Do meiofauna consume primary production? About many questions and how to answer them

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Abstract

In view of their high densities, benthic meiofauna are potentially important consumers of primary production. Feeding on diatoms and other microalgae has been documented in a variety of benthic meiotaxa, including many species of the numerically dominant nematodes and harpacticoids. Still, a detailed account of the exact diet of most species, and of the quantitative importance of primary producers in it, is lacking. For nematodes, the presumed nutritive importance of diatoms mostly derives from rather hypothetical links between buccal morphology and food. On the basis of such links, the proportion of nematodes supposedly feeding on diatoms may amount to as much as 85 %, suggesting meiofauna to importantly graze on microalgae. In estuarine and shallow coastal environments, the importance of photoautotrophs for meiofauna is further supported by correlations of meiofauna abundance patterns to phytopigment concentrations.

However, as observations on the feeding behaviour of nematodes increasingly show the bias involved in stringently linking morphological characters to food, any quantification of grazing based merely on this kind of information remains putative. As many meiofauna are opportunistic feeders, which may change feeding behaviour in relation to available food, no simple relations between meiofauna and primary production can be drawn.

Published estimates of meiofauna grazing on benthic bacteria and microalgae on average approximate 0.01 h^{-1} (Montagna, 1995). Put differently: meiofauna consume about 1 % of bacterial and microalgal standing stock per hour, which suggests a tight coupling of benthic meiofauna to benthic microbiota (Montagna, 1995). There are,

however, serious flaws in the presently used techniques to measure meiofaunal microbivory, and questions pertaining to relevant experimental incubation times, sample preservation procedure, periodicity in meiofauna feeding activity etc. have so far received too little attention.

While from the foregoing, it is obvious that important questions about quantitative aspects of the links between primary production and meiofauna remain unanswered, it becomes increasingly clear that, apart from direct grazing, other interactions, e.g. involving exopolysaccharide secretions, may exist between microalgae, bacteria and meiofauna.

1. Introduction

A substantial part of primary production in estuaries and shallow coastal environments occurs in the sediment (Heip *et al.*, 1995). Moreover, also in seas and oceans, significant primary production from out of the water column may reach the seafloor. In order to obtain an integrated view of the primary production and fate of organic matter in the marine environment, it is therefore vital to improve our understanding of routes and pathways of organic matter down to and in the sediment, and of the role benthic biota play in these processes.

The meiobenthos is operationally defined as those benthic organisms which are retained on a 40 μm mesh size sieve, but which pass through a 1 mm sieve (Giere, 1993). Hence, meiofauna includes organisms belonging to a variety of metazoan taxa, such as nematodes, harpacticoid copepods, oligochaetes, gastrotrichs, kinorhynchs, turbellarians, tardigrades etc., but also to some of the larger Protozoa taxa like foraminiferans.

Metazoan meiobenthos densities typically are in the range of 10^5 to 10^7 ind.m^{-2}, with on average 1 to 2 million ind.m^{-2} in estuarine and shallow coastal environments. This corresponds to a biomass range of 0.01 to 10 g C.m^{-2} and average values approximating 1 g C.m^{-2}, respectively (Heip *et al.*, 1985; Heip *et al.*, 1995). Especially in fine sands with a high silt content, nematodes are by far the numerically dominant representatives of the meiofauna (up to 98 %), which is why this paper will mainly focus on nematodes.

Meiofauna is further characterized by a high species diversity, with e.g. more than 735 nematode species so far reported for the North Sea (Heip *et al.*, 1983). Species diversity is higher in marine than in brackish water habitats, while this trend does not hold for density (Heip *et al.*, 1985).

