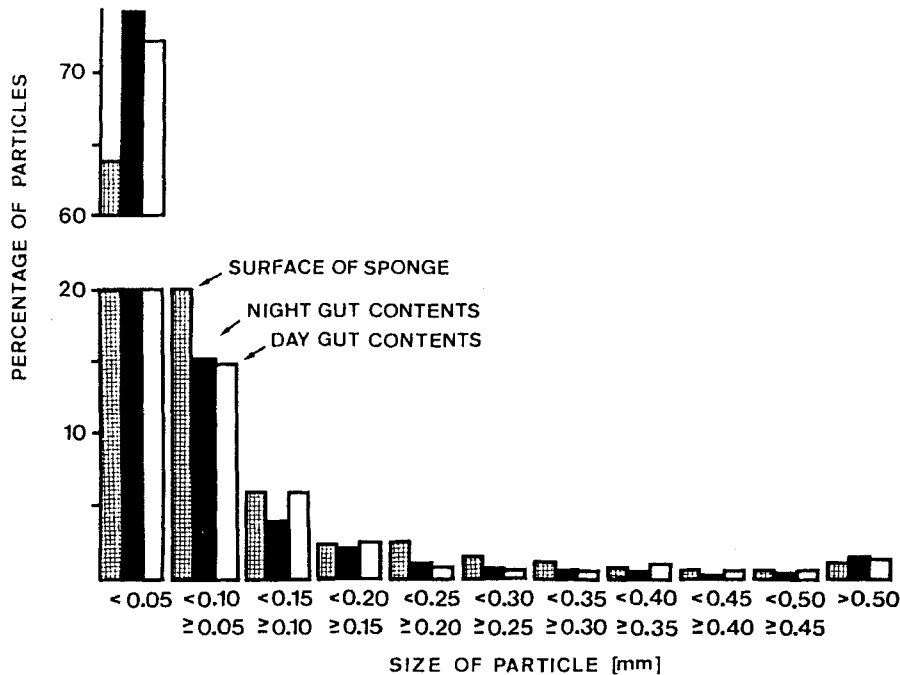


Fig. 7. Comparison of the size-distributions of particles: siphoned off the surface of *Callyspongia vaginalis* (number of particles = 1,369), removed from the stomachs of *Ophiothrix lineata* sampled during the day ($n = 499$), and removed from the stomachs of *O. lineata* sampled at night ($n = 3,109$).

It is noteworthy that although the food-particle size distribution is similar for the stomach contents of brittlestars during the day and at night, only 21 % (n = 91) of the brittlestars were feeding during the day compared to 86 % (n = 71) at night. This difference in the incidence of full and empty stomachs in day and night samples is significant (FISHER'S Exact Test: n = 162, P < 0.001). The volume of material in the stomachs of animals sampled at night was compared with that in the stomachs of animals collected during the day, by ranking the volume of material from 1 (low volume) to 3 (high volume). For night samples the number of specimens showing values 1, 2, and 3 is, respectively, 28, 21, and 12. For the day samples there is a lower volume of stomach contents per specimen, with 18, 2, and 0 individuals in the same categories. Moreover, the hypothesis that the occurrence of the three ranks was the same in the night and day samples is rejected ($\chi^2 = 12.2568$ with d. f. = 2, P = 0.0027). Thus, more brittlestars feed at night and their volume of stomach contents is greater than that of day-specimens.

4. Fish predation

Attacks on brittlestars in the lumen of *Callyspongia vaginalis*, and those placed experimentally on the outside of the sponge, and on the sand beneath the sponge were analysed. At night, potential predators on brittlestars, such as hermit crabs, squirrelfish, and grunts were present. However, these predators did not approach the experimental sponges or attack *Ophiothrix lineata*. During the day, fish reached the experimental sponges within 3 to 112 sec. The predominant species were *Halichoeres bivittatus* (BLOCH), *Halichoeres garnotti* (CUVIER & VALENCIENNES), and *Scarus croicensis* BLOCH. Other fish attracted, with much lower frequency, were *Sparisoma chrysopterygum* (BLOCH & SCHNEIDER), *Calamus bajonado* (BLOCH & SCHNEIDER), and *Thalassoma bifasciatum* (BLOCH).

