

Food, Feeding Behavior and Feeding Ecology of Nemerteans¹

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SYNOPSIS. The feeding biology of nemerteans is reviewed, new information is presented, and the role of nemerteans in natural communities is discussed and evaluated. Most nemerteans are carnivorous, the majority feeding on live, often specific, prey, while some are scavengers. Macrophagous feeding is found in the Palaeonemertea, Heteronemertea and some of the Hoplonemertea; the more specialized suctorial feeding is limited to five of the hoplonemertean families, and suspension feeding (omnivorous diet) occurs only in the highly specialized symbiotic monogeneric Bdellonemertea.

Feeding adaptations seem to be related to the nature and employment of the proboscis, the dilatibility of the mouth, and the structure of the anterior part of the digestive tract. The transport of dissolved organic materials from seawater has been demonstrated, but its role in nemertean nutrition is just being contemplated. Present meager information on predation has shown nemerteans to have actually and potentially large effects on prey populations and thus on the communities in which they live. As the feeding biology of only a relative handful of species has been studied, much basic comparative research is needed before we can corroborate or refute our present ideas concerning the ecological roles of nemerteans.

INTRODUCTION

The food-catching proboscis apparatus is both a unique and a visibly outstanding feature of the Nemertea. The feeding biology of these worms shows them to be elegantly adapted in behavior, physiology and morphology to the particular foods they eat, and they are consequently integral and potentially important members of natural communities. In this paper we will relate these adaptive strategies in four parts: foods, patterns of feeding behavior, the role of dissolved organic material in nemertean nutrition, and feeding ecology. Finally, we will discuss areas of research needed before the importance of nemerteans in their communities can be appreciated.

FEEDING BIOLOGY

Foods of nemerteans

Foods are basically semi-fluid, soft, or partly digested parts of arthropods, anne-

lids and other worm-shaped animals, plus a scattering of molluscs, fish, etc., living and dead (Table 1). Although there is little published information on the food of palaeonemerteans, it appears that they feed on annelids compatible with their size. Evidence for heteronemerteans indicates that their food may be living or dead with a predilection for polychaetes; they also utilize molluscs, crustaceans and other nemerteans. Although scavenging may be a way of life for many species, clear-cut evidence from nature exists only for *Parborlasia corrugatus* (Dayton *et al.*, 1970, 1974; Gibson, 1983).

All data continue to show that the free-living marine suctorial hoplonemerteans are primarily predators of live amphipods, especially tubicolous types (Bartsch, 1973, 1975; McDermott, 1976a, 1984, unpublished), although other crustaceans are eaten by some. Brünberg's (1974) suggestion that polychaetes may be in the diet of *Nipponnemertes* seems to belie all evidence. Insects and myriopods are the only known prey of the two terrestrial species of *Argonemertes*. Members of the symbiotic family Carcinonemertidae feed in a suctorial fash-

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TABLE 1. Food of Nemertea belonging to the orders Palaeonemertea, Heteronemertea, Hoplonemertea and Bdellonemertea.^a

