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FEEDING BEHAVIOR OF *ASTEROPORPA ANNULATA*, A GORGONOCEPHALID BRITTLESTAR WITH UNBRANCHED ARMS

Gordon Hendler and John E. Miller

ABSTRACT

Using the research submersible JOHNSON-SEA-LINK I, a population of the simple-armed gorgonocephalid brittlestar, *Asteroporpa annulata*, was discovered on a deep-water coral pinnacle off east-central Florida. Information on the habitat, population structure, circadian activity and feeding was obtained for this previously unstudied species, the only simple-armed member of the suborder Euryalina ever directly examined in situ. The brittlestars were associated with the scleractinian, *Oculina varicosa*. The clumps of coral bearing *Asteroporpa* usually carried only one specimen. *Asteroporpa* remained perched in an exposed position during the day and night. Some individuals extended single arms during the day, but most brittlestars did not take a suspension-feeding posture until at least several hours after dusk.

At that time, they oriented with their aboral surface facing the current. Generally three or four arms were extended vertically; sometimes, however, the tips of the arms bent into the current, or the arms were thrown into a sinusoidal pattern. The diet mostly consisted of pelagic organisms, predominantly copepods, some veligers and ostracods, and more rarely larvaceans, bivalve larvae, fecal pellets, eggs, amphipods and larval fish. An unidentified, siphonostome copepod associate was attached to the stomach wall of 26% of the specimens. Twenty percent of the brittlestar arms examined were regenerated, an indication that the species suffers from predation despite its heavy armor.

Members of the brittlestar suborder Euryalina possess some of the most highly specialized morphological attributes of all the brittlestars, yet they are classified as a primitive group (Baker, 1980). The Euryalina are characterized by a thick skin covering their disc and arms, reduced calcareous body armature, unique hooklike arm spines and the ability to throw their arms into tight vertical coils. They exhibit a remarkable spectrum of arm structures: many species with five unbranched ("simple") arms, others with increasing degrees of arm forking, and the most morphologically complex taxa (the basketstars) with intricate, arborescent arms. Moderately detailed in situ observations have been made on the behavior of only two species of basketstars, *Astroboa nuda* and *Astrophyton muricatum* (references in Hendler, 1982). Euryalina with simple arms have been sampled by dredging and their natural activities observed with automatic underwater cameras in situ, as in Dearborn's (1977) study of *Astrotoma agassizii*. Thus, the manner in which arm branching morphology is related to the biology of the Euryalina is not known (Warner, 1982).

Euryalina are often epizoic on colonial cnidarians and it has been suggested that the simple-armed forms may feed on the polyps of their hosts (Gislén, 1924; MacGinitie, 1949; Fell, 1961) or on plankters from the water column (Mortensen, 1912; Dearborn, 1977). If the simple-armed forms suspension feed, are they as efficient as the nocturnal basketstars or do they need to "fish" day and night to capture sufficient prey? Such possibilities have been impossible to evaluate because Euryalina are generally not abundant and most occur below the typical range of scientific SCUBA research (Baker, 1980). Only Warner's (1979) report on an *Asteroschema* sp. indicated that simple-armed species could be observed by divers.

Therefore we are fortunate to be able to report on one of the simple-armed Euryalina in the family Gorgonocephalidae, *Asteroporpa annulata* (Ørsted and Lütken). We observed it in situ from the research submersible, JOHNSON-SEA-LINK I.

A. annulata is a particularly attractive brittlestar with five long, tapering, chocolate brown and tan banded arms (Fig. 1A). The species ranges from North Carolina, Bermuda, and the northern Gulf of Mexico, throughout the West Indies, to at least as far south as the Rio Orinoco (Lyman, 1883; Döderlein, 1911; Clark, 1948; John and Clark, 1954). *A. annulata* is not restricted by substratum, occurring on a number of cnidarian species, most often gorgonians (Verrill, 1899; 1901). It has been collected in depths from 37 to 305 m with a variety of benthic gear, even hook and line (Verrill, 1901; Döderlein, 1911). Though its geographic range is documented, the biology of *A. annulata* has remained entirely unexplored. This is also true for the other seven Caribbean and Indo-Australasian *Asteroporpa* species, all living at depths below 55 m (Baker, 1980).

