

## INTERACTIONS AMONG TEMPORARY AND PERMANENT MEIOFAUNA: OBSERVATIONS ON THE FEEDING AND BEHAVIOR OF SELECTED TAXA

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### ABSTRACT

Meiofauna diets and behavioral patterns are relatively unknown despite the fact that in any system, predatory relationships and behavioral responses may play an important role in determining community structure. Therefore, observations on food preferences, feeding behavior, and encounter interactions of members of a meiofauna assemblage were made in the laboratory in dishes of natural sediment. The diets and behavior of two turbellarian species, *Neochildia fusca* and *Archiloa wilsoni* were examined in detail. Both are predators and both feed on a variety of other taxa, including the temporary meiofauna. Based upon the results of these experiments, a potential food web was constructed among the temporary and permanent meiofauna. The behavioral responses of these turbellarians and other members of the meiofaunal assemblage at times of encounter were also observed, categorized, and quantified. Implications of these behaviors are discussed.

### INTRODUCTION

The meiofauna represent a very abundant and potentially important component of marine soft-sediment communities and yet knowledge about the feeding habits of and behavioral interactions among the meiofauna are scarce. The food preferences of some microbial-feeding harpacticoid copepods (Lee *et al.*, 1977; Rieper, 1978, 1982; Vanden Berghe and Bergmans, 1981) and nematodes (Tietjen and Lee, 1977) are partially known from experiments using radiolabeling techniques. Information about turbellarian diets arises mostly from remains visible in the guts of occasional animals (Straarup, 1970, and references therein), although a few largely anecdotal observations have been reported (Meixner, 1938; Pawlak, 1969; Straarup, 1970). For many turbellarian species, gut contents are unidentifiable, or items in the gut (such as diatom frustules) may have a secondary origin (*i.e.*, may have been present in the gut of the prey species consumed). Systematic observations of the feeding behavior of and the various predatory and aggressive behavioral interactions among the meiofauna are almost completely lacking.

In any system of interacting species, species recognition and differential behavioral responses at times of encounter should play a role in establishing and maintaining patterns of co-existence. Therefore, the study of behavioral interactions and natural history of the fauna is extremely important, especially since interpretations of manip-

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ulative field experiments often rest heavily on assumptions about the natural history and behavior of the manipulated species (Dayton, 1979; Peterson, 1979). If the manipulated species is known to be a predator on another species, then a reduction in the abundance of that prey species seems easily interpretable. However, behavioral avoidance of the manipulated species by the prey species could equally well explain lower densities of this prey species in experimental plots. Without some independent observation on mechanism, it is impossible to tell if the negative result of a manipulation is due to predation, behavioral avoidance, competition, or physical disturbance.

Therefore, observations on the food preferences, feeding behavior, and encounter interactions of members of a meiofauna assemblage were undertaken. Because the meiofauna are both small and live in the sediments, field observations are difficult. Thus laboratory experiments were designed to get initial information on some common meiofaunal taxa. Since so little is known about the diets of turbellarians, and yet turbellarian predators could be feeding on both permanent and temporary meiofauna (*i.e.*, the juvenile macrofauna, as defined by McIntyre, 1969), major emphasis was placed on determining the diets and behavioral patterns of two turbellarian species common in muddy-sand habitats, an acoel, *Neochildia fusca* (Bush, 1975), and a proseriate, *Archiloa wilsoni* (Stirewalt *et al.*, 1940). The behavioral responses of other assemblage members to encounter with these two turbellarian species were also observed.

#### MATERIALS AND METHODS

Sediment was collected from several shallow-water muddy-sand sites in Bogue and Back Sounds, North Carolina, but principally from Tar Landing Bay, a shallow-water embayment on the southeast end of Bogue Sound (34° 42' N, 76° 42' W). The surface 2 to 3 cm of sediment was collected and transported back to the laboratory. Sediment was then spooned into flasks and mixed with a MgCl<sub>2</sub> solution isotonic to seawater (30 ppt), shaken, and allowed to sit for 15 minutes. Then the flasks were shaken again, and the supernatant decanted through a 63  $\mu$ m sieve. The material collected on the sieve was rinsed gently with seawater, and the sieve placed in a Petri dish with a small amount of seawater. After at least 1 hour, sieves and Petri dishes were examined under a dissecting microscope and experimental animals were removed by pipette.

##### *Feeding experiments*

Experimental animals were placed into culture dishes (3 cm diameter) which contained approximately 5 ml of 63  $\mu$ m filtered natural seawater and approximately 1 ml of sediment in the center of the dish. Seawater in each dish was changed daily by pipette (under the microscope). Combinations of individual meiofauna and their suspected prey were established. Each combination was checked twice daily under the dissecting microscope to determine if the prey had been eaten. Animals usually stayed in the center of the dish, and could be easily located by spreading the sediment grains apart with a dissecting needle. As soon as the prey was eaten, or if, after three successive days, no predation had occurred, the trial was terminated.

Combinations of *Neochildia fusca* and *Archiloa wilsoni* with their suspected prey were emphasized. Unless otherwise stated, only robust, active individuals were used in the experiments. Some specific trials were made with wounded animals (either the body wall was pricked with the dissecting needle, or the shell was broken), to see if there was a greater response to prey in this condition.



### *Interaction observations*

Interactions between meiofauna (both permanent and temporary, *i.e.*, the juvenile macrofauna) were observed under two sets of conditions.

*Under the dissecting microscope (observations from above).* Specific pairs of meiofauna were placed in culture dishes, set up in the same way as in the feeding experiments, or whole assemblages were placed in Petri dishes with a layer of sediment several sand grains thick. The majority of the observations were made on animals in the Petri dish situation. Fields of view in the center of the Petri dish were haphazardly located until an individual was observed. This individual was then observed until it disappeared under the sediment surface again or 30 min had passed. Then a new field of view and a new individual were located to prevent making too many observations on the same individual. Usually, this was not a problem, as animals disappeared from view long before the half hour was over. After several such observations, major encounter types and responses were put into categories and the frequency of each response to a particular type of encounter was recorded. Truly unique behaviors also were recorded separately.

*Under the inverted microscope (observations from below).* Again, whole assemblages were placed in Petri dishes with enough sediment to cover the dish completely with a layer of sediment several sand grains thick. Since most meiofauna are positively geotactic (Boaden, 1977) and burrow down into the sediments, this was an attempt to observe the animals in as nearly a natural condition as possible. A red filter was placed over the light source to minimize light interference with behavior. Observations were made in the same manner as under the dissecting microscope.