Marauding fish more frequently attacked brittlestars that were on the sand than those that were on the exterior of sponges (48 versus 18 attacks), and the survival of brittlestars on the sponges was higher than for those on the ground (82 % versus 64 %). In the experiments, *Ophiothrix lineata* living within the sponges were never attacked by fish. The brittlestars on the sponge and on the ground exhibited frenzied movements that probably intensified attacks by fish and increased the mortality of brittlestars in the experiments.

In another series of experiments, comparing fish attacks on injured *O. lineata* beside *Callyspongia vaginalis*, versus attacks on injured brittlestars within the sponge tubes, confirmed the effectiveness of the protection provided by the sponge. Fish attacked the brittlestars on the bottom within 4 to 102 sec, but fish did not molest the individuals in the sponge, even when the arms of injured brittlestars protruded from the osculum.

The film record shows that most of the fish in the study area were present during the day. Between 0530 and 0800 h, when brittlestar activity virtually ceased, 61 fish were counted by observing a film frame for every 6 min interval. Using the same sampling interval only 9 fish were counted over the much longer period from 1830 to 0530 h. Thus, fish were recorded in greater numbers during

the day. The diurnal and nocturnal fish populations were composed of different species. At night, mostly squirrelfish and grunts were filmed, but during the daytime predominantly wrasses, parrotfish, and damselfish were recorded. The latter 3 taxa attacked brittlestars in the predation experiment.

5. Regeneration

Regeneration indices (RI) are tabulated in Fig. 4; higher values indicate higher frequency of autotomy or breakage and regrowth. *Ophiothrix lineata* specimens from the lumen of *Callyspongia vaginalis* have a higher RI value than specimens collected from the outer surface of the sponge. The same trend is shown by *Ophiothrix angulata*. Notably, Fig. 4 also shows that brittlestars on the outside of the sponge are considerably smaller than brittlestars on the inside.

The RI values of brittlestars were compared between populations from *Callyspongia vaginalis* and *Neofibularia nolitangere* to gauge the relative degree of protection provided by the two species of sponges. *Ophiothrix suenisoni* has a higher RI value on *Neofibularia* than on *Callyspongia*, but *O. angulata* has a lower RI value on *Neofibularia* than on *Callyspongia*. Interestingly, *Ophiothrix suenisoni* and *Ophiothrix angulata* both are generally of larger size on *Neofibularia* than on *Callyspongia* (see Fig. 4 and "Distribution" – Results section).

Discussion

1. Obligate commensalism

HYMAN (1955, p. 687) noted that for brittlestars "Their small size and flexible arms fit them for clinging to other animals, especially branching types, and hence it is not surprising that they often occur in association with sponges and coelenterates". Despite their obvious morphological specializations for occupying large, sessile organisms, the adaptive value of such associations for the brittlestars and sponges is not well understood. Fortunately, it is possible to gauge the significance of the dependence by observation and experiment on brittlestars requiring sponge hosts.

It appears that *Ophiothrix lineata* invariably is associated with sponges. KISSLING & TAYLOR (1977) suggested that the presence of *O. lineata* was governed by the availability of suitable sponges, an observation supported by other investigations (CLARK, 1933; DEVANEY, 1974). In contrast, the other brittlestar species that live on the same sponges as *O. lineata*, live on substrata besides sponges as well (CLARK, 1933; DEVANEY, 1974; KISSLING & TAYLOR, 1977). These findings support the hypothesis that *O. lineata* is an obligate commensal of sponges.

2. Sponges as a refuge from predation

Abundant evidence has been published showing that brittlestars suffer heavily from predation. RANDALL (1967) reported on 33 species of Caribbean fish that

feed on brittlestars. They occurred in more than 10 % of the stomach content samples for 10 fish species. He found that *Ophiothrix* was the most common brittlestar genus identified from fish stomach contents, at least in part because the spines of *Ophiothrix* species are so easily recognized. Of the 10 fish species referred to for which brittlestars are an important dietary component, 6 fed on *Ophiothrix*. Those include 3 diurnal wrasses, *Bodianus rufus* (L.), *Halichoeres garnotti*, *Halichoeres poeyi* (STEINDACHNER); 2 porgies, *Calamus calamus* (CUVIER & VALENCIENNES), *Calamus pennatula* GUICHENOT, and the nocturnal grunt, *Anisotremus virginicus* (L.). Another wrasse, *Thalassoma bifasciatum*, which also ingests *Ophiothrix* may consume a diet of 30.8 % brittlestars (FEDDERN, 1965; RANDALL, 1967).

