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RATES OF METAZOAN MEIOFAUNAL MICROBIVORY: A REVIEW

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INTRODUCTION

During the 1970's, little was known about how, what, and how much meiofauna consumed (Fenchel, 1978; Coull and Bell, 1979). A lot has changed. The kinematics of meiofaunal feeding has been defined. There are four harpacticoid feeding groups: point feeders that are selective epistrate pickers, line feeders that scrape edges of particles, plane sweepers that sweep food into their mouths from two-dimensional surfaces, and solid feeders that either eat or clean whole particles (Marcotte, B.M. 1977, Ph.D. Thesis, Dalhousie University, 212 pp., described in Hicks and Coull, 1983). There are also four nematode feeding groups: deposit feeders, epistrate feeders, scavengers and predators (Jensen, 1987). Although some nematodes (as well as meiofaunal sized annelids) are deposit feeders, most metazoan meiofauna behavior is adapted to pick specific microbial food items, e.g., microalgae, bacteria, and protozoans. Some workers have referred to this feeding habit as «grazing,» and have measured...
how much microbial biomass is consumed by meiofauna (Montagna, 1984; Decho, 1988; Blanchard, 1991). Whereas macrofaunal (and presumably meiofaunal) deposit feeders have adaptations to acquire food by ingesting large volumes of sediment (Lopez and Levinton, 1987), meiofaunal grazers have adaptations to pick out specific microbial particles (Marcotte, 1977 in Hicks and Coull, 1983; Jensen, 1987).

One of the most successful areas of study during the 1980's was to measure how much meiofauna eat in the field. It was found that meiofauna can vary their ingestion rates of microbes in response to changes in food quality or quantity (Deco, 1988; Montagna and Yoon, 1991). These results suggest that meiofaunal grazing rates are a functional response to changes in the environment. I use this term in the same way that Taghon and Green (1990) defined functional response: «how any animal changes its feeding rate in response to changes in abundance of its food.» Meiofauna, particularly harpacticoids, can exponentially increase feeding rates as a function of increased microphytobenthos (Montagna, et al., 1995). More information is needed on how to apply models to meiofauna feeding, but we need a reliable and easy way to obtain feeding rate measurements. The current radioisotope techniques are neither well understood, nor easy to use (Montagna, 1993).

Together nematodes and harpacticoids usually make up 90-98% of the meiofaunal community (McIntyre, 1969; Coull and Bell, 1979; Dye and Furstenburg, 1981; Platt, 1981). This paper focuses on nematodes and harpacticoids because they dominate the community. So, when I refer to metazoan meiofauna, I am referring to mainly nematodes and harpacticoids and exclude benthic microfauna (flagellates, ciliates and foraminifera). There is no doubt that microfauna are important, but they may have different behavior and metabolism than metazoan meiofauna (Rivkin and De Laca, 1990). Meiofauna can utilize organic matter in diverse forms, but this review is focusing on the utilization of the microflora: bacteria and microphytobenthos. The main purpose of this paper is to review the current literature on meiofaunal feeding rates, so that the role of meiofauna in transferring microbial carbon into food webs can be better appreciated.

**TECHNIQUES**

Most meiofaunal grazing rate studies have employed radioisotopic tracers. There are two notable exceptions. One study used chlorophyll-pigment gut-content analysis to measure grazing on microalgae (Deco, 1988), and one study used fluorescence-labeled bacteria to measure grazing on bacteria (Epstein and Shiaris, 1992). Both of these fluorescence techniques are very powerful and have advantages for studies specific to bacteria or microalgae. The radioisotope approach has problems, but it is currently the only way to measure grazing on both bacteria and microalgae. Therefore, this review will mostly cover radioisotope tracer studies. There are two techniques for employing radioactive tracers to measure the invertebrate feeding via grazing. Microbial food is either pre-labeled (Haney, 1971) or labeled while it is being grazed (Daro, 1978). Both techniques have advantages and disadvantages that limit their use to either laboratory or field studies. The pre-labeling technique requires growing microbes with a radioactive tracer, introducing the labeled microbe to the existing microbial community and knowing the specific activity of the food source. Such conditions are best achieved in laboratory studies. The synoptic labeling technique is more amenable to in situ studies, because only the radioactive tracer is introduced and microbial uptake of the tracer and meiofaunal grazing can be measured at the same time.

