



A handy method for measuring meiobenthic respiration

Tom Moens*, Andy Vierstraete, Sandra Vanhove, Mattias Verbeke,
Magda Vincx

University of Gent, Zoology Institute, Marine Biology Section, K.L. Ledeganckstraat 35, B-9000 Gent,
Belgium

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Abstract

Our current understanding of meiofaunal respiration rates, and especially of the way they are influenced by changing abiotic factors, is still far from complete. Meiofaunal respiration is traditionally measured using Cartesian divers or related manometric techniques, but these are extremely time-consuming and labour-consuming. We have evaluated the use of the Strathkelvin polarographic electrode model 1302 and the O_2 monitor model 781 in determining the O_2 consumption of meiofaunal animals. Respiration rates obtained in this way of the terrestrial nematode *Caenorhabditis elegans* compared well with results obtained from Cartesian diver respirometry. Experiments with 3 estuarine nematode species show that 5% accuracy levels are obtained with respiration rates down to $200 \text{ nl } O_2 \text{ h}^{-1}$. This involves the use of a few tens to a few hundred individuals, depending on the size and the respiratory activity of the animals. Several practical problems that relate to accurate determinations of O_2 consumption are discussed. It is concluded that short-term measurements and fairly easy procedures make polarographic O_2 electrodes an interesting and reliable tool for routine measurements of meiofaunal community respiration and of the influence of abiotic factors on meiofaunal aerobic metabolism.

Keywords: Respiration; Electrode; Method; Meiobenthos; Nematodes

1. Introduction

The role of meiofauna in benthic energy flow processes is still a controversial matter. Calculations of production (e.g. Faubel et al., 1983; Heip et al., 1984; Witte and Zijlstra, 1984) are commonly based on an annual P/B -ratio of 9 (Gerlach, 1971). Warwick and Price (1979) re-evaluated this P/B -ratio using an empirical relationship between

*Corresponding author. Fax: (32) (9) 264-5344.

respiration and production (McNeil and Lawton, 1970), while Vranken and Heip (1986) recalculated annual *P/B* for marine nematodes from data obtained from laboratory experiments. Nematodes are by far the dominant component in marine and estuarine meiobenthic communities, but energy budgets have been established for only four marine species (Tietjen, 1980; Warwick, 1981), and annual production has but been estimated for one (Herman and Vranken, 1988; Vranken et al., 1988). Relatively more data are available on fresh-water nematodes (e.g. Duncan et al., 1974; Marchant and Nicholas, 1974; Schiemer et al., 1980; Schiemer, 1983, 1987; Woombs and Laybourn-Parry, 1985). Thus there remains a wide gap in our knowledge of meiofaunal respiration and energetics, and of the way these are influenced by varying abiotic factors.

The paucity of papers on meiofauna respiration is evidence of the difficulties involved in its study. Nematode respiration has hitherto been measured using Cartesian divers or related techniques (Linderstrom-Lang, 1937, 1943; reviews in Lasserre, 1976; Heip et al., 1985). Although the fairly high sensitivity of this method allows respiration measurements with few (less than 10) individuals, it is less suited for studies on community respiration; moreover, Cartesian diver respirometry is extremely time-consuming and labour-consuming, and it is therefore an unlikely tool for routine use or for respiration studies under a range of abiotic conditions (temperature, salinity, pO_2 , etc.). O_2 electrodes have only rarely been used to study nematode respiration, mainly because of methodological problems (for a discussion of technical problems involved in electrode-based respiration studies of small aquatic invertebrates, see, for example Gnaiger, 1983a). Respiration of large enoplid nematodes has, however, been measured on individual animals (Atkinson and Smith, 1973; Atkinson, 1973a,b). The present study evaluates the use of the Strathkelvin polarographic electrode model 1302 and the oxygen monitor model 781 in determining meiofaunal respiration rates. Results so obtained of experiments on nematode respiration are verified on the basis of previously published data. Finally, the applicability of the described method to other than nematode research is stressed.

