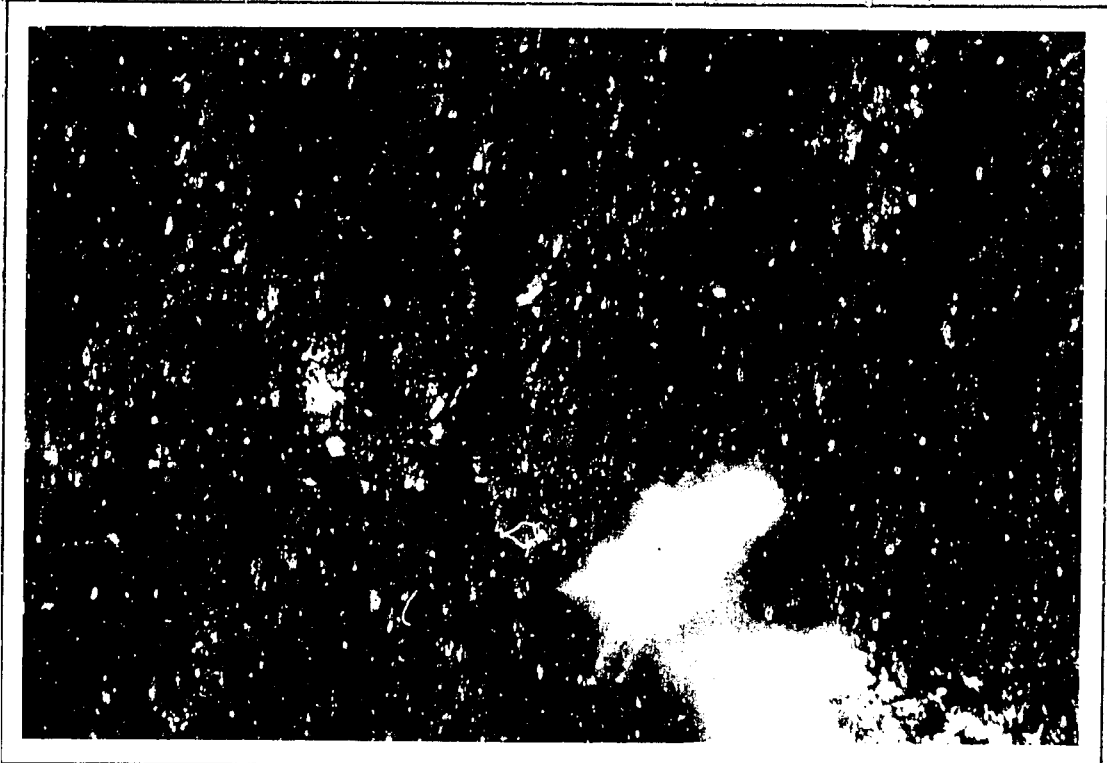


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Detritus and Microbial Ecology in Aquaculture

Edited by
D. J. W. Moriarty
R. S. V. Pullin



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Cover: Decomposing plant detritus, with associated
colonies of filamentous bacteria and a fungal
hypha (red). Photomicrograph by D.J.W. Moriarty.

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Meiofauna: Their Role in Marine Detrital Systems

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Abstract

Detritally enriched marine habitats are characterized by high densities of meiofauna which are generally confined to a few taxa: nematodes of the genera *Rhabditis*, *Diplo-laimella* and *Diplo-laimelloides* and copepods of the genus *Tisbe*, the latter often in multispecies guilds. All species are opportunistic with the ability to utilize a wide variety of food sources, a high reproductive potential and rapid rates of population growth. The nematodes are bacterial feeders and convert detrital to nematode biomass with an efficiency of about 1% in a simple two-step food chain: their presence enhances the rate of bacterial decomposition of the detritus. The feeding behavior of copepods of the genus *Tisbe* is more complex and they may occupy several trophic levels. Meiofauna, particularly copepods, are the main dietary item for the juvenile stages of many commercially important marine food species including fish and crustaceans, and they therefore play a crucial role in the rearing of such species in aquaculture systems.

Introduction

The meiofauna can be defined as an assemblage of small benthic metazoans, ranging in dry adult body mass from about 0.01 to 50 μg and having a coherent set of life-history and feeding characteristics which sets them apart as a separate evolutionary unit from larger macrofauna (Warwick 1984). Arranged roughly in order of numerical abundance, the meiofauna consists of nematodes, copepods (principally harpacticoids), turbellarians, gastrotrichs, tardigrades, kinorhynch, gnathostomulids, small annelids, hydrozoans and in addition some aberrant members of other phyla which mainly comprise larger organisms.