It is difficult to review the literature and determine the comparative quantitative differences in meiofaunal microbiory, because of differences in approach to measuring feeding rates and differences in reporting the rates measured. In large part, the differences exist because different endpoints are desired. Studies on carbon flow might report rates on a biomass specific basis (e.g., µg C·ind·h⁻¹), whereas studies on the impact of meiofauna grazing on microbial populations might report the flow rate (e.g., h⁻¹). The focus of this review is on assessing the latter issue, therefore I have reported flow rates. This requires that the amount of food (e.g., carbon, chlorophyll, or number of cells) offered or available for eating is known and reported. In this case it is simple to calculate the flow rate, i.e., the percent grazed per unit time. An advantage to reporting the flow rate is that the inverse is the turnover time required for the microbial population to maintain itself under the grazing pressure of meiofauna. Turnover time is an interesting number, because if the grazing rate is near the prey population growth rate then there is a tight linkage between predator and prey.

**MEIOFAUNAL GRAZING RATE STUDIES IN THE LABORATORY**

The earliest study on nematodes was performed by Duncan et al. (1974). They pre-labelled bacteria, *Acinetobacter* sp., with ¹⁴C-glucose and fed
them to a freshwater nematode, *Plectus palustris*, in hanging drops on slides. Although the grazing rate was low (Table I), the amount of bacteria consumed was 650% of the nematode body weight $d^1$. Another early study on the marine nematode, *Adoncholaimus thalassophygas*, demonstrated that this predator could take up dissolved organic matter (DOM) in the form of $^{14}C$-glucose, but did not eat pre-labelled bacteria (Lopez et al., 1979).

Admiraal et al. (1983) fed the nematode *Eudiplogaster pararamatus* $^{14}C$-labelled algae, *Navicula pygmaea*. They used an interesting technique. The diatoms were solidified in agar and nematodes introduced to the agar drops. This is one of the most complete studies in terms of measuring functional responses, since they used three concentrations of food, two ages of nematodes, and two species of food. Feeding rates increased with increasing food concentration. In two of the three experiments, there appears to be a saturation of the feeding rate. Feeding rates doubled with doubled nematode age, but the weight specific grazing rate decreased nearly an order of magnitude. One experiment was performed with the diatom *N. salinarum*, and the feeding rate was four times higher on this diatom, indicating that selection of food species exists.

Herman and Vranken (1988) fed the nematode *Monohystera disjuncta* with the bacterium *Aleromonas haloplanktis* in bacto-agar. Feeding rates increased with age, but females had greater feeding rates than males (Table I). They also measured defecation rates and used a model to calculate assimilation efficiency. The assimilation efficiency was low: 18% for juveniles, 27% for adult males, and 26% for adult females.

Diatom ingestion rates increase with age and size for the nematode *Chromadorita tenuis* (Jensen, 1984). The nematode body weight increases about 20 times during its life cycle, and the ingestion rate increases from about 1 to 3 $\mu$g algae $d^1$.