| Nemertean | Prey | Reference |
|---|--|---|
| Palaeonemertea | | |
| Cephalothricidae and Hubrechtidae | | |
| <i>Cephalothrix linearis</i> (Rathke) and <i>C. rufifrons</i> (Johnston) ^{b,c} | Oligochaetes (id. sp. or gen.), nematode (id. gen.); oligochaete (id. sp.) | Jennings and Gibson (1969); McDermott (unpublished) |
| <i>Cephalothrix</i> sp. | Cannibalistic | McIntosh (1873–74) |
| <i>Hubrechtella dubia</i> Bergendal ^b | Polychaetes (unid.) | Hylbom (1956) |
| Heteronemertea | | |
| Lineidae | | |
| <i>Cerebratulus lacteus</i> (Leidy) ^b | <i>Nereis</i> sp.; <i>Ensis directus</i> | Wilson (1900), Coe (1943); McDermott (1976b), Schneider (1982) |
| <i>Cerebratulus</i> sp. | <i>Syndosmya nitida</i> | Brunberg (1964) |
| <i>Gorgonorrhynchus bermudensis</i> Wheeler ^b | <i>Atherina harringtonensis</i> (dead); crustacean exoskeletal remains | Wheeler (1940); Gibson (1974) |
| <i>Lineus bilineatus</i> (Renier) | Polychaetes (id. sp. or gen.) | Joubin (1894), McDermott (1984) |
| <i>Lineus desori</i> Schmidt | Polychaetes (id. gen.) | Beklemishev (1955) |
| <i>Lineus lacteipitatus</i> Wheeler | Polychaetes (unid.) | McDermott (unpublished) |
| <i>Lineus longissimus</i> (Gunnerus) ^b | Polychaetes (id. sp. or gen.), <i>Ascidia intestinalis</i> , <i>Anomia</i> sp; polychaetes (id. sp., gen. or fam.) | McIntosh (1873–74); Piéron (1914), Beklemishev (1955) |
| <i>Lineus ruber</i> (Müller) ^b | Polychaetes (id. sp. or gen.); living and dead polychaetes, oligochaetes and small crustaceans (all unid.); <i>Clitellio arenarius</i> ; <i>Littorina saxatilis</i> ; dissolved organics | Verrill (1892), ^d Gontcharoff (1948, 1961), Rassmussen (1973), Bartsch (1975); Jennings and Gibson (1969); Jennings (1960), McDermott (unpublished); Muus (1967); Fisher and Cramer (1967), Fisher and Oaks (1978) |
| <i>Lineus sanguineus</i> (Rathke) | Polychaetes (id. sp. or fam.), oligochaetes (id. gen.), ^c nemertean (id. sp.) ^c | Jennings and Gibson (1969) |
| <i>Lineus vegetus</i> Coe ^b | Liver, dead mussels and shrimp | Roe (unpublished) |
| <i>Lineus viridis</i> (Fabricius) ^b | Polychaetes (unid.) | Gontcharoff (1959), Cantell (1975) |
| <i>Lineus</i> sp. | <i>Nephtys</i> sp. | McIntosh (1873–74) |
| <i>Micrura corallifila</i> Cantell | Polychaetes (unid.) | Cantell (1975) |
| <i>Micrura fasciolata</i> Ehrenberg | Polychaetes (id. fam.) | Cantell (1975) |
| <i>Micrura purpurea</i> (Dalyell) | Nemerteans (id. sp.) | Riches (1893), Cantell (1975) |
| <i>Parborlasia corrugatus</i> (McIntosh) ^{b,f} | <i>Acodontaster conspicuus</i> (dead); <i>Limatula hodgsoni</i> and unid. bivalve; "almost anything" | Dayton <i>et al.</i> (1970, 1974); Dayton (unpublished); Gibson (1983) |
| <i>Polybrachiorhynchus dayi</i> Gibson | <i>Upogebia africana</i> ; other crustaceans, polychaetes and gastropods (unid.) | Day (1974), Branch and Branch (1981); Branch and Branch (1981) |
| <i>Uchidana parasita</i> Iwata ^g | <i>Mactra sulcataria</i> (gill tissue) | Iwata (1967) |
| Hoplonemertea | | |
| Suctorial Feeders | | |
| Amphiporidae | | |
| <i>Amphiporus bioculatus</i> McIntosh | Amphipods (id. sp.) | McDermott (1984) |
| <i>Amphiporus dissimulans</i> Riches | Amphipods (id. sp.) | Brunberg (1964), ^b McDermott (1984) |
| <i>Amphiporus formidabilis</i> Griffin | Amphipods (unid.); <i>Petrolisthes</i> sp. (claws); isopods (id. gen.) | Stricker and Cloney (1982); Roe (unpublished); Kohn, A. J. (unpublished) |