There is no evidence of a guild of fish that feed primarily on sponge-dwelling brittlestars, though there is a group of fish which prey largely on sponges (RANDALL & HARTMANN, 1968). Only one of the fish that feeds on sponges, *Cantherhines pullus* (RANZANI), has been found to ingest brittlestars, and *Ophiothrix* spp. were found in its stomach contents (RANDALL, 1967; RANDALL & HARTMANN, 1968). Certain fish may occasionally feed on both sponges and brittlestars. For example, BEEBE & TEE-VAN (1928) reported some sponge material in the guts of *Halichoeres radiatus* (L.), a fish that feeds on brittlestars (RANDALL, 1967). Both brittlestars and sponges are a minor component in the diets of the fishes *Anisotremus surinamensis* (BLOCH) and *Haemulon album* CUVIER & VALENCIENNES (RANDALL, 1967). In European waters crustacean predators that attack *Ophiothrix quinquemaculata* associated with sponges include the crab *Pilumnus hirtellus* (L.), the hermit crab *Paguristes oculatus* (FABR.), and the spiny lobster, *Palinurus vulgaris* LATR. (VASSEROT, 1965; WURZIAN, 1977; STACHOWITSCH, 1979, 1980).

There is ambiguous evidence in the literature regarding whether brittlestars are protected from predation by their association with sponges. The potential of the sponge as a physical barrier to predation is obvious. In addition, fish might avoid the toxins or noxins (noxious compounds) synthesized by sponges. BAKUS & THUN (1979) reported that 57 % of the Caribbean sponge species tested were toxic to fish. *Neofibularia nolitangere* causes intense pain and dermatitis when handled by humans, and it is strongly toxic to fish (BAKUS & THUN, 1979). *Callyspongia vaginalis* was reported by HALSTEAD (1965) to be toxic to fish, but BAKUS & THUN (1979) found that the species liberated noxins that were not lethal to the fish they tested. Not surprisingly, sponge-eating fish feed more often on *C. vaginalis* than on *N. nolitangere* (RANDALL & HARTMANN, 1968). However, perhaps because of their chemistry and the presence of spicules in many species, sponges are generally not an attractive food source for most fish. RANDALL & HARTMANN (1968) concluded that, overall, sponge-eating fish are of little importance in controlling populations of Caribbean sponges.

Considering the contrasting effects on fish of toxins from the two sponges, *Callyspongia vaginalis* and *Neofibularia nolitangere*, it would be expected that brittlestars associated with the latter, distasteful species would show less damage from predation. However, the results of the regeneration index measurements of brittlestars on *C. vaginalis* and *N. nolitangere* were equivocal on this point, perhaps because of the inadequacies of the RI as an index of predation. While the incidence of arm regeneration may parallel the intensity of predation, it is

not necessarily directly related to fatal encounters. Brittlestar species that are not ingested by fish can still exhibit a considerable amount of arm regeneration (SHIRLEY, 1982). Moreover, regeneration index values are probably biased by the differing regenerative abilities of particular brittlestar size classes and species.

The trends in RI values for particular brittlestar species on *Callyspongia* and *Neofibularia* were inconsistent. This implies that factors other than sponge toxicity may be involved in the intensity of predation directed at brittlestars on various sponge species. It is possible that the presence or absence of brittlestar species on certain sponge species (Fig. 4) is related to brittlestar requirements for such factors as sponge morphology or microhabitat.

The more straightforward data of the fish predation experiments show that *Callyspongia vaginalis* offers *Ophiothrix lineata* protection from fish. Mortality from fish attacks increases for brittlestars inside sponges, over those placed on the outside surface of sponges, to those placed on the substratum near sponges. These results, and evidence of regeneration of *O. lineata* on *C. vaginalis*, indicate that the brittlestar normally suffers a degree of predation while on the sponges. It appears (somewhat unexpectedly) to be the larger individuals, which extend their arms outside the sponge only at night, that are most seriously affected by predators. The small specimens (both *O. lineata* and *O. angulata*), primarily found on the outer wall of the sponge, show less evidence of regeneration. If this observation is not a technical artifact (a product of the difficulty of identifying damage and regeneration in small specimens), it is likely that the tiny specimens on the outside of the sponge simply are not detected by visual predators. Certainly, they are not easily seen by the human observer, because of their small size and their pale coloration.