2. Materials and methods

2.1. Description of the oxygen monitor and the respiration vials

Essentially, the Strathkelvin respirometer consists of a polarographic Clark-electrode (Clark, 1956), contained in a polystyrene-based coat. The electrode can be inserted into different types of respiration vials. The polypropylene membrane spanning the electrode tip is kept taut by a neoprene 'O'-ring. When it is in measurement position, the membrane forms part of the respiration chamber (Fig. 1). O_2 concentration is displayed on a decimal meter, which is connected to a potentiometric pen recorder for continuous registration of O_2 consumption. The temperature during measurements is regulated by connecting the water mantle of the respiration vial to a thermostatic water bath; a Haake KT 38 was used in our experiments. All presently reported tests were performed at 20°C, unless stated otherwise. This paper discusses the use of the RC 200 and the RC 300 respiration vials, which have respiration chambers with adaptable volumes of 50–180 μ l

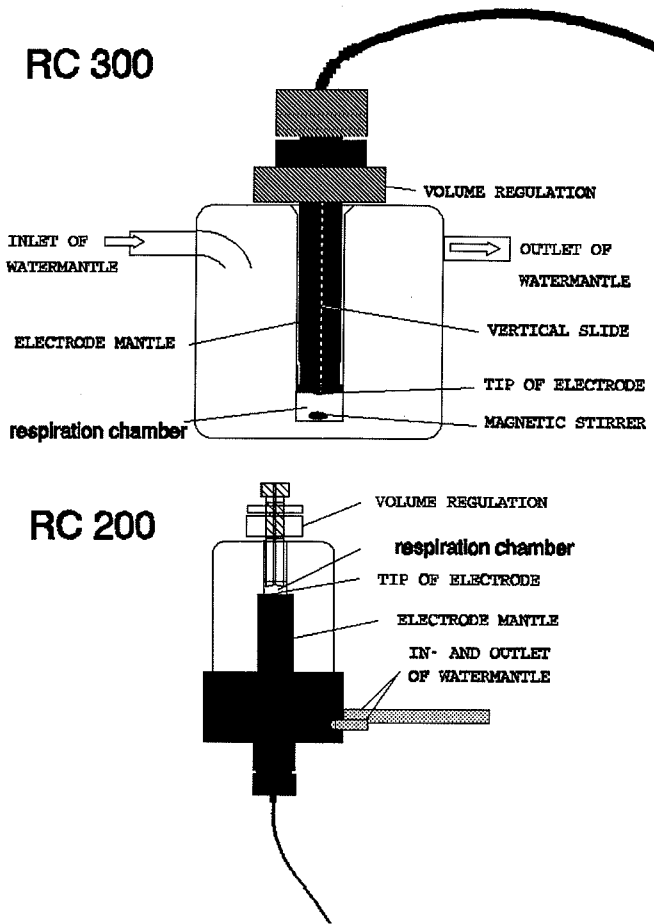


Fig. 1. The RC 300 and the RC 200 respiration vials. The drawings are not to relative size. Both respiration chambers have a diameter of 1.5 cm; the diameter \times height dimensions are 5 \times 5.6 cm and 3.7 \times 7.7 cm for the RC 300 and the RC 200 vials, respectively.

and of 300–1000 μ l, respectively (Fig. 1). The reason for testing both vial types was to check on methodological aspects, such as reproducibility, sensitivity and O_2 consumption of the electrode, etc. in the RC 300, and then to further improve the sensitivity of the procedure—and hence reduce the number of animals needed per experiment—by decreasing the sample volume in the RC 200.

2.2. Calibration of the electrode

Zero O_2 was calibrated in a 3% solution of sodiumsulfide or sodiumdithionite. 100% saturation was determined using presaturated distilled water. The accuracy of the monitor was then tested by comparing O_2 measurements of a set of tap water samples of

different concentrations obtained with the electrode with a parallel series of measurements following the Winkler method (as described in Strickland and Parsons, 1972). These measurements were performed at 15.7°C.

To determine O₂ consumption by the electrode itself, the respiration chamber of the RC 300 vial was filled with 1 ml of a presaturated 1% formaldehyde solution, and O₂ concentration was registered for 2 h. The influence of temperature and salinity on the O₂ consumption by the electrode was assessed in the following way: O₂ consumption of the electrode was measured at 2, 5, 10, 15, 20, 25 and 30°C during 20 min incubations of 600 µl samples of 0.22 µm Millipore-filtered water from the Westerschelde estuary (southwest Netherlands), with a salinity of 20‰. A parallel test was run on a series of 600 µl samples of water of different salinities as prepared from 35‰ of artificial seawater (Dietrich and Kalle, 1957) through the addition of distilled water. Distilled water served as the 0‰ control.

