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SLOW FLICKS SHOW STAR TRICKS: ELAPSED-TIME ANALYSIS OF BASKETSTAR (*ASTROPHYTON MURICATUM*) FEEDING BEHAVIOR

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ABSTRACT

Aspects of the nocturnal activity of the basketstar, *Astrophyton muricatum*, were studied with elapsed-time cinematography. A basketstar, situated on a coral pinnacle in a tidal channel, fed during the periods of moderate water speed associated with ebb and flood currents. It changed feeding position in response to tidal flow by directing its arms into the current. At slack tide (2110–2154 h) prey capture ceased and the basketstar's arms covered its disc. Also, in a strong flood tide (0225 h), *Astrophyton* did not ingest prey. Instead, it held its arms stiffly outstretched for an hour and retreated to its diurnal niche by 0400 h. Although feeding activity commenced at dusk, the cessation of feeding before dawn and absence of response to changes in moonlight intensity indicated that feeding behavior is not a rectilinear function of ambient light. The timing of feeding movements may reflect a response to randomly distributed patches of prey plankters. Feeding movements did not occur at regular intervals or in fixed series, but generally only one arm curled at a time. The central arms in the feeding fan were more active, and therefore may have captured more plankters than the lateral arms. In each feeding sequence, a feeding branch curled against the disc in about 1 min, remained near the disc for about 5 min, and uncurled in 1–2 min. The movements of feeding branches seemed to be coordinated with shifts in the position of adjacent locomotor branches. An examination of the pattern of curling and uncurling movements suggested that food was transferred to the mouth by side arm-branches while the main axis of the feeding branch remained coiled against the disc. When relocating and for repositioning the disc, locomotor branches released the substratum, formed an umbrella over the disc, and acted as ambulatory appendages. The basketstar appeared to follow an identical course during the ascent and descent from its feeding perch.

Astrophyton muricatum (Lamarck) is one of the most imposing echinoderms on Caribbean coral reefs. Large specimens reach over a meter in diameter with arms extended. Each of the basketstar's five arms gives rise to two relatively smooth and stubby locomotor branches and two longer, more slender feeding branches. The fully expanded arms have a lacelike appearance owing to numerous, successive, unequal bifurcations. Close inspection of the branches reveals multitudes of minute, scimitar-shaped spines arranged in close-set annuli (Atz, 1960; Davis, 1966; Fricke, 1968; Macurda, 1976; Meyer and Lane, 1976; Wolfe, 1978, illustrate arm morphology).

For centuries, the elaborate structures of basketstars piqued the curiosity of naturalists, but the inaccessibility of living specimens thwarted attempts to interpret the "curious composure" of such "stellar fish" (Winthrop, 1671). During the last 50 years contradictory descriptions of the biology of *A. muricatum* evolved from aquarium and diving studies. Recently, the species has attracted the attention of forward-looking paleontologists because of its similarity in form, and potentially in function, to certain Paleozoic crinoids (Macurda, 1976; Meyer and Lane, 1976).

Initially, the deduction that *A. muricatum* fished for plankton vied with the conclusion that it stripped polyps from gorgonians (Boone, 1933; Pearson, 1937). The status of *A. muricatum* as a suspension feeder is no longer in question. However, contradictory results indicate that it either ingests plankters as they are captured or that the prey are sequestered in the arms at night and ingested during the day (Fricke, 1968; Wolfe, 1978 and in press).

The living habits of *A. muricatum* have hampered *in situ* investigations of its ecology. It is strictly nocturnal, so slow-moving that it appears to remain motionless unless disturbed, and it has a pronounced negative reaction to underwater lamps. In addition, in aquaria its large size and rheophilic behavior confound observations of its normal activity. Fortunately, elapsed-time photography can provide an unbiased record, over long periods, of the behavior of undisturbed basketstars. This report, based on underwater cinematography, focuses on the movements of *A. muricatum* during feeding, locomotion in response to tidal currents, and diurnal migrations. Patterns of behavior too difficult to study while diving are quantified and correlated with records of environmental variables.

METHODS

A specimen of *A. muricatum* was filmed in a sandy cut in the Belize Barrier Reef to the east of Carrie Bow Cay (Ruetzler, 1976, for location). The basketstar was found during a night dive (27 April 1981) at about 5 m depth, and the prefocused photographic system was emplaced on 28 April, 2 m from the subject, and activated at 1836 h.