Table I. – Meiofaunal grazing rates using prelabelled food. The grazing rate was calculated as the fraction of radioactivity incorporated per individual. Units are in $x 10^{-4}$ h$^{-1}$, which is equivalent to $% x 100$ h$^{-1}$.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Bacteria</th>
<th>Microalgae</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Plectus palustris</em></td>
<td>3.2</td>
<td>-</td>
<td>Duncan et al. (1974)</td>
</tr>
<tr>
<td><em>Adoncholaimus thalassophygas</em></td>
<td>0.016</td>
<td>-</td>
<td>Lopez et al. (1979)</td>
</tr>
<tr>
<td><em>Eudiplogaster pararamatus</em></td>
<td>-</td>
<td>0.02</td>
<td>Admiraal et al. (1983)</td>
</tr>
<tr>
<td><em>Monohystera disjuncta</em> (Juvenile)</td>
<td>17.8</td>
<td>-</td>
<td>Herman and Vranken (1988)</td>
</tr>
<tr>
<td><em>Monohystera disjuncta</em> (Male)</td>
<td>15.3</td>
<td>-</td>
<td>Herman and Vranken (1988)</td>
</tr>
<tr>
<td><em>Monohystera disjuncta</em> (Female)</td>
<td>53.1</td>
<td>-</td>
<td>Herman and Vranken (1988)</td>
</tr>
<tr>
<td><em>Tisbe californicus</em></td>
<td>-</td>
<td>1.6</td>
<td>Lear &amp; Oppenheimer (1962)</td>
</tr>
<tr>
<td><em>Tisbe holothuriae</em></td>
<td>-</td>
<td>1.2</td>
<td>Vanden Berghe &amp; Bergmans, (1981)</td>
</tr>
<tr>
<td><em>Tisbe holothuriae</em> (sand)</td>
<td>19.7</td>
<td>-</td>
<td>Rieper (1978)</td>
</tr>
<tr>
<td><em>Tisbe holothuriae</em> (suspension)</td>
<td>0.059</td>
<td>-</td>
<td>Rieper (1978)</td>
</tr>
<tr>
<td><em>Tisbe battaglai</em></td>
<td>-</td>
<td>1.2</td>
<td>Vanden Berghe &amp; Bergmans, (1981)</td>
</tr>
<tr>
<td><em>Tisbe furcata</em></td>
<td>-</td>
<td>0.51</td>
<td>Vanden Berghe &amp; Bergmans, (1981)</td>
</tr>
<tr>
<td><em>Paramphiacella vararensis</em> (sand)</td>
<td>0.059</td>
<td>-</td>
<td>Rieper (1978)</td>
</tr>
<tr>
<td><em>Paramphiacella vararensis</em> (suspension)</td>
<td>0.0049</td>
<td>-</td>
<td>Rieper (1978)</td>
</tr>
</tbody>
</table>
It appears that all aspects of nematode biology is strongly influenced by the amount of food available. Schiemer (1982) measured respiration, growth, and reproduction of *Caenorhabditis briggsae* as a function of different concentrations of the bacterium, *Escherichia coli*. Nematode body length and weight increased concordantly when grown with increasing concentrations of bacteria. Nematode respiration increased with increasing food. Growth rates increased with increasing food to a threshold value, and maturation was earlier at higher food densities. Fecundity, egg size, and egg production also increased with increasing food. The nematode *Plectus palustris* showed a similar response (Shiemer et al., 1980). Both species have increased assimilation, growth, and population rate with an increase in bacterial food density (Schiemer, 1983). These studies demonstrate the tight linkage between nematodes and the amount of bacterial food available.

The first study on harpacticoids was performed by labelling the green alga, *Platymonas subcordiformis*, with $^{90}$Sr and $^{90}$Y (Lear and Oppenheimer, 1962). However, they used *Tigriopus californicus*, a harpacticoid that is not benthic. *Tigriopus* is a littoral tide pool species. Syvitski and Lewis (1980) studied sediment ingestion and mineral transformation by *T. californicus*. They found that ingestion rate was dependent on suspension concentration.

Rieper (1978) performed one of the first studies feeding bacteria to harpacticoids. She used a planktonic species, *Tisbe holothuriae*, and a benthic species, *Paramphiascella vararensis*. She prelabelled five different strains of bacteria with $^3$H-glucose or $^3$H-leucine, and offered the harpacticoids a sand-paste consisting of pelleted bacteria in sterilized beach sand and bacteria in suspension. We don’t know in which experiments glucose or leucine were used, and this could have affected the results. Both species had higher grazing rates when offered bacteria in a sand paste over bacteria in suspension. Unexpectedly, the planktonic species grazing rate was three orders of magnitude greater on sand than suspension, but the difference was only one order of magnitude for the benthic species (Table I). This suggests that even planktonic harpacticoids are episubstrate feeders. Rieper obtained three other results: the planktonic species ate more than the benthic species, both species had different rates on different species of bacteria, and both species had higher grazing rates when the cell concentration were increased.

Harpacticoids also may have intrageneric differences in feeding rates and preferences. Three species of the planktonic genus *Tisbe* were fed pre-labelled algae (*Dunaliella tertiolecta*) and unlabelled bacteria (Vanden Berghe and Bergmans, 1981). One species had a low feeding rate on algae and preferred the bacteria, and two had the same rate and preferred the algae (Table I). However, I think that Vanden Berghe and Bergmans may have misinterpreted the results. They performed seven experiments, but the experiments usually contained different amounts of added algae and bacteria for different replicates. Within the experiments, there are trends of increasing grazing rates with increasing added algae (Fig. 1). Although, *T. furcata* had an average grazing rate four times lower than the other two species, the experiments also contained an average of 40% less food in each replicate. Rather than an intrageneric effect, they may have simply observed a functional response to the amount of added food (Fig. 1).

