

Respiration of an Interstitial Ciliate and Benthic Energy Relationships*

Winona B. Vernberg and Bruce C. Coull

Belle W. Baruch Institute for Marine Biology and Coastal Research and Department of Biology,
University of South Carolina, Columbia, S.C. 29208

Received July 11, 1974

Summary. Respiration of the interstitial ciliate *Tracheloraphis* sp. was measured with the Cartesian diver. Ciliate respiration ranged from 2353–7088 $\mu\text{l O}_2/\text{hr/g}$ wet weight, averaging 4477 $\mu\text{l O}_2/\text{hr/g}$ wet weight. These metabolic data on *Tracheloraphis* expand the known size range-metabolic rate differential of the omnipresent meiofauna.

The metabolic-size relationship of meiofauna has been calculated based on data from the literature and this study. Results indicate that these smaller organisms maintain the same proportionality of metabolism to body weight ($b=0.74$) as do larger animals.

When the ciliate data, and published meio- and macrofauna data, are used to estimate the portion each component plays in total benthic metabolism it is apparent that the metabolic role of each can vary significantly. Only when the ratio of macrofauna to ciliate biomass is 90 or more, or when meiofauna/ciliate biomass is 3 or more do the other components play a more important energetic role than do the ciliates.

Within recent years there has been a growing interest in the role of the meiofauna in benthic community metabolism. Some data are available on meiofauna larger than 1 μg (see review of Gerlach, 1971). None, however, are available for the smaller-sized animals despite the fact that some of them, such as the ciliates, often greatly outnumber the metazoan meiofauna. Fenchel (1967), for example, pointed out that ciliates constituted 93% of the total number of meiofauna living in a Danish bay, yet it was not possible to assess the metabolic importance of these forms since —“technical difficulties still prevent obtaining values of respiration for the large number of protozoan species”. Data are presented here on the respiratory rate of one species of marine benthic ciliate, *Tracheloraphis* sp., and results are compared with those obtained for other interstitial fauna. Combining known respiratory data of meio- and macrofauna with our ciliate data, an attempt is made to estimate the contribution of each component to total benthic metabolism.

Materials and Methods

Tracheloraphis sp. were collected in August and September 1973 from subtidal sands in the North Inlet Estuary, Georgetown, South Carolina, when water temperatures were 25–28°C. The sediment was a well sorted ($S_o=1.2$) fine sand (Md 175–200 μ), lying subtidally to an intertidal sand flat approximately 1 Km N-W from the mouth of the North Inlet Estuary at 33° 20.1'N, 79° 10.1'W. Plastic buckets were used as scoops to collect the upper 2–5 cm of sediment, filled to 1/2 their volume, capped and transported to the laboratory in air conditioned vehicles at constant temperature.

* Research supported by NSF Grant GA-35508. Contribution No. 74 from the Belle W. Baruch Institute for Marine Biology and Coastal Research.

In the laboratory ciliates were extracted from the sediment by the sea water ice technique (Uhlig, 1968). Each *Tracheloraphis* was sorted from the other meiofauna by mouth pipette and used experimentally within 24 hrs after collection.

Respiration rates were determined using Cartesian diver respirometers having a total volume of 9–13 μ ls. Due to the small size of the ciliates it was necessary to use 9–11 in each diver. The medium in the diver was filtered 30⁰/₀₀ sea water, a salinity equivalent to that in the field. All determinations were made at 25°C for 4–6 hrs; readings were taken at approximately 90 min intervals. Ciliates were checked at the end of each determination and all were alive; none were used more than once. A total of 12 determinations were made.

Wet weights were calculated from Fenchel's length-weight diagram (Fenchel, 1967; Fig. 5). The length of representative specimens was measured live to ascertain if the North Inlet *Tracheloraphis* population fell within the limits of Fenchel's Danish Specimens. Measurements of 9 specimens indicated that they were within the range reported by Fenchel. Since there were no statistically significant differences in the two sets of data, Fenchel's mean value of 0.34 μ g was used as a wet weight value. [Results are expressed as μ ls O₂/hr/g wet weight.

To determine the metabolic-weight relationship in meiofauna, results of the present study and metabolic studies reported by other authors in Gerlach (1971) were combined after all respiration rates were converted to 20°C using the correction factor in Winberg (1971). Data then were analyzed using the least squares regression analysis package of the SAS programs. The program was run on an IBM 360 computer.