In addition, the occurrence of small individuals outside the sponge and large individuals inside the sponge suggests that there may be settlement and recruitment of *Ophiothrix lineata*, *O. angulata*, and possibly even *O. suenisoni* on the outside of *Callyspongia vaginalis*. Subsequently, larger specimens may take residence inside the sponge. However, it is also possible that competition or other negative interactions between size classes (or species), or the activities of predators results in the observed distributions.

Since *Ophiothrix lineata* is a detritus feeder its circadian cycle is likely not a function of the periodical availability of its food, as detritus is generally in constant supply. Rather, the circadian feeding pattern detected with elapsed-time cinematography is probably related to the damage inflicted by predators on the larger specimens of *O. lineata*. The results of several studies on echinoderms suggest that nocturnal activity is a predator avoidance tactic (references in NELSON & VANCE, 1979).

NELSON & VANCE (1979) demonstrated experimentally that the sea urchin, *Centrostephanus coronatus* (VERRILL), which is normally active only at night, is preyed upon by fish when exposed in daytime experiments. The results of the predation experiments using *Ophiothrix lineata* were analogous. The greater abundance of diurnal than nocturnal predators shown in the elapsed-time film suggest that the brittlestar's circadian rhythm is an adaptation for predator avoidance. Interestingly, the Mediterranean species, *Ophiothrix quinque maculata*, sometimes a facultative associate on sponges and sometimes

found in dense monospecific aggregations, maintains its feeding posture continuously rather than hiding during the day. Individuals of *O. quinque maculata* only shift position in response to changing current or to direct disturbance by predatory benthic invertebrates (FEDRA & MACHAN, 1979). The sort of circadian behavior shown by *O. lineata* on *Callyspongia vaginalis* would be nonadaptive for *O. quinque maculata* because *O. quinque maculata* does not associate with a permanent host which provides a refuge from predation.

A problem with this interpretation of the nocturnal activity pattern of *Ophiothrix lineata* (as an escape from predation) is that certain fish which prey on Caribbean *Ophiothrix* spp. are active at night as well as during the day. For example, the nocturnal porkfish (*Anisotremus virginicus*) preys on brittlestars (RANDALL, 1967). STACHOWITSCH (1979) found that in the North Adriatic Sea, the brittlestar-eating hermit crab, *Paguristes oculatus*, is more active during daylight hours than after dark. However, brittlestar-eating pagurids in the Caribbean, such as *Petrochirus diogenes* L., feed nocturnally (unpubl. obs.). These inconsistencies must be weighed against the observation that the diurnal wrasses were the most important group of brittlestar-predators reported by RANDALL (1967) and were the dominant predators in the predation experiments discussed in the present paper. Evidently, the diurnal crypsis of *Ophiothrix lineata* enhances the survival of the species.

3. Sponges as a source of food

WARNER (1982, p. 168) wrote that "All members of the genus *Ophiothrix* so far studied – *O. quinque maculata*, *O. spiculata*, *O. angulata*, and *O. fragilis* – are specialized suspension feeders". For example, *Ophiothrix fragilis* (ABILDGAARD) raises its arms in moderate currents and unselectively ingests particles of suspended material that adhere to the tube feet and spines of its arms (WARNER & WOODLEY, 1975). In fact, the elevation on sponges of the closely related *Ophiothrix quinque maculata* has been estimated to provide the filter-feeding brittlestar a threefold increase in availability of suspended food particles (FEDRA, 1977).

The feeding mode of *Ophiothrix lineata* differs fundamentally from that of its congeners. The combined observation of arm movements of *Ophiothrix lineata* on the surface of *Callyspongia vaginalis*, and their ingestion of particles (*i. e.*, brine-shrimp eggs) on the surface of the sponge, indicate that *O. lineata* is a deposit feeder. This conclusion is also affirmed by the similar nature and the size distribution of particles on the surface of the sponge and in the stomachs of the brittlestars. In addition, *O. lineata* maintains its arms in contact with the sponge, whereas filter-feeding brittlestars characteristically project their arms into the water above their substratum. Apparently, KISSLING & TAYLOR (1977) were mistaken in supposing that *O. lineata* (because of its arm morphology) filter-feeds.

