Food Habits of the Gastropod *Mitra litterata* Lamarck: Relation to Trophic Structure of the Intertidal Marine Bench Community in Hawaii[1]

ALAN J. KOHN[2]

ABSTRACT: The stenoglossan gastropod *Mitra litterata* Lamarck, common on intertidal solution benches on Oahu, preys on sipunculids occurring in burrows in reef limestone. *Phascolosoma scolops* Selenka and DeMan is the main component of the diet. *Phascolosoma* sp. cf. *P. heronis* Edmonds and *Aspidosiphon elegans* Chamisso and Eysenhardt are also eaten. This is the first report of the nature of the food of a member of the family Mitridae. *Mitra litterata* belongs to a distinct trophic subweb from other co-occurring predatory gastropods of similar size and population density—*Morula granulata* (Duclos), which preys mainly on herbivorous gastropods, and *Conus* spp., which eat herbivorous polychaetes.

RELATIVELY SMALL to moderate-sized predatory gastropod molluscs of the genera *Conus, Morula,* and *Mitra,* all belonging to the prosobranch suborder Stenoglossa, are abundant and prominent carnivores in the biotic community of intertidal solution benches that comprise almost one-third of the shoreline of Oahu, Hawaii (Wentworth, 1939). Up to eight species of *Conus* (superfamily Toxoglossa), with mean shell lengths 20–35 mm, occur at densities of 0.2–0.6/m^2. Most are specialized predators on different species of Eunicidae and Nereidae, families of herbivorous polychaetes (Kohn, 1959).

In order to determine the position of the other predatory gastropods in the trophic structure of the community and to relate this to their taxonomic position, their feeding activities have been examined. *Morula granulata* (Duclos) (superfamily Muricacea) is smaller than the *Conus* spp. (mean shell length 14 mm) but more numerous (8/m^2), and it eats only other molluscs, mainly small browsing gastropods of the genera *Cerithium, Rissoina, Heliacus,* and *Bittium,* and the mussel *Hormomya* (Miller, 1968).

Mitra litterata (superfamily Volutacea) (mean shell length 17 mm) is the second most abundant predatory gastropod. Two small quantitative samples, at Kahuku and Kapoho Point, Oahu, contained 3 individuals in 65 m^2 (0.05/m^2) and 2 individuals in 9.3 m^2 (0.22/m^2), respectively. This note reports a study of the trophic position of *M. litterata* in the solution bench community. *M. litterata* probably preys exclusively on sipunculids, thus exploiting a resource not known to be utilized by any other co-occurring gastropods. Little is known of other predators of sipunculids: Fischer (1925) lists anemones (*Sagartia* and others), crabs (*Carcinus* and *Eupagurus*), and fishes (plaice and cod), but he gives no further information.

Virtually no information exists on the nature of food and feeding in the Mitridae, although members of the suborder Stenoglossa are generally assumed to be carnivores. Cernohorsky (1965) noted that *Vexillum* spp. are attracted by carrion, on which they feed. In a popular book, Abbott (1962) mentioned worms and clams as food of mitrids but gave no further information. Risbec (1955) proposed a toxoglossan feeding mechanism in the Mitridae, but this is incorrect. The mitrid radula is typically rachiglossan and is borne at the end of an extremely long pleurembolic proboscis, which may extend the length of the shell. In *Strigatella,* the subgenus to which *Mitra litterata* belongs, the radular teeth are laterally elongate. Cernohorsky (1966) described and figured the radula of *M. litterata.* The rachidian teeth of the speci-

[1] Contribution No. 356, Hawaii Institute of Marine Biology. Manuscript received February 25, 1970.

[2] Department of Zoology, University of Washington, Seattle, Washington 98105.

mens I examined had four, and the lateral teeth seven or eight conical denticles of nearly uniform height.

OBSERVATIONS

Feeding

The feeding process of *M. litterata* has been observed in the laboratory, specimens have been observed feeding in nature, and the food of others in nature has been identified from the examination of alimentary tracts of preserved specimens and of fecal material recovered from specimens kept alive in the laboratory after collection. In every case, the food has been a sipunculid worm of species that characteristically occur in burrows in calcareous rock. The papillae and hooks of sipunculids pass undigested through the gut of *Mitra,* facilitating identification of the prey. Species identifications were made primarily from the monograph of Selenka, DeMan, and Bülow (1883).

Observations on feeding in the laboratory were made at night, when *M. litterata* is normally active and when the introverts of burrowing sipunculids are extended. When placed on a piece of reef limestone containing one or more specimens of *Aspidosiphon elegans* Chamisso and Eysenhardt, *Mytra litterata* extends the siphon along the substrate, waving it from side to side. When the siphon contacts a sipunculid, the head is extended and also moved from side to side until one of the extended tentacles contacts the worm. Usually the proboscis extends only after both siphon and tentacle have touched the sipunculid. The padlike proboscis lip, bearing projecting, nonmotile, and evidently sensory cilia, then contacts the sipunculid and moves over its exposed body surface. The proboscis begins to engulf the sipunculid when the lips are affixed to the introvert, or to the anterior end of the trunk if the introvert is withdrawn. The rate of ingestion probably varies with the size of the sipunculid. In laboratory observations, *M. litterata* did not succeed in extracting *Aspidosiphon elegans* from its burrow; it required several minutes to ingest a small specimen of *A. elegans* removed from its burrow and placed in a dish. The distal end of the proboscis is not expansible and probably limits the diameter of prey that can be eaten.

In no case was the "accessory proboscis" visible during the feeding process. This muscular, vermiform structure, considered by Risbec (1955) to release a venom, originates in the proboscis behind the radula and was observed to extend and retract through the mouth during dissection of living specimens. Its function remains unknown.