MATERIALS AND METHODS

Observations were made from JOHNSON-SEA-LINK I, a submersible described by Fike and Dolan (1976). Four dives (Table 1) were devoted to collecting *Asteroporpa* and observing diurnal and nocturnal activities of the brittlestars. Data were collected simultaneously by observers in the forward and aft compartments of the vessel, and visual records were made using a color video system (Subsea, Inc.), and a 35 mm Edgerton camera and strobe (Benthos, Inc.). A Savonius rotor current meter was used to measure water flow around the submersible. Specimens were captured with the submersible's manipulator grab and transferred underwater to a closed container. At the completion of a dive, the specimens were placed in concentrated formalin and subsequently transferred to 70% ethanol within 24 h. Preserved material was then measured and scrutinized for evidence of arm regeneration. For this purpose, accidentally broken arms were ignored since the incidence of regeneration could not be assessed for the missing portion of the arm. Only instances where an abrupt narrowing of arm width indicated regrowth were tallied to calculate a conservative index of regeneration, although less extreme, irregular configurations of the arm annuli were observed (indicative of arm damage and repair). After removing the dorsal surface of the disc with a razor blade, sex was determined and stomach contents were examined. Specimens for stomach content analyses were available from a late morning dive (JSL-1267) and a late evening dive (JSL-1269). Large particles were picked from the gut with forceps and the remainder of the gut contents were washed out with a stream of ethanol.

