

Habitat and Feeding Observations on Species of *Ophiocoma* (Ophiocomidae) at Enewetak

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Abstract—Habitat and feeding differences among seven species of the Genus *Ophiocoma* (Ophiuroidea: Ophiocomidae) were examined at Enewetak, Marshall Islands. A variety of suspension, deposit, and water surface feeding mechanisms were employed by these species, but dietary differences were not distinguished. The four abundant species, *O. anaglyptica*, *O. erinaceus*, *O. pica*, and *O. scolopendrina*, were ecologically separated by habitat (patch type) rather than particle size of food. Three closely related and relatively rare species, belonging to the *Brevipes* intrageneric group, *O. brevipes*, *O. dentata*, and *O. doederleini* were not ecologically separated based on food or habitat. It is possible that neither food nor habitat availability were limiting factors for this group, but rather some feature not discovered in this study. *Ophiocoma* that were primarily bottom feeders had stronger dentition and a lower spine to arm length ratio than suspension feeding species.

Introduction

The genus *Ophiocoma* consists of 19 recent species of shallow-water brittlestars (Devaney, 1970, 1974a). Within tropical and subtropical latitudes it has a circum-global distribution, but the greatest number of species are Indo-Pacific. In many shallow-water areas associated with atolls, islands, and continental land masses, representatives of this genus are among the most abundant ophiuroids. The present study was undertaken to evaluate ecological differences among seven species in this genus which are commonly encountered in shallow water habitats of an Indo-West Pacific atoll (Fig. 1).

Devaney (1968, 1970) has divided the genus into four intrageneric groups: the *Brevipes* group, the *Pica* group, the *Pumila* group, and the *Scolopendrina* group. Members of the *Brevipes* group have an Indo-Pacific distribution and are characterized by having: closely packed disk granules that give a smooth appearance; a short, broad dental plate; and arm plates that have rounded margins. At Enewetak this group includes *O. brevipes* Peters, *O. dentata* Müller and Troschel, and *O. doederleini* DeLoriot and are included in this study.

The *Pica* group has long, tapered, and generally regular number of arm spines;

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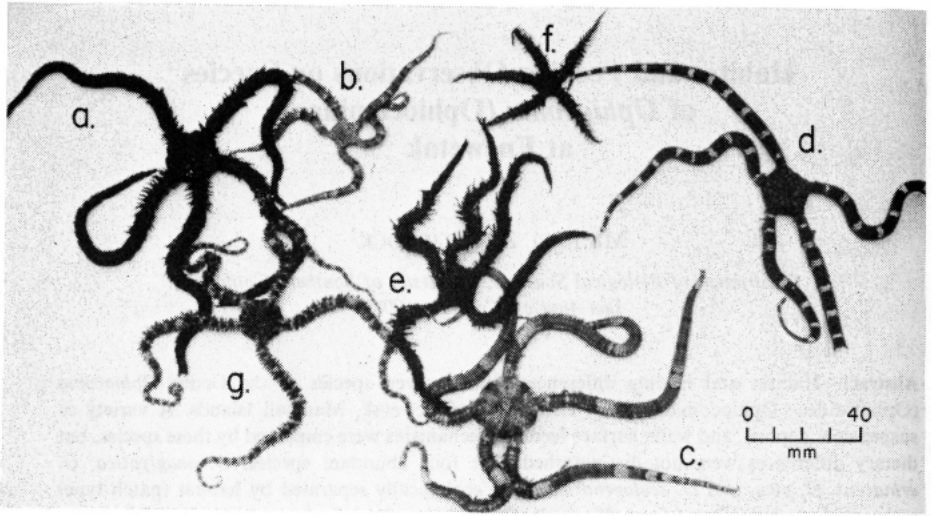


Fig. 1. Seven species of *Ophiocoma* included in the study: a. *Ophiocoma anaglyptica*; b. *Ophiocoma brevipes*; c. *Ophiocoma dentata*; d. *Ophiocoma doederleini*; e. *Ophiocoma erinaceus*; f. *Ophiocoma pica*; g. *Ophiocoma scolopendrina*.

angular lateral margins of the arm plates; and even disk granulation. There are three Indo-West Pacific species in this group. Only *O. pica* Müller and Troschel was included in the present study although *O. pusilla* has also been reported from Enewetak (Devaney, 1970).

The *Pumila* group has variable disk granulation, some granules being elongate or spiniform. It is not represented at Enewetak but is found in the eastern Pacific, the West Indies, West Africa, East Africa, and the western Indian Ocean.

The *Scolopendrina* group has a pantropical distribution and contains nine species. Of these, *O. anaglyptica* Ely, *O. erinaceus* Müller and Troschel, and *O. scolopendrina* Lamarck were abundant at Enewetak. The group is characterized by having an alternating number of spines on the arm segments, the uppermost arm spine thicker and often longer than the lower ones, and the disk granulation typically coarse and spherical.

In laboratory studies at the Red Sea, Magnus (1962, 1964) found that *O. scolopendrina* may feed by a number of different mechanisms, eating benthic material as well as suspended particles and neuston. Devaney (1974b) provides a comprehensive account of the distribution of species of *Ophiocoma* in southeastern Polynesia, and Sloan et al. (1979) provide a detailed account of the echinoderms of Aldabra, with a review and evaluation of microhabitats of the Ophiocomidae found worldwide.