More than 500 hours were spent observing these animals, about 400 from above, and 100 from below. A total of more than 1600 interactions were witnessed. Observations from above and below were combined in all the following tables.

### *Observations on undisturbed sediment cores*

Square cores (10 cm by 10 cm) were taken with a coring box which fit into a freezer box with the same dimensions. Cores were covered, transported back to the laboratory and placed in aquaria with running seawater, uncovered, and left for approximately 12 hours. Then an individual core was placed into a smaller aquarium where the surface of the core was covered by approximately 3 cm of seawater and over which a dissecting microscope was mounted on a swing arm. Again fields of view were located haphazardly, and no individual was watched for more than one half hour. Observations were made on the animals visible or appearing at the sediment surface. All observations were timed and all animal movements were recorded.

## RESULTS

### *Feeding experiments*

Both *Neochildia* and *Archiloa* did eat a wide variety of the prey species offered, including both temporary and permanent meiofauna (Table I). But both also could be very selective in some instances, for example neither would eat the maldanid *Axiiothella mucosa*, but both would eat *Clymenella torquata*. *Archiloa* fed much more readily on nematodes and copepods than *Neochildia* did. Neither ate bivalves, and *Neochildia* would not eat juvenile amphipods. The percentage eaten in Table I includes both animals completely consumed and those where one third or more of the body was missing. These animals usually died within 24 hours. Table II summarizes these incidences of partial predation. *Archiloa* was much more prone to eat only part of its



TABLE I

The results of the feeding experiments with *Neochildia fusca* and *Archiloea wilsoni*

Prey species	<i>Neochildia fusca</i>		<i>Archiloea wilsoni</i>	
	n	% eaten	n	% eaten
Temporary Meiofauna				
Spionidae				
<i>Streblospio benedicti</i>				
7–12 setigers	5	100	5	80
13–18 setigers	11	73	12	58
>18 setigers	6	33	6	33
<i>Polydora</i> sp	2	50	3	0
<i>Prionospio</i> sp	3	100	3	67
Capitellidae				
<i>Mediomastus</i> sp	3	100	3	100
<i>Heteromastus filiformis</i>	4	100	3	67
<i>Capitella</i> sp	3	67	3	67
Cirratulidae				
<10 setigers	5	60	5	40
>10 setigers	2	50	5	40
Orbiniidae	5	80	3	33
Maldanidae				
<i>Clymenella torquata</i>	4	50	3	33
<i>Axiiothella mucosa</i>	3	0	3	0
Terebellidae	4	25	4	25
Nereidae				
<7 setigers	4	50	3	0
8–12 setigers	4	0	6	50
>12 setigers	3	0	3	0
Nephtyidae	3	33	2	0
Hesionidae	3	0	3	0
Syllidae				
<8 setigers	3	33	3	0
>8 setigers	3	0	3	0
Arabellidae				
<i>Drilonereis magna</i>	not tested		2	0
Oligochaeta				
<1 mm	6	67	7	86
> 1 mm	4	0	4	50
Bivalvia	4	0	6	0
Amphipoda	3	0	4	50
Permanent Meiofauna				
Nematoda	6	0	9	55
Copepoda				
<i>Enhydrosoma</i> sp	4	0	9	67
Others	8	25	6	60
Turbellaria				
<i>Neochildia fusca</i>	6	0	9	0
<i>Archiola wilsoni</i>	9	89	6	0
<i>Convoluta</i> sp	7	57	7	71
<i>Macrostomum beaufortensis</i>	2	50	3	0
Species A	3	67	3	33
Species B (acoel)	3	33	3	67
Ostracoda	2	0	3	0
Gastrotricha				
<i>Turbanella</i>	not tested		2	0

n = the number of trials with that potential prey taxon.  
% eaten = the percentage of trials in which *Neochildia* or *Archiloea* consumed the prey.



TABLE II

*Incidences of partial predation by Neochildia fusca and Archiloea wilsoni*

<i>Neochildia fusca</i>	Partial predation	Total no. eaten	<i>Archiloea wilsoni</i>	Partial predation	Total no. eaten
Oligochaeta >1 mm	1	1	<i>Streblospio benedicti</i>		
Terebellidae	1	1	>18 setigers	1	2
Nephtyidae	1	1	Oligochaeta >1 mm	1	6
Orbiniidae	1	4	Capitellidae		
			<i>Heteromastus filiformis</i>	1	2
			Cirratulidae		
			>10 setigers	1	2
			Nereidae		
			8–12 setigers	3	4
			Nematoda	2	5

The partial predation column represents the number of times where less than the whole animal was consumed. The total no. eaten column represents the total number of individuals eaten in the feeding experiments.

prey than was *Neochildia*. Also *Archiloea* ate almost every wounded animal which was offered to it (Table III), whereas *Neochildia* did not eat a single wounded animal.

#### *Behavioral observations*

*Neochildia fusca*. *Neochildia fusca* is a relatively large (0.1–3 mm in length) elongated-oval shaped turbellarian with a ventral mouth in approximately the center of the body. *Neochildia*, like all acoels, does not have a true gut, but rather a central digestive parenchyma. *Neochildia* moves rapidly and easily through the sediment. It employs several different strategies in feeding. The first is a “sit and wait” strategy. The posterior portion of the body is anchored down in the sediment and the anterior one half to two thirds of the body is arched up above the sediment with the sides of the body folded slightly underneath and inward. Bush (1975) also observed this behavior and as she notes, it makes the animal an excellent trap for passing prey. An animal moving under the raised end of the turbellarian is quickly pounced upon. The cupped portion of *Neochildia*’s body serves to hold the prey from escaping as it is quickly pushed and sucked up into the mouth.

TABLE III

*Incidences of predation on wounded animals*

Prey species	<i>Neochildia fusca</i>	<i>Archiloea wilsoni</i>
<i>Streblospio benedicti</i> 13–18 setigers	0	3
Terebellidae	0	3
Copepoda	0	4
Bivalvia (broken shell)	0	2
Oligochaeta	0	3

*Streblospio*, terebellids, copepods, and oligochaetes were pricked with a dissecting needle. The bivalve shells were broken with forceps. Four replicates of each taxa were offered to each of the two turbellarians.