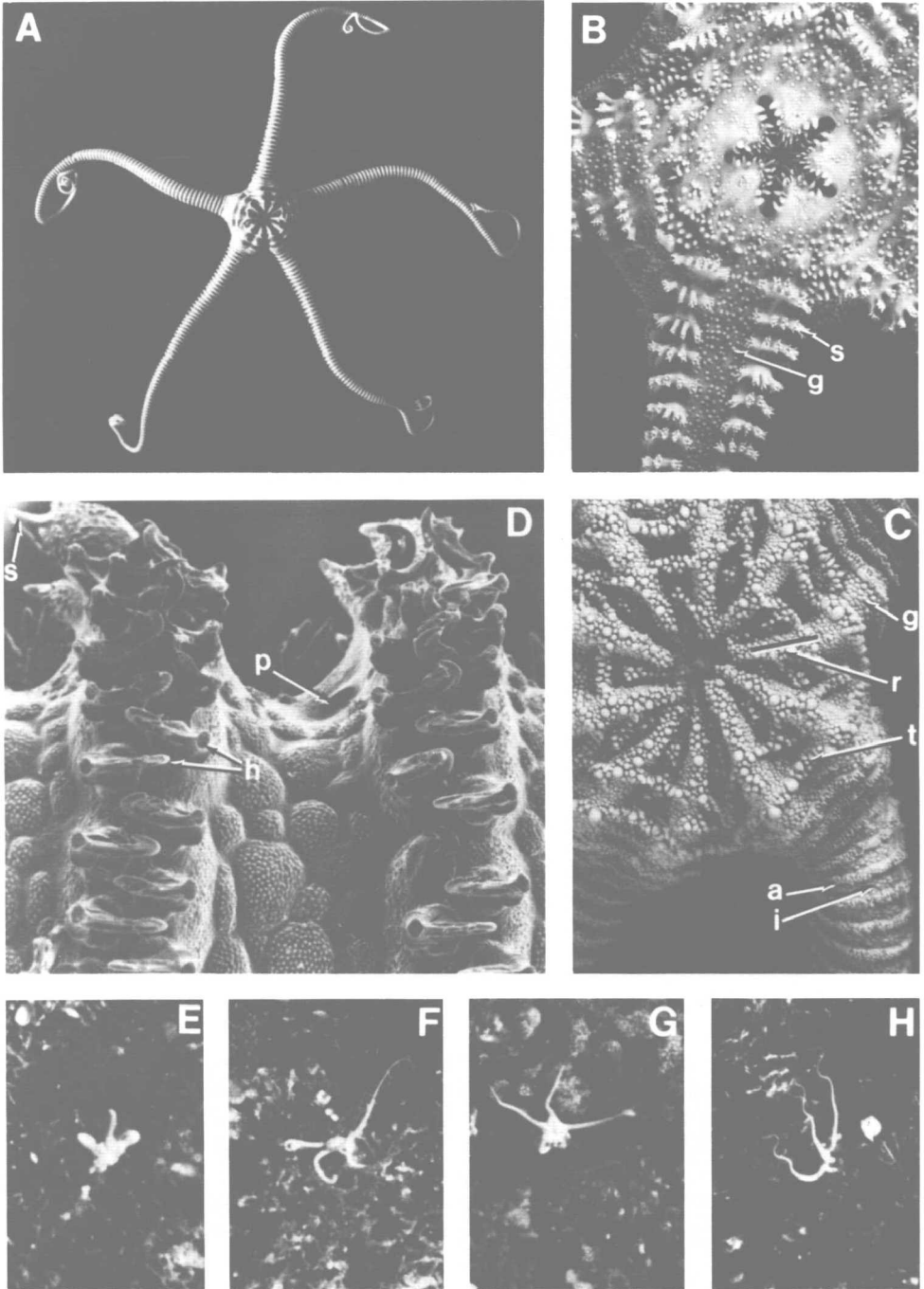
RESULTS

Description of the Specimens

Forty-one brittlestars were measured for disc diameter and arm length. Arms were approximately eight times longer than the diameter of the disc. Disc diameters ranged from 1.4 to 2.2 cm (1.8 ± 0.2 , $\bar{x} \pm SD$) and arm lengths from 10.9 to 20.7 cm (14.4 ± 2.1). The arms gently tapered and were quite slender near the tip. Most remained undamaged during collecting, and 179 unbroken arms could be measured. Of those, 20% (35 arms) had regenerated distally.

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Figure 1. A–D, external morphology of *Asteroporpa annulata*. A. Photograph of entire preserved specimen. In life, black and white banded patterns in illustration are, respectively, chocolate brown and pale tan. Note that slender tips of the unbranched arms are thrown into tight coils by dorso-ventral flexure. Size of individual: 1.8 cm disc diameter, 15 cm arm length. B. Ventral surface of a brittlestar showing colonades of thorny-tipped spines (s) and scattered granules (g) on arm. Spinulose teeth and oral papillae border the mouth at the center of the disc. C. Dorsal surface of a brittlestar showing intermeshed network of pyramidal tubercles (t) and solid pavement of granules (g) overlaying the riblike radial shields (r) and the remainder of the disc. From the edge of the disc to the tips of the arms, annuli (a) bearing hooks alternate with granulose interannuli (i). Note that the dorsal surface of the disc is more heavily armored than the ventral surface. Size of the individual in B–C: 1.7 cm disc



diameter. D. SEM micrograph of a brittlestar arm showing a granulose interannulus flanked by annuli composed of plates surmounted with batteries of moveable hooks (h). Note that hooks (each about $250\ \mu\text{m}$ long) are arranged in opposing series (arrows). Arm spines (s) and a tube-foot pore (p) are shown. E-H, *A. annulata* photographed in situ. E. Prone brittlestar with 5 arms clasping branches of a colony of *Oculina varicosa*. F. Individual in typical daytime stance with one fully extended arm and other arms grasping the substratum. G. Brittlestar in typical nighttime suspension-feeding posture with three upraised arms. H. Individual with arms in sinusoidal array.