When considering the role of meiofauna in detrital systems, in the particular context of aquaculture, three main questions seem important: what kinds of meiofaunal organisms are generally associated with detritus both in natural and culture systems; what is the role of the meiofauna in the breakdown and mineralization of the detritus and is the presence of meiofauna detrimental or beneficial in aquaculture systems which use plant detritus as the primary food source? In attempting this review it has become abundantly clear that there is a dearth of published information on these topics and it is obvious that much more research needs to be done.

Meiofauna Associated with Detritus

The meiofaunal taxa which favor habitats which are highly enriched with organic detritus are remarkable in two respects, first they are virtually confined to a few restricted groups of nematodes and copepods, and second these same groups are of ubiquitous occurrence in such situations, at least in temperate latitudes where they have been most studied.

Nematodes are found in very high densities in decaying plant material derived from both macroalgae and terrestrial macrophytes. For example, Odum and Heald (1972) found nematodes in "extremely high numbers" in decaying mangrove leaves and suggested that they "play an important role in the decomposition process". Koop et al. (1982) similarly reported "large populations of nematodes" associated with beds of decomposing kelp. I have examined nematodes collected from South African kelp beds described in this last paper, and found that the community is dominated by a single species, *Rhabditis marina*. This species has a cosmopolitan distribution (Inglis 1966) and is commonly associated with stranded decomposing algae. Inglis and Coles (1961) consider that it is a typical member of the beach fauna and is not a truly marine species: indeed it belongs to a large class of nematodes, the Secernentea, only two species of which have been found as free living organisms in the marine environment.

Detrital systems where marsh vegetation or mangrove leaves predominate are usually dominated by two closely related genera of the nematode family Monhysteridae, namely *Diplolaimella* and *Diplolaimelloides* (Lorenzen 1969; Hopper 1970; Hopper et al. 1973). These two genera are also associated with high-shore and brackishwater environments and may not be truly marine. A particular feature of these three genera of nematodes which are prevalent in detrital systems is their ease of laboratory culture in comparison with truly marine forms, and they have been used extensively in experimental studies (Tietjen et al. 1970; Tietjen and Lee 1975; Tenore et al. 1977; Milton 1981; Warwick 1981; Findlay 1982; Findlay and Tenore 1982; Pamatmat and Findlay 1983; Alongi and Tenore 1985).

A wide variety of environments enriched by particulate organic material are also characterized by the predominance of a limited number of copepod species, notably members of the genus *Tisbe* (Fava and Volkmann 1975). This genus comprises a number of very closely related and morphologically similar species (Volkmann

1979) which are often found in the field in multispecies guilds (Bergmans 1979): the maintenance of this diversity probably results from behavioral adaptations for spatial resource partitioning (Marcotte 1984), or it may be that a temporary superabundance of food obviates interspecific competition for resources. *Tisbe* species are again noted for their ease of culture and many species, particularly the scavenging *T. gracilis* group, are frequently found in neglected aquaria in large numbers (Volkman 1979). In controlled experiments in which sublittoral muddy sediments were enriched with powdered *Ascophyllum*, Gee et al. (1985) found that the enriched sediments became dominated by a guild of five *Tisbe* species. There is no doubt that these copepods are fully marine, and they appear to be favored in relation to nematodes in sublittoral habitats which are detritally enriched.

Common features of both the nematode and copepod components of the meiofauna of detrital systems are their opportunistic characteristics. Both the nematodes (this paper) and the *Tisbe* species (Berghe and Bergmans 1981) have the capacity to utilize a wide variety of food sources. They also both have a high reproductive potential and rapid rates of population growth as indicated by Warwick (1981) for the nematodes and by Battaglia (1970) and Bergmans (1981) for *Tisbe*. These characteristics enable them to exploit the highly unpredictable environment that natural detrital systems offer, depending as they do on the occurrence of storms or other climatic events.

Role of Meiofauna in Detrital Systems

It can be deduced from the structure of their buccal cavity (Wieser 1953) that the main nematode taxa associated with detritus are selective bacterial feeders. They all have simple unarmed buccal cavities capable of processing bacterial sized particles: for example in *Rhabditis marina* the buccal cavity is about 1.8 μm wide (Inglis and Coles 1961) and in *Diplolaimelloides brucei* about 1.5 μm wide (Hopper 1970), whilst the larger benthic intertidal bacteria are usually 1-1.5 μm in diameter (I.R. Joint, pers. comm.).