Inspite of their numeric abundance, little is known of the role of meiofauna in the functioning of the benthos. For a long time, the meiobenthos has been considered as a sort of black box, receiving energetic inputs from the lower trophic levels (primary producers and microheterotrophs), but otherwise not participating in benthic energy flow (McIntyre, 1969; McIntyre *et al.*, 1973). In more recent years, meiofauna have been demonstrated to play a potentially substantial role in the energy flows to the higher trophic levels, both directly, since meiofauna can be significant prey to macrofauna (e.g. shrimps and surface-dwelling fishes) (e.g. Gerlach *et al.*, 1969; Bell *et al.*, 1978; Gee, 1989; Coull, 1990; Ellis *et al.*,1989;Feller *et al.*, 1995; Hamerlynck *et al.*, 1983; Sevice *et al.*, 1993; Smith *et al.*, 1987; Sogard, 1984), and indirectly, as they may contribute to

nutrient recycling processes. It has been suggested that meiofauna stimulate heterotrophic breakdown of organic matter in sediments (e.g. Findlay *et al.*, 1982; Tietjen, 1980; Tietjen *et al.*, 1990; Schiemer, 1987; Alkemade *et al*, 1992a; Pieper-Kirchner, 1989) through their grazing activity on bacteria (e.g. Montagna, 1995), through mucus production (Riemann *et al.*, 1978), and through bioturbation of the sediment, which increases both the penetration depth of oxygen into the sediment (Alkemade *et al.*, 1992b, Cullen, 1973) and the available space for heterotrophic processes (Nehring *et al.*, 1990; Nehring *et al.*, 1991; Alkemade *et al.*, 1992a).

While our understanding of the basic qualitative aspects of the meiofauna's functional position in sediments is still far from complete, reliable attempts to quantify some of these processes are thusfar almost non-existing. The key problem is yet to obtain a more profound knowledge of the feeding habits of the meiofauna, and to develop a reliable methodology for their quantitation.

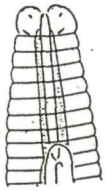
2. What do meiofauna feed on?

As a group, meiofauna consume a wide variety of food sources, including detritus, bacteria, diatoms and other small photoautotrophs, cyanophytes, ciliates, other meiofauna (by predation or scavenging) etc.. However, what genus or species feeds on which sources remains largely unknown.

For nematodes, a feeding type classification, based on the morphology of the buccal cavity and on a few scattered observations of gut contents of preserved specimens, has been proposed as early as 1953 (Wiezer, 1953). It discriminates between four feeding types (Figure 1), mainly on the basis of mouth size and presence/absence/prominence of a buccal armature (teeth, denticles, onchia...).

4 feeding-categories:

* 1A: selective deposit feeders
  - no buccal armature
  - minute buccal cavity
  - mainly bacterial feeders



* 1B: non-selective deposit feeders
  - no buccal armature
  - bacteria, diatoms, algae, macromolecules...

* 2A: epistrate-feeders
  - buccal armature
  - especially diatoms and algae

* 2B: omnivores or predators
  - strong buccal armature
  - variable feeding strategies, including predation

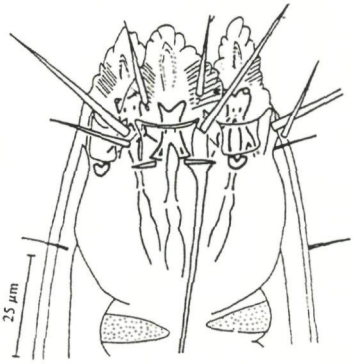


Figure 1: Representation of the four feeding types recognized among the free-living marine nematodes by Wieser, 1953.

This scheme has been widely used since, primarily because it enables the putative assignment of any nematode specimen to a trophic guild. However, the reduction of a huge species diversity into four feeding types, suggesting but a very limited functional diversity, is likely to underestimate the true functional complexity of nematode communities. The same may hold for the four feeding groups recognized among harpacticoid copepods (B.M. Marcotte, cited in Hicks *et al.*, 1983), often the secondmost dominant meiofaunal taxon.

Wieser's scheme, and the modifications subsequently proposed to it, are primarily lacking in factual data obtained from observations of live nematodes in the presence of different candidate food particles. Moens & Vincx (Moens *et al.*, in press.) observed a variety of species from an intertidal mudflat in the Westerschelde estuary (SW Netherlands) and recognized six feeding guilds which may mediate energy flows through the benthos via a variety of pathways (Figure 2).

