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THE DIET OF WORMS: A STUDY OF POLYCHAETE FEEDING GUILDS

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INTRODUCTION

Polychaetes are among the most frequent and abundant marine metazoans in benthic environments. In bathyal and abyssal areas (Hessler & Jumars, 1974), in shelf depths on open coasts (Barnard & Hartman, 1959; Boesch, 1972), in estuaries (Boesch, 1971; Orth, 1973), in man-made harbours (Reish, 1959), and on coral reefs (Kohn & Lloyd, 1973), polychaetes are also among the most 'species-rich' groups. They often comprise over one third the number of macrobenthic species and may be even more dominant in numbers of specimens (Knox, 1977). Polychaetes may be numerically less important on hard substrata, and bivalves and various peracarid crustaceans may co-dominate in soft sediments, but of all metazoans only the nematodes are more ubiquitous. Polychaetes must thus be included in calculations of community trophic structure and in community energy budgets (*e.g.* Banse, Nichols & May, 1971; Pamatmat, 1977). Despite their obvious importance the literature on ecological rôles of polychaetes remains largely anecdotal.

This review attempts to summarize current information about the feeding biology of these animals. We have organized the information into a limited number of patterns, using the guild concept to define our patterns. The concept of a guild (in the sense of a functional grouping) has proved to be a valuable tool both in generalizations and for continuing investigations in various animal and plant taxa (*e.g.* Grime, 1974; Karr & James, 1975). Provisional attempts at delineating feeding guilds among benthic polychaetes (Jumars & Fauchald, 1977) allowed generalizations to be drawn and revealed several unexpected trends. There are other useful ways to form functional groups of polychaetes (*e.g.* by reproductive behaviours or degrees of opportunism), but the morphology and behaviour of feeding appears so important that we suspect most alternative functional groups will show considerable overlap with the one developed here.

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The paper consists of two sections. In the first we have summarized current information about food and feeding habits within each polychaete family. The families are arranged in alphabetic order, and in the summary for each family we have included predictions on the most likely feeding habits where we found this possible or appropriate. The predictions are in the form of hypotheses capable of being tested (or can be so treated) and our intent was to create a suitable framework for continued work on the topic. We are now, with some of our associates, in the process of testing some of the predictions; we invite our colleagues to join us in this endeavour.

The second section of the paper is an interpretation of the data presented in the first section. We formally define feeding guilds for all polychaetes based on a joint consideration of food, feeding habits and locomotory patterns. We also draw some synecological conclusions about these patterns. We were particularly interested in understanding the sympatric occurrence in the deep sea of several congeners with extremely limited morphological differentiation. This problem started us thinking along these lines; we believe we have at least a partial solution to our problem.

THE FEEDING BIOLOGY OF THE POLYCHAETES

ALCIOPIDAE

Alciopids are holoplanktonic animals with muscular, eversible pharynges. Smaller alciopids, such as *Torrea pelagica* and *Vanadis minuta*, feed on copepods and young euphausiaceans whereas larger species feed on thaliaceans (Dales, 1955a). All species are carnivores, and considering the structure of the large, complex eyes (Hermans & Eakin, 1974), probably hunt by sight. The family includes about 30 species; no quantitative investigations have been attempted.

AMPHARETIDAE (Table I, Fig. 1)

Most ampharetids are surface deposit-feeders, using their retractable, ciliated tentacles to pick up food particles (Yonge, 1928; Remane, 1933; Dales, 1963; Day, 1964, 1967). The process was detailed for *Ampharete grubei* by Fauvel (1897). The tentacles are short (in comparison with those of the terebellids) and are attached to the roof of the mouth, which in some cases can be a folded or ribbon-shaped eversible membrane (*Amythas membranifera*, *Isolda whydahaensis*, and *Pabits deroderus*; see Day, 1964).

All ampharetids make mucus-lined tubes covered with sediment particles. Bacescu (1972, figs 7–14) showed *Melinna palmata* in the feeding position. The tube projects obliquely above the substratum and is distally curved towards the mud. The worm stretches out of the tube, spreading the tentaculate palate over the substratum, keeping the branchiae up in the water. We have observed other ampharetids in the same feeding position; it may be common to the family as a whole. The feeding tentacles are generally no longer than the body-length, and the worms are apparently sessile and tubicolous. Nevertheless, the family is well represented bathyally where food is sparse (Hartman, 1965; Hessler & Jumars, 1974). Some form of locomotion seems necessary. The shallow-water species, *Ampharete grubei*, will build horizontal tubes in aquaria when the bottom is covered with a thin layer of sediment (Fauvel, 1897). Fauvel mentioned that his specimens would continue tube-building indefinitely. Our own records indicate that most ampharetids have very long tubes, compared with the length of the specimens. One of us (P. A. Jumars) has maintained an intertidal ampharetid (of the genus *Hobsonia*) for several months both with and without added food. The worms in the tank without food added markedly to their tubes. In contrast, certain populations of *Melinna cristata* off northeastern England can contain more than 5000 specimens per square metre (Buchanan, 1963; Hutchings, 1973) with tubes forming a turf binding up the soft sediments. These tubes are oriented vertically making continuous tube-building unlikely. Continuous tube-building may represent a form of locomotion in ampharetids and certain other tube-building polychaetes, and orientation of the tubes, horizontally or vertically, may depend on the amount of food available for each individual.

TABLE I

Literature on feeding modes of the ampharetids: approximate number of known species, 204.

Alkmaria rominji	Hartmann-Schröder, 1971
Ampharete acutifrons	Pearson, 1971; Wolff, 1973
,, *grubei*	Fauvel, 1897
Amphicteis floridus	Zottoli, 1974
,, *gunneri*	Fauvel, 1897; Hessle, 1925; Hunt, 1925; Southward, 1957
Amythas membranifera	Day, 1964
Anobothrus gracilis	Hessle, 1925
Hypania invalida	Gruia & Manoleli, 1974
Hypaniola kowalewskii	Gruia & Manoleli, 1974
Isolda whydahaensis	Day, 1964
Melinna cristata	Hessle, 1925; Nyholm, 1951
,, *palmata*	Hunt, 1925; Mare, 1942; Dragoli, 1961; Bacescu, 1972
Pabits deroderus	Day, 1964
Samytha adspersa	Fauvel, 1897
Ampharetidae, general	Yonge, 1928; Remane, 1933; Dales, 1963; Day, 1964, 1967

Gut content has been examined in a few species (Fauvel, 1897; Hessle, 1925; Hunt, 1925; Mare, 1942) including two freshwater species (Gruia & Manoleli, 1974); ingested material includes detritus, unicellular algae and larval invertebrates. Ampharetids start feeding as newly settled juveniles with two or three setigers (Nyholm, 1951; Zottoli, 1974). The first tube is formed immediately upon settling (*M. cristata*, Nyholm, 1951) or first after a few days (*Amphicteis floridus*, Zottoli, 1974). In the latter, juveniles feed by a muscular pumping of the lips before the tentacles are developed.

There is no published evidence to show selectivity in feeding of marine ampharetids, and the amount of food taken has not been investigated for a single species, freshwater or marine. We argue that most marine species are selective and that in cases of sympatry, resource partitioning between the different species is present in analogy with what Gruia & Manoleli (1974)

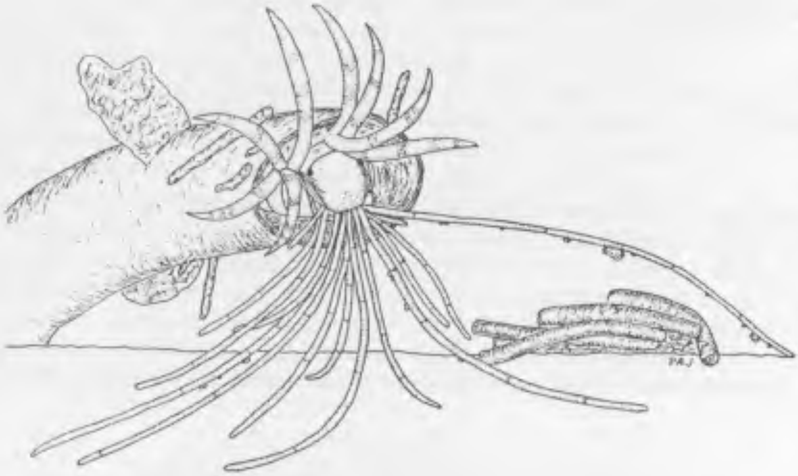

Fig. 1.—AMPHARETIDAE: near *Amphicteis* transporting detrital particles along its feeding tentacles; the tentacles and pointed branchiae have a jointed appearance because of the pigment bands indicated by stippling; particle selection may be mediated by winnowing during particle transport along the tentacles (Self & Jumars, in press); × 10.

reported for the two freshwater forms, *Hypania invalida* and *Hypaniola kowalewskii*. *Hypania invalida* will ingest blue-green algae in addition to green algae and diatoms; *Hypaniola kowalewskii* avoids ingesting blue-green algae. *Hypania invalida* digests nearly exclusively diatoms, whereas *Hypaniola kowalewskii* is also capable of digesting green algae. Most species ingested by these two ampharetids are pelagic. Since both live under riverine conditions, this does not appear unlikely even if they use the same feeding position as *Melinna cristata*.

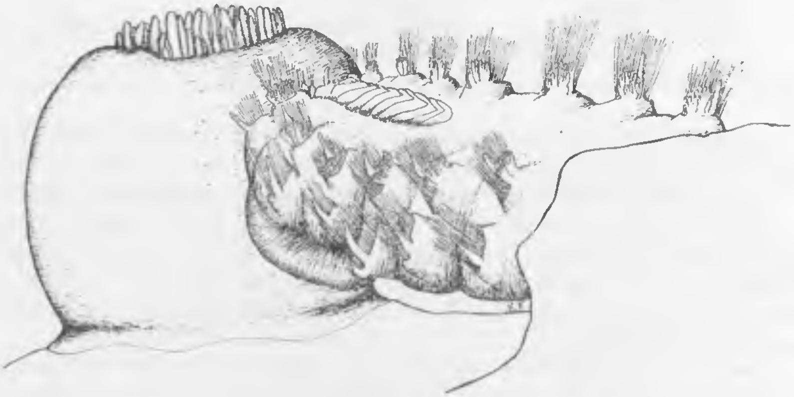

Fig. 2.—AMPHINOMIDAE: *Hermodice carunculata* attacking a sea anemone; other members of the family appear capable of feeding on carrion or on detrital material as well; natural size.

AMPHINOMIDAE (Table II, Fig. 2)

Amphinomids are best represented in shallow warm-water areas where they are found in coral sand under beach-rock (Kudenov, 1974) or with corals and other cnidarians (Marsden, 1962, 1963b). Gustafson (1930) in a description of their anatomy, implied that they were carnivores and this implication has been borne out. The mouth has a muscular eversible lower lip used for rasping and possibly squeezing food material.

TABLE II

Literature on feeding modes of the amphinomids: approximate number of known species, 110.

Eurythoe complanata	Kudenov, 1974
Hermodice caruncculata	Ebbs, 1966; Lizama & Blanquet, 1975; Marsden, 1962, 1963a,b
Hipponoa gaudichaudi	MacGinitie & MacGinitie, 1968; Kudenov, 1977a
Hipponoa sp.	Day, 1967
Notopygos crinita	Ebbs, 1966
Pherecardia sp.	Day, 1967
Amphinomidae, general	Gustafson, 1930; Dales, 1963; Day, 1967

Most amphinomids are associated with cnidarians: they browse on corals and anemones (Ebbs, 1966), on sponges and hydroids (Dales, 1963) or on sponges, hydroids, and ascidians (Day, 1967). *Hipponoa* spp., however, are associated with pelagic barnacles (*Lepas*) and may be semi-parasitic on their hosts (Day, 1967; MacGinitie & MacGinitie, 1968; Kudenov, 1977a; V. Loeb, pers. comm.) *Pherecardia* sp. is more active than most amphinomids in that it may hunt and feed on specimens of *Marphysa* (Polychaeta: Eunicidae) (Day, 1967). The best investigated species is *Hermodice caruncculata* which may browse on corals (*Porites*) or feed on sea anemones. Prey is found by contact rather than by distant sensing, but semi-digested coral matter in the water will attract other specimens (Lizama & Blanquet, 1975). The worms attack single coral polyps or anemones by everting the ventral rasping pad onto prey. Some predigestion takes place before the polyp remnants are swallowed (Lizama & Blanquet, 1975). The enzymatic complement is appropriate (Marsden, 1963a).

Amphinomids are least active during the middle part of the day (Marsden, 1962; Kudenov, 1974). *Eurythoe complanata* is usually hidden during daylight hours, whereas *Hermodice caruncculata* will sit out in the open and feed during late afternoon and early morning. The notosetae of the amphinomids are extremely fragile and contain an irritant; thus the animals may be protected against predators.

Marsden (1963b) reported the gut content of *Hermodice caruncculata*; she remarked that specimens found on sand contain sand, spines, setae and algal fragments, whereas specimens found on corals contain zooxanthellae, coral fragments, eunicid jaws, radulae and setae, indicating that sand-dwelling specimens may be carrion-feeders. *Eurythoe complanata* also appears to be more of a carrion-feeder than a carnivore, at least when nestling under rocks (Kudenov, 1974). *Pherecardia striata* has been observed feeding on the internal organs of *Acanthaster plancii*. The starfish had probably been previously attacked by the shrimp, *Hymenocera picta* (P. W. Glynn, pers. comm.). This observation appears to fit in with the earlier reports of carrion-feeding by members of this family. We postulate that other hard-bottom amphinomids will be found to be carnivores, whereas populations associated with sand and mud (mainly species of *Chloeia*) will turn out to be carrion-feeders.

APHRODITIDAE (Table III)

Aphroditids are large scale-worms most commonly found in sands and muds. All aphroditids are non-tubicolous; none are commensal with other organisms. All the authors cited in Table III, apart from Day (1967) state that the aphroditids are carnivores. Day (1967) reported that the aphroditids lack jaws and that *Aphrodita* spp. fed on detritus and microscopic animals and that *Laetmonice* spp. are often found with the gut diverticula distended by foraminiferans. Gut content in *Aphrodita aculeata* was listed by Blegvad (1914) and Hunt (1925), both of whom examined a number of specimens. Both agree that the most common items in the gut were remnants of other polychaetes, especially terebellids and sabellids.

TABLE III

Literature on feeding modes of the aphroditids: approximate number of known species, 66.

Aphrodita aculeata	Biedermann, 1911; Jordan, 1913; Blegvad, 1914; Fordham, 1925, Hunt, 1925; Hempelmann, 1931; Yonge, 1954a; Evans, 1971; Pearson, 1971; Wolff, 1973
Aphrodita sp.	Yonge, 1928; Day, 1967
Hermione hystrix	Hempelmann, 1931
Laetmonice filicornis	Hartmann-Schröder, 1971
Laetmonice sp.	Day, 1967

The number of independent investigations on which Table III is based is actually very low. Biedermann (1911), Jordan (1913) and Fordham (1925) all claim Darboux (1899) as their source of information about the food habits of *A. aculeata*. Darboux gave a summary of the food habits for all scale-worms, *i.e.* for the superfamily Aphroditacea; he did not specify the food of any species. Yonge (1928, 1954a), Evans (1971), and Pearson (1971), based their statements on Hunt's and Blegvad's findings. Hartmann-Schröder (1971) tentatively identified *Laetmonice filicornis* as a carnivore, apparently in analogy with the other reports. Hempelmann (1931) called *Hermione hystrix* a carnivore, without giving any evidence; this finding may represent an independent investigation.

Aphroditids do have jaws, even if they are irregularly shaped and less obviously grasping than those found in other scale-worms (K. Fauchald, pers. obs.). We consider the aphroditids as slow-moving carnivores, taking as prey microscopic animals if nothing else is available, but specializing on sessile or slow-moving animals if encountered. There is insufficient evidence to show that they can sustain themselves on non-living detritus. The gut content cited by Day (1967) for *Laetmonice* sp., indicates that considerable selectivity may also be found for other aphroditids.

ARABELLIDAE

The arabellids are long, slender euniceans with a variably developed jaw apparatus. Pettibone (1957) and Emerson (1974), summarizing life histories, indicated that a number of them are parasitic as juveniles. They are found in the body cavity of other polychaetes (eunicids, onuphids, syllids, and terebellids) or in echiurans. Free-living members are considered carnivores (Pettibone, 1957, 1963; Southward, 1957), but no direct evidence is available. *Drilonereis longa* has sand as the main gut content, and this species was considered a sediment ingestor by Sanders *et al.* (1962).

We have been unable to find any reports of the food habits or gut content of any arabellid, other than the report by Sanders *et al.* (1962). We argue that they will be shown to have similar habits to the morphologically and ecologically very similar lumbrinerids. They would thus generally be considered carnivores, with the proviso that some species may have switched to highly selective deposit-feeding. The approximate number of known species is 79.

ARENICOLIDAE (Table IV, Fig. 3)

Table IV indicates that considerable effort has been exerted in evaluating "the life of the lugworm" (to quote the title of the well known article by Wells, 1957). The early literature, including Rauschenplat (1901), Jordan (1913), Blegvad (1914), and Hempelmann (1931), detailed the gut content of the lugworm as sand and detritus, or as detritus only (Yonge, 1954a).

TABLE IV

Literature on feeding modes of the arenicolids: approximate number of known species, 28 (including recognized subspecies).

Abarenicola affinis africana	Day, 1967
,, *gilchristi*	Day, 1967
,, *pacifica*	Hobson, 1967; Hylleberg, 1975
,, *vagabunda*	Hobson, 1967; Hylleberg, 1975
Arenicola laveni	Day, 1967
,, *marina*	Rauschenplat, 1901; Jordan, 1913; Blegvad, 1914; Yonge, 1928, 1954a; Hempelmann, 1931; Remane, 1933; Thamdrup, 1935; Linke, 1939; Wells, 1945, 1952, 1953b, 1957, 1966; Newell, 1949; Smidt, 1951; Kermack, 1955; Krüger, 1959; Schäfer, 1962; Amoureux, 1963; Dales, 1963; Jacobson, 1967; Retière, 1967; Longbottom, 1970a,b; Hartmann-Schröder, 1971; Wolff, 1973; Kozyar, 1974; Cadée, 1976
Arenicola sp.	MacGinitie & MacGinitie, 1968

Remane (1933) characterized *Arenicola marina* as a semi-sessile detritus swallower and Yonge (1928) reported the same species as swallowing inactive material in large masses (Yonge's feeding mode II A).

The first detailed description of the feeding mode was given by Thamdrup (1935): *A. marina* occupies a U-shaped burrow system consisting of a sand-filled head-shaft, an open horizontal gallery, and an open tail-shaft. At the upper end of the head-shaft, a shallow funnel is formed and around the opening of the tail-shaft are deposited the characteristic, coiled faecal masses. The animal feeds by taking in sand at the base of the head-shaft. Much of this sand was originally derived from the surface and represents material that has slumped or been deposited into the funnel formed by the removal of sand at the base of the sand column. Thamdrup thus characterized *A. marina* as a surface deposit-feeder, even if the actual food intake takes place at depth. This interpretation has been accepted by most subsequent workers (Linke, 1939; Wells, 1945, 1957; Smidt, 1951; Kermack, 1955; Amoureux, 1963; Longbottom, 1970a; Wolff, 1973; Kozyar, 1974).

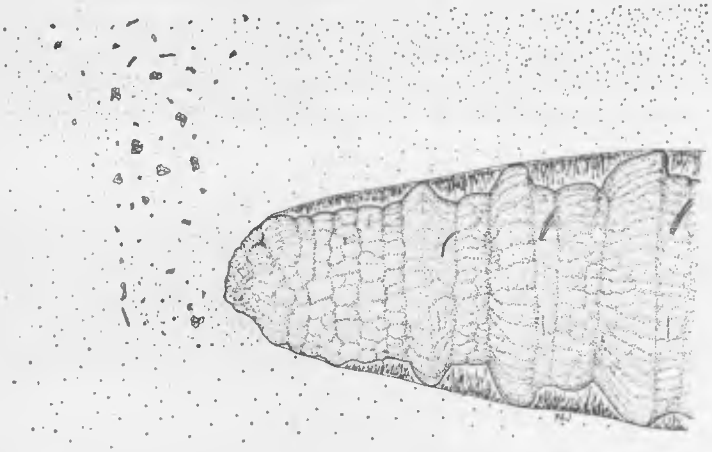

Fig. 3.—ARENICOLIDAE: *Abarenicola pacifica* bracing its anterior flanges against the incipient, sediment-dilatating thrust of its pharynx; its feeding causes sediments to slump downward, as indicated by the organic detrital and fine surface sediments portrayed at the head of the burrow; ×4.

Krüger (1959, followed by Hartmann-Schröder, 1971) pointed out that the maintenance of an irrigation current going headwards in the open part of the burrow (Wells, 1945, 1957, 1966) would lead to the capture of the plankton in the irrigation water in the sand immediately in front of the worm. He marshalled evidence to show that this enrichment of the sand could be of nutritional importance to the animal. Krüger's findings led to a renewed interest in the question. Jacobson (1967) quantified the organic content of the surrounding water, in the sand of the head-shaft and in the surrounding sand. He found that the water contained too little to be of any importance and while the head-shaft had higher organic content than the surrounding sand, this could be explained as a mechanical effect of the funnel, which would tend to concentrate organic detritus of low specific gravity.

Hobson (1967) demonstrated experimentally that filtering is possible, but concluded that the two Pacific species she worked with, for all practical purposes could be considered as feeding from a sinking column of sand in the head-shaft. Hylleberg (1975) reinvestigated the same species, *Abarenicola pacifica* and *A. vagabunda* and came to the same conclusion.

Wells (1966) and Schäfer (1962) pointed out that feeding could be in both the Thamdrupian and Krügerian modes and that the importance of each might be related to the sediment composition. In low-nutrient, coarse sand, filtration may be relatively more important than in high-nutrient fine sand. The pumping effort would also be much greater in fine than in coarse sands. We accept this interpretation with the comment that in nearly all locations investigated, the surface deposit-feeding mode has proved to be the most important. This inconsistency with our earlier classification (Jumars & Fauchald, 1977) is based on a more thorough literature review and on more recent references (Hylleberg, 1975; Cadée, 1976).

Traditionally, the arenicolids have been considered non-selective (Linke, 1939; Smidt, 1951; Kermack, 1955; Retière, 1967; Wolff, 1973). Large particles, such as shell fragments, are sorted out at the base of the head-shaft and are not taken into the body (Wells, 1945, 1966). Where worm populations are dense, this will lead to the formation of a more or less continuous layer of coarse particles 15–20 cm below the surface of the mud. MacGinitie & MacGinitie (1968) remarked that only fine particles are taken into the body and that the mucus secreted while feeding differs in quality from the secretions made while burrowing, suggesting a higher level of selectivity.

A. pacifica, while ingesting the surrounding medium more or less indiscriminately, will digest mainly the contained ciliates, flagellates, small nematodes, and bacteria associated with the interstitial water, while leaving diatoms undigested. *A. vagabunda* will digest a similar array of materials, but appears much more adept at digesting particle-bound bacteria than is *A. pacifica* (Hylleberg, 1974). Hylleberg also demonstrated that sand having passed through the digestive tract rapidly gains a much larger population of bacteria than the surrounding sand; he characterized this as a form of gardening.

The anatomy of the digestive system was described by Kermack (1955). Enzymatic properties were detailed by Longbottom (1970b) who demonstrated that most enzyme production takes place in the esophageal diverticulae and in the stomach. A cellulase is absent; carbohydrases, lipases, and proteases are present. Considering the high rate of transport of sand through the gut of the lugworms (14 min from ingestion to egestion according to Kermack, 1955), most digestion must be extracellular. This agrees with studies on absorption of neutral and charged amino acids by Bamford & Stewart (1973a,b). Cadée (1976) demonstrated both short-term and long-term periodicities in production rates of faecal matter and related them to tidal exposure, temperature, and benthic primary production.

Behavioural and mechanical studies of feeding and irrigation rhythms in *Arenicola marina* and *A. ecaudata* (Wells & Albrecht, 1951a,b; Wells, 1952a, 1953, 1954) have shown that close similarity in morphology is not necessarily paralleled by similar behavioural patterns. Thus information about feeding and irrigation available for one species cannot be applied uncritically to other members of the same genus. Ontogenetically, the lugworm way of life starts when the post-larvae are about 5 mm in length (Newell, 1949). Smaller larvae are encased in a thick mucous tube and feed from the surface of the mud.

Population densities are positively correlated with the amount of organic matter present in the sediment (Longbottom, 1970a), again pointing to the importance of the Thamdrupian interpretation of feeding in the arenicolids; the Krügerian mode would not predict any relation between the organic content of the sediment and the population size.

We know more about feeding in the arenicolids, specifically in *A. marina*, than about feeding in any other polychaete. The results of Wells & Albrecht (1951a,b) showing differences between closely related forms and the demonstration of resource partitioning by Hylleberg (1975) are object lessons. We believe that studies made on one population or on one species cannot be applied to other populations of the same species, or to congeners, without carefully examining the purpose of the application, or without at least a cursory examination of the new population to demonstrate that the accuracy of the results remains adequate.

CAPITELLIDAE (Table V)

Capitellids are simple-bodied, earthworm-like polychaetes. All feed by everting a papillose, sac-like pharynx. The pharyngeal epithelium secretes a mucopolysaccharide (Michel, 1967, 1970b, 1972) apparently used to agglutinate sand grains, and possibly to select organic particles of low specific gravity.

TABLE V

Literature on feeding modes of the capitellids: approximate number of known species, 134.

Capitella capitata	Eisig, 1887; Biedermann, 1911; Jordan, 1913; Reish, 1957; Muus, 1967; Hartmann-Schröder, 1971; Pearson, 1971; Wolff, 1973; Augustin & Anger, 1974; Stephens, 1975;
,, *ovincola*	Hartman, 1947; MacGinitie & MacGinitie, 1968
Capitella sp.	Frankenberg & Smith, 1967
Capitomastus giardi	Hartmann-Schröder, 1971
,, *minimus*	Hauenschild, 1954; Hartmann-Schröder, 1971; Pearson, 1971
Capitomastus sp.	Bacescu, 1972
Dasybranchus caducus	Hempelmann, 1931; Yonge, 1954a; Southward, 1957
Heteromastus filiformis	Thamdrup, 1935; Linke, 1939; Smidt, 1951; Sanders *et al.*, 1962; Schäfer, 1962; Jepsen, 1965; Hartmann-Schröder, 1971; Wolff, 1973
Leiochone sp.	Bacescu, 1972
Notomastus latericeus	Blegvad, 1914; Hunt, 1925; Wilson, 1937; Hertweck & Reineck, 1966; Michel, 1970b; Hartmann-Schröder, 1971; Pearson, 1971;
,, *magnus*	Ronan, 1978
Notomastus sp.	Yonge, 1928; MacGinitie & MacGinitie, 1968
Capitellidae, general	Dales, 1963; Day, 1967

All capitellids are considered non-selective. The list of gut contents, however, nearly always includes algal fragments, suggesting that some selection is probable.

Some capitellids build tubes at or near the surface of the sediment (*e.g.*, *Capitella capitata*), others build horizontal or vertical tubes or burrows stretching up to 15 cm below the surface (*e.g.*, *Heteromastus filiformis*). These tubes maintain contact with the surface and allow the worm to feed in black, anoxic muds, getting the necessary oxygen from the overlying waters by irrigation of the burrow (Linke, 1939; Schäfer, 1962; Jepsen, 1965). Closely similar forms may vary in their activities: *Capitomastus minimus* is tubicolous, while its congener, *C. giardi* lacks a tube (Hauenschild, 1954; Hartmann-Schröder, 1971). Some capitellids, such as *Notomastus latericeus*, are tubicolous as juveniles but become free-living as adults (Wilson, 1937). Adult *Notomastus* spp. build partially spiralled burrows that maintain integrity for some time after construction, but which lack a distinct wall structure (Hertweck & Reineck, 1966; Ronan, 1978). *Capitella ovincola* lives in the egg-masses of squids and apparently feeds on the jelly in which the eggs are embedded without harming the developing squid embryos (Hartman, 1947; MacGinitie & MacGinitie, 1968).

