# AN ANTIPREDATION MECHANISM OF THE POLYCHAETE *PHYLLODOCE MUCOSA* WITH NOTES ON SIMILAR MECHANISMS IN OTHER POTENTIAL PREY[1]

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ABSTRACT

The polychaete *Phyllodoce mucosa* exhibits an antipredation response via the extrusion of a repulsive mucoid secretion. The mucus, secreted by large glandular regions of the dorsal and ventral parapodial cirri, prevents immediate ingestion of the worm by several species of small or juvenile fish. A sipunculid, *Phascoleopsis gouldi*; a nemertean, *Lineus ruber*; and a large flatworm, *Stylochus zebra*, are also distasteful to some potential predators. Antipredation responses found in some organisms may play an important role in regulating benthic community dynamics by mediating the feeding habits of certain predators during at least some stage of their development.

Feeding habits of many species of fish have been well established, but few studies have extended analyses beyond stomach contents. Results of such research frequently lead to labeling food found in the stomach as "preferred" (Onyia 1973; Smith and Daiber 1977). Reports of selective feeding behavior based mainly on stomach contents reveal the major types of food eaten by a fish but do not add substantially to our understanding of the interactions between predator and prey.

Ivlev (1961), discussing selective feeding by fishes, included the role of "constitutional defenses" of potential prey species as a mechanism which may contribute to predatory selectivity. Selectivity in food thus entails not only "preference" but avoidance of specific potential food items (Berg 1979). Bakus (1966) considered the possible role of antipredatory responses by some tropical reef inhabitants. He noted that several members of a reef community that are not readily able to retreat into the security of a coral crevice or not naturally protected by skeletal armor are either poisonous, venomous, or distasteful to predators. Acidic secretions from epidermal glands of some opisthobranch gastropods (Graham 1957; Thompson 1960, 1969) and some nemerteans (Gibson 1972) function as predatory deterrents. In view of the fact that predation is a well established cause of quantitative changes in a population of prey species, the ability of some members of a community to thwart extensive predatory cropping by using inherent protective devices may also affect community structure.

An accurate picture of community dynamics demands a closer examination of direct interactions between potential prey and predatory species. A start in this direction has been made on a limited number of fish. Hynes (1950), Tugendhat (1960), and Beukema (1968) examined some of the behavioral feeding patterns of the threespine stickleback, *Gasterosteus aculeatus*. They found that selective feeding of the stickleback is influenced by degree of satiation and palatability of food. This may have implications extending into the natural environment with regard to seasonal, predatory, or man-induced changes in community structure. In food-limited situations "selectivity" may decrease. The presence of a predatory deterrent in an organism may thus be functionally operative only in a nonstressed community with nonstarved predators.

Polychaetes often dominate marine benthic communities (Sanders et al. 1965) and many bottom feeding fish eat substantial quantities of these worms (Qasim 1957; Nikolsky 1963; Kislalioglu and Gibson 1977). Obscurance of taxonomic characters due to digestion often prevents identification of prey to species, so food items tend to be listed in terms of higher taxonomic levels (Hynes 1950; Kneib and Stiven 1978). This is especially true for soft bodied prey organisms and means that accurate feeding records are often nonspecific and possibly biased relative to the researcher's taxonomic expertise.

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Phyllodocid polychaetes secrete copious amounts of mucus when irritated (Fauchald 1977). Pettibone (1963) briefly noted that the mucoid secretion of *Phyllodoce maculata* may be offensive to predators. Preliminary observations of *P. maculata* and *P. mucosa* (Prezant 1975, unpubl. data) have confirmed that an epithelial, mucoid secretion acts as an antipredatory mechanism against at least one species of fish, the rock gunnel, *Pholis gunnellus*.

The present study extends these observations by quantitative experiments on behavioral interactions of *Phyllodoce mucosa* with several species of small or juvenile fish, and examines the possible defensive mechanism of this polychaete. Initial observations concerning antipredatory mechanisms in the phyllodocids *Eumida sanguinea* and *P. maculata*, the large flatworm *Stylochus zebra*, the sipunculid *Phascoleopsis gouldi*, and the nemertean *Lineus ruber* are also reported.

## METHODS

*Phyllodoce mucosa* (Phyllodocidae) was collected in late August 1978 in Nahant Bay, Mass., by epibenthic sled from a fine sand substratum at a depth of about 17 m. *Eumida sanguinea* and the orbiniid *Scoloplos fragilis* were collected intertidally from Henlopen Flat, Lewes, Del., in early September 1978. *Scoloplos fragilis* was used as a control in the behavioral experiments because, despite its overall gross similarity to phyllodocids (i.e., long, thin worms of similar proportions), *S. fragilis* produces considerably less external mucus than *P. mucosa*. Worms were maintained in separate finger bowls on a running seawater table at 17° C and 32‰ salinity.

Fish used in behavioral experiments (Table 1) were collected in July 1978 and allowed to acclimatize for 30-60 days in separate compartments on the seawater table. During acclimatization, the fish were fed a variety of foods from a widemouthed glass pipette. Foods included bits of fresh blue mussel, *Mytilus edulis*; and American oyster, *Crassostrea virginica*; live tubificid oligochaetes, *Tubifex* spp.; brine shrimp, *Artemia marina*; and, infrequently, frozen brine shrimp.

*Phyllodoce mucosa*, typically found on fine sand substrata from low water to depths over 500 m, ranges from Labrador to Mexico (Pettibone 1963) thus geographically overlapping with all fish species used in this study (Table 1).

Since this research dealt principally with the inability of certain predators to eat *P. mucosa*, it was important to insure that the fish used would actively feed throughout the experimental period. Accordingly, several other species of polychaetes

TABLE 1.—The range, habitat, food habits, and collection sites of the species of fish used in the feeding experiments. The last column lists the test organisms offered to fish. Quantitative results are available only for *Phyllodoce mucosa*. Range, habitat, and feeding habit data for the fish are from Hildebrand and Schroeder (1928), Bigelow and Schroeder (1953), Chao and Musick (1977), and Kneib and Stiven (1978).