The objective of this study was to evaluate the food and habitat resources utilized by species of *Ophiocoma* and to distinguish factors that may be important in possible ecological separations among species. In addition, these observations might serve to

identify ecological differences among the major intrageneric groups and enhance the understanding of morphological characteristics and systematic relationships.

Materials and Methods

Seven transects were established on three islets, two on Bokandretok, four on Enewetak, and one on Japtan during the period of June through August of 1968, 1969 and 1970 (Fig. 2). In addition, observations were made in the intertidal and shallow sublittoral areas on Alembel, Ananij, Bijire, Bokoluo, Ikuren, Jinedrol, Kidrinen, Medren, Mut, Ribewon, and Runit islets. The transects ranged between 20 and 80 meters in length and extended from the upper intertidal zone to about three meters below mean low water, although in certain transects on the windward reef subtidal observations were not possible due to persistent large waves. The substrate along the transect was carefully inspected, using a crowbar to overturn large rocks and break apart coral heads. The numbers of ophiuroids found along the transect were recorded, along with substrate data and other qualitative descriptive infor-

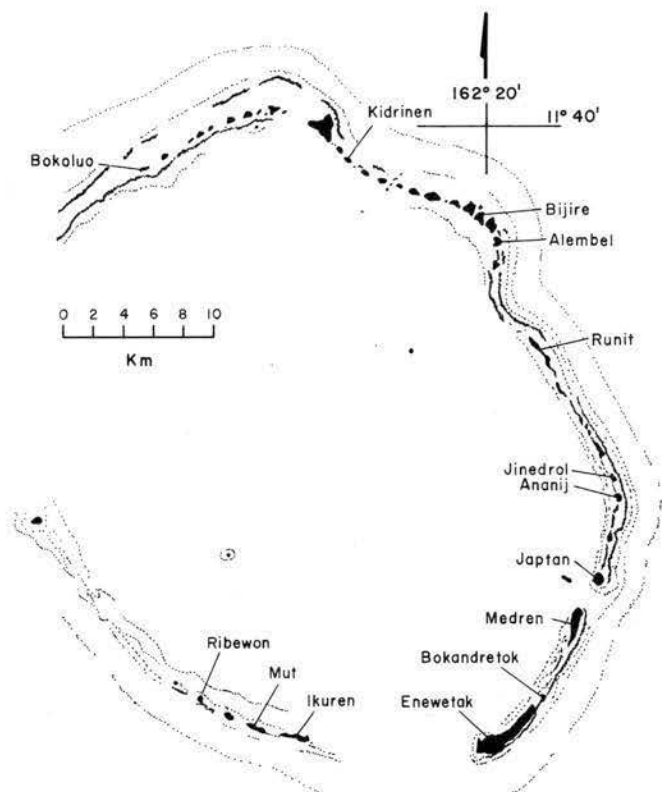


Fig. 2. Enewetak Atoll, Marshall Islands.

mation. Densities were measured, using one-half or one-meter-square quadrats. In other instances, the overall volume of coral heads or the area of crevice habitat under beach rock slabs were measured to determine density per unit of habitat.

Ophiuroids were collected during day and night and individually placed in vials. Within several minutes, stomach contents were regurgitated, and in the laboratory these contents were preserved either in alcohol or fixed and imbedded in permount for subsequent examination. Regurgitation typically included repeated pumping of the stomach which resulted in complete voiding its contents. Dissection and microscopic inspection of more than ten specimens indicated that stomachs were empty although it is possible that some of the smallest size particles remained in the stomachs. Stomach content particle diameters were measured with a calibrated reticle under a compound microscope.

Observations on feeding behavior were conducted at night and during the day both in the field and in the laboratory. Observations were documented with 8- and 16-mm color movies and still photographs. Field notes included information on podial and arm movements, body orientation, degree of activity, and other qualitative observations (Chartock 1972).

Laboratory observations of ophiuroid feeding were conducted using glass aquaria and plexiglass chambers fitted with artificial crevices. Observations were conducted under red light, which produced no observable changes in ophiuroid behavior when compared to almost total darkness. Food material tested in chamber feeding studies included filamentous algae, fine and coarse calcareous material (to 1 cm in diameter), and suspended and benthic detritus from shallow water environments and fish (*Acanthurus guttatus* and *A. triostegus*) muscle. Some feeding observations were also made using carmine particles and powdered charcoal.

Results

HABITAT OBSERVATIONS

Members of the genus *Ophiocoma* were found in a variety of zones of the atoll. These zones (Fig. 3) extended from the seaward slope or buttress area across the reef flat to the lagoon slope which descends to the lagoon floor (Fosberg et al. 1956; Odum and Odum, 1955, 1957). Species habitat preference apparently existed for one or several of these zones and some species were more abundant on certain substrates (Table 1). The number of individuals reported in Table 1 did not reflect relative abundance as substantial time was spent collecting rare species.

The degree in which species pairs cooccur in the same habitat represents a convenient index of habitat overlap (Hurlbert, 1969). The degree that cooccurrences deviated from random expectation is listed in Table 2. Thirteen species pairs had negative associations, where cooccurrences were observed less frequently than would be expected from random distribution. Five species pairs tended to positively cooccur, and three had no significant deviation from random cooccurrence.