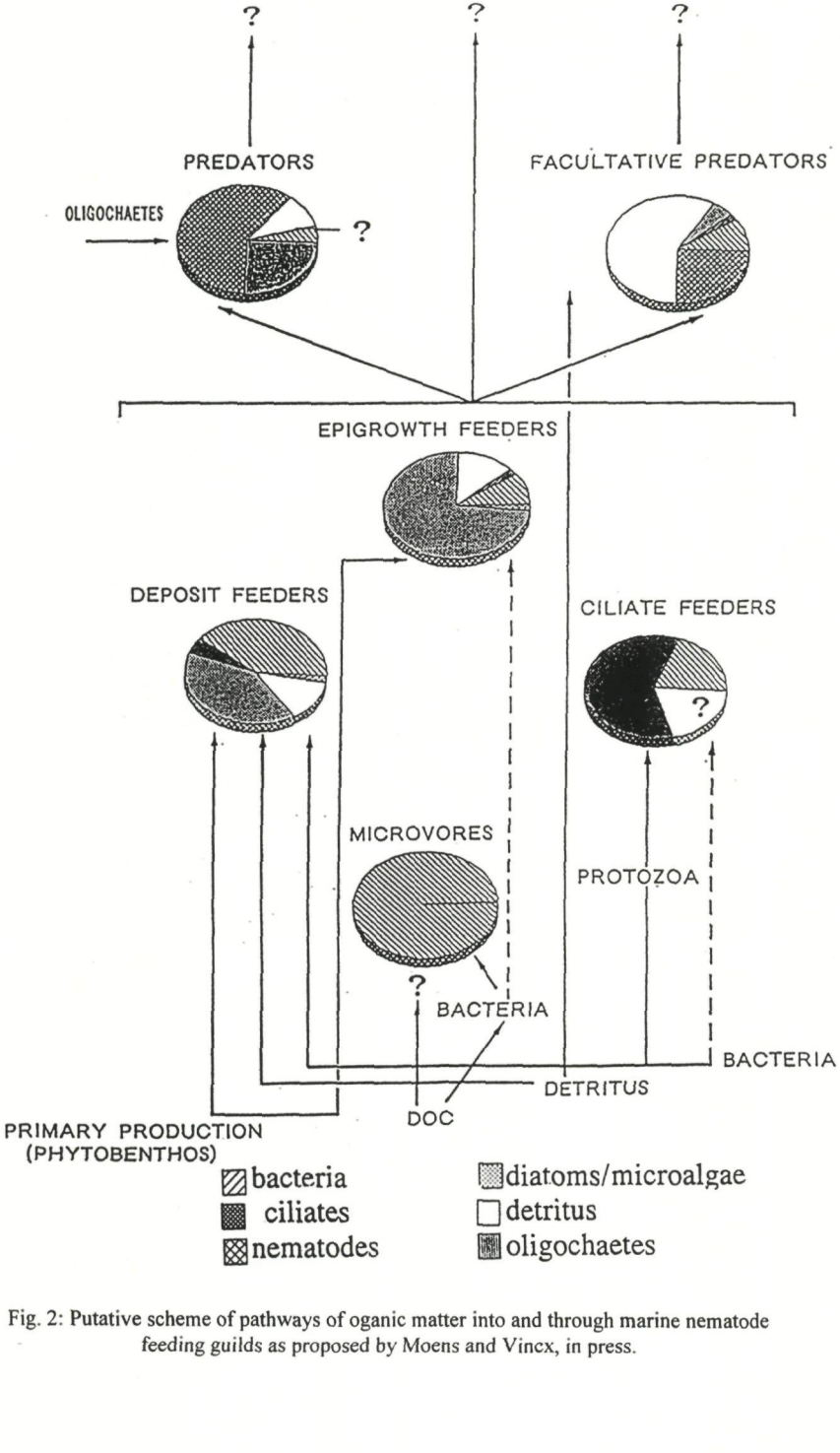


Fig. 2: Putative scheme of pathways of oganic matter into and through marine nematode feeding guilds as proposed by Moens and Vincx, in press.

However, perhaps the main conclusions from this study highlight that nematodes are often very opportunistic feeders, which may change their feeding habits in relation to available food, and that probably very complex and intricate nematode-food interactions must exist in order to explain the coexistence of functionally related species.

3. Confirming links between meiofauna distribution and suspected food

It has been suggested, on the basis of Wieser's scheme, that up to 85 % of nematodes from an intertidal community feed mainly on diatoms and other microalgae (Bouwman, 1983). The possible importance of diatoms and microalgae to free-living marine nematodes is corroborated by results from observational and experimental studies. In order to substantiate such links, several field studies have looked at the correlation between the distribution of meiofauna and suspected foods, mainly microalgae and bacteria.