| Fish species | Range and habitat | Feeding habits | Fish collection site | Test organism |
|---|---|---|---|---|
| Atlantic silverside, *Menidia menidia* | Nova Scotia to northern Florida; often over sandy or gravelly shores | Small crustaceans and molluscs, annelids, small fish, eggs, and plant material | Lewes Beach, Lewes, Del. | *Phyllodoce mucosa*<br>*Scoloplos fragilis* |
| Weakfish, *Cynoscion regalis* | Nova Scotia to Florida; shallow coastal waters in summer | Fish, crabs, amphipods, mysids, shrimp, molluscs, annelids | Lewes Beach | *P. mucosa*<br>*Phascoleopsis gouldi*<br>*S. fragilis* |
| Windowpane flounder, *Lophopsetta maculata* | Gulf of St. Lawrence to South Carolina; sand bottoms from low water to 50 m | Mobile prey such as mysids, fish, shrimp, errant polychaetes | Lewes Beach and near Delaware Bay mouth at 18 m | *Phyllodoce mucosa*<br>*Eumida sanguinea*<br>*S. fragilis* |
| Sheepshead minnow, *Cyprinodon variegatus* | Cape Cod to Mexico; shallow waters of inlets and bays; salt marshes | Mobile epifauna including annelids | Lewes Beach | *P. mucosa*<br>*S. fragilis* |
| Mummichog, *Fundulus heteroclitus* | Labrador to Mexico; shallow coastal waters especially salt marshes | Omnivorous (at least when >30 mm) including small crustaceans, annelids, and carrion | Canary Creek, Lewes, Del. | *P. mucosa*<br>*Phascoleopsis gouldi*<br>*S. fragilis* |
| Threespine stickleback, *Gasterosteus aculeatus* | Labrador to Virginia; salt and fresh waters | Small invertebrates, fish fry, eggs | East Point, Nahant, Mass., tide pool | *Phyllodoce mucosa*<br>*S. fragilis* |
| Striped sea robin, *Prionotus evolans* | Gulf of Maine to South Carolina; coastal bottom dweller | Crustaceans, molluscs, annelids, small fish | Near Delaware Bay mouth at 18 m | *Stylochus zebra*<br>*Phascoleopsis gouldi*<br>*Lineus ruber* |
| Rock gunnel, *Pholis gunnelus* | Hudson Strait to Delaware; generally on rocky bottoms from low water to over 200 m | Molluscs, crustaceans, annelids | East Point, Nahant tide pool | *Phyllodoce mucosa*<br>*P. maculata*<br>*Nephtys incisa* |

were fed to the fish before and following behavioral experiments. These worms, which were from various size classes, included: *Spio filicornis* (Spionidae) and *Nephtys incisa* (Nephtyidae) collected from Nahant Bay; and *Glycera americana* (Glyceridae), *Nereis virens* (Nereidae), *Scolecolepides viridis* (Orbiniidae), and *Hydroides dianthus* (Serpulidae) collected from Henlopen Flats.

The feeding behavior of each species of fish, excluding *Prionotus evolans* and *Pholis gunnellus*, was tested quantitatively with *Phyllodoce mucosa* and *Scoloplos fragilis*. Fish were starved for 24-48 h prior to testing. An individual fish was then placed in a separate 4 l glass aquarium or in a small compartment on the seawater table and allowed to acclimate for 60 min prior to experimentation. Each test session was composed of two sets of observations separated by a 5-min interval. A set consisted of five 1-min trials each separated by a 2-min interval. The trials entailed repeated exposure of randomly chosen worms to potential predation by each fish by dropping the worm from a widemouthed glass pipette in close proximity to the head of the fish. Since the fish were previously fed from a pipette, they showed no hesitation in accepting potential food items delivered in this manner. Following release from the pipette, several possible combinations of behavioral responses of the fish were noted: 1) ingestion of the worm, 2) rejection of the worm following an active attempt at ingestion, 3) presence or absence of investigations of the worm by the fish (investigation is defined here as an obvious "enticement" of the fish to the worm without an attempt at ingestion), and 4) avoidance of the fish to the worm. The behavior of *P. mucosa* was also noted following release from the pipette and after rejection or avoidance by the fish.

If the worm sank to the floor of the aquarium, either after rejection or without any contact with the fish, it was taken off the bottom and again dropped in front of the fish. This process was repeated as often as a 1-min trial would allow. Discounting delays due to behavioral interactions, this averaged one exposure every 6 s. Prior to the start of the first set of each test session and 1 min after each trial ended, the fish was fed a small portion of frozen brine shrimp to ensure active feeding. If at any time during a test the fish refused to eat the brine shrimp, the experiment was terminated. Because of terminations, the number of sessions per species of fish varied. Initial qualitative tests subjecting various other test organisms found on Henlopen Flats to potential predation are also noted on Table 1.

To test whether the mucoid secretion truly acts as the predatory inhibitor in *P. mucosa*, two further tests were carried out. First, mucus was removed from the surface of *P. mucosa* by repeatedly sucking the worm in and out of a narrow-mouthed glass pipette and then gently dabbing it with a clean, lintless cloth. The worm was then fed to a rock gunnel. Second, mucus from *P. mucosa* was collected by placing several of the worms in a small, dry stendor dish, allowing the worms to physically irritate each other and thus produce a copious supply of mucus. After the phyllodocids were removed from the dish, a small *Nephtys incisa*, which secretes very little external mucus, was placed in it and allowed to accumulate a thick mucoid coat. The nephtyd was then fed to the rock gunnel.

For histological study of the mucus-producing organs of *P. mucosa*, entire worms were fixed in Zenker's or Hollande's fixatives and embedded in polyester wax. Blocks were cut at 5 $\mu$m and sections stained with Mallory's "Azan" or toluidine blue in 1.0% borax.

To examine the ultrastructure of the parapodial cirri of *P. mucosa*, small worms were fixed for 1 h in cold Anderson's fixative, cut into 2 mm sections with a razor blade, thoroughly rinsed with phosphate buffer (pH 7.2), and postfixed for 1 h in 2.0% osmium tetroxide in a phosphate buffer. Following dehydration in a graded acetone series, the specimens were embedded in Spurr's low viscosity medium and polymerized at 60° C for 48 h. Thin sections, cut on a Porter-Blum[3] MT1 ultramicrotome using glass knives, were stained with uranyl acetate and Sato lead citrate. Sections were examined with a Philips EM201 transmission electron microscope at an accelerating voltage of 80 kV.

## RESULTS

### Response of Fish

Results of the feeding experiments for the various species of fish being fed *P. mucosa* along with the length of each are summarized in Tables 2 and

[3]Reference to trade names does not imply endorsement by the University of Delaware, College of Marine Studies or by the National Marine Fisheries Service, NOAA.