TABLE 1. *Continued.*

| Nemertean | Prey | Reference |
|---|--|---|
| <i>Amphiporus imparispinosus</i> Griffin | Amphipods (unid.) | Roe (unpublished) |
| <i>Amphiporus lactifloreus</i> (Johnston) | Amphipods (id. sp.) | Gontcharoff (1948), Jennings and Gibson (1969), McDermott (unpublished) |
| <i>Amphiporus ochraceus</i> (Ver-rill) | Amphipods (id. sp.) | McDermott (1976a) |
| <i>Zygonemertes virescens</i> (Ver-rill) | Amphipods (id. sp.), isopods (id. sp.) | McDermott (1976a and unpublished) |
| Carcinonemertidae | | |
| <i>Carcinonemertes carcinophi-la</i> (Kölliker) ^a | Host crab embryos | Humes (1942) |
| <i>Carcinonemertes epialti</i> Coe ^a | Host crab embryos | Kuris (1978), Roe (unpublished) |
| <i>Carcinonemertes errans</i> Wickham ^a | Host crab embryos; dissolved or-ganics | Wickham (1978, 1979a, b, 1980), Wickham and Fisher (1977); Roe <i>et al.</i> (1981), Crowe <i>et al.</i> (1982) |
| <i>Pseudocarcinonemertes hom-ari</i> Fleming and Gib-son ^a | <i>Homarus americanus</i> (probably embryos) | Fleming and Gibson (1981) |
| Cratenemertidae | | |
| <i>Nipponnemertes pulcher</i> (Johnston) | Amphipods (id. sp.); polychaetes (unid.) | Brunberg (1964), Berg (1972a), McDermott (1984); Brunberg (1964) |
| Prosorhochmidae | | |
| <i>Argonemertes dendyi</i> (Dak-in) | Collembolans, nymphs of del-phacid bugs | Waterston and Quick (1937) |
| <i>Argonemertes australiensis</i> (Dendy) | <i>Collembola</i> , other small insects, young myriopods (all unid.); myriopods (unid.) | Hickman (1963); Gibson (1982a) |
| <i>Oerstedtia dorsalis</i> (Abild-gaard) | Amphipods (id. sp.) | McDermott (unpublished) |
| Tetrastemmatidae | | |
| <i>Tetrastemma candidum</i> (Müller) | <i>Artemia</i> nauplii | Roe (unpublished) |
| <i>Tetrastemma elegans</i> (Gir-ard) | Amphipods (id. sp.) | McDermott (1976a) |
| <i>Tetrastemma laminariae</i> (Uschakow) | Small crustaceans (unid.) | Sundberg (1979a) |
| <i>Tetrastemma melanocephalum</i> (Johnston) | Amphipods (id. sp. or gen.), co-pepods (unid.); amphipods (id. sp.) | Bartsch (1973, 1975); Gibson (1982a) |
| <i>Tetrastemma</i> sp. | Amphipods (id. sp. or gen.) | Stricker and Cloney (1982) |
| Macrophagous Feeders | | |
| Emplectonematidae | | |
| <i>Emplectonema gracile</i> (Johnston) | Barnacles (unid.), acmaeid lim-pets (unid.); injured barnacles (id. sp.), eggs of <i>Nucella emar-ginata</i> ; barnacles (unid.) | Dayton (1971); Glynn (1965); Lel-lelid, N. (unpublished) |
| <i>Paranemertes peregrina</i> (Coe) | Polychaetes (id. sp. or gen.); dis-solved organics | Roe (1970, 1976, 1979), Gibson (1970); Roe <i>et al.</i> (unpublished) |
| <i>Nemertopsis gracilis</i> Coe | <i>Lasaea cistula</i> | Glynn (1965) |
| Ototyphlonemertidae | | |
| <i>Ototyphlonemertes brevis</i> Corrêa ^b | Crustaceans (unid.) and setae of polychaetes in gut; fresh fish (bait) | Corrêa (1948) |

TABLE 1. *Continued.*

| Nemertean | Prey | Reference |
|--|---|---|
| <i>Ototyphlonemertes pallida</i> (Kerferstein) | Copepods (harpacticoids) | Mock (1978) |
| Tetrastemmatidae | | |
| <i>Prostoma asensoriatum</i> (Montgomery) | Oligochaetes (unid.) | Child (1901) ^c |
| <i>Prostoma graecense</i> (Böh-mig) | Insect larvae (id. gen.) <i>Cyclops</i> sp.; oligochaetes (id. sp. or gen.) | DuPlessis (1893, from Gibson, 1972); ^d Reisinger (1926), Loden (1974) ^e |
| <i>Prostoma jenningsi</i> Gibson and Young | Oligochaetes (id. fam.), serological ident. of oligochaete remains | Gibson and Young (1976) |
| <i>Prostoma rubrum</i> (Leidy) | Oligochaetes (unid.), insects, crustaceans, unicellular organisms, cannibalistic; oligochaetes (id. gen.), insect larvae (id. gen.) | Coe (1943); Jennings and Gibson (1969) |
| Bdellonemertea | | |
| <i>Malacobdella grossa</i> (Müller) ^g | Plankton from mantle cavity of many bivalve hosts | Gibson (1968), Gibson and Jennings (1969) |

^a Families and species arranged alphabetically, and hoplonemerteans divided into suctorial and macrophagous feeders; id. sp., id. gen., id. fam. = items in food groups identified to species, genus and family, respectively; unid. = unidentified; semicolon separates references for different food groups.

^b Scavenging indicated.

^c Formerly *C. bioculata* in Jennings and Gibson (1969).

^d Called worm *L. viridis*, but apparently *L. ruber* (see Coe, 1943).

^e Eaten by starved worms.

^f Formerly *Lineus corrugatus*.

^g Symbiotic nemertean.

^h Called worm *A. lactifloreus*, but apparently *A. dissimulans* (see Berg, 1972b).