Ophiocoma scolopendrina was negatively associated with all other species of

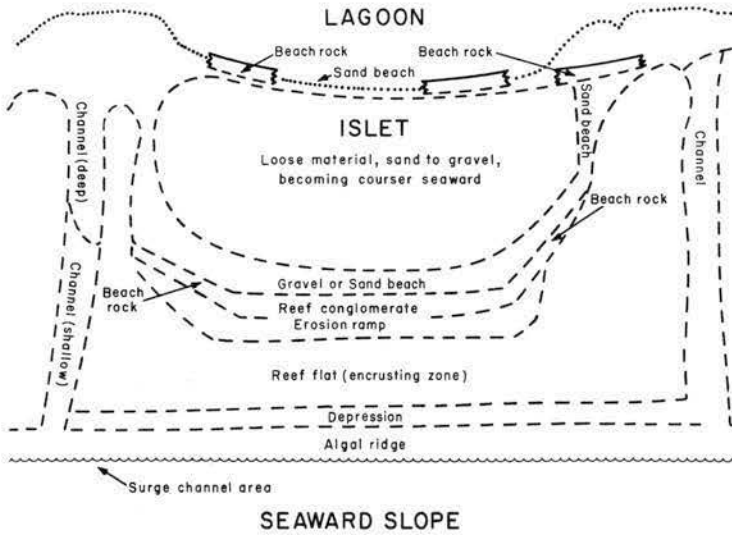


Fig. 3. Diagrammatic aerial view of a typical Marshall Islands windward islet and reef (Modified from Fosberg, et al., 1956).

Ophiocoma. *Ophiocoma anaglyptica* was also negatively associated with all species except *O. brevipes*. *O. pica* was only positively associated with *O. erinaceus*, but microhabitat differences tended to separate these two species as *O. pica* lived near the extremities of the coral branches and *O. erinaceus* occurred in the medial portions of the coral heads.

The three members of the *Brevipes* intrageneric group had considerable habitat overlap. *Ophiocoma brevipes* was most numerous in the midreef. *Ophiocoma brevipes* was small, however, and occupied crevices inaccessible to the majority of larger *O. dentata* and *O. doederleini*. Both *O. dentata* and *O. doederleini* were most common in similar locations and substrate. The following species descriptions characterize in greater detail these habitat preferences.

1. *O. anaglyptica*

Ophiocoma anaglyptica occurred in high densities along the algal ridge where surf was intense and became less numerous towards the lagoon. It appeared to be gregarious, attaining densities of 150 individuals/m² under slabs of dead coral and reef conglomerate. Under every algal ridge slab pried up with a crowbar, numerous individuals were found. The moist weight of *O. anaglyptica* biomass in this habitat was about 240 g/m², and it was the predominant benthic invertebrate. *Ophiocoma pica* was the only other ophiocomid found on the algal ridge.

Ophiocoma anaglyptica was also found under heads of *Porites lobata* in the shallow areas of the reef flat behind the algal ridge (the "encrusting zone" of Odum

Table 1. Number of ophiuroids captured in habitats.

Habitat Zone (meters above low water)	<i>O.</i> <i>anaglyptica</i>	<i>O.</i> <i>brevipes</i>	<i>O.</i> <i>dentata</i>	<i>O.</i> <i>doederleini</i>	<i>O.</i> <i>erinaceus</i>	<i>O.</i> <i>pica</i>	<i>O.</i> <i>scolopendrina</i>	Number of visits*
Intertidal								
Algal ridge (0-1)	230	—	—	—	—	2	—	14
Mid reef (.3-6)	88	17	1	2	2	—	4	10
Back reef (0-.3)	42	10	4	27	7	3	—	7
Reef crevices (.6-1.2)	—	—	—	—	—	—	201	7
Reef beach rock (.6-1.2)	—	—	—	—	—	—	63	14
Lagoon beach rock (0-1)	2	—	—	—	—	—	2	3
Subtidal								
In <i>Pocillopora</i>	—	—	—	—	30	89	—	13
In <i>Heliopora</i>	—	—	—	—	64	23	—	13
Lagoon patch reefs	—	—	—	1	4	—	—	10
In crevices and under rocks	3	—	2	3	12	2	—	8
Under <i>Porites</i>	—	1	1	5	18	1	—	7
In <i>Millepora</i>	—	—	—	—	5	2	—	3
Total	365	28	8	38	142	122	270	109

* Visits to the habitat zone during which at least one species was found.

Table 2. Coefficients of interspecific association.*

Species	<i>O.</i> <i>brevipes</i>	<i>O.</i> <i>dentata</i>	<i>O.</i> <i>doederleini</i>	<i>O.</i> <i>erinaceus</i>	<i>O.</i> <i>pica</i>	<i>O.</i> <i>scolopendrina</i>
<i>O. anaglyptica</i>	+0.13	-0.15	-0.29	-0.37	-0.28	-0.24
<i>O. brevipes</i>		+0.42	+0.13	0.00	-2.28	-0.28
<i>O. dentata</i>			+0.60	0.00	-0.33	-0.29
<i>O. doederleini</i>				0.00	-0.15	-0.21
<i>O. erinaceus</i>					+0.39	-0.58
<i>O. pica</i>						-0.34

* -1.00 = no cooccurrences.

0.00 = no deviation from randomness.