TABLE 2.—Number of attempts to ingest *Phyllodoce mucosa* by several species of fish. An attempt is defined as a single intake and expulsion of the worm. The number following the abbreviated fish binomial stands for an individual fish and the small letter that follows stands for an individual worm. The two numbers in parenthesis in the first column are the standard lengths of the fish and maximum length of the worm, in millimeters, respectively. Fh = *Fundulus heteroclitus*, Ga = *Gasterosteus aculeatus*, Mm = *Menidia menidia*, Cv = *Cyprinodon variegatus*, Lm = *Lophopsetta maculata*, Cr = Cynoscion regalis, † =experiment terminated, * = worm eaten.

| | Set A, trial | | | | | Set B, trial | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Session | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | Total |
| Fh1a (63,22) | 3 | 5* | | | | | | | | | 8 |
| Fh1b (63,29) | 9 | 4* | | | | | | | | | 13 |
| Fh2c (66,18) | 4 | 2* | | | | | | | | | 6 |
| Fh3d (52,19) | 13* | | | | | | | | | | 13 |
| Fh4e (61,19) | 10* | | | | | | | | | | 10 |
| Ga1a (18,9) | 4 | 7 | 3 | 1 | 0 | 6 | 5 | 0 | 0 | 0 | 26 |
| Ga2a (18,15) | 21 | 4 | 0 | 2 | 1 | 20 | 5* | | | | 53 |
| Ga2b (18,12) | 2 | 4 | 0 | 2 | 1 | 20 | 5* | | | | 34 |
| Ga3c (18,13) | 29 | 5* | | | | | | | | | 34 |
| Ga3d (18,24) | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| Ga4e (18,12) | 14 | 5 | 0 | 0 | 0† | | | | | | 19 |
| Ga5e (18,12) | 8 | 0 | 0 | 0 | 0† | | | | | | 8 |
| Mm1a (44,24) | 5 | 2 | 1 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 12 |
| Mm2b (37,22) | 4 | 3 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 11 |
| Mm3c (51,17) | 10 | 4 | 4 | 0 | 0† | | | | | | 18 |
| Mm4d (54,14) | 3 | 2 | 2* | | | | | | | | 7 |
| Mm5e (64,18) | 1* | | | | | | | | | | 1 |
| Mm5f (64,23) | 2* | | | | | | | | | | 2 |
| Mm6g (67,13) | 4* | | | | | | | | | | 4 |
| Cv1a (46,24) | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 2 | 15 |
| Cv1b (46,24) | 1 | 1 | 1 | 1 | 2 | 2 | 3 | 4 | 1 | 0 | 16 |
| Cv2c (46,14) | 3 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 8 |
| Cv2d (46,12) | 2 | 3 | 3 | 1 | 2 | 2 | 3 | 3 | 3 | 2 | 24 |
| Lm1a (69,29) | 3 | 1 | 1 | 2 | 1 | 2 | 0 | 0 | 1 | 0 | 11 |
| Lm1b (69,21) | 6 | 4 | 3 | 1 | 3 | 5 | 5 | 3 | 0 | 1 | 31 |
| Lm2a (91,29) | 2 | 1 | 2 | 2 | 2 | 2 | 0 | 0 | 1 | 1 | 13 |
| Lm2c (91,17) | 2 | 5 | 5 | 1 | 3 | 3 | 3 | 0 | 0 | 0 | 22 |
| Lm2d (91,21) | 7 | 3 | 3 | 4 | 3 | 3 | 3 | 0 | 0 | 1 | 27 |
| Cr1a (42,24) | 1 | 2 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 6 |
| Cr1b (42,16) | 2 | 2 | 4 | 2 | 2 | 2 | 2 | 3 | 2 | 2 | 23 |
| Cr1c (42,26) | 0† | | | | | | | | | | 0 |
| Cr2d (46,14) | 2 | 6 | 1 | 6 | 5 | 4 | 5 | 6 | 4 | 5 | 44 |
| Cr2e (46,22) | 0† | | | | | | | | | | 0 |
| Cr2f (46,17) | 2 | 4 | 5 | 5 | 3 | 4 | 5 | 3 | 5 | 4 | 40 |

TABLE 3.—Number of investigations undertaken by four species of fish when exposed to *Phyllodoce mucosa*. This table excludes *Fundulus heteroclitus* and *Cyprinodon variegatus* because these species showed no or insignificant investigatory behavior without attempts at ingestion. Abbreviations and notations as in Table 2.

| | Set A, trial | | | | | Set B, trial | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Session | 1 | 2 | 3 | 4 | 5 | 1 | 2 | 3 | 4 | 5 | Total |
| Ga1a (18,9) | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 4 | 3 | 3 | 14 |
| Ga2a (18,15) | 0 | 0 | 0 | 0 | 2 | 0 | * | | | | 2 |
| Ga2b (18,12) | 0 | 0 | 0 | 0 | 3 | 2 | * | | | | 5 |
| Ga3c (18,13) | 0 | * | | | | | | | | | 0 |
| Ga3d (18,24) | 3 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 9 |
| Ga4e (18,12) | 0 | 0 | 5 | 1 | † | | | | | | 6 |
| Ga5e (18,12) | 0 | 2 | 2 | 1 | † | | | | | | 5 |
| Mm1a (44,24) | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 1 | 0 | 1 | 6 |
| Mm2b (37,22) | 4 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| Mm3c (51,14) | 0 | 1 | 3 | 1 | † | | | | | | 5 |
| Mm4d (54,14) | 0 | 0 | * | | | | | | | | 0 |
| Mm5e (64,18) | * | | | | | | | | | | 0 |
| Mm5f (64,23) | * | | | | | | | | | | 0 |
| Mm6g (67,13) | * | | | | | | | | | | 0 |
| Lm1a (69,29) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| Lm1b (69,21) | 0 | 2 | 0 | 3 | 3 | 2 | 2 | 1 | 2 | 3 | 18 |
| Lm2a (91,29) | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 3 |
| Lm2c (91,17) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lm2d (91,21) | 0 | 0 | 0 | 3 | 2 | 1 | 2 | 2 | 0 | 2 | 12 |
| Cr1a (42,24) | 3 | 0 | 1 | 6 | 2 | 3 | 4 | 0 | 3 | 1 | 23 |
| Cr1b (42,16) | 2 | 1 | 1 | 3 | 1 | 3 | 2 | 4 | 2 | 4 | 23 |
| Cr1c (42,26) | † | | | | | | | | | | 0 |
| Cr2d (46,14) | 2 | 0 | 3 | 2 | 3 | 2 | 3 | 1 | 4 | 3 | 23 |
| Cr2e (46,22) | † | | | | | | | | | | 0 |
| Cr2f (46,17) | 1 | 2 | 2 | 2 | 2 | 1 | 1 | 3 | 1 | 4 | 19 |

TABLE 4.—Number of attempts to ingest the control polychaete *Scoloplos fragilis* and size of fish and worm used. Abbreviations and notations as in Table 2.

| | Trial | | | Trial | |
|---|---|---|---|---|---|
| Session | 1 | 2 | Session | 1 | 2 |
| Fh1x (48,15) | 1 | | Lm1w (69,16) | 4 | |
| Fh1y (48,20) | 1 | | Lm1x( 69,25) | 1 | |
| Ga1x (18,11) | 1 | | Lm2y (91,17) | 12 | 9 |
| Ga2y (18, 9) | 1 | | Lm2z (91,23) | 11† | |
| Mm1x (37,14) | 1 | | Cr1x (42,14) | 1 | |
| Mm2y (64,13) | 1 | | Cr1y (42,17) | 5 | |
| Cv1x (46,13) | 1 | | | | |
| Cv2y (46,26) | 1 | | | | |

3. The large number of ingestive attempts in a given trial (Table 2) resulted from the rapid, repetitive actions of a fish not allowing the worm to settle to the floor of the aquarium following initial attempts. Results of the control series using *S. fragilis* and sizes of fish and worms are given in Table 4.

