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OBSERVATIONS ON THE FOOD AND FEEDING BEHAVIOR OF ESTUARINE NEMERTEAN WORMS BELONGING TO THE ORDER HOPLONEMERTEA[1]

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The majority of nemerteans are carnivores or scavengers, but the exact nature of the food and the feeding habits of most species is poorly documented. Certain species belonging to two classes, Anopla and Enopla, capture and ingest whole animals from many of the invertebrate phyla (Hyman, 1951; Gibson, 1972). Under laboratory conditions, some nemerteans may be maintained on homogenized liver, starch paste, and cooked beef fat (Gibson, *op. cit.*). In the laboratory they also may be cannibalistic or may feed on other nemertean species.

Hoplonemerteans (Enopla), all of which have armed proboscides, in some cases strike a prey species with the proboscis and immobilize it with an injected toxin. As is the case in the larger heteronemerteans (Anopla), the prey is then either ingested whole (Roe, 1970) or, by other hoplonemerteans which feed on arthropods, sucked out of the exoskeleton (Hickman, 1963; Jennings and Gibson, 1969). Some hoplonemerteans are known to consume a variety of prey species, but some are such specialists that they may starve in the laboratory if not provided with the correct prey (Jennings and Gibson, 1969; Roe, 1970).

The purpose of this paper is to present laboratory observations on the capture and ingestion of live prey by three species of estuarine hoplonemerteans of the suborder Monostylifera. Their food, food preferences and feeding behavior will be compared with findings from similar studies on other monostyliferans, thus developing a more comprehensive understanding of feeding within the group, and defining more precisely the niches of these worms.

Materials and Methods

The three species studied were *Tetrastemma elegans* (Girard, 1852), *Zygonemertes virescens* (Verrill, 1879), and *Amphiporus ochraceus* (Verrill, 1873). They were identified according to the criteria described by McCaul (1963). All were collected during the summers of 1971, 1973 and 1974 from beds of eelgrass (*Zostera marina* L.) located at Gloucester Point, Virginia, where the salinity of the water was approximately 20‰. Marsh (1973) found both *Tetrastemma and Zygonemertes* in equal abundance in his study of the epifauna of eelgrass near Gloucester Point, but I found *Tetrastemma* to be far more common. *Amphiporus*, though not a rare species on eelgrass, is much less common than the other two (Marsh, 1973; Orth, 1971). Specimens of *Zygonemertes* were obtained also from among hydroids and bryozoans on wooden pilings at Wachapreague, Virginia, where the salinity was

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about 30‰. This species is the only one of the three that is found also on the Pacific coast of the United States (McCaul, 1963).

Nemerteans living on the eelgrass were obtained by placing the freshly-collected grass into large rectangular or circular plastic containers and periodically removing the worms that surfaced around the periphery [see Kirsteuer (1967) for other details on collecting]. Once isolated, these worms were easily maintained for weeks in the laboratory without food or frequent water change.

The length of relaxed, moving specimens was determined by averaging several measurements taken with a millimeter scale. The latter was manipulated beneath a petri dish into which individual worms were placed.

Prey species used in these observations were crustaceans (amphipods, isopods and a mysid shrimp), polychaetes and molluscs. These were collected mostly from the eelgrass beds but some amphipods, especially members of the Corophiidae, were collected from scrapings of local pilings. Generally, only common species of prey were used in feeding preference tests. Amphipods, which were the most difficult of the prey to classify were identified with the aid of the descriptions and keys in McCain (1965), Feeley and Wass (1971) and Bousfield (1973). Total lengths of crustaceans (front of head to tip of telson) were measured with a calibrated ocular micrometer. Measurements of polychaetes were made to the nearest millimeter in the same manner used for the nemerteans.

Feeding tests were run with worms fresh from their habitat and also with those starved in the laboratory for known periods of time. Individuals of a prey species were presented to individual nemerteans in Syracuse watch glasses or in plastic compartmentalized covered boxes (length × width × depth: 51 × 43 × 39 mm, or 37 × 33 × 30 mm). Sometimes two different prey species were placed with each worm. Other procedures are described in the text. Water of approximately 20‰ salinity, usually filtered with a one micron filter, was used in the tests. Temperatures were 21–23° C. Tests were usually of short duration (*i.e.*, approximately 24 hours or less), but some were run for longer periods of time.