+1.00 = all specimens cooccur (see Hurlbert, 1969).

and Odum, 1955, 1957). In this habitat it overlapped with *O. brevipes*, *O. dentata*, and *O. doederleini*. It was relatively rare in this midreef habitat; some of the individuals were possibly swept to the midreef area which was down-current from the algal ridge.

2. *O. brevipes*

Ophiocoma brevipes, a solitary species, was most abundant under *Porites lobata* and rocks and boulders firmly set on reef-rock substrate. It was found from the middle of the encrusting zone back to the shallow subtidal corals adjacent to the lagoon. Only 28 individuals were encountered, so it is possible the optimum habitat was not found. However, specimens collected by other investigators (Clark, 1921, 1946; Devaney, 1974) were found in a similar reef-flat habitat. Its density was 0.5 to 2 individuals/m² in optimum microhabitat under *Porites*. This habitat only covered about 10 percent of the reef-flat surface. In the midreef area it cooccurred with *O. anaglyptica*, and toward the lagoon in slightly deeper water it was found in the same under-rock habitat as *O. dentata*, *O. doederleini*, *O. erinaceus*, and *O. pica*. It rarely cooccurred in the same crevice with these species. *Ophiocoma brevipes* was smaller and was observed to occupy narrower crevices than the above-mentioned larger species.

3. *O. dentata*

Ophiocoma dentata was the rarest species studied and only eight specimens were found during three summers on the reef. It was typically found in subtidal areas under heads of *Porites* which were firmly attached to the reef floor. Specimens were also found under heads of dead *Acropora* at lagoon patch reefs. *Ophiocoma dentata* had a maximum density estimated to be 0.1 animal/m² in areas of the reef floor with *Porites*.

Ophiocoma dentata occurred as solitary specimens and, when disturbed, moved rapidly to crevices in the coarse rubble substrate. These areas of retreat resembled burrows, although there was no direct evidence to ascribe these burrows to ophiuroid activity. This species occupied the same zone as *O. doederleini* and overlapped with *O. brevipes*, *O. erinaceus*, and *O. pica*.

4. *O. doederleini*

Ophiocoma doederleini was the most common member of the *Brevipes* in-trageneric group encountered at Enewetak. It was usually found in the low intertidal zone or subtidally under boulders or coral heads (e. g., *Porites lobata*) which were firmly attached to the substrate. *Ophiocoma doederleini* occurred under approximately one out of four such undisturbed coral heads from the low-tide area to a depth of several meters. The maximum density of this species was about 1/m². *Ophiocoma dentata*, *O. erinaceus*, and, to a lesser extent *O. anaglyptica*, *O. brevipes*, and *O. pica* would also be encountered in this zone.

Ophiocoma doederleini was occasionally found on the shallow reef-flat and in deeper channel or lagoon areas under rock or rubble piles. On rare occasions, more than one individual would be found under a given slab or rock; apparently this species, like *O. dentata*, and *O. brevipes* was solitary. Other investigators in the Marshall Islands have not found it in great abundance (Dr. Dennis Devaney, pers. comm.; Capt. Fred Zieshenne, pers. comm.).

5. *O. erinaceus*

Ophiocoma erinaceus was the most abundant and widespread ophiuroid in subtidal areas. It was most common in *Heliopora coerulea*, where a head of 0.002 m³ held 6 individuals. Moderate-sized heads of 0.01 m³ frequently contained 15 or more individuals. Heads of *Heliopora* were often a meter high and in interisland channels they would be 3 to 5 m high. In the *Heliopora* zone, *O. erinaceus* achieved estimated densities between 150 to 15,000 per m² reef surface. All heads of *Heliopora* examined contained at least several *O. erinaceus*. *Ophiocoma erinaceus* also occurred in *Pocillopora elegans* and occasionally in the staghorn coral *Acropora* sp. and in *Millepora platyphylla*. It was also found in subtidal locations under large rocks and *Porites lobata*.

Ophiocoma erinaceus cooccurred with several other *Ophiocoma* species to varying degrees. In the crevice dwelling habitat in subtidal areas it overlapped with *O. brevipes*, *O. dentata*, and *O. doederleini*, but was less abundant (5/m²) than in its coral-branch habitat. *Ophiocoma pica* was found with *O. erinaceus* in *Acropora*, *Millepora*, and *Heliopora*.

6. *O. pica*

Ophiocoma pica commonly occurred in subtidal waters in both living and dead heads of *Heliopora coerulea* and in *Pocillopora elegans*. Several specimens were found under rocks or in crevices other than those of coral. In small heads of *P. elegans*, less than 10 cm on a side, only *O. pica* was found, but in larger heads both it and *O. erinaceus* were common. *O. pica* occupied the distal interstices; *O. erinaceus* the proximal spaces of coral heads. In the coral habitat, *O. pica* was typically less abundant than *O. erinaceus*.

7. *O. scolopendrina*

Ophiocoma scolopendrina was confined to the upper intertidal zone, near the high-tide mark from the +0.6 m to the +1.2 m levels. It was thus associated with islet beaches, raised beach rock, and reef conglomerate distant from intense surf. Only one specimen of the hundreds collected was found subtidally, in this case under the giant clam, *Tridacna* sp. Several specimens were found under lagoon beach-rock slabs, in an area which overlaps with a minor habitat of *O. anaglyptica*. The area of maximum abundance was crevice-laden reef conglomerate, where the highest density measured was 100/m². However, densities of 20/m² were more frequent.