Of the six species of fish quantitatively tested, only the mummichog, *Fundulus heteroclitus*, consistently ingested *P. mucosa* early in set A (Table 2). This species of fish showed no investigative behavior before taking the worm into its mouth. Nevertheless, *F. heteroclitus* did show some distaste for this polychaete; in two cases the mummichog sucked the worm in and out 13 times prior to ingestion. When *F. heteroclitus* did eat the worm, ingestion was immediately followed by a variable period (10-45 s) of choking or "coughing" (rapid protraction and retraction of jaws and intake and expulsion of water). In session Fh1a, the worm was held in the mouth and only partially ejected many times prior to ingestion. During trial 2 of set A in session Fh1b, the fish, on the fourth attempt, took in the worm and exhibited a choking response which lasted 15 s before spitting out the posterior portion of the worm. The remaining portion of the polychaete was eaten after two further attempts. The maximal number of attempts prior to ingestion by *F. heteroclitus* was demonstrated by the smallest mummichog (Fh3d) and in trials involving the largest phyllodocid (Fh1b) (Table 2). *Scoloplos fragilis* was consumed on the first attempt by *F. heteroclitus* in each control test (Table 4).

While only one size class of *Gasterosteus aculeatus* was used, there was no trend between size of the worm and ingestion by the fish (Table 2). The largest as well as some of the smaller worms were not consumed. Sessions Ga1a, 2b, and 3a all resulted in ultimate ingestion of *P. mucosa* but involved 34-53 prior ingestive attempts. Of the seven sessions observed with *G. aculeatus*, these three sessions showed the highest number of attempted ingestions prior to consumption. In session Ga2a, there was a renewed expression of the antipredation mechanism at the start of set B (Table 2). Thus, sets A and B start with 21 and 20 attempts, respectively, followed by a decrease in the number of attempts in set A and consumption in trial 2 of set B.

In most of the sessions between *G. aculeatus* and *P. mucosa*, lack of ingestive attempts seemed to correspond with the presence of investigative responses (Tables 2, 3). These investigations involved a close approach to the worm as it sank through the water column, and in some cases a recoil from the worm without evidence of direct contact. In cases where the worm was consumed, the fish exhibited a coughing response which lasted several seconds. *Gasterosteus aculeatus* readily consumed *S. fragilis* (Table 4).

A correlation between the size of the Atlantic silverside, *Menidia menidia*, and its ability to consume *P. mucosa* is suggested (Table 2). Smaller fish showed little interest in the worms following initial experiences in set A, while the larger fish often consumed the worm very early in the first set. During set A, fish <50 mm initiated several attacks on the phyllodocids, and the worm was easily taken into the buccal cavity before rejection. A rejected worm was often so densely covered with mucus that it would cling to the lower lip of the fish by a mucus thread for several seconds. *Menidia menidia* also exhibited coughing reactions following attempted and successful ingestions. Larger silversides were quick to respond to potential food items released into the aquarium and swiftly sucked them in. In set Mm5f, a 64 mm fish was fed a 23 mm worm. On the first attempt at ingestion by the fish, the worm was quickly taken, whereupon the fish reacted with a coughing response lasting 45 s. The fish also exhibited a violent lateral head shaking during this time. Following this, the worm was totally ejected but the fish continued reacting as described for several seconds. This was the only case where an entire worm was injured prior to ejection. The worm, though alive, lost several parapodia and cirri and appeared sluggish. This same worm was again placed in the aquarium with the fish and was again set upon, producing a coughing response lasting 30 s but was not rejected. This fish did postfeed on *A. marina* and *M. menidia* showed no hesitation in consuming *S. fragilis*.

Only a single size class of sheepshead minnow, *Cyprinodon variegatus*, was available. This species was exposed to *P. mucosa* ranging in size from 12 to 24 mm and showed a consistent rejection of each size class (Table 2). In no case was a coughing reaction noted. *Cyprinodon variegatus* appeared able to distinguish between *P. mucosa* and *A. marina* from short distances (up to 15 cm). The fish showed almost no investigatory behavior after initial ingestive attempts in a given trial but did quickly swim over to feed on *A. marina* in every case of exposure. *Scoloplos fragilis* was eaten on the first attempt in each control test with *C. variegatus* (Table 4).

The windowpane flounder, *Lophopsetta maculata*, was the largest fish used in this study. This species rejected the phyllodocids without fail, showing 11-31 attempts at ingestion (Table 2) and also exhibited coughing responses following ingestive attempts. The two sessions with *L. maculata*, making the greatest number of attempts to ingest (Lm1b and 2d) (Table 2), also registered the greatest degree of inquisitiveness (Table 3). There was no relation between size of fish and size of worm in these interactions. As Table 4 shows, there was some hesitation by the larger *L. maculata* in the control series when offered *S. fragilis*. In all of these control tests but one (Lm2z was terminated), the fish eventually ate the worm, but in Lm2y the fish made 21 attempts and ran into the second trial of set A prior to ingestion. Less than 1 h later, this same fish actively and quickly fed on 12 mm *Scolecolepides viridis* and 31 mm *Nereis virens*.

Juvenile weakfish, *Cynoscion regalis*, also refused to eat *P. mucosa* (Table 2). There may be a relationship between the number of attempts to ingest and the size of the worm in these cases (Table 2). In Cr1c and 2e, the worms used were among the three largest (26 and 22 mm, respectively), and in both cases the fish showed a violent headshaking response to void its buccal chamber. It thereafter became "nervous" and would not feed on *A. marina*. In Cr1a a 24 mm worm was used, and in the entire session only six attempts at ingestion were made. All the remaining *P. mucosa*

tested with *C. regalis* were <20 mm long, and ingestive attempts ranged from 23 to 44/session. *Cynoscion regalis* exhibited frequent investigative responses (Table 3) which, unlike those of most of the other fish, usually involved direct contact with the worm by bumping it with its snout. In some cases following this contact, the fish would show a headshaking reaction similar to that produced by attempted ingestion. *Cynoscion regalis* consumed *Scoloplos fragilis* during the first trials of the control series (Table 4).

During the course of these experiments, individuals of each species of fish were given the opportunity to feed on several other species of polychaetes. These included *Spio filicornis, Nephtys incisa, Nereis virens, Glycera americana, Scolecolepides viridis,* and *Hydroides dianthus.* Each fish readily consumed each of these species from several size classes, in almost every case on the first attempt.