Ontogenetic feeding shifts also occur within the harpacticoids (Decho and Fleeger, 1988). *Nitocra lacustris* feed on diatoms only from the second or third copepodite stage. Nauplii and early copepodite stages ingest bacteria by scraping the outer surface of diatoms. Adults ingest bacteria coincidently with ingested diatoms.

Food quality, as measured by C:N ratios, does not affect ingestion rates of *Tisbe cucumariae*. Guidi (1984) fed *T. cucumariae* seven pre-labelled foods with varying C:N ratios and protein content. Whereas nitrogen, protein level, and C:N ratios significantly correlated with survival and development times, ingestion rates were not greatly affected.
One measure of food quality is egg production. The harpacticoid copepod, *Heteropsyllus pseudonunni*, produced more eggs when fed detritus from *Juncus roemerianus* than when fed the microalga, *Dunaliella* sp. (Ustach, 1982). The copepod also produced more eggs when fed *Juncus* detritus and bacteria than when fed the microalga *Nitzschia* sp. (Ustach, 1982). These results suggest that detritus and the associated bacteria are important to *H. pseudonunni*. However, the copepod *Scotolana canadenensis* produced more eggs on a mixed diet of algae and bacteria than either diet alone (Heinle et al., 1977).

**IN SITU GRAZING RATE STUDIES**

Microbial prey can also be labeled while they are being grazed (Daro, 1978). I have adapted this technique for use in sediments to measure meiofaunal grazing rates (Montagna, 1984; Montagna and Bauer, 1988; Montagna, 1993). This allows for in situ studies to be performed. Meiofaunal grazing rates on bacteria and microalgae are calculated using a model proposed by Daro (1978). The meiofaunal grazing rate (G) is the proportion of material flowing from the donor (or prey) compartment to the recipient (or grazer) compartment per unit time. The model assumes that label is in excess and that during the incubation period label does not become limiting, prey uptake is linear, and grazer label recycling is zero. In this case, G is expressed in units of h⁻¹ and is calculated as follows:

\[
G = 2F/t 
\]

\[
F = M/B 
\]

where F is the fraction of label uptake in the grazer, M (in this case meiofauna), relative to the prey, B (bacteria or microalgae), at time, t in hours. M and B are in units of disintegrations per minute (DPM). Since 2/t is a constant, variability in G is due to variability in F, i.e., M and B. In situ grazing studies require controls, because meiofauna may absorb DOM (Montagna and Bauer, 1988), or adsorb dissolved inorganic carbon (Montagna, 1983). A properly designed in situ meiofaunal grazing experiment must consider and correct for isotopic uptake by microbes, meiofauna, and macrofauna via non-grazing processes. This requires parallel incubations to obtain experimental and control values.

Carman and Thistle (1985) used this technique to study species interactions and feeding strategies. They injected ¹⁴C-bicarbonate or ¹⁴C-acetate into undisturbed sediment cores and incubated for 4 and 8 hours. They found that three co-occurring species had three different feeding strategies. *Thompsonula hyaenae* preferred microalgae, *Halicyclops coulli* preferred bacteria, and *Zausodes arenicolus* did not exhibit preferences (Table II). In general, the grazing rates from field studies (Table II) are much lower than the grazing rates obtained from laboratory studies (Table I). This could be explained in two ways. There may be methodological problems with the in situ technique, or the lower rates may be a response to lower amounts of food. It is more likely that food is added in excess in laboratory culture experiments than is available in the natural sediments during field studies. Therefore, it is possible (and perhaps likely) that the lower grazing rates are reflecting lower amounts of available food.

Recently, Carman (1990) has suggested that these differences in grazing rates among the three species were due to label uptake by epicuticular bacteria, and not grazing on labeled bacteria. Male copepods do not feed while clasping females, but the females continue to feed. No bacteria associated label was seen in copepod guts by autoradiography, and non-feeding males still incorporated label on their cuticle. Carman (1990) concluded that differences in feeding rates on bacteria among the harpacticoids listed in Table II is due to differences in uptake by epicuticular bacteria, not grazing on labeled bacteria. This study illustrates the importance of using live controls to subtract label uptake by non-grazing processes.