Findlay (1982) showed that the nitrogen content of plant detritus was the best measure of nutritional quality for *Diplolaimella chitwoodi*. Population growth rate (r) and carrying capacity (K) were measured in laboratory culture using different types of plant detritus. Population growth was scarcely affected by the nature or quantity of the detritus except in a few isolated cases, but K was strongly affected by both the food quality and ration. I have done some similar experiments with *Diplolaimelloides brucei* which largely confirm these conclusions. Freeze-dried and ground material of three brown algae (*Fucus*, *Pelvetia* and *Ascophyllum*) and two salt-marsh phanerogams (*Halimione* and *Spartina*) from the nematode's estuarine habitat were added to 50 ml of 26 ppt autoclaved seawater in 100 ml conical flasks. Three ration levels, 25, 50 and 100 mg per culture, for each food source and five replicates for each treatment were used. The cultures were inoculated with 1 ml of a suspension of *D. brucei* containing a mean of 16.6 nematodes ml^{-1} . The flasks were stoppered with cotton wool and incubated in the dark at 20°C. After various

intervals of time the population density was estimated by withdrawing 1 ml aliquots and counting the nematodes on a Hawksley eelworm slide. Population growth rate and maximum population density were compared with control cultures containing 50 mg of ground baby food (Gerber mixed cereal) (Fig. 1) on which the stock cultures had been maintained.

The initial exponential increase is represented by a straight line on the graph of log abundance against time, with slope r . It can be seen that this slope is very similar for all food sources except that it is rather greater for *Spartina*. Final population density varies both with the ration and with the food type, being lowest for *Spartina*.