TABLE IV

*Response of Neochildia fusca to encounter with a variety of other taxa*

Other taxa	Encounter type	Response of <i>Neochildia fusca</i>			
		Violent recoil	Stop, back away	Move over	Attack
<i>Streblospio benedicti</i> , sm.	Head on	0	4	9	2
	Side on	0	2	10	7
<i>Streblospio benedicti</i> , med.	Head on	0	7	6	3
	Side on	0	1	9	7
<i>Streblospio benedicti</i> , lg.	Head on	1	6	4	1
	Side on	0	3	8	5
<i>Polydora</i> spp.	Head on	0	7	3	0
	Side on	0	4	7	4
unmetamorphosed spionid larvae		2	5	0	0
Capitellidae	Head on	1	4	3	1
	Side on	0	2	6	3
Cirratulidae	Head on	2	4	1	0
	Side on	0	6	5	3
Orbiniidae	Head on	1	5	2	0
	Side on	0	4	7	2
<i>Clymenella torquata</i>	Head on	0	3	3	0
	Side on	0	2	5	1
<i>Axiiothella mucosa</i>	Head on	0	4	2	0
	Side on	0	5	7	0
Terebellidae	Head on	4	3	1	0
	Side on	0	4	3	1
Nereidae, sm.	Head on	0	1	7	0
	Side on	0	1	8	1
Nereidae, med.	Head on	2	6	7	0
	Side on	0	8	9	0
Syllidae, sm.	Head on	0	2	5	0
	Side on	0	1	7	1
Syllidae, med.	Head on	1	6	2	0
	Side on	0	5	6	0
<i>Glycera</i> sp.	Head on	1	5	0	0
	Side on	0	4	2	0
Oligochaeta	Head on	0	4	8	1
	Side on	0	3	10	5
Bivalvia		0	3	5	2
Nematoda	Head on	0	3	1	0
	Side on	0	4	8	0
Copepoda	Head on	0	6	3	0
	Side on	0	4	7	1



TABLE IV (Continued)

Other taxa	Encounter type	Response of <i>Neochildia fusca</i>			
		Violent recoil	Stop, back away	Move over	Attack
<i>Neochildia fusca</i>	Head on	14	0	0	0
	Side on	12	3	0	0
<i>Archiloa wilsoni</i>	Head on	0	3	5	6
	Side on	0	1	8	12
<i>Convoluta</i> sp.	Head on	0	3	5	0
	Side on	0	3	6	2
Ostracoda		0	2	5	0

See text for more complete descriptions of encounter type and response categories. Sm., med., lg. refer to the sizes listed in Table I.

Other strategies are more active. *Neochildia* often swims along the surface of the sediment, again with the anterior end of the body slightly raised and cupped inward. It also moves through the sediment in a flattened position. When a prey is encountered on its side or from the rear, *Neochildia* very rapidly moves over it or pins it to a sand grain, again cupping its body around the prey to prevent escape. Events of partial predation usually occurred with larger, vermiform prey. The victim's body was broken off when there appeared to be no more room in *Neochildia*'s digestive parenchyma. However *Neochildia*'s central parenchyma appeared to be very extensible, and *Neochildia* ate many animals as big or slightly bigger than itself.

Encounter types were put into two categories, head on, and side on. Head on is defined as the meeting of the animal being observed (in this case *Neochildia*) and the other animal on the anterior most one fourth of the body (for turbellarians and nematodes) or the part of the body defined as the head (for polychaetes, oligochaetes, and copepods). Side on is defined as the meeting of the head of the animal being observed with the lower three fourths of the body of the animal it encounters.

Responses of the animal under observation were put into four categories; (1) violent recoil, (2) stop and back away, (3) move over or under, and (4) attack. For *Neochildia*, these categories are further defined as follows: (1) violent recoil—as soon as body contact is made between the two animals, *Neochildia* immediately and violently draws back by very abruptly contracting the muscles in the anterior end of the body. This is immediately followed by a change in direction and rapid movement away from the animal it just encountered. (2) Stop and back away—when body contact is made, *Neochildia* quickly stops forward motion, then moves backwards and away from the animal it encountered. When forward motion ceases, the body does not contract as it does in category one. (3) Move over or under—*Neochildia* simply changes the plane of motion very slightly and moves over or under the animal it encountered. (4) Attack—*Neochildia* may back off for a fraction of a second, but then rapidly moves over the animal it encountered, cups its body around it, and then consumes, or tries to consume all or part of it.

Table IV summarizes *Neochildia*'s responses to both types of encounter with a wide variety of other taxa. The violent recoil reaction never occurred when *Neochildia* encountered the other individual on the side except in the case of *Neochildia*-*Neochildia*



interactions. This strong intraspecific avoidance reaction was more pronounced than *Neochildia*'s reaction to any other species. With all taxa, *Neochildia* was much more likely to attack and eat an individual if it was encountered from the side rather than head on.

The two attacks on bivalves were both unsuccessful. In both cases, *Neochildia* encountered the foot of the bivalve and then cupped its body around the clam. However, the bivalve quickly withdrew its foot and closed its shell before *Neochildia* could ingest any clam body parts, and *Neochildia* did not try to engulf the whole animal, shell and all. Once the bivalve was closed, *Neochildia* let go of it and moved on.

*Archiloea wilsoni*. *Archiloea* is slightly smaller than *Neochildia* (0.1–2 mm length) and thinner with a pointed tail. The mouth, with a long, cylindrical plicate pharynx, is located about two thirds of the way down the body, opening on the ventral side. It also moves readily and rapidly through the sediment. The feeding behavior of *Archiloea* was observed much less often than that of *Neochildia* even though more individuals of this species were observed. It rarely ate the first day after extraction. In the feeding experiments, its prey, with few exceptions, were only found missing on the second or third day. Initially some animals were observed until the sixth day. However if *Archiloea* had not eaten by day 3, it never ate. By day 4, it appeared emaciated and behaved abnormally.