ⁱ Originally *Stichostemma asensoriatum* (see Gibson and Moore, 1976).

^j Originally *Emea lacustris* (see Gibson and Moore, 1976).

^k Originally *Prostoma rubrum* (see Gibson and Moore, 1976); annelid food supplied in laboratory only.

ion on the embryos of their decapod hosts. Among the marine macrophagous hoplonemerteans, polychaetes are important prey and there is a preference for certain species (Roe, 1970, 1976, 1979, for *Paranemertes peregrina*). Members of the interstitial genus, *Ototyphlonemertes*, apparently feed on associated small crustaceans and polychaetes, but our knowledge of this family's biology is meager. All data indicate that oligochaetes and worm-like insect larvae are utilized by species of the freshwater genus *Prostoma*.

Patterns of feeding behavior

Two major feeding patterns occur among the nemerteans—suctorial and macrophagous. Both patterns are found in the hoplonemerteans, while the palaeonemerteans and heteronemerteans are macrophagous. The scavenging mode of life falls into the

macrophagous category. Suspension feeding is found only among the specialized symbiotic bdellonemerteans. We will describe each feeding pattern employing information from well-known examples, and will discuss general principles involved in each behavior.

Suctorial feeding. Suctorial behavior is found in five of the seven families within the Monostilifera (Table 1). It has been confirmed for only 19 species in 8 genera among the estimated 260 species in 53 genera (Gibson, 1982b) in the five families. Only members of the genus *Tetrastemma* (~80 species) within the Tetrastemmatidae are herein considered suctorial.

The description of the general feeding behavior of free-living suctorial species that follows, is based on laboratory observation made primarily with *Amphiporus lactifloreus*, *A. ochraceus*, *Nipponnemertes pulcher*,

Oerstedtia dorsalis, *Tetrastemma elegans*, *T. melanocephalum* and *Zygonemertes virescens* (Jennings and Gibson, 1969; Bartsch, 1973, 1975; McDermott 1976a, 1984, unpublished). The pattern, which involves various species of amphipods as prey, is remarkably similar for these and related species.

As the nemertean makes contact with an amphipod, the proboscis is everted with considerable force (still unmeasured), so that its tip strikes the prey on the more vulnerable ventral side at the base of the appendages. It may strike this location directly or by coiling halfway around the prey before the tip makes ventral contact. The thin exoskeleton of the sternal plate is pierced by the stylet and a toxin is introduced into the body. The everted proboscis may remain apposed to the plate from several seconds to 2 min. Usually, however, the prey is immobilized and apparently killed (McDermott, 1976a) in <1 min after eversion of the proboscis. Following inversion of the proboscis, the nemertean uses its head to probe among the appendages seeking to penetrate one of the sternal plates. The proboscis may be everted one or more times onto the ventral side of the amphipod before the head penetrates. Worms may move away from the prey before penetration, but they apparently maintain contact by means of a mucus-trail. The head is eventually wedged past the partially dislodged sternal plate (usually on the peraeonal section of the body), and the anterior gut (esophagus-stomach complex) is everted into the opening as a shallow cup-like structure.

As the suctorial action begins, due to peristaltic movements of the body wall, the prey's fluid, tissues and organs flow into the gut of the nemertean. Eventually the prey is completely evacuated leaving the otherwise intact exoskeleton. Internal fluids and organs are obviously partially replaced with fluid from the external medium because the exoskeleton does not collapse from the vigorous suctorial action.

The entire feeding sequence (initial proboscis eversion to the end of feeding) takes from 3 to >40 min depending on a variety of conditions particularly related to pre-

penetration behavior. Once a worm penetrates, the evacuation process proceeds at a more uniform rate (McDermott, unpublished).

Jennings and Gibson (1969) suggested that the sternal plates are subjected to histolytic action by glandular secretions from the anterior proboscis prior to penetration by the head, and that proteolytic enzymes may be forced through the stylet-produced hole in the exoskeleton and thus begin some internal digestion of the body parts prior to suctorial action. While these ideas may be true (still not proven) for *A. lactifloreus* and also for *N. pulcher* (McDermott, 1984), it is unlikely to be the case for other species that hold the proboscis against the prey for only a few seconds (McDermott, 1976a).

Free-living marine suctorial species are food specialists. Laboratory experiments have shown that they feed primarily on amphipods (Table 1), especially the tubicolous Ampeliscidae and Corophiidae (Bartsch, 1973; McDermott 1976a, 1984, unpublished). A notable exception is *Z. virescens* which may also utilize the abundant isopods in its eelgrass habitat (McDermott, 1976a, unpublished). Attempts to feed them other small crustaceans, polychaetes and molluscs have been negative (Jennings and Gibson, 1969; Bartsch, 1973; McDermott, 1976a). Little is known about specialization in terrestrial species (Table 1).