Meiofauna samples are taken with perspex cores covering a surface area of 10 cm^2. These cores are subsampled for the determination of chlorophyll a (as a measure of microphyton biomass/density) and fucoxanthin (as a measure of diatom standing stock) via HPLC, and of bacterial densities via epifluorescence microscopy. Meiofauna is isolated through centrifugation in the colloidal silicagel Ludox (de Jonge *et al.*, 1977). Most previously published studies have identified meiofauna but to major taxa, while in our lab we are identifying to species level.

In general, no or only week spatial correlations between meiofaunal and bacterial densities have been reported in the literature (e.g. Montagna *et al.*, 1983), whereas in some studies, meiofauna and chla were positively correlated (e.g. Blanchard, 1990; Montagna *et al.*, 1983). A possible explanation for the apparent lack of a positive correlation between meiofauna and suspected microalgal foods in other studies may be the sample size. The benthos is an extremely heterogeneous environment, where bacteria, microphyton and meiofauna are very patchily distributed, the size of these patches typically being over an order of magnitude smaller than the meiocores. Each meiocore is therefore likely to cover several patches. Blanchard (1990) studied meiofauna and microphytobenthos on a scale of 10 cm^2 and of 0.64 cm^2, and found a much clearer (positive) correlation on the latter scale.

4. How to quantify meiofauna grazing activity?

Most experiments to date investigating rates of meiofauna grazing on either bacteria or microalgae have used radioactive tracer techniques, the label either being added directly *in situ* (i.e. to sediment samples) (Daro, 1978; Montagna, 1983; Montagna, 1984b) or indirectly (as prelabelled food particles added *in situ* or under laboratory conditions) (Haney, 1971).

No insurmountable methodological problems are to be expected from experiments performed with prelabelled food under laboratory conditions. This, however, only holds true if meiofauna can be maintained alive and active under the conditions of the test. Several mainly bacterivorous species from soil, freshwater and marine environments are fairly easy to culture in the lab, and give little problems in this respect. Most of these species are, however, typical saprobionts, and therefore not directly represen-

tative for the benthos, of which many species seem to need a very particular environment in order to remain active. Successful culture of marine benthic nematodes has been restricted to very few species. Many more species remain alive and - to a variable extent - active when kept in a thin layer of habitat water, with or without addition of a little sediment. It is, however, doubtful whether uptake rates obtained under such conditions can be extrapolated to the field. For this to hold true, not only should meiofauna have the same activity level under laboratory conditions as in the field, but also should the prelabelled food be representative for field microbial communities and their exploitation by the meiofauna. Experiments with addition of prelabelled food under controlled conditions are therefore especially useful in testing mechanisms of food selectivity and influence of abiotic factors on food uptake, but perhaps not in determining absolute grazing rates which are directly pertinent to field situations.

Even in a two-compartment model with grazers and prelabelled food, some significant methodological problems exist. Recycling of label from the food compartment during the test incubation period should be low, since free label may enter grazers via non-grazing activity (Montagna *et al.*, 1988), which in this setup is not corrected for. It also tends to yield higher control values for adsorption of label to the grazers. More important yet is the fixation procedure used to stop an experimental incubation. Formaldehyde has commonly been used in trials with meiofauna (Montagna, 1993), but apart from permeabilizing their cuticle to some extent, it may also induce egestion or defaecation of (parts of) the grazers' gut contents. Other chemical preservatives are likely to cause similar bias, though probably to a variable extent (Montagna, 1993). We are presently comparing bacterial grazing rates in meiofauna preserved chemically (formaldehyde in several concentrations, glutaraldehyde, ethanol,...) or physically (freezing or heating) or with a combined chemical and physical approach, with rates obtained from non-preserved meiofauna. Apparently, the traditional preservation with formaldehyde yields rates one third lower than in non-preserved meiofauna, a discrepancy which significantly increases with sample storage time. Another important question is how long a grazing trial should be incubated in order to yield values representative of grazing and not of assimilation. Most studies have hitherto used incubations of at least two hours (Montagna, 1993), a period during which actively feeding rhabditid nematodes, e.g., can fill and subsequently empty their guts as often as eight times (Mapes, 1965; personal observation).