The feeding behavior of *Archiloea* was similar with all types of prey. After encountering a potential prey, *Archiloea* would swim along side of it, quickly evert its pharynx, thrust it into the victim, and suck the animal, or only the internal organs and fluids, into its own digestive cavity. Copepods were attacked on the ventral side, between the legs. Usually the carapace was not ingested. Several times with larger polychaetes, only a portion of the body was consumed before the animal broke away or was released by *Archiloea*. This must have been the case with the victims of partial predation in Table II. Once with a larger spionid and twice with larger oligochaetes, *Archiloea* would feed for a minute or two, then begin to move through the sediment with the victim still only partly ingested, but still tightly held by the pharynx. With one oligochaete, a few minutes later *Archiloea* stopped and ingested a little more of its victim, then started moving again. Eventually, in all three cases, the sand grains pulled what remained of the prey away from the pharynx, and *Archiloea* kept going without it.

*Archiloea* readily preyed on wounded animals (Table III). This was first observed with a copepod, and subsequently with another copepod and an oligochaete. In all three of these cases, within 5 minutes, *Archiloea* swam over to the injured individual, moved along side of it, then quickly attacked and ate it.

Encounter types and categories of responses are defined for *Archiloea* as they were for *Neochildia*, except for attack. In an attack, *Archiloea* swims along side the encountered animal, and rapidly everts the pharynx trying to thrust it into its victim to consume all or part of it.

Table V summarizes *Archiloea*'s responses to encounter with other taxa. *Archiloea* showed the violent recoil reaction to a much wider array of taxa than did *Neochildia*. Again, however, this response was much more common in head on encounters than in encounters to the side. The response of *Archiloea* to intraspecific encounters most frequently yielded the violent recoil reaction, but not as overwhelmingly as *Neochildia*'s reaction to intraspecific encounter. In all encounters of *Archiloea* with *Neochildia*, the response was the violent recoil. Several times after an encounter of this type, *Neochildia* quickly turned, chased, and attacked *Archiloea*. Three of *Archiloea*'s attacks on *Streblospio* (2 medium, 1 large) were not completed. The pharynx was everted and touched *Streblospio*'s body, but there appeared to be no suction and the animal was quickly released.



TABLE V

*Responses of Archiloea wilsoni to encounter with a variety of other taxa*

Other taxa	Encounter type	Response of <i>Archiloea wilsoni</i>			
		Violent recoil	Stop, back away	Move over	Attack
<i>Streblospio benedicti</i> , sm.	Head on	0	12	17	2
	Side on	0	10	14	7
<i>Streblospio benedicti</i> , med.	Head on	2	17	13	1
	Side on	0	12	11	6
<i>Streblospio benedicti</i> , lg.	Head on	3	9	8	0
	Side on	0	6	5	4
<i>Polydora</i> spp.	Head on	0	3	5	0
	Side on	0	4	6	2
Unmetamorphosed spionid larvae		4	8	0	0
Capitellidae	Head on	3	5	4	1
	Side on	0	3	5	4
Cirratulidae	Head on	5	6	0	0
	Side on	0	3	5	2
Orbiniidae	Head on	3	6	1	0
	Side on	1	2	4	2
<i>Clymenella torquata</i>	Head on	2	3	1	0
	Side on	1	4	1	1
<i>Axiiothella mucosa</i>	Head on	3	4	2	0
	Side on	1	3	4	0
Terebellidae	Head on	4	4	1	0
	Side on	2	5	4	1
Nereidae, sm.	Head on	1	2	4	0
	Side on	0	2	5	0
Nereidae, med.	Head on	3	4	3	0
	Side on	0	2	4	1
Syllidae, med.	Head on	1	4	1	0
	Side on	0	3	4	0
<i>Glycera</i> sp.	Head on	1	5	0	0
	Side on	0	3	2	0
Oligochaeta	Head on	0	7	2	0
	Side on	0	1	4	5
Bivalvia		0	1	8	0
Nematoda	Head on	0	2	1	0
	Side on	0	4	6	1
Copepoda	Head on	0	6	1	0
	Side on	0	8	3	2
<i>Neochilda fusca</i>	Head on	18	0	0	0
	Side on	20	0	0	0
<i>Archiloea wilsoni</i>	Head on	7	6	0	0
	Side on	8	3	0	0
<i>Convoluta</i> sp.	Head on	0	2	5	0
	Side on	0	1	6	2
Ostracoda		0	3	7	0

See text for more complete descriptions of encounter type and response categories. Sm, med., lg. refer to the sizes listed in Table I.



*Enhydrosoma* sp. *Enhydrosoma* is frequently the most abundant harpacticoid copepod in the Tar Landing Bay assemblage. It is a small (200–500  $\mu\text{m}$ ) vermiform copepod which moves easily and quickly between and around sand grains. It is assumed to be a deposit feeder. Some observations were made (Table VI). Encounter types are as described for *Neochildia*. Response categories differ as follows. (1) Violent recoil—no perceptible stopping is observed. *Enhydrosoma* nearly instantaneously changes direction  $180^\circ$  and rapidly swims away from the encountered individual. (2) Stop and move away—All forward motion ceases. Then *Enhydrosoma* changes direction and swims away. The primary difference between this response and the first response is in the presence of the stop and the speed with which the whole reaction takes place. (3) Move over or under—as with *Neochildia*, the plane of movement is slightly altered, and *Enhydrosoma* simply swims over, under, or around the encountered animal. (4) Circle—the response category is unique to *Enhydrosoma*. It simply moves off the animal, then swims around it in a circle several times, appearing occasionally to touch it with the legs or antennae.

The circle response was exhibited particularly to *Streblospio* and bivalves (Table VI). In the case of *Streblospio*, the response seemed to be elicited by encounter with the partial tube of *Streblospio* as much as it was by an encounter with the animal itself. The violent recoil response was only exhibited in six cases, all of these head on

TABLE VI

*Responses of Enhydrosoma sp. to encounter with a variety of other taxa*

Other taxa	Encounter type	Response of <i>Enhydrosoma</i> sp.			
		Violent recoil	Stop, move away	Move over/under	Circle
<i>Streblospio benedicti</i>	Head on	2	1	1	0
	Side on	0	2	5	4
Capitellidae	Head on	0	2	3	1
	Side on	0	0	4	3
<i>Axiiothella mucosa</i>	Head	0	3	0	0
	Side on	0	1	1	2
Oligochaeta	Head on	2	1	1	0
	Side on	0	3	0	0
Bivalvia		0	0	1	4
Nematoda	Head on	0	3	0	0
	Side on	0	1	9	0
Copepoda, other	Head on	0	4	3	0
	Side on	0	3	4	0
Small Turbellaria	Head on	0	2	5	0
	Side on	0	1	6	0
<i>Neochildia fusca</i>	Head on	1	4	2	0
	Side on	0	4	4	0
<i>Archiloea wilsoni</i>	Head on	1	3	1	0
	Side on	0	3	3	0

See text for more complete descriptions of encounter type and response categories.



encounters. While major attention was focused on *Enhydrosoma* in these observations, some note was taken of what the other animal did after *Enhydrosoma* encountered it. Bivalves quickly closed their shells. Particularly when the circle response was initiated, *Streblospio*, capitellids, and *Axiiothella* withdrew or tried to move away from *Enhydrosoma*. Nematodes always responded by moving away.