Table 1. Station data for JOHNSON-SEA-LINK I research submersible dives to observe and sample *Asteropora annulata*

Dive Number	Date	Duration (h)	Operating Depth on <i>Oculina</i> Reef (m)	Current Speed (knots)
JSL-1266	22 Sep 82	1222-1514	56-83	0.2
JSL-1267	23 Sep 82	0809-1213	56-85	0.3-0.4
JSL-1268	23 Sep 82	1920-2058	56-83	0.1-0.2
JSL-1269	23 Sep 82	2139-2258	56-83	0.3-0.4*

* Current measured on top of pinnacle.

The general lack of damage to specimens, despite rather drastic collection and preservation techniques, reveals the species' physical robustness and restraint from autotomy. *A. annulata* is an extremely tough and resilient species due to its multilayered, heavily calcified skeletal elements embedded in thick strata of connective tissue. For example, the disc is encased by multilaminar radial ribs that are buttressed by cross-layered connective tissue and overlaid with substantial tubercles set in an unbroken pavement of thick granules (Fig. 1A-C). The massive vertebral core of the arms is protected by annuli of heavy skeletal plates bearing both spines and hooks set in batteries of opposing series and interannuli covered by granules (Fig. 1A-D).

A total of 34 specimens was dissected and all were found to be sexually mature; 62% male and 38% female. A siphonostome copepod (probably new to science, *A. G. Humes*, pers. comm.) was found in the stomachs of 26% of the specimens. The copepod associate somehow escapes digestion by its host. Generally, one and sometimes two or three copepods infested a host, but because of their ability to cling to stomach wall folds, some of the copepods may have been overlooked.

Description of the Habitat

Our observations were made on a deep-water pinnacle supporting an *Oculina varicosa* reef located at 27°46.2'N, 79°58.52'W. This pinnacle is typical of the deep-water reefal structures near the shelf/slope break along the central Atlantic Coast of Florida described and illustrated by Avent et al. (1977) and Reed (1980). The pinnacle was elongated in an east-west direction with a narrow ridge at 56 m, steep sides (30°-50°), and a broad base at 84 m. Mounds of *Oculina* (mostly, intact dead colonies) were largest and most numerous below the ridge on the SW portion of the pinnacle and a region of relatively barren sand surrounded the reef. The temperature ranged from 29.2°C at the surface to 16.7°C at the bottom of the pinnacle. Presumably the 7.5 to 26.5°C annual range (mean of 15°C), characterizing other *Oculina* reefs, (Reed, 1980; Reed et al., 1982) could be expected at the study site.

The study site supported a rich community of invertebrates and fish. The fauna, like that of previously described deep-water *Oculina* pinnacles, was associated with mounds of the scleractinian coral, *Oculina varicosa*, colonizing a relic oolitic limestone ridge. Although *Asteropora annulata* was abundant at the study site, the dominant species of motile invertebrate megafauna were the same as those on other pinnacles, namely the diadematomid sea urchin, *Centrostephanus longispinis rubricingulus* and the cidaroid, *Stylocidaris affinis*. Within the coral colonies, the bivalve *Barbatia candida* and the brittlestar *Ophiothrix angulata* were abundant. During night observations a large population of the cowrie, *Cypraea cervus*, was active on the reef.

Table 2. Numbers of *Asteroporpa annulata* counted from the lock-out chamber port of the submersible during one day- and two night-dives. During each dive, tallies of brittlestars were made for 5 or 6 of the locations occupied by the submersible where *Asteroporpa* was observed. The co-occurrence of specimens of *Asteroporpa* on colonies of *Oculina* is presented for each location

Dive Number	Location Number	Clumps of <i>Oculina</i> with 1-4 <i>Asteroporpa</i>				Total Number of <i>Asteroporpa</i>
		1	2	3	4	
JSL-1267	1	4	1	—	—	6
	2	6	1	—	—	8
	3	6	—	—	—	6
	4	—	—	—	1	4
	5	3	—	—	—	3
						27
JSL-1268	1	1	—	—	—	1
	2	4	—	—	—	4
	3	2	—	—	—	2
	4	1	—	—	—	1
	5	—	1	—	—	2
						10
JSL-1269	1	3	—	—	—	3
	2	1	—	—	—	1
	3	1	—	—	—	1
	4	1	—	—	—	1
	5	1	—	—	—	1
	6	1	—	—	—	1
						8