In the association between *Callyspongia vaginalis* and *Ophiothrix lineata*, the sponge provides the brittlestar with detrital material and a suitable surface from which to feed. The brittlestar ingests, for the most part, unidentifiable particles of debris, although several taxa of animals and plants are observed in the

brittlestar stomach contents. The observations of the brittlestar's pattern of activity, the contrasting proportion of animals feeding during day and night, and the fluctuations in the volume of stomach contents, all indicate that feeding is primarily a nocturnal behavior.

The dependence of *Ophiothrix lineata* on *Callyspongia vaginalis* for food is clear evidence for a commensal relationship. *Ophiothrix lineata* could be regarded as a parasite if its food were of value to the sponge, but several lines of evidence indicate that brittlestars do not collect material which can be utilized by sponges. For example, *Ophiothrix fragilis* responded to both phytoplankton and 60–90 μm particles of radioactively labelled detritus, but under the same experimental regime, three species of sponges showed relatively low uptake of labelled detritus (BEVISS-CHALLINOR & FIELD, 1982).

Brittlestars are clearly capable of feeding on particles larger than those readily accessible to digestion by sponges (HENDLER, 1982 b). Brittlestar digestion is extracellular, mediated by enzymes secreted into the lumen of the stomach. Particles, reduced to suitable size by extracellular digestion, are absorbed through the stomach lining by pinocytosis (PENTREATH, 1969; DESCHUYTENEER & JANGOUX, 1978). On the other hand, detrital particles accounted for only about 3% of the microscopically resolvable, particulate, organic biomass available as food to sponges (REISWIG, 1971 a). Seemingly, much of the material ingested by brittlestars is detritus, unavailable to sponges as food.

The incurrent flow of demosponges traverses several filter systems including pores in the dermal membrane, inhalent canals, prosopyles, and choanocyte collars (references in REISWIG, 1971 a). The size of the opening in these filters restricts the upper size limit for particles taken by the sponge. In *Callyspongia diffusa* (RIDLEY), incurrent pores in the dermal membrane are 50 μm , and major incurrent canals from subdermal spaces open into lacunae around choanocyte chambers via 25 μm apertures. The prosopyles are 1 μm triangular spaces between choanocyte cell bodies. The size of the pores in the dermal membrane dictates an upper limit of 50 μm for particles entering the sponge and particles between 1 and 50 μm in size must be phagocytized outside the choanocyte chambers (JOHNSTON & HILDEMAN, 1982). The parameters for *C. vaginalis* are probably similar to those for *C. diffusa* (RÜTZLER, pers. comm).

REISWIG (1971 a) found that most of the food of sponges was small enough to be phagocytized by the choanocytes. He characterized 95% of the total plankton collected by sponges as bacteria, unarmored cells, armored cells (fungi, diatoms, etc.), and detritus. However, such plankters (2.5 to 13.5 μm diameter) were an insignificant portion of the sponge diet. Almost all of the sponge's dietary, particulate organic carbon was composed of particles less than 1.5 μm . The microscopically unresolvable, particulate organic carbon component "provides by far the major carbon source" (REISWIG, 1971 a, p. 582; REISWIG, 1974).

Although *Ophiothrix lineata* ingested particles of a size theoretically suitable as food particles for *Callyspongia vaginalis*, the majority of the particles utilized by the sponge for food could not even be measured with the techniques employed to examine the brittlestar diet. Therefore, the question of brittlestars as parasites of sponges is, at present, unresolved. Although sponge spicules were found in the brittlestar stomach contents, they also were found in the

siphon samples from the surface of the sponge and can be assumed to be part of the sediment. Identifiable pieces of sponge tissue were not found in the brittlestar stomach contents, indicating that *O. lineata* does not prey on *C. vaginalis*.