*Nematodes.* Identification of nematodes was not undertaken. Therefore it is not known how many species are included in this group. The only criterion used in selecting individuals to observe was reasonably large size. These results are only intended to indicate the general breadth of nematode behavior. Encounter types and response categories are as described for *Enhydrosoma*, except that the direction change in violent recoil is rarely as great as  $180^\circ$ .

Nematodes move through the sediments by both pushing on sand grains and moving sand grains from their directional paths (Pitcher, 1975). When there is very little sediment, nematodes flex their muscles, but do not move in any direction, and simply whiplash back and forth. This behavior was observed frequently in culture dishes, and did sometimes result in damage to individuals of other species (*i.e.*, tentacle loss in spionids). However when sufficient sediment is present, muscle contraction results only in the nematode moving quickly through the sediment. Therefore only reactions seen while following nematodes in sufficient sediment in Petri dishes are reported here.

Table VII summarizes the responses of nematodes to other taxa. Like the two turbellarians and *Enhydrosoma*, the violent recoil response most often followed head on encounters. Unlike the two turbellarians, the nematode-nematode encounter did not yield the violent recoil reaction. In most cases the two nematodes simply moved past each other, or stopped, changed direction, and moved away from each other. In general, the other taxa responded to nematode encounter by movement away.

Nematodes are known to excrete mucus (Riemann and Schrage, 1978). Some secrete copious amounts which very visibly binds the sediment and detritus together in long strings. This mucus apparently remains sticky for quite awhile after it has been secreted, and I have often observed that other meiofauna become tangled in this mucus. In four cases, these tangled individuals were encountered by one of the two turbellarians predators, and became easy prey, as they could not swim away.

*Temporary meiofauna.* Reactions of temporary meiofauna to encounters with *Neochildia* and *Archiloa* also were observed (Table VIII). Because many of these taxa are not mobile, following an individual and recording its responses to encounter with other individuals was not always feasible. Therefore animals were first observed and put into mobility categories. Sedentary species never moved more than half a body length. The two maldanid species (*Clymenella torquata*, *Axiiothella mucosa*) would construct partial tubes around themselves and usually only moved within the confines of these tubes. The occasionally mobile taxa usually stayed in one place, but would occasionally move away a short distance, and then remain stationary again. The spionids (*Streblospio benedicti* and *Polydora* sp.) also constructed tubes around themselves and would move their anterior ends in and out of the tube, but only occasionally would leave their tubes and move to a new area. This was usually in response to some outside disturbance. Sedentary and occasionally mobile taxa were observed in place. Since they rarely ran into other individuals, their responses to other animals running into their head region were also recorded. Mobile taxa moved actively through the sediments and were followed through the sediments in the same manner as before.

Responses of these temporary meiofauna to *Neochildia fusca* and *Archiloa wilsoni* again were put into categories. The categories are defined as follows: (1) withdraw—the animal rapidly draws back into its tube in the case of the tube dwellers, or simply



TABLE VII

*Responses of nematodes to encounter with a variety of other taxa*

Other taxa	Encounter type	Response of Nematoda		
		Violent recoil	Stop, back away	Move over
<i>Streblospio benedicti</i>	Head on	2	3	0
	Side on	2	5	3
Capitellidae	Head on	2	3	0
	Side on	0	3	5
Terebellidae	Head on	3	3	0
	Side on	0	2	5
Oligochaeta	Head on	2	4	0
	Side on	0	6	6
Bivalvia		0	2	8
Nematoda	Head on	1	4	3
	Side on	0	3	4
Copepoda	Head on	2	3	0
	Side on	2	5	3
<i>Neochilda fusca</i>	Head on	2	4	0
	Side on	1	3	1
<i>Archiloea wilsoni</i>	Head on	3	4	0
	Side on	0	5	1
Small Turbellaria	Head on	3	4	4
	Side on	0	5	6

See text for more complete descriptions encounter type and response categories.

draws or backs away rapidly in the case of the non-tube dwellers. This response does not include movement of more than one body length of the animal. (2) Move away—the animal may draw back momentarily, but then quickly moves off in a direction away from the turbellarian it encountered. (3) Move forward—the animal moves forward, directly into the turbellarian it has just encountered, forcing it to alter its path. (4) No movement—the animal simply stops all forward motion and remains still.

The spionids responded to both turbellarians in the same way, either withdrawing into the tube and then just remaining there for several minutes afterwards, or by moving out of the tube and away from the turbellarian. Moving out of the tube twice resulted in the spionid being chased and eaten by *Neochilda*. *Archiloea* on two occasions went down into a spionid tube after the animal withdrew. In neither case, however, did *Archiloea* attack the spionid. This does not, however imply that *Archiloea* could not attack and eat a spionid in its tube.

Terebellids also responded in one of two ways. If the encounter was with one or several of the terebellid's tentacles, it would draw in the tentacles and back away. However if the encounter was with the very base of the tentacle or with the head of the animal, it immediately and violently moved forward, thrashing its tentacles and whiplashing its body. This response quickly moved the animal away from the turbellarian, and made it very difficult to chase and capture.