Figure 4 indicates the abundance of *O. scolopendrina* from the sandy-beach reef-rock interface towards the algal ridge in two transects each 16 m long. In both instances the location of maximum density was 6 m from the beach, in an area where the microtopography of the reef conglomerate was very coarse, affording numerous crevices for ophiuroid retreat. Areas without ophiuroids lacked these small crevices,

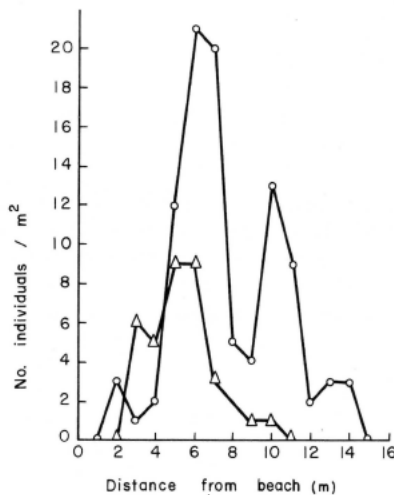


Fig. 4. Density of *Ophiocoma scolopendrina* in two transects on Enewetak Island.

suggesting that the limiting factor on *O. scolopendrina* density might be microhabitat availability.

FEEDING ACTIVITIES

Stomach contents of *Ophiocoma* species consisted almost exclusively of sand, intact algae, and algal detritus. In addition, stomachs of specimens inhabiting the reef floor occasionally contained foraminiferans, sponge spicules, crustacean (e.g., isopod) skeletal parts, nematodes, and juvenile snail shells. The mean particle diameters of 50 particle samples from each stomach of 78 specimens are given in Table 3.

Table 4 indicates the degree of difference among pairs of species in the mean particle diameter of stomach contents, using a Student's *t*-test (Bailey, 1981). Although the mean particle diameter ranged from 40 to 90 μ , in no cases were these means significantly different ($P \geq 0.05$) when compared between species. However, at the $P=0.1$ level, *O. scolopendrina* apparently consumed larger material than *O. anaglyptica* and *O. brevipes*.

Behavioral observations of all seven species of *Ophiocoma* indicated a wide range

Table 3. Diameter of particles in stomach contents of seven species of *Ophiocoma*.

Species	Number of stomachs examined	Mean particle diameter (μ)	Standard error of particle diameter
<i>O. anaglyptica</i>	11	43	5.9
<i>O. brevipes</i>	2	40	6.0
<i>O. dentata</i>	4	74	34.0
<i>O. doederleini</i>	4	63	17.0
<i>O. erinaceus</i>	16	66	11.0
<i>O. pica</i>	25	56	5.8
<i>O. scolopendrina</i>	12	94	16.0

Table 4. Comparison of stomach-content particle sizes indicating tail-probability of differences between pairs of species of *Ophiocoma*.

Species	<i>O. brevipes</i>	<i>O. dentata</i>	<i>O. doederleini</i>	<i>O. erinaceus</i>	<i>O. pica</i>	<i>O. scolopendrina</i>
<i>O. anaglyptica</i>	0.5	0.3	0.35	0.2	0.25	0.1
<i>O. brevipes</i>		0.3	0.3	0.15	0.2	0.1
<i>O. dentata</i>			0.45	0.45	0.4	0.4
<i>O. doederleini</i>				0.5	0.45	0.3
<i>O. erinaceus</i>					0.35	0.25
<i>O. pica</i>						0.15

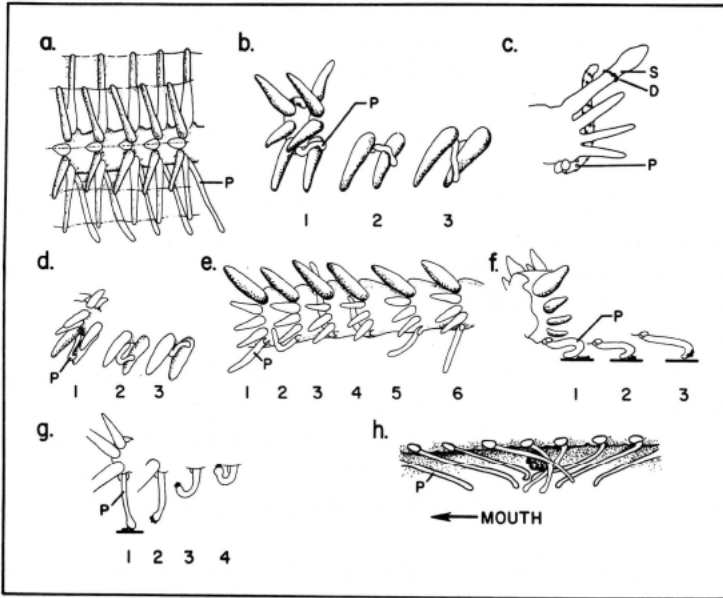


Fig. 5. Diagrammatic representations of feeding methods in species *Ophiocoma* (D=detritus; P=podium; S=spine; numbers represent temporal sequences of podial movement in an arm segment): a. mucus net of *Ophiocoma pica*; b. medial to distal spine cleaning movement of a podium in *Ophiocoma dentata*; c. podium of *Ophiocoma erinaceus* in a posture prior to sweeping down a row of spines; d. distal to medial spine cleaning movement of podium in *Ophiocoma brevipes*; e. oral-aboral sweep of podium in *Ophiocoma scolopendrina*; f. podium picking-up detritus in *Ophiocoma anaglypica*; g. podium picking-up detritus in *Ophiocoma dentata*; h. podial transport along the oral surface of an arm in *Ophiocoma doederleini*—podia near the mouth swing out and pull, those nearer the arm tip push.