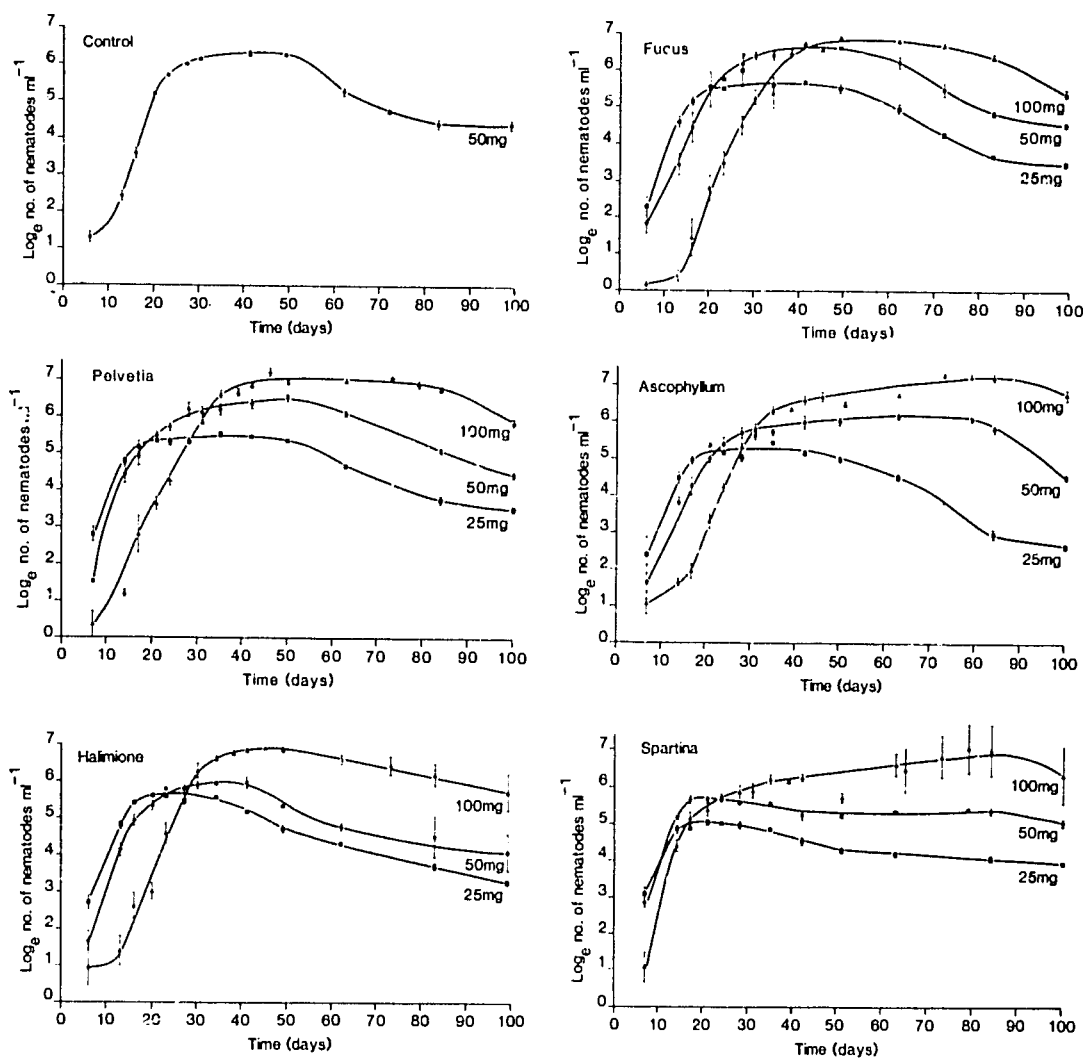


Fig. 1. Population growth of the marine nematode *Diplolaimellodes brucei* cultured on different detrital sources at three ration levels.

The carbon and nitrogen content of the detrital sources, and the values of maximum population density achieved, are given in Table 1. Linear regression of the maximum population density attained (numbers per ml) against the carbon ration (Fig. 2a) and nitrogen ration (Fig. 2b) indicate a much closer correlation with the nitrogen,

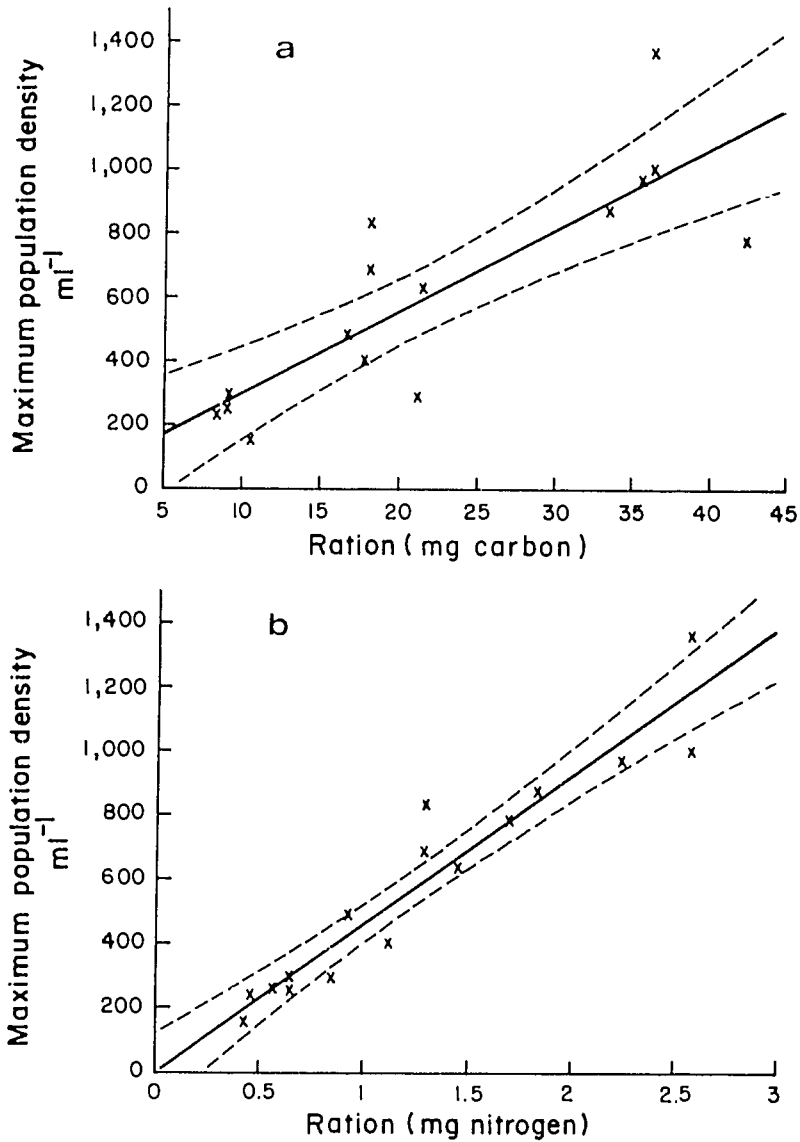


Fig. 2. Maximum population density of the marine nematode *Diplo-laimelloides brucei* attained on different detrital sources and rations (from Fig. 1 and Table 1) regressed by the method of least squares against the carbon ration (a) and nitrogen ration (b). Broken lines are 95% confidence limits of the regression lines.

confirming Findlay's (1982) observation that the nitrogen content of the detrital source is the best measure of its nutritional quality for nematodes.