TABLE VIII  
Responses of temporary meiofauna to encounter with *Neochildia fusca* and *Archiloa wilsoni*

Macrofaunal taxa	Mobility	Neochildia fusca				Archiloa wilsoni				
		With- draw	Move away	Move forward	No movement	With- draw	Move away	Move forward	No movement	
Streblospio benedicti	Occasionally mobile	12	7	0	0	11	5	0	1	
Polydora spp.	Occasionally mobile	10	8	0	0	9	6	0	0	
Capitellidae	Mobile	12	7	0	0	7	6	0	0	
Cirratullidae	Occasionally mobile	9	6	0	0	7	5	0	0	
Orbiniidae	Occasionally mobile	4	9	0	0	3	8	0	0	
Chlymenella torquata	Sedentary	8	2	0	2	4	3	0	4	
Axiobella mucosa	Sedentary	2	9	0	0	3	8	0	0	
Terebellidae	Sedentary	10	0	11	0	9	0	13	0	
Nereidae	Mobile	0	4	9	7	0	4	6	7	
Syllidae	Mobile	0	5	6	8	0	3	4	5	
Glycera sp.	Mobile	0	1	7	4	0	0	5	6	
Arabellidae	Mobile	1	2	0	6	1	0	1	5	
Oligochaeta	Mobile	0	13	0	4	0	10	0	0	
Bivalvia	Occasionally mobile		Shell closure (6)				Shell closure (7)			
Unmetamorphosed spionid larvae	Mobile		Balls up, spines protruding				Balls up, spines protruding			

See text for more detailed descriptions of categories.



Cirratulids responded, like spionids, by either withdrawing (though they did not build tubes, so they just moved back) or moving away. On one occasion each with both *Neochildia* and *Archiloa*, the animal autonomized part of its gills and left them behind.

Among the four mobile, predatory taxa (syllids, nereids, *Glycera*, and arabellids), withdrawal was almost never a response. *Glycera* on two occasions everted its pharynx upon encountering *Neochildia*, although on neither occasion did it successfully hit the turbellarian. Three nereids also everted their jaws (at 2 *Neochildia*, 1 *Archiloa*) although they also did not actually catch the turbellarian.

On all occasions, bivalves responded to turbellarians by drawing in the foot and closing up the shell. The bivalve usually remained closed for several (2–5) minutes after the encounter.

### *Observations of undisturbed sediment cores*

These observations showed that most of the permanent meiofauna spend very little time exposed on the sediment surface. Animals frequently moved just under the uppermost layer of sand grains. In over 30 hours of observations, nematodes were never seen on the surface for more than a few seconds. They would break the sediment surface, then quickly burrow back down again. Copepods, turbellarians, and ostracods were more active on the surface, but still spent the majority of their time in the sediment. Copepod and ostracod movements were responsible for stirring up and moving around fecal pellets and sediment grains.

Both *Neochildia* and *Archiloa* frequently came to the surface, would move along the surface for a short while (30 s to 5 min), then burrowed back down underneath the sediment grains again. Only one attack on the surface was witnessed. This was a *Neochildia* which swam (flat) into another small turbellarian (*Convoluta* sp.), pinned it to a sediment grain, and ate it. Right after ingestion, *Neochildia* moved below the sediment surface again.

Spionids were active in the cores. A few juvenile *Streblospio* were observed feeding, usually with the tentacles up in the water column. Copepods sometimes swam into the base of a *Streblospio* tube, which resulted in the spionid's withdrawal response in three out of five encounters. A large epibenthic copepod simply swam up into the water column and swam over *Streblospio*'s tentacle field. One *Archiloa* was observed swimming around a *Streblospio* tube, after which it burrowed down between the sediment grains near the tube.

## DISCUSSION

### *Feeding experiments*

In interpreting feeding experiments of this type, it is important to remember that what an animal does in the laboratory is not always the same as what it does in nature. These experiments offered the turbellarians only one potential food source at a time. In nature, they, of course, would have a whole range of food sources to choose from. Nevertheless, these experiments do adequately test the simple capability and/or inclination of the predators to eat the various prey offered to them and indicate the general breadth of their diets.

Clearly *Neochildia fusca* and *Archiloa wilsoni* share a number of prey species in common. However it is difficult to make comparisons between species on relative preference for a particular prey species since *Archiloa* was somewhat more reluctant to feed in the laboratory. Very large differences in percentages eaten (Table I) though



may in fact be meaningful. *Archiloea* seemed to have a greater preference for copepods, juvenile amphipods, and nematodes than did *Neochildia*. This may have something to do with the way each feeds. A copepod or amphipod, with its unmalleable carapace may be difficult for *Neochildia* to stuff into its mouth. Nematodes may be difficult for *Neochildia* to pin down and/or position under its mouth. Bush (1975), however, reports finding copepod and nematode pieces in the parenchyma of mature *Neochildia*. Thus, either *Neochildia* will occasionally feed on these animals, or these animals were in the gut of another prey species which *Neochildia* ate, like *Archiloea*, a nereid, or a syllid.

It is difficult to know exactly why *Clymenella* was eaten by both turbellarians, and the confamilial *Axiiothella* was not (Table I). *Clymenella* has a pelagic larval stage, while *Axiiothella* has benthic larvae which develop in a mucus egg case (Newell, 1951). *Axiiothella* is not available to the turbellarians until it leaves the egg case. Both *Neochildia* and *Archiloea* seem to be incapable of penetrating the egg case. The juvenile *Axiiothella* offered were those which had just left the decomposing egg case, and perhaps had a bit of the mucus still clinging to their bodies. Maybe this mucus prevents their being recognized as prey upon encounter. The replication of these trials was not as large as with some others, so the possibility remains that these results are artificial. The behavioral observations (Tables IV, V) also show an attack on *Clymenella* and not *Axiiothella*, but generally the turbellarians withdrew from, or ignored both mal-danids.

*Archiloea* was much more likely to consume only part of its prey than was *Neochildia*. Again this may largely be due to differences in feeding mechanisms. *Neochildia* consumed its prey with extraordinary speed and its central parenchyma is extremely extensible. There is very little time for the prey to escape. *Archiloea* takes much longer to suck out or consume its prey, and is less effective in pinning its prey down, affording the prey greater opportunity for escape. Also, *Archiloea* is not capable of entirely consuming a prey individual much larger than itself (as a  $>1$  mm oligochaete is). A portion of these larger prey appears to be enough to completely fill the gut.

It has been suggested that patterns of turbellarian feeding are directly related to the type of pharynx that each turbellarian possesses (Meixner, 1938; Hyman, 1951; Bilio, 1967; Straarup, 1970). Turbellarians with simple pharynges or lacking pharynges must engulf their prey whole, and thus are limited in the size of prey that they can ingest. Those with plicate or rosulate pharynges which are eversible are able to suck out larger prey. The results of these experiments tend to support this idea. *Archiloea*, with its plicate pharynx, was able to feed on some large prey (*i.e.*, large oligochaetes and nereids) which seemed to be unavailable to *Neochildia* which does not have a pharynx (Table I).