To observe the feeding behavior, predator and prey were placed into small dishes or depression slides. Use of a minimum amount of water promoted the desired contact between predator and prey. The complete sequence of events from the initial attack to the end of feeding was observed with a dissecting microscope. Individual events in the feeding process were timed with a stopwatch.

RESULTS

Tetrastemma elegans

This species fed only on amphipods, although presented with a wide range of possible prey (Table I). *Corophium acherusicum* was attacked and consumed much more readily than any of the others. As 90–100% of these crustaceans were usually consumed, the species became a useful control for most tests with other prey. Thus, the propensity to feed by an experimental population of *Tetrastemma* was easily determined by providing an aliquot sample with amphipods of this species.

The data in Table II show that *Tetrastemma* has a definite preference for *Corophium* over three other species of amphipods. In the first 15 minutes of Experiment 3, twelve individuals of *Corophium* were killed versus only two spec-

TABLE I

Summary of all feeding tests with Tetrastemma elegans, *involving one worm with one specimen of prey in each test.*

Species of prey	Number of prey		Per cent killed
	Presented	Killed	
Amphipoda			
Corophium acherusicum Costa	94	87	92.5
Ampithoe longimana Smith	19	2	15.5
Ampithoe valida Smith	2	1	
Cymadusa compta (Smith)	1	1	
Gammarus mucronatus Say	21	5	
Mixed (*Ampithoe* sp. and *Gammarus* sp.)	9	0	
Stenothoe gallensis (Walker)	6	0	
Caprella penantis Leach	36	6	16.7
Isopoda			
Erichsonella attenuata (Harger)	10	0	
Idotea baltica (Pallis)	17	0	
Edotea triloba (Say)	7	0	
Mysidacea			
Mysidopsis bigelowi Tattersall	7	0	
Polychaeta			
Nereis succinea (Frey and Leuckart)	9	0	
Sabella microphthalma Verrill	6	0	
Polydora ligni Webster	6	0	

imens of *Caprella.* There was a nine to one differential in Experiment 4, during the same time interval. Other numerous observations showed that if worms which were unresponsive to caprellids were presented with specimens of *Corophium,* they killed them at the first contact. An analysis of these data as well as all data dealing with *Corophium,* showed that there was no obvious selection by the worms for prey of a certain sex, or ovigerous females or smaller individuals.

Preferential feeding by *Tetrastemma* was tested further with other species of amphipods. Five specimens of *Corophium* (length: 3.13 mm mean, 2.28–4.05 mm range) were placed into each of five chambers, and one worm was added to each chamber. Two other chambers with five amphipods each but without worms served as a control for natural mortality. Predation was followed over a 20-hour period. Within five minutes all worms had attacked at least one amphipod; four had attacked more than one. At 15 minutes three had completed feeding and all of the other worms were feeding actively. At the end of the experiment, 19 of 25 amphipods were killed (4.56 corophiids/worm/day). Four other worms, each placed with five amphipods (mixed species: *Ampithoe valida, Gammarus mucronatus* and *Gammarus* sp.), killed a total of four individuals in 15 hours (1.6 amphipods/worm/day). Three of the four amphipods were *A. valida.*

The rate of predation on *C. acherusicum* by *Tetrastemma* was compared with that produced by *Zygonemertes virescens* on the same species. Two standard petri dishes (10 cm in diameter) were used to hold 25 amphipods each. Five worms of

TABLE II

Summary of experiments demonstrating food preferences of Tetrastemma elegans *for different species of amphipod prey.*

Experiment number	*Tetrastemma*		Amphipod prey			
	Number of worms	Mean length, mm	Species	Number	Mean length, mm	Number killed
1*	9**	9	*Corophium acherusicum*	9	—	8
			Ampithoe longimana	9	—	0
2*	9	8	*Corophium acherusicum*	9	—	9
	9	7	*Ampithoe* sp. and *Gammarus* sp.	9	—	0
3***	18	7	*Corophium acherusicum*	18	3.22	18
	18	7	*Caprella penantis*	18	5.15	5
4***	18	7	*Caprella penantis*	18	5.04	1
	18	7	*Corophium acherusicum*	18	3.07	13

* 24 hr experiment.