As indicated above, little is known about selectivity in the capitellids. A series of closely similar species of *Capitella* may be present in one small area (Grassle & Grassle, 1974, 1976); it is thus possible that a reported lack of selectivity may be due to a confusion of sibling species. In the laboratory, *C. capitata* can be maintained on a diet of *Enteromorpha* sp. or on alfalfa powder (Reish, 1957). *Capitella* sp. is also coprophagous; under culture conditions it will take in as much as 19% of its body weight in faecal pellets in a 48-h period (Frankenberg & Smith, 1967). *Capitomastus minimus* can be maintained in culture on a diet of killed plant cells of various kinds (Hauenschild, 1954). Finally, *Capitella capitata* can take up dissolved primary amines from the surrounding medium (Stephens, 1975), although it is not clear that any net energy gain ensues. All of this indicates that the complexity of feeding modes and selectivity of these species may have been underestimated.

The digestive system of the capitellids has been poorly investigated; in fact, nothing has been done since the early studies summarized by Biedermann (1911) and Jordan (1913), which indicate that the gut cells of capitellids are in part secretory. The anatomy was detailed masterfully by Eisig (1887).

Despite the tube-building habits of some capitellids, we believe that normally they are all motile deposit-feeders. We suggest that the most opportunistic of these species, such as *C. capitata* may be relatively non-selective, whereas less opportunistic species, such as *Notomastus latericeus* and *Dasybranchus caducus* will prove to be more selective. We believe that both particle size and composition are important environmental parameters for the less opportunistic species.

CHAETOPTERIDAE (Table VI, Figs 4, 5)

Chaetopterids are tubicolous polychaetes common in shallow water; members of the genera *Phyllochaetopterus* and *Spiochaetopterus* are also found in bathyal and abyssal samples. The highly characteristic morphology of the widespread *Chaetopterus variopedatus* led to an early interest in its structure and life history as summarized by Joyeux-Laffuie (1890). Gut contents for this species include planktonic skeleta, unicellular algae and protozoans, small metazoans, and detritus (Hunt, 1925; Hempelmann, 1931; Yonge, 1954a), indicating a pelagic derivation of the food. The feeding mechanism has been analysed several times. Strings of mucus secreted from the aliform parapodia, moved by cilia, were considered responsible for food capture by Enders (1909). The food boluses were transported forwards on the dorsal side from the cupule, called the accessory feeding organ by Enders, to the mouth along a ciliated groove. The mouth is displaced to the dorsal side in adults of this species. A similar method, using strings of mucus and cilia, was described for *Mesochaetopterus* sp. by MacGinitie & MacGinitie (1968).

TABLE VI

Literature on feeding modes of the chaetopterids: approximate number of known species, 41.

Chuetopterus variopedatus	Joyeux-Laffuie, 1890; Enders, 1909; Hunt, 1925; Yonge, 1928, 1954a; Hempelmann, 1931; MacGinitie, 1939; Wells & Dales, 1951; Seilacher, 1953; Werner, 1953; Dales, 1963; MacGinitie & MacGinitie, 1968; Hartmann-Schröder, 1971;
Mesochaetopterus prolifica	MacGinitie & MacGinitie, 1968
,, *sagittaria*	Barnes, 1964b
,, *taylori*	Barnes, 1964b
Mesochaetopterus sp.	MacGinitie & MacGinitie, 1968
Phyllochaetopterus socialis	Barnes, 1964b
Spiochaetopterus costarum	Barnes, 1964b
,, *oculatus*	Enders, 1909; Barnes, 1964a
,, *typicus*	Hartmann-Schröder, 1971
Chaetopteridae, general	Day, 1967

MacGinitie (1939) described the production of a continuous mucous net from the edges of the aliform parapodia in *Chaetopterus variopedatus* (Fig. 4). The net was suspended from the edge of these parapodia to the cupule which is centrally placed on the dorsal side. At the cupule the net could be rolled up, formed into a food bolus and transported to the mouth, as indicated by Enders, along a ciliated groove. The necessary water current is set up by three fan-shaped notopodia immediately posterior to the cupule. MacGinitie's observations have been repeated successfully by others, including both the present authors; the method must be considered the norm in this species. Under some conditions especially with heavy particle loads, shreds of mucus containing food material are produced from the aliform parapodia, rather than the complete net (Wells & Dales, 1951). This corresponds to the description given by Enders, who probably used particle loads too heavy to produce the mucous net.

Werner (1953) found that pelagic metatrochophores of *C. variopedatus* produce mucus from the pygidial region and will drift around in the water with trailing strings of mucus. Periodically these strings are rolled up and a food bolus transported to the mouth, in this case on the ventral side of the animal. Feeding by mucous devices is thus the only mode of feeding in this species, whether larval or adult. *C. variopedatus* is permanently tubicolous from the time of settling (Enders, 1909; Seilacher, 1953). The tube is U-shaped and narrowed towards both ends. As the animal grows, the tube becomes too small. The animal uses the large spines of setiger 4 to cut open the old tube; it will then add new material, both lengthening and widening the tube as it does so (Seilacher, 1953). When the animal lives in soft bottoms this will leave remnants of the old tube easily visible between the two arms of the U.

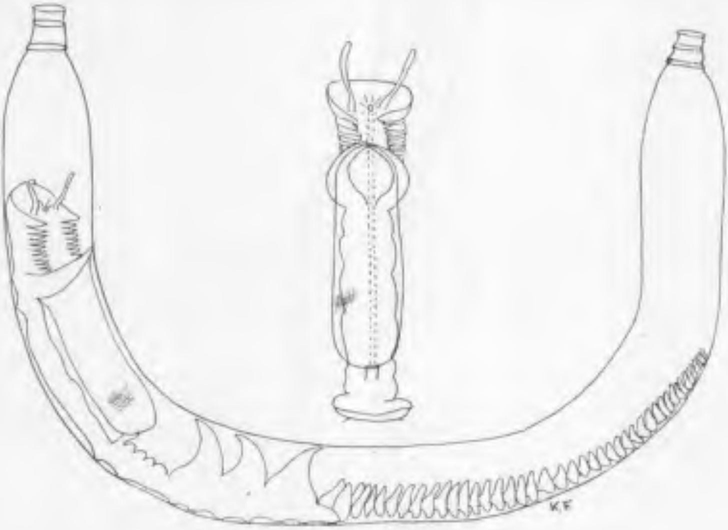

Fig. 4.—CHAETOPTERIDAE: *Chaetopterus variopedatus* in feeding position, drawn as though the tube were transparent, after MacGinitie (1939); the mucous bag used in feeding is indicated by crosshatching; ×0·7.

The family Chaetopteridae is unusually well known in terms of feeding modes thanks to two excellent studies by Barnes (1964a,b) in addition to the studies listed above for *C. variopedatus*. Barnes demonstrated that filter-nets, similar to the ones produced by *C. variopedatus* are used by all chaetopterids he investigated. In some instances a single net is formed; in others several nets are formed on successive segments. In these chaetopterids, the current is set up by notopodial cilia rather than by muscular motion. Open canals are left between the notopodia and the tube-wall making a series of filter-nets useful. Chaetopterids other than the genus *Chaetopterus* have well developed, spioniform palps. These have been implicated in the food uptake (Enders, 1909; MacGinitie & MacGinitie, 1968). Barnes demonstrated that the palps are used as aids in defaecation and only rarely for feeding. Under conditions of low particle concentrations, *Spiochaetopterus* sp. will search the sediment surface with the palps (Fauchald & Jumars, pers. obs. Fig. 5). Surface deposit-feeding is likely to be important for species living in bathyal and abyssal regions, such as *Spiochaetopterus costarum* and *Phyllochaetopterus limnicolus* in the Pacific Ocean.


PAJ

CIRRATULIDAE (Table VII)

Cirratulids are simply constructed polychaetes with either two groups or a single pair of palps attached anteriorly. Some forms live in mud-covered tubes (Jumars, 1975); others drill in coral or other calcareous substrata (Hartman, 1954) or build calcareous tubes (Hartmann-Schröder, 1971), but most species are free-living. Shallow-water species often nestle in small quantities of mud in crevices, under rocks or in algal hold-fasts (Gardiner, 1903; Kensler, 1964; Kennedy, 1978). *Tharyx* spp. may be extremely abundant in polluted areas; other members of the same genus are among the most abundant macrofaunal species in the deep sea (Jumars, 1975).

TABLE VII

Literature on feeding modes of the cirratulids: approximate number of known species, 134.

Caulleriella caputesocis	Pearson, 1971
Chaetozone setosa	Wolff, 1973
Cirratulus cirratus	Olive, 1970
Cirratulus sp.	Yonge, 1928
Cirriformia spirabrancha	Ronan, 1978
,, *tentaculata*	Flattely, 1916; Hempelmann, 1931; Yonge, 1954a; George, 1964a,b
Tharyx marioni	Southward, 1957; Wolff, 1973
,, *parvus*	Jones, 1961
Tharyx sp.	Sanders *et al.*, 1962
Cirratulidae, general	Dales, 1963; Day, 1967

The cirratulids are deposit-feeders (Hempelmann, 1931; Southward, 1957; Jones, 1961; Sanders *et al.*, 1962; Dales, 1963; George, 1964b; Day, 1967; Olive, 1970; Ronan, 1978). They are usually considered non-selective but *Chaetozone setosa* and *Tharyx marioni* may be selective feeders (Wolff, 1973) and *Caulleriella caputesocis* may be both a surface deposit-feeder and a burrowing deposit-feeder (Pearson, 1971). Ronan (1978) found that *Cirriformia spirabrancha* fed at and below the sediment-water interface. Flattely (1916) claimed that the cirratulids use only the eversible pharynx in feeding and that the palps are wholly without feeding function; all other authors indicate that this is not the case. Investigations are few in number and consist mainly of casual observations; a few quantitative observations have been made. *C. tentaculata* is capable of utilizing about 8% of the organic content of the food taken compared with a 14% rate calculated from enzymatic digestion

Fig. 5.—CHAETOPTERIDAE: *Phyllochaetopterus prolifica* shown utilizing two feeding modes other than the mucous bag method described for *Phyllochaetopterus* by Barnes (1964b); when the currents are moderately strong, the palps are often held erect until impacted by a detrital particle; the uppermost individual is about to engulf a detrital particle, caught in this fashion, by forcing the particle into its everted pharynx with the aid of both palps; the other individual, in the more slowly moving waters deeper in the benthic boundary layer, is deposit-feeding on the fouled tube of the first individual; ×5.

of the same material (George, 1964a). According to George, the difference between the predicted and measured values is due to the short time the food stays in the gut.

We predict that all cirratulids will be found to be surface deposit-feeders using their palps for food collecting. We also expect that they will show selectivity, both in terms of particle composition and in the size of the particles. We have some observations to support this: *C. luxuriosa* and *C. spirabrancha* in aquaria will change the particle composition of the sediments immediately next to them (K. Fauchald, pers. obs.).

CTENODRILIDAE (Fig. 6)

The ctenodrilids are very small, maggot-shaped worms found in sandy and muddy bottoms, among seaweed and hydroids in shallow water. Wilfert (1973) showed that in culture they will feed on *Dunaliella* sp. and in the field they stir up detritus with the eversible lower lip, feeding on benthic diatoms in addition to detrital material. A population of *Ctenodrilus serratus* at Santa Catalina Island, California, is commensal with sea urchins (especially *Centrostephanus coronatus* and *Strongylocentrotus franciscanus*) so other modes of feeding may be possible (K. Fauchald, pers. obs.). At present eight species are recognized.

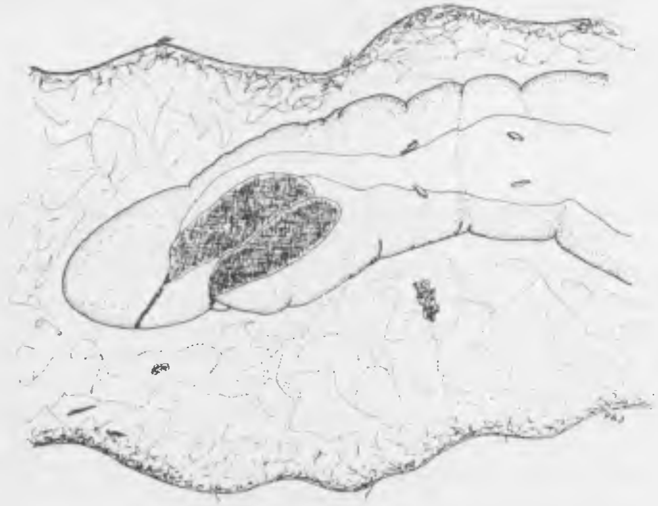

Fig. 6.—CTENODRILIDAE: *Ctenodrilus* sp. shown against the *Enteromorpha* sp. fragment from which it was taken; the musculature associated with the eversible lower lip (densely crosshatched) and the gut outline are clearly visible through the body wall; ×50.

DINOPHILIDAE

Dinophilids are tiny, interstitial polychaetes with a plate-muscle pharynx which can be everted through the mouth and presumably used in a licking motion (Rieger & Rieger, 1975). They feed on bacteria, protozoans, unicellular algae, diatoms, and organic debris (Jennings & Gelder, 1969; Wolff, 1973).

They are also capable of catching suspended particles with a ciliary mucoid mechanism (Jennings & Gelder, 1969). Quantitative investigations are lacking; the family is known for 17 species.

DORVILLEIDAE (Table VIII, Fig. 7)

The dorvilleids have a jaw apparatus consisting of paired series of independent maxillary plates and paired mandibles mounted in partially eversible muscular bulbs. All dorvilleids are free-living, and are found in all sublittoral environments, including heavily polluted areas. Some species, especially of the genus *Ophryotrocha*, are easily cultured and have been used for a variety of studies (*e.g.*, Åkesson, 1975). In culture, members of both *Ophryotrocha* and *Schistomeringos* do well on a diet of plant material, including such items as dried *Enteromorpha* sp., frozen spinach, alfalfa powder, *etc.* Larvae do well on diatoms and dinoflagellates (Düsing, 1961; Müller, 1962; Åkesson, 1967; Dohle, 1967; Richards, 1967). Freshly killed *Artemia* nauplii are also often used successfully as a diet for *Ophryotrocha.*

TABLE VIII

Literature on feeding modes of the dorvilleids: approximate number of known species, 47.

Dorvillea sp.	Day, 1967
Ophryotrocha gracilis	Dohle, 1967
,, *puerilis*	Düsing, 1961; Müller, 1962; Åkesson, 1967; Day, 1967; MacGinitie & MacGinitie, 1968
Protodorvillea kefersteini	Rasmussen, 1973; Wolff, 1973
Schistomeringos longicornis	Richards, 1967
,, *neglecta*	Pearson, 1971
,, *rudolphii*	Hempelmann, 1931; Yonge, 1954a

Day (1967) indicated that *Dorvillea* is carnivorous and that no algal food nor detritus had been found in its gut. The gut content of one of the species listed by Day, *Schistomeringos rudolphii*, is known to include algae and detritus (Hempelmann, 1931; Yonge, 1954a), so the generalization cannot be made for all species referred to *Dorvillea* (see Jumars, 1974, for a revision of the family). *Schistomeringos neglecta* and *Protodorvillea kefersteini* are carnivores (Pearson, 1971; Rasmussen, 1973; Wolff, 1973). Rasmussen detailed the diet of the latter as a "variety of small invertebrates".

Ophryotrocha puerilis may capture prey or feed on macerated meat while crawling on the surface of the mud in aquaria (MacGinitie & MacGinitie, 1968). This species also scrapes diatoms and filamentous algae (growing on aquarium walls) with the anterior maxillary plates which are beset with comblike rows of microscopic teeth resembling the radula of a limpet (Day, 1967). Other dorvilleids have long, slender, often hollow anterior maxillary plates (Fauchald, 1970; Jumars, 1974); it is unlikely that these delicate objects can be used for grazing.

We postulate that all dorvilleids are facultative carnivores and will feed as such if given the opportunity. We further suggest that all species will be

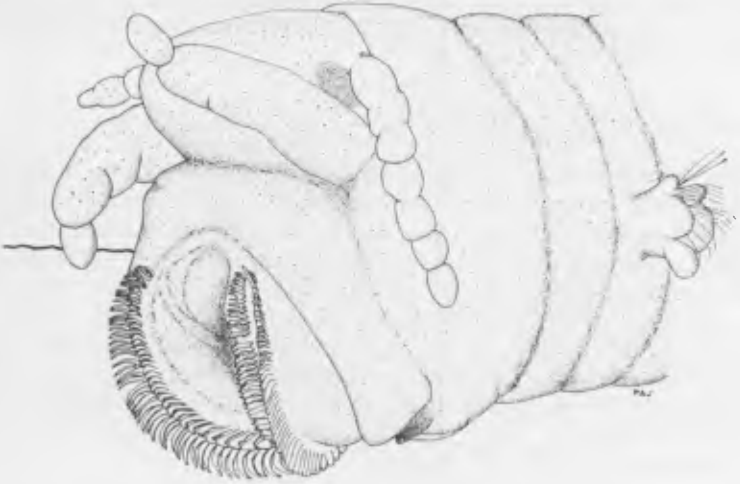

Fig. 7.—DORVILLEIDAE: *Schistomeringos annulata* with jaws everted; it is unknown to what degree the species is a detritivore, carnivore or herbivore, or to what extent the jaws are used in grasping or scraping food items; ×20.

able to survive on a mainly plant-derived diet and that some of the smaller species are specifically adapted to such a diet. There are some glaring contradictions in the literature; these may be due to our inability to distinguish all species on morphological grounds (Åkesson, 1972) and may be clarified by experimental work.

EUNICIDAE (Table IX, Fig. 8)

Eunicids have paired mandibles and complex sets of maxillae in a strongly muscular, eversible pharynx. At least as juveniles, *Eunice* spp. are mostly free-living; as they become larger, they may become tubicolous (Day, 1967; Fauchald, pers. obs.). Other species may be tubicolous through most of their life (Day, 1967). Members of other genera burrow in sand and mud (*Marphysa*; Day, 1967) or in old coral (*Lysidice*, *Palola*; Hartman, 1954). The eunicids associated with coral reefs are reported to do considerable damage to the reef by burrowing (Gardiner, 1903); however, Hauenschild, Fischer & Hofmann (1968) indicated that *Palola viridis* occupies burrows made by other organisms, especially sipunculans, and that they do not make their own burrows. The issue needs clarification.

Eunice aphroditois is a carnivore (Hempelmann, 1931; Evans, 1971); its gut content includes annelids chaetognaths ostracods, copepods, bivalves, a few diatoms, and some detritus (Yonge, 1954a). *E. tubifex* will emerge from its tube in search of prey (Day, 1967) and large, free-living species of *Eunice* from various tropical beaches will feed on carrion (Mortensen, 1922).

On the other hand, *Palola siciliensis* will do well on a diet of phytoflagellates and nettle-powder in aquaria (Hofmann, 1974). *P. viridis* feeds on red algae, including coralline algae in the field and in laboratory experiments; a yellow sponge may also be included among the food items

(Hauenschild *et al.*, 1968). *P. paloloides* burrow in corallinaceous algae (Fauchald, 1970). *Lysidice* spp. burrow in old coral and appear to get their nutrition from it (Hartman, 1954; Day, 1967) as does *Eunice schemacephala* (Ebbs, 1966); the latter may also feed from the entrance to its burrow on plant material (Clark & Hess, 1940). *Marphysa* spp. may be herbivores (Yonge, 1954a), carnivores (Desière, 1967) or omnivores (Day, 1967); Day also found that they could live largely on detritus.

Table IX

Literature on feeding modes of the eunicids: approximate number of known species, 241.

Eunice afra	Hartman, 1954
,, *aphroditois*	Hempelmann, 1931; Yonge, 1954a; Evans, 1971
,, *pennata*	Pearson, 1971
,, *schemacephala*	Clark & Hess, 1940; Ebbs, 1966
,, *tubifex*	Day, 1967
Eunice sp.	Mortensen, 1922
Lysidice collaris	Hartman, 1954
Lysidice sp.	Day, 1967
Marphysa bellii	Desière, 1967
,, *depressa*	Day, 1967
,, *mossambica*	Day, 1967
,, *sanguinea*	Yonge, 1954a; Day, 1967
Nematonereis unicornis	Southward, 1957
Palola siciliensis	Hartman, 1954; Hofmann, 1974
,, *viridis*	Hauenschild *et al.*, 1968
Eunicidae, general	Gardiner, 1903

Eunicids are thus not exclusively carnivores. The emerging pattern can be summarized as follows: free-living or tubicolous species of *Eunice* are primarily carnivores, feeding on all kinds of small invertebrates. Burrowing species of this and other genera (*Lysidice* and *Palola*) feed on old coral and contained organisms or on corallinaceous and other red algae. The information about *Marphysa* spp. cannot be summarized simply. No quantitative studies of the food habits of eunicids have as yet been undertaken.

EUPHROSINIDAE

These short-bodied amphinomid-like polychaetes are all carnivores. Gustafson (1930) who investigated their anatomy in detail, indicated that they feed mainly by scraping sponges off rocks, but will also feed on bryozoans and corals. Both *Euphrosine foliosa* and *E. cirrata* have been found with sponge spicules and chitin fragments as major components of the gut content (McIntosh, 1894) and *Euphrosine* sp. from South Africa lives on sponges (Day, 1967). A deep-water species of *Euphrosine* from the Atlantic Ocean feeds exclusively on foraminiferans (Sanders, Grassle & Hampson, pers. comm.); the exact mechanism is under investigation (K. Fauchald, in prep.). The family contains 42 known species; it is better represented in deep water than are the very similar Amphinomidae.

Fig. 8.—EUNICIDAE: *Eunice valens* palpitating a piece of the green alga, *Ulva* sp.; the eunicids as a group appear to be mainly herbivorous and carnivorous, but the diets of individual species remain largely unknown; twice natural size.

FLABELLIGERIDAE (Table X, Fig. 9)

Flabelligerids are non-tubicolous worms often covered with thick mucous sheaths or with sand incrustations. The anterior end, with a branchial field and paired grooved palps, is retractable within a space formed by the first setigers. The numbers of independent investigations of the feeding mode are few; thus Remane (1933), Yonge (1954a), Southward (1957), Hartmann-Schröder (1971), and Pearson (1971) all base their statements on previous investigations, especially on those by Blegvad (1914) and Hunt (1925). It is unclear how Hempelmann (1931) got his information.

Some flabelligerids (*Flabelligera affinis*) are motile surface deposit-feeders (Rasmussen, 1973), and closely related forms may be commensals (*Flabelliderma commensalis*). The latter uses its palps to feed on the faecal matter of its host (the sea urchin *Centrostephanus coronatus*); it will also employ its own respiratory current for feeding on loose detritus (Spies, 1975). Most flabelligerids are discretely motile and feed while sitting in cracks and crevices (Hartmann-Schröder, 1971). The gut content indicates that some sorting takes place; it consists of unicellular algae and fragments of larger algae and detritus (Blegvad, 1914; Yonge, 1928; Remane, 1933; Rasmussen, 1973).

All flabelligerids are surface deposit-feeders, usually using their grooved palps to gather food particles. Little seems to be known about their locomotory habits in the field. While sessile, the branchial field sets up a current which may be used for feeding. The commensal form mentioned above feeds in the same manner as the free-living members of the family.

TABLE X

Literature on feeding modes of the flabelligerids: approximate number of known species, 126.

Brada villosa	Blegvad, 1914; Hartmann-Schröder, 1971
Brada sp.	Pearson, 1971
Diplocirrus glaucus	Southward, 1957; Hartmann-Schröder, 1971; Pearson, 1971
Diplocirrus sp.	Day, 1967
Flabelliderma commensalis	Spies, 1975
Flabelligera affinis	Rauschenplat, 1901; Hartmann-Schröder, 1971; Rasmussen, 1973
Pherusa plumosa	Blegvad, 1914; Hempelmann, 1931; Yonge, 1954a; Hartmann-Schröder, 1971; Pearson, 1971
Pherusa sp.	Remane, 1933
Flabelligeridae, general	Hunt, 1925; Yonge, 1928

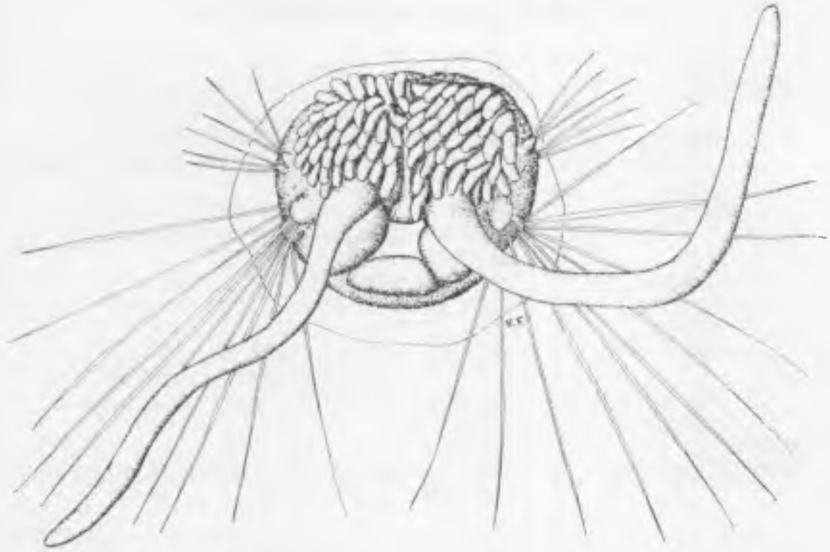

Fig. 9.—FLABELLIGERIDAE: *Pherusa* sp. in a front view with the anterior end everted; the two palps are used to collect material which deposits around the worm and on the setae of the first two setigers; the strongly ciliated branchiae (in dense masses inserted above the palps) set up a considerable current near the animal; ×2·5.

GLYCERIDAE (Table XI, Fig. 10)

Glycerids are slender, long-bodied polychaetes with enormous eversible pharynges tipped by four jaws. The jaws are penetrated by a canal connected basally to a gland (Hartman, 1950; Michel, 1966). In *Glycera convoluta* the secretion from this gland is toxic to small crustaceans (Michel, 1966, 1970b; Michel & Robin, 1972; Michel & Kiel, 1975). The jaws are made of tanned proteins impregnated with iron and copper compounds (Michel, Fonce-Vignaux & Voss-Foucart, 1973). Some glycerids form semi-permanent burrow systems in soft substratum (Ockelmann & Vahl, 1970; Stephens, 1972); other species are free-living under rocks and crawling on algae (Fauchald, pers. obs.).

The largest group of investigators characterize glycerids as carnivores (Blegvad, 1914; Hunt, 1925; Yonge, 1928; Hempelmann, 1931; Mare, 1942; Southward, 1957; Retière, 1967; MacGinitie & MacGinitie, 1968; Michel, 1970b; Ockelmann & Vahl, 1970; Evans, 1971; Pearson, 1971; Ronan, 1978). Other authors have declared them to be detritivores or capable of feeding on faecal pellets (Stolte, 1932; Klawe & Dickie, 1957; Sanders *et al.*, 1962; Frankenberg & Smith, 1967; MacGinitie & MacGinitie, 1968; Wolff, 1973). Some forms may fulfil part of their energy requirements by absorption of dissolved organic matter (summarized in Stephens, 1972).

TABLE XI

Literature on feeding modes of the glycerids: approximate number of known species, 72.

Glycera alba	Blegvad, 1914; Hunt, 1925; Ockelmann & Vahl, 1970; Hartmann-Schröder, 1971; Pearson, 1971
„ *capitata*	Hartmann-Schröder, 1971; Wolff, 1972
„ *convoluta*	Michel, 1966, 1970b; Evans, 1971; Michel & Robin, 1972; Michel *et al.*, 1973
„ *dibranchiata*	Klawe & Dickie, 1957; Sanders *et al.*, 1962; Frankenberg & Smith, 1967; MacGinitie & MacGinitie, 1968; Stephens, 1972
„ *gigantea*	Hartmann-Schröder, 1971
„ *lapidum*	Hunt, 1925; Southward, 1957
„ *robusta*	Ronan, 1978
„ *rouxii*	Blegvad, 1914; Hunt, 1925; Mare, 1942; Southward, 1957; Hartmann-Schröder, 1971
„ *siphonostoma*	Hempelmann, 1931; Yonge, 1954a; Evans, 1971
„ *unicornis*	Stolte, 1932
Glycera sp.	Yonge, 1928
Glyceridae, general	Day, 1967; Retière, 1967; MacGinitie & MacGinitie, 1968; Pearson, 1971

Hartmann-Schröder (1971) separated a group of detritivorous forms (*G. capitata* and *G. gigantea*) from a group of carnivores (*G. alba* and *G. rouxii*). She claimed the detritivorous habit as the major mode of feeding of the glycerids. All glycerids examined by Blegvad (1914, 23 specimens) had empty stomachs and he concluded from this that they are carnivores. Sanders *et al.* (1962) found the stomachs of *G. dibranchiata* empty in most cases, but containing detritus in a few instances and concluded from this that *G. dibranchiata* is a detritivore.