A 16-mm elapsed-time movie camera set to expose frames of film (Kodachrome ASA 25) at 20-sec intervals was connected to an electronic strobe supplying 50 watt-seconds illumination (equipment described in detail by Edgerton et al., 1968). The camera and strobe units were attached to tripod stands hammered into coral rock.

As a current meter, a buoyant float (whiffle-type plastic ball) was tethered just below the basketstar on a short monofilament line and filmed. The water velocity was calculated from the angle of the float by calibrating the float in a flow tank. However, the tilted position of the movie camera introduced a discrepancy between the real and apparent float angles, and interfered with the correlation of the float angle and water speed. Therefore, only approximations of water speed are considered below.

During filming the relative intensity of ambient illumination was monitored continuously with a photometer (United Detector Technology, Inc. 40× 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.

The film was studied using a stop-motion 16-mm projector (L-W International 224-A MK VI Photo-Optical Data Analyzer). The movement of the basketstar was examined frame-by-frame at speeds from 2 to 24 frames per second.

The Wilcoxon two-sample test was used in lieu of the *t*-test to assess the significance of differences between samples because sample data did not meet the requirements of normality or equal variances.

RESULTS

Sequences of Activity

The chronology of the basketstar's behavior is presented in Table 1. Major modes of activity included ascent to the feeding station on a coral pinnacle, an initial feeding period, reorientation, a second feeding period, and descent to the diurnal shelter. Between the first and second feeding periods a flood tidal current significantly altered the velocity of water flow across the study area (Wilcoxon two-sample test of float angle readings: $n_1 = 38$, $n_2 = 53$, $U_s = 1{,}871.0$, $P < 0.001$). Water speed was roughly 6 cm/sec during the first period, 8–13 cm/sec during the second period, and in excess of 18 cm/sec afterwards. Figure 1 illustrates the temporal pattern of the basketstar's arm movements and the current velocity.

The basketstar used its locomotor branches for propulsion from the diurnal shelter to the nocturnal feeding perch. During relocation the feeding branches remained curled against the disc, and the locomotor branches were partially extended and flattened against the substratum. As it neared the crest of the pinnacle, the basketstar gradually extended a feeding branch, then retracted the branch

Table 1. The sequence of events in the nocturnal behavior of *Astrophyton muricatum* (the chronology is related in hours, local time)

1816	Sunset.
1836	Camera activated. Basketstar is moving between the diurnal shelter and the top of the pinnacle.
1856	Crest of the pinnacle is reached.
1859	Disc is in position.
1900–1904	Feeding branches are extended into the current; locomotor branches are loosely arranged.
1905	Prop branches are fixed to the substratum.
1922	Locomotor branches are in a stable configuration surrounding the disc.
1929–2109	First feeding period.
2110–2154	Feeding and locomotor branches are held against the disc, with some movement of distal branches.
2218 and 2248–2251	Prop branches shift point of attachment; increasing agitation of locomotor branches around the disc.
2301	Locomotor branches are lifted off the surface of the disc.
2316	Prop branches release the substratum.
2327	The disc is reoriented.
2327–2341	Feeding branches are extended into the current.
2356–2406	Readjustment of the prop branches and positioning of the feeding fan.
0007–0224	Second feeding period.
0225–0330	Feeding branches are fully extended into the current without showing feeding movement.
0330–0337	Feeding branches are furled against the disc.
0337–0343	Increasing movement of locomotor branches on the disc culminates in loosening and lifting of the branch tips.
0344	Prop branches detach from the substratum.
0345	Reorientation of the disc and locomotor branches, preceding descent from the feeding perch.
0352	Basketstar is below the top ot the pinnacle, out of camera range.
0540	Sunrise.

and shifted to an unobstructed position closer to the top of the pinnacle. The locomotor branches loosely held over the disc soon grasped the nearby coral-and-sponge substratum. Two locomotor branches (referred to hereafter as "prop branches") extended obliquely well beyond the disc like prop roots, in a direction perpendicular to the current, and further anchored the basketstar (Fig. 2). As the feeding branches uncoiled, portions of the locomotor branches moved above the disc and then settled to the periphery of the disc.