The difference in response of *Neochildia* and *Archiloea* to wounded prey was striking (Table III). Other proseriates have been found in the field clumped around dead animals (Bush, 1966) or have been collected using freshly killed meat as bait (Bush, 1966; Riser, 1981). Vernberg and Coull (1981) reported proseriates swarming around and rapidly consuming recently killed copepods, and suggested that these flatworms had chemotactic abilities. Perhaps the proseriates as a group are able to biochemically detect the presence of wounded animals, by diffusing body fluids, and follow the gradient in these fluids to their source. Also relying on baited trap evidence, Gerlach (1977) suggested that nematodes could do this. If *Archiloea* is at least partially a scavenger as much as a true predator, this would make available to it a food resource which *Neochildia* does not appear to utilize.

Clearly the temporary meiofauna are potentially an important component of both these turbellarian's diets, however the temporary meiofauna are not always abundant. During the times of the year when young macrofauna are not settling in high densities,



perhaps food does become limiting. The seasonal influx of large numbers of juvenile polychaetes may allow turbellarian densities to increase to a level not otherwise possible, and may give some of the other permanent meiofauna, such as the copepods, some relief from intense predation, and the opportunity for population density increase as well.

### *Behavioral observations*

Neither observational method, from above or below, proved to be superior to the other. In both cases, if sediment is present in the dish, as it must be for observations to even approach natural conditions, animals are lost from view as soon as they move under or over a single layer of sand grains. This is the major stumbling block to good observations of meiofauna behavior. Even when the animals are visible, they will only be doing something of interest to the observer (like encountering each other) in a fraction of that time. I chose to do more observations from above because the dissecting microscope, with its zoom lens, made it possible to follow an animal longer when it did appear (by zooming down to lower power if it was moving out of the field of view too quickly), or to see something in more detail as it was happening (by zooming up to a higher power). Switching lenses on the inverted scope to do this often resulted in losing the animal or missing the action. Thus perhaps the most important criterion is not viewing angle, but the lens capabilities of the microscope.

Because time was taken to observe these animals in the sediments, most behaviors observed probably do approach natural responses. Mobile taxa moved around, tubedwellers did build tubes. The angle of the tubes was probably more horizontal than it would have been in the field and appeared in the undisturbed cores, and it is possible there is some artifact associated with this. Juvenile terebellids did not construct well defined tubes or burrows, but only covered themselves with a few sediment grains and detritus particles and laid on the surface of the sediments. This may be normal behavior for juvenile terebellids. Hunt (1981) speculated that juvenile terebellids may be relatively immobile as soon as they settle, but did not know whether they constructed burrows immediately. A juvenile terebellid has only a few tentacles and very incomplete segmentation. The whiplash/thrashing response is a good indication that the musculature is already fairly well developed, but most polychaetes rely on complete inter-segmental walls and a complete coelom to burrow efficiently (Trueman and Ansell, 1969). Juveniles may not yet be capable of effective burrowing. The whiplash response may be a uniquely juvenile response, which effectively protects them from small predators like turbellarians, until they are able to burrow into the sediments, and can respond by withdrawal, or they are simply too big to be eaten by these predators.

Many side encounters of *Neochildia* and *Archiloa* occurred with *Streblospio* (Tables IV, V). In dishes of sediment, *Streblospio* builds a tube which may be shorter than it is in nature. When *Streblospio* is withdrawn in its tube, often its posterior end would be out of the end of the tube, and attack would occur on this portion of the animal. Of course *Streblospio* had no tube when dishes of animals were first established, and during this time, animals encountered on the side were very frequently attacked and eaten. Extrapolating to nature then, *Streblospio* is probably most vulnerable right after settlement, but before it has constructed a complete tube. Once the tube is made, the animal is afforded some protection, but is still vulnerable to (less frequent) head on attack when extended out of the tube, or attack from behind when the animal is down in the base of its tube. Since it is nearly impossible to observe animals in the base of their tubes in the natural bottom (or in undisturbed cores), I do not know how common the latter may be. Certainly as the animal grows larger, and its tube extends below the



redox layer where these turbellarians are not found, attack from behind would not occur. Also the natural sediments tend to be more consolidated than sediments in a Petri dish, and penetration of the spionid beyond the end of the tube is probably more difficult and less common.

All the animals observed responded much more abruptly to head on encounters than to side on encounters (Tables IV–VII). For the predators (*Neochildia* and *Archiloa*), the overwhelming majority of attacks on prey came from the side rather than from the front. Most of the sensory apparatus is located on the anterior of these animals. Perhaps the response of the prey is important in the decision to attack. In head on encounter, the potential prey has also just sensed the presence of the predator, and is in equally good position to react in a way which might injure the predator. In side encounter, the prey may not be “aware” of what has just touched its side (predator or benign species), or even that something has encountered it, and may make no attempt to move away.

The temporary meiofauna can be divided into two groups based on their responses to encounters with *Neochildia* and *Archiloa*. The first group responded by withdrawal or movement away from the turbellarians (spionids, capitellids, orbinids, cirratulids, maldanids, oligochaetes), whereas the second group either did not respond at all, or continued moving forward, forcing the turbellarian out of its way (syllids, nereids, glycerids, arabellids) (Table VIII). The first group consists of non-aggressive, largely deposit feeding taxa (Fauchald and Jumars, 1979; pers. obs.). Despite the ability of some spionids to interact aggressively intrafamiliarily (Levin, 1981), spionids and indeed all the taxa in group one probably have little defense against a predator except moving away. The taxa in group two are all themselves predatory (Fauchald and Jumars, 1979) and aggressive. They could defend themselves against, and even prey upon these turbellarians, although I never witnessed such predation.

Avoidance reactions, particularly the movement away of the taxa in group one above, and the unique thrashing movement of terebellid juveniles are, of course, adaptive, since both *Neochildia* and *Archiloa* can prey on these animals. However, independent of such predation, these reactions could result in negative correlations between densities of both *Neochildia* and *Archiloa* and these taxa in the natural environment. Data from other field experiments (Watzin, 1983), show that experimental increases in turbellarian density did result in reduced densities of some of these groups. Both predation and behavioral avoidance probably contributed to this result. A survey of benthic habitats generally shows much higher densities of turbellarians in sands than in muds (McIntyre, 1969). The opposite trend tends to hold for the polychaetes, especially some of the opportunistic groups such as spionids and capitellids (Sanders, 1958; Commito, 1976). While it may be argued that this distribution pattern is, in part, due to higher organic carbon concentrations in muds (more food), or substrate stability requirements of polychaetes, it may also be due, in part, to the higher densities of turbellarian predators in sandy habitats which may be discouraging settlement of polychaete juveniles, and reducing densities of those that do settle by predation.