of feeding patterns. Each species apparently employed several mechanisms for obtaining food. Based on observations described below, the ophiocomids were suspension and deposit feeders and also fed at the air-water interface. The methods of suspension feeding could employ either a "net" of mucus connected between erect arm spines (Fig. 5a) or by cleaning mucus that was on the spines alone (Fig. 5b, c, d). Typically, in suspension feeding the tube feet would also repeatedly sweep from an outstretched position above (aboral to) the spines, and then sweep down a row of spines, removing the mucus and entrapped detritus (aboral-oral tentacle sweep) (Fig. 5e). In these methods of suspension feeding the podia would pick up particles from the spines, pass the particles to the oral surface of the arms, and then toward the mouth.

Differences in deposit feeding methods were based on how the arms, podia, and mouth were used. The podia alone could pick up material after they were pressed on or swept across the bottom (Fig. 5f, g). Portions of the arm could curl or flex laterally around larger particles or boluses of food (arm curling). A wave of arm flexure would

pass from the tip of the arm to the mouth, moving along a large particle in the concave surface of the wave. Direct ingestion or rasping with the oral papillae on the bottom surfaces was also observed where the mouth directly ingested material, without the use of arms.

Feeding at the air-water interface on the film of particles held by surface tension was also employed. Here the distal portion of the arm was recurved so that the oral surface was directed upwards to contact the water surface film, and the tentacles picked up food particles. In both deposit and suspension feeding, a bolus of food was often collected and passed toward the mouth in a coordinated movement of tentacles along adjacent arm segments (Fig. 5h).

Food material on the podia would thus originate either from spines, other podia, or directly from the substrate or surrounding water. Transfer of small particulate matter from the podia along the arms to the mouth was by podial movement. A podium with food on or near its tip would bend toward the mouth to the next adjacent podium; the next podium would flex and wipe material from the first podium and again bend toward the mouth for a subsequent transfer (podial transport).

Table 5 compares feeding activities based on examination of gut contents, available food supply and substrate, and notations on field and laboratory behavior. The categories "method observed most frequently," "method observed occasionally," and "method not observed," were based on field and laboratory observations.

All species were observed to employ at least two methods of feeding, and some were observed using up to four methods. *Ophiocoma anaglyptica*, *O. erinaceus*, and *O. pica* were almost always observed suspension feeding. *O. brevipes* was almost always deposit feeding. The remaining species were often observed with a wide

Table 5. Feeding methods of seven species of *Ophiocoma*.

Species	Feeding methods observed*					Water surface
	Suspension		Deposit			
	Mucus-net	Mucus-spine	Podia only	Arm-curling	Rasping	
<i>O. anaglyptica</i>	×	× ×	×	×	—	—
<i>O. brevipes</i>	—	×	× ×	—	—	—
<i>O. dentata</i>	—	×	×	×	×	—
<i>O. doederleini</i>	×	×	×	×	—	—
<i>O. erinaceus</i>	×	×	×	—	—	—
<i>O. pica</i>	× ×	×	—	—	—	—
<i>O. scolopendrina</i>	×	×	×	—	—	×

* × × = method observed most frequently; × = method observed occasionally; — = method not observed.

Table 6. Rank of seven species of *Ophiocoma* according to relative degree of suspension feeding, and ratio of arm spine length to arm length.

Relative degree of suspension feeding (rank)	Species	Spine length/ arm length ratio	Rank of spine length/ arm length
1	<i>O. pica</i>	0.064	1
2	<i>O. erinaceus</i>	0.063	2
3	<i>O. anaglyptica</i>	0.063	3
4	<i>O. scolopendrina</i>	0.025	6
5	<i>O. doederleini</i>	0.0289	5
6	<i>O. dentata</i>	0.022	7
7	<i>O. brevipes</i>	0.0291	4

Spearman's rank correlation: $r_s = 0.75$.

variety of methods. Only *O. scolopendrina* was observed to feed on particles at the air-water interface.

Species that were often observed deposit feeding, such as *O. brevipes*, *O. dentata*, and *O. doederleini*, were more prone to stroke an individual spine with their podia, typically the more oral spines (Fig. 2b, 2d). In contrast, animals that were often suspension feeding, *O. erinaceus*, *O. pica*, *O. anaglyptica*, and *O. scolopendrina* would flex their podia oral-aborally to clean all the spines in a single stroke (Fig. 5c, 5e).

A close relationship seemed to exist between feeding method and relative arm-spine length. The degree of suspension feeding was ranked subjectively using the relative proportion of observations of suspension feeding. This ranking is listed in Table 6, along with the ratio of spine length to arm total length. Spearman's rank correlation (Sokal and Rolf, 1981) of 0.75 indicated that a strong relationship may exist between the spine to arm length ratio and suspension feeding. The relatively longer spines may afford a greater surface area for suspension feeding, especially in species in the *Pica* group. The following descriptions elaborate on these feeding observations.