Before the first "feeding period" (an extended interval of feeding activity), some locomotor branches at the oral side of the disc relaxed and lifted from the disc. Portions of the locomotor branches were also loosened while the feeding branches were in motion and were drawn against the disc in the intervals between feeding sequences (note that a "feeding sequence" consists of incoiling followed by extension of a feeding branch, presumably for transfer of food to the mouth). Some feeding branches coiling past a stationary locomotor branch later extended at a different point in the feeding fan, revealing that branches do not maintain fixed positions around the disc.

Activity During Transitional and Non-feeding Intervals

At the end of the first feeding period, the ebb-tide current slowed to roughly 5 cm/sec or less. The feeding branches, one at a time, coiled towards the disc in 45 min. Before the second feeding period, the basketstar displayed relatively little

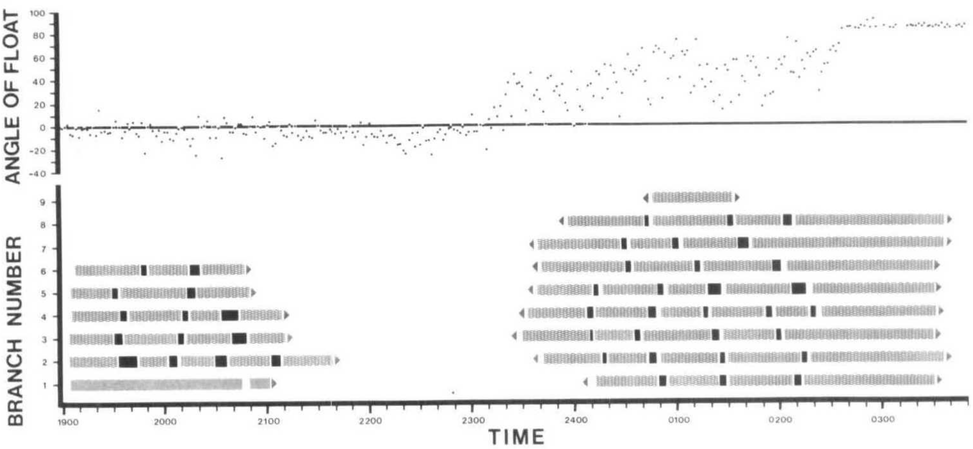

Figure 1. Diagram of *Astrophyton muricatum* behavior during the period between ascent and descent from the feeding perch, and of ambient water velocity. The angle of a float, measured as degrees deviation from the vertical, indicates current speed. Positive angles denote flood tide flow and negative angles indicate seaward water movement. Activities of the feeding arm-branches are indicated for two major periods of feeding activity. Branch numbers denote the position of a branch (left to right, facing the camera) in the feeding fan. Because of a reversal of the orientation of the disc, the same branch may have different numerical designations in the first and second feeding periods. Cross-hatched bars represent the time when branches were extended and black bars indicate when they were coiled against the disc. The intervals of curling and uncurling are shown by narrow white bands. A wavy bar designates arm movements that were not clearly filmed. Bars are omitted for the interval between the feeding periods.

activity. Locomotor branches near the mouth moved, but most of the locomotor branches stayed securely fixed to the disc or the substratum.

Between the first and second feeding periods the locomotor and feeding branches were held against the disc and the basketstar resembled a large knot of line. Twice during this period there were marked changes in the velocity of the water current. These resulted in shifts in the position of the prop branches followed by agitated movements of the locomotor branches.

As the current reversed direction the prop branches released the substratum, and immediately afterwards other locomotor branches rose to form a flattened "umbrella" above the disc. This configuration was maintained while the body of the basketstar reoriented.

After the position of the disc was adjusted and the distal portion of some locomotor branches lifted off the disc, the feeding branches extended, one at a time, over a 14-min period. The feeding branches formed a nearly paraboloid filter concave into the current (which had reversed direction after the first feeding period). Up to nine feeding branches were extended during the second feeding period. One, pointing downward toward "6 o'clock," was extended for only 46 min. There were two prop branches at one side of the disc and one on the other side (one more than for the first feeding period). Shifts in the position of the prop branches preceded repositioning of the feeding fan, such as during intensification of the current at 0102 h.