2.3. Experimental procedures

The respiration in different sample volumes and of different nematode species was compared. Measurements were performed with the brackish-water nematodes *Diplo-laimeloides meyli* (Timm, 1966), *Pellioditis marina* (Bastian, 1865) and *Panagrolaimus* (Fuchs, 1930) sp. and with the terrestrial *Caenorhabditis elegans* (Maupas, 1900). Adult sizes of these species are approximately 0.75–1.25, 1.4–2.4, 0.6–1.2, and 1.15–1.75 mm, respectively. The latter species was cultured either monoxenically on *E. coli* or axenically (Vanfleteren et al., 1990). The other species were cultured on agar plates, consisting of a mixture of bacteriological and nutrient agar in a 4/1 or a 10/1 ratio, synxenically with unidentified bacteria from the natural habitat as a food source.

For all experiments described, nematodes were harvested from the stock cultures, either by washing them from the agar surface with small volumes of sterile water, or, if only low numbers were required, by hand-sorting. Nematodes were aseptically washed prior to measurements, and antibiotics were added to the sample medium in order to block microbial development. Applicability of different aseptic washing techniques was compared by determining the antibiotic efficiency and the recovery rate of nematodes (defined as the actual number of nematodes that were still present and alive after treatment). Antibiotic efficiency was qualitatively assessed by plating 10 µl subsamples on nutrient-enriched agar plates, and observing bacterial growth after 3, 5, and 10 days of incubation at 22°C in the dark. Aseptic washing techniques were modified after Koenning and Barker (1985); washing with sterile habitat water, or through serial changes of antibiotic solutions (basically 10 mg/ml streptomycin and 10 000–20 000 units/ml penicillin), and preincubation with the same antibiotics, were performed. After treatment, nematodes were collected by centrifugation (5 min, 3000 rpm). *C. elegans* was freed from contaminants by washing with sucrose (Sulston and Brenner, 1974).

All measurements with nematodes were accompanied by blanks, in which the O₂ consumption of the 0.22 µm Millipore-filtered sample medium was determined. All results presented below have been corrected for this 'background-respiration'. 100% saturation was calibrated whenever the temperature or the sample medium was changed.

The reproducibility of the respiration measurements was determined using bacteria

(unidentified species) or nematodes (*C. elegans*). Stocks were adequately mixed to ensure subsample homogeneity. A magnetic stirrer was added in all of the following experiments with the RC 300 vial to ensure optimal O₂ diffusion. The reproducibility of the measurements as a function of the sample volume (1000, 600 and 500 µl in the RC 300; 150, 100 and 50 µl in the RC 200) was also determined with bacteria and nematodes (*C. elegans*). Both respiration vials were compared on the basis of measurements of O₂ consumption of *C. elegans*.

The respiration of a dense sample of monoxenically cultured *C. elegans* was compared with that of subsamples of declining nematode numbers. The respiration rates of monoxenically cultured and axenically cultured *C. elegans* were compared with values from the literature to independently assess the accuracy of our measurements. To determine the minimum number of nematodes necessary for reproducible measurements of O₂ consumption, small numbers (in between 20 and 500) were hand-picked from laboratory cultures, aseptically washed and the respiration measured and calculated per individual, following the equation:

$$R = \frac{(a - b) \cdot v \cdot 60}{1000 \cdot t \cdot n}$$

with:

<i>a</i> and <i>b</i>	the oxygen concentration at the beginning and at the end of a measurement, respectively
<i>v</i>	sample volume (ml)
<i>t</i>	time in minutes (we usually measured for 20–40 min)
<i>n</i>	number of individuals
<i>R</i>	respiration rate in mg O ₂ ind ⁻¹ h ⁻¹

or, if respiration was measured as a percentage of the O₂ used from the initial concentration:

$$R = \frac{x \cdot v \cdot z \cdot 60}{1000 \cdot y \cdot t \cdot n}$$

with:

<i>x</i>	difference in oxygen concentration between the beginning and the end of a measurement
<i>z</i>	maximal concentration of oxygen dissolved in the sample medium at the temperature of measurement
<i>y</i>	% of oxygen at the beginning of the experiment

3. Results

3.1. Calibration of the electrode

The measurements of the O₂ concentration with the Strathkelvin monitor and according to the Winkler method, respectively, differed from 0.18 to 0.20 mg O₂ l⁻¹

Table 1

Comparison of O₂ measurements with the Strathkelvin 1302 electrode and the Winkler method

Electrode measurement	Winkler measurement
9.92	9.73
9.92	9.74
8.24	8.05
7.00	6.80
5.56	5.38
4.48	4.29

Experiments were performed at 15.7°C.