The diet of the suctorial symbiotic Carcinonemertidae is as might be expected, very specialized, i.e., it feeds on the host's embryos. However, Roe (unpublished) has shown that *Carcinonemertes* spp. from the west coast of the U.S. will feed and reproduce on both natural and unnatural host crab embryos.

Free-living suctorial feeders probably find food by chance contact with their often abundant prey. Jennings and Gibson (1969) showed that *A. lactifloreus* apparently does not detect food from a distance. It seems likely that in comparison to some of the macrophagous scavengers, distance chemoreception is poorly developed, but this has yet to be demonstrated experimentally.

The heavily folded walls of the stomach in suctorial feeders appear to be an adap-

tation for their mode of feeding (Jennings and Gibson, 1969; Berg, 1972a), allowing the worms to consume prey larger than themselves. In all species studied to date, the esophagus-stomach complex is everted into the body of the prey after the head has penetrated the sternal plate; it then expands to form the cup that collects the soft parts of the prey.

Macrophagous feeding. In this type, the nemertean consumes the entire prey organism rather than taking fluids and organs from inside the prey. Macrophagous feeders may be divided into two groups: 1. those hoplonemerteans that use the stylet of the proboscis to immobilize the prey—Monostilifera of the families Emplectonematidae, Ototyphlonemertidae and some members of the Tetrastemmatidae; and 2. anoplans in which the proboscis may or may not be used to capture prey. Scavenging occurs in members of the Anopla, some species showing evidences of both predatory and scavenging behavior (Table 1).

Feeding has been observed in only 9 (5 genera) of an estimated 95 species (Gibson, 1982b) in the three hoplonemertean families. Approximately 30 of the 110 known species of Tetrastemmatidae are herein considered *potentially* of the macrophagous type, although this has been demonstrated only in four species of *Prostoma*.

Paranemertes peregrina is a typical example of a hoplonemertean macrophagous feeder (Roe, 1970). Upon contact of the anterior edge of the nemertean's head with the polychaete prey, the nemertean retracts its head, everts its proboscis, wraps it around the prey and punctures the prey several times with the stylet. After the prey is paralyzed, the nemertean retracts the proboscis, losing contact with the prey, then crawls to the prey and engulfs it whole. Peristaltic waves can often be seen passing along the body apparently to help the worm gain traction or to move the food into the digestive tract. As with suctorial feeders, some prey selectivity occurs, *e.g.*, nereid polychaetes are preferred (Roe, 1970, 1976).

Jennings and Gibson (1969) gave a sim-

ilar description of feeding for the freshwater species *Prostoma rubrum*, and showed that oligochaetes and chironomid larvae were acceptable prey while the crustaceans *Gammarus* and *Asellus* were not attacked or eaten.

An example of a typical anoplan macrophagous feeder is *Lineus ruber* (Jennings, 1960; Jennings and Gibson, 1969; Bartsch, 1975). The nemertean everts the proboscis in a spiral coil around the prey when it comes within range (prior contact is not required as in the hoplonemerteans). A sticky mucus released by the proboscis seems to help bind the prey. As the proboscis retracts it pulls the prey toward the ventral mouth. The body anterior to the mouth is raised and curls downward over the prey, even gripping the prey, thus gradually forcing it into the highly expandable mouth. The ingestion process may take minutes to hours depending on the size of the prey. Non-living foods in this and other species are ingested without the aid of the proboscis.

The genus *Cephalothrix* uses its proboscis in the same manner as *Lineus*. Jennings and Gibson (1969) suggested that the barbs in the proboscis epithelium (proboscoidal rhabdoids—see Stricker and Cloney 1983) may be used both to paralyze and grip the oligochaete prey. They hypothesized that a toxin is introduced into the holes produced by the barbs. Recent observations with *C. rufifrons* (McDermott, unpublished), however, showed that oligochaetes do not become paralyzed and may continue their writhing activity even when fully ingested. Although *Cerebratulus* uses its proboscis to capture worms (Wilson, 1900; Coe, 1943) it seems unlikely that this organ is used in attacking *Ensis* in its burrow (McDermott, 1976b).