Results and Discussion

The taxonomy of the meiobenthic ciliates has been subject to some confusion. Fenchel (1968) states "it has not been possible to define the apparently numerous species in a satisfactory way" and Dragesco (1963) suggests that the taxonomic confusion is a result of various polymorphic stages. From hours of observation we feel quite certain that our experimental animal is but one species, but the true test of our determination must await a revision of the Trachelocercidae.

The metabolic rate of *Tracheloraphis* sp. averaged 4477 ± 476 μ ls O₂/hr/g wet weight (Table 1). It has long been recognized that generally smaller-sized organisms have higher metabolic rates than larger-sized ones. Data from body size-respiration studies are commonly expressed as a power function of body size. For weight-specific data, the formula is

$$\frac{O_2}{W} = a W^{b-1}$$

where O₂=oxygen consumed per unit time, W=weight of animal, *a* and *b*=coefficients, in which *a* represents the intercept of the *y*-axis and *b* represents the slope of the function in logarithmic plot. Zeuthen (1953) postulated that the metabolism of organisms larger than 40 mg is proportional to 0.75 (*b* value) of the body weight, but in organisms ranging in size from 1 μ g to 40 mg, the *b* value is 0.95. However, Hemmingsen (1960) argued convincingly that the proportionality of metabolism to body size is the same among all organisms whether they are unicellular organisms, plants, poikilothermal or homoiothermal animals, and that this value is approximately 0.75. He considered this proportionality to be adaptive and that it has... "evolved by orthoselection, resulting perhaps from a struggle between proportionality of metabolism to body weight and proportionality to surface functions".

Metabolic data for *Tracheloraphis*, the smallest micro-meiofaunal organism yet measured, expands the known size range—metabolic rate differential for the omnipresent meiofauna. Using this data along with respiratory data (corrected to

Table 1. Oxygen uptake rates of *Tracheloraphis* sp. under thermal-salinity regime of 25° C to 30‰. A mean wet-weight value of 0.34 µg per ciliate was calculated (see text)

Determina- tion no.	Number of ciliates	µl O ₂ /hr g wet weight
1	9	2353
2	9	2941
3	8	2941
4	8	3147
5	8	3375
6	15	3824
7	8	4029
8	8	5529
9	7	5853
10	16	5882
11	9	6764
12	9	7088
		4477 ± 476.2 (S.E.)

20°C) compiled by Gerlach (1971) for meiofauna, the calculated *b* value is 0.74. This value closely approximates Hemmingsen's predicted 0.75, supporting his thesis and the data of Banse *et al.* (1971) and Klekowski *et al.* (1972). Gerlach (1971) also shows a non-calculated plot for the same data (excluding the newly acquired ciliate data) assuming Zeuthen's predicted *b* value of 0.9. Thus his Fig. 1 (p. 182) is misleading.

It is well-known that many factors other than size influence the metabolic rate of an organism, including activity, thermal history, and stage in the life cycle. Earlier we have shown that even within the phylogenetically related Harpacticoida, metabolic rate differs significantly depending on sex and activity of an animals (Coull and Vernberg, 1970). Overall, however (Fig. 1), the meiofauna maintain the same metabolic rate—body size proportionality as do the macrofauna.

Recently much research effort has been directed toward analysis of total benthic metabolism. To estimate energy utilization of the "micro" components, respiration rates of the macrofauna and bacteria are totaled and subtracted from the total community respiration; the remainder of the respiration rate is attributed to micro-meiofaunal components. Without exception these studies conclude that the microfauna and flora account for the majority (>50%) of total benthic oxygen consumption (Wieser and Kanwisher, 1961; Carey, 1967; Pamatmat, 1968; Pamatmat and Banse, 1969; Banse *et al.*, 1971; Smith *et al.*, 1972; Smith *et al.*, 1973). However, there has been considerable speculation and less unanimous agreement about the comparative contributions of the microfaunal (unicellular) and meiofaunal (metazoan) components. Smith *et al.* (1972) concluded that the microfauna were responsible for 60–65% of the total community respiration in a benthic community near Bermuda. Banse *et al.* (1971) attributed the greater fraction of measured community metabolism to organisms smaller than 1 mm, while Pamatmat (1968) attributed from 17 to 54% (depending on season of the