Preliminary data has also been collected on *Eumida sanguinea* tested with *L. maculata.* Test worms ranged from 9 to 13 mm long and were consistently rejected. A 69 mm *L. maculata* rejected a 13 mm long *E. sanguinea* 20 times over a single session, while a 91 mm flounder rejected a 12 mm long worm 38 times in a session. Investigations ranged from 6 to 10/session and showed no obvious relationship with ingestive attempts. In qualitative observations, it was also noted that the rock gunnel rejected both *P. mucosa* and *P. maculata.*

Removal of the mucus coat from *P. mucosa* resulted in quick consumption by *Pholis gunnellus.* Emplacement of the phyllodocid mucus on a small *Nephyts incisa*, which were previously a quick meal for *P. gunnellus*, resulted in rejection of the nephtyd polychaete by the rock gunnel many times prior to ingestion.

Initial observations were also made on the sea robin, *Prionotus evolans*, fed *Stylochus zebra, Lineus ruber,* and *Phascoleopsis gouldi. Fundulus heteroclitus* and *C. regalis* were also tested with *P. gouldi.* In each case the fish showed adverse reactions (coughing, headshaking, and rejection) after ingestive attempts. The sea robin rejected *S. zebra* 75 times over eight trials before consuming the flatworm. In many cases, the turbellarian was held in the buccal chamber for as long as 21 s before ejection. Both the nemertean and the flatworm produced copius quantities of mucus when irritated, whereas the sipunculid did not.

## Behavior of *Phyllodoce mucosa*

*Phyllodoce mucosa* showed relatively consistent reactions upon release into the aquarium and following rejection. When first released, the worm fell slowly through the water in a semicurl position, or curled in a tight ball and fell at a slightly faster rate. After a worm was taken and rejected by a fish, it was covered with a thick layer of viscous mucus. Immediately after rejection, the worm coiled into the tight, spheroid position. In this position, it was either retaken by the fish and the process repeated until the worm was eaten, or the worm was dropped, after initial attempts, to the floor of the tank. If the worm drifted unharmed to the floor of the aquarium, it usually started what appeared to be an exploratory phase which consisted of several short excursions in various directions before setting out on a single, straight path toward one of the corners of the aquarium. During this exploratory period, the worm held its dorsal parapodial cirri folded against its dorsum.

## Histology and Ultrastructure of *Phyllodoce mucosa* Parapodial Cirri

The glandular and sensitive dorsal and ventral parapodial cirri of *P. mucosa* are the primary sources of externally released mucoid secretion.

The dorsal cirrus possesses a large nerve which runs along the cirral axis and then radiates centrally into several smaller nerves which wind between the large cirral mucocytes (Figure 1). Numerous free neural extensions penetrate the cirral epithelium. Large, ovoid mucocytes, which stain beta-metachromatically with toluidine blue (Figure 1, lower), fill most of the cirrus. These broad and elongated cells have small basal nuclei. In worms that have been irritated prior to fixation, the previously metachromatic mucocytes appear as large, empty vacuoles surrounded by many immature mucus cells (Figure 1, upper). The latter are usually small, irregularly shaped cells which are densely packed with basophilic but orthochromatic secretory granules. The outer, central portion of the dorsal cirrus has a narrow bank of melanic pigment cells. There are also thin muscle bands which enter the cirrus along the dorsal region of the cirral peduncle.

Electron microscopy reveals a dense microvillar and ciliary border lining the short, columnar epithelium of the dorsal cirrus (Figure 2). The epithelial cells have large, irregular nuclei with

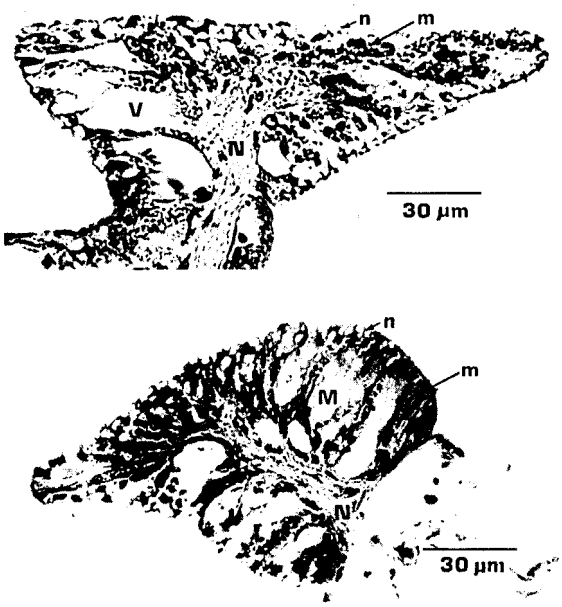


FIGURE 1.—Upper: An oblique-frontal section of the dorsal parapoidial cirrus of the polychaete *Phyllodoce mucosa*. This specimen was irritated prior to fixation resulting in the loss of the mucoid secretion produced by mature cirral mucocytes. The vacuolated regions mark the remnants of the mature mucocytes. The large cirral nerve is also evident. Zenker's fixative, "Azan" stain. m = immature mucocyte; n = neural extension; N = cirral nerve; V = vacuolated mucocyte. Lower: The dorsal parapodial cirrus of a relaxed specimen of *P. mucosa* in transverse section, fixed without excessive mucus loss. The cirral mucocytes show a beta-metachromatic reaction with toluidine blue. Hollande's fixative, toluidine blue stain. M = metachromatic mucocyte.

abundant heterochromatin material. Many immature secretory inclusions are present near the epithelial surface as well as subepithelially. The immature secretory droplets occur in a loose formation and are surrounded by a dense array of smooth endoplasmic reticulum. The larger, less electron dense, mature secretory droplets occur in tighter, membrane bound accumulations. Figure 2 shows a portion of a vacuolated mucous cell bounding a central nucleus. Both the mature and vacuolated secretory cells have numerous, small mitochondria associated with them.

The smaller, ventral cirrus is histologically and cytologically similar to the dorsal cirrus, and is equipped with oblong mucocytes in both mature and immature stages. Also present is a large cirral nerve and thin longitudinal muscle bands. Melanic pigmentation is not obvious in sections of the ventral cirri.

## DISCUSSION AND CONCLUSIONS

Many factors influence successful predation. Griffiths (1975) believed that prey abundance and prey size are two of the prime variables affecting predation success but that situations do occur in which predators react to prey characteristics other than body size. These characteristics include physical avoidance by potential prey (Fagade and Olaniyan 1973) which may be chemically mediated by a secretion released by the predator (Mackie et al. 1968; Doering 1976; Mayo and Mackie 1976), physical deterrents of the potential prey species such as spines (Hoogland et al. 1956; Bakus 1966), or innate defense mechanisms of the potential prey such as toxicity or unpalatability (Thompson 1960; Bakus 1966, 1968; Gibson 1972; Rahemtulla and Løvtrup 1974). An epidermal, mucoid secretion is responsible for the protection of at least some phyllodocid polychaetes from active predation by some small or juvenile fish. Since phyllodocids are relatively small benthic worms, it is unlikely that many large fish would expend the energy needed to use them as a primary food source; thus only smaller fish would potentially make any notable impact on the phyllodocid populations.