Unlike the suctorial species, macrophagous feeders do not have an enlarged, folded stomach nor a distinct esophagus (Jennings and Gibson, 1969; Gibson, 1970). The size of prey is generally limited to the nemertean diameter or dilatibility of the mouth; therefore prey is usually of worm-like proportions (annelids, elongated aquatic insect larvae, *Ensis*). Having worm-

shaped prey is probably an adaptation to maximize the amount of food per prey diameter.

Distance chemoreception is not well developed in the enoplan *P. peregrina* (Roe, 1970), but Amerongen and Chia (1982) showed that the cerebral organs of this worm function in close-range chemoreception for prey detection and recognition. As with free-living suctorial species, prey tend to be abundant, and are captured when contacted by the nemertean.

Scavengers are apparently limited primarily to the orders Palaeonemertea and Heteronemertea. Lineids provide the most studied laboratory examples of scavenging, but their feeding behavior differs from predatory behavior mainly in that the proboscis is not used in the process, certainly an energy conserving behavioral adaptation.

Few lineids have been observed to scavenge in nature. Dayton *et al.* (1974), however, showed that large numbers of *Parborlasia corrugatus* moved onto and fed on recently killed Antarctic sea stars, *Acodontaster conspicuus*.

Scavenging species tend to have well-developed distance chemoreception and little food selectivity. Specimens of *Lineus vegetus* will congregate on pieces of mussel, shrimp or liver from scattered places in a 200 liter aquarium within several minutes after their introduction (Roe, unpublished). Jennings and Gibson (1969) reported that *Lineus sanguineus* and *L. ruber* locate food up to 8 cm by chemotaxis. Dayton (personal communication) found *Parborlasia corrugatus* to have effective chemoreception of 10–20 m. Fisher and Cramer (1967) listed a variety of organic compounds that attract *L. ruber* (cellobiose, glucose, histidine, n-acetyl-glucosamine, proline and taurine).

Suspension feeding. This specialized mechanism has evolved only in *Malacobdella* (Bdellonemertea), symbiotic in bivalves (Gibson, 1972). The following account is from Gibson and Jennings (1969). *Malacobdella grossa* is primarily an unselective plankton feeding omnivore that utilizes the mollusc's incurrent water.

Associated with this behavior are unique morphological characteristics of the digestive tract: the rhynchodaeum and buccal cavity are incorporated into a large papillate, ciliated, distensible pharynx. In feeding, the worm closes off its esophagus and expands the pharynx, thus drawing in water. Then the pharynx is contracted slightly, causing the papillae to form a meshwork that prevents particles from escaping. Further pharyngeal contraction forces the water back out, and food is carried via cilia into interpapillate ciliary tracts that lead to the esophagus. The same authors showed that the digestive enzymes of *Malacobdella* are carbohydrases in contrast to the proteases of typically carnivorous nemerteans.

Role of dissolved organic uptake

Many soft-bodied marine invertebrates absorb dissolved organic material (DOM) directly through the epidermis (Stephens, 1982). Absorption of DOM by nemerteans has been shown in *Lineus ruber* (Fisher and Cramer, 1967; Fisher and Oaks, 1978), *Paranemertes peregrina* (Roe *et al.*, unpublished) and *Carcinonemertes errans* (Roe *et al.*, 1981; Crowe *et al.*, 1982). Fisher and Oaks (1978) presented strong evidence that epidermal cells of *L. ruber* are the primary site of uptake, and that DOM is used in a nutritional sense, both in providing energy and in protein synthesis. In addition, Jennings and Gibson (1969) found nonspecific esterases and exopeptidases in the epidermis (*L. sanguineus*) and blood vascular system of most species studied. They suggested that these enzymes are concerned with extracorporeal digestion of simple proteins or polypeptides, and that the products of this digestion supplement the normal diet.

The role of DOM in nutrition of free-living marine organisms is only beginning to be realized (Stephens, 1981, 1982), and its quantitative role in nutrition of nemerteans has not been established. However, some information on its importance in the symbiotic *Carcinonemertes* is available. Individuals of *C. errans* on male and non-berried female crabs (9 months/yr) appar-

ently do not feed. Roe *et al.* (1981) and Crowe *et al.* (1982) not only showed that non-feeding individuals absorb dissolved amino acids, but also demonstrated that the crab hosts leak amino acids across arthrodial membranes in excess of surrounding water levels. These amino acids are the same ones most readily absorbed by the worms, and there is net influx at concentrations found in this worm habitat.