** One of each prey species with each worm.

*** 4 hr experiment; same worms used in experiments 3 and 4, but food presented to each reversed on successive days.

the first species were placed into one dish and five of the other into the second dish. All of these worms had been used in previous feeding experiments, and most had fed within four days prior to the beginning of the test; four specimens of *Tetrastemma* had fed the previous day. At the end of 18 hours, 19 of the 25 amphipods had been killed by *Tetrastemma* (5.05 amphipods/worm/day). Nine were killed within the first half hour. *Zygonemertes* killed twelve in 18 hours (3.20 amphipods/worm/day), but only two were killed in the first half hour.

The complete feeding process of *Tetrastemma* was observed many times in the laboratory. Most of the worms upon which the following account is based were 7 to 9 mm in length; the amphipods (*Corophium*) were 2.5 to 4.0 mm in length. Some observations were made also with other species of amphipods and larger worms.

Immediately upon contact of predator and prey, the armed proboscis is thrust out rapidly and usually strikes the amphipod somewhere on the ventral side. It may strike either in the anterior or posterior half of the prey. Occasionally the proboscis wraps around the body, but the tip still strikes ventrally. A single strike completely immobilizes the prey in from 15 to 90 sec (usually in less than 60 sec). The larger prey individuals are generally immobilized more slowly, but the size of the worm may be equally important with regard to immobilization time.

During this period of developing paralysis, the worm often moves away from the prey (up to a few worm-lengths) and then doubles back on its mucous-trail. It begins probing with its head, sometimes violently, on the ventral side of the amphipod, often everting the proboscis one or more times. The worm finally makes internal contact on the ventral side, probably penetrating between the sternal plates. Bleeding of the prey is occasionally discerned when an opening is produced. A large worm of 19 mm, feeding on *Gammarus mucronatus*, dislodged two thoracic gills in the process of probing and penetrating.

The head is inserted into the opening and the stomach is everted out of the rhynchodaeal pore, expanding to a hemispherical suctorial process. Feeding commences from 2.5 to 6 min (mean about 4 min) after the initial strike of the proboscis.

The body of the worm begins a series of peristaltic undulations while the ventral surface remains attached to the substratum. Muscular contraction of the body may be partially responsible for the suctorial action which begins to remove blood, tissue, organs, pigment, etc. from the prey. The flow of these materials can be seen through the transparent exoskeleton. Usually, all of the internal structures, including such organs as the eyes, are eventually sucked out leaving a completely transparent test. Occasionally the posterior part of the prey's digestive tract may remain intact, being the only opaque structure.

Feeding is completed in from 3.5 to 12 min with an average of about 7 min. The time taken for the whole process, *i.e.*, initial attack to the end of feeding, is approximately 6 to 17 min. The actual feeding time is greater for larger prey. Worms may stay with the prey for 1–2 min after feeding is discontinued, and then move away. Occasionally a worm may kill but not feed on the amphipod.

While completely sucking out the soft parts of ovigerous female corophiids, the worms never ingested the eggs or embryos. However, recently hatched young still living in the marsupium of the female were killed readily. Feeding on these minute animals (<1 mm long) is also suctorial, and takes place from the ventral side. Because they are so small, the worm's feeding time is very much shorter than the minimum figures noted above for adult amphipods.

To determine whether the immobilized prey is killed or only narcotized, starved worms (4 to 6 mm in length) were allowed to strike amphipods (*Corophium acherusicum*, 2.28–4.75 mm) with one thrust of the proboscis. The pair was separated and the amphipod was placed in clear sea water in a covered watch glass. Six pairs were treated in this manner. All of the six amphipods were immobilized in from 15–120 sec. None recovered during an observation period of several hours.

Zygonemertes virescens

A total of 20 worms was used for the following observations on *Zygonemertes*. Worms ranged in size from 12–40 mm (mean 23 mm). *Zygonemertes* attacked and fed on the amphipods and on one of the isopods (Table III). *Corophium* was attacked and killed more readily than the other species.