Both groups of investigators may be correct: each species investigated has been unanimously assigned to a mode. *G. alba*, *G. convoluta*, *G. lapidum*, *G. robusta*, *G. rouxii*, and *G. siphonostoma* are considered carnivores (Blegvad, 1914; Hunt, 1925; Mare, 1942; Yonge, 1954a; Ockelmann & Vahl, 1970; Michel, 1970b; Ronan, 1978). *G. capitata*, *G. dibranchiata*, *G. gigantea* and

G. unicornis are considered detritivores (Stolte, 1932; Klawe & Dickie, 1957; Sanders *et al.*, 1962; Frankenberg & Smith, 1967; MacGinitie & MacGinitie, 1968; Hartmann-Schröder, 1971).

Attempts at feeding glycerids with pieces of meat have generally been unsuccessful (Stolte, 1932; Klawe & Dickie, 1957) and this has been considered evidence for a detritivore habit. The description of the feeding behaviour of *G. alba* given by Ockelmann & Vahl (1970) indicates that this conclusion may be erroneous. *G. alba* has a complex burrow system with several openings on the substratum surface. The worm is sensitive to small changes in water pressure such as created by an animal moving around. The glycerid will track the moving prey in its burrow system and will move to the opening that gives the best angle of attack and the easiest possiblity of cutting off the path of the prey. The prey is grasped by a rapid eversion of the pharynx. Ockelmann & Vahl (1970) found *G. alba* to prefer moving prey, such as small polychaetes and amphipods; it is less interested in sessile prey and will not attack animals encased in tubes. These results were generally confirmed for *G. robusta* by Ronan (1978).

Fig. 10.—GLYCERIDEA: *Hemipodus borealis* shown eating the scale-worm *Eunoe uniseriata*; some other glycerids are considered deposit-feeders; ×2·5.

The stated prey preferences agree with the gut contents listed for the carnivorous species (Mare, 1942: polychaetes; Yonge, 1954a: polychaetes and crustaceans; Retière, 1967: polychaetes, amphipods, and organic debris; Michel, 1970b: polychaetes and amphipods). The enzymatic complement of two carnivores (*G. alba* and *G. convoluta*) has been investigated and fits the expected pattern in that an array of lipolytic and proteolytic enzymes are present (Michel, 1970a; Michel & Imhoff, 1975; Vahl, 1976).

The mechanism of food uptake has not been described in detail for the detritivorous forms. The detailed knowledge of the carnivorous habit must not be considered evidence on the frequency of this habit in the family.

On morphological grounds we postulate that the carnivorous habit is the primary feeding mode among the glycerids, but that an unknown, probably small number of species have become detritivores. We further postulate that bathyal and abyssal glycerids may be able to use both modes and that glycerids living in nutrient-rich environments may supplement either feeding mode by direct uptake of dissolved organic matter. Finally, we suggest that construction of a burrow system is associated primarily with a carnivorous habit and secondarily, with the uptake of dissolved organic matter, and that detritivorous forms may not maintain burrow systems.

GONIADIDAE

Goniadids resemble glycerids in that they are long, narrow polychaetes with conical prostomia and enormous eversible pharynges tipped with series of small jaws. The 93 known species are found at all depths; goniadids tend to be more common in deeper water than are the glycerids. All species are considered carnivores, but only the following species have been specifically mentioned in the literature: *Glycinde armigera*, *G. nordmanni*, and *Goniada maculata* (Blegvad, 1914; Hunt, 1925; Southward, 1957; Jones, 1961; Wolff, 1973). *Goniada* sp. is capable of absorbing dissolved organic matter according to Southward & Southward (1972a). Nothing has been done to quantify the food uptake of a single goniadid, and in fact, the information listed above is mainly indirect. Blegvad (1914) concluded that *G. maculata* was a carnivore, because all nine specimens investigated by him were empty and Hunt (1925) came to a similar conclusion, based on twelve empty specimens. Southward (1957) followed by Wolff (1973) considered the same species a carnivore, apparently on the basis of morphology.

We agree that the goniadids probably are carnivores, but there is no direct evidence to show that this is so. The locomotory patterns are unknown; goniadids are not tubicolous, but whether they form burrows or move freely in the sediment is unknown.

HESIONIDAE (Table XII, Fig. 11)

Hesionids possess an eversible muscular, armed or unarmed pharynx. They comprise one of the least known of the major polychaete families, systematically as well as biologically. A major reason is their fragility, making well preserved material difficult to obtain. While frequent, the hesionids are rarely abundant, so apparently there has been little reason to take them into account in synecological contexts. The interstitial forms are best known, thanks to the efforts of Westheide (see *e.g.*, 1977) and others.

TABLE XII

Literature on feeding modes of the hesionids: approximate number of known species, 130.

Hesionides arenaria	Westheide, 1967; Wolff, 1973
,, *gohari*	Westheide, 1967
,, *maxima*	Westheide, 1967
Kefersteinia cirrata	Rasmussen, 1973
Microphthalmus aberrans	Westheide, 1967; Wolff, 1973
,, *listensis*	Westheide, 1967; Wolff, 1973
,, *sczelkowii*	Westheide, 1967
Nereimyra punctata	Schäfer, 1962; Pearson, 1971
Syllidia armata	Rasmussen, 1973
Hesionidae, general	Day, 1967

Most interstitial forms feed on diatoms (*Hesionides arenaria* and *H. gohari*, *Microphthalmus aberrans* and *M. sczelkowii*) and at least partially on bacteria-rich detritus (*Hesionides arenaria* and *Microphthalmus listensis*) according to Westheide (1967) and Wolff (1973). Wolff indicated that some species may take copepods and foraminiferans as well. The larger hesionids (*Hesionides maxima*, *Kefersteinia cirrata*, *Nereimyra punctata*, and *Syllidia armata*) are carnivores (Westheide, 1967; Pearson, 1971; Rasmussen, 1973); they feed on a variety of small invertebrates. *Nereimyra punctata* also is capable of feeding on detritus as a surface deposit-feeder (Schäfer, 1962; Pearson, 1971); documentation of this habit is weak.

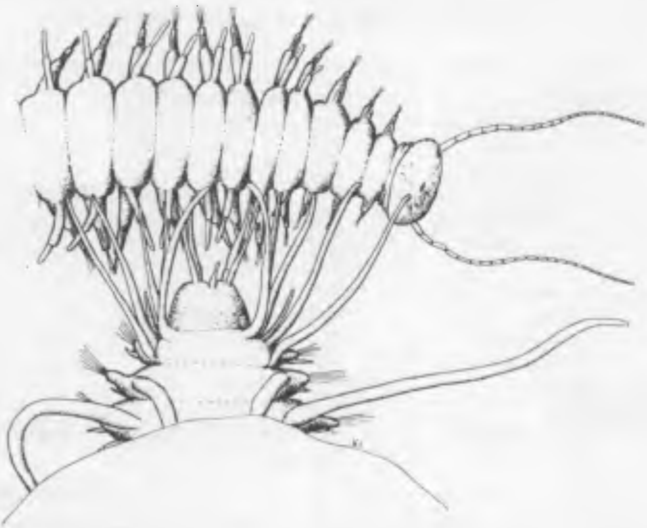

Fig. 11.—HESIONIDAE: *Ophiodromus pugettensis* shown just before striking at the posterior end of *Schistomeringos annulata*; the food habits of most large hesionids are otherwise unknown; ×2·5.

We postulate that non-interstitial hesionids are carnivores. The small hesionids feed on a variety of diatoms, bacteria, and other small forms, as do most mesopsammic polychaetes. Resource partitioning by food type may take place among the interstitial forms (Westheide, 1967); no such information is available for the larger species. All non-commensal hesionids are freely motile (Remane, 1933). No quantitative information is available.

ICHTHYOTOMIDAE

The family is known for a single species, *Ichthyotomus sanguinarius*, parasitic on eels from Naples, Italy (Eisig, 1906). The parasites are attached to the gills of the fish and feed by taking in host cells and blood.

LOPADORHYNCHIDAE

The family is known for 16 species of exclusively pelagic habits. All species are carnivores, grasping their prey with the enlarged, muscular anterior parapodia which have strong, gently curved spines (Dales, 1955a); prey items are unknown.

LUMBRINERIDAE (Table XIII, Fig. 12)

Lumbrinerids are long, slender polychaetes with unadorned, usually conical prostomia, uniramous parapodia, and large eversible jaw complexes that consist of a pair of mandibles and four pairs of maxillae. The most dorsal pair of maxillae is tong-shaped and at least one pair has series of blunt teeth.

TABLE XIII

Literature on feeding modes of the lumbrinerids: approximate number of known species, 188.

Lumbrineris bicirrata	Banse & Hobson, 1968
,, *californiensis*	Banse & Hobson, 1968
,, *cruzensis*	Banse & Hobson, 1968
,, *flabellicola*	Zibrowius *et al.*, 1975
,, *fragilis*	Blegvad, 1914; Hartmann-Schröder, 1971
,, *hibernica*	Southward, 1957; Pearson, 1971
,, *impatiens*	Hunt, 1925; Hempelmann, 1931; Yonge, 1954a; Hartmann-Schröder, 1971
,, *latreilli*	Wolff, 1973
,, *luti*	Banse & Hobson, 1968
,, *minima*	Reish, 1959
,, *tenuis*	Sanders *et al.*, 1962
Lumbrineris sp.	Yonge, 1928
Ninoe nigripes	Sanders, 1960
Lumbrineridae, general	Gardiner, 1903; Day, 1967; Hartmann-Schröder, 1971

The lumbrinerids are considered carnivores or carrion-feeders by most authors (Gardiner, 1903; Blegvad, 1914; Hunt, 1925; Yonge, 1928; Southward, 1957; Day, 1967; Pearson, 1971; Wolff, 1973; Zibrowius, Southward & Day, 1975). This list of investigators dwindles if more accurate documentation is required. Blegvad (1914) listed the gut content for *Lumbrineris fragilis* as consisting of other polychaetes (*Pherusa plumosa* and tube-worms), the ophiuroid *Amphiura* sp., nemerteans, small crustaceans and bivalves. Zibrowius *et al.* (1975) showed that *Lumbrineris flabellicola* is a commensal with cnidarians of the genera *Caryophyllia* and *Flabellum*, feeding on the food of its hosts, and Gardiner (1903) claimed that lumbrinerids might drill in newly formed coral. There is evidence of a carnivorous habit for two species.

At least one species, *Lumbrineris impatiens*, is known to be herbivorous (Hempelmann, 1931; Yonge, 1954a; Hartmann-Schröder, 1971); however, Hunt (1925) reported this species as a carnivore. It is supposed to feed on large plant fragments, usually of *Zostera*. We have been unable to find the original documentation of this herbivorous habit, unless Hempelmann was responsible for the observations. We accept the claim, however, as being consistent with our own, rather casual observations. *Ninoe nigripes* is a selective deposit-feeder, feeding on the surface of the mud (Sanders *et al.*, 1962). Specimens of four species investigated by Banse & Hobson (1968) contained detritus and sand, suggesting deposit-feeding habits.

We postulate that all three modes of feeding are utilized among the lumbrinerids, but that each species will use only one mode. The lumbrinerids are notoriously difficult to identify, so reports of two different modes in one species may be due to misidentifications. Lumbrinerids are not usually tubicolous, but are capable of secreting temporary mucous housings, at least in aquaria. In bare-walled aquaria they rarely demonstrate agonistic behaviour, but become territorial when sediments, algae or other materials are added (K. Fauchald, pers. obs.). This territoriality could place a limit on their realized motility; however, they must be considered motile forms, until better evidence becomes available.

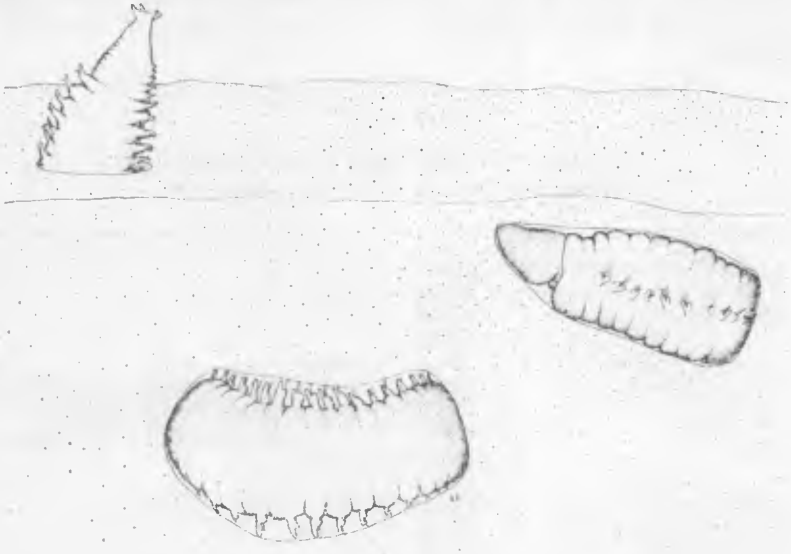

Fig. 12.—LUMBRINERIDAE: *Lumbrineris tetraura* shown burrowing as a sub-surface deposit-feeder; the feeding selectivity of this species and of most other lumbrinerids is unknown; ×2·5.

LYSARETIDAE

Lysaretids are tropical, large-bodied euniceans with a complex eversible jaw apparatus. The family contains about ten species and is extremely poorly known. One species, *Oenone fulgida*, is circumtropical and appears associated with coral reefs in that it has been reported as boring in coral both from the Caribbean Sea (Ebbs, 1966) and the Marshall Islands (Hartman, 1954). Yonge (1954a) reports the gut content of *Halla parthenopeia*, which is less strictly tropical than *Oenone fulgida*, as consisting of algae, diatoms, and copepods, perhaps indicating a scraping mode of life on hard substrata. The lysaretids are non-tubicolous, but whether they form their own burrows, or live in burrows made by other organisms, remains an open question.

MAGELONIDAE

Magelonids are long, slender spioniform polychaetes with a flattened, spade-shaped prostomium and a pair of very long, ventrally attached palps. These palps are papillose over the distal two-thirds of their length and are smooth proximally. The magelonids are very good burrowers, living in sands and muds; they are present at all depths. The burrows are poorly supported, and no distinct tubes are formed (McMahon & Jones, 1967; Hartmann-Schröder, 1971).

The feeding habits of a species traditionally called *Magelona papillicornis* have been reported by Hunt (1925), Linke (1939), Retière (1967), Hartmann-Schröder (1971), Wolff (1973), and Kühl (1974). Jones (1977) pointed out that this name has been incorrectly applied to the European material and that this species should be called *M. mirabilis*, at least temporarily. The species concept used by most authors is confused and more than one species may be involved in the European reports on the feeding habits of members of *Magelona*.

TABLE XIV

Literature on feeding modes of the maldanids: approximate number of known species, 218.

Axiothella rubrocincta	Kudenov, 1977b
Branchioasychis americana	Mangum, 1964a,b
Clymenella californica	Kudenov, 1977b
,, *cincta*	Pearson, 1971
,, *mucosa*	Mangum, 1964a,b
,, *torquata*	Ullman & Bookhout, 1949; Sanders *et al.*, 1962; Stephens, 1963; Mangum, 1964a,b; Rhoads & Stanley, 1965; Rhoads, 1967, 1974; Southward & Southward, 1972b
,, *zonalis*	Mangum, 1964a,b
Maldane sarsi	Hartmann-Schröder, 1971
Petaloproctus socialis	Mangum, 1964a,b
Praxillella affinis	Pearson, 1971
,, ,, *pacifica*	Kudenov, 1977b
,, *gracilis*	Pearson, 1971
Rhodine loveni	Pearson, 1971
Maldanidae, general	Blegvad, 1914; Dales, 1963; Day, 1967; Hunt, 1925; Yonge, 1928; Southward & Southward, 1972a

McMahon & Jones (1967) and Jones (1968) described feeding in *Magelona* in detail. Food particles are captured on the papillated surface of the palps and are transferred to more proximal groups of papillae by a looping motion of the palp, as if an inch-worm would transfer the ground from one set of feet to the next. Eventually the food particle will reach the unpapillated, innermost part of the palp. The particle apparently falls freely from this point to the mouth, but mucus may be involved in this last transfer. There is no evidence for the use of cilia in feeding (Jones, 1968).

The food consists of detritus, diatoms, and small animals (Jones, 1968). The fraction of crustacean fragments was very high in specimens examined by Mare (1942); she concluded that these specimens were at least partially to be considered carnivores. Other authors have indicated selectivity in terms of food particles (Hunt, 1925; Linke, 1939), but did not report the grounds for their statements. Retière (1967) indicated that particle size selection is present, but gave no evidence. Hartmann-Schröder (1971) and Wolff (1973) indicated that some suspension-feeding may take place. The feeding procedure described by McMahon & Jones (1967) and Jones (1968) makes this unlikely, but not impossible. Magelonid larvae feed on veligers (Kühl, 1974).

We conclude that the magelonids are motile surface deposit-feeders. When feeding on poorly sorted material, we believe that selectivity may be shown in that the magelonids prefer to handle larger particles and will take small crustaceans as prey when given the opportunity. Such selectivity may not be seen in well sorted sand, or in ripples where relatively coarse-grained, high-organic particles have been already concentrated by physical means. The presence of pelagic organisms in the digestive tracts of worms living in a high-energy environment such as a well sorted beach, is more indicative of feeding on the organic debris in ripples than of filter-feeding.

No quantitative investigations have been done; the number of species is unsettled, possibly about 35.

MALDANIDAE (Table XIV, Fig. 13)

The bamboo-worms all feed by eversion of a sac-like pharynx (Kudenov, 1977b) and are common in soft substrata at all depths. Most are tubicolous, but the construction of the tubes varies a great deal. Some forms have strong tubes with thick linings and a thick outer covering of mud (*Maldane sarsi*); others lack the sediment cover, so the tube consists of the organic matrix only (*Rhodine* spp.) and in several the tubes are no more than poorly consolidated burrows (some species of *Clymenella*).

The food is usually characterized as detritus (Mangum, 1964a); Ullman & Bookhout (1949) specified protozoa and diatoms contained in the sediment as the true source of food for *C. torquata*. This species has been the subject of a number of studies, and more biological information is available for this than for any other maldanid. It feeds at the bottom of a 20-cm long tube (Mangum, 1964a,b; Rhoads & Stanley, 1965; Rhoads, 1967, 1974). As it ingests the sediments, voids are left, and the surrounding sediments collapse to bring more material to the feeding worm. Mangum (1964a) showed that all five species (three genera) investigated by her fed in essentially the same manner; Day (1967) generalized to the whole family.

It is not clear how much selectivity the worms show while feeding. Mangum (1964a) showed that the five species were, in part, spatially separated, or could be separated on preference for particular grain sizes. Mangum (1964b) also showed that there are differences in the activity patterns of the five species. *Clymenella* spp., living in anoxic sands, showed distinct rhythmic activity patterns, whereas *Branchioasychis americana* and *Petaloproctus socialis* did not. *Branchioasychis americana* is branchiated, and *Petaloproctus socialis* lives in well aerated sands. Maldanids thus use several environmental factors to partition their environment. *Clymenella torquata* is capable of taking up dissolved organic matter (Stephens, 1963; Southward & Southward, 1972b) as are other, unidentified maldanids (Southward & Southward, 1972a). The importance of this capability is unknown.

Because of their burrowing activities, maldanids are of interest to stratigraphers. *C. torquata* (Rhoads & Stanley, 1965; Rhoads, 1967, 1974) and

Fig. 13.—MALDANIDAE: *Axiothella rubrocincta* with pharynx partially everted, cephalic plaque braced against the recoil; the degree to which this feeding mechanism is selective is largely unknown; ×20.

some species from sandy areas in Europe (Schäfer, 1962) have been well investigated; the bioturbation is a consequence of the feeding activity as described above. Maldanids may continue building tubes throughout life, and thus move slowly from one location to another. We suggest that all species with poorly constructed tubes and all deep-water species have this capability. It is unlikely that forms living in food-rich environments will keep on constructing tubes for an extended time. We predict, however, that all maldanids are capable of continuous tube building and that experimental work will connect the amount of food available and the tube-building activity in any population.

Mangum (1964b) calculated the food necessary for *C. torquata* and related this to turnover rates of sediments and oxygen consumption, creating what comes close to being a complete energy budget for this species. She found that each individual will turn over about 1 ml of sediment per day at 26 °C; the oxygen consumption was the equivalent of 1 cal. day^{-1} . $worm^{-1}$ and the food consumed had the caloric value of 10 cal. day^{-1} . $worm^{-1}$. The calculation shows there is sufficient energy available in the sediment to maintain this species. The activities of a dense bed of *C. torquata* can in fact turn over a considerable volume of sediment in a short time.

NEPHTYIDAE (Table XV)

Nephtyids have very large eversible pharynges. Internally the pharynx has a pair of small jaws consisting of tanned protein (Michel *et al.*, 1973). In some instances the jaws show growth rings (Kirkegaard, 1970) which in some

TABLE XV

Literature on feeding modes of the nephtyids: approximate number of known species, 103.

Aglaophamus malmgreni	Schäfer, 1962
,, *rubella*	Hunt, 1925
Nephtys caeca	Rauschenplat, 1901; Schäfer, 1962; Hartmann-Schröder, 1971; Wolff, 1973
,, *caecoides*	Ronan, 1978
,, *ciliata*	Rauschenplat, 1901; Schäfer, 1962; Hartmann-Schröder, 1971; Pearson, 1971
,, *cirrosa*	Hunt, 1925; Clark, 1962; Schäfer, 1962; Wolff, 1973
,, *hombergii*	Hunt, 1925; Hempelmann, 1931; Thamdrup, 1935; Linke, 1939; Yonge, 1954a; Smidt, 1951; Clark, 1962; Schäfer, 1962; Jepsen, 1965; Michel, 1970c; Hartmann-Schröder, 1971; Pearson, 1971; Michel *et al.*, 1973; Rasmussen, 1973; Wolff, 1973
,, *hystricis*	Hunt, 1925; Pearson, 1971
,, *incisa*	Hunt, 1925; Sanders, 1956, 1960; Southward, 1957; Clark, 1962; Hartmann-Schröder, 1971; Rhoads, 1974
,, *longosetosa*	Schäfer, 1962; Wolff, 1973
Nephtyidae, general	Blegvad, 1914; Yonge, 1928; Remane, 1933; Mare, 1942; Schäfer, 1962; Day, 1967; Retière, 1967; Southward & Southward, 1972a

areas have been related to the reproductive periodicity (Olive, 1977). This does not seem to be the case in animals from warm-water regions (Fauchald, pers. obs.). The nephtyids are common in soft substrata from the intertidal to abyssal depths and may be extremely abundant (Sanders, 1960). All are free-living burrowers which may periodically form poorly agglutinated burrows (Ronan, 1978).

Nephtyids are usually considered vagile carnivores, feeding on small invertebrates including molluscs, crustaceans, and other polychaetes (Rauschenplat, 1901; Blegvad, 1914; Hunt, 1925; Yonge, 1928, 1954a; Hempelmann, 1931; Thamdrup, 1935; Linke, 1939; Mare, 1942; Smidt, 1951; Southward, 1957; Clark, 1962; Jepsen, 1965; Day, 1967; Retière, 1967; Hartmann-Schröder, 1971; Pearson, 1971; Schäfer, 1972; Rasmussen, 1973; Wolff, 1973; Ronan, 1978). Rauschenplat (1901) found that *Nephtys caeca* and *N. ciliata* often had large quantities of sand in the gut, in addition to remnants of polychaetes and crustaceans.

Sanders (1956, 1960) reported that *N. incisa* from Long Island Sound and Buzzard's Bay, New England, was a typical motile subsurface deposit-feeder. He found no evidence of a carnivorous habit in this species, which has been reported as a carnivore from Europe (Southward, 1957; Clark, 1962). Members of the genus *Nephtys* have extremely limited capabilities of taking up dissolved organic matter so this potential source of nutrition appears unlikely (Southward & Southward, 1972a).

We generally consider the nephtyids as motile predators, but some species have taken up other modes of living. We strongly suggest that the identity of the two populations of *N. incisa* be carefully tested. We do not suggest that the reports of detritus feeding by Sanders are incorrect: in fact, Sanders' observations were unusually carefully made. On the other hand, the observations of carnivorous habits in this and related species from Europe, have been well made and frequently repeated. We propose that despite the close similarity between the two populations, morphology is in this instance a very poor predictor of ecology.

We know nothing about the energy requirements of any species, nor do we know anything about possible food selectivity in terms of prey species or in terms of particle selection.

NEREIDAE (Table XVI, Fig. 14)

All nereids have jawed eversible pharynges, often adorned with small auxiliary jaw pieces called paragnaths. They are most common in shallow water, but some species, especially of the genus *Ceratocephale*, have been reported from deep water as well (Hartman & Fauchald, 1971). One species, *Pseudonereis gallapagensis*, drills in corals (Hartman, 1954); coral experts indicate that the nereids may nestle in holes made by other organisms (Gardiner, 1903).

Feeding in nereids was recently and extremely ably reviewed by Goerke (1966, 1971a,b,c) and references to additional literature can be found in those papers, particularly in Goerke (1971a). Only about eight species can be said to have well known feeding habits: these include *Eunereis longissima*, *Nereis (Hediste) diversicolor*, *N. (Neanthes) arenaceodentata*, *N. (N.) fucata*, *N. (N.) succinea*, *N. (N.) virens*, *N. (Nereis) pelagica*, and *N. (N.) grubei*. In feeding

TABLE XVI

Literature on feeding modes in the nereids: approximate number of known species, 439.