Density and Distribution

Asteroporpa annulata was concentrated on the portion of the pinnacle with the thickest coral cover, the SW quadrant between 60 and 75 m. Few individuals were seen on the pinnacle ridge (56 m) or near the base of the pinnacle (81 m). The brittlestars were found almost exclusively (33 of 34 specimens) on dead branches of *Oculina*; most of the *Oculina* branches at the study site were dead. Where *Oculina* mounds were relatively large, we estimated that *Asteroporpa* was situated at about 0.5 m from the bottom, with the brittlestars usually near the top of the mound. On smaller or more fragmented coral mounds, the brittlestars were closer to the bottom. In most cases clumps of coral bearing *Asteroporpa* usually carried only one specimen. Thirty-five coral mounds supported single specimens, three mounds were noted with two individuals, and a very large mound supported four specimens (Table 2).

Position and Movement

Asteroporpa grasped the *Oculina* by coiling one or more arms around branches or larger portions of a coral colony (Fig. 1E-H). Evidently, the ventrally directed spines (Fig. 1B) on their prehensile arms enabled them to exert a tenacious hold on the substratum. Brittlestars that were not entirely prone maintained one or more arms extended in the water column (Fig. 1E-H). The arms were either partially extended with the distal portion in a tight coil, or fully extended with the arm nearly straight. The extended arms were held with a slight bow near the disc or exhibited a slight lateral bending (Fig. 1F-H), resembling the sinusoidal arm posture displayed by other simple-armed *Euryalina* (Dearborn, 1977). The individuals with several arms fully extended held the dorsal surface of their disc

towards the current, and the tips of the arms were sometimes slightly bent into the current. *Asteropora* with partially extended arms or with fully extended arms arrayed near the substratum did not orient their arms into the prevailing current.

During the day, many of the brittlestars partly extended their arms, and some were observed rolling the proximal portion of one arm and unrolling another arm. Thus, the same arrangement of extended or curled arms was not maintained throughout the day. Undisturbed individuals moved slowly. One animal coiled half of an extended arm within two minutes. Another individual, video-taped under strong artificial illumination, extended a partially coiled arm in 15 sec. We did not observe *Asteropora* ingest food.

In more than 100 observations, only one specimen of *Asteropora* was seen sweeping the substratum with its arms (at night), and another was recorded crawling on the bottom (during the day). The arrangement of an animal's arms depended somewhat on the shape of the piece of coral to which the specimen was clinging. *Asteropora* attached to a narrow piece of coral could hold the branch tightly. They could also extend the base of their arms over a wider expanse of *Oculina* and grasp the colony with the tips of their arms. At night when their arms were extended in a feeding fan, we did not observe brittlestars bringing coiled arms to their mouth. Their fully extended arms were held rather rigidly but showed small movements apparently in response to changes in water flow.

Reaction to Disturbance

At night, *Asteropora annulata* responded to the 200 watt video lights and 1,000 watt arc lights on the submersible and to contact with the submersible's manipulator. In daylight, brittlestars with fully extended arms did not respond to video lights or to prodding with the manipulator. However, brittlestars confined in the manipulator grab (during day or night) extended their arms and crawled about. At night, specimens with extended arms reacted by coiling their arms towards the substratum when illuminated by the powerful arc light or when prodded by the manipulator. The irritated animals completely coiled their arms in 30 sec or less. It is noteworthy that these specimens did not attempt to withdraw into the interstices of the *Oculina* mounds but simply tightened their grasp on the coral branches. At night, an individual illuminated by the submersible's arc light was attacked by fish. The fish appeared to nip at the brittlestar's arms and dispersed after all the arms had been coiled against the disc.

Stomach Contents

Thirty-four specimens were dissected to examine stomach contents. Half were collected during a day dive (JSL-1267) and half during a night dive (JSL-1269). The number and sizes of ingested objects are given in Table 3.