At 0225 h, sharp movements of the current float indicated a strong perturbation in water flow. For an hour or more afterwards, the feeding branches remained extended from the disc. This probably marked a period of increasing water velocity. However, the water speed exceeded the metering capability of the float (approximately 18 cm/sec). It is possible that the actual speed was in the range of maximum currents previously measured near the study site, in excess of 41 cm/sec (Ruetzler, 1976). Strong oscillations in water movement, however, were registered by the disc and arms of the basketstar which bent backwards and snapped forwards with each surge. Between current shocks (at 1.2 ± 1.8-min intervals) the side branches of the feeding branches resumed a U-shaped configuration facing into the direction of the water current.

Preceding the retreat of the basketstar from the summit of the pinnacle, the feeding branches were furled over a 7-min span. One or two branches at a time were retracted until all were pressed under the disc. At the conclusion of the second feeding period, as at the end of the first period, distal extensions of the locomotor branches were positioned on the surface of the disc. Then the branch tips loosened and extended above the disc. Within a few minutes the disc shifted, and the animal descended from the pinnacle. The basketstar's descent took approximately the same amount of time as the ascent. The same path and "handgrips" were covered by the locomotor branches of the basketstar when moving both up and down the crest of the pinnacle.

Analysis of the Feeding Sequence

During each feeding sequence a feeding branch flexed towards the disc in a plano-spiral coil and moved adorally through the loosely furled locomotor branches (Fig. 2). Extension of the feeding branch was the reverse of this sequence. The axis of the feeding branch lifted off the disc in a coiled posture and uncurled as it extended aborally into the current. The motion of the side-branches of a feeding branch was not distinguishable in the film, and the position of the feeding branches in relation to the mouth was obscured by locomotor branches and projections from the substratum.

Feeding branches coiled towards the disc in 1.07 ± 0.22 min ($\bar{x}$ ± SD), and extension took 1.89 ± 0.66 min, for all sequences examined. These intervals, though similar, were significantly different ($n_1 = 30$, $n_2 = 30$, $U_s = 827.0$, $P < 0.01$). During the first feeding period, feeding sequences were generally of longer duration than during the second feeding period (Fig. 1). Overall, branches remained coiled against the disc for 4.68 ± 1.86 min during each feeding sequence. During the first feeding period the feeding branches remained coiled against the disc for 5.78 ± 2.13 min, a value significantly different from the 4.21 ± 1.55 min interval during the second period ($n_1 = 21$, $n_2 = 9$, $U_s = 141.5$, $P < 0.001$, excluding the first feeding sequence in each period). There were significantly more feeding sequences per hour during the first feeding period (1.74 ± 0.12) than during the second period (1.44 ± 0.10) ($n_1 = 8$, $n_2 = 5$, $U_s = 40.0$, $P < 0.01$).

Timing of Successive Feeding Sequences

The median delay between successive feeding sequences was 4.33 min. Despite some drastic deviations from the mean value (5.47 ± 5.43 min), feeding sequences rarely exceeded 6 min (Fig. 3). In contrast, feeding movements of a particular branch only recurred at 35.86 ± 6.86 min (Fig. 3). Between consecutive curls of any one branch, there were approximately six feeding sequences of other branches. Generally, only one arm at a time coiled towards the disc. Only on two occasions did two arms curl simultaneously, and there were no more than three feeding branches held at the disc at any one time. There were 33 instances of one branch at the disc, 18 of two, and three of three branches.