1. *O. anaglyptica*

Both suspension and deposit feeding, were often observed for *O. anaglyptica*. During high tide (when submerged) the arms were outstretched with the spines erect, and the podia extended beyond the spines to trap suspended particles settling from the water column. During low tide, animals usually had material in the stomach of similar particle size and composition to the detritus that settled on the substrate. About two-thirds of the gut content volume was calcareous material; the remainder was mostly algal fragments.

In most laboratory experiments, *O. anaglyptica* would become active about two minutes after introduction of food (e.g., cubes of fish muscle 5 mm on a side). An arm

would extend toward the food and the tube feet would pick it up and pass it along the oral surface of the arm to the mouth, but the pieces were not ingested. *Ophiocoma anaglyptica* would also pick up smaller particulate materials by pushing the podia repeatedly against the substrate (Fig. 5-f) and subsequently ingest them.

Suspended particles were captured by mucus on the spines or sheets of mucus stretching between spines. Food-bolus formation was also observed in *O. anaglyptica*. Food would collect in the area of the mouth as it was passed down the arms. With the mouth pressed against the substrate, the particle laden mucus would collect in the area between the mouth and the substrate, below the oral frame. The buccal tentacles would compact the bolus. After several hours of accumulation, the food bolus was ingested.

2. *O. brevipes*

Ophiocoma brevipes, in contrast with *O. anaglyptica* and other species, had spines with only slight quantities of mucus, insufficient for the formation of a mucus net. In addition, the aboral-oral tentacle sweep was not often observed; rather the predominant mode of spine cleaning was by movement of the podia over an individual spine (Fig. 5d).

Ophiocoma brevipes had the shortest aboral (upper) spines in relation to its arm length (Table 6). In contrast with other species, the oral (lower) arm spine of *O. brevipes* was the longest. Specimens frequently did not have erect spines and the arms were always flat on the substrate. These behavioral and morphological features suggest that *O. brevipes* may feed predominantly on deposited material.

3. *O. dentata*

Ophiocoma dentata employed a variety of feeding techniques, and was even observed in the laboratory, consuming or tearing the aboral surface of the disks in *O. erinaceus*, *O. anaglyptica* and *O. scolopendrina*. Morphologically, this carnivorous activity may relate to its dentition, as the oral papillae (teeth) project outward to a great degree, and the mouth is shallower (permitting feeding on the surface of objects) than in suspension feeders such as *O. pica*. Large pieces of food would be ingested, including algal masses over several centimeters in length. When the particles were too large, they were frequently rotated about in the buccal area, with some rhythmic contractions of the teeth. This activity might resemble rasping but was not substantiated by a noticeable removal of material from rocks. Large particles were rapidly transferred by a combination of arm curling and tentacle activity. In both feeding and rejection, movement of a particle along 10 cm of arm took from 8 to 15 seconds.

Pieces of algae (*Enteromorpha* sp.) and fish muscle (*Acanthurus triostegus*) when added to the aquarium at a distance of 5 to 10 cm from the animal, would elicit a feeding response involving capture, transport down the arm, and ingestion. Particles

of food placed under plexiglass, with space available for only several tube feet and not the arm, would elicit podial behavior to probe at the food object and extract it from the crevice.

Podial activity indicated feeding on bottom sediments, in addition to eating larger particles as described above. Typically, the podia would be extended to the substrate to pick-up material, then bend toward the oral arm surface to transfer the food to other podia (Fig. 5g). The tips of the podia were expanded with a terminal knob and this may represent an adaptation for deposit feeding.

Suspension feeding was also documented in *O. dentata*. Although a mucus net was not observed, particles flowing past the organism would become trapped on the mucus of the spines and podia. This material would then be cleaned off and passed to the mouth by the podia (Fig. 5b). A posture with upturned arm tips, typical of suspension-feeding ophiuroids, was occasionally observed.

4. *O. doederleini*

Feeding by *O. doederleini* was basically similar to that of *O. dentata*. In the laboratory *O. doederleini* would feed on fragments of benthic algae and pieces of fish, using both podial transport (Fig. 5h) and arm curling. Suspension feeding with the formation of a mucus net between spines was also observed.

5. *O. erinaceus*

Ophiocoma erinaceus, like other species of *Ophiocoma*, employed several mechanisms of feed gathering, but the predominant behavior was suspension feeding. Unlike other species studied, however, *O. erinaceus* has an expanded fleshy tip on many of the dorsal arm spines (Fig. 5c). Mucus on the spines collected suspended particles, which infrequently formed a ring around the spines. This ring moved down the spine and was picked up by the podia, which stroked the row of spines. Sheets of mucus extending along the spines were also observed.

6. *O. pica*

Ophiocoma pica always maintained a posture with arms curved upwards, exposing the spines and podia to the water current. The edges of the arms were usually extended perpendicular to the current, which may provide a large exposed surface for food capture. The spines of *O. pica* were covered with mucus (Fig. 5a), which not only formed sheets, but at times formed a three-dimensional mass. Periodically the particles attached to the spines and mucus were removed by the podia and transferred to the mouth.