Of the specimens collected during the day, only seven individuals had material in their stomachs. Three of the seven specimens contained fecal strands (presumably produced in the brittlestar stomach) surrounded by a thin membrane. Within the strands, there were masses of cyclopid copepods mostly less than 1 mm in length, particularly *Oncaea* spp. In lesser numbers were *Lubbockia* spp. and *Corycaeus* spp. (also cyclopoids), *Macrosetella* spp. (harpacticoids), *Candacia* spp. and aetideids (calanoids). Also within the strands, veligers and pelagic ostracods were relatively more numerous than the rarer copepod taxa, and a bivalve larva and an unidentified egg were also represented. The other daytime-sample specimens contained a piece of an amphipod, larvaceans, non-ophiuroid fecal pellets, and a small piece of fibrous tissue.

Six individuals from the nighttime sample had material in their stomachs. None of the items was incorporated in membrane-bound fecal strands. One of these specimens contained a small (non-ophiuroid) fecal pellet and another specimen a piece of fibrous tissue (these objects may have been contaminants in the sample rather than ingested food items). The remaining four animals contained, collectively, one amphipod, an amphipod exoskeleton, a larvacean house, a larval labrid fish and a piece of sponge tissue. The ingested items from the night-sample, such as a 12 mm long larval fish and a 4 mm long sponge-fragment, tended to be larger than the items from the day-sample which were bound within brittlestar fecal strands.

Diurnal Trends in Activity

Our impression is that *Asteropora annulata* was seen as commonly at night as during the day, indicating that animals did not emerge from concealment after dark. Although fewer *Asteropora* were counted at night from the aft chamber port, the lower figures probably reflect the restricted field of view illuminated by the submersible lights after dark.

Indicative of increased suspension feeding, there was a marked increase in the number of *Asteropora* with extended arms after dark, particularly late at night. The varying counts of coiled, partially extended and fully extended arms are illustrated in Figure 2. Clearly, the majority of arms are coiled against the substratum during the day though some individuals maintain a single extended arm (Fig. 1F). Transition to a suspension-feeding posture, with several extended arms (Fig. 1G-H), did not occur until well after dusk. Figure 2 shows that extended arms are considerably more prevalent later at night (Dive JSL-1269, 2139-2258 h) than early in the evening (Dive JSL-1268, 1920-2058 h).

DISCUSSION

All four families of Euryalina include species with simple arms, but only two families contain taxa with branching arms. It is therefore of interest to know whether the behavior of various species of Euryalina is more closely allied to their arm morphology than to their phylogenetic affinities. Unfortunately, the issue is difficult to resolve by comparative examination since the simple-armed species are scarcely mentioned in the literature. However, knowledge of the behavior of species with branched arms is summarized in the following paragraphs and compared to our observations on *Asteropora annulata*, a species with simple arms.

Based primarily on studies of *Astroboa nuda* and *Astrophyton muricatum* (references in Hendler, 1982), it appears that tropical shallow-water basketstars are active nocturnally and cryptic by day. They emerge at dusk, assume a feeding position on an elevated perch, and retire at dawn or when water currents are either too weak or too strong. While feeding, the basketstars maintain their arms in a paraboloid array, holding their aboral surface towards the current. Movements are rather slow, and each arm-branch fishes in the current for about 20 min. Small plankters (usually 0.2-2.0 mm long copepods) are secured using the hooked spines and coils of the finest arm branches. However, *Gorgonocephalus eucnemis* and *Astroboa nuda* take some benthonic prey, and the basketstars are capable of capturing large plankters (up to 25 mm long) attracted to their vicinity by dive lights (Patent, 1970; Davis, 1966; Tsumamal and Marder, 1966). The basketstars transfer prey to the mouth by periodically coiling and uncoiling an arm-branch in approximately 5 min. The rate of digestion in basketstars is rapid and much of the material captured at night is digested by dawn. In *A. nuda* the remains of