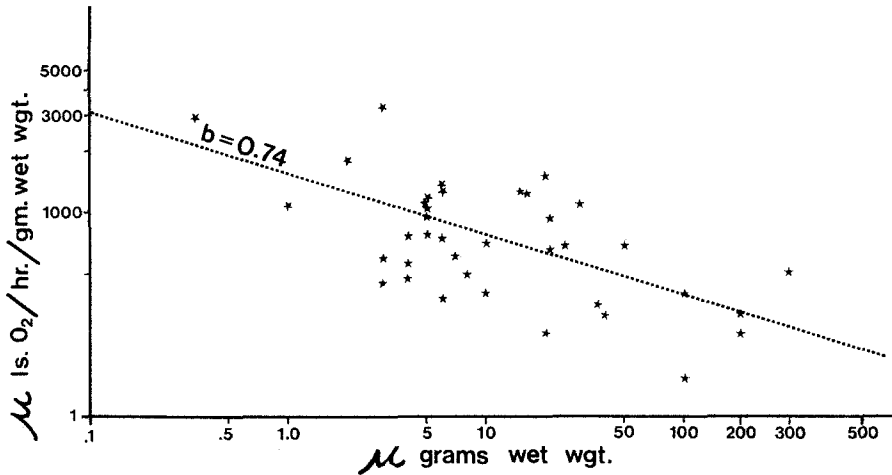


Fig. 1. The relation of metabolism to body weight of some meiofauna and the ciliate *Tracheloraphis* sp. Oxygen uptake rates of the meiofaunal data are from Gerlach (1971). All data were corrected to 20°C using the correction factor of Winberg (1971)

Table 2. Biomass ratios and calculated metabolic rate (arbitrary units) for Fenchel's (1969) stations. The metabolic rate is calculated for ciliates using the *Tracheloraphis* data from this paper, for meiofauna, assuming 1500 μ l s O_2 /g/hr (calculated from Gerlach, 1971) and for macrofauna assuming 49.7 μ l s O_2 /g/hr (calculated from Pamatmat, 1968)

Fenchel's station, depth	Biomass	O_2 consumption (relative units)
Ålsgårde (10 m)		
Ciliates	1	4477
Meiofauna	1.5	2250
Macrofauna	190	9443
Helsingør (intertidal)		
Ciliates	1	4477
Meiofauna	1.6	2400
Macrofauna	3.9	193
Nivå Bay (0-1 m)		
Ciliates	1	4477
Meiofauna	10	15000
Macrofauna	70	8449

year) of total community metabolism to the bacteria, microfauna and meiofauna. Fenchel (1969) suggested that ciliates alone may account for 8 times the metabolism of a sandy beach community when compared with macrofaunal components.

The only study available to date that gives relative numbers and biomass data of ciliates and other component fauna are those of Fenchel (1967, 1968, 1969). Fenchel's 1967 study deals exclusively with meiofauna and microfauna and therefore no comparisons with the macrofauna can be made. However, in his 1969

paper he lists number, biomass, and metabolic rate ratios of macrofauna, meiofauna, and ciliates for 3 Danish localities. Since he simply estimated metabolic rates on a 10-fold increase per unit weight but did base his biomass and numbers ratios on real numbers, we have calculated the metabolic role each component played at his three stations (Ålsgårde, Helsingør Beach and Nivå Bay). Total ciliate respiration was calculated using our *Tracheloraphis* data, and since Fenchel lists ciliates as the base of 1, all ciliate metabolic rates are assumed to be $4477 \mu\text{l O}_2/\text{g/hr}$. Meiofauna respiration was calculated using $1500 \text{ mm}^3 \text{ O}_2/\text{g/hr}$, an average meiofaunal value derived from Gerlach (1971). Macrofaunal respiration was calculated from Pamatmat (1968, Table 24), who gives wet weight values and respiration for several species over several temperature regimes which total 543 mg and $27 \text{ mm}^3 \text{ O}_2/\text{animal/hr}$. Therefore, a mean metabolic rate of $49.7 \text{ mm}^3 \text{ O}_2/\text{g/hr}$ is assumed here. All calculations are based on wet weight biomass. The calculated metabolic rates in arbitrary units (since we were working with ratios not real numbers) for Fenchel's (1969) three stations are presented in Table 2. It becomes apparent that at different stations each benthic component plays a different energetic role depending on the biomass. The argument that the microfauna are most important is not necessarily true. Ciliates will only be the most important metabolic constituents if the macrofauna to ciliate biomass ratio is 90 or less and the meiofauna to ciliate biomass ratio is 3.0 or less. Literature generalizations stating the microfaunal component must be the most important because of the addition and subtraction method of estimating their role may well be misleading. It appears that for each station the relative contribution by each component is highly dependent on its size and population density and therefore at time x any one of the three categories of benthic animals may be energetically the most active.