Cheilonereis cyclurus	MacGinitie & MacGinitie, 1968
Dendronereis sp.	Day, 1967
Eunereis longissima	Hammond, 1966; Goerke, 1971a; Southward & Southward, 1972a; Wolff, 1973
Laeonereis culveri	Mazurkievicz, 1975
Micronereis variegata	Rullier, 1954
Nereis (Hediste) diversicolor	Rauschenplat, 1901; Blegvad, 1914; Thamdrup, 1935; Linke, 1939; Rees, 1940; Harley, 1950, 1953; Smidt, 1951; Seilacher, 1953; Bogucki, 1954; Perkins, 1958; Schäfer, 1962; Goerke, 1966; 1971a; Muus, 1967; MacGinitie & MacGinitie, 1968; Cazaux, 1969; Southward & Southward, 1972a,b; Losovskaya, 1973; Rasmussen, 1973; Theede *et al.*, 1973; Wolff, 1973; Evans *et al.*, 1974; Stephens, 1975
,, *(Neanthes) arenaceodentata*	Sanders *et al.*, 1962; MacGinitie & MacGinitie, 1968; Reish & Stephens, 1969; Goerke, 1971a
,, ,, *brandti*	MacGinitie & MacGinitie, 1968; DeVillez & Reid, 1971
,, ,, *fucata*	Goerke, 1971a,c; Wolff, 1973
,, ,, *succinea*	Frankenberg & Smith, 1967; Goerke, 1971a; Losovskaya, 1973; Rasmussen, 1973; Theede *et al.*, 1973; Southward & Southward, 1974b
,, ,, *virens*	Blegvad, 1914; Gross, 1921; Copeland & Wieman 1924; Hempelmann, 1931; Yonge, 1954a; Sanders *et al.*, 1962; Chapman & Taylor, 1968; MacGinitie & MacGinitie, 1968; Taylor, 1969; Goerke, 1971a,b; Southward & Southward, 1972b; Kay & Brafield, 1973; Rasmussen, 1973; Theede *et al.*, 1973; Wolff, 1973; Kay, 1974
Nereis (Nereis) grubei	Reish, 1954; Goerke, 1971a
,, ,, *irrorata*	Goerke, 1971a
,, ,, *limnicola*	Southward & Southward, 1972b
,, ,, *accidentalis*	Goerke, 1971a
,, ,, *pelagica*	Rauschenplat, 1901; Blegvad, 1914; Hempelmann, 1931; Yonge, 1954a; Goerke, 1971a; Theede *et al.*, 1973
,, ,, *procera*	Goerke, 1971a
,, ,, *vexillosa*	Goerke, 1971a; Roe, 1975
,, ,, *zonata*	Hunt, 1925; Losovskaya, 1973
Perinereis cultrifera	Hempelmann, 1931; Yonge, 1954a; Cazaux, 1968; Goerke, 1971a; Michel *et al.*, 1973
,, *marioni*	Goerke, 1971a
Platynereis bicanaliculata	Jones, 1961; MacGinitie & MacGinitie, 1968; Goerke, 1971a; Roe, 1975
,, *dumerilii*	Hunt, 1925; Remane, 1933; Korringa, 1951; Day, 1967; Cazaux, 1969; Goerke, 1971a; Rasmussen, 1973
,, *massiliensis*	Goerke, 1971a
,, *megalops*	Goerke, 1971a
Pseudonereis gallapagensis	Hartman, 1954
,, *variegata*	Day, 1967; Goerke, 1971a
Nereidae, general	Gardiner, 1903

experiments, these species with few exceptions were found to be omnivorous (Reish, 1954; Goerke, 1971a). *Nereis* (*Neanthes*) *fucata*, which is commensal with the hermit crab, *Pagurus bernhardus*, will feed only on various animal tissues. It feeds normally by stealing food from its host (Goerke, 1971a,c) as does *Cheilonereis cyclurus* in a similar association in the Pacific Ocean (MacGinitie & MacGinitie, 1968). They are apparently protected from their hosts by living in mucous tubes, which the host cannot grasp. The other species listed will take both animal and plant food as well as detritus.

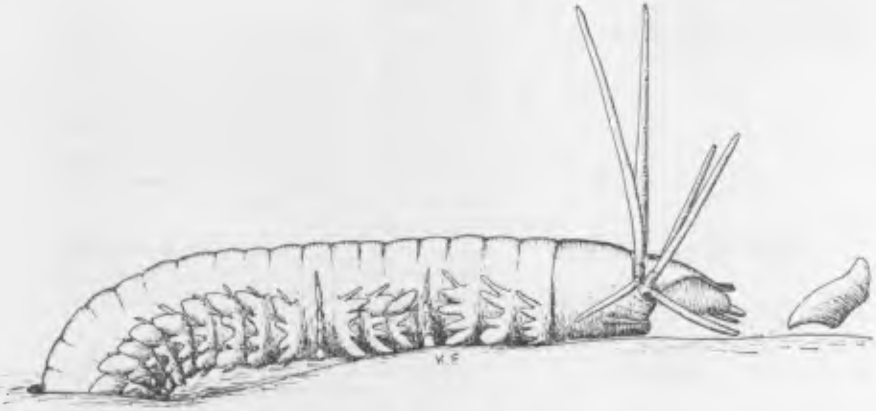

Fig. 14.—NEREIDAE: *Nereis vexillosa* emerging from a burrow and exploring a piece of the green alga *Ulva* sp.; ×2·5.

All species so far examined, can form mucous tubes and feed preferentially from the mouth of such tubes, and all species are capable of leaving their tubes and do so when conditions become unacceptable. They will rapidly and repeatedly move and set up new tubes in other locations, both in the field and in laboratory experiments. This ability indicates that the nereids as a group function as discretely motile, rather than fully motile, animals. One species, *Nereis* (*Hediste*) *diversicolor*, is capable of filter-feeding with the aid of a mucous cone suspended within its tube (Harley, 1950, 1953; Goerke, 1966). As many as 25 filters may be set up in the course of 1·5 h. The process consists of four distinct steps. First is the secretion of mucous threads, then the formation of the filter, followed by irrigation of the tube, and finally ingestion of the filter with contained food (Goerke, 1966). We do not know if this feeding behaviour is unique to *N.* (*H.*) *diversicolor*; it is used in the field as well as in laboratory experiments.

Gut content investigations (summarized in Table 7 of Goerke, 1971a) indicate that even the most omnivorous of nereids may have a relatively limited realized diet. The realized diet of most nereids consists of algae and diatoms (*Nereis* (*Neanthes*) *arenaceodentata*, *N.* (*N.*) *brandti*, *N.* (*Nereis*) *irrorata*, *N.* (*N.*) *procera*, *Perinereis cultrifera*, *P. marioni*, *Platynereis bicanaliculata*, *P. dumerilii*, and *P. massiliensis*). A few nereids may be shown to be carnivores (*e.g.*, *N.* (*Nereis*) *grubei*) and some species are also omnivores in the field (*N.* (*Nereis*) *vexillosa*, *N.* (*Hediste*) *diversicolor*, some populations of *N.* (*Neanthes*) *virens*, and *Pseudonereis variegata*). Some species (*Dendro-*

nereis sp., *Eunereis longissima*, *N.* (*Neanthes*) *succinea*) are surface deposit-feeders. Several nereids show two different feeding patterns (MacGinitie & MacGinitie, 1968). In a few cases one population shows a limited diet while others are less restricted: *N.* (*Neanthes*) *virens* is a herbivore near Woods Hole and is omnivorous elsewhere (Copeland & Wieman, 1924; Goerke, 1971a; Theede *et al.*, 1973). Similarly, the importance of filter-feeding in *N.* (*Hediste*) *diversicolor* varies from one population to the next and the habit may be entirely missing in some populations. Alternatively, populations may switch from one mode to the other. Several species are capable of absorbing dissolved organic matter (Southward & Southward, 1972a,b; Stephens, 1975); it remains unclear how important this may be.

NERILLIDAE

Nerillids are small, interstitial polychaetes with an eversible pharynx. The family is known for 25 species of which two have been partially investigated in terms of feeding habits. *Nerilla antennata* feeds on diatoms, bacteria, and plant and animal debris with the largest particles taken being ≈ 50 μm long and 15 μm wide (Gelder & Uglow, 1973). This species is selective in that it will avoid taking in non-nutritive particles. The feeding takes place as an abrading or rubbing of the surface of sand grains by the eversible pharynx. *Thalassochaetus palpifoliaceus* feeds on diatoms that are cracked by the armature in the pharynx (Ax, 1954).

We assume that other species in the family will be shown to have similar food habits, and that the different species may be separated more on habitat preference than on food habits (Gelder, 1974).

ONUPHIDAE (Table XVII, Fig. 15)

Onuphids are tubicolous euniceans found mainly on soft substrata and in rubble; they are common in shallow water and are better represented in bathyal and abyssal areas than any other eunicean group (Fauchald, 1972). Most forms have permanently fixed tubes, but some are capable of moving around with their tubes (*e.g.*, *Nothria conchylega* and *Hyalinoecia* spp.). All species are capable of leaving their tubes and constructing new tubes.

TABLE XVII

Literature on feeding modes of the onuphids: approximate number of known species, 190.

Diopatra cuprea	Sanders *et al.*, 1962; Day, 1967; Mangum *et al.*, 1968; Myers, 1970, 1972; Mangum & Cox, 1971
„ *monroi*	Day, 1967
„ *neapolitana*	Hempelmann, 1931; Yonge, 1954a
„ *ornata*	Lipps & Ronan, 1974; Rosenthal *et al.*, 1974
Epidiopatra gilchristi	Day, 1967
Hyalinoecia tubicola	Hunt, 1925
Nothria conchylega	Schäfer, 1962; Hartmann-Schröder, 1971
Onuphis brittanica	Hunt, 1925
„ *quinquedens*	Day, 1967
Onuphidae, general	Hartmann-Schröder, 1971

Opinion on the feeding biology of onuphids is more than usually divided. Hartmann-Schröder (1971) characterized them as carnivores and Schäfer (1962) gave evidence of this. Hempelmann (1931) called *Diopatra neapolitana* a herbivore; Yonge (1954a) listed its gut content as algae, sponges, bryozoans, crustaceans, and detritus, indicating a rather more catholic taste. *D. ornata* feeds largely on kelp, according to evidence gathered by Emerson (see below), but Rosenthal, Clarke & Dayton (1974) called it a scavenger. This species may also feed on foraminiferans (Lipps & Ronan, 1974), and feeding experiments have shown that it will accept any plant or animal material, dead or alive, fresh or rotten (R. R. Emerson, pers. comm.). Emerson did show, however, that one population did well on a realized diet of kelp (*Macrocystis pyrifera*) and formed dense stands where the supply of drift kelp was high. A closely related form, *Diopatra cuprea*, has been extensively studied along the Atlantic coast of the U.S.A. (Sanders *et al.*, 1962; Mangum, Santos & Rhodes, 1968; Myers, 1970, 1972; Mangum & Cox, 1971) and has been shown to use the curved tube cap as a food catching device. It feeds on members of the tube cap community, as well as on any living or recently dead animals it can catch. At least in the population most intensively studied, it showed no distinct signs of herbivorous habits. Specimens from the same population in Barnstable Harbor, Massachusetts, may contain large quantities of sediment in addition to algal fragments, according to Sanders *et al.* (1962); so plant- and detritus-feeding may take place from time to time. The question needs resolution. Day (1967) argued that *D. monroi* and *Epidiopatra gilchristi* may be capable of feeding on plankton, based largely on the density of populations in relation to obvious benthic food sources. We suggest that it is more likely that these species feed on drift material, such as drift algae, than that they feed on plankton directly.

Fig. 15.—ONUPHIDAE: *Diopatra ornata* feeding on a frond of the giant kelp, *Macrocystis pyrifera*; closely related onuphids differ greatly in food habits, making it unclear whether these animals should be considered herbivores or generalized scavengers. ×0·5.

Observations in aquaria (MacGinitie & MacGinitie, 1968) and with baited monster cameras (Dayton & Hessler, 1972) show that *Hyalinoecia* spp. will come to carrion; in fact, hundreds of specimens will aggregate on a single rotten fish. We consider the onuphids primarily omnivorous scavengers. Members of shallow-water sessile populations may specialize on the food items most readily available and, if a single food item dominates, may functionally become food specialists. We believe that this specialization is a matter of opportunism, rather than of genetics. Onuphids living in less nutrient-rich environments have two major ways of increasing their food supply. They may retain a truly omnivorous habit or they may become motile. Members of the motile genus *Hyalinoecia* are better represented in nutrient-poor, shifting sands than any other onuphids, and the genus is also extremely well represented in deep water. This argument does not hold for the numerous deep-water species of *Nothria*, all of which are thought to be sessile. These species may be truly omnivorous, but this remains unknown. No quantitative investigations have been done on any onuphid.

OPHELIIDAE (Table XVIII)

Opheliids are burrowers in sandy or muddy sediments. They are considered non-selective deposit-feeders (Blegvad, 1914; Hunt, 1925; Yonge, 1928; Retière, 1967; Hartmann-Schröder, 1971; Pearson, 1971; Wolff, 1973). Guerin (1971) indicated that *Polyophthalmus pictus* feeds on dead copepods and other organic debris, strongly suggesting selectivity in this species. *Euzonus mucronatus* feeds primarily on organic matter adsorbed on sand grains, but also on bacteria, protozoans, and other small organisms associated with the sand. This species does not appear to digest diatoms (McConnaughey & Fox, 1949).

TABLE XVIII

Literature on feeding modes of the opheliids: approximate number of known species, 138.

Euzonus flabelligerus	Hartmann-Schröder, 1971
,, *mucronatus*	McConnaughey & Fox, 1949
Ophelia bicornis	Wilson, 1952, 1955
,, *borealis*	Wolff, 1973
,, *limacina*	Blegvad, 1914; Hartmann-Schröder, 1971
,, *rathkei*	Hartmann-Schröder, 1971; Wolff, 1973
Ophelina acuminata	Blegvad, 1914; Hunt, 1925; Hartmann-Schröder, 1971; Pearson, 1971
Ophelina sp.	Yonge, 1928
Polyophthalmus pictus	Guerin, 1971
Travisia forbesi	Retière, 1967, 1971, 1972; Wolff, 1973
Opheliidae, general	Dales, 1963; Day, 1967

The low level of food specialization in adults contrasts sharply with the high level of precision in the selection of substrata by the juveniles (Wilson, 1952, 1955; Retière, 1971, 1972). We believe that the opheliids are rather more selective of their food sources than has been suggested, but that all species have the same general habit, in that all ingest sediment for the contained organic matter. The selection will be at the level of differential digestion among different species.

McConnaughey & Fox (1949) calculated that the turnover rate in *Euzonus mucronatus* was ≈84 g sand . year^{-1} . worm^{-1}. Based on the average organic content of the sand in the habitat and the faecal material an absorption efficiency of 96% is indicated. This is much higher than expected, especially considering that the total passage time of sediment through the digestive tract was measured by the same authors to be about 15 min.

ORBINIIDAE (Table XIX)

Orbiniids have sac-like or dendritic eversible pharynges. They are common in muddy areas and are found from salt marshes to abyssal depths.

All authors cited agree that all orbiniids are non-selective deposit-feeders burrowing freely through the sediments. We have been unable to find a single reference to the testing of the level of selectivity in these worms. In fact, most authors give no evidence whatever for their statements. The dendritically branching eversible pharynx present in many species, indicates that a test of the level of selectivity might prove fruitful. Larvae start feeding after metamorphosis, in the early stages using the pharynx for burrowing as well as for feeding (Anderson, 1961). Later in life they burrow in the fashion similar to the other annelids (Clark, 1964; Fauchald, 1974). Eisig (1914) stated that the larval pharynx was non-eversible; this appears unlikely considering Anderson's findings. While the orbiniids are freely motile, the presence of cocoons in *Scoloplos armiger* may be useful for keeping populations in appropriate habitats (Gibbs, 1968).

TABLE XIX

Literature on feeding modes of the orbiniids: approximate number of known species, 124.

Haploscoloplos fragilis	Anderson, 1961; Sanders *et al.*, 1962
Orbinia cuvieri	Schäfer, 1962
,, *kuppferi*	Schäfer, 1962
,, *sertulata*	Wolff, 1973
Orbinia sp.	Hunt, 1925; Yonge, 1928
Scoloplos armiger	Blegvad, 1914; Thamdrup, 1935; Linke, 1939; Smidt, 1951; Schäfer, 1962; Jepsen, 1965; Gibbs, 1968; Wolff, 1973
,, *robustus*	Sanders *et al.*, 1962
Orbiniidae, general	Eisig, 1914; Dales, 1963; Day, 1967

We postulate that the orbiniids will show distinct and identifiable levels of food preferences and that the same basic mode of feeding is displayed by all species. We also propose that sympatric species will demonstrate resource partitioning in the food items ingested or digested.

OWENIIDAE

The only oweniid so far investigated is *Owenia fusiformis* (Hempelmann, 1931; Yonge, 1954a; Dales, 1957; Southward, 1957; Schäfer, 1962; Hartmann-Schröder, 1971; Pearson, 1971; Wolff, 1973). These references represent two or possibly three independent investigations (Hempelmann, 1931; Dales, 1957; Schäfer, 1972); of these, only the investigation by Dales (1957) is very detailed and it gives excellent evidence on the feeding modes.

O. fusiformis has a shallow, lobed tentacular crown. The flat marginal lobes have raised ridges with lateral cilia and with ciliary paths leading to the mouth, which is guarded by paired lips. These tubicolous worms will project the tentacular crown from one end of the tube. They can feed in an upright position or bent over towards the substratum; thus they are capable both of filter-feeding and of surface deposit-feeding. While doing the latter, the lips are used to pick up particles directly. Schäfer (1962) indicated that *O. fusiformis* might move around in the substratum and feed on small invertebrates in a buried position. Dales indicated that the species feeds at the surface. We do not know what evidence Schäfer had for his statements and thus cannot exclude subsurface feeding as a possibility.

Others of the 25 or more species of oweniids differ from *Owenia* in major morphological features. *Myriowenia* spp. have paired, grooved palps and *Myriochele* spp. and others lack all anterior appendages apart from the paired lips. Dales (1957) suggested that *Myriochele* spp. might feed by picking up particles from the surrounding sediment using the lips.

We suggest that the bipalpate oweniids are surface deposit-feeders that feed in a manner similar to the surface deposit-feeding spionids. The species that entirely lack anterior appendages feed in a buried position. Considering the size of the tubes in relation to the size of the contained specimen, they probably do not move around, but feed in a manner similar to that of the maldanids. The structure of the feeding apparatus in all oweniids indicates the potential for high levels of selectivity, both in terms of particle size and composition. Quantitative investigations are lacking.

PARAONIDAE

Paraonids have short, eversible, sac-like pharynges. The feeding biology has been investigated in only one of the 50 or more species in the family.

Paraonis fulgens is usually called a non-selective, burrowing deposit-feeder (Day, 1967; Pearson, 1971) or surface-feeder (Retière, 1971; Rasmussen, 1973). These statements are often generalized to the family. According to Rasmussen, *P. fulgens* has the posterior end buried in a cork-screw fashion in the sediment, projecting the anterior end up into the water searching in the surf zone for plant debris and dead animals—an idea first suggested by Mortensen (1922). This would associate *P. fulgens* with ripple troughs in sandy beaches; however, this species has also been reported from deeper waters and in muddy environments.

The burrow pattern of this species is highly characteristic, consisting of a series of spiralled or meandering parts connected by shorter straight stretches (Gripp, 1927). Röder (1971) in an extremely valuable contribution, described the meander pattern in detail as consisting of a series of horizontal spiralling patterns connected from one level to another in the sediment by short, oblique or vertical burrows. Similar meandering patterns have been found in the fossil record (Raup & Seilacher, 1969), and modelling of the pattern has proved interesting from an evolutionary and ecological point of view (Papentin, 1973).

The food of *P. fulgens* consists of pennate diatoms taken singly (Röder, 1971); they may feed on a few other organisms such as foraminiferans and small crustaceans, and Röder specifically stated that this species does not feed on detritus or sediment. For the only paraonid investigated we have, therefore, two distinct and very different feeding modes described. In one instance, it is considered a highly selective burrowing form, feeding nearly exclusively on diatoms and in the other, as feeding on drifting debris. Two different species may have been confused under one name; this is certainly easily done in this family. The spiralling burrow pattern is probably present in most forms; when preserved the paraonids curl up in spirals, indicating the presence of obliquely acting longitudinal muscles. The frequency and abundance of paraonids in deep water (Fauchald, 1972) makes investigations of their feeding biology important for our understanding of community structure in the deep sea; many of them have guts distended with foraminiferans (Jumars, pers. obs.).

PECTINARIIDAE (Table XX, Fig. 16)

Pectinariids are burrowing, tubicolous worms, digging with the stout paleal setae and sorting particles with their tentacles. Judging from the gut content all species are selective deposit-feeders (Rauschenplat, 1901; Blegvad, 1914; Hessle, 1925; Hunt, 1925; Yonge, 1928; Remane, 1933; Linke, 1939; Southward, 1957; Hartmann-Schröder, 1971; Pearson, 1971; Wolff, 1973).

TABLE XX

Literature on feeding modes of the pectinariids: approximate number of known species, 46.

Amphictene auricoma	Blegvad, 1914; Hunt, 1925; Southward, 1957; Hartmann-Schröder, 1971; Pearson, 1971; Vovelle, 1971
Cistenides gouldii	Sanders, 1956; Gordon, 1966; Rhoads, 1967; Whitlatch, 1974
Lagis koreni	Blegvad, 1914; Hessle, 1925; Hunt, 1925; Watson, 1928; Remane, 1933; Linke, 1939; Wilcke, 1952; Schäfer, 1962; Hartmann-Schröder, 1971; Pearson, 1971; Vovelle, 1971, 1973; Wolff, 1973
Pectinaria belgica	Rauschenplat, 1901; Blegvad, 1914; Hessle, 1925; Hartmann–Schröder, 1971; Vovelle, 1971
,, *californiensis*	Nichols, 1974; Ronan, 1978
Pectinaria sp.	Hunt, 1925
Petta pusilla	Hessle, 1925; Vovelle, 1971
Pectinariidae, general	Yonge, 1928; Day, 1967; MacGinitie & MacGinitie, 1968

The tubes are conical; they are open at both ends and are only a little longer than the worm itself. The worms are oriented with the head end down and the upper narrow chimney of the tube projecting above the surface of the sediment. This limits the activity of the worm to the upper 10 cm of the sediment in most species. There is some disagreement as to the motility of the pectinariids. Schäfer (1962) considers *Lagis koreni* to be highly motile in the sand flats of the Wadden Sea. Watson (1928) and Wilcke (1952) indicated

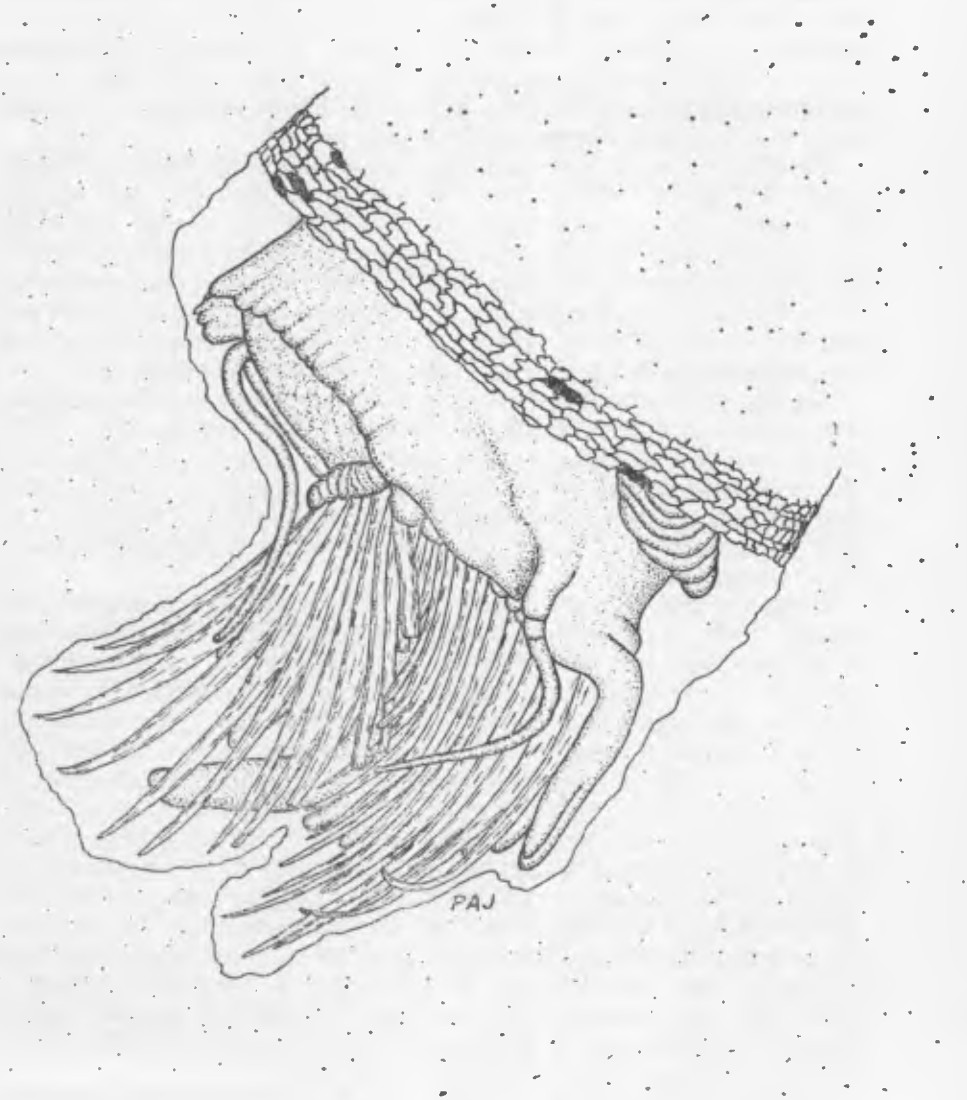

Fig. 16.—PECTINARIIDAE: *Pectinaria californiensis*, paleae splayed, loosening sediment particles to fall on the oral tentacles below; while *Pectinaria* can select particles (Whitlatch, 1974), the mechanisms of selection remain unknown; × 10.

that the same species might be discretely motile or nearly sessile in other areas, forming a U-shaped burrow with an open headshaft leading into a chamber in front of and below the worm, and with the tube leading up to the surface as the other arm of the U. Ronan (1978) found in laboratory experiments that *Pectinaria californiensis* moves only 1–2 cm per week and is dependent on small-scale slumping for its food. We posulate that U-shaped tubes are formed when the specimens are found in nutrient-rich, oxygen-poor, fine-grained sediments, whereas higher motility is associated with well oxygenated, coarse sediments relatively poor in food.

Cistenides gouldii is dependent on 'caved-in' sediments for food (Sanders, 1956). Whitlatch (1974) found that larger specimens eat larger particles than do smaller ones, that organic-encrusted particles are selected over clean particles and that flocculent organic aggregates and faecal pellets are preferred to other, less nutritive materials. Schäfer (1962) indicated that pectinariids may also feed on small organisms they encounter; this may vary from one species to the next. On the average, 30% of the organic content was removed by *Cistenides gouldii* from the sediments it reworked (Whitlatch, 1974).

The selectivity demonstrated in feeding is paralleled by a similar selectivity for particles used in tube-building (Watson, 1928; Vovelle, 1971, 1973). Small specimens will select smaller particles than will larger specimens of the same species. Each of the four species investigated by Vovelle (1971) had a characteristic maximal particle size incorporated; furthermore, all four species took particles in proportions different from their occurrence in the environment.

Gordon (1966), Rhoads (1967) and Nichols (1974) demonstrated the turnover rates of sediments in two different pectinariids. The turnover rate of *Cistenides gouldii* in Barnstable Harbor, Massachusetts, was 6 g sediment . worm^{-1} . day^{-1}; taking into account the annual active season in Massachusetts, this extrapolates to 600 g sediment . worm^{-1} . year^{-1} (Gordon, 1966). Gordon also found that the higher the organic content, the lower the turnover rate. The rates might be reduced by as much as one third in areas of high organic content (measured as pigment concentration in the sediment). This is consistent with what we postulated above about the motility patterns in the pectinariids. *C. gouldii* removes about one-half of the organic content of the sediment according to Gordon; this is a higher value than reported by Whitlatch for the same species and the same population. Two thirds of the sediment disturbed by the worms is passed over the dorsum of the animals within the tubes and deposited on the surface as pseudofaeces (Rhoads, 1967); this may account for the low level of removal of organic material reported by Gordon and Whitlatch, and may also account for differences in utilization rates reported by the last two authors.

The same pattern appears to apply to *Pectinaria californiensis*, except that the fraction characterized as pseudofaeces may be as much as 77·5% of the total disturbed material (Nichols, 1974). Nichols gave empirical formulae relating turnover rates and production of faecal matter (both in mg . worm^{-1} . h^{-1}) to the size of the animals, measured as the width of the cephalic plate (mm).

$$\log_{10} \text{sediment turnover rate} = 2{\cdot}0501 \,.\, \log_{10} \text{cephalic plate width} - 0{\cdot}5290 \qquad r = 0{\cdot}71$$

$$\log_{10} \text{faecal matter} = 2{\cdot}0513 \,.\, \log_{10} \text{cephalic plate width} - 1{\cdot}2308 \qquad r = 0{\cdot}61$$

It would be interesting to apply these formulae to populations of *Cistenides*, perhaps to predict the width of cephalic plates from measured turnover rates or production rates of faecal matter. One should be able to account for differences in habitat among species from the values of the fitted constants.

We propose, in summary, that the pectinariids are selective deposit-feeders with more than half of all the disturbed sediment passed over the dorsum as pseudofaeces. It should be possible to show that the pseudofaeces differ from the environmental sediment and from the material ingested by the animal, both in terms of grain size and food value. We further propose that in organic-rich environments the pectinariids will form U-shaped burrows and remain sessile for long periods and that the motility pattern will be closely related to the organic content of the surrounding substratum.