The following account of the feeding behavoir of *Zygonemertes* is based primarily on three worms consuming three amphipods (*Corophium*). The worms were 23, 25 and 30 mm long, while the amphipods were 3.7, 3.0 and 3.0 mm.

Upon contact with the prey, the proboscis was everted rapidly and penetrated the prey ventrally in two of three cases; in the other, it was a dorsal strike as the proboscis wrapped around the body of the crustacean. The amphipods were completely immobilized in 10 to 60 sec; the largest worm paralyzed its prey in the shortest time. In the latter case, the proboscis was attached to the amphipod for no longer than 2 sec. This indicates that the toxin is injected at the strike and not pumped into the "wound" by the proboscis. During the period of immobilization the worms moved away from the prey but kept contact by their posterior ends or by the attached mucus. Upon return to the prey, the worms actively probed the

TABLE III

Summary of all feeding tests with Zygonemertes virescens, *involving one worm with one specimen of prey in each test.*

Species of prey	Number of prey		Per cent killed
	Presented	Killed	
Amphipoda			
Corophium acherusicum Costa	41	29	70.6
Ampithoe longimana Smith	13	3	13.8
Gammarus mucronatus Say*	3	0	
Melita nitida Smith	13	1	
Caprella penantis Leach	17	6	35.2
Isopoda			
Erichsonella attenuata (Harger)	4	2	50.0
Idotea baltica (Pallis)	2	0	
Edotea triloba (Say)	3	0	
Polychaeta			
Nereis succinea (Frey and Leuckart)	14	0	
Gastropoda			
Bittium varium Pfieffer	3	0	
Crepidula convexa Say	3	0	

* This species is known to serve as prey for *Zygonemertes* (unpublished observations of T. A. Bernard, Jr., a former student).

ventral sides of the amphipods, exerted a few thrusts of the proboscis, penetrated, everted the stomach, and commenced sucking out all of the soft parts, leaving a transparent exoskeleton. The peristaltic action of the body was not as vigorous as in *Tetrastemma.*

In the case of the largest nemertean, the entire process from attack to end of feeding took less than 3 min. In the other two cases the whole process took 8.75 min and 9.75 min, actual feeding time being approximately 5 min in each case. The largest nemertean, which had entered the amphipod postero-ventrally, exited out of the anterior end. Amphipod embryos were not ingested. These observations further demonstrated the worms' preference for *Corophium.* In each case the worms had previously been kept in depression slides with *Ampithoe longimana* for 16 hours but had not fed. When specimens of *Corophium* were introduced, they were immediately attacked in all three cases.

Feeding on the isopod *Erichsonella* was also observed. The two isopods that were consumed measured 6.3 and 7.5 mm, and the worms were about the average length. These crustaceans were attacked with the proboscis, and appeared to be at least partially paralyzed almost immediately. The worms probed ventrally with their heads, eventually penetrating the exoskeleton. One worm penetrated at the base of the second left peraeopod, while the other worm inserted its head under the uropods in among the pleopods. In each case the head was inserted a short distance and the stomach was everted to produce a funnel-like suctorial organ. In one case the worm fed for 30 min, and then left after evacuating the anterior two-fifths of the isopod's body; the gut remained intact. The other worm was forcibly removed from the isopod after it had sucked out a part of the posterior end of the body.

Amphiporus ochraceus

Only seven worms were available for study, six collected from eelgrass at Gloucester Point and one at Wachapreague, Virginia on a wooden piling. The prey species tested were *Corophium acherusicum, Ampithoe longimana, Gammarus mucronatus,* and *Idotea baltica.* Six worms were starved for nine days prior to a 24 hour test. Each of three worms were given one *Ampithoe* and each of three given one *Gammarus.* One of each prey was killed and consumed. Another worm, starved for three days and then given two specimens of *Corophium,* consumed both animals within 24 hours. The embryos of the prey were not harmed. Three days later this worm consumed two more of the same amphipods within two hours. It failed to attack two specimens of *Idotea* within a two day period.

Observations on the feeding behavior of *A. ochraceus* are very limited in comparison to the other two species. It feeds by paralyzing its prey with thrusts of the proboscis, and in all cases fed from the ventral side of the amphipod. In one observation, a specimen of *Ampithoe* (5.7 mm long) was completely immobilized in less than 60 sec, and was then fed upon by suctorial action for five minutes. There was a slight peristalsis of the body, but it was less pronounced than in *Tetrastemma.* All amphipods were completely evacuated.