Roe (unpublished) also isolated non-trophic worms in fingerbowls in sea water with and without amino acids. She was unable to get long-term maintenance of worms with the amino acids. However, worms kept in sea water subjected to ultraviolet light and passed through a 1 μ m filter plus a charcoal filter to remove organic materials shrank from an average weight of 4.5 μ g/worm (800 worms in 4 samples) to 3.1 μ g/worm (480 worms in 1 sample) in 22 days. These results, coupled with the lack of any obvious mechanism of feeding by the worms, and the fact that little organic material besides the small molecules leaked by the crab is present in arthrodial membrane areas, lend support to the hypothesis that absorption of DOM is the primary method of nutrition for *C. errans* during much of its life span.

Nemerteans in community ecology

Three topics will be discussed with respect to feeding ecology of nemerteans and the community: a) the adaptive strategies of nemerteans as optimal foragers; b) the effects of nemerteans on community structure; and c) the role of nemerteans as prey.

Nemerteans as optimal foragers. We have seen that several features of behavior, gut morphology, prey detection, etc., function together to result in each nemertean being highly adaptive with respect to feeding. A relatively large body of ecological literature exists which describes optimal foraging patterns for different types of predators under different conditions (*e.g.*, Pyke *et al.*, 1977). For predators that pursue relatively large prey, the most adaptive strategy is to specialize when preferred food is abundant, but become less specialized when that food becomes scarce (Ivlev, 1961,

Emlen, 1966 and MacArthur and Pianka, 1966 in Roe, 1976; Pyke *et al.*, 1977). *Paranemertes peregrina* pursues its prey (Roe, 1976) and prefers nereid polychaetes (Roe, 1970). Studies of its diet in several study sites that differed in abundances of preferred nereid food, showed that *P. peregrina* was most selective in the area where preferred nereids were most abundant. Nereids comprised a higher proportion of the diet where they were most abundant, and more polychaete families were represented in the nemertean diet where nereids were less abundant (Roe, 1976, 1979). These studies indicate that *P. peregrina* is an optimal forager, emphasizing again the adaptive nature of nemertean feeding biology.

Effects on community structure. Some predators have a large effect on community structure and diversity (*e.g.*, Paine, 1966; Dayton, 1971). Predators that have the greatest effect on their communities are those that eat abundant, competitively dominant prey (Paine, 1966) and those that cause a moderate level of disturbance (Connell, 1978). Although such effects are less clear-cut in soft-sediment communities (Peterson, 1979; Dayton and Oliver, 1980) than in rocky intertidal communities (Paine, 1966) some evidence exists for community structural changes as a consequence of predation (reviewed in Peterson, 1979; Dayton and Oliver, 1980). On intertidal mud flats on San Juan Island, Washington, *P. peregrina* prefers and eats primarily *Platynereis bicanaliculata*. The latter is not only one of the most abundant polychaetes on these mud flats, but its presence negatively affects at least the polychaetes *Armandia brevis* and *Axiiothella rubrocincta* (Woodin, 1974). By feeding mainly on this numerically and biologically important polychaete, *P. peregrina* has much potential secondary effect on community structure. Although questions of community effect were not tested, Roe (1976) did show that *P. peregrina* feeds on a substantial portion of the nereid population. At one mud flat the nereids averaged 819/m² and *P. peregrina* was estimated to eat approximately 38% of the population. At a similar area the nereids averaged 3,240/m² and the

nemerteans ate about 15% of the population. Although diversity indices were not calculated nor other factors considered, the first community appeared qualitatively more diverse, having more polychaete species than the second. It appears that *P. peregrina* may, therefore, by feeding heavily on a prey that is important, affect structure and diversity of these soft-sediment communities.

From her studies on the biology of *Tetrastemma melanocephalum*, Bartsch (1973) was able to calculate the effect of this nemertean on a population of *Corophium volutator*. Applying a laboratory-determined feeding rate of 3 corophiids/day to a concentration of 116 nemerteans/m² on a particular mud flat, she calculated that the potential predation was over 10,000 amphipods/m²/mo in a population estimated at 118,000 corophiids/m². She also suggested (Bartsch, 1977) that *T. melanocephalum* is not a serious food competitor of the more opportunistic feeder *Nereis diversicolor*, whose tubes it occupies simultaneously with impunity. Commiato (1982) showed that *Nereis virens* regulates numbers of *C. volutator* in Maine, and where population levels of *C. volutator* are low, other infaunal species show increased numbers. Heavy predation by *T. melanocephalum* of *C. volutator* could produce similar results in the *C. volutator* community.

Cerebratulus lacteus, in feeding on razor clams, feeds on larger prey than most of the macrophagous nemerteans. Its predation has the added effect of making individuals it misses more susceptible to epibenthic predators and desiccation. In their escape response the clams project much of the body above the surface, or may even leave the burrow altogether (McDermott, 1976b). Schneider (1982) also found that the naticid snail *Polinices duplicatus* competes with *Cerebratulus* for the same prey.