PHYLLODOCIDAE (Table XXI, Fig. 17)

The eversible pharynges of the phyllodocids are long and unarmed. No phyllodocid is tubicolous and few appear to be territorial. Phyllodocids on coral reefs are nestlers according to Gardiner (1903). In Dutch estuaries, *Eumida sanguinea* is always found with *Lanice conchilega*, a terebellid polychaete, indicating a possible symbiotic relationship (Wolff, 1973).

TABLE XXI

Literature on feeding modes of the phyllodocids: approximate number of known species, 295.

Anaitides groenlandica	Wolff, 1973
,, *maculata*	Evans, 1971; Wolff, 1973
,, *mucosa*	Michel, 1970b,c; Rasmussen, 1973; Cazaux, 1975
Eteone heteropoda	Sanders *et al.*, 1962; Simon, 1965; Evans, 1971
,, *longa*	Remane, 1933; Khlebovich, 1959; Retière, 1967; Michaelis, 1971; Wolff, 1973
Eulalia pallida	Gravier, 1896
,, *viridis*	Gravier, 1896; Michel, 1970b,c; Evans, 1971; Pearson, 1971; Wolff, 1973
Eumida sanguinea	Korringa, 1951; Wolff, 1973
Phyllodoce laminosa	Gravier, 1896; Cazaux, 1975
Phyllodocidae, general	Gardiner, 1903; Pearson, 1971

The phyllodocids are considered hunting carnivores, catching their prey with the muscular pharynx (Gravier, 1896; Michel, 1970b; Evans, 1971; Pearson, 1971; Rasmussen, 1973; Wolff, 1973). Evidence is accumulating however, that they may be scavengers rather than carnivores (Michel, 1970b; Wolff, 1973; Emson, 1977). They are in part non-selective, feeding on all kinds of polychaetes (Gravier, 1896; Rasmussen, 1973), and in part highly selective. Among the latter, intertidal species of *Eteone* will follow mucous trails on mudflats at low tide and feed on the organism that made the trail. Khlebovich (1959) reported that *E. longa* feeds exclusively on the spionid *Spio filicornis*; Michaelis (1971) found that the same species would feed exclusively on another spionid, *Scolelepis squamata*. A related species, *Eteone heteropoda* feeds on the nereid polychaete, *Nereis* (*Neanthes*) *succinea* and cannibalistically (Simon, 1965). Sanders *et al.* (1962) found that *Eteone heteropoda* ingests sediment and that this was the only source of food for the species. Simon (1965) suggested that it might be a detritus-feeder when the tide was in, and a carnivore when the tide was out, leaving the mucous trails easier to follow. Retière (1967) found *E. longa* to be less selective than indicated by either Khlebovich or Michaelis, feeding on a variety of small metazoans.

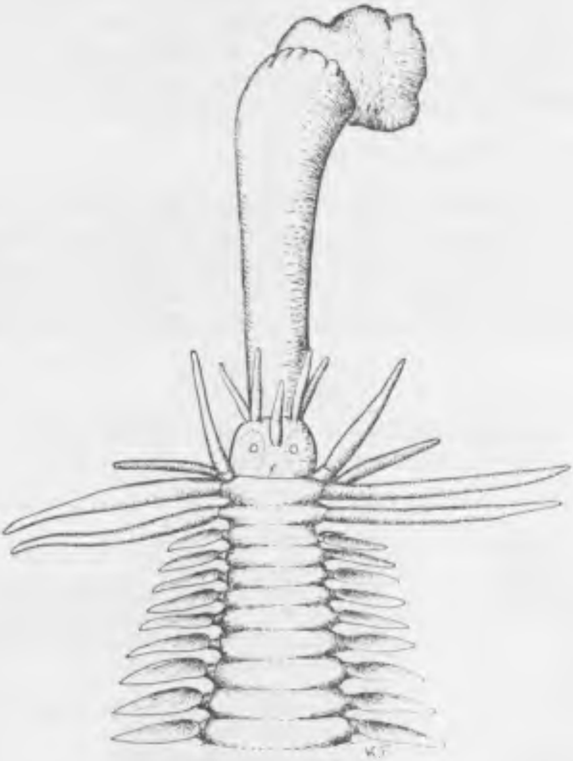

Fig. 17.—PHYLLODOCIDAE: *Eumida* cfr. *tubiformis* striking at a piece of carrion; while most phyllodocids are considered carnivores, carrion may be an important source of food; ×2·5.

The subfamily Eteoninae, to which *Eteone* belongs, is much better represented in deep water than the other major subfamily, Phyllodocinae, perhaps reflecting sediment-feeding habits in one subfamily, but not in the other. Phyllodocids start their carnivorous habits from the first meal after metamorphosis (*e.g.*, Cazaux, 1975).

We postulate that all phyllodocids are hunting predators, feeding on a variety of small invertebrates; we find it likely that olfactory 'search images' may lead to a high apparent selectivity in any population and that olfactory clues, such as mucous trails, are used generally by members of this family. Cannibalism is widespread. Members of the subfamily Eteoninae also have the possibility of sustaining themselves on ingested sediments. We are uncertain as to the relation between the carnivorous habit and sediment-feeding within one species, and suggest that population studies of species with both habits might be rewarding.

PILARGIIDAE

Pilargiids do not form tubes and have eversible muscular pharynges. They are considered carnivores or omnivores (Day, 1967). *Litacorsa stremma* is probably an active predator or scavenger (Pearson, 1970). We have been able to find no evidence whatsoever on the food habits of the pilargiids; the above statements are based on anatomical analogies with other polychaetes. The family contains 48 species.

POECILOCHAETIDAE

Poecilochaetids are spioniform polychaetes that always live in long, branching tubes in sand and mud (Allen, 1904; Fauchald, pers. obs.). They have paired palps and may use these for suspension-feeding on small algae and diatoms (Allen, 1904; Wolff, 1973) or in selective deposit-feeding from the surface of the substratum (Schäfer, 1962; Hartmann-Schröder, 1971). Whether both modes are used, which appears most likely, or under what conditions these animals feed in either of the two ways remains unknown. The family contains 13 species in two genera, and is found infrequently but abundantly in sand and mud both in shallow and deep water. Characteristically, they are extremely patchy in distribution (Allen, 1904) and can wholly dominate small areas.

POLYNOIDAE (Table XXII, Fig. 18)

Polynoids are common intertidal and shallow-water scale worms on all substrata; they are infrequent in deeper water, but have been reported from abyssal and hadal depths (Hartman, 1971). All polynoids have a muscular eversible pharynx armed with jaws; none are tubicolous, but they are otherwise represented by a wide variety of life habits.

The polynoids are considered carnivores, feeding on small crustaceans, echinoderms, polychaetes, gastropods, sponges, and hyroids (Darboux, 1899; Rauschenplat, 1901; Blegvad, 1914; Meunier, 1930; Hoop, 1941; Korringa, 1951; Ebbs, 1966; Streltzov, 1966; Hartmann-Schröder, 1971; Pearson, 1971; Sarvala, 1971; Schäfer, 1972; Rasmussen, 1973; Wolff, 1973; Hughes, 1975). A number of authors mention algal fragments as important for *Harmothoe imbricata* and *Lepidonotus squamatus* (Rauschenplat, 1901; Streltzov, 1966; Schäfer, 1972). Streltzov specified that in his investigation of *Harmothoe imbricata*, algal remnants made up 18·2% by weight and occurred in 83% of the specimens investigated; in comparison, the most common prey, amphipods, made up 65·6% by weight and occurred in 87% of the specimens. Algal fragments were thus almost as frequent as the most important food item and may be of major nutritional importance to the animal, but may also be a contaminant of encrusting animals taken in as food. *Thormora johnstoni* has a deviant carnivorous habit in that it sucks coelomic fluid and blood from the abdomen of the eunicid polychaete, *Palola viridis* (Hauenschild *et al.*, 1968); it would qualify as an ectoparasite by most definitions.

There is some disagreement as to the food habits of the hemipelagic *Antinoella sarsi*. Schäfer (1962) and Hartmann-Schröder (1971) considered it to be a detritus-feeder; Meunier (1930) and Sarvala (1971) referred to it as a carnivore. Sarvala listed dietary items in detail and related a shift in the diet from smaller to larger arthropods with increasing size of the worm. Documentation of the detrital feeding habits is not available in similar detail.

A number of polynoids are commensals with various other invertebrates, including other polychaetes, molluscs, and echinoderms (Davenport, 1953; Southward, 1957; MacGinitie & MacGinitie, 1968; Wolff, 1973; Ajeska & Nybakken, 1976). Davenport (1953) suggested that *Acholoe astericola* might feed on the gut content of its host, the starfish *Astropecten irregularis*.

TABLE XXII

Literature on feeding modes of the polynoids: approximate number of known species, 567.

Acanthicolepsis asperrima	Pearson, 1971
Acholoe astericola	Davenport, 1953
Antinoella sarsi	Meunier, 1930; Remane, 1933; Schäfer, 1962; Hartmann-Schröder, 1971; Sarvala, 1971; Wolff, 1973
Enipo kinbergi	Blegvad, 1914
Gattyana cirrosa	Blegvad, 1914; Hartmann-Schröder, 1971; Wolff, 1973
Halosydna brevisetosa	Ajeska & Nybakken, 1976
,, *gelatinosa*	Cazaux, 1968
Harmothoe imbricata	Rauschenplat, 1901; Blegvad, 1914; Remane, 1933; Hoop, 1941; Dean & Blake, 1966; Streltzov, 1966; Cazaux, 1968; Hartmann-Schröder, 1971; Schäfer, 1972; Daly, 1973; Rasmussen, 1973; Wolff, 1973; Hughes, 1975
,, *impar*	Korringa, 1951; Hartmann-Schröder, 1971; Wolff, 1973
,, *lunulata*	Hartmann-Schröder, 1971; Wolff, 1973
Harmothoe sp.	Pearson, 1971
Hesperanoe complanata	MacGinitie & MacGinitie, 1968
Lagisca extenuata	Cazaux, 1968
Lepidonotus squamatus	Rauschenplat, 1901; Blegvad, 1914; Cazaux, 1968; Hartmann-Schröder, 1971; Pearson, 1971; Schäfer, 1972; Rasmussen, 1973; Wolff, 1973
Scalisetosus pellucidus	Southward, 1957
Thormora johnstoni	Hauenschild *et al.*, 1968
Polynoidae, general	Darboux, 1899; Ebbs, 1966; Day, 1967; MacGinitie & MacGinitie, 1968

Ajeska & Nybakken (1976) reported that *Halosydna brevisetosa* as a commensal of the nudibranch *Melibe leonina* would feed on the faecal matter of its host and gave experimental evidence to prove this. This report is disturbing in that *Halosydna brevisetosa* is now known as free-living in mussel beds, as a commensal with terebellid polychaetes (Blake, 1975), and as a commensal with a nudibranch snail. A related form, *H. johnsoni*, has been shown to have special developmental requirements (Rossi, 1976); we suggest that population studies of *H. brevisetosa* will yield interesting insights into habitat segregation of morphologically extremely similar polynoids.

Juvenile polynoids become carnivores immediately upon metamorphosis (Dean & Blake, 1966; Cazaux, 1968; Rasmussen, 1973), independent of the length of the preceding larval life. The larvae, when planktotrophic, feed on various phytoplankton (Cazaux, 1968).

Daly (1973) experimentally analysed the prey-capture technique of *Harmothoe imbricata*; this species is a 'sit-and-wait' predator. The palps are sensitive to vibration, and it will attack live prey only. It will explore vibrating non-food particles, but will not attack, and it will explore neither homogenates of prey nor dead food. The experimental items offered included amphipods and polychaetes. We find Daly's description convincing; all reliable evidence indicates that the polynoids are primarily carnivores and that only a few species have modified their diet to include plant material.

A large fraction of the polynoids will probably turn out to be commensals; Dr Olga Hartman used to surmise that at least all polynoids with little or no

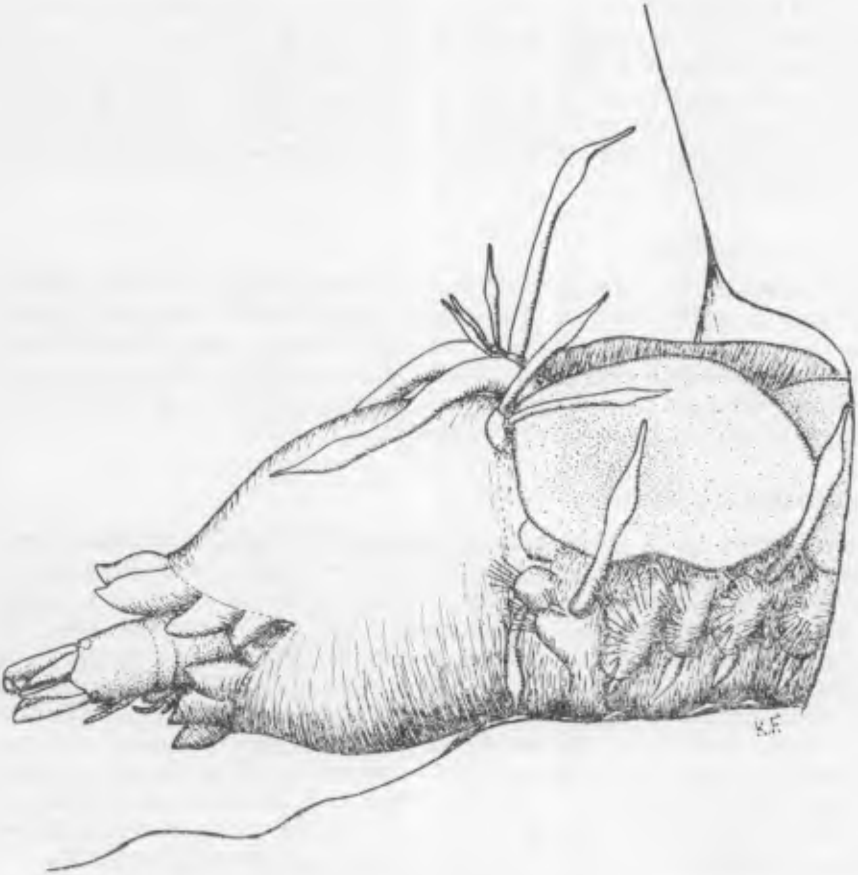

Fig. 18.—POLYNOIDAE: *Halosydna johnsoni* pulling in an amphipod of the genus *Corophium*; this worm may not be exclusively a sit-and-wait predator; members of the genus *Corophium*, typically found in its gut contents, are tubicolous; ×5.

elytral ornamentation would turn out to be commensals. So far her conjecture has not been discredited. The commensals may feed in one of four ways. (1) They may feed on the food of the host (MacGinitie & MacGinitie, 1968); in cases where the host is a carnivore, this represents a simple extension of the normal feeding habits in the family. (2) They may feed more or less ectoparasitically on the host as in the case of *Thormora johnstoni.* These forms should perhaps be called parasites rather than commensals. The mode is under any circumstances easily derived from the normal habits of polynoids. (3) They may feed on the faecal matter of the host, as indicated by Ajeska & Nybakken (1976); in the only known case, the host is a carnivore, so the habit is not surprising. (4) They may feed on the food or the pseudofaeces of a selective deposit-feeding or filter-feeding host. This fourth method is difficult to derive from the (presumably) carnivorous habits of the ancestral polynoids. There has been no study of the food habits of commensal polynoids on such hosts.

The Polynoidae is the most rich in species of the non-tubicolous polychaete families. We have feeding information of variable reliability for 14 of the 550 known species. A major interest in the study of polynoid feeding habits lies in the change from free-living to commensal habits within the family. This has not been accompanied by morphological changes, and such a study could, therefore, isolate behavioural modifications as requisites for radical changes in habits.

POLYODONTIDAE

Polyodontids are large, tubicolous scale-worms found down to bathyal depths on muddy bottoms. They have a large, eversible muscular pharynx with four jaws and are considered carnivores (Darboux, 1899; Blegvad, 1914), scavengers or omnivores (Day, 1967). Darboux (1899) reports that one can fish polyodontids by baiting hooks with pagurid-abdomens or freshly killed goldfish. The family consists of 39 species.

PROTODRILIDAE (Table XXIII)

Protodrilids are tiny interstitial polychaetes with eversible muscular lower lips used to scrape food from the environment. There is some disagreement as to what they scrape. Gray (1966, 1967a,b, 1974) has shown that various protodrilids are attracted to sand covered with specific bacterial films. He indicated that these films are of great nutritional importance to the worms, as did Boaden & Erwin (1971). Jägersten (1940) and Wolff (1973) claim that diatoms are the major food items for these animals. Both food sources may be used, with varied relative importance, based on the density of either bacteria or diatoms. Jägersten (1952) showed that early larvae of *Protodrilus rubropharyngeus* feed on unicellular algae and described the method of swallowing in detail. He also showed that late larvae have non-functional digestive tracts that become functional again only after metamorphosis.

PSAMMODRILIDAE

Psammodrilids are small, interstitial polychaetes, described from shallow water; only two species are known to date. They feed by a muscular pumping action of the prostomial and peristomial muscles (Swedmark, 1955) or by licking of the sand grains (Hartmann-Schröder, 1971); it is possible that they may use both methods towards the same end—intake of benthic diatoms.

SABELLARIIDAE

Sabellariids are tubicolous, reef-building polychaetes, common in shallow water where there is a good supply of sand (Gruet, 1972). They are of considerable geological interest, and the tube-building conditions have been

TABLE XXIII

Literature on feeding modes of the protodrilids: approximate number of known species, 22.

Protodriloides symbioticus	Gray, 1966, 1974; Boaden & Erwin, 1971; Wolff, 1973
Protodrilus chaetifer	Remane, 1933
,, *hypoleucus*	Gray, 1967a
,, *rubropharyngeus*	Jägersten, 1940, 1952; Gray, 1967b

TABLE XXIV

Literature on feeding modes of the sabellids: approximate number of known species, 292.

Branchiomma bombyx	Johansson, 1927; Hartmann-Schröder, 1971
Chone infundibuliformis	Pearson, 1971
Chone sp.	Hunt, 1925
Euchone sp.	Remane, 1933
Fabricia sabella	Remane, 1933; Lewis, 1968; Muus, 1967; Hartmann-Schröder, 1971
Fabriciola baltica	Hartmann-Schröder, 1971
Hypsicomus phaeotaenia	Hartman, 1954
Jasmineira elegans	Hughes, 1975
Laonome kroyeri	Hartmann-Schröder, 1971
Laonome sp.	Remane, 1933
Manayunkia aestuarina	Schäfer, 1962; Muus, 1967; Lewis, 1968; Hartmann-Schröder, 1971; Wolff, 1973
,, *speciosa*	Pettibone, 1953
Megalomma vesiculosum	Hempelmann, 1931; Yonge, 1954a
Megalomma sp.	Soulier, 1891; Orton, 1914; Yonge, 1928
Myxicola infundibulum	Hempelmann, 1931; Wells, 1953b; Yonge, 1954a; Hartmann-Schröder, 1971
Myxicola sp.	Soulier, 1891
Sabella penicillus	Hunt, 1925; Nicol, 1930; Thomas, 1940; Wells, 1951, 1953a; Schäfer, 1962; Dales, 1963; Hartmann-Schröder, 1971
Sabella sp.	Soulier, 1891; Orton, 1914; Yonge, 1928
Sabellastarte magnifica	Fitzsimons, 1965; Sander, 1973
Spirographis spallanzanii	Soulier, 1891; Hempelmann, 1931; Wells, 1951; Yonge, 1954a
Sabellidae, general	Gardiner, 1903; Blegvad, 1914; Day, 1967; MacGinitie & MacGinitie, 1968

described in detail (Schäfer, 1962; see also Wilson, 1971). The feeding apparatus consists of paired ciliated groups of tentacles on either side of the prostomium, creating water currents that lead towards the mid-line. Mucus-embalmed food particles are transported along ciliated paths to the mouth from the medially attached edge of the tentacular fields. The water current is deflected anteriorly at the same edge (Johansson, 1927; Dales, 1963). The food consists of phytoplankton (Johansson, 1927; Schäfer, 1962; Hartmann-Schröder, 1971). In aquaria, the larvae feed well on small phytoplankton and as they grow older will move to larger organisms (Wilson, 1968, 1970). Roy (1974) described defaecation in *Phragmatopoma californica* as stretching the long post-abdomen forward over the dorsum, depositing the faecal matter there, with ciliary transport over the most anterior part of the body. The family is known for 61 species. Quantitative information is not available.

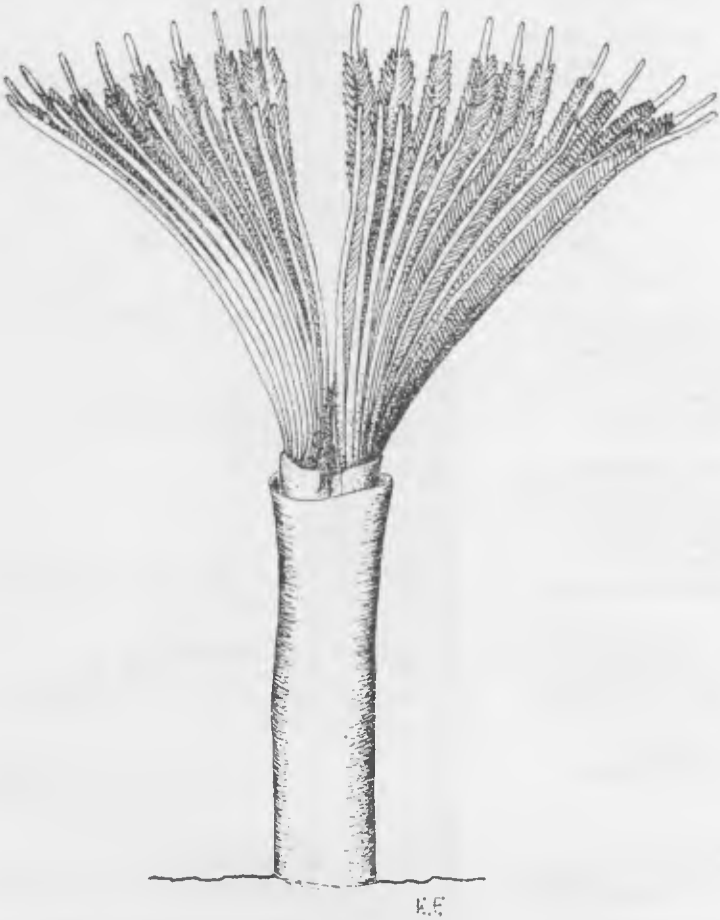

Fig. 19.—SABELLIDAE: *Sabella* sp. suspension-feeding in its normal feeding posture, holding the branchial funnel erect; ×2.

SABELLIDAE (Table XXIV, Figs 19–21)

Sabellids are tubicolous polychaetes with the prostomium and peristomium modified into a tentacular crown. Members of the subfamily Sabellinae remain in their tubes for life (Soulier, 1891; Schäfer, 1962); members of the subfamilies Fabriciinae and Myxicolinae may leave their tubes (Soulier, 1891; Remanc, 1933; Pettibone, 1952; Day, 1967; MacGinitie & MacGinitie, 1968; Hartmann-Schröder, 1971).

All authors agree that the filter-feeding habit is by far the most important in the family. *Manayunkia* spp. are also capable of feeding by turning over and touching the substratum with their tentacular crowns in a form of selective deposit-feeding; the method may be of primary importance in freshwater and brackish water sabellids (Pettibone, 1953; Muus, 1967; Lewis, 1968). Major food items include pelagic diatoms, dinoflagellates, and other unicellular algae, as well as small invertebrates including larvae.

Nicol (1930) in one of the best studies ever done on a polychaete, described the structure and function of the tentacular crown, the feeding paths and the rejection paths in *Sabella penicillus*. Figure 20 has been redrawn from her publication and imparts better than words the details of the complex system.

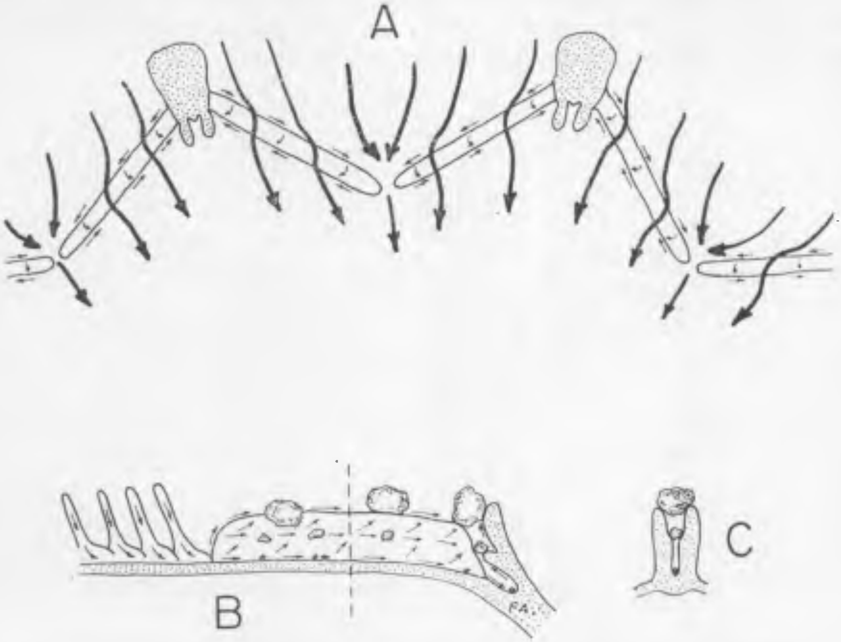

Fig. 20.—SABELLIDAE: diagrammatic representation of particle handling by *Sabella penicillus*, after Nicol (1930); A, cross-section through a segment of the branchial funnel, showing directions of the ciliary beat (fine arrows) and of the resulting flow of water (heavy arrows); B, longitudinal section through the basal portion of a gill filament, showing the beat of the cilia (fine arrows) and the transport of particles of three size classes; C, cross-section through the basal portion of a gill filament at the level of the dashed line in B; particle handling in other sabellids is much more scantily known.

Sabellastarte magnifica separates the filtered particles into three fractions: the finest fraction (3–5 μm for small worms, 6–8 μm for larger worms) consists of unicellular algae, filamentous green algae and various debris, and is used as food. The two larger fractions are either used in tube building or are rejected (Fitzsimons, 1965). Sabellids apparently select particles exclusively on size; no evidence has been presented for selection on other particle characteristics.

Sabellid tubes may be open at both ends, in which case irrigation currents run in both directions. When the tube is buried in sand or otherwise closed off, the current runs tailwards (Wells, 1951). The rôle of the tentacular crown in respiratory exchange depends on the structure of the tubes. If these are open posteriorly, the importance of the crown is minimal, if the tube is closed, the crown becomes a very important respiratory organ (Wells, 1953a).

There are major differences in the activity levels of the sabellids. Some, such as *Sabella penicillus* and *Sabellastarte magnifica*, are very active in the tubes (Wells, 1953a; Sander, 1973); others, such as *Myxicola infundibulum* are very quiescent. This behaviour implies major differences in the energy requirements. Unfortunately, no quantitative studies have been done on any species.

Reef-dwelling sabellids may be capable of drilling their own holes in the coral (Gardiner, 1903; Hartman, 1954). How this is done, and how prevalent the habit is among reef-dwelling species, is unknown.

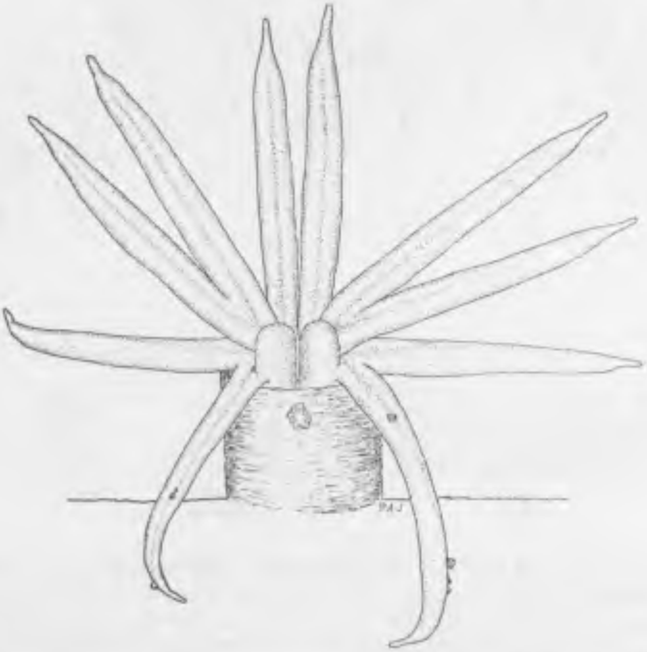

Fig. 21.—SABELLIDAE: *Manayunkia aestuarina* in its frequent feeding posture with a pair of branchial filaments being used in deposit-feeding; the large particle falling in front of the tube has just been expelled from the branchial crown by the ejection current; see Lewis (1968) for other aspects of the broad behavioural repertoire; ×150.