One factor most energy flow ecologists have overlooked is the probable rate of turnover as related to population growth. Fenchel (1968) lists population parameters for several ciliates, with generation time ranging from 2.5–26.0 hrs and r ranging from 1.4–1000.0 per day. Heip (1972) gives r values of between 0.042–0.144 per day for some meiofauna. Corresponding macrofaunal values would probably be in the range of 0.001–0.05 per day. However, if ciliate reproduction and turnover rates are 1–4 orders of magnitude greater than those of meiofauna and macrofauna, the total amount of energy utilization with time would be much greater among the microfaunal components than with the others. Obviously, total turnover rates must be considered before an accurate assessment of energetic roles of the various components can be made.

Acknowledgments. We most gratefully acknowledge the assistance of Bettye W. Dudley in various phases of this research.

References

- Banse, K., Nichols, F. M., May, D. R.: Oxygen consumption of the seabed III. On the role of the macrofauna at three stations. *Vie et Milieu*, Suppl. 22, 31–52 (1971)
- Carey, A. G.: Energetics of the benthos of Long Island Sound. I. Oxygen utilization of sediment. *Bull. Bingham Oceanolog. Coll.* 19(2), 136–144 (1967)
- Coull, B. C., Vernberg, W. B.: Harpacticoid copepod respiration: *Enhydrosoma propinquum* and *Longipedia helgolandica*. *Mar. Biol.* 5(4), 341–344 (1970)

- Dragesco, J.: Compléments a la connaissance des Ciliés mesopsammiques de Roscoff. 1. Holotriches. Cahiers Biol. Mar. 4, 91-119 (1963)
- Fenchel, T.: The ecology of marine microbenthos. I. The quantitative importance of ciliates as compared with metazoans in various types of sediments. Ophelia 4(2), 121-138 (1967)
- Fenchel, T.: The ecology of marine microbenthos. II. The food of marine benthic ciliates. Ophelia 5(1), 73-122 (1968)
- Fenchel, T.: The ecology of marine microbenthos. IV. Structure and function of the benthic ecosystem, its physical factors and the microfauna communities with special references to the ciliated protozoa. Ophelia 6, 1-182 (1969)
- Gerlach, S. A.: On the importance of marine meiofauna for benthos communities. Oecologia (Berl.) 6, 176-190 (1971)
- Heip, C.: The reproductive potential of copepods in brackish water. Mar. Biol. 12(3), 219-222 (1972)
- Hemmingsen, A. M.: Energy metabolism as related to body size and respiratory surfaces, and its evolution. Rep. Steno. Hosp. (Kbh.) 9(2), 1-110 (1960)
- Klekowski, R. Z., Wasilewska, L., Paplinska, E.: Oxygen consumption by soil inhabiting nematodes. Nematologica 18, 391-403 (1972)
- Pamatmat, M. M.: Ecology and metabolism of a benthic community on an intertidal sand flat. Int. Rev. ges. Hydrobiol. 53(2), 211-298 (1968)
- Pamatmat, M. M., Banse, K.: Oxygen consumption by the seabed. II. *In situ* measurements to a depth of 180 m. Limnol. Oceanogr. 14(2), 250-259 (1969)
- Smith, K. L., Burns, K. A., Teal, J. M.: *In situ* respiration of benthic communities in Castle Harbor, Bermuda. Mar. Biol. 12(3), 196-199 (1972)
- Smith, K. L., Rowe, G. T., Nichols, J. A.: Benthic community respiration near Woods Hole sewage outfall. Est. Coastal Mar. Sci. 1(1), 65-70 (1973)
- Uhlig, G.: Quantitative methods in the study of interstitial fauna. Trans. Amer. micr. Soc. 87(2), 226-232 (1968)
- Wieser, W., Kanwisher, J.: Ecological and physiological studies on marine nematodes from a small salt marsh near Woods Hole, Mass. Limnol. Oceanogr. 6(3), 262-270 (1961)
- Winberg, G. G.: Methods for the estimation of production of aquatic animals, (translation by A. Duncan), 161 pp. London-New York: Academic Press 1971
- Zeuthen, E.: Oxygen uptake as related to body size in organisms. Quart. Rev. Biol. 28, 1-12 (1953)

Dr. Winona B. Vernberg
Belle W. Baruch Institute
for Marine Biology and Coastal Research
University of South Carolina
Columbia, South Carolina 29208, USA