Several morphological features appeared to represent adaptations for suspension feeding. The arm spines were the longest, in respect to arm length, of any of the species studied. These spines may also function in locomotion and in holding the

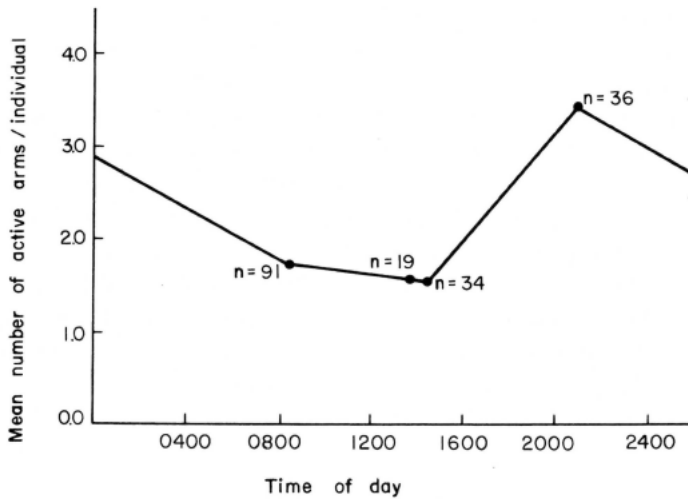


Fig. 6. Mean number of active arms of *Ophiocoma scolopendrina* at various times of the day (n=number of individuals in each sample).

animal in its habitat in the interstices of coral heads. The arm segments were also short, permitting a dense array of spines. The dentition is delicate, in contrast to the more massive teeth and oral papillae of *O. dentata*.

7. *O. scolopendrina*

In the field, *Ophiocoma scolopendrina* employed several methods of food gathering, depending on currents and tide level. Similar to Magnus's (1962) observations, three types of feeding were observed: deposit feeding, suspension feeding, and feeding on neuston from the water-air interface.

Benthic feeding was accomplished by sweeping the arms over the substrate to pick up particles of sand, algae, fecal pellets and other detritus. More arms were employed in feeding (rather than attachment) during the night than during the day (Fig. 6).

On the rising tide, when water first reached the ophiuroid, bottom feeding was initiated, but as the water level rose several centimeters above the substrate, feeding at the water-air interface began. The water surface supported a thick film of surface detritus, and the animals exploited this food supply until the water-air interface extended beyond the arm tips. Most *O. scolopendrina* lived in the upper intertidal zone so that during high tide feeding at the water-air interface could be continued for a considerable length of time (up to three hours). Suspension feeding was frequently employed as the water rose above the *O. scolopendrina* habitat zone. Suspension feeding employed either a mucus net or mucus on the spines.

Discussion

Some habitat and feeding differences occur among the seven species of *Ophiocoma*. Habitat differences in all but three rare species were statistically significant, but differences in the particle size of food were not.

Feeding behavior may be related to habitat; for example, *O. pica* was abundant in coral heads and was exclusively a suspension feeder. In contrast, *O. scolopendrina* lived on hard bottoms and was a suspension, deposit, and water surface feeder. Feeding mechanisms may account for ecological separations, but the apparent wide behavioral range for most species seemed to permit each species to use the mechanism most appropriate in its habitat.

Kohn (1971) suggests that detritivores may contrast with carnivores in mechanisms of niche separation, and the present study also supports that contention. Kohn (1971: 345) states that "...cooccurring predatory invertebrates might tend to adopt a strategy of apportioning resources by specializing more on different prey species rather than subdividing habitats distinctly. On the other hand, cooccurring congeners that feed less selectively, especially those eating mainly particulate organic detritus, might specialize more to different microhabitat patch types, while apparently overlapping more with respect to the nature of their food." This study supports Kohn's hypothesis.

Devaney (1970: 12) notes the close relationship of *O. brevipes*, *O. dentata*, and *O. doederleini*, primarily based on "...having a dental plate that is relatively much shorter, and broader than long. . .". These three species were assigned to the *Brevipes* intrageneric group. Clark (1921) regarded the *Brevipes* group as ancestral, from which the *Scolopendrina* and *Pumila* groups evolved. The *Pica* group also shows divergence from generalized *Ophiocoma* attributes (Devaney, 1970). The primitive nature of *O. brevipes* was based primarily on the limited number of dental papillae, a criterion criticized by Devaney (1970). The three species comprising the *Brevipes* group share the feature of a short dental plate and similar relatively short spination in relation to length of arms. These features may reflect the habitat and how members of the *Brevipes* group feed, most often consuming deposited detritus rather than suspension feeding. If these species were ancestral as Clark contended, this study suggests that one interpretation of possible adaptive radiation of *Ophiocoma* might be related to habitat and feeding: from predominantly bottom feeding (under rocks, on a planar surface) species to more "specialized" areas occupied by representatives of the *Scolopendrina* and *Pica* groups, such as the wave-swept algal ridge, the rigorous upper intertidal area, and the interstices of coral heads. These latter groups commonly employed a range of suspension or sediment feeding mechanisms.

However, an accepted phylogeny among the intrageneric groups of ophiocomids has not been established. The *Brevipes* group is confined to the Indo-Pacific whereas the other groups are more pantropical. Suspension feeding has also been noted in the most primitive groups of echinoderms. Thus, differences in resource utilization by *Ophiocoma* species may be difficult to relate to the intrageneric groups or to other

phylogenetic relationships.

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