Members of the subfamily Fabriciinae are common in deep water (Hartman, 1971; Fauchald and Jumars, pers. obs.). As mentioned above, they are capable of moving around. When they move, aquarium observations show that they move with the posterior end first, trailing the tentacular crown (Day, 1967; Lewis, 1968; Fauchald and Jumars, pers. obs.). They leave mucous trails and frequently drag along a tangle line of mucus which they will pull in from time to time. This amounts to a method of selective surface deposit-feeding, even while moving from place to place. Day indicated that they may also sweep the surface of the substratum with the tentacular crown while sitting in their tubes, giving them a sessile form of surface deposit-feeding. The tentacular crown in most Fabriciinae is simply constructed, with few radioli, and in some genera, is proportionally much smaller than in other sabellids. We believe that the reduced tentacular crown is associated with a discretely motile existence and that the Fabriciinae are secondarily becoming selective deposit-feeders in addition to retaining a moderate filter-feeding capacity as adaptations to life in nutrient poor or physically unstable environments.

SCALIBREGMIDAE

Two scalibregmids, *Scalibregma inflatum* and *Polyphysia crassa* of a total of 33 species have been investigated. The two are rather similar biologically and will be treated together.

The scalibregmids have sac-like eversible pharynges. They do not form tubes, but live in galleries in soft sediments, often buried as much as 30–60 cm below the surface (Ashworth, 1901; Hertweck & Reinneck, 1966). They are active burrowers and feed on detritus found in the sediment (Ashworth, 1901; Blegvad, 1914; Hunt, 1925; Yonge, 1928; Mare, 1942; Schäfer, 1962; Dales, 1963; Day, 1967; Hartmann-Schröder, 1971; Pearson, 1971; Elder, 1972; Wolff, 1973). *Scalibregma inflatum* may also feed at the surface, and has been called non-selective (Mare, 1942). It is unclear what evidence Mare had for her statement; we have been unable to find any evidence for or against selectivity for any member of this family.

We postulate that the permanence of the galleries as well as the depth to which these forms can burrow depends on the composition of the sediment and that varying levels of selectivity will be found in different populations of the same species, depending on the productivity of the area.

SERPULIDAE AND SPIRORBIDAE (Table XXV)

The serpulids and spirorbids resemble the sabellids in the possession of a tentacular crown and in their tubicolous habits. The tubes are calcareous and the worms never leave them. Most members of both families live on hard substrata. A rapidly increasing number of species are reported from hard bottoms in deep water; however, the bulk of both serpulids and spirorbids are in highly productive areas of shallow water.

All members of both families filter-feed, using the tentacular crown. There is no information about the selectivity of feeding, nor is any quantitative information available. Descriptions of feeding currents and the functions of the tentacular crown are found in Orton (1914), Johansson (1927), and Thomas (1940). In general, they resemble the feeding mode in the sabellids.

TABLE XXV

Literature on feeding modes of the serpulids and spirorbids: approximate number of known species (both families), 497.

Filigrana implexa	Blegvad, 1914
Hydroides norvegica	Blegvad, 1914; Orton, 1914; Hunt, 1925; Yonge, 1928; Hartmann-Schröder, 1971; Pearson, 1971
Pomatoceros triqueter	Blegvad, 1914; Orton, 1914; Hunt, 1925; Johansson, 1927; Yonge, 1928; Remane, 1933; Pearson, 1971
Serpula vermicularis	Hunt, 1925; Johansson, 1927; Hartmann-Schröder, 1971
Spirorbis nautiloides	Rauschenplat, 1901
Spirorbis sp.	Orton, 1914; Yonge, 1928; Remane, 1933
Serpulidae/Spirorbidae, general	Gardiner, 1903; Jordan, 1913; Soulier, 1891; Dales, 1963; Day, 1967

SIGALIONIDAE (Table XXVI)

Sigalionids are especially frequent in soft sediments; some of them are tubicolous. They are more frequent in abyssal depths than any other scale worms, but are most abundant in shelf depths.

TABLE XXVI

Literature on feeding modes of the sigalionids: approximate number of known species, 156.

Pholoe minuta	Remane, 1933; Korringa, 1951; Southward, 1957; Hartmann-Schröder, 1971
Psammolyce arenosa	Hempelmann, 1931; Yonge, 1954a; Evans, 1971
Sigalion squamatum	Hempelmann, 1931
Sthenelais boa	Cazaux, 1968; Hartmann-Schröder, 1971; Pearson, 1971; Michel *et al.*, 1973; Wolff, 1973
Sigalionidae, general	Day, 1967

The sigalionids have muscular eversible pharynges with four jaws of similar composition to other polychaete jaws (Michel *et al.*, 1973). They are unanimously considered carnivores although there is little evidence available. Yonge (1954a) gives the gut content of *Psammolyce arenosa* as polychaetes and detritus. The larvae, when planktotrophic, feed on phytoplankton and become predators after metamorphosis to the nectochaete stage (Cazaux, 1968).

We postulate that all sigalionids are active, non-tubicolous predators feeding on a variety of small invertebrates. No quantitative information is available.

SPHAERODORIDAE

Sphaerodorids have muscular, eversible, unarmed pharynges. Little is known about them. Reimers (1933) examined the gut content of *Sphaerodoropsis balticum* and found it to consist of organic remnants and sand grains. Remane (1933) called the same species a truly vagile form, indicating a lack of tube-building. Schäfer (1962) characterized *Sphaerodoridium claparedii* as a surface deposit-feeder, but gave no evidence for this opinion.

For once, the presence of an eversible muscular pharynx has not led to the conclusion that these animals are carnivores. Using Occam's Razor, we postulate that all sphaerodorids are free-living deposit-feeders, probably feeding most frequently at the surface of the muds. This is compatible with their depth distribution in that they are well represented in samples from both bathyal and abyssal areas (Fauchald, 1974). The family consists of 46 species.

SPINTHERIDAE

Spintherids are flattened, more or less disc-shaped polychaetes associated with sponges. They have long, muscular eversible pharynges, resembling those found in the turbellarians (Manton, 1967). They are carnivorous or ectoparasitic on sponges (McIntosh, 1894; Hartmann-Schröder, 1971). It is also possible that they live by scavenging dead parts of the sponge. Twelve species are known, and no quantitative information is available.

SPIONIDAE (Table XXVII, Fig. 22)

Spionids are bipalpate, usually tubicolous worms both frequent and abundant in shallow water on all substrata. Certain genera (*e.g. Spiophanes*) are also well represented in deep water. Some members of *Polydora* and allied genera drill in calcareous substrata (Hartman, 1941; Korringa, 1951; Blake & Evans, 1973; Zottoli & Carriker, 1974), but most live in mud-tubes in other substrata. All spionids, except possibly some members of the *Polydora*-complex, are capable of leaving their tubes (Remane, 1933) and will build new tubes when necessary. Certain species (especially of the genera *Aonides* and *Scolelepis*) living in shifting sand, build only loosely constructed burrows or are entirely free-living (Hartmann-Schröder, 1971; Foster, 1971).

Despite the extensive literature on spionid feeding, little quantitative information is available. Spionids are generally considered surface deposit-feeders, using their ciliated palps to select food particles from the surrounding medium (Mortensen, 1922; Thamdrup, 1935; Linke, 1939; Mare, 1942; Smidt, 1951; Seilacher, 1953; Hempel, 1957a,b; Southward, 1957; Jones, 1961; Schäfer, 1962; Jepsen, 1965; Muus, 1967; Retière, 1967; Febvre, 1969; Eleftheriou, 1970; Hartmann-Schröder, 1971; Pearson, 1971; Daro & Polk, 1973; Losovskaya, 1973; Rasmussen, 1973; Sleeter & Coull, 1973; Wolff, 1973). Certain species of *Polydora* and related genera are partially or wholly filter-feeders, in that they catch planktonic organisms on the palps (Linke, 1939; Korringa, 1951; Dorsett, 1961; see also Wolff, 1973 for a summary). Korringa (1951) contended that *Polydora* spp. drilling on oysters compete with these for food, in addition to damaging their shells. Dorsett described the "lassoing" motions of the palps of the *P. ciliata* used while catching plankton from the water. We have made similar observations on several unidentified species of *Polydora.*

Sympatric species of the *Boccardia-Polydora* complex may partition food on particle size. *Polydora ligni* and *Boccardia ligerica* can feed on particles up to 600 μm in diameter, whereas *Polydora ciliata* does not feed on particles larger than 30–50 μm (Hempel, 1957a,b; Dorsett, 1961). These studies did not directly investigate competitive interactions, so it remains to be shown that the discrimination will function as a resource partitioning device.

Pygospio elegans is the most versatile of the spionids studied to date. It can filter by building a mucous net within its tube, it can catch plankton with the help of its palps, or it can feed on surface deposits (Hempel, 1957a,b).

The late larvae of spionids can feed on phytoplankton (Breese & Phibbs, 1972) and have been successfully raised on a variety of artificial substrata (see *e.g.*, Dean & Blake, 1966). A number of larvae are lecithotrophic and do not start feeding until after settling. Those that do feed, however, apparently start using their palps for feeding as soon as these have developed. *Scolelepis*

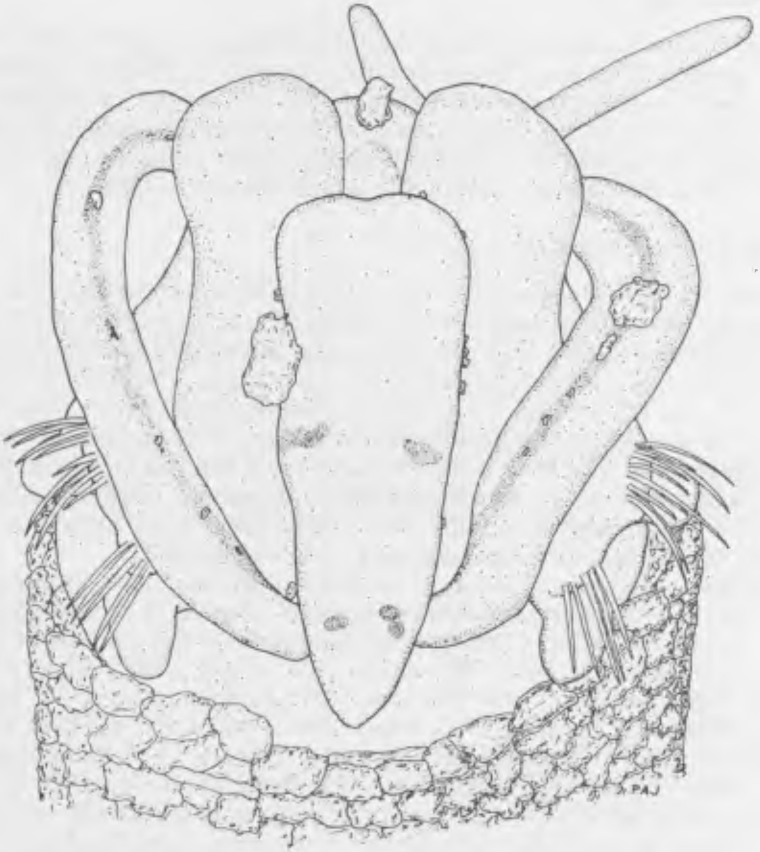

Fig. 22.—SPIONIDAE: *Pygospio elegans* transporting particles from the surface deposit along its palps and prostomial ciliary tracts; the particle poised on the midventral cleft of the distended lower lip is about to be rejected by ciliary transport over the lip; ×90.

TABLE XXVII

Literature on feeding modes of the spionids: approximate number of known species, 275.

Aonides oxycephala	Mare, 1942
Boccardia hamata	Dean & Blake, 1966
,, *ligerica*	Hempel, 1957a,b; Schäfer, 1962; Wolff, 1973
Laonice cirrata	Southward, 1957
Malacoceros tetracerus	Hartmann-Schröder, 1971
Microspio mecznikowianus	Febvre, 1969
Polydora ciliata	Rauschenplat, 1901; Linke, 1939; Korringa, 1951; Smidt, 1951; Hempel, 1957a,b; Dorsett, 1961; Schäfer, 1962; Hartmann-Schröder, 1971; Daro & Polk, 1973; Rasmussen, 1973; Wolff, 1973
,, *hoplura*	Korringa, 1951
,, *ligni*	Hempel, 1957a,b; Sanders *et al.*, 1962; Schäfer, 1962; Muus, 1967; Hartmann-Schröder, 1971; Breese & Phibbs, 1972; Wolff, 1973
,, *limnicola*	Losovskaya, 1973
,, *quadrilobata*	Hempel, 1957a,b; Schäfer, 1962; Hartmann-Schröder, 1971
,, *websteri*	Zottoli & Carriker, 1974
Polydora sp.	Hartman, 1954; Sleeter & Coull, 1973
Prionospio cirrifera	Pearson, 1971
,, *malmgreni*	Southward, 1957
Pseudopolydora pulchra	Eleftheriou, 1970; Hartmann-Schröder, 1971; Wolff, 1973
Pygospio elegans	Remane, 1933; Thamdrup, 1935; Linke, 1939; Smidt, 1951; Hempel, 1957a,b; Sanders *et al.*, 1962; Schäfer, 1962; Jepsen, 1965; Muus, 1967; Hartmann-Schröder, 1971; Wolff, 1973
Scolelepis agilis	Sanders *et al.*, 1962
,, *cirratulus*	Hempelmann, 1931; Yonge, 1954a; Retière, 1967
,, *foliosa*	Hempelmann, 1931; Jepsen, 1965; Wolff, 1973
,, *fuliginosa*	Yonge, 1954a; Gray, 1971; Pearson, 1971; Wolff, 1973
,, cf. *fuliginosa*	Guerin, 1973
,, *girardi*	Pearson, 1971
,, *squamatus*	Mortensen, 1922; Seilacher, 1953; Jepsen, 1965; Hartmann-Schröder, 1971; Wolff, 1973
,, *tridentatus*	Wolff, 1973
Spio martinensis	Wolff, 1973
,, *setosa*	Sanders *et al.*, 1962
Spiophanes bombyx	Retière, 1967; Hartmann-Schröder, 1971; Wolff, 1973
,, *kroyeri*	Southward, 1957; Hartmann-Schröder, 1971; Pearson, 1971
Streblospio benedicti	Jones, 1961; Sanders *et al.*, 1962
,, *shrubsolii*	Hartmann-Schröder, 1971
Spionidae, general	Yonge, 1928; Remane, 1933; Dales, 1963; Day, 1967

fuliginosa settles preferentially on substrata covered with specific amounts of bacteria (Gray, 1971), but the level of discrimination is not as great as in some truly sessile polychaetes. This is to be expected since the adults are capable of moving away from a marginally suitable habitat.

We postulate that spionids in principle are surface deposit-feeders with good discriminatory powers to select particles both on size and on content. They are discretely motile, in that they can move around as adults, but do not do so while feeding. Some species, such as the rock, shell and coral drilling forms, are probably wholly sessile as adults. Supplementary filter-feeding or lassoing may take place in most species but it will be difficult to distinguish from feeding on bedload materials.

SYLLIDAE (Table XXVIII, Fig. 23)

Syllids are most frequent in shallow water associated with hard substrata and are especially abundant on coral reefs (Kohn & Lloyd, 1973). Members of the subfamily Exogoninae are also well represented in bathyal and abyssal areas. All syllids have eversible, cylindrical, often armed pharynges, followed by strongly muscular pumping structures called proventricles. The pharyngeal armature is most commonly in the form of a single, dagger-shaped tooth, but a series of large or small teeth encircling the pharyngeal opening may also be present (*e.g.*, *Trypanosyllis*, *Eusyllis*).

Syllids generally are considered non-tubicolous. Forms associated with hydroids, however, often build mucous tubes along the colonies (Hughes, 1975; Fauchald and Jumars, pers. obs.).

Members of the subfamily Autolytinae feed largely on hydroids (Okada, 1928; Hamond, 1969; Hughes, 1975) each species is more or less a specialist on a single kind of hydroid or on a few related kinds. Other syllids feed on

TABLE XXVIII

Literature on feeding modes of the syllids: approximate number of known species, 602.

Autolytus alexandri	Hamond, 1969
,, *brachycephala*	Hamond, 1969; Evans, 1971
,, *edwardsi*	Okada, 1928; Hamond, 1969; Evans, 1971
,, *prolifer*	Hamond, 1969
Autolytus sp.	Hughes, 1975
Eusyllis blomstrandi	Hughes, 1975
Exogone gemmifera	Rasmussen, 1973
Haplosyllis cephalata	Treadwell, 1909
Procerastea cornuta	Hamond, 1969; Evans, 1971
,, *halleziana*	Okada, 1928; Hamond, 1969
Sphaerosyllis hystrix	Hughes, 1975
,, *pirifera*	Jones, 1961
Sphaerosyllis sp.	Schäfer, 1962
Streptosyllis bidentata	Remane, 1933
,, *websteri*	Wolff, 1973; Zmudzinski, 1973
Syllis armillaris	Southward, 1957
Syllidae, general	Malaquin, 1893; Korringa, 1951; Day, 1967; Neumann *et al.*, 1970

hydroids or bryozoans and other colonial invertebrates (Malaquin, 1893; Okada, 1928). They pierce the surface of their prey with the pharyngeal tooth and suck out the content with the help of the proventricle. *Haplosyllis cephalata* is an ectoparasite on a eunicid polychaete (Treadwell, 1909) and Korringa (1951) reported the presence of a number of syllids on oyster shells in the absence of hydroids, so other sources of nutrition are also available for the syllids.

Completely divergent food-habits have been reported for a few species. *Sphaerosyllis hystrix* and *S. pirifera* feed on diatoms and detritus (Jones, 1961; Hughes, 1975), and Schäfer (1962) claimed that *Sphaerosyllis* sp. is a surface deposit-feeder. Another member of the Exogoninae, *Exogone gemmifera*, feeds on reproductive products of other organisms including fish larvae, according to an analysis of gut contents done by Rasmussen (1973). Neumann, Gebelein & Scoffin (1970) demonstrated that a syllid (judging from their Plate 4D, an exogonin of some sort) was an important grazer on green algal mats in the Bahamas. A eusyllin, *Streptosyllis websteri*, is known to feed on diatoms (Hartmann-Schröder, 1971; Wolff, 1973).

Fig. 23.—SYLLIDAE: *Syllis spongicola* grazing on the sponge *Mycale* sp.; members of the subfamily Syllinae are otherwise usually considered predators of hydroids; × 10.

We postulate that all members of the subfamilies Autolytinae and Syllinae are carnivores feeding on hydroids, bryozoans, and other colonial invertebrates. Some may be tubicolous, but most are free living. Most members of the Eusyllinae live in a similar fashion but, especially species associated with muddy bottoms, feed on diatoms. We further postulate that members of Exogoninae are highly selective deposit-feeders, feeding on the surface of the mud and that they will function as carrion-feeders or carnivores as opportunity arises. Some serious contradictions are present in the literature, and only additional work can resolve them.

TEREBELLIDAE (Table XXIX)

The terebellids are rather large, strongly cephalized, usually tubicolous polycheates. The anterior end is equipped with series of very extensible tentacles and the lips are usually heavily muscular and pliable. Terebellids may leave their tubes when necessary, and some species are capable of swimming (Hessle, 1925; Polloni, Rowe & Teal, 1973; Rasmussen, 1973; Eckelbarger, 1974). We have made observations on polycirrin terebellids pulling themselves across the substratum with the help of the tentacles, but a more usual mode of locomotion is a peristaltic crawling. The food is detritus, usually including diatoms, other unicellular algae, and various small invertebrates, including larvae (Rauschenplat, 1901; Blegvad, 1914; Hunt, 1925; Hempelmann, 1931; Yonge, 1954a; Sanders *et al.*, 1962; Ronan, 1978). The method of feeding has been described in detail for some species (Hessle, 1925; Welsh, 1934; Dales, 1955; Sutton, 1957; Hartmann-Schröder, 1971). The tentacles

TABLE XXIX

Literature on feeding modes of the terebellids: approximate number of known species, 357.

Amaeana trilobata	Pearson, 1971
Amphitrite cirrata	Blegvad, 1914; Hartmann-Schröder, 1971; Pearson, 1971
,, *ornata*	Sanders *et al.*, 1962; Gordon, 1966; Rhoads, 1967
,, *rubra*	Hempelmann, 1931; Yonge, 1954a
Amphitrite sp.	Hunt, 1925
Artacama proboscidea	Blegvad, 1914; Hessle, 1925; Dales, 1955; Hartmann-Schröder, 1971
Eupolymnia crescentis	Ronan, 1978
,, *heterobranchia*	Dales, 1961
,, *nebulosa*	Hessle, 1925; Hunt, 1925; Hempelmann, 1931; Yonge, 1954a; Hartmann-Schröder, 1971; Pearson, 1971
,, *nesidensis*	Hessle, 1925
Lanice conchilega	Watson, 1890, 1916; Blegvad, 1914; Hempelmann, 1931; Seilacher, 1951, 1953; Ziegelmeier, 1952, 1969; Yonge, 1954a; Schäfer, 1962; Ernst & Goerke, 1969; Hartmann-Schröder, 1971; Wolff, 1973; Buhr, 1976
Lysilla loveni	Hessle, 1925
Neoamphitrite figulus	Rauschenplat, 1901; Blegvad, 1914; Dales, 1955b; 1963; Hartmann-Schröder, 1971; Wolff, 1973
,, *groenlandica*	Pearson, 1971
,, *robusta*	Dales, 1961
Nicolea zostericola	Blegvad, 1914; Remane, 1933; Hartmann-Schröder, 1971; Rasmussen, 1973; Wolff, 1973
Nicolea sp.	Hunt, 1925
Pista cristata	Hessle, 1925
Polycirrus aurantiacus	Dales, 1955b
,, *plumosa*	Hessle, 1925
Scionella lornensis	Pearson, 1971
Terebella lapidaria	Sutton, 1957
,, *magnifica*	Welsh, 1934
Thelepus cincinnatus	Hunt, 1925; Pearson, 1971
,, *crispus*	Dales, 1961
Terebellidae, general	Jordan, 1913; Yonge, 1928; Remane, 1933; Dales, 1963; Day, 1967

are usually held in a shallow inverted U or V over the bottom. The cells along the edges of the V are mucous-producing and the median cells are ciliated. Smaller particles are transported in a mucous string along the median strip of the V down to the lower part of the tentacles. The proximal part of the tentacles are smooth and rounded, and the mucous string is transferred to the mouth region by the muscular lips. Large particles are pulled in close to the body by muscular contraction of the tentacle, and in most instances several tentacles will collaborate in pulling in large particles (Watson, 1916; Dales, 1955b).

The tubes of the terebellids have occasioned some comment. Some of them, such as the ones made by *Lanice conchilega*, are topped by a fan-shaped branching structure, and several functions have been suggested for it, such as snares for food, support for filter-feeding tentacles, closure of tubes at low tide, and protective mimicry (Watson, 1890). Of these, the first two have been investigated. There is now agreement that *L. conchilega* feeds on material in bedload transport. The fans of *Lanice* are oriented at right angles to the current; this orientation will make them function as baffles in the current, allowing transported material to drop in the quiet areas behind the fans (Ziegelmeier, 1952, 1959). Buhr's (1976) experimental design attempting to demonstrate filter-feeding, does not exclude Ziegelmeier's finding as a likely possibility. Most tubes of terebellids are supposed to be blind-ended, but according to Seilacher (1953) terebellid tubes are open at both ends in coarse sediments. According to Dales (1961) irrigation is headwards in the three species investigated, indicating that the tube must be open at the lower end, and Rhoads (1967) described the tube of *Amphitrite ornata* as U-shaped. Ziegelmeier (1952) suggested that the latter tube morphology is associated with a low flux of food material.

The sedimentary effects of a population of terebellids may be considerable. Gordon (1966) mentioned that the tentacles of a single *A. ornata* can cover several hundred square centimetres; we have made similar observations on *Neoamphitrite robusta*. A large specimen of this species can easily include the whole bottom of a 1 m^2 aquarium under its influence. Rhoads (1967) described how *Amphitrite ornata* sorts out large particles and high-nutrient particles, thereby creating large heaps of coarse sands where they are common; similar mounds were found in dense populations of *Eupolymnia crescentis* by Ronan (1978).

Terebellids may be capable of absorbing dissolved organic matter (Ernst & Goerke, 1969; Southward & Southward, 1972a). Quantitative calculations have shown that three species may be capable of removing 50–60% of the contained oxygen from the irrigation water in the burrow (Dales, 1961). This gives a good starting point for calculations of the energy needed for each of the three species, but other than this, little quantitative information is available.

While terebellids may have the possibility of locomotion, apparently few of them use this ability regularly; we shall consider them to be sessile or discretely motile organisms, until evidence to the contrary has been amassed.

We have observed that *Pista brevibranchiata* and *Eupolymnia heterobranchia* build tubes continuously in the laboratory and that the latter will do this in the field as well.

TOMOPTERIDAE

Tomopterids are large, pelagic polychaetes. All information available indicates that they are carnivores (Lebour, 1923; Yonge, 1928; Rakusa-Suszczewski, 1968; Evans, 1971; Hartmann-Schröder, 1971). Hartmann-Schröder claimed that they are greedy carnivores, attacking large prey. Lebour, somewhat more soberly, indicates that they may feed on herring larvae or on *Sagitta*, which she had found in their guts. She also reported the presence of various unicellular algae, such as diatoms and dinoflagellates. Rakusa-Suszczewski reported that tunicates as well as chaetognaths were present in the gut and claimed that the unicellular algae found by Lebour might be coelomic cells from the chaetognaths, which she described as being perforated and sucked out, rather than ingested.

There are some obvious contradictions here; more direct observations are needed before they can be resolved. The family is known for 41 species.

TRICHOBRANCHIDAE (Table XXX)

Trichobranchids are tubicolous and strongly cephalized. They feed on the surface as selective deposit-feeders, using their tentacles in a fashion similar to that described for the terebellids. Food items include unicellular algae, small animals, and detritus. *Filibranchus roseus* has non-ciliated tentacles (Hessle, 1925) and is capable of feeding only by looping or contracting the tentacles. A number of trichobranchids have some tentacles with rounded cross-sections along the margin of the cephalic region; these may be sensory rather than feeding appendages.

TABLE XXX

Literature on feeding modes of the trichobranchids: approximate number of known species, 27.

Filibranchus roseus	Hessle, 1925; Mare, 1942; Pearson, 1971
Terebellides stroemi	Blegvad, 1914; Hessle, 1925; Hunt, 1925; Remane, 1933; Southward, 1957; Hartmann-Schröder, 1971; Pearson, 1971
Trichobranchus glacialis	Southward, 1957; Pearson, 1971

We have found no published evidence on the locomotory capabilities of trichobranchids. Our observations indicate that the tubes of *Terebellides stroemi* are remarkably long, compared with the size of the contained specimen; they are also usually oriented horizontally or obliquely in the substratum, and we contend that this represents a form of locomotion similar to that found in the ampharetids. *T. stroemi* sometimes uses the expanded upper lip as a scoop and employs the fine feeding tentacles to sort through sediments excavated by this scoop (Jumars and Fauchald, pers. obs.).

TROCHOCHAETIDAE

Trochochaetids are bipalpate spioniform polychaetes that live in long, branching tubes in sand and mud bottoms. They use the palps as selective devices on the surface of the sediment, and the tubes are continuously lengthened. Thus the populations keep moving around in a complex pattern, creating dense mats of tubes in some areas (Remane, 1933; Hartmann-Schröder, 1971). The trochochaetids are not dominant anywhere, and the family consists of only nine species.