Russell (1966) tested the palatability of tissues from 48 species of marine organisms with two marine (*Pelatus quadrilineatus* and *Torquigener hamiltoni*) and two freshwater (*Gambusia affinis* and *Carassius auratus*) species of fish ranging from 25 to 90 mm. This involved choice experiments with the fish simultaneously offered a known palatable organism and a test organism of unknown palatability. The results revealed many unpalatable species which were rejected by the fish. The majority of these tests involved only three or fewer trials and there is little note concerning specific reaction of fish to potential prey items. Among the palatable items found by Russell was *Phyllodoce malgremi*. Phyllodocids, as all other test organisms, were cut to acceptable sizes based on preliminary trials which noted size limits of prey for each fish. *Phyllodoce malgremi* might indeed be consumed by these particular fish but the limited number of trials (two per fish) and lack of corresponding worm size data plus the previous treatment of the worms (i.e., sectioned into fragments) may have led to misleading data concerning palatability.

Few reports list phyllodocids as a major portion of a fish's diet; however, Wigley (1956) did list four

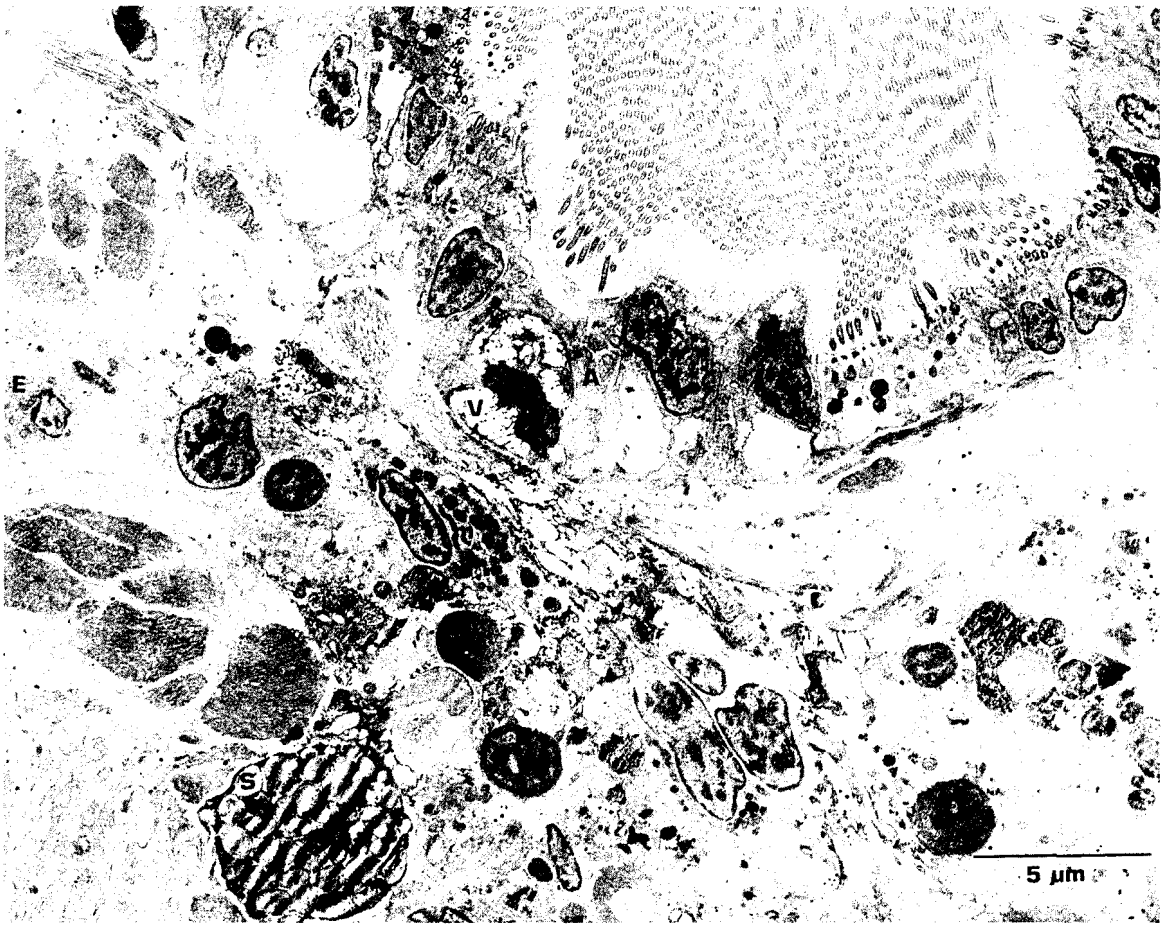


FIGURE 2.—The ultrastructure of the dorsal parapodial cirrus of the polychaete *Phyllodoce mucosa*. The micrograph shows the dense array of cilia and microvilli which line the cirral epithelium as well as mature and immature secretory droplets and associated organelles. Anderson's and osmium tetroxide fixation, uranyl acetate, and Sato lead stain. S = mature secretory droplets; A = mitochondria; E = smooth endoplasmic reticulum. Other abbreviations as in Figure 1.

species of phyllodocids in the food of the haddock, *Melanogrammus aeglefinis*. No phyllodocids were among the 11 dominant prey species of the larger fish examined. Wigley noted, however, that because of the small, subterminal mouth, most of the haddocks' prey were small and thin. Small invertebrates, including phyllodocids, were listed as dominant foods of the few smaller (14-30 cm) haddock examined. Annelids composed only 1.9% of the prey items found in the haddock study and no note was made of the diet of fish <14 cm. Data for small juveniles is found in only a few studies involving bulk analysis of fish stomach contents (Stickney et al. 1975; Chao and Musick 1977).

In nature, initial rejection and adverse reaction of a fish to *P. mucosa* may give the potential prey sufficient time to retreat from harm. Chiszar and Windell (1973) found that satiated bluegill, *Lepomis macrochirus*, have more selective feeding habits than starved fish. This may imply that in natural conditions a normally feeding fish may not persist in an attack on an unpalatable prey organism.