4. Speculation regarding a cleaning symbiosis

The feeding activities of *Ophiothrix lineata* may benefit *Callyspongia vaginalis*. As the brittlestars feed, the incurrent filtering surface of the sponge is cleaned, and this may promote greater pumping efficiency. There is no question that pumping efficiency is of primary importance to sponges. Vital activities of sponges such as feeding, respiration, and reproduction all depend on unobstructed flow of water (GERRODETTE & FLECHSIG, 1979). Sponges survive in plankton-poor tropical waters by virtue of their remarkably efficient filter-feeding activities. Thus, they cannot afford to reduce their pumping rates for extended periods of time (REISWIG, 1971 a, b; 1974).

The amount of sediment in suspension can limit distribution of sponges (BAKUS, 1968). Some demosponges are excluded from low-turbulence environments because they cannot maintain the sediment-free incurrent surfaces necessary for adequate pumping rates (REISWIG, 1971 a, 1974). For instance, the sponge *Verongia lacunosa* (LAMARCK) is more sensitive to suspended sediments than any other filter-feeding organism previously tested (GERRODETTE & FLECHSIG, 1979).

Sponges are not without means of cleansing themselves. REISWIG (1971 a) indicated that amoebocytes in the inhalent aquiferous system, capable of capturing 2–5 μm particles, must operate continuously to prevent occlusion of the aquiferous system by suspended particles. Sponges also employ reorganization of subdermal canals and sloughing of particles trapped in sponge mucus for self-cleansing (REISWIG, 1971 a).

Callyspongia vaginalis commonly occurs in sandy lagoons (RANDALL & HARTMANN, 1968). In such habitats it would likely be exposed to relatively heavy sedimentation. Not all specimens of *C. vaginalis* at the study site had associated brittlestars. Thus, a continuous association with *Ophiothrix lineata* is not necessary for the survival of the sponge. However, the effectiveness of the brittlestar in removing sediment coating the incurrent surface of the sponge has been amply demonstrated. This is consistent with the hypothesis that the sponge benefits from the activities of the brittlestar.

Whether the interaction between *Ophiothrix lineata* and *Callyspongia vaginalis* (or other brittlestars and sponges) is truly mutualistic remains to be determined. It may be a facultative relationship (of mutual benefit) rather than obligate mutualism (where both partners are dependent on each other). It would be valuable to evaluate directly the pumping rate of *Callyspongia vaginalis* with and without associated *Ophiothrix lineata*. However, LEWIS (1982) has shown that the pumping behavior of *C. vaginalis* is difficult to record. Certainly, reliable information on the pumping behavior and growth rates of sponges with and without associated brittlestars will be of the utmost interest in determining the true nature of sponge-brittlestar associations.

Summary

1. Large specimens of *Ophiothrix lineata* are concealed in the tubes of *Callyspongia vaginalis* during the day. At night the brittlestars sweep their arms across the outer surface of the sponge as they feed, simultaneously cleaning the sponge's inhalent surface.

2. *Ophiothrix lineata* unselectively ingests detritus (and occasionally, microscopic organisms). Most of these particles are larger than the microscopically unresolvable material utilized as food by sponges.

3. Diurnal fishes such as wrasses, parrotfish and porgies attack *O. lineata* placed outside *C. vaginalis*, but not those dwelling inside *C. vaginalis*. Predation on brittlestars was not detected at night. Apparently, the nocturnal activity of the brittlestars is a predator avoidance strategy.

4. It is hypothesized that the brittlestar-sponge relationship is mutualistic. *Callyspongia vaginalis* provides food and a refuge from predation for *O. lineata*, and it is suggested that the pumping efficiency of the sponge may be enhanced by the feeding/cleaning activity of the brittlestar.

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References

- BACESCU, M., 1971: Les spongiaires; un des plus intéressants biotopes benthiques marins. Rapp. Comm. Int. Mer Médit., **20**: 239-241.
- BAKUS, G. J., 1968: Sedimentation and benthic invertebrates of Fanning Island, Central Pacific. Mar. Geol., **6**: 45-51.
- & M. A. THUN, 1979: Bioassays on the toxicity of Caribbean sponges. In: C. LEVI & N. BOURY-ESNAULT (Eds.), Biologie des Spongiaires. Colloques internationaux du C. N. R. S., **291**: 417-422.
- BEEBE, W. & J. TEE-VAN, 1928: The fishes of Port-au-Prince Bay, Haiti with a summary of the known species of marine fish of the island of Haiti and Santo Domingo. Zoologica, **10**: 1-279.
- BEVISS-CHALLINOR, M. H. & J. G. FIELD, 1982: Analysis of a benthic community food web using isotopically labelled potential food. Mar. Ecol. Prog. Ser., **9**: 223-230.