There were trends in the responses of juvenile macrofauna to encounter with copepods. *Streblospio*, capitellids, oligochaetes, and *Axiiothella* all responded to encounter with *Enhydrosoma* by moving away. Particularly the circling response of *Enhydrosoma* induced these animals to move away. This, combined with my observations and those of others (Cullen, 1973; Rhoads *et al.*, 1977), of the ability of copepods to disrupt the sediment surface which may make it difficult for these animals to construct and maintain tubes and burrows, suggests a negative effect of copepods on these taxa. Again, other experiments (Watzin, 1983) show reduced densities of some of these groups in the field in the presence of high densities of copepods and nematodes.



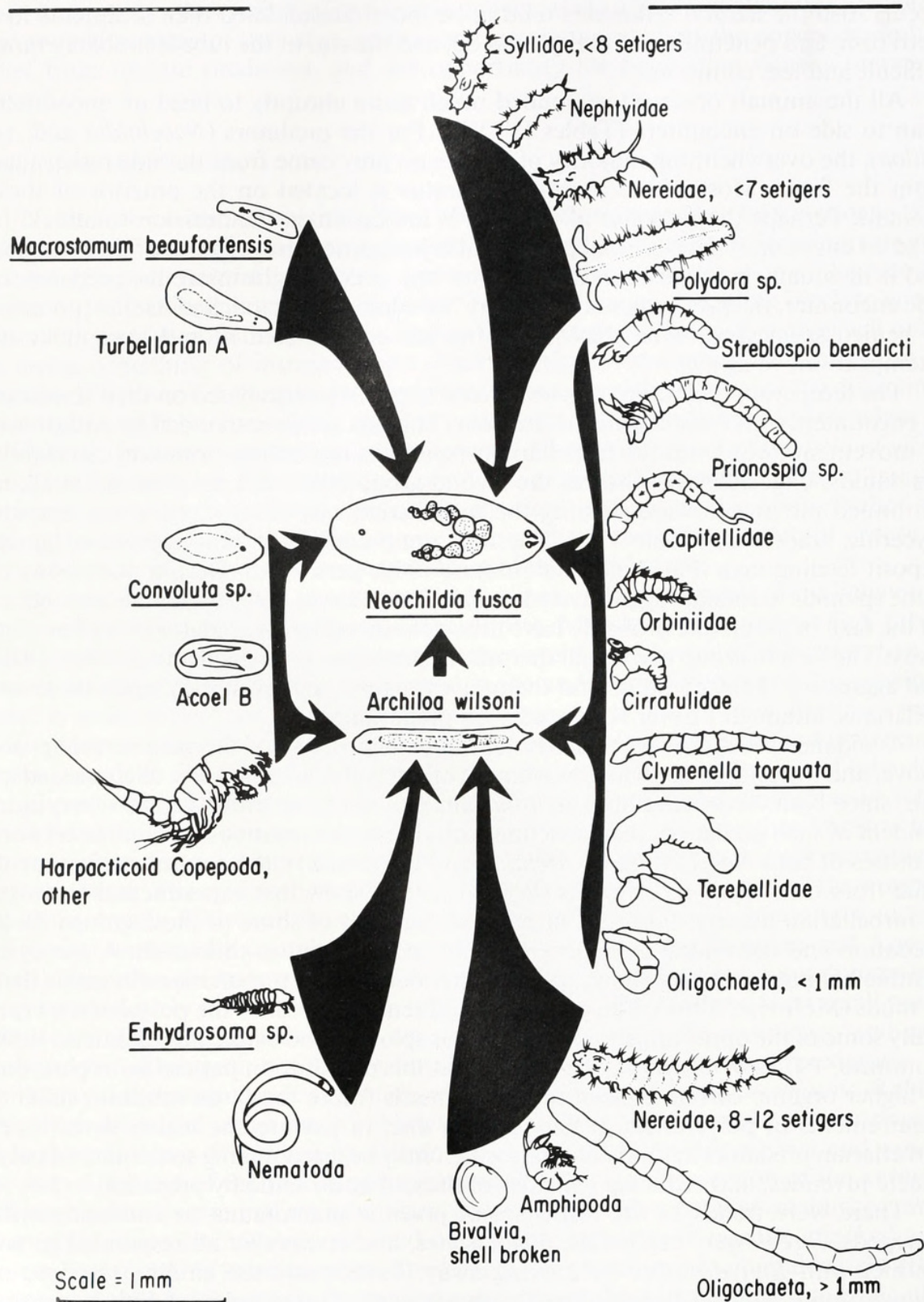
Permanent Mei faunaTemporary Mei fauna

FIGURE 1. A potential food web among the permanent and temporary mei fauna. All animals were drawn to the same scale using a camera lucida.



This paper represents a first attempt to directly observe and interpret the "black-box" of meiofaunal trophic and behavioral relationships. All meiofauna are not simply "packagers" of microbial biomass (Coull and Bell, 1979), but occupy several trophic levels even before passage to epibenthic predators or deposit feeders such as fish (Bregnballe, 1961; Feller and Kaczynski, 1975) or shrimp (Bell and Coull, 1978). Previous attempts have been made at constructing benthic food webs which include the meiofauna, but they have focused on the pathways between micro-organisms and meiofauna (Fenchel, 1970; Coull, 1973), or between permanent meiofauna and macrofaunal consumers (Ankar, 1977; Elmgren, 1978). Based upon the results of these feeding experiments, I have constructed a hypothetical food web among the permanent and temporary meiofauna (Fig. 1).

Turbellarians prey on a wide variety of other meiofaunal taxa, and may play a role in structuring meiofaunal and macrofaunal communities independent of the structure imposed on these communities by even higher trophic levels. Some nematodes are also probably predaceous, but the appropriate feeding experiments and observations have not yet been done to determine this. Before we can completely understand either what factors and interactions control meiofaunal densities and diversities, or what role the meiofauna play in benthic systems as a whole, the complex of interactions between the meiofauna must be better documented.

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