The progression of feeding movements shown in Figure 1, visually suggested

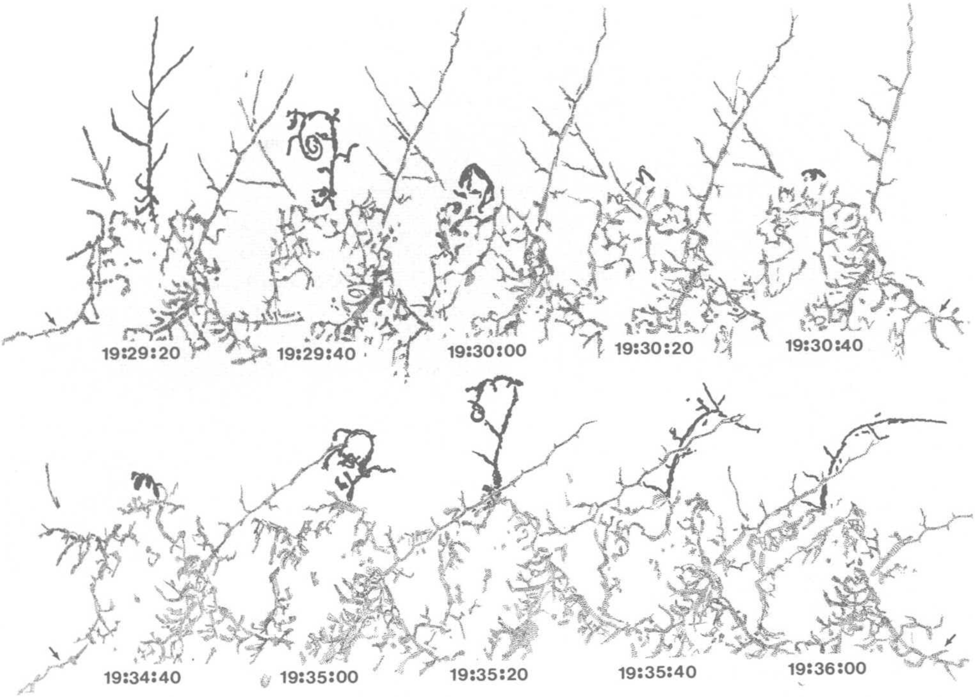

Figure 2. Tracings from the film of *Astrophyton muricatum* arms during a feeding sequence. The plano-spiral configuration of a feeding branch (black) is evident. In sequential frames, it curls orally, is obscured by the locomotor branches (stippled) around the disc, then uncoils as it extends aborally. The prop branches (extended locomotor branches) are indicated by arrows. The oral surface of the basketstar is towards the viewer, but it is hidden by a sponge (not drawn) to which the locomotor branches cling. Local time (h:min:sec) is indicated for each frame. There is a discontinuity in the sequence of frames during the interval that the feeding branch remained at the disc, presumably transferring food to the mouth.

cyclical movements of the feeding branches in one direction across the feeding fan and then in a series in the opposite direction. However, a runs test for trend data (Sokal and Rohlf, 1969) indicated no significant trend in the order of arm movement during the first feeding period ($n = 14$, $t_s = -1.359$, $P > 0.05$) and during the second feeding period ($n = 29$, $t_s = 0.303$, $P > 0.05$). Since the number of runs did not exceed that expected in a random sequence of values, it appears that feeding behavior is not a fixed, cyclical activity. Similarly, there seemed to be runs of feeding sequences interspersed with periods when the arms were not moving. However, a runs test for dichotomized data (Sokal and Rohlf, 1969) for the first and second feeding periods indicated that the pattern was not significantly different from the expectation for randomly alternating feeding and filtering events ($n_1 = 10$, $n_2 = 10$, $r = 9$, $P > 0.05$, and $n_1 = 19$, $n_2 = 8$, $r = 9$, $P > 0.05$).

The data suggested that the central arms (those pointing toward 12 o'clock in the feeding fan) curled more frequently and remained at the disc for a longer time than the lateral branches (those directed toward 9 and 3 o'clock). However, the data were not extensive enough to warrant a test for significance. The three central branches averaged 4.0 feeding sequences during the second period and the five lateral branches that were visible each averaged 3.4 feeding sequences.