DISCUSSION

Feeding behavior in the three species of nemerteans is very similar. It appears that the prey is found fortuitously. At least there is no general evidence that chemoreception or visual senses are involved, but critical experiments are needed to evaluate such stimuli. Contact must be made before the lethal trust of the nemertean's proboscis. Roe (1970) found that *Paranemertes peregrina* had to come in contact with a nereid worm or with its fresh products, such as a trail of mucus, before it would initiate the sequence of events in the capture and feeding process. Jennings and Gibson (1969) came to the same conclusion in dealing with the predator-prey relationship between *Amphiporus lactifloreus* and *Gammarus locusta.*

In all cases, the proboscis is everted rapidly onto the prey, sometimes wrapping around the body, and the stylet-bearing portion usually makes contact with the ventral side. One strike of the proboscis is ordinarily sufficient not only to paralyze but also to kill the prey. It appears that the venom of *P. peregrina* only paralyzes the polychaete prey (Roe, 1970). Presumably the stylet-bearing part of the proboscis in some way penetrates the integument of the crustacean and a toxin is transmitted into the hemocoel. It seems unlikely that the penetration of the exoskeleton is anything other than mechanical. Immobilization of the prey, as seen in the present study, is too rapid for any significant histolytic action to take place, although Jennings and Gibson (1969) suggested this mode of toxin entry in the case of amphipods attacked by *A. lactifloreus.* The proboscis is not used to draw the prey to the head of these hoplonemerteans as is the case with some of the heteronemerteans (Jennings and Gibson, 1969).

Table IV

Food of suctorial and macrophagous nemerteans belonging to the order Hoplonemertea, suborder Monostylifera.

Nemertean species	Prey species	Source
Suctorial feeders		
Amphiporidae		
Nipponnemertes pulcher (Johnston, 1837)	*Haploops tubicola* Liljeborg	Brunberg (1964); Berg (1972)
	small polychaetes	Brunberg (1964)
Amphiporus lactifloreus (Johnston, 1928)	*Haploops tubicola* Liljeborg	Brunberg (1964)
	Gammarus locusta	Jennings and Gibson (1969)
Amphiporus ochraceus (Verrill, 1873)	*Ampithoe longimana* Smith	McDermott (this paper)
	Corophium acherusicum Costa	
	Gammarus mucronatus Say	
Zygonemertes virescens (Verrill, 1879)	*Ampithoe longimana* Smith	McDermott (this paper)
	Ampithoe valida Smith	
	Corophium acherusicum Costa	
	Gammarus mucronatus Say	
	Melita nitida Smith	
	Caprella penantis Leach	
	Erichsonella attenuata (Harger)	
Prosorhochmidae		
Geonemertes australiensis Dendy, 1892	young myriapods and small insects, particularly *Collembola*	Hickman (1963)
Tetrastemmatidae		
Tetrastemma elegans (Girard, 1852)	*Ampithoe longimana* Smith	McDermott (this paper)
	Ampithoe valida Smith	
	Cymadusa compta (Smith)	
	Corophium acherusicum Costa	
	Corophium simile Shoemaker	
	Gammarus mucronatus Say	
	Caprella penantis Leach	
Macrophagous feeders		
Emplectonematidae		
Paranemertes peregrina Coe, 1901	*Platynereis bicanaliculata*	Roe (1970)
	Nereis vexillosa	
	Neanthes brandti	
	Lepidonotus squammatus	
	Armandia brevis	
	Syllis sp.	
	Polydora sp.	
Ototyphlonemertidae		
Ototyphlonemertes brevis Correa, 1948	crustaceans and many setae of polychaetes in gut; fresh fish used as bait	Correa (1948)
Tetrastemmatidae		
Prostoma rubrum (Leidy, 1850)	oligochaetes (naids and others); insects, crustaceans and unicellular organisms; cannibalistic	Coe (1943)
	Aeolosoma sp.	Jennings and Gibson (1969)
	Stylaria sp.	
	Tubifex sp.	
	Chironomus larva	
Prostoma lacustris	*Chironomus* and *Tanypus* larvae; *Cyclops*.	DuPlessis (1893) *from* Gibson, 1972

The relationship between size of prey, size of nemertean and lethal doses of toxin have not been determined quantitatively. Nevertheless, my observations reveal that the time for immobilization of the prey species is inversely related to the size of the nemertean and directly related to the size of the prey. These relationships could be quantified by accurately measuring the volume and dry weights of predator and prey.