By converting maximum population density in Table 1 to biomass, it is possible to calculate rough conversion efficiencies (nematode weight/food weight). Warwick (1981) found that these cultures comprise 8.91% adult males (body volume = 0.319 nl), 4.69% adult females (b.v. = 0.411 nl) and 86.4% juveniles (b.v. = 0.0217 nl): an average nematode thus has a body volume of 0.06645 nl, and assuming a specific gravity of 1.13 and dry/wet weight of 0.25 (Wieser 1960) this gives a dry weight of 0.0188 μ g. Conversion efficiencies of about 1% are normal (Table 1), but mean values are slightly better on algae (*Fucus* 1.20%, *Pelvetia* 1.17%) than on phanerogams (*Spartina* 0.62%, *Halimione* 0.88%), although the conversion efficiency on the alga *Ascophyllum* (0.87%) is comparable with that of *Halimione*. Interestingly, conversion efficiencies on baby cereal (1.19%), which has a high C and N content and is balanced with vitamins, are no better than on brown algae.

Newell (1982) has reviewed evidence that the conversion of both algal debris and of detritus derived from salt-marsh plants to bacterial biomass has an efficiency of approximately 10%. In laboratory microcosms, in the absence of meiofauna, colonization of such debris follows a characteristic succession of bacteria, followed by flagellates and ciliates which utilize the bacteria with an efficiency also around 10%, so that the overall incorporation of detritus into Protozoa is about 1%. This figure is

Table 1. Conversion efficiency (C.E. = dry weight of nematodes/dry weight of food) for *Diploaimelloides brucei* fed on different types of detritus at three ration levels.

Detrital type	mg D.W.	Ration mg C	mg N	Max. nematode density (ml^{-1})	C.E.(%)	Mean C.E.
<i>Ascophyllum</i>	25	8.34	0.455	232	0.87	0.87
	50	16.68	0.910	488	0.92	
	100	33.36	1.821	874	0.82	
<i>Fucus</i>	25	9.06	0.643	292.8	1.10	1.20
	50	18.13	1.285	832	1.56	
	100	36.26	2.571	1,006	0.94	
<i>Pelvetia</i>	25	9.04	0.641	251.4	0.94	1.17
	50	18.07	1.283	686	1.28	
	100	36.15	2.565	1,370	1.29	
<i>Halimione</i>	25	8.86	0.558	258.4	0.97	0.88
	50	17.73	1.116	402	0.75	
	100	35.46	2.231	972	0.91	
<i>Spartina</i>	25	10.56	0.421	153.8	0.58	0.62
	50	21.12	0.842	292	0.55	
	100	42.23	1.683	785	0.74	
Mixed cereal	50	21.47	1.443	634	1.19	

the same for meiofaunal nematodes, suggesting that they are indeed primary consumers of bacteria: if they incorporated plant debris directly, conversion efficiencies an order of magnitude higher would be expected, as are found in the macro-consumers in such systems (Cammen 1980; Newell 1982), and if they were secondary consumers of Protozoa the conversion efficiency would be an order of magnitude lower. The relative development of meiofauna and Protozoa in the potentially competitive situation of natural detrital systems has not been investigated.

As bacterial consumers, nematodes may play an important role in the decomposition of plant detritus. Gerlach (1978) postulated that a large part of the bacterial population is in the stationary phase: grazing by meiofauna stimulates active metabolism and rapid duplications, and this enhanced bacterial productivity is important for the breakdown of organic matter. In sediments, this was shown to be the case by Milton (1981), who found that *Diplolaimella shiewoodi* enhanced bacterial numbers (determined from direct acridine orange counts) in freeze-thawed sediments. However, the evidence is still equivocal as Pamatmat and Findlay (1983) found that *Diplolaimella chitwoodi* inhibits bacterial metabolism as measured by heat production in sand samples. In detrital systems, however, the effect of nematodes on the mineralization rate is significant. Findlay and Tenore (1982) labelled *Gracilaria* (an alga) and *Spartina* by growing them in the presence of $^{14}\text{CO}_2$ and measured the mineralization rates (organic ^{14}C mineralized to $^{14}\text{CO}_2$) with and without *Diplolaimella chitwoodi*. They found that, at natural nematode densities, mineralization rates of *Gracilaria* were enhanced by 300%, but of *Spartina* by only 50%. This increase in mineralization by nematodes would reduce the overall standing stock of detrital carbon for macro-consumers, but concurrent changes in microbial biomass and/or production might increase the nutritional quality of the detritus.