Most experiments to date have been performed to determine meiofauna community grazing rates on bacteria or microalgae, and have for this purpose used direct addition of radioactive label ($NaH^{14}CO_3$ for microalgae and [methyl-^{3}H]-thymidine for bacteria) to sediment samples. This is the so-called three-compartment model, where grazing rates can be calculated from the equation

$$G = 2M/m.t$$

where G = grazing rate, M = the amount of label entering grazers via feeding on bacteria or microalgae , m = the amount of label in the bacteria or microalgae, and t = incubation time (Daro, 1978; Montagna, 1984b; Montagna *et al.* 1988). For this equation to yield accurate grazing rates, two essential assumptions should be met: 1. label uptake in the grazed compartment should be linear, and 2. label uptake in the grazer compartment should be hyperbolic with time (as the grazers are feeding on increasingly more labeled food). It is further assumed that added label is not depleted and that grazer label

recycling is zero during the experimental time course. In this case, G is expressed in units of t^{-1}, mostly h^{-1} (Daro, 1978; Montagna *et al.*, 1988; Montagna 1984b; Montagna, 1993).

A first methodological difficulty in trials with sediments is how to administer the label in such a way that it is rapidly and evenly distributed, at the same time, however, minimizing disturbance to sediment microbial and meiofaunal organisms. Frequent use has been made of slurries, which cause severe disruption of the sediment, but ensure rapid and homogeneous distribution of the label. Alternatives to this are the pore water replacement method, which also yields a good homogeneous label distribution, but may still adversely affect the benthos, and horizontal injection of label into the sediment, which does not significantly disrupt the sediment, but results in a poorer label homogenization (Carman *et al.*, 1989; Montagna, 1983; Montagna 1984b).

Once a tracer has been added to a sediment, controls have to be adopted for label adsorption to grazers' body surfaces, and for the ingestion of free label (i.e. not assimilated by the grazed compartment) (Montagna, 1983; Montagna *et al.*, 1988; Montagna, 1993). Poisoned controls, typically using formaldehyde-preserved samples, account for the former aspect, while the latter can be balanced by running parallel dark (in the case of grazing on microalgae) or inhibitor-poisoned (in the case of grazing on bacteria) incubations, where label uptake by the grazed compartment is considered non-existent or minimal (in the latter case strongly influenced by the efficacy of the prokaryote inhibitor used) (Montagna, 1983; Montagna *et al.*, 1988; Montagna, 1993). Whereas ingestion of inorganic free label ($NaH^{14}CO_3$) by meiofauna is apparently all together not very high, and the use of parallel dark incubations remains pretty straightforward, uptake of free organic label in, e.g., the deposit-feeding fraction of the meiobenthos, together with surface adsorption, may account for more than 80 % on average of label entering grazers (Montagna *et al.*, 1988), and the use of prokaryotic inhibitors requires time-consuming efficiency screening and may adversely affect meiofauna activity. It is therefore not surprising that fairly well reproducible grazing rates on microalgae have been obtained in some studies, while rates of bacterivory remain prone to unacceptably high variance.

A further problem in determining rates of bacterivory is the choice of label. Thymidine, though traditionally used to measure bacterial production (Furhrmann *et al*, 1982), has recently been shown not to be incorporated by a variety of, e.g., chemolithotrophic bacteria (e.g. Johnstone *et al.*, 1989; Roberts *et al.*, 1993; Wellsbury *et al.*, 1994), so that rates calculated from trials using this tracer will not accurately reflect grazing on total bacterial standing stock. Using leucine instead of thymidine may solve this problem. Even then, the observation that but a minor proportion of sediment bacteria actively incorporate label (Carman., 1990), complicates interpretation of rates measured in this way.

Alternatively, fluorescently labelled food (bacteria or diatoms) or food analogues (similarly sized but inert microbeads) is now almost routinely used in studies mainly on protozoan grazing (Epstein *et al.*, 1992 and references therein). As quantification of ingested particles is through epifluorescence microscopy, this method is perhaps still more laborious than the radiotracer methodology. The question as to how representative the introduced food (analogue) is for determining grazing rates, and whether it will be selected for or against by members of the meiofauna, remains as in trials where

radiolabelled food is introduced. On the other hand, it may prove an interesting tool in the study of size- and shape-selective feeding processes.