The head of each nemertean species probes the ventral side of the paralyzed (dead) prey and eventually penetrates in this region. Here again penetration seems to be a mechanical process with the head wedging itself between the sternal plates. While it is possible that the probing head is continually secreting some lytic substance that softens the cuticular membranes, the rapidity of the penetration obviates such speculation.

It appears to be the stomach that is extruded through the rhynchodaeal pore, in the form of a bulbous sucker-like extension of the head. Peristaltic waves of the body are the external manifestation of a process producing the suctorial action which evacuates the whole exoskeleton. Although the stomach of *A. lactifloreus* is applied to various organs of the amphipod, the stomach of the present species usually remains in one position and there is a flow of organs and tissues into this organ. Again, the process is so rapid and continuous that histolytic secretions from the glands of the stomach wall participating in this phenomenon need not be postulated. Jennings and Gibson (1969) suggested that such secretions were utilized by *A. lactifloreus.* Overall, the feeding process described above is really very similar to that described in *A. lactifloreus* by the last authors. They also showed that *A. lactifloreus* will ingest dead specimens of *Gammarus* but without initial proboscis eversion. I did not attempt a confirmation of this behavior.

Other suctorial, arthropod feeders are the marine species, *Nipponnemertes pulcher* and the terrestrial form, *Geonemertes australiensis* (Table IV). Berg (1972) noted that after the former species kills the amphipod prey the stylet makes a hole between the ventral plates. He postulated that proteolytic enzymes are injected; the proboscis is then withdrawn, and the esophagus is everted into the hole and used to suck out the soft parts. Berg neither confirmed nor commented on Brunberg's (1964) observation that "small polychaetes" are also eaten by *N. pulcher.* If polychaetes are a regular part of its diet, this would be the only exception to the generalization that the suctorial species feed exclusively on arthropods.

When the insect prey of *Geonemertes* comes into contact with the viscous mucus surrounding the body of the worm, the proboscis is everted rapidly. The prey either adheres to the adhesive papillae of the proboscis or is wrapped within the proboscis. It is pierced eventually by the stylet of the proboscis and immobilized. Hickman observed that the rhynchostome is applied to the insect and the soft parts are sucked out, leaving the exoskeleton and any internal hard parts. Note that this worm differs from those discussed above in that the head of the worm is not inserted into the body and the anterior part of the intestinal tract is not everted.

Jennings and Gibson (1969) observed that ingestion of *Gammarus locusta* takes 30–40 min, whereas the whole feeding process in the three worms under present study was never longer than about 15 min. However, the size relationships of predator and prey need to be evaluated in order to document differences in feeding times.

The three hoplonemerteans studied here are all crustacean feeders, and with one exception, all feed primarily on amphipods. Indeed, one amphipod, *Corophium,* is attacked and ingested more readily than all others. At first I thought that the apparent preference for *Corophium* might be due partially to its relative sluggishness. *Caprella* also is quite sluggish, and it also appears to be more susceptible to predation than the laterally-flattened amphipods which move much more rapidly. However, many observations have shown that while numerous contacts with other amphipods may not induce a specimen of *Tetrastemma elegans* to attack, one or two contacts with *Corophium* will elicit an attack and capture by the same worm.

Jennings and Gibson (1969) showed that the freshwater species *Prostoma rubrum* was primarily an oligochaete feeder, paralyzing the prey and ingesting it whole. The two crustaceans they tested, *Gammarus* sp. and *Asellus* sp., were not harmed by *Prostoma.* Coe (1943) also lists oligochaetes as its preferred prey. This nemertean is, therefore, primarily an annelid feeder, but may also feed on slender, worm-like insect larvae such as the chironomids (Table IV).