The trophic position and role of the copepods in detrital systems is more problematical and probably more complex. Harpacticoids may graze bacterial cells off detrital particles or ingest some detrital fragments whole. The mucilage released from macroalgal detritus, with its associated microbiota, may also be an important resource (Hicks and Coull 1983). Members of the Tisbidae may be cultured in the laboratory using a wide variety of plant and animal food sources (Hicks and Coull 1983), but the exact method of utilization of the resource is often unknown. *Tisbe holothuriae* ingests ciliates of the genus *Urcnema* (Rieper and Flotow 1981), but the extent to which predation on ciliates occurs in nature is also unknown. *Tisbe furcata* has been known to attack both larval fish and nematodes (Garstang 1900), and there is indirect evidence that its predation on nematodes might be quite significant: Marcotte (1977) noted an inverse density relationship between *T. furcata* and nematodes, and it certainly appears to be the case that detrital systems either become dominated by nematodes or *Tisbe* spp., but rarely by both. Ciliates and flagellates may be important in this relationship: nematodes may outcompete Protozoa for the bacterial food supply in some situations so that if *Tisbe* fed primarily on Protozoa this inverse relationship would become apparent. Alternatively, the inverse relationship may simply be due to conditions of the physicochemical environment, nematodes being favored by brackish intertidal situations and copepods by marine sub-

tidal ones. Such mechanisms are, of course, pure speculation. Much more work needs to be done on the succession of microbial and animal communities on fresh plant detritus of different kinds under differing environmental conditions.

Meiofauna in Aquaculture Systems

Dense populations of meiofaunal nematodes and/or copepods are likely to develop naturally in aquaculture systems which utilize plant detritus as the primary food source, but the question arises as to whether such development is beneficial or detrimental to the production of the target species. Do meiofauna compete with the cultured organisms for the detrital food source and its associated bacterial flora, constituting an energy sink, or are they a crucial step in the transfer of energy up the food chain to the target species?

If the cultured species does not utilize meiofauna as a food source at any stage of its life-history, then the presence of meiofauna could be detrimental to its growth rate. Alongi and Tenore (1985) have shown that, in the presence of both *Diplolaimella chitwoodi* and *Tisbe holothuriae*, the weight specific growth rate of the deposit-feeding polychaete *Capitella capitata* was reduced when mixed cereal and red seaweed detritus were used as food sources. On the other hand, Tenore et al. (1977) showed that the presence of meiofauna enhanced the rate of incorporation of aged *Zostera* detritus in another polychaete *Nephtys incisa*. The influence of meiofauna in such cases is unpredictable, and clearly not well understood. Of course, neither *Capitella* nor *Nephtys* are likely candidates for aquaculture, but such experiments serve to illustrate the regulatory role of meiofauna in detrital food chains.

However, many food species reared under aquaculture feed on meiofauna, especially in their juvenile stages. Gut content analysis of the larvae and juveniles of many commercially important species of bottom feeding fish have shown the dominance of harpacticoid copepods in their diet (review by Hicks and Coull 1983), including various species of flatfish (Castel and Lasserre 1982; de Morais and Boudiou 1984) and salmon (Kaczynski et al. 1973; Feller and Kaczynski 1975; Sibert et al. 1977; Sibert 1979). It is probably true to say that harpacticoids are a crucial dietary item in the early life stages of these species. Gut content analyses reveal that nematodes are much less important, although they do not have such permanent exoskeletons and are likely to be more rapidly digested than copepods, so that their importance may have been underestimated. Hofsten et al. (1983) fed four species of nematodes to the fish *Danio* sp. and no identifiable nematodes were found in the gut when the digestion period was 3 hours or more. However, copepods in detrital systems are usually larger and more active than nematodes, and are often brightly colored, and so would be much more attractive to predators foraging visually. With regard to crustaceans, J.M. Gee (pers. comm.) found that harpacticoids comprised the major item in the diet of shrimps (*Crangon*) foraging over sand, and in young individuals (15-19 mm in length) they represented virtually the entire gut content. Bell and Coull (1978) showed experimentally that shrimp populations regulated

meiofaunal densities, and Gerlach and Schrage (1969) showed that shrimps consumed nematodes under laboratory conditions (when given no other choice). Juvenile crabs are also significant meiofaunal predators (Scherer and Reise 1981).