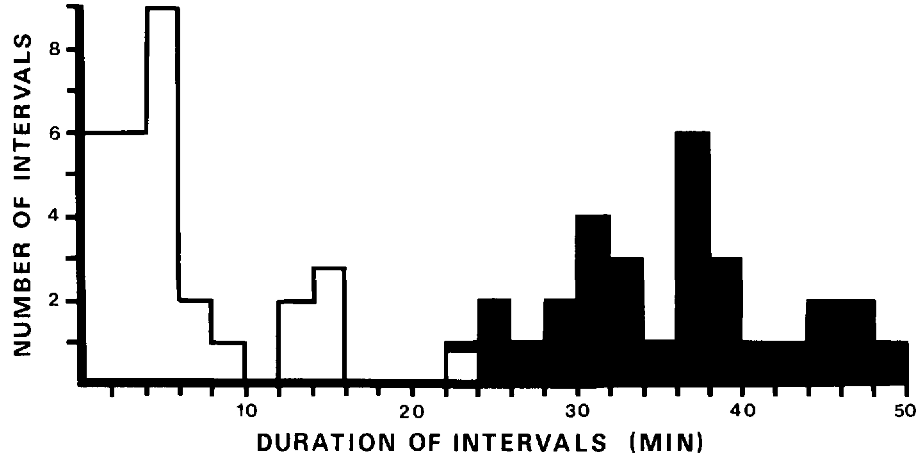

Figure 3. The frequency of occurrence of intervals of various lengths between successive feeding sequences. The intervals between the feeding sequence of a branch and the next feeding sequence of any other branch, shown by white bars, averaged 5.5 min. In contrast, the delays between a feeding sequence of a particular branch and the next feeding sequence of the same branch, shown by black bars, averaged 35.9 min.

Likewise, the central arms each remained coiled beneath the disc for 4.19 min, and the lateral branches were each at the disc for an average of 2.96 min per feeding sequence.

A correlation between changes in the basketstar's activity and the intensity of moonlight was not found. Therefore, illumination is not considered in the discussion below. The continuously recording photometer registered light only during 7-, 10-, and 50-min segments in the interval of "inactivity" between feeding periods. During the study the moon was late in the last quarter phase, and the recorded light level was equivalent to that registered by the meter for a full moon behind dense cloud cover.

Discussion

Prior to this study the most detailed accounts of the behavior of *Astrophyton muricatum* were the underwater observations of Fricke (1968) and Wolfe (1978 and in press). They found that *Astrophyton* emerged at sunset and maintained an elevated perch while extending its feeding arms. They also noted that the feeding branches formed a parabolic array concave to the current. The branches with captured prey were seen to droop, rolling in branchlets and massing as they descended towards the mouth.

The present study clarified the movements of the locomotor and feeding branches during the basketstar's ascent and descent from the pinnacle crest and during shifts in speed and direction of water flow. Migration involved integrated activity of the locomotor branches and retraction of the feeding branches. When the prop branches released the substrate the locomotor branches formed an umbrella arched over the disc. The significance of the umbrella was not apparent but it might serve for physical protection of the animal, as a sensory array, for maintaining balance, or as a potential supporting apparatus.

Distinctions between the function of the locomotor and feeding branches were apparent during feeding sequences. The locomotor branches served to fix the disc to the substratum. The prop branches (the locomotor branches most easily observed) seemed to allow minimal slack. They compensated for small changes in the orientation of the disc by releasing and altering their position of attachment. Locomotor branches might conceivably protect the disc and transfer food particles, but such activity was not seen.

The basketstar seemed to detect the current direction without extending its feeding branches. At the beginning of the feeding periods, the disc was emplaced before the feeding arms were extended into the current. In the second feeding period the current changed direction and the position of the disc changed before the feeding branches lifted from the disc.

At the initiation and conclusion of the feeding periods the feeding branches were gradually, one by one, moved into the current or toward the disc, rather than moving all at once. The feeding branches extended more rapidly during the first feeding period when water current was low, than during the period of increasing water velocity at the start of the second feeding period. Thus, the rapidity with which the feeding branches were raised seemed to be related to the speed of water flow. Perhaps the water speed was tested by locomotor or feeding branches. The agitation of the locomotor branches during the interval between the first and second feeding periods might have constituted an assessment of water movement.

Astrophyton fed over an extended period in agreement with Wolfe's (1978 and in press) but contrary to Fricke's (1968) observations. However, feeding activity ended during the night, in contrast to the expectation based on previous studies that it would persist until dawn (Fricke, 1968; Macurda, 1976; Wolfe, 1978 and in press). The buffeting of the disc and arms and the cessation of feeding movements prior to the retreat of the specimen perhaps indicated that excessive current or turbulence had interfered with feeding. Water may have been allowed to spill from the feeding fan (diminishing pressure against the arms) by reflexion and straightening of the main feeding branches and side branches throughout the period of turbulence. That the feeding branches remained fully extended in rapid water currents for an hour after the last feeding sequences is noteworthy, but difficult to interpret. Whether or not food was captured in this period is not known. The water speed, probably >20 cm/sec at the end of the feeding period, is indicative that the upper limit for feeding tolerated by *A. muricatum* may be lower than the >50-cm/sec value suggested by Meyer and Lane (1976).