Most authors have used the in situ technique to measure carbon flow, and not individual species responses to environmental factors. The goal in these types of studies is to determine the impact

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Bacteria</th>
<th>Microalgae</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Thompsonula hyaenae</em></td>
<td>0.002</td>
<td>0.056</td>
<td>Carman &amp; Thistle (1985)</td>
</tr>
<tr>
<td><em>Halicyclops coulli</em></td>
<td>0.016</td>
<td>0.002</td>
<td>Carman &amp; Thistle (1985)</td>
</tr>
<tr>
<td><em>Zausodes arenicolus</em></td>
<td>0.008</td>
<td>0.007</td>
<td>Carman &amp; Thistle (1985)</td>
</tr>
</tbody>
</table>
of meiofauna on benthic microbial productivity, and the flow of carbon from microbes to meio-
fauna. I have performed five such studies (Table III).

The community grazing rates on bacteria range only within one order of magnitude, from 0.003
to 0.03 h\(^{-1}\). The range on microalgae is five times greater, i.e. a 50 fold difference, from 0.0008 to
0.04. The range on both grazing rates reflects the range of environmental conditions, e.g., temperature,
season, and food quality. In my studies, the differences can be explained by temperature and
organic carbon content of the sediment (Montagna and Yoon, 1991). In each study, different taxa
dominate the grazing process, reflecting differences in community structure in each locale and
experiment. The average grazing rate over all studies is the same for both bacteria and microalgae:
0.01 h\(^{-1}\). This suggests, that on average the meio-
faunal community is removing 1 % of the (heter-
otrophic and autotrophic) microbial standing stock
per hour worldwide (in shallow ecosystems).

The mesocosm study by Nilsson et al. (1991)
was the only experimental study. They were in-
vestigating the effect of increased nitrogen (N)
and phosphorous (P) loading on the lower trophic
levels of a sand system. Additions of N and P in-
creased primary production within 2-3 weeks, and
this lead to increases in meiofaunal grazing rates. During the four week experiment, bacterial pro-
duction was not stimulated, and grazing rates on
bacteria did not change. This study shows that
meiofaunal communities can respond to changes
in the quantity of food abundance with changes
in ingestion rates.

Only one study has come to the conclusion that
meiofauna grazing has no impact on bacterial dy-
namics (Epstein and Shiaris, 1992). They con-
cluded that meiofauna consumption only accounted for about 0.03 % of the bacterial stand-
ing stock per day. This is equivalent to a meio-
faunal grazing rate of 0.0000125 h\(^{-1}\), which is
about three orders of magnitude lower than all
other estimates reported in the literature (Table III). In fact, the estimate is comparable to
rates of individual organisms, and not communi-
ties (Tables I and II). This result is at odds with
most published literature. The difference must be
attributed to one or more unique circumstances,
e.g., the use of a different technique, the specific
location, or the bacteria used. The technique,
fluorescence-labeled bacteria, appears to be a very
powerful method. However, rather than staining a
broad natural community, four strains of coliform

Table III. – Meiofaunal community grazing rates from studies that label food while grazing occurs. Grazing rate was
calculated as two times the fraction of radioactivity incorporated per unit time (Daro, 1978). Units are in h\(^{-1}\), which
is equivalent to % × 100 h\(^{-1}\).