The proboscis and radula appear to function exclusively as conveyors, capturing the sipunculid and moving it, intact and undamaged, into the mid-esophagus and stomach. In one instance, Mrs. S. Miller collected a *Mitra litterata* in the act of swallowing a *Phascolosoma scolops* Selenka and DeMan. The predator was dissected five hours later, revealing the prey in the stomach, markedly distending the stomach wall. The trunk of the sipunculid was mostly intact, the introvert mostly digested; all damage appeared to have been caused by chemical digestion. The sipunculid was removed from the stomach and remained alive until it was fixed two hours later.

Food in Nature

Results of examination of the alimentary tracts and feces of *Mitra litterata* are summarized in Table 1. Of the 24 specimens examined, each of 16 contained the remains of one sipunculid. All specimens were collected during the morning or late at night, and it is likely that they fed at night. Furthermore, attempts to induce feeding in the laboratory succeeded only at night. The

TABLE 1

GUT AND FECES CONTENTS OF 24 *Mitra litterata* INDIVIDUALS ON INTERTIDAL BENCHES AT KAHUKU, KAPOHO POINT, AND HAUULA, OAHU

FOOD ITEM FOUND	No. *M. litterata*
Sipunculids	
Phascolosoma scolops (Selenka and DeMan)	9
Phascolosoma sp. cf. *P. heronis* Edmonds	3
Aspidosiphon elegans (Chamisso and Eysenhardt)	4
Total sipunculids	**16**
Minute, unidentifiable, soft fecal material	3

rate of passage of food through the gut is not known, but, if the mean number of food items per gut is taken as the daily feeding rate, as seems reasonable from studies of *Conus* of similar size (Kohn, 1959), this rate is about 0.7 sipunculid per *Mitra litterata* per day.

The sipunculid fauna of Hawaii is incompletely known. Edmonds (in preparation) lists four species of *Phascolosoma,* but not *P. scolops,* the commonest prey of *Mitra litterata* on intertidal benches. Except for slight differences in the platelets of the trunk papillae, the specimens studied agree in all details with the original description of *Phascolosoma scolops.* However, the identification should be regarded as tentative because the taxonomy of this group of sipunculids is not settled. The genus *Aspidosiphon* has been reported from Hawaii by Edmondson (1946) and Edmonds (in preparation), but neither author identified the species. The commonest sipunculids in areas where *Mitra litterata* occurs are *Phascolosoma scolops* and *Aspidosiphon elegans,* found in burrows, probably of their own construction, in the reef limestone. The species listed as *Phascolosoma* sp. cf. *P. heronis* Edmonds (Table 1) differs from the original description of that species only in the pigmentation of the tentacles, the nephridium, and the spots on the trunk. A fourth sipunculid, *Phascolosoma pelma* Selenka and DeMan, previously reported from Hawaii by Edmondson (1946) and Edmonds (in preparation), was found in the same habitat but was not eaten by any of the *Mitra litterata* examined. *Phascolosoma* spp. share the same microhabitat as *Aspidosiphon* but may be found also in sand bound by algae and animals on the surface of the reef rock, and in crevices. Several species of sipunculids of these genera frequently co-occur in adjacent burrows in the same rock (Rice, 1969).

Four 100–625-cm^2 samples from the solution bench at Kahuku (Sta. 5 of Kohn, 1959) contained 6 to 26 sipunculids each and gave a mean density of $470/m^2$. *Phascolosoma scolops* was the most abundant species. A substrate sample of 270 cm^2 from the solution bench at Kapoho Point contained 20 sipunculids, of which 19 were *Aspidosiphon elegans,* suggesting a density of $740/m^2$. A crude estimate of the feeding rate of the *Mitra litterata* population, based on the minimal data presented above, is about 0.08 sipunculid eaten per square meter per day. *M. litterata* would thus consume about 5 percent of the standing crop of sipunculids per year, an estimated rate quite similar to the feeding rate of *Conus* on polychaetes at Kahuku (Kohn, 1959).

DISCUSSION

Mitra litterata preys on *Phascolosoma* and *Aspidosiphon* on intertidal solution benches, apparently extracting the sipunculids from their burrows with the long proboscis and radula and conveying the prey, intact and alive, to the capacious stomach. It thus exploits a food resource that is not utilized at all by *Morula granulata* and *Conus* spp., co-occurring predatory stenoglossan gastropods of roughly similar size and population density. The diets of the three genera, belonging to three different superfamilies, do not overlap, and the different species are the primary carnivores in distinct food subwebs.

Paine (1963) described in detail a subweb of predatory gastropods on an intertidal sand bar in Florida. On Hawaiian solution benches, however, there is no equivalent of the large fasciolariid gastropods found there, that prey generally on smaller carnivorous gastropods. This is probably because of the hard, rather smooth topography of solution benches and their exposure to desiccation at low tide and to violent wave action at high tide (Kohn, 1967). The habitat does not provide shelter suitable for large, motile invertebrates, and selection appears to favor small body size (Kohn, 1968). The harshness of the environment may thus effectively preclude a secondary carnivore level in the trophic structure of the benthic community.

ACKNOWLEDGMENTS

This study was supported by National Science Foundation grant GB-6134, and in part by GB-5942X. I thank participants in the Summer Training Program, Hawaii Institute of Marine Biology, for aid with the field work; Dr. Mary E. Rice for aid in identifying the sipunculids; Dr. Vera Fretter and Dr. R. T. Paine for discussion and criticism of the manuscript; and

Dr. L. G. Eldredge for providing the manuscript of the second edition of *Reef and Shore Fauna of Hawaii.*

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