INTERPRETATION OF THE FEEDING HABITS

This section consists of an evaluation of the data presented above with comments on various problems and some suggested solutions. The next part is a development of a theoretical framework for our interpretation. This section is followed by a demonstration of the fit of our data into the framework and by a brief discussion of how we view our results in relation to the development of marine benthic ecology.

The following section may be read and understood separately; this was done because we believe that the ideas are of considerable interest to persons not directly involved in research on polychaetes. In order to keep the paper to reasonable proportions, however, we have rarely cited the original literature in this section. For a complete understanding of the grounds for the positions we have taken concerning the feeding habits of any given polychaete family, the readers must refer to the material presented above.

EVALUATION OF DATA

Certain polychaetes, mostly members of speciose families, appear to vary their diets a great deal. Normally, such observations lead to the conclusion that these species are omnivores (Goerke, 1966, 1971a; Day, 1967). We have two different kinds of objections to such conclusions. First, each population of a widely dispersed species feeds on a limited range of materials (*e.g.*, *Diopatra ornata*, Rosenthal, *et al.*, 1974; Emerson, in prep.), indicating that, while the species as a whole may be omnivorous, each population may be functionally specialized. Secondly, reports of omnivorous habits are often based on laboratory experiments showing that a species is capable of feeding on all materials offered (*e.g.*, Goerke, 1971a). We believe it is of greater interest to know what each population does in the field than to know what it potentially can do in the laboratory or what the species as a whole might do.

Consequently, we distinguish between potential and realized diets where possible. The potential diet of a species includes all food items it is enzymatically and behaviourally capable of using in its diet; the realized diet is the subset of the potential diet found in any given population of that species. The distinction suggests that the ecological (trophic) rôle of any population may be only partially predictable from investigations of conspecific populations. Feeding modes may, therefore, remain unpredictable at any (taxonomic) level down to that of populations. Species-rich families appear to have predictable feeding modes at lower taxonomic levels than is the case in species-poor families. This may be an artifact of sampling, in that species-rich families have been more intensively studied.

Determination of the potential diet can be done by experiment. Some caution is advisable in the experimental design: glycerids and polynoids will attack living prey, but are less interested in pieces of tissue of the same prey, indicating that behavioural aspects must be carefully considered (Stolte, 1932; Ockelmann & Vahl, 1970; Dyal, 1973). *Glycera alba*, furthermore, will not attack prey unless it is allowed to construct a burrow in natural sediments (Ockelmann & Vahl, 1970).

In general three sets of experiments are advisable; *i.e.*, one set with live prey, one with freshly killed prey (or pieces of prey, where appropriate), and one with water extracts of the macerated prey. Together these three sets of experiments should give reasonable results. They will also indicate the probable sensory mode used in prey finding. Similar sets of experiments should also be done with plant material and with detritus. Detritivores should also be tested for their ability to use living or dead fractions of the detrital organic matter. Determination of aspects of the potential diet is thus not difficult, even if laborious. Determination of the realized diet is more troublesome. Experiments must be interpreted cautiously since they usually reveal only the potential diet. The time course of enzymatic breakdown of different food classes differs, so especially proteins of animal origin will be under-estimated in a gut content analysis. Nevertheless, repeated and careful microscopic examination and other direct methods such as immunological assays (Pickavance, 1970) seem to offer the best possibilities for determination of the realized diet. Experiments may again be required, however, to distinguish incidentally ingested detritus from *bona fide* sources of nutrition (*e.g.*, Prinslow, Valiella & Teal, 1974). Realized diets may be expected to differ from one population to the next. As an example, *Nereis* (*Neanthes*) *virens* is functionally a herbivore near Woods Hole, Mass., U.S.A., but an omnivore on European coasts (Goerke, 1971a,b). In this instance a simple examination of the gut content would be adequate to show the difference. We believe that the concepts of potential and realized diets are useful because they allow recognition of an ecological differentiation with or without reproductive implications.

Wherever possible, we have distinguished between potential and realized diets, giving greater weight to the latter in classifying polychaetes by feeding guilds. Gut contents and other direct observations are given highest weighting in the analysis. Functional morphology and other information on potential diets is used when other data are lacking. Anecdotal observations are employed when no other sources are available.

THE THEORETICAL FRAMEWORK

Data about feeding biology could be arranged in a number of different patterns, depending on the purpose of the study. One can envisage energetic arrangements, diversity-classification patterns, and other more or less sophisticated treatments. These methods would have been useful, if the actual information available had been sufficiently precise and developed for all groups of polychaetes. We are effectively without any quantitative data on polychaete feeding. The only form of quantitative treatment we can give, is a numerical summarization for each habitat (sample) of the proportion of specimens showing each feeding mode. We developed geographical patterns based on such summaries in our preliminary report (Jumars & Fauchald, 1977); a similar analysis was developed, but with a different emphasis by Woodin (1976).

What we have developed below are a series of verbal models, using the guild concept. The predictions of these models are subject to Popperian rejection, and the models can be formalized in a mathematical sense in the future, when the qualitative predictions have been tested.

The concept

The feeding guild of any organism may be defined as the set of relations among food particle size and composition, the mechanism involved in food intake, and the motility patterns associated with feeding. Involved are the efficiencies of removal of food items, including digestive and assimilatory efficiencies, and the size of the search area (or volume) necessary to allow a single specimen to survive and reproduce. These considerations are stated or implied in ecology texts and have been partially axiomatized by Schoener (1971).

Discussion of the conceptual components

Polychaetes have no special enzymatic gifts allowing them access to materials unavailable to members of other phyla (Jeniaux, 1969). They can feed on large or small particles, on live or dead material of plant as well as of animal origin, and in some cases are capable of absorbing dissolved organic material directly (Stephens, 1972; Erokhin & Vaichijulis, 1976). Decomposing organic material, generally referred to as detritus, is a major source of food. It consists of two fractions: the remnant reduced carbon (often in the form of high-polymer carbohydrates, such as cellulose) and micro-organisms. Some invertebrates may elect to feed on or to digest one fraction rather than the other (Hylleberg, 1975; Yingst, 1976). Whether this is the general case among polychaetes is not known, but certain polychaetes are attracted as settling larvae to bacterial films made by specific bacteria (Gray, 1974), suggesting that acute selectivity may be present.

Feeding modes and functional morphology. The term feeding mode is here used to describe the mechanism of food transport from the environment into the organism. A set of terms defining different modes have been applied to polychaetes as well as to other metazoans (Hunt, 1925; Remane, 1932; Yonge, 1954a; and others). The terms give the erroneous impression that animals are adapted to one or possibly two clearly defined modes and show little or no overlap with other modes. The terms make it easier to discuss a mass of separate observations, but they do not represent a system of mutually exclusive classes.

The modes are defined on particle size and composition. Macrophages handle food particles singly, or at most a few at a time; they handle each particle separately and with all parts of the feeding apparatus involved in handling every or almost every particle. Microphages handle food particles in bulk; each particle is handled by only part of the feeding apparatus. While macrophages generally feed on large particles and microphages on small ones, no absolute particle size measurements can be used to make the distinction. Small species, such as the interstitial forms, show transitions between handling benthic diatoms as single objects and bulk-feeding on material containing benthic diatoms. Post-larval juveniles of microphagous adults may show a gradual shift from macrophagy to microphagy as they grow. The classification is useful only as a first approximation.

Macrophages are subdivided according to the trophic origin of their food—plant or animal. A category for carrion-feeders is usually included (*e.g.*, Yonge, 1954b), but we consider carrion-feeders a subgroup of carnivores because the distinction is usually impossible in practice.

Microphages are subdivided according to the stratum from which their food is derived. Suspension-feeders extract their nourishment from particles carried in the water column. Surface deposit-feeders take their food from the sediment surface. Subsurface deposit-feeders seek particles in buried positions. In order to avoid the confusion of similar names and abbreviations, we refer to all suspension-feeders as 'filter-feeders' (not maintaining the distinction held by Jørgensen, 1966, and others) and to all subsurface deposit-feeders as 'burrowers'. Assignments among these three feeding strata, however, are not without ambiguity, particularly for forms that feed on material in transport as part of the bedload or suspended load sediments.

Among the microphages, surface deposit-feeders and burrowers have similar sets of feeding structures. They may use jawed or unarmed eversible pharynges, or tentacular structures, thus providing three subgroups for each of these two submodes. For filter-feeders, a different system must be recognized. Tentaculate filter-feeders usually use ciliary means to set up feeding currents. Other filter-feeders employ various mucous devices, generally pumping water through a mucous web by muscular or ciliary means.

The total feeding system, therefore, consists of two modes (macrophagy and microphagy), five submodes (herbivores, carnivores, filter-feeders, surface deposit-feeders, and burrowers), and a total of a dozen morphological subgroups. We have consciously avoided the terms 'selective' and 'non-selective deposit-feeder'. Careful studies which are not destructive of the natural sediment fabric and its associated biota reveal that most forms are highly selective in their choice of food particles (Whitlatch, 1974, and in prep.) and that others, which may ingest particles with little prior sorting, are capable of highly selective digestion (Hylleberg, 1975). Consideration of the principles of resource partitioning (Schoener, 1971) militates against application of the label 'non-selective' except in cases where the problem was specifically investigated. We find non-selectivity to be a convenient null hypothesis—one that can usually be disproved with little difficulty.

Motility. Another component of foraging strategy is motility and three motility patterns may be related to feeding. The structure of the feeding apparatus may force the animal to remain sessile while feeding, or the use of the feeding apparatus may be independent of, or require locomotion for proper function. Among sessile organisms, one can distinguish between forms that remain sessile at all times and forms that move between bouts of feeding. We have been unable to separate between species that require locomotion for feeding and those in which the feeding apparatus is independent of locomotion. We have no information suggesting that the former possibility has been realized in any polychaete; it may be a rewarding object of future study. Jumars & Fauchald (1977) defined three motility patterns based on the above considerations. Sessile are organisms which through their lifespan do not move sufficiently to feed in an area appreciably different from the one in which they settled as larvae. Discretely motile are organisms capable of moving between bouts of feeding, but which are sessile during food uptake. Motile are organisms which generally do move independently of the use of the feeding apparatus or in which the efficient working of the feeding apparatus requires locomotion. These motility patterns were originally recognized for microphagous polychaetes from sandy and muddy bottoms (Jumars & Fauchald, 1977). The patterns are also valid for macrophages and for species from hard substrata, and we are here applying the patterns to all benthic polychaetes. They are not directly applicable to pelagic animals, which live in a Lagrangian reference frame.

Some species considered sessile in the current scheme may have a limited locomotion in one sense. The tubes of tubicolous polychaetes are often very long compared to the length of the animal; they are also sometimes oriented obliquely or horizontally in the substratum, and one end of the tube may fill in while the worm is still living in the other end. This indicates that an apparently sessile, tubicolous polychaete may in fact move slowly from one location to another. The problem has not been investigated in detail for any form. It is thus unknown how important this form of locomotion may be.

The term discretely motile is defined similarly to Remane's (1933) term "hemisessile". We believe our term is somewhat more descriptive, in that it implies periods when stationary interrupted by relatively distinct periods of movement. As an example, nereids may not move much during their adult life. In fact, several species may develop recognizable ambits (*sensu* Lloyd, 1967). Thus, while nereids in general can and do move around, under favourable circumstances some species are functionally sessile (Goerke, 1966, 1971a; Woodin, 1974, 1976). This must be taken into account when an analysis of feeding behaviours is undertaken.

Guilds. Until more specific information on the components of foraging (*i.e.*, on the details of search, pursuit, handling, and eating) becomes available, we choose to define polychaete feeding guilds on the basis of feeding mode and submode, morphological subgroup (see above), and motility. We thus consider all of the 36 potential combinations of (12) morphological subgroups and (3) motility classes as feeding guilds. For example, tentaculate, discretely motile surface deposit-feeders form one guild, and motile surface deposit-feeders employing eversible pharynges constitute another. Not all of the combinations are actually represented among the polychaetes, as is indicated in Table XXXIII (see p. 274).

RESULTS

We present the summary of feeding in polychaetes according to our definition of feeding guilds. First, we deal with available information on polychaete feeding modes and functional morphology. Next, we briefly treat motility. Finally, we rearrange the available data into our scheme of feeding guilds, which hopefully correspond to functional ecological units.

For more than 90% of all species, even information about the food eaten is not available. A survey of all families *sensu* Fauchald (1977) shows that for 22 families no information is available, and for another ten families only anecdotal remarks made during taxonomic and anatomical studies can be found. Even for the remaining 49 families, the biology of only a few species has been well explored (*Arenicola marina, Chaetopterus variopedatus, Clymenella torquata, Glycera alba, Harmothoe imbricata, Nereis* (*Hediste*) *diversicolor*, and *N.* (*Neanthes*) *virens*). Two partial energy budgets have been compiled (*N.* (*Neanthes*) *virens*, Kay & Brafield, 1973; *Clymenella torquata*, Mangum, 1964b).

Feeding modes and functional morphology

Table XXXI lists the available information on feeding mode and morphological subgroup by family. Herbivores are found among ten families and may be represented in three more families. They can be separated into diatom- and macrophyte-feeders.

Most diatom-feeding polychaetes are small and are often considered interstitial. Dorvilleids, hesionids, and syllids use jaws or teeth to crack the diatom frustules and have strongly muscular pharynges that can be used as pumps to suck out the cell content. The rasping action of dorvilleid denticles may bring in frustule fragments as well as cell contents. Members of the other diatom-eating families crush the diatoms with their muscular pharynges (usually a muscularized lower lip) and swallow frustule fragments as well as cell contents. Gut content analysis should give clearly different results depending on the method of preying on the diatoms. Microscopic analysis will show unrecognizable organic matter in the gut of the jawed diatom-feeders, while recognition of frustule fragments in the guts of the non-jawed ones should be easy. Since the latter group contains mainly fragments of frustules, some of them have been called deposit-feeders. The ctenodrilids, dinophilids, and protodrillids very probably belong to this group despite current evidence of surface deposit-feeding. Most diatom-feeding herbivores are specialists.

The macrophyte herbivores usually have considerably less restricted diets. While any one population of a species may be herbivorous, other populations may be carnivorous or surface deposit-feeding. As herbivores, they feed on seaweeds and sea grasses; they sometimes specialize on drift kelp and other drifting plant material. All species have strong jaws capable of cutting plant fragments, and most have grinding surfaces that can be used to fracture cell walls. Some eunicids in this category should perhaps be considered epifaunal grazers (*Eunice antennata, E. aphroditois*); however, documentation of their herbivorous diets has so far been much more convincing than documentation of their epifaunal grazing habits.

Carnivores are found in 19 families. All holoplanktonic polychaetes, with the exception of Poeobiidae, are carnivores; we have no clear explanation for this pattern. Among the benthic families, all or nearly all species of Amphinomidae, Aphroditidae, Euphrosinidae, Polynoidae, and Sigalionidae are carnivores. The available evidence indicates that Goniadidae should be included in this list; however, the closely similar Glyceridae contain both carnivores and detritivores. Disregarding for the time being the goniadids, the exclusive carnivores fall into two distinct taxonomic groups. The amphinomids and euphrosinids (order Amphinomida) feed by everting a strongly muscular, chitinized lower lip and rasping sessile or hemisessile prey such as cnidarians and sponges. Deep-water euphrosinids may feed mainly on foraminiferans. One genus of amphinomids, *Hipponoa*, falls outside the pattern in that its species are commensals associated with lepadid barnacles. The three other families listed are the largest scaleworm families (superfamily Aphroditacea). They grasp their prey with the help of one or two pairs of strong jaws mounted in an eversible, muscular pharynx. We postulate that the remaining three families in this superfamily, Eulepethidae, Pholoididae, and Polyodontidae, will be found to have similar habits.

Of the remaining families with carnivorous members, Dorvilleidae, Eunicidae, Lumbrineridae, Lysaretidae, and Onuphidae include most members of the superfamily Eunicea; we believe that at least some species of the two remaining eunicean families, Arabellidae and Iphitimidae, will also prove to have carnivorous habits. These two families contain parasitic members and form a transition to the fully parasitic families of the order Eunicida, *i.e.*, Histriobdellidae and Ichthyotomidae. Members of *Eunice*, *Marphysa*, and *Lumbrineris* appear to have extremely varied food habits. Nevertheless, we believe that in principle these polychaetes are carnivores and have adopted other habits secondarily.

The glycerids and goniadids are very similar to each other in that they have extremely long, eversible pharynges tipped by jaws. One half of the glycerids investigated are carnivores, the others are burrowers. Some populations of two nephtyid species have been reported as burrowers; other populations of the same species and all other species of nephtyids are considered carnivores. The nereids and some hesionids have paired jaws in an eversible pharynx. The syllid pharyngeal apparatus is more varied: most species have a single, dart-like tooth, others have a crown of teeth, and some are unarmed. The hesionids and nereids (in their guise as carnivores) feed on crustaceans, bivalves, and other polychaetes, while syllids feed mainly on hydroids and sponges. The phyllodocids lack a jaw-apparatus. The pharynx is long, glandular and muscular, but does not appear to have poison glands or any other form of aggressive devices.

Members of one subfamily in each of the Phyllodocidae and Syllidae have penetrated with considerable success into deep water; these differ from other members of the two families in their food habits. The Eteoninae (Phyllodocidae) retain basically the carnivorous habits of the rest of the family, but are also capable of sustaining life as detritivores. The Exogoninae (Syllidae) feed on diatoms which they handle singly; in deeper water they seem to specialize on foraminiferans.

Most of the symbiotic (*sensu latu*) polychaetes are members of otherwise carnivorous groupings. Commensals are also present in Ctenodrilidae and Flabelligeridae, neither of which have carnivorous members. In these two families, the commensal relationship appears to be informal, and both commensals appear to feed on the food collected by the host (sea urchins in both cases) or use the host for a ride. Among the carnivore-derived symbionts, the relations vary greatly. In the Eunicida, the histriobdellids, ichthyotomids, and iphitimids are obligate symbionts, mostly ectoparasites; the arabellids are temporary endoparasites in other polychaetes and echiurans, living in the body cavities of their hosts for a period of their post-larval lives. Among the hesionids and polynoids the relationships seem less fixed, and all stages of the transition from obligate commensals, through species surviving both as

TABLE XXXI

Feeding guilds for each polychaete family: where possible, the dominant guild is in italics; in the three letter codes, the letter in first position indicates major mode, the second the motility pattern, and the last letter the morphological structure used in feeding; in position 1—B, subsurface deposit-feeder; C, carnivore; F, filter-feeder; H, herbivore; S, surface deposit-feeder; in position 2—D, discretely motile; M, motile; S, sessile; in position 3—J, jawed; P, pumping; T, tentaculate; X, other structures, usually eversible sac-like pharynges.

Family	Guild	Number of species
Acrocirridae		
Flabelligella	?BMT, SMT	5
all others	SMT	14
Alciopidae	CMX	30
Ampharetidae	SST	204
Amphinomidae	CMX	110
Antonbruunidae	CDX	1
Aphroditidae	CMJ	66
Apistobranchidae	SDT	3
Arabellidae	CMJ, SMJ	79
Arenicolidae	FDP, *SDX*	28
Bogueidae	BSX	2
Calamyzidae	CDJ	1
Caobangiidae	FST	7
Capitellidae	SMX, *BMX*	134
Chaetopteridae	*FSP*, SST	41
Chrysopetalidae	CMX	24
Cirratulidae		
Dodecaceria + *Tharyx luticastellus*	SST	16
some *Tharyx* sp.	SDT	118
all others	SMT	
Cossuridae	BMX	15
Ctenodrilidae	?HMX, *SMX*	8
Dinophilidae	?HMX, FDM, *SMX*	17
Dorvilleidae		
Meiodorvillea	BMJ	3
all others	HMJ, CMJ, SMJ	44
Eulepethidae	CMJ	12
Eunicidae	HMJ, HDJ, CMJ, CDJ, ?BMJ	241
Fauveliopsidae	BMX, BSX	8
Flabelligeridae	?FDT, SMT, *SDT*	126
Glyceridae	CDJ, BMJ	72
Goniadidae	CDJ	93
Hesionidae		
Microphthalaminae	HMJ	17
all others	HMJ, CMJ, ?SMJ, BMJ	113
Heterospionidae	SDT	4
Histriobdellidae	CDJ	5
Ichthyotomidae	CDJ	1
Iospilidae	CMX	7
Iphitimidae	CDJ	5
Lacydoniidae	BMX	8

TABLE XXXI—*continued*

Family	Guild	Number of species
Lopadorhynchidae	CMX	16
Lumbrineridae	HMJ, CMJ, CDJ, BMJ	188
Lysaretidae	CMJ, SMJ	10
Magelonidae	SDT	35
Maldanidae	BSX	218
Nephtyidae	*CMJ*, BMJ	103
Nereidae	HMJ, CMJ, CDJ, FDP, SDJ	439
Nerillidae	SMX	25
Onuphidae	HDJ, CMJ, CDJ, SDJ	190
Opheliidae	BMX	138
Orbiniidae	BMX	124
Oweniidae		
Myriowenia	SDT	2
Owenia	FDT, SDT	
all others	BMX	23
Palmyridae	CMX	3
Paraonidae	HMX, SMX	50
Parergodrilidae	?HMX, *SMX*	2
Pectinariidae	BMX	46
Pholoididae	CMJ	4
Phyllodocidae		
Eteoninae	CMX, BMX	66
all others	CMS	229
Pilargiidae	CMJ	48
Pisionidae	?HMX, *BMX*	14
Poecilochaetidae	SDT	13
Poecobiidae	FDT	1
Polygordiidae	SMX	16
Polynoidae	CMJ, CDJ	567
Polyodontidae	CMJ	39
Pontodoridae	CMX	1
Protodrilidae	?HMX, *SMX*	22
Questidae	BMX	2
Sabellariidae	FST	61
Sabellidae		
Fabriciinae	FST, SDT	136
all others	FST	156
Sabellongidae	BSX	1
Saccocirridae	BMX	12
Scalibregmidae	BMX	33
Serpulidae–Spirorbidae	FST	439
Sigalionidae	CMJ	156
Sphaerodoridae	BMX	46
Spintheridae	CMX	12
Spionidae	FDT, SDT	275
Sternaspidae	BMX	10
Syllidae		
Exogoninae	HMJ, CMJ	106
all others	CMJ	496
Terebellidae		
Polycirrinae and *Nicolea*	SDT	78
all others	SST	279
Tomopteridae	CMX	41
Trichobranchidae	SST	27
Trochochaetidae	SDT	9
Typhloscolecidae	CMX	13

commensals and free-living, to completely free-living species can be found in highly similar genera. A systematic search of both families may show conceptually interesting features in parallel development of symbiotic relationships in the polychaetes.

The largest number of polychaetes are microphagous. As stated above (see p. 258) we recognize three microphagous feeding modes: filter-feeding, surface deposit-feeding, and burrowing (subsurface deposit-feeding). Grazers and scrapers are usually included among the microphages when other phyla are treated (Hunt, 1925; Yonge, 1954a). Grazers remove the mucoid film that covers hard substrata—with contained diatoms, microalgae, incrusting animals, and organic debris. Some dorvilleids, eunicids, lumbrinerids, and lysaretids may belong to this category, but the mode has not been adequately documented for a single species.

Filter-feeding has been documented for eight families. It may also be performed by species of Arenicolidae, Flabelligeridae, and Onuphidae. Some feeding methods verge on filter-feeding. One is found in the Spionidae and may perhaps best be characterized as fishing in the sediment bedload. The spionids have paired ciliated palps which they may lash or hold erect in the water. On contact with food particles, these palps will 'lasso' the particles and transport them, partially by muscular methods and partially with the aid of ciliary tracts, to the mouth. We have observed a similar mode in *Phyllochaetopterus.*

Two other methods are more properly called filter-feeding. Chaetopterids, dinophilids, and nereids use mucous-devices. The dinophilid method is a simple mucous rope trailing the animal in the water. The ropes are gathered in from time to time and ingested with the debris adhering to the mucus. Chaetopterids and nereids (*e.g., Nereis* (*Hediste*) *diversicolor*) are both tubicolous filter-feeders. Both set up mucous nets across the tube and create a water current by (at least partially) muscular means. They feed on the net when sufficient particles have accumulated on it. In the nereids the water current is created by undulating motions of the body. *Chaetopterus variopedatus* uses three modified notopodia to set up the current. Other chaetopterids have marginally ciliated notopodia, and the cilia, together with the muscular motion, are used to set up the necessary current. All chaetopterids live in permanent tubes; the nereids build temporary tubes. *Nereis* (*Hediste*) *diversicolor* has other feeding modes as well, and adaptation to filter-feeding is behavioural rather than structural; it is not known whether filter-feeding is of primary importance for any population of this species. The chaetopterids are strongly modified for filter-feeding, and this mode of feeding is by far the most important in the family; some long-palped chaetopterids function as surface deposit-feeders as well.

The remaining filter-feeding polychaetes have ciliated tentacular structures. The sabellariids have paired groups of ciliated tentacles projecting forward on either side of the prostomium. Ciliated paths lead from the tentacular bases medially and posteriorly to the mouth, where the food is ingested with the help of the lips. The overall water current runs towards the midline and anteriorly. The only oweniid investigated (*Owenia fusiformis*) has a low tentacular crown consisting of flattened lobes. The lobes are marginally and medially ciliated. The marginal cilia set up a water current leading anteriorly and centrally. The frontal cilia collect debris falling out of the water as the current slows after passing the edge of the crown; ciliated paths lead towards the mouth, and rejection paths are also present.

Members of Sabellidae, Serpulidae, and Spirorbidae have complex tentacular crowns involving modification of both pro- and peristomia. Each crown consists of a varying number of radioli usually carrying pinnules (Fig. 19). The pinnules and the radioli are ciliated. Lateral cilia on the pinnules set up a water current leading anteriorly and centrally; food particles are collected by the frontal cilia on the pinnules and led to the frontal side of the radioli where ciliated grooves transport them to the mouth. Folds and ridges make it possible for the worm to sort particles by size (Fig. 20). The smallest particles are used for food, medium sized ones are used for tube building (in Sabellidae) and the largest ones are rejected. The complexity of the sorting mechanism varies a great deal; it is most complex in the subfamily Sabellinae, less complex in other members of Sabellidae, and in all Serpulidae and Spirorbidae.

The Sabellariidae, serpulids, and spirorbids are exclusively filter-feeders. The chaetopterids are predominantly filtering forms, but some species may also be surface deposit-feeders. Dinophilids are primarily surface deposit-feeders. Oweniids may surface deposit-feed and feed as burrowers; most oweniids do not have tentacular crowns, but have paired palps or lack anterior appendages entirely. Some sabellids are surface deposit-feeders, and Spionidae comprises surface deposit-feeders and burrowers as well as filter-feeders. Finally, nereids can feed in most feeding modes. Flabelligerids are usually considered surface deposit-feeders, using their paired grooved palps; they have, however, been observed to set up a ciliary current through the branchial field and, with the help of mucus, gather in particles caught in this field. Onuphid filter-feeding appears closely related to surface deposit-feeding on material in bedload.

Arenicolid filter-feeding is a controversial subject. It is mechanically possible and may take place, but most authors feel that it is at best of minor importance. Arenicolids live in blind-ending burrows where they sit with the mouth at the end of the burrow, feeding on sand in front of them; the sand has been loosened compared with the sand surrounding it. The worm maintains a headwards current through the burrow and the water percolates from the end of the tube into the sand in front of the worm. Seston in the irrigation current will be collected in the sand filter just in front of the animal and will be eaten as the worm feeds on the sand. Thus, filter-feeding does take place as a by-product of the irrigation current. The importance of the mechanism is disputed. We believe that the importance varies with the consistency of the sediment. Coarse sand allows for better water circulation; it is also poorer in organic matter than finer sands; so in coarse sand the method may be of some importance, although surface deposit-feeding must be considered the major mode of feeding in the arenicolids.

Surface deposit-feeding is found in 19 families and may also be present in Chaetopteridae, Hesionidae, and Syllidae. Ctenodrilids, dinophilids, and protodrilids are all very small animals; they feed mainly on diatoms and should possibly be considered herbivores; members of all three families may, however, feed on bacteria and organic debris as well; this would justify their inclusion among the microphagous surface deposit-feeders. The importance of diatom feeding is unknown for any member of these families.