5. What the papers say

Two recent papers have reviewed the existing literature on meiofauna grazing (Montagna, 1995; Heip *et al.*, 1995). Montagna (1995) lists available data in terms of carbon flow, which facilitates interpretation of meiofauna impact on benthic microbial productivity. In general, for temperate shallow coastal environments, community grazing rates on bacteria appear to range only within one order of magnitude, from 0.003 to 0.03 h^{-1}, whereas the range on microalgae is 50-fold, from 0.0008 to 0.04 (Montagna, 1995). A grazing rate averaged over the studies listed by Montagna (1995) would be approximately 0.01 h^{-1}, and be the same for microalgae and bacteria. This suggests that the meiofauna is removing about 1 % of the microbial standing stock per hour. So if on average microbial turnover times are about four days or less, meiofauna grazing would roughly be in equilibrium with microbial production (Montagna, 1995), leading Montagna to the conclusion that meiofauna have a significant impact on sediment microbial processes (e.g. by keeping microbiota in a log phase of growth, hence also strongly influencing rates of heterotrophic breakdown processes).

Blanchard (1991) even suggests meiofauna to be limited by benthic primary production. Considering that, apart from the permanent metazoan meiofauna, Protozoa and temporary meiofauna (mostly larvae from macrofauna) may also be significant consumers of microbiota (Montagna, 1995), one could presumptuously hypothesize that, on a community scale, benthic meiofauna have to balance their energy requirements with organic matter precipitated from the water column. It may be a relevant observation in this respect that in the deep-sea, where no *in situ* benthic primary production (except chemoautotrophic) is to be expected, microalgae-feeding nematode feeding types can be almost equally abundant as in shallow subtidal or even intertidal environments (e.g. Vincx *et al.*, 1994; Thistle *et al.*, 1995).

As an alternative, it could be hypothesized that meiofauna are able to consume dissolved organic matter (DOM). To date, few studies have convincingly shown that meiofauna are capable of taking up DOM under environmentally relevant conditions (Chia *et al.*, 1969; Lopez *et al.*, 1979; Rieman *et al.*, 1990; Montagna, 1984a), but it is generally assumed that meiofauna cannot compete for DOM with bacteria, in view of their much longer turnover times. The benthos is, however, a complex environment, where the binding of DOM to, e.g., EPS (exopolysaccharide secretions) from bacterial, microalgal or meiofaunal origin may facilitate its uptake and utilization by deposit-feeding organisms (Decho, 1990; Decho *et al.*, 1992; Decho *et al.*, 1990).

6. Are meiofaunal grazing rates over- or underestimated?

As a consequence of methodological shortcomings in meiofauna grazing experiments, it can be argued that rates so far obtained have consistently been over- or underestimated. There are arguments on both sides, and it is yet to be established whether they are in balance or tend to either direction.

Possible causes for underestimated grazing rates are function of sample preservation (chemical sample preservation may cause both egestion and defaecation of particles and label leakage, and may for the latter reason also bias background controls

for label adsorption), tracer administration to the sediment (slurries, which have frequently been used, may disrupt patches of microalgae and bacteria, and from our own observations it would appear that nematodes are attracted to and feed more efficiently on patchily rather than homogeneously distributed food), and experimental incubation time (are we measuring ingestion or rather assimilation?).

The latter aspect, however, can also be held as an argument to suggest that grazing rates have so far been overestimated. The key question here is whether or not rates obtained from relatively short incubations can be extrapolated to 24h rates. In an intertidal environment, e.g., it seems plausible that there would be a significant tidal impact on feeding, as meiofauna migrate vertically in the sediment in response to a tidal cycle, and as a significant part of their suspected microalgal food (e.g. epipelic diatoms) is tidally resuspended and therefore only available during ebb tide. In subtidal environments, hydrodynamics and perhaps other abiotic factors may similarly influence feeding activity.

Either way, it is clear that attention has to be focused on improving methodology. A comparison between rates obtained from radioactive and fluorescent tracer trials could yield new insights. At present, the main study suggesting bacterial grazing rates much lower than the above-mentioned range used fluorescently labelled bacteria (Epstein *et al.*, 1992).

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