- CLARK, H. L., 1933: A handbook of the littoral echinoderms of Porto Rico and the other West Indian islands. Scient. Surv. Porto Rico and Virgin Is. N. Y. Acad. Sci., **16**: 1-147.
- CLARK, K. B., 1971: The construction of a collecting device for small aquatic organisms and a method for rapid weighing of small invertebrates. *Veliger*, **13**: 364-367.
- DESCHUYTENEER, M. & M. JANGOUX, 1978: Comportement alimentaire et structures digestives d'*Ophioderma longicauda* (RETZIUS) (Echinodermata, Ophiuroidea). *Ann. Inst. Océanogr.*, Paris, **54**: 127-138.
- DEVANEY, D. M., 1974: Shallow-water echinoderms from British Honduras, with a description of a new species of *Ophiocoma* (Ophiuroidea). *Bull. Mar. Sci.*, **24**: 122-164.
- EDGERTON, H. E., V. E. MACROBERTS & K. R. H. READ, 1968: An elapsed-time photographic system for underwater use. In: N. R. NILSSON & L. HÖGGER (Eds.), *Proceedings of the 8th International Congress on High-speed Photography*, Stockholm. Wiley, New York: 488-491.
- FEDDERN, H. A., 1965: The spawning, growth, and general behavior of the bluehead wrasse, *Thalassoma bifasciatum* (Pisces: Labridae). *Bull. Mar. Sci.*, **15**: 896-941.
- FEDRA, K., 1977: Structural features of a North Adriatic benthic community. In: B. F. KEEGAN, P. O. CEIDIGH & P. J. S. BOADEN (Eds.), *Biology of benthic organisms*. 11th European marine biology symposium, Galway, October 1976. Pergamon Press, Oxford: 233-246.
- & R. MACHAN, 1979: A self-contained underwater time-lapse camera for *in situ* long-term observations. *Mar. Biol.*, **55**: 239-246.
- , E. M. ÖLSCHER, C. SCHERÜBEL, M. STACHOWITSCH & R. S. WURZIAN, 1976: On the ecology of a North Adriatic benthic community: Distribution, standing crop and composition of the macrobenthos. *Mar. Biol.*, **38**: 129-145.
- GERRODETTE, T. & A. O. FLECHSIG, 1979: Sediment-induced reduction in the pumping rate of the tropical sponge *Verongia lacunosa*. *Mar. Biol.*, **55**: 103-110.
- HALSTEAD, B. W., 1965: *Poisonous and Venomous Marine Animals of the World*. Vol. I. Invertebrates. U. S. Govt. Printing Off., Washington, (D. C.).
- HENDLER, G., 1982 a: Slow flicks show star tricks: Elapsed-time analysis of basketstar (*Astrophyton muricatum*) feeding behavior. *Bull. Mar. Sci.*, **32**: 909-918.
- , 1982 b: The feeding biology of *Ophioderma brevispinum* (Ophiuroidea: Echinodermata). In: J. M. LAWRENCE (Ed.), *Echinoderms*. *Proceedings of the International Echinoderms Conference*, Tampa Bay. Balkema, Rotterdam: 21-27.
- HYMAN, L., 1955: *The Invertebrates*. Vol. 4. *Echinodermata*. McGraw-Hill, New York.
- JOHNSTON, I. S. & W. H. HILDEMAN, 1982: Cellular organization in the marine demosponge *Calyspongia diffusa*. *Mar. Biol.*, **67**: 1-7.
- KISSLING, D. L. & G. T. TAYLOR, 1977: Habitat factors for reef-dwelling ophiuroids in the Florida Keys. *Proc. Third Int. Coral Reef Symp.*, **1**: 225-231.
- LEWIS, S. M., 1982: Sponge-zoanthid associations: Functional interactions. In: K. RÜTZLER & I. G. MACINTYRE (Eds.), *The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I: Structure and Communities*. *Smithson. Contrib. Mar. Sci.*, **12**: 465-474.
- MACGINITIE, G. E. & N. MACGINITIE, 1949: *Natural History of Marine Animals*. McGraw-Hill, New York.
- MURPHY, G., 1980: The omnipresent brittle star. *Skin Diver*, **29**: 54-55.
- NELSON, B. V. & R. R. VANCE, 1979: Diel foraging patterns of the sea urchin *Centrostephanus coronatus* as a predator avoidance strategy. *Mar. Biol.*, **51**: 251-258.
- PEARSE, A. S., 1950: Notes on the inhabitants of certain sponges at Bimini. *Ecology*, **31**: 149-151.
- PENTREATH, R. J., 1969: The morphology of the gut and a qualitative review of digestive enzymes in some New Zealand ophiuroids. *J. Zool., Lond.*, **159**: 413-423.
- RANDALL, J. E., 1967: Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.*, **5**: 665-847.
- & W. D. HARTMANN, 1968: Sponge-feeding fishes of the West Indies. *Mar. Biol.*, **1**: 216-225.
- REISWIG, H. M., 1971 a: Particle feeding in natural populations of three marine demosponges. *Biol. Bull.*, **141**: 568-591.
- , 1971 b: *In situ* pumping activities of tropical *Demospongiae*. *Mar. Biol.*, **9**: 38-50.
- , 1974: Water transport, respiration and energetics of three tropical marine sponges. *J. Exp. Mar. Biol. Ecol.*, **14**: 231-249.
- RÜTZLER, K., 1975: Ecology of Tunisian commercial sponges. *Tethys*, **7**: 249-264.
- & I. G. MACINTYRE, 1982: The habitat distribution and community structure of the Barrier Reef complex at Carrie Bow Cay, Belize. In: K. RÜTZLER & I. G. MACINTYRE (Eds.), *The*

- Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I: Structure and Communities. *Smithson. Contrib. Mar. Sci.*, **12**: 9-45.
- SEFTON, N., 1982: The stars at night. *Sea Frontiers*, **28**: 87-92.
- SHIRLEY, T. C., 1982: The importance of echinoderms in the diet of fishes of a sublittoral rock reef. In: B. R. CHAPMANN & J. W. TUNNELL (Eds.), *South Texas Fauna*. Caesar Kleberg Wildlife Research Institute: 49-55.
- STACHOWITSCH, M., 1979: Movement, activity pattern, and role of a hermit crab population in a sublittoral epifauna community. *J. Exp. Mar. Biol. Ecol.*, **39**: 135-150.
- , 1980: The epibiotic and endolithic species associated with gastropod shells inhabited by the hermit crabs *Paguristes oculatus* and *Pagurus cuanensis*. *P. S. Z. N. I.: Marine Ecology*, **1**: 73-101.
- VASSEROT, J., 1965: Un prédateur d'échinodermes s'attaquant particulièrement aux ophiures: La langouste *Palinurus vulgaris*. *Bull. Soc. Zool. Fr.*, **90**: 365-384.
- WARNER, G., 1982: Food and feeding mechanisms: *Ophiuroidea*. In: M. JANGOUX & J. M. LAWRENCE (Eds.), *Echinoderm Nutrition*. Balkema, Rotterdam: 161-181.
- & J. D. WOODLEY, 1975: Suspension-feeding in the brittle-star *Ophiothrix fragilis*. *J. Mar. Biol. Assoc. U. K.*, **55**: 199-210.
- WESTINGA, E. & P. C. HOETJES, 1981: The intrasponge fauna of *Sphaciospongia vesparia* (Porifera, *Demospongiae*) at Curaçao and Bonaire. *Mar. Biol.*, **62**: 139-150.
- WURZIAN, R. S., 1977: Predator-prey interaction between the crab *Pilumnus hirtellus* (LEACH) and the brittlestar *Ophiothrix quinquemaculata* (D. CHIAJE) on a mutual sponge substrate. In: B. F. KEEGAN, P. O'CEIDIGH & P. J. S. BOADEN (Eds.), *Biology of Benthic Organisms*. Proc. 11th Europ. Mar. Biol. Symp., Galway, October 1976. Pergamon Press, Oxford: 613-620.