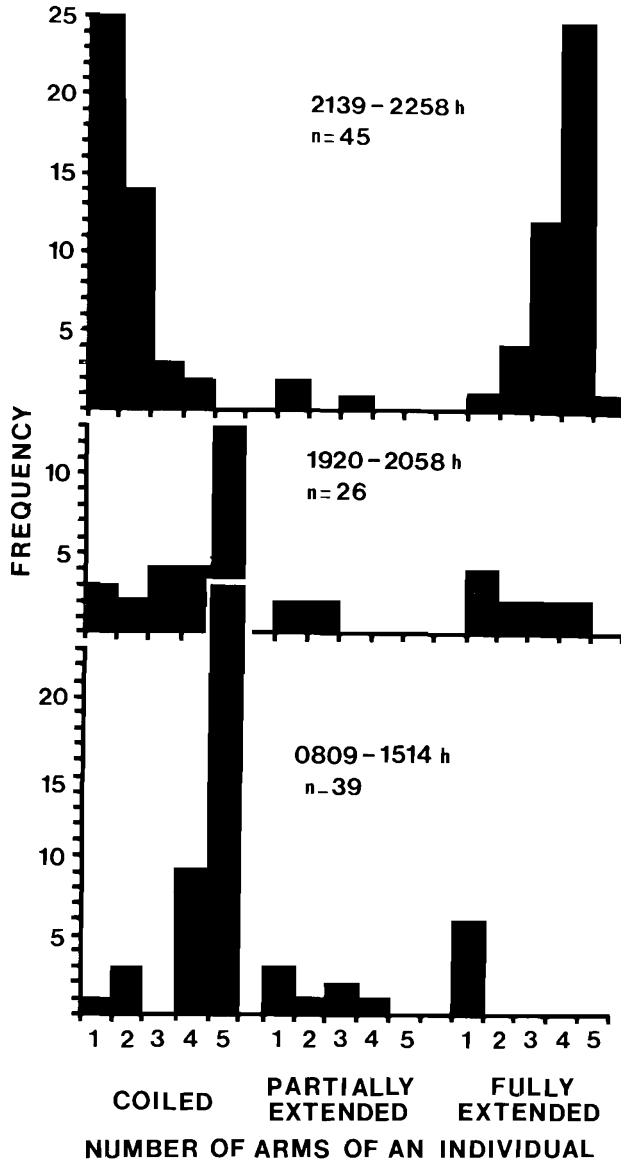


Figure 2. An index of the fluctuations in suspension feeding activity of *Asteroporpa annulata* is illustrated by counts of the numbers of arms in the extended ("fishing") position, partially extended, or coiled against the substratum. The number of arms of each individual in each position are plotted cumulatively for all the individuals observed during a dive. Numbers of individuals observed (n) are indicated. Data for daytime dives (JSL-1266, 1267) from 0809 to 1514 h are combined, and counts for nighttime dives from 1920 to 2058 h (JSL-1268) and from 2139 to 2258 h (JSL-1269) are presented separately.

prey are bound by a "gelatinous secretion" in the stomach (Tsurumal and Marder, 1966), and the ingested prey of *G. eucnemis* are enveloped in mucus (Patent, 1970).

When actively feeding, the discs of *A. muricatum* and *A. nuda*, which lack

heavy scaling or spination, are protected by the locomotory arm branches. Basketstars rapidly respond to dive lights or mechanical disturbance, quickly coiling their arms and retreating to shelter. Apparently these defense mechanisms effectively limit predation. Davis (1966) reported a few specimens of *A. muricatum* with missing arms but, during Wolfe's (1978) extensive observations on that species, predation on adults was not detected and arm regeneration was rare. Interestingly, Wolfe (1978) concluded that small fish which nipped at the arms of *Astrophyton* were attracted to the plankton trapped in the basketstar's arms.