Wickham's studies (1979a, 1980) of *Carcinonemertes errans* have demonstrated adverse effects on its host *Cancer magister*. With a population averaging 43,000 worms/crab near San Francisco, and each worm eating about 70 crab embryos during the 30 day crab brooding season, the worms are consuming about 55% of the

total egg production of central California dungeness crabs. *C. errans* is obviously a significant predator, and has been implicated in the collapse of the central California dungeness crab fishery.

Part of the adaptive feeding strategy for both macrophagous and suctorial feeding types, especially among hoplonemerteans, is to utilize only a few species as food (they specialize or show preference although capable of feeding on a greater variety). Such food is often abundant enough that the worm finds the prey by simple contact rather than having well-developed long-distance chemoreception. Since most structural and macrophagous hoplonemerteans do specialize on abundant prey, if they themselves are abundant, these worms have high potential for affecting community structure through their feeding activities. That nemerteans are important to their communities as predators seems obvious, but supporting data are meager.

Nemerteans as prey. Little information exists indicating that nemerteans are eaten by other animals. *Cerebratulus lacteus* may be consumed by *Cyanea capillata* (Coe, 1943), *Limulus polyphemus* (Shuster, 1982) and the black-bellied plover, *Pluvialis squatarola* (Hicklin and Smith, 1979; Schneider and Harrington, 1981). Some nemerteans will feed on other nemerteans, e.g., *Micrura purpurea* has been observed feeding on the related nemertean *Micrura fasciolata* (Cantell, 1975) and *Emplectonema neesii* (Riches, 1893). Starved *Lineus sanguineus* will feed on *Amphiporus lactifloreus* (Jennings and Gibson, 1969). Small specimens of *Paranemertes peregrina* are preyed upon by the cephalaspidian gastropod *Aglaia diomedea*, and worms are sometimes consumed by black-bellied plovers (Roe, 1976, 1979). The gastropod *Tricolia* has been observed to eat *Carcinonemertes errans* (Wickham, personal communication).

Nemerteans (rarely identified) occasionally occur in the diet of fishes, polychaetes and crustaceans (e.g., Feller *et al.*, 1979; Jewett and Feder, 1980; Hacunda, 1981; Lasiak, 1982). Limited experimental studies have shown, however, that nemerteans were rejected by various species of predatory fishes and decapod crustaceans (Gib-

son, 1970; Kem, 1973; Prezant, 1979; Sundberg, 1979b; Prezant *et al.*, 1981; McDermott, 1984). Kem (1971, 1973) suggested that toxins of the nemertean body wall must serve as antipredatory adaptations. Such information is not in harmony, however, with the fact that *C. lacteus* and the large South African heteronemertean, *Polybrachiorhynchus dayi*, are commonly used, and often prized, as bait for sport fishing (Branch and Branch, 1981; McDermott, unpublished). These limited data suggest that nemerteans are more important as predators than prey.

FUTURE STUDIES ON FEEDING BIOLOGY

Effects of nemerteans on community structure are almost completely unknown, often misinterpreted and often ignored. The studies discussed herein, however, indicate that nemerteans are potentially important predators and perhaps influential scavengers in a variety of communities. Recent research, indicating the important role that *Nipponnemertes pulcher* may have on the *Haploops* community in the Danish Øresund, further emphasizes this point (McDermott, 1984).

Before the ecological relationships of these worms can be properly evaluated, more work is necessary in taxonomy. In addition, the feeding biology of many more species, especially with respect to quantitative information on trophic interactions between nemerteans and prey, needs to be investigated, so that the patterns we described can be tested and modified and hopefully become more predictive. No attention has been given to the whole sub-order Polystilifera.

Although the suctorial nemerteans present greater difficulties for analysis, some quantitative studies have begun in the *Zostera* community (McDermott, unpublished). By investigating feeding rates in laboratory situations and by determining densities of nemerteans and prey in nature, one can estimate the potential feeding impact of suctorial species. Laboratory data can be verified and enhanced by employing serological analysis on entire mud flat communities (Feller *et al.*, 1979) and on the amorphous gut contents of freshly col-

lected specimens, as have been done recently for *Prostoma* (Gisbon and Young, 1976) and *Paranemertes* (Feller *et al.*, 1979).

The role of nemerteans as prey is a virtually untouched area for study. Finally, the ecological role of prey or host metabolites in attracting nemerteans, needs considerable attention.

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