(Table 1). The observed discrepancy can be accounted for by a small calibration error of the 100% saturation value, which was due to a loss of O₂ from the saturated sample upon transfer to the respirometer. As a consequence, the 100% sample was only 97.5% saturated. The sensor output is linear with O₂ concentration, and so the discrepancy with the Winkler method is fairly constant over the entire concentration scale (Table 1). Hence, calculations of O₂ consumption, which use the difference between O₂ content at the beginning and at the end of a measurement, are not affected.

O₂ consumption by electrodes depends on the cathode surface area and on the O₂ partial pressure of the buffer (Haller et al., 1994). O₂ consumption by the Strathkelvin electrode ranged from 0 to 1% (mostly from 0.2 to 0.6%) of a saturated water sample over a 20 min. period at 20°C; this percentage did not differ between water samples of different salinity, so O₂ consumption was indeed proportional to O₂ partial pressure. Equally, O₂ consumption by the electrode, expressed as a percent of O₂ used, should not be influenced by temperature. At a room temperature of about 21°C, this was true for sample temperatures from 15 to 25°C. At 2–10°C and at 30°C, however, we found, in terms of percentage, a higher (1 to 2%) and lower (0 to –0.6%) consumption, respectively. This was overcome by using longer equilibration times at the more extreme temperatures; this problem is probably due to the signal being transferred between the highly different temperatures of the sample/electrode and the monitor.

Next to O₂ consumption by the electrode, O₂ diffusion into the respiration chamber via the vertical slit in the electrode jacket is a potential problem in respiration measurements (Hinkle and Yu, 1979; Haller et al., 1994). This rate of O₂ diffusion is proportional to the pO₂ gradient between the respiration chamber and the surrounding air. Haller et al. (1994) found the diffusion rate in their setup to be typically in between +1 and +3 pmol O₂ s⁻¹, far less than values reported for several other respirometers. In their study, the gateway for O₂ diffusion from outside was an injection cannula of 100 mm length and 1.2 mm diameter, which compares well with a slit of 65 mm length but only 1 mm diameter in the protective coat of the Strathkelvin electrode. At low sample pO₂, however, this aspect deserves closer attention.

3.2. Experiments

Table 2 presents data on the recovery rate and the antibiotic efficiency of four aseptic treatments. Aseptic washing was most efficient through serial changes of antibiotics.

Table 2

The applicability of different aseptic washing techniques for experimental nematodes

Treatment	% nematodes recovered after treatment \pm SD		Infected spots (x/15 inocula)
	A (without agar)	B (with agar)	
a	53.74 \pm 4.78	81.69 \pm 2.62	13
b	45.93 \pm 5.31	73.82 \pm 2.87	2
c	44.27 \pm 2.62	77.95 \pm 3.40	3
d	32.97 \pm 3.68	69.12 \pm 4.64	0

Treatments: (a) rinsing with sterile habitat water; (b and c) overnight preincubation at 22 and 6°C, respectively; (d) washing through serial changes of an antibiotic solution. Nematodes were harvested after treatment by centrifugation. More than 98% of the recovered nematodes were alive, without significant differences between treatments. A and B refer to treatment without and with addition of 0.1% agar, respectively. Both series (A and B) are averages of 3 replicate treatments. The number of infected spots was determined after a 5-day incubation.

Loss of nematodes from the samples during centrifugation was strongly reduced through addition of a small volume of 0.1% agar. This improved pellet formation during centrifugation but did not interfere with antibiotic efficiency. For most respiration measurements, however, a simple preincubation with antibiotics will sufficiently reduce bacterial contamination, even at treatments as short as 1 h. The combination of antibiotics did not significantly affect the respiration rates of the four nematode species used in our experiments. However, if toxicity of the antibiotics is a problem, transferring the experimental animals through a sterile medium will also strongly reduce the number of microbial contaminants, except when there is a prominent microbial epiflora coating the body surface of the animals.