Strong similarities exist between the behavior of *A. annulata* and the basketstars investigated to date. For example, *Asteroporpa* takes an elevated position and perches alone rather than gregariously. The presence of large numbers of tiny digested plankters in the gut of *A. annulata* late in the morning (Dive JSL-1267), and a lesser number of large items in the gut when a suspension-feeding posture is assumed late in the evening (Dive JSL-1269), indicates that the species may capture the majority of its prey between midnight and early morning. Additional samples are needed to bear this out. Although *Asteroporpa* preys on tiny plankters similar in size to the food of basketstars, the presence of a 12 mm fish larva and amphipods in the stomach contents reveals that it too can feed on larger prey, both planktonic and benthic.

The greatest numbers of the prey (small cyclopoid copepods) are pelagic, found in rather low concentrations, and probably strike *Asteroporpa* arms with low frequency. In addition, they are agile swimmers and should be able to avoid entrapment (F. Ferrari, pers. comm.). Moreover, like the basketstars, the undisturbed *Asteroporpa annulata* move slowly, though they respond quickly to mechanical prodding or to illumination by artificial lights at night. Presumably, they secure prey within loops of the whiplike distal portion of the arm and the batteries of hooks girdling the arms. But, the mechanism whereby *Asteroporpa* captures and ingests active planktonic prey is problematical.

Allredge's (1972) observation that *Oncaea mediterranea*, *Microsetella norvegica* and other copepods and ostracods settle and feed on larvacean houses lends itself to the hypothesis that *Asteroporpa* may capture crustaceans clinging to larvacean houses as well as free swimming prey. The presence of larvacean houses in several brittlestar stomachs is consistent with this speculation. It is also noteworthy that *Asteroporpa* produces encased fecal strands, perhaps similar to the gelatinous substance binding the digested prey of *Astroboa nuda* or the mucus enveloping the prey of *Gorgonocephalus eucnemis*, but entirely different from the stomach contents of many species of Atlantic and Caribbean ophiuroids (G. H., pers. obs.). Is it possible that the material coating the fecal strands of *Asteroporpa* is composed of the residue of partially digested larvacean houses? This might explain the absence of larvacean houses in specimens with copepod-prey bound in fecal strands and their presence in some specimens without fecal strands.

Asteroporpa annulata and basketstar behavior differs in some interesting respects. Although *A. annulata* is relatively inactive during daylight and apparently feeds primarily at night, the presence of a small number of unconsolidated food items in the daytime-sample guts indicates that animals may occasionally ingest food during the day. They keep their arms coiled against the substratum during the day, remaining in an exposed position rather than seeking shelter in the coral substratum. Evidence that this behavior is a function of their resistance to predation is ambiguous. For, although their discs are more heavily armored than some basketstars, and they do not protect their disc with locomotory arm branches, they do react to attacks by fishes and have a high proportion of regenerating arms (presumably caused by predation).

The feeding activity of *Asteroporpa*, which increases sharply after about 2100 h, is surprisingly different from the dusk-to-dawn pattern of basketstars (Hendler, 1982). While suspension feeding, *A. annulata* maintains a posture with the aboral surface facing the current, but its arms do not assume the paraboloid array characteristic of basketstars. Some individuals hold their arms in a sinusoidal design, as does the simple-armed *Astrotoma agassizii* studied by Dearborn (1977). This posture may be typical of simple-armed Euryalina, although the upraised arms of most *Asteroporpa* were held rather straight.

During feeding, *Asteroporpa* kept its arms extended in currents of at least 0.4 knots (21 cm/sec), quite near the estimated upper limit of water speed (approx. 20 cm/sec) suitable for suspension feeding by the basketstar *Astrophyton muricatum* (Hendler, 1982). However, it would be premature to deduce that the streamlined design of the simple-armed Euryalina permits them to feed effectively in stronger currents than basketstars with considerably greater surface area and resistance to flow. It is also too early to presume that the traits of *Asteroporpa annulata* can be generalized to the other simple-armed species of Euryalina. We still know too little about the natural history of the Euryalina, but the observations to date are tantalizing and further investigations are clearly merited.

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