The evidence therefore suggests that the presence of meiofauna is essential in bringing many commercially important marine food species through their early developmental stages. In general, harpacticoid copepods seem to be the favored resource. In pilot studies, *Tisbe* species and several other harpacticoid copepods have been reared in mass culture on a variety of vegetable and other food sources (Kahan 1979 and references therein) with a view to using them a food source in marine fish hatcheries. Kahan et al. (1982) devised a method of presenting the naupliar larvae of harpacticoids to very young hatchlings by culturing them in floating net-bottomed trays with a mesh size of 80-100 μm , through which the older copepods could not pass. Whether nematodes might outcompete the copepods in such systems in the longer term is not known. I have alluded earlier to our lack of knowledge about what conditions favor the relative development of copepods or nematodes in detrital systems, and research into this field is required urgently in order that the conditions favoring harpacticoids can be reproduced. Such research may be crucial in the development of many detrital systems for aquaculture.

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Discussion

ANDERSON: In Dr. Gray's opening comments, there was reference to a 'microbial loop'. If you use Steele's figures for organic carbon transfer, i.e., with 10% conversion efficiency from one level to another, you find that the transfer of energy to zooplankton is negligible. They appear as a very small energy compartment. Dr. Warwick has shown us that the biomass of the nematodes is clearly related to the N-content of their food resources. I would say that when we consider transfers, as energy or carbon transfer, we are missing the point of transfer of *protein* across trophic levels. We saw from previous papers that the food quality (protein quality) of detritus is very important. Have you looked at N transfer efficiencies? Perhaps many of the organisms that we classify as detritivores or even some herbivores and omnivores are using a lot of this animal protein. Many herbivorous or omnivorous animals can cope with a large intake of animal protein if such is available, for example, consumption of the placenta after parturition by ruminants. The capacity to cope with digestion of animal protein is there. Some of our definitions may be somewhat artificial.

WARWICK: Well, the meiofauna are really best considered as predators on bacteria. I have not looked at N transfer efficiencies. I have only measured transfer efficiencies in terms of biomass—a very crude measure.

ANDERSON: But an animal feeding on detritus could be taking in lots of valuable protein from bacteria and meiofauna.

WARWICK: Yes, I am sure it could.

ANDERSON: In that case, an N-transfer budget would show much higher efficiencies than those which you have measured.

MORIARTY: This is very important. If the conversion efficiency of available food to meiofauna really is say 0.5 or 1.0%, then they are not beneficial to aquaculture systems. However, it is the

step between the detritus and the meiofauna which is important, namely the bacteria. We must find out what they are doing in the detritus and their conversion efficiency not only in terms of C but also in terms of N. If the bacteria are converting detrital N into protein which is then available for use by the meiofauna and higher organisms, then this is a key point for our discussions. Only then can we work out how to utilize detritus to maximum benefit. We need to get the best possible conversion efficiencies from the bacteria to meiofauna or high organisms.

WARWICK: Then perhaps we should avoid the meiofaunal step in aquaculture. They may compete with fish for the detrital resource and the bacteria.

MORIARTY: But the meiofauna can be important mineralizers of N and P. In a fertilized pond in which there is a rich layer of organic material on the bottom, perhaps a rich meiofaunal population could help to mobilize dissolved nutrients for algal production.

WARWICK: Meiofauna also excrete lots of ammonia.

MORIARTY: We need to look at all these options and then build systems for specific purposes.

SCHROEDER: Let us reconsider the question of transfer and losses: the idea of a 1% efficiency with respect to carbon fixation in meiofauna. If this is so, the system could not supply enough carbon to produce meiofauna and still support fish production as well. However, for every 100 g food consumed, perhaps about 90 g is released to the system by excretion and respiration. All of this is not lost. If say 20-40 g go off as CO₂, still say 40-50 g are recycled to the system in other compounds. So, the real efficiency may be much higher.

ANDERSON: This is why decomposers are so effective. There is continuous recycling. There are feedback systems.

GRAY: I did some measurements on ammonia excretion by meiofauna in Australia. Their input is very significant and could be taken up by bacteria.

WARWICK: We must not think only in terms of conversion efficiencies. The target species must be able to grow and complete their life cycles.

BILIO: What evidence is there that nematodes are consumed by fish, young fish for instance?