There may also be a threshold water velocity below which feeding ceases. For example, during the period of relative inactivity between the two major feeding periods, the basketstar remained in an exposed position rather than retreating to its diurnal shelter. It held this posture for a longer time than it remained in a stiff, upright position during the period of high water velocity that followed the final feeding sequences. Whether this reflects different behaviors elicited by low and high current regimes, or perhaps indicates a learned response to predictable tidal fluctuations, is not determinable from the film.

It is noteworthy that the basketstar moved along the same path, over the same sponge colonies, when ascending and descending from the pinnacle crest. This suggests that the route followed was a learned pattern of behavior. This hypothesis is supported by *Astrophyton*'s long-term occupation of a single feeding perch and diurnal shelter (Wolfe, 1978 and in press).

The feeding sequence was examined in detail to address the question (Atz, 1960) of how food is transferred to the basketstar's mouth. The manipulation of food in the oral area was obscured from the camera by the substratum and the basketstar's disc and arms. However, the position of the feeding branches at the mouth could be inferred from the posture of the incoiling and extending arms. Therefore it was particularly interesting that the uncoiling sequence was essentially the reverse of the coiling sequence. A parsimonious explanation of these reciprocal motions is that the main axis of the feeding branch remains coiled during the ingestion of food, though the coil may perhaps loosen and free the side branches to enter the mouth. It appears that the entire incoiled feeding branch is not inserted in the oral cavity and then straightened and extended as it is drawn across the rows of serrated teeth along the jaws.

These deductions are supported by Fricke's (1968) aquarium observation that the feeding branches of *A. muricatum* were held in a flat coil against the oral area. Patent (1970), also making observations with aquaria, noted that portions (size unspecified) of the feeding branches of *Gorgonocephalus eucnemis* entered the basketstar's mouth during the feeding process. It may be that only the tightly coiled side-branches of the feeding branches of *A. muricatum* are directed into the mouth, or that the locomotor arms mediate in the transfer of prey from the feeding branch to the oral cavity. For *Astroboa nuda,* Tsurnamal and Marder (1966) thought that proximal side-branches lying against the disc might conduct food to the mouth. Critical observations on undisturbed basketstars in the field will be difficult to make but are essential to unravel the mechanics of the feeding sequence.

There were apparent differences of activity between the arms at the center and those at the side of the feeding fan. If these differences are indicative of differential feeding intensity, the pattern of activity would support Warner's (1977) filter-feeder model. Warner found that in an experimental flume, curved filters captured more particles than flat filters of equal area, especially at speeds in excess of 4.7 cm/sec. In addition, he found that the central portion of a curved filter captured more particles than the edges of the filter. Similarly, the curved feeding fan of *A. muricatum* may entrain a higher concentration of prey in the central, rather than the lateral arms. Thus the preponderance of feeding movements by the central branches may reflect a greater availability of prey near the center of the feeding fan. This suggests that the outspread arms of *A. muricatum* function as a passive filter collecting inanimate particles. However, movements of the fine terminal arm branches, possibly "chasing" prey, have been noted by Fricke (1968) and Wolfe (1978 and in press) for specimens in aquaria.

The "random" timing and order of arms engaged in feeding was quite unlike the invariable cycle of tentacle movements described by Ölscher and Fedra (1977) for a dendrochirotid holothuroid. *Astrophyton* moves only one branch at a time toward the mouth. This is evidence for coordination among arms. Moreover, the marked delay between feeding sequences of individual branches suggests that a particular amount of food is captured by a branch before it coils. The variable length of the delays might reflect a haphazard or patchy distribution of prey impinging on the basketstar's feeding fan. The patchiness of zooplankton in time and space has been demonstrated in reef habitats (Tranter et al., 1981), but additional observations are necessary to assess the relationship of plankton availability to basketstar feeding movements. Further application of elapsed-time analysis may clarify this and other questions posed by this study.

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