The information in Table IV compares the present observations on the food of the Monostylifera with most of the findings in the literature. Practically all of these data were obtained from observations and experiments run in the laboratory with prey species from the same general habitat as the worms. The nemerteans are divided into suctorial and macrophagous feeders, but all paralyze or kill their prey with the stylet-bearing proboscis before they feed.

In the macrophagous nemerteans, annelids or worm-like aquatic insect larvae make up the known prey species. Oligochaetes are taken in fresh water (*Prostoma rubrum*) and polychaetes in the marine environment (*Paranemertes peregrina*). Only in the macrophagous species is it possible to identify the prey of freshly collected worms. The hard, secreted portions of the bodies of annelids or insects (*e.g.*, setae, jaws, denticles and exoskeletons) are readily seen and identified in the intestinal tract of compressed or dissected worms. On the other hand, at present it is not possible to identify the natural food in the intestine of the suctorial species. One therefore must carry out careful laboratory experiments with potential prey species in order to determine whether they actually are eaten.

In terms of the two feeding categories of Table IV, all members of the Amphiporidae for which information is available are suctorial. Members of the Tetrastemmatidae fall into each group, *i.e., Tetrastemma elegans* is suctorial and *Prostoma* is macrophagous. I prefer to withhold judgment on *T. melanocephalum* (Johnston, 1837), a species studied by Jennings and Gibson (1969). Only three worms were used for all of their observations, and these refused to attack or eat living annelids, crustaceans or molluscs. Jennings and Gibson noted similarities in the proboscis structure, stylet apparatus and gut structure of *T. melanocephalum* and *Amphiporus lactifloreus*, which suggest that the feeding process may be quite similar in the two species. Hence I suspect that when *T. melanocephalum* is studied carefully it may fall into the suctorial category with *T. elegans*.

Sanders, Goudsmit, Mills and Hampson (1962) examined the intestines of nine specimens of *Amphiporus* sp. (see Table 4, p. 68). In view of the evidence presented here that members of the genus *Amphiporus* are suctorial feeders of crustaceans, it is not surprising that they found seven with "empty" digestive tracts and two with only sand and benthic diatoms in their guts.

Roe (1970) noted that nereid worms show a distinct swimming escape response upon contact with the macrophagous species, *Paranemertes peregrina*. This response was not elicited upon contact with *Amphiporus formidabilis, Zygonemertes virescens* or *Emplectonema gracile*, nemerteans found in the same habitats as *Paranemertes* and the nereids. To her knowledge these three species did not prey on nereids. Information in the present study would confirm that *Zygonemertes* and probably *A. formidabilis* are crustacean feeders. According to Gibson (1972, p. 194) the genus *Emplectonema* is in the same family as *Paranemertes*. Further study is needed to determine whether it is also of the same feeding type.

The present observations make clear the necessity of laboratory study as well as field study if one is to delineate the feeding niches of suctorial nemerteans. For example, Marsh (1973) in his extensive study of the epifauna of the eelgrass (*Zostera marina*) community in the York River of Virginia, made erroneous inferences about the food of the suctorial species discussed in this paper. He identified a number of monostyliferans in this community with *Zygonemertes virescens* and *Tetrastemma elegans* being equally common. He suggested, referring to Barnes (1968), that they feed on polychaetes and other small invertebrates in the eelgrass, and in his diagram (Fig. 5, p. 95) of presumed trophic relationships, indicated that *Zygonemertes* feeds on the polychaete *Polydora ligni.* He indicated this prey presumably because it was the most common polychaete on the eelgrass. The evidence presented here shows that both of these nemerteans are in a different niche of the presumed food web, *i.e.,* they are primarily crustacean feeders with a decided preference for amphipods.

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Summary

1. It is shown, by laboratory observations, that the marine hoplonemerteans *Tetrastemma elegans* (Girard, 1852), *Zygonemertes virescens* (Verrill, 1879), and *Amphiporus ochraceus* (Verrill, 1873), feed in a suctorial manner on small crustaceans.