Murdoch et al. (1975) suggested that predators distribute attacks among prey species in response to the prey's relative densities. These authors broke down events leading to final ingestion of prey into a series of predatory behaviors, including "choosing" to attack the prey species. Once a potential prey is perceived and located, the "choice" is up to the predator whether to attack or not. If the organism is attacked and successfully

consumed, the predator may set up a "specific searching image" (Tinbergen 1960), which would increase its chance of locating additional specimens provided more of the same prey species can be found while reinforcement is still fresh. Thus, this pattern is only relevant when prey species occur in relatively high densities. *Phyllodoce mucosa* is found in moderately high densities in Nahant Bay with many other polychaetes such as *Prionospio malmgreni, Scoloplos armiger,* and *Nephtys* spp. If a small fish encounters and attempts to eat a *Phyllodoce mucosa* but is repulsed by the worm's defenses several times, the fish may eventually set up a negative searching image and thus avoid further "discomfort" caused by attempted ingestion. While simultaneous choices of food may be a rare event in nature (Beukema 1968), when it does occur between a phyllodocid and another type of prey of similar size, a fish with a negative image may "select" the nonphyllodocid prey. This is indicated in the present data by the relationship between ingestive attempts and investigations of *Gasterosteus aculeatus* and the "loss of interest" shown by the smaller *Menidia menidia.*

Kneib and Stiven (1978) recently found that the diet of *F. heteroclitus* in a North Carolina salt marsh varied with the size of the fish (smaller fish were carnivorous while larger individuals were omnivorous). In this case, alteration in diet seemed to reflect a physiological and morphological change in the fish with growth. This conversion of food habits may be based upon the ability of the fish to eat different food items because of its proportionally larger size or it might indicate a change in the "ability" of the fish to consume less appealing food items if the "need" arises. Data presented here indicate that larger *M. menidia* might be more effective in consuming phyllodocids than smaller *M. menidia.* Smaller fish may not be able to "handle" a phyllodocid of a size that a larger fish might readily consume. This is based solely upon the reaction of the fish to the mucoid secretion since smaller fish were able to consume comparatively large nonphyllodocid polychaetes.

The largest fish used in the present study, a juvenile *Lophopsetta maculata*, about 9 cm long, consistently rejected *P. mucosa. Lophopsetta maculata* is an active predator of mobile prey (Table 1). The large buccal chamber and distensibility of the esophagus of this flounder preclude the possibility that the phyllodocid mucus acts as a physical barrier to ingestion (i.e., an occlusive plug) but instead indicate that the mucus contains some irritating or obnoxious substance which repels the fish.

The high sensitivity and secretory nature of the parapodial cirri is reflected in the complex ultrastructure shown in Figure 2, however, *P. mucosa* does not seem able to continually produce an adequate supply of protective mucus. This is indicated by ingestion of the worm by *G. aculeatus* following numerous rejections from this fish's small, sharply toothed buccal cavity which may have removed the protective cover. Similar results are obtainable with a smallmouthed pipette, which simulates this. The large, empty vacuoles in the dorsal cirri surrounded by immature mucocytes indicate a lag between total loss of available secretion and maturation of additional, functional mucocytes.

Beukema (1968) suggested that *G. aculeatus* hunts by sight only and its sense of smell plays little if any role in finding food. This is supported in the data presented here by the correlation between investigations and ingestive attempts. Investigations involved no direct contact but only close observation of the worm by the fish.

Ejectory behavior by *G. aculeatus* feeding on clumps of *Tubifex* spp. oligochaetes was discussed by Tugendhat (1960) who found that this action caused a breakdown of the clumps into individual worms which were easily ingested. Hynes (1950) noted that young *G. aculeatus* feed on proportionally smaller prey items and that the diet changed to larger prey as the fish grew. The largest phyllodocid fed to a *G. aculeatus* in the present study was 24 mm long, and it was investigated but only one attempt at ingestion was made. In this case, the worm probably was too large for the fish to deal with.

The only species of fish tested which consistently ate *P. mucosa* was *F. heteroclitus. Fundulus heteroclitus*, a well-known inhabitant of salt marshes, is only rarely found in strictly saline environments (Hildebrand and Schroeder 1928). Vince et al. (1976) showed that *F. heteroclitus* may cause an impact on the abundance and distribution of some prey species, and Fraser (1973) found that *Fundulus* spp. would consume prey items in proportion to prey densities. Since *P. mucosa* is not a normal resident of salt marshes the question must be asked: does the fact that these two organisms occur in different environments influence the predator-prey interactions between these species when brought together? According to Tin-

bergen (1960), there may be an obvious delay in the attack on a potential prey if it is new to the predator. No such delay was seen in these experiments using semistarved fish. It is unlikely that *P. mucosa* has developed a defense mechanism which is specific in its action only to marine fish. The ability of *F. heteroclitus* to consistently consume *P. mucosa* probably reflects the predaceous mummichog's lack of sensitivity or its ability to overcome the irritation or unpalatability of this worm.

*Cyprinodon variegatus* always rejected the phyllodocids and rarely investigated the worm without attempted ingestion. The small, terminal mouth of this fish, with its large tricuspid teeth and protractile premaxillaries, was quite efficient at quickly devouring all nonphyllodocid polychaetes offered to the fish during these experiments.

*Cynoscion regalis* is primarily an active pelagic predator (Table 1). There has been some research concerning the feeding habits of juvenile sciaenids (Thomas 1977; Chao and Musick 1977) which found that small *C. regalis* feed mainly on mysids, copepods, and small fish. Annelids do form, however, a portion of the weakfish's diet (Table 1). Bigelow and Schroeder (1953) noted that the diet of *C. regalis* varies with locality and availability of prey. Small weakfish reject *P. mucosa* as a food item. *Cynoscion regalis* showed active investigatory behavior which usually consisted of tapping or bumping the sinking worm with its snout. Direct contact often resulted in a rapid shunning of the worm by the fish. This may indicate the presence of sensitive nares chemoreceptors. The juvenile fish would not be a major threat to these worms even were they readily available.

Preliminary work indicates that antipredation responses are active in *P. maculata, E. sanguinea, Phascoleopsis gouldi, Stylochus zebra,* and *Lineus ruber*. All these organisms, except the sipunculid, secrete large quantities of mucus. The epidermis of many sipunculids is densely packed with gland cells (Tétry 1959) and some secretion from these glands may serve to protect the animal from predation. *Stylochus zebra*, is a commensal of pagurid crabs; abundant production of mucus by this worm may tend to keep this relationship commensal.

The role of secretory defense mechanisms is well established in many species of marine animals (Graham 1957; Thompson 1960, 1969; Bakus 1968), but many questions concerning the broader aspects of antipredational responses remain unanswered. Are antipredation responses reflected in the composition of marine benthic communities? How does effectiveness of antipredation mechanisms vary with size of predators or degree of predator satiation? In similar-sized predators, what differences allow one species to prey on a given organism and not on the other? What changes in diet would be found if feeding studies involving analyses of stomach contents typically were extended to include all size classes of fish? Does previous exposure to an antipredation mechanism produce "learning" in potential marine predators?

In responding to slow-moving predators many potential prey species have evolved escape reactions (Doering 1976). In dealing with highly mobile fish predators, many species of potential prey have developed such defense mechanisms as protective secretions. Lagler et al. (1977:142) stated, "In general the esophagus [of fish] is so distensible that it can accommodate anything that the fish can get into its mouth . . . . " With the discovery of the repulsive characteristics of certain phyllodocids, the indications of antipredation mechanisms in a sipunculid and turbellarian reported here, added to what is known of nemerteans and opisthobranchs, it is clear that a closer examination must be made of interspecific molecular interactions which occur within marine communities.