WARWICK: They are consumed by fish and shrimp. Work done by Gerlach and Schrage (1969)* has shown that laboratory cultures of shrimps can be sustained by nematodes alone. However, this was in the absence of other food items. Copepods are usually the preferred item for fish. Many *Tisbe* spp. in detritus are brightly colored—reds and blues—and are easy to locate.

BILIO: What about the digestibility of nematodes? They have a strong cuticle. Wouldn't they be as resistant or more resistant to digestion than copepods?

WARWICK: Maybe. I don't know of any work on this.

BILIO: I suspect this from my observations on nematodes ingested by Turbellaria.

WARWICK: The copulatory apparatus of nematodes, particularly spicules, should be good indicators of their digestion. These should remain very prominent in the gut of consumers.

BILIO: Yes. There was once a new tubellarian species described in error because of the presence of a nematode spicule.

SRINIVASAN: When considering digestibility, we should not forget that some bacteria are also chitinoplastic.

PULLIN: You did not mention rotifers. These are important in aquaculture, particularly in hatchery and nursery systems. Perhaps they are best defined as zooplankton, not meiofauna. In carp hatchery ponds, one technique used is to develop a rich mixed zooplankton and then to apply an insecticide which selectively kills the arthropods. A 'bloom' of rotifers then follows to provide excellent food for carp larvae. Are any rotifers important components of the meiofaunal systems which you have discussed?

WARWICK: Certainly not in marine benthic situations. Rotifers are present but they are very uncommon.

BILIO: They can become abundant in some special situations, for example, in littoral pools.

PULLIN: What about freshwater ecosystems?

WARWICK: I really do not know. Probably they are more important. I would not like to speculate on their importance in systems with rich detritus. I doubt that meiofauna could be important foods, say for fattening up tilapia. However, they may be useful foods during the early life history stages of some fish.

SCHROEDER: Yes. The early life history stages of many fish require high animal protein food—like zooplankton.

WOHLFARTH: Larval feeding may indeed be the most critical part of the growth cycle for fish. David Kahan in Israel has mass-cultured nematodes and copepods for feeding fish larvae and fry and is now at the stage of setting up a pilot plant for harpacticoid copepod culture.

WARWICK: Where is this work in progress?

WOHLFARTH: The Hebrew University of Jerusalem.

MORIARTY: Regarding the need for a link to the heterotrophic food web to generate nutrients, what about the Protozoa? Would they be the main regulators of bacterial production, by grazing on bacteria in the sediments. Certainly, as Dr. Gray has pointed out in the water column, the microflagellate Protozoa have an important role in limiting bacterial production and biomass. Fenchel and Jørgensen (1977) in their review suggested that Protozoa were the main controllers of bacterial production in the sediments, but I know of no clear evidence for this. What do you think are the relative roles of Protozoa and meiofauna?

GRAY: My feeling is that in most sediments the Protozoa play a minor role and the meiofauna are the major bacteria grazers. However, it may be different in highly flocculent material. Here, there may be large ciliate populations. These are very difficult to study.

WARWICK: I agree. I don't think the Protozoa are as important as the meiofauna. Fenchel (1969)** found that they were important in so-called capillary sediments, that is, sediments like muddy sand with a definite pore structure. In most muds and detritus, they are not important bacteria grazers compared to meiofauna.

MORIARTY: Which meiofauna?

WARWICK: Nematodes, which are overwhelmingly abundant.

BILIO: On part of the seashore, where plant detritus accumulates and there may be anaerobic conditions, you can also find large populations of ciliates.

GRAY: Yes, where you get a mass macroalgal debris you can find this, but not say, on the floor of a fjord. So, it depends upon conditions. However, what we can say is that microflagellates are not

important in the sediments. Their role, as performed in the water column, is taken over by meiofauna and sometimes perhaps by ciliates.

BILIO: There is obviously a need for more work on the nematode meiofauna and the ciliates in fishponds and natural systems.

* Gerlach, S.A. and M. Schrage. 1969. Freilebende Nematoden als Nahrung der Sandgarnele *Crangon crangon*. Experimentelle Untersuchungen über die Bedeutung der meiofauna als Nahrung für das marine Makrobenthos. *Oecologia (Berl.)* 2: 362-375.

** Fenchel, T. 1969. The ecology of marine microbenthos. IV. Structure and function of the benthic ecosystem, its chemical and physical factors and the microfauna communities with special reference to the ciliated protozoa. *Ophelia* 6: 1-182.