2. Amphipods are the preferred crustacean prey, with an overwhelming preference being shown for *Corophium acherusicum* Costa, over several other species tested. *Tetrastemma* kills this amphipod at a greater rate than does *Zygonemertes.*

3. The prey is killed with a violent thrust of the proboscis, which in some manner punctures the exoskeleton and injects a toxin. The head is inserted into an opening produced on the ventral side, and the stomach is everted. A peristaltic action of the whole body is associated with a suction that removes nearly all of the internal contents of the prey.

4. The feeding behavior of the suctorial monostyliferans is compared with the macrophagous species. In at least one family, the Tetrastemmatidae, both feeding mechanisms are represented.

5. Laboratory studies on the food and food preferences of the suctorial species are essential in determining their particular ecological niches.

LITERATURE CITED

Barnes, R. D., 1968. *Invertebrate zoology.* W. B. Saunders Co., Philadelphia, 733 pp.

Berg, G., 1972. Studies on *Nipponnemertes* Friedrich, 1968 (Nemertini, Hoplonemertini). *Zool. Scr.,* **1**: 211–225.

Bousfield, E. L., 1973. *Shallow-water gammaridean Amphipoda of New England.* Cornell University Press, Ithaca, New York, 312 pp.

Brunberg, L., 1964. On the nemertean fauna of Danish waters. *Ophelia,* **1**: 77–111.

Coe, W. R., 1943. Biology of the nemerteans of the Atlantic coast of North America. *Trans. Conn. Acad. Arts Sci.,* **35**: 129–327.

Correa, D. D., 1948. *Ototyphlonemertes* from the Brazilian coast. *Comun. Zool. Mus. Hist. Natur. Montevideo,* **2**: 1–12.

DuPlessis, G., 1893. Organisation et genre de vie de l'*Emea lacustris* nemertien des environs de Genève. *Rev. Suisse Zool.,* **1**: 329–357, (from Gibson (1972) p. 84).

Feeley, J. B., and M. L. Wass, 1971. The distribution and ecology of the Gammaridea (Crustacea: Amphipoda) of the lower Chesapeake estuaries. *Spec. Papers Mar. Sci., Virginia Institute of Marine Science, Gloucester Point,* 2: 1–58.

Gibson, R., 1972. *Nemerteans.* Hutchinson University Library, London, 224 pp.

Hickman, V. V., 1963. The occurrence in Tasmania of the land nemertine, *Geonemertes australiensis* Dendy, with some account of its distribution, habits, variations and development. *Pap. Proc. Roy. Soc. Tasmania,* **97** : 63–71.

Hyman, L. H., 1951. *The invertebrates. Volume II*: *Platyhelminthes* and *Rhynchocoela.* McGraw-Hill Book Co., Inc., New York, 550 pp.

Jennings, J. B., and R. Gibson, 1969. Observations on the nutrition of seven species of rhynchocoelan worms. *Biol. Bull.,* **136** : 405–433.

Kirsteuer, E., 1967. Marine, benthonic nemerteans: how to collect and preserve them. *Amer. Mus. Novitates, 2290* : 1–10.

Marsh, G. A., 1973. The *Zostera* epifaunal community in the York River, Virginia. *Chesapeake Sci.,* **14** : 87–97.

McCain, J. C., Sr., 1965. The Caprellidae (Crustacea :Amphipoda) of Virginia. *Chesapeake Sci.,* **6** : 190–196.

McCaul, W. E., 1963. Rhynchocoela: nemerteans from marine and estuarine waters of Virginia. *J. Elisha Mitchell Sci. Soc.,* **79** : 111–124.

Orth, R. J., 1971. Benthic infauna of eelgrass, *Zostera marina,* beds. *M.S. Thesis, University of Virginia, Charlottesville,* 78 pp.

Roe, P., 1970. The nutrition of *Paranemertes peregrina* (Rhynchocoela: Hoplonemertea). I Studies on food and feeding behavior. *Biol. Bull.,* **139** : 80–91.

Sanders, H. L., E. M. Goudsmit, E. L. Mills, and G. E. Hampson, 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.,* **7** : 63–79.

Mcdermott, John J. 1976. "OBSERVATIONS ON THE FOOD AND FEEDING BEHAVIOR OF ESTUARINE NEMERTEAN WORMS BELONGING TO THE ORDER HOPLONEMERTEA." *The Biological bulletin* 150, 57–68. https://doi.org/10.2307/1540589.