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## LITERATURE CITED

BAKUS, G. J.
1966. Some relationships of fishes to benthic organisms on coral reefs. Nature (Lond.) 210:280-284.
1968. Defensive mechanisms and ecology of some tropical holothurians. Mar. Biol. (Berl.) 2:23-32.

BERG, J.
1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). Mar. Biol. (Berl.) 50:263-273.

BEUKEMA, J. J.
1968. Predation by the three-spined stickleback (*Gasterosteus aculeatus* L.): the influence of hunger and experience. Behaviour 31:1-126.

BIGELOW, H. B., AND W. C. SCHROEDER.
1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv., Fish. Bull. 53, 577 p.

CHAO, L. N., AND J. A. MUSICK.
1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fish. Bull., U.S. 75:657-702.

CHISZAR, D., AND J. T. WINDELL.
1973. Predation by bluegill sunfish (*Leopomis macrochirus* Rafinesque) upon mealworm larvae (*Tenebrio molitor*). Anim. Behav. 21:536-543.

DOERING, P. H.
1976. A burrowing response of *Mercenaria mercenaria* (Linnaeus, 1758) elicited by *Asterias forbesi* (Desor, 1848). Veliger 19:167-175.

FAGADE, S. O., AND C. I. O. OLANIYAN.
1973. The food and feeding interrelationship of the fishes in the Lagos Lagoon. J. Fish. Biol. 5:205-225.

FAUCHALD, K.
1977. The polychaete worms. Definitions and keys to the orders, families and genera. Nat. Hist. Mus. Los Ang. Cty., Sci. Ser. 28:1-190.

FRASER, A.
1973. Foraging strategies in three species of *Fundulus*. M.S. Thesis, Univ. Maryland, College Park, 54 p.

GIBSON, R.
1972. Nemerteans. Hutchinson Univ. Library, Lond., 224 p.

GRAHAM, A.
1957. The molluscan skin with special reference to Prosobranchs. Proc. Malac. Soc. Lond. 32:135-144.

GRIFFITHS, D.
1975. Prey availability and the food of predators. Ecology 56:1209-1214.

HILDEBRAND, S. F., AND W. C. SCHROEDER.
1928. Fishes of Chesapeake Bay. Bull. U.S. Bur. Fish. 43, 366 p.

HOOGLAND, R., D. MORRIS, AND N. TINBERGEN.
1956. The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as a means of defence against predators (*Perca* and *Esox*). Behaviour 10:205-236.

HYNES, H. B. N.
1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. J. Anim. Ecol. 19:36-58.

IVLEV, V. S.
1961. Experimental ecology of the feeding of fishes. (Translated from Russ. by D. Scott). Yale Univ. Press, New Haven, 302 p.

KISLALIOGLU, M., AND R. N. GIBSON.
1977. The feeding relationship of shallow water fishes in a Scottish sea loch. J. Fish. Biol. 11:257-266.

KNEIB, R. T., AND A. E. Stiven.
1978. Growth, reproduction, and feeding of *Fundulus heteroclitus* (L.) on a North Carolina salt marsh. J. Exp. Mar. Biol. Ecol. 31:121-140.

LAGLER, K. F., J. E. BARDACH, R. R. MILLER, AND D. R. M. PASSINO.
1977. Ichthyology. Wiley, N.Y., 506 p.

MACKIE, A. M., R. LASKER, AND P. T. GRANT.
1968. Avoidance reactions of a mollusc *Buccinum undatum* to saponin-like surface-active substances in extracts of the starfish *Asterias rubens* and *Marthasterias glacialis*. Comp. Biochem. Physiol. 26:415-428.

MAYO, P., AND A. M. MACKIE.
1976. Studies of avoidance reactions in several species of predatory British seastars (Echinodemata: Asteriodea). Mar. Biol. (Berl.) 38:41-49.

MURDOCH, W. W., S. AVERY, AND M. E. B. SMYTH.
1975. Switching in predatory fish. Ecology 56:1094-1105.

NIKOLSKY, G. V.
1963. The ecology of fishes. (Translated from Russ. by L. Birkett). Acad. Press, London and N.Y., 352 p.

ONYIA, A. D.
1973. A contribution to the food and feeding habit of the threadfin *Galeoides decadatylus*. Mar. Biol. (Berl.) 22:371-378.

PETTIBONE, M. H.
1963. Marine polychaete worms of the New England region. I. Families Aphroditidae through Trochochaetidae. U.S. Natl. Mus. Bull. 227, 356 p.

QASIM, S. Z.
1957. The biology of *Centronotus gunnellus* (L.) (Teleostei). J. Anim. Ecol. 26:389-401.

RAHEMTULLA, F., AND S. LØVTRUP.
1974. The comparative biochemistry of invertebrate mucopolysaccharides. II. Nematoda; Annelida. Comp. Biochem. Physiol. 49B:639-646.

RUSSELL, E.
1966. An investigation of the palatability of some marine invertebrates to four species of fish. Pac. Sci. 20:452-460.

SANDERS, H. L., R. R. HESSLER, AND G. R. HAMPSON.
1965. An introduction to the study of deep-sea benthic faunal assemblages along the Gay Head-Bermuda transect. Deep Sea Res. 12:845-867.

SMITH, R. W., AND F. C. DAIBER.
1977. Biology of the summer flounder, *Paralichthys dentatus*, in Delaware Bay. Fish. Bull., U.S. 75:823-830.

STICKENEY, R. R., G. L. TAYLOR, AND D. B. WHITE.
1975. Food habits of five species of young southeastern United States estuarine Sciaenidae. Chesapeake Sci. 16:104-114.

TÉTRY, A.
1959. Classe des sipunculiens. *In* P.-P. Grassé (editor), Traité de zoolgie, Tome V, p. 785-854. Libraires de l'académie de médecine, Paris.

THOMAS, D. L.
1977. The early life history and ecology of six species of drum (Sciaenidae) in the lower Delaware River, a brackish tidal estuary. Ichthyol. Assoc. Bull. 3, 247 p.

THOMPSON, T. E.
1960. Defensive acid-secretion in marine gastropods. J. Mar. Biol. Assoc. U.K. 39:115-122.
1969. Acid secretion in Pacific ocean gastropods. Aust. J. Zool. 17:755-764.

TINBERGEN, L.
1960. The natural control of insects in pine wood. I. Factors influencing the intensity of predation by songbirds. Arch. Neerl. Zool. 13:265-343.

TUGENDHAT, B.
1960. The normal feeding behavior of the three-spined stickleback (*Gasterosteus aculeatus* L.) Behaviour 15:284-318.

VINCE, S., I. VALIELA, N. BAKUS, AND J. M. TEAL.
1976. Predation by the salt marsh killifish *Fundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance. J. Exp. Mar. Biol. Ecol. 23:255-266.

WIGLEY, R. L.
1956. Food habits of Georges Bank haddock. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 165, 26 p.