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Location</th>
<th>Bacteria</th>
<th>Microalgae</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salt marsh</td>
<td>North Inlet, SC</td>
<td>0.0337</td>
<td>0.0065</td>
<td>Montagna (1984)</td>
</tr>
<tr>
<td>Beach</td>
<td>San Francisco Bay, CA</td>
<td>0.0028</td>
<td>0.0008</td>
<td>Montagna &amp; Bauer (1988)</td>
</tr>
<tr>
<td>Subtidal</td>
<td>San Antonio Bay, TX</td>
<td>0.0099</td>
<td>0.0411</td>
<td>Montagna &amp; Yoon (1991)</td>
</tr>
<tr>
<td>Ocean 18m</td>
<td>Santa Barbara, CA</td>
<td>0.0058</td>
<td>0.0018</td>
<td>Montagna et al. (1994)</td>
</tr>
<tr>
<td>Oyster pond</td>
<td>La Rochelle, France</td>
<td>-</td>
<td>0.0070</td>
<td>Blanchard (1991)</td>
</tr>
<tr>
<td>Mesocosm</td>
<td>Tjärnö, Sweden</td>
<td>0.003</td>
<td>0.004</td>
<td>Nilsson et al. (1991)</td>
</tr>
<tr>
<td>Mud flat</td>
<td>Ems-Dollard,</td>
<td>-</td>
<td>0.003(^a)</td>
<td>Admiraal et al. (1983)</td>
</tr>
<tr>
<td></td>
<td>Netherlands</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mud flat</td>
<td>Marennes-Oléron Bay,</td>
<td>-</td>
<td>0.0014</td>
<td>Montagna et al. (1995)</td>
</tr>
<tr>
<td></td>
<td>France</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mud flat</td>
<td>Boston Harbor, MA</td>
<td>0.00001(^b)</td>
<td>-</td>
<td>Epstein &amp; Shiaris (1992)</td>
</tr>
</tbody>
</table>

\(^a\) Different technique: estimate based on laboratory cultures

\(^b\) Different technique: estimate based on fluorescence-labeled bacteria
bacteria were used, two extracted from sewage treatment plant effluent. The natural community was reported to be dominated by rod-shaped bacteria. There are two of one two possibilities that must be explored in future research: technology and spatial variability. Perhaps grazing rate results are a function of the technique used and one technique (or the application of it) may be flawed. Alternatively, grazing rate results are always unique to the study area and not general (in this case Boston Harbor just represents the low end of the spectrum). In either case, much more work is needed.

Results from freshwater studies are in the same ranges as those found in marine studies. *Attheyella* sp. in freshwater streams ingest bacterial carbon at rates of 0.03-0.47 µg ind⁻¹ d⁻¹ (Perlmutter and Meyer, 1991). This is comparable to rates of 0.05-0.12 µg ind⁻¹ d⁻¹ that is reported for *Tisbe* sp. (Vanden Berghe and Bergmans, 1981). The total stream community is grazing bacteria at rates that range from 0.0004 to 0.0092 h⁻¹, which is in the low range for marine meiofauna (Table III). The lower rates are concordant with the densities of meiofauna in streams, which is about an order of magnitude lower than in marine sediments. The comparability of these rates indicate that the conclusions drawn from marine habitats have generality to all aquatic habitats that support meiofauna communities.

Metazoan meiofauna are not the only grazers in the benthos (Lee et al., 1966). Protozoans are also important in some environments (Fenchel, 1977; Epstein and Shirar, 1992), but perhaps not others (Kemp, 1988). Temporary meiofauna, and taxa other than harpacticoids and nematodes can also be important grazers. For example, polychaetes (Montagna, 1984), mollusks (Montagna and Yoon, 1991), and oligochaetes and turbellarians (Meyer-Reil and Faubel, 1980) have been shown to be dominant grazers in some ecosystems. The total impact of meiofauna on microbes is a complex issue.

**CONCLUSIONS**

Metazoan meiofaunal grazing rates appear to be functional responses to available food. Grazing rates increase when meiofauna are offered increased abundances of microbial food as predicted by optimization models. Since ingestion varies as a function of food, it is imperative that all future studies measure and report the total amount of food available in the experiment or the concentration of food available in the field. Meiofauna taxa apparently have different grazing rates on different food, as well as different selectivity of different foods. Ontogenetic grazing rate differences also exist. Intrageneric grazing rates may exist, but more work is needed on this issue. It is possible that most bacteria ingested by meiofauna in shallow water, is coincidental ingestion. There is much variability from site to site worldwide, because of differing amounts of food available due to different environmental conditions and meiofauna community structure differences. Despite this variability, grazing rates only vary by an order of magnitude, and on average meiofauna graze at a rate of 0.01 h⁻¹, or 1% of the standing stock of both heterotrophic bacteria and autotrophic microalgae. As long as the average global microbial turnover time is about 4 days or less, meiofauna grazing will be roughly in equilibrium with microbial production. This suggests that meiofaunal communities are tightly coupled to microbial communities. This coupling implies that meiofauna have a significant global impact on microbially mediated processes by allowing microbial growth rates to be maintained in log phase.

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**REFERENCES**


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