Ampharetids, cirratulids, flabelligerids, magelonids, oweniids, sabellids, spionids, terebellids, and trichobranchids use variously developed tentacular structures to collect food particles. Surface deposit-feeding capitellids, ctenodrilids, dinophilids, lysaretids, nereids, onuphids, paraonids, and protodrilids lack such structures and use eversible pharynges to gather food. Arenicolids also use eversible pharynx, but their method is rather idiosyncratic and is considered separately. As mentioned above, each arenicolid lives in a burrow consisting of an open, vertical tail-shaft leading into a horizontal gallery at about 20 cm depth in the sediment. The vertical head-shaft is filled with sediment, and the worm feeds at the base of the head-shaft. The feeding activity causes the overlying sand to collapse and a low, conical depression appears on the surface of the sediment. Due to water movement and slumping, material from the surrounding area is transported into this funnel, and as the worm feeds, this material will sink down the head-shaft and be eaten. The material eaten by the worm is thus predominantly surface material, transported from the head-shaft by the activities of the worm. Because of the difference in specific gravity between organic detritus and sand grains, under low velocities of water flow detritus will differentially collect in the funnel, which thus functions as a food gathering device. The feeding mode described here was originally documented by Thamdrup (1935); a more detailed account was given above. Arenicolids must derive at least a portion of their food from subsurface deposits; they occasionally move from one area to another through the sediment and subsurface sediments are ingested until the funnel is formed. Depending on the extent of this movement, these worms might be considered burrowers rather than surface deposit-feeders, or as representing both modes.

The tentaculate surface deposit-feeders may be separated into three groups: forms with paired palps, forms with numerous tentacles, and forms with tentacular crowns. Paired palps are found among cirratulids (in part), flabelligerids, magelonids, oweniids (in part), and spionids. The paired palps are muscular structures with a V-shaped groove running along them. There is usually a band of cilia in the groove, and the margins of the palps are well supplied with mucus glands and nerves. Forms with multiple tentacles (often prostomial, sometimes modified palps) are the ampharetids, cirratulids (in part), terebellids, and trichobranchids. Each tentacle is usually constructed like the palps described above, but each may have a circular or ovate rather than a V-shaped cross-section. Functionally all these structures are similar. Where a V-shaped groove is present, the tentacle (palp) is usually held with the V upside down onto the sediment. When a food particle is encountered, one of two things may happen. If the particle is large, the tentacle may 'lasso' it and pull it in by muscular contraction, or several tentacles may aid in doing this. If the particle is small, it will be entangled in mucus and transported in the groove by ciliary action. In species with cylindrical tentacles, two or more of these may be held together to form a groove, or the particle may be transported superficially on ciliary tracts. When the particle comes close to the mouth, most surface deposit-feeders have lips allowing them to sort the particles; ciliary rejection paths are present in some species. Surface deposit-feeders with tentacular equipment are capable of selection at least at two points: initially in the decision to pick up the particle, and later at the point of ingestion. Both selection points function in some species; the relative importance of either site has not been determined for any species. Some recent experiments (Self, pers. comm.) suggest that selection may also occur in transit along the tentacles.

Some oweniids and the surface deposit-feeding sabellids use a tentacular crown in feeding. *Owenia fusiformis* may use its lips directly, rather than its tentacular crown, but potentially the crown may also be used. The sabellids use their tentacular crowns as feather dusters on the surfaces surrounding their tubes. The fabriciins may also gather food particles from the surface by trailing mucous strings from the tentacular crown while moving from one location to the next. Of the surface deposit-feeders that use an eversible pharynx, lysaretids, nereids and onuphids have jaws and function as scavengers as well as deposit-feeders. The distinction is mainly one of particle size in relation to the size of the worm. The capitellids are at least partially tubicolous; few are associated with sediment surfaces and burrowing is much more important than is surface deposit-feeding in this family. *Paraonis fulgens*, the only paraonid investigated, has been observed to feed by grasping particles from the bottom in ripple marks, but also been characterized as a specialist on diatoms. It is unclear which of the two methods is the more important or if the conflicting evidence is based on taxonomic confusion.

Burrowing (subsurface deposit-feeding) is found among 13 families and is possibly also present in Eunicidae, Paraonidae, Spionidae, and Syllidae, but has been poorly documented in these four families. Three different subsidiary modes may be recognized. One group feeds by everting a more or less muscular pharynx onto the substratum; this group includes all families, except the oweniids and pectinariids. Functionally, eversible pharynges are similar whether they are muscular or non-muscularized, and as far as burrowing activities are concerned, the presence of jaws appears unimportant. It is unclear how much sorting can take place with this sort of feeding, but evidence is gathering that papillae, mucus, and cilia on the surface of the pharynges are used for this purpose. The issue needs investigation. Burrowing oweniids use their lips to gather food. Pectinariids loosen the sediment by digging with stout, specialized, anteriorly directed setae (paleae) and sort through the loosened material with the aid of tentacles. Both oweniids and pectinariids appear well equipped to sort particles, but little of this ability has been demonstrated for feeding activities (in contrast to tube-building).

Motility

Motile species have been reported in 31 families and may be present in another two (Table XXXI); motile species are thought to be absent in ten families. Discretely motile species are in 15 families, doubtfully present in three families and absent in 25 families. Sessility is known in nine families, may be present in one additional family (Cirratulidae) and is known to be absent in 33 families.

At the family level, polychaetes are thus very largely motile animals, and only few of them have been capable of adapting to a wholly sessile existence. In fact, four of the families here characterized as sessile, Ampharetidae, Maldanidae, Terebellidae, and Trichobranchidae, may turn out to have a limited form of locomotion in that they can move by building tubes from one area to another. The polychaetes are overwhelmingly motile also when

TABLE XXXII

*Demonstrated and hypothetical feeding guilds: * taxa for which a single category can be assigned and the numbers indicate the numbers of species in such taxa.*

Demonstrated guilds	Hypothetical assignments
HMJ (herbivore, motile, jawed)	
Dorvilleidae	
Eunicidae	
*Hesionidae (Microphthalminae) 17	
Lumbrineridae	
Nereidae	
Syllidae (Exogoninae)	
HMX (herbivore, motile, non-jawed)	
?Ctenodrilidae	?Parergodrilidae
?Dinophilidae	?Pisionidae
Paraonidae	?Psammodrilidae
?Protodrilidae	
HDJ (herbivore, discretely motile, jawed)	
Eunicidae	
Onuphidae	
CMJ (carnivore, motile, jawed)	
*Aphroditidae 66	Arabellidae
Dorvilleidae (except *Meiodorvillea*)	*Eulepethidae 12
Eunicidae	*Pholoididae 4
Hesionidae	*Pilargiidae 48
Lumbrineridae	*Polyodontidae 39
Lysaretidae	
*Nephtyidae (except some populations of *Nephtys incisa* and *N. picta*) 103	
Nereidae	
Onuphidae	
Polynoidae	
*Sigalionidae 156	
Syllidae	
CMX (carnivore, motile, non-jawed)	
*Alciopidae 30	*Chrysopetalidae 24
*Amphinomidae 110	*Iospilidae 7
*Euphrosinidae 42	*Lopadorhynchidae 16
Phyllodocidae (includes Eteoninae, in part)	*Palmyridae 3
*Tomopteridae 41	*Pontodoridae 1
	*Spintheridae 12
	*Typhloscolecidae 13
CDJ (carnivore, discretely motile, jawed)	
Eunicidae	*Calamyzidae 1
Glyceridae	*Histriobdellidae 5
*Goniadidae 93	*Ichthyotomidae 1
Lumbrineridae	*Iphitimidae 5
Nereidae	
Onuphidae	
Polynoidae	

TABLE XXXII—*continued*

Demonstrated guilds	Hypothetical assignments
CDX (carnivore, discretely motile, non-jawed)	
	*Antonbruunidae 1 (inquiline in bivalve)
FDT (filter-feeding, discretely motile, tentaculate)	
?Flabelligeridae	*Poeobiidae 1
Oweniidae (*Owenia*)	
Sabellidae (Fabriciinae)	
Spionidae	
FDP (filter-feeding, discretely motile, pumping)	
Nereidae (*Nereis* (*Hediste*))	
Arenicolidae	
FDM (filter-feeding, discretely motile, mucous devices)	
Dinophilidae	
FST (filter-feeding, sessile, tentaculate)	
*Sabellariidae 61	*Caobangiidae 7
Sabellidae (except Fabriciinae)	
*Serpulidae–Spirorbidae 439	
FSP (filter-feeding, sessile, pumping)	
*Chaetopteridae 41	
SMJ (surface deposit-feeding, motile, jawed)	
Dorvilleidae	Arabellidae
?Hesionidae	
Lumbrineridae	
Lysaretidae	
SMT (surface deposit-feeding, motile, tentaculate)	
Cirratulidae (except *Dodecaceria* and some *Tharyx*)	*Acrocirridae (except Flabelligella) 14
Flabelligeridae	
SMX (surface deposit-feeding, motile, non-jawed)	
Capitellidae	*Parergodrilidae 2
*Ctenodrilidae 8	*Polygordiidae 16
*Dinophilidae 17	*Psammodrilidae 2
*Nerillidae 25	
Paraonidae	
*Protodrilidae 22	
SDJ (surface deposit-feeding, discretely motile, jawed)	
Nereidae	
Onuphidae	

TABLE XXXII—*continued*

Demonstrated guilds	Hypothetical assignments
SDT (surface deposit-feeding, discretely motile, tentaculate)	
Cirratulidae (except *Dodecaceria* and some *Tharyx*)	*Apistobranchidae 3
*Flabelligeridae 126	*Heterospionidae 4
*Magelonidae 35	*Poecilochaetidae 13
*Oweniidae (*Myriowenia*) 2	*Trochochaetidae 9
Sabellidae (Fabriciinae)	
Spionidae	
*Terebellidae (Polycirrinae and *Nicolea*) 78	
SDX (surface deposit-feeding, discretely motile, non-jawed)	
*Arenicolidae 28	
SST (surface deposit-feeding, sessile, tentaculate)	
*Ampharetidae 204	
Chaetopteridae (non-*Chaetopterus*)	
Sabellidae (some Sabellinae)	
*Terebellidae (except Polycirrinae and *Nicolea*) 279	
*Trichobranchidae 27	
BMJ (burrowing, motile, jawed)	
*Dorvilleidae (*Meiodorvillea*) 3	
?Eunicidae	
Glyceridae	
Hesionidae	
Lumbrineridae	
Nephtyidae (some populations of *Nephtys incisa* and *N. picta* only)	
BMT (burrowing, motile, tentaculate)	Spionidae
BMX (burrowing, motile, non-jawed)	
*Capitellidae 134	*Acrocirridae (*Flabelligella*) 5
*Opheliidae 138	Arenicolidae
*Orbiniidae 124	*Cossuridae 15
*Pectinariidae 46	Fauveliopsidae
Phyllodocidae (some Eteoninae)	*Lacydoniidae 8
*Scalibregmidae 33	Paraonidae
	*Pisionidae 14
	*Questidae 2
	*Saccocirridae 12
	*Sphaerodoridae 46
	*Sternaspidae 10
BDX (burrowing, discretely motile, non-jawed)	
BSX (burrowing, sessile, non-jawed)	
*Maldanidae 218	*Bogueidae 2
	Fauveliopsidae
	*Sabellongidae 1

Summary

50 families have 1 guild, with 2229 species, *i.e.* 44·58 species/family;
22 families have 2 guilds, with 2698 species, *i.e.* 122·64 species/family;
5 families have 3 guilds, with 710 species, *i.e.* 142·00 species/family;
2 families have 4 guilds, with 429 species, *i.e.* 214·50 species/family;
2 families have 5 guilds, with 680 species, *i.e.* 340·00 species/family.

analysed at lower taxonomic level, and in most habitats, motile forms usually outnumber sessile ones by considerable margins. Exceptions are serpulid and sabellariid reefs where these are formed, but even in these, the numbers of specimens of associated motile polychaetes may be nearly as high as those forming the substratum.

Guilds

Demonstrated and hypothetical guilds are listed in Table XXXII. All macrophagous polychaetes have muscular eversible pharynges, often with jaws or teeth. Among the herbivores, three guilds are realized, HMJ, HMX, and HDJ; the sessile guilds are missing. There is no particular energetic reason why herbivores, using non-jawed eversible pharynges could not be discretely motile; nevertheless, this guild is not represented.

Members of HMJ belong to the orders Phyllodocida (Hesionidae, Nereidae, and Syllidae) or Eunicida (Dorvilleidae, Eunicidae, and Lumbrineridae) and include representatives of most jawed polychaetes except the scaleworms and the glycerid-like forms. All members of HMX are diatom-feeders; all are small species, and in fact several of the major interstitial families have been included in this guild, partially as hypothetical assignments. No taxa are uniquely present in this guild; this may be an artifact of the system. HDJ is represented by various eunicids and onuphids. These animals tend to be tubicolous, but are capable of leaving their tubes; they feed on algae, either drifting past them as part of the bedload, or growing on their tubes.

Motile, jawed carnivores (CMJ) is one of the major categories of polychaetes. All scale-worms are in this category, with the exception of the polynoids, which also include discretely motile members, since they usually act as sit-and-wait predators. The polyodontids are at least in part tubicolous and may be discretely motile; we need more information before we can move them to a category different from the one including most other scaleworms. The non-jawed, motile carnivores include all the holoplanktonic families, except the Poeobiidae, the phyllodocids and members of the order Amphinomida, the related order Spintherida and two closely similar families, Chrysopetalidae and Palmyridae, usually considered related to the scaleworms. Several tube- or burrow-dwelling, jawed carnivores may leave their tubes, but will usually feed from the tube opening; they are thus discretely motile. Hypothetically associated with this grouping are all symbiotic, jawed polychaetes. They are appended mainly for the sake of the completeness of the system. A single species, *Antonbruunia viridis*, is hypothetically assigned to the corresponding non-jawed category; we would not be surprised if the assignment were incorrect.

Most discretely motile filter-feeders are sabellids or spionids; one genus of oweniids is included in the tentaculate group. The fabriciins are well represented in deep water compared to other sabellids, whereas the spionids are found at all depths. *Owenia* has been reported from all depths, but is probably most common in shelf depths. We have suggested that the poeobiids should be considered in this guild; they are holoplanktonic, but have palps resembling those found in the flabelligerids. *Nereis* (*Hediste*) *diversicolor* can use pumping filter-feeding as its major mode of feeding, and is definitely discretely motile in this activity. More nereids will probably be shown to belong to this guild. Several species of *Platynereis* and *Pseudonereis* construct tubes and maintain irrigation currents through the tubes; so far no observations of filter-feeding have, however, been made on them. The arenicolids in this guild have been discussed above. If a substantial fraction of their food is derived from burrowing, an assignment to the guild BDX would be appropriate.

The sessile tentaculate filter-feeders are the traditional examples of filter-feeders, *i.e.*, sabellariids, sabellids, and serpulids-spirorbids. Among the pumping filter-feeders, the classical studies on chaetopterids have made this feeding mode one of the best described and understood ones.

Among the motile surface deposit-feeders, the euniceans are all members of the jawed guild (SMJ). It is unclear how important surface deposit-feeding is for any member of this guild; most of them graze on surface materials, and most could also be considered scavengers. The motile tentaculate surface deposit-feeders (SMT) are non-tubicolous members of Cirratulidae and most of the closely similar Acrocirridae. These are frequently members of the crevice habitat in intertidal areas, where they dig burrows in the small amounts of sediments that collect in crevices and interstices in algal holdfasts. Most members of the motile surface deposit-feeders with eversible, non-jawed pharynges are small forms. The dinophilids and nerillids should perhaps be considered herbivores feeding on single diatoms rather than as surface deposit-feeders. The discretely motile, jawed, surface deposit-feeders include tubicolous onuphids and burrow-dwelling nereids, including relatively large animals. These forms could also be considered scavengers in that they appear to prefer large particles to small ones. Ecologically, they resemble the corresponding free-living guild but are, since they have reduced motility, tied to environments with relatively higher influx of food than are the corresponding motile species.

The discretely motile, surface deposit-feeding, tentaculate guild is one of the major groupings of polychaetes. The bulk of the bipalpate spioniform polychaetes belong here, as do the flabelligerids, some sabellids, and at least one subfamily of terebellids. The number of species has not been indicated in the tables; we anticipate that at least 200 of the 275 species of spionids will probably belong to this guild. Most guild members are moderately large and are burrow dwellers rather than true tube dwellers. If they build tubes, these are relatively flimsy in construction. The next guild (SDX) includes the arenicolids only; they have been discussed above. The sessile, tentaculate, surface deposit-feeders (SST) form a major guild. It contains most terebellids all trichobranchids and ampharetids, and some sabellids; a few chaetopterids could also possibly be included in this category. It represents what could be called the terebellid way of life. The question of sessility in these animals has been discussed above.

Burrowing (subsurface deposit-feeding) is of minor importance in all jawed and tentaculate forms. Only a few free-living, sand beach spionids are included in BMT and it is unclear whether these species use their palps in feeding; if they do, it is more likely that they are discretely motile than motile. The deposit-feeding glycerids are considered motile; they may live in burrows, but are too active to be called discretely motile. Arenicolids may belong to a discretely motile burrowing guild in cases where they derive the bulk of their food from subsurface deposits.

The guild combining subsurface deposit-feeding with sessility (BSX) is an apparent contradiction in terms. Under specific conditions this may not be the case. By removing sediment these animals will create open, water-filled spaces in the substratum and this, provided the water content is high enough, will slump and fresh sediment will be brought to the feeding animal. If slumping does not continue, there will be a limit to the period animals can keep feeding in this manner. We suspect that the maldanids, the only members of this guild, are capable of moving by building tubes from one location to another. Nothing is known about the biology of either bogueids or sabellongids, but their body forms suggest modes of living similar to that found in the maldanids. The fauveliopsids are hypothetically included here; they live encased in mud burrows in empty shells of gastropods, scaphopods, and others of similar structure. They can evert the anterior end and have no other food gathering devices; nothing more is known about their feeding.

DISCUSSION

Table XXXIII is a matrix of possible feeding guilds. Some of the potential categories are not realized. To be sessile seems a poor habit for a macrophage. The flux of large particles to one feeding site has apparently been too small or too variable to result in the evolution of wholly sessile forms. Similar reasoning may explain the absence of discretely motile macrophages with unarmed pharynges. Jaws allow the utilization of a wider food size range and thus provide access to a greater food supply overall. Among filter-feeders, on the other hand, motile species are unknown. Because of the generally low concentration of food particles in suspension, filter-feeders usually have rather sizeable and cumbersome food catching devices. Motility cannot add substantially to the physically or biologically generated flux of particles in suspension, although discretely motile species have the advantage of being able to leave locally deteriorating conditions for more favourable micro-environments. Discretely motile fabriciin sabellids, for example, numerically dominate sessile sabellins in physically unstable sediments and in the nutrient-poor deep sea.

Motility is advantageous for surface deposit-feeders. Of all the potential sessile guilds, only the tentaculate group is realized. An energetic explanation again seems most likely, the tentaculate forms having a larger foraging radius than would a hypothetical sessile form without feeding tentacles.

We are least comfortable with the state of knowledge about the burrowing forms, especially since it is virtually impossible to gather direct information about their locomotory habits. According to arguments concerning flux of food, sessile forms should be extremely rare among the burrowers. It is not surprising then, that jawed and tentaculate sessile burrowers are unknown. Maldanids (BSX), however, have been reported to be sessile, existing on material slumping toward the head end of the vertical tube. We do not deny this possibility, but suggest that many species of maldanids may periodically move by building lateral tube extensions. They are clearly capable of doing so in the laboratory, but field data are lacking. The entire issue of discrete motility in burrowers requires field observation to determine, for example, whether natural populations of (jawed) lumbrinerids or (tentaculate) pectinariids move continuously or episodically. Burrowers are of additional interest because motile subsurface deposit-feeders are considered the most primitive of the polychaetes (Clark, 1969; Fauchald, 1974, 1977).

Of the 81 polychaete families 50 belong to only one guild (Table XXXII summary) and only two families have as many as five guilds. The species-poor families have fewer guilds than the species-rich ones. Hypothetically, this might be caused by varying morphological separation between families in the class Polychaeta. This is not the case; most polychaete families are similar in morphological uniformity. The taxonomic system used here contains the highest number of families recognized by anybody for the class. We tried to re-calculate the distribution of guilds based on the much more conservative taxonomic systems proposed by Ushakov (1955) and Day (1967). There was no difference in the average number of guilds; what seemed to happen was that families that already were heterogenous in terms of feeding guilds became grouped with similarly heterogenous families, rather than with families with uniform patterns.

TABLE XXXIII

*Feeding guilds of polychaetes: several combinations are unknown as indicated by the absence of an abbreviation for them; * BDX will be occupied by Arenicolidae if these worms get a substantial portion of their food from subsurface deposits.*

	Motile	Discretely motile	Sessile
Macrophagous modes			
Herbivores			
Unarmed pharynx	HMX		
Jawed pharynx	HMJ	HDJ	
Carnivores			
Unarmed pharynx	CMX		
Jawed pharynx	CMJ	CDJ	
Microphagous modes			
Filter-feeders			
Tentaculate		FDT	FST
Mucous devices		FDP	FSP
Surface deposit-feeders			
Unarmed pharynx	SMX	SDX	
Jawed pharynx	SMJ	SDJ	
Tentaculate	SMT	SDT	SST
Burrowers			
Unarmed pharynx	BMX	*BDX	BSX
Jawed pharynx	BMJ		
Tentaculate	BMT		

A deduction from this result is that members of species-rich families must be capable of behavioural changes in their feeding modes. It is probably this capability that has led to their success in terms of exploiting various food sources. Morphologically, nereids with five recognized feeding guilds are as similar to each other as are the phyllodocids with two guilds or the ampharetids with only a single guild. Families with several guilds (*e.g.* eunicids, lumbrinerids, and nereids) are morphologically simpler than families with a restricted number of guilds (*e.g.* ampharetids, terebellids, and sabellids). The contrast is especially striking in the species-rich families.

Feeding guilds are predictable at some supra-specific level for about 3700 species of polychaetes at the present time; they are predictable only at a specific or lower level for nearly 2600 species. We believe that we will eventually be able to identify a single guild for about 5700 species, but that guilds are going to remain unpredictable at the species level for about 1000 species. The total number of species will change as taxonomic descriptions and revisions accumulate. We believe, however, that the proportion of species with unpredictable guilds will remain at about the same level. The 1600 species that we believe can be removed from the unpredictable to the predictable category include a series of ecologically vicariate species, *i.e.* species that are morphologically similar, but have different ecological requirements. Identification of these problem taxa will probably be possible based on comparisons of large samples and with the use of sophisticated methods of data analysis (see Fauchald, 1974, 1976, 1977). We believe that investigations of the 2600 species, will leave a remnant of about 1000 species which show a variety of food habits and motility patterns. Most of the species in this category are extremely widely dispersed; they were largely described from Europe, and usually before 1850. Some may be extreme opportunists with few predictable habits at all. In most instances, however, we believe that partial isolation may have led to different 'traditions' in different parts of the range of each of these species so that predictable habits could be identified at the population level. To name species we believe are in this category is not easy, since none have been adequately analysed. Good candidates include some nereids, such as *Nereis* (*Hediste*) *diversicolor*, *N.* (*Neanthes*) *virens*, and *N.* (*N.*) *succinea* and the eunicids *Eunice antennata* and *E. aphroditois*. We are not suggesting that this is the only possible explanation of the success of widespread species; there are series of cosmopolitan polychaetes species each belonging to a single, well-defined guild, such as *Terebellides stroemi* (SST) and *Chaetopterus variopedatus* (FSP). For these species, other explanations of wide dispersal must be sought.

For the species that belong to more than one guild, separate investigations of their biology must be undertaken for each locality of interest. The sort of detailed investigations needed are accurate energy budgets or precise determinations of interrelations between taxa and influx of food. An important outcome of such investigations would be a clarification of the relation between morphological and non-morphological differentiation of sibling taxa. It may also be of interest to know if a region is capable of invasion by species not at present in the area and in that case, what sorts of taxa would be likely to invade. We believe that this will be possible to predict on the basis of guilds, provided that information about taxa already present is sufficiently detailed.

The proposed system should also facilitate predictions about which groups of polychaetes one is less likely to find under specified environmental conditions. Since light is reduced with depth of water, so will be actively growing plants and so we predict that a group wholly tied to feeding on benthic diatoms is unlikely to be found in water deeper than about 100 metres; herbivores feeding on drift algae, on the other hand, could theoretically be capable of living anywhere in the ocean. We would expect, however, that dependency on drift kelp would rapidly decline with increasing distance from shore and increasing depth. We would not expect to find sessile groups dominant in nutrient-poor environments. The 'catch-apparatus' of any sessile organism is usually considerably larger than that of a motile animal in relation to the size of the body. Beyond a certain point it simply becomes uneconomical for a sessile organism to increase the food-catching surface in order to live in increasingly nutrient-poor waters. Predation, especially of exposed food-catching devices such as palps, may also contribute to selection against very large food gathering devices.

In really shallow water, currents and wave action are strong, so again it would be a poor policy to be a sessile organism in soft substrata. Such an organism would stand the risk of being buried by sediment, or being left completely out of the sediment. Food-catching mechanisms would be clogged by drifting sediment and abrasion would be of considerable importance. Shallow water is eminently desirable for a sessile animal when it is capable of attaching to firm substrata and of protecting itself against abrasion. The food and oxygen supplies as well as the temperature in these waters allow for higher production and more rapid turnover rates, and thus to a closer evolutionary tracking of environmental variables than in deeper water. As stated above, these rewards may be difficult to reap in shallow-water soft substrata.

There are some intriguing trends among the surface deposit-feeders. The motile forms are much smaller than the sessile ones; in fact, the latter guilds include some of the largest of all polychaetes. With the increase of the sessile habit there is a decrease in the relative size of the preferred particles. The sessile, very large terebellids feed on particles as small as or smaller than the particles preferred by the tiny motile dinophilids. Among the surface deposit-feeders there is thus an increased dependency on true bulk feeding with increasingly sessile habits. There are good energetic reasons why these two trends should show up. A small animal can move from one potential food particle to another with relatively low energetic costs. Locomotion is a considerably more expensive process for larger animals since bulk is related to the cube of linear dimensions. Transport of relatively small particles can be done with energy inexpensive processes such as ciliary motion and provides a large amount of energy per unit volume of sediment processed (Taghon, Self & Jumars, 1978). In addition, ciliary collecting devices allow sorting of the particles by specific gravity, so that less dense and thus usually energy-rich particles are transported more readily than the energy-poor, heavier sand grains (Self & Jumars, in press).

Obviously polychaetes do not make up the sum total of benthic organisms in any environment. Nevertheless, it could be of great interest to be able to predict an expected trophic composition of the polychaete fraction of the fauna in such environments. Based on the organisms known to be present and the range of organic particle distribution, it would be possible to make testable statements about the sorts of organisms one would expect in similar sorts of environments. This kind of treatment could also lead to predictions of species that could invade the areas tested. For example, if a surface deposit-feeding group lacks an obvious sessile guild member adept at handling small particles, a prediction of invasion by a terebellid or an ampharetid could be made, especially if the worm already feeding on small particles also could handle larger ones (as could, *e.g.*, a nereid). An accurate guild classification thus permits 'natural experiments' of the sort commonly applied in geographical ecology.

It will remain impossible to predict exactly which of many possible taxa are likely to invade an area; what we want to be able to do is to predict the most probable kind of organism in terms of its feeding behaviour. Since few of the guilds listed in Table XXXIII are unique to one family, accurate prediction at the family level will remain impossible. The overlap in guilds between different taxa represents an irreducible level of unpredictability which cannot be removed. In addition, we are not truly certain that predictability at a lower taxonomic level would be of great interest except to the narrow circle of polychaete taxonomists.

Summarizing the literature on polychaete feeding has made us painfully aware of the lack of information on this topic. Most of the general conclusions are based on limited material; for all families crucial information is missing. We have started to collect information ourselves, and urge all polychaetologists to do the same. Without this very specific information we shall remain incapable of making any sort of predictive statements about the marine benthos at any level.

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