Determinations of bacterial or nematode respiration using the RC 300 were not significantly influenced by the sample volume (500, 600 or 1000 μ l; $P >> 0.05$, post hoc test). Measurements with bacteria gave low variances as percentages of the mean (Fig. 2). Values obtained with dense nematode samples, however, were extremely variable during early experiments. This could be attributed to inefficient O₂ diffusion upon use of the small stirrer provided with the RC 300 vial. A second set of measurements with a rectangular magnetic stirrer (0.8 \times 0.3 \times 0.2 cm), gave highly reproducible results (Fig. 2). Survival of the nematodes was checked after a series of measurements using three different types of stirrer at different stirring speeds (10–200 rpm). Only occasional mortality (usually less than 1%) of nematodes was observed upon use of the above-mentioned rectangular stirrer at a speed of up to 30 rpm; occasional increases in mortality during measurements were due to 'irregular' stirring, either at too high a speed or with contact between the stirrer and the vial wall, causing physical damage to the nematodes (see also Marks and Sørensen, 1971). Larger stirrers at a speed of well above 60 rpm caused highly variable mortality rates, sometimes exceeding 50%.

Measurements of O₂ consumption by homogeneous bacterial samples, using the RC 200 vial, were highly reproducible. Values obtained with dense nematode cultures, however, showed large variation. Furthermore, respiration was significantly influenced by the sample volume (50, 100 and 150 μ l; $P < 0.005$, post hoc test). The high variance

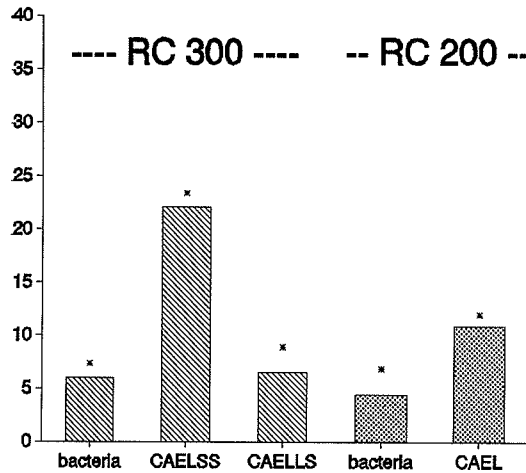


Fig. 2. The variance levels of the respiration measurements with bacterial and nematode samples, using the RC 300 and RC 200 vials. The average variance and the STD are shown for 3 series of 3 replicate measurements each. CAEL, CAELSS and CAELLS represent data on the nematode *C. elegans*, without stirring, with a small stirrer and with a larger stirrer, respectively.

on measurements with the RC 200 can be accounted for by the position of the electrode, which is at the bottom of the RC 200. Nematodes will precipitate during measurements and cover the electrode, thus causing local O_2 depletion. This explanation was verified by changing the position of the respiration vial during measurements (Fig. 3). Although reproducibility of the measurements was greatly enhanced by altering the position of the

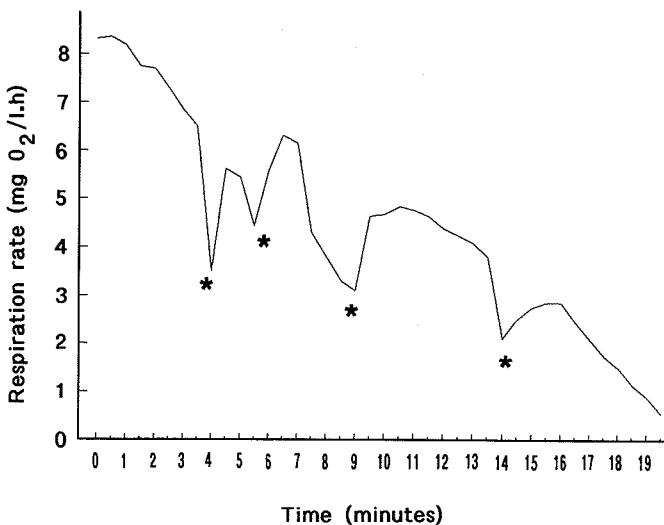


Fig. 3. The respiration profile as a function of the vial position. The measurements were taken with the RC 200 vial. * marks changes caused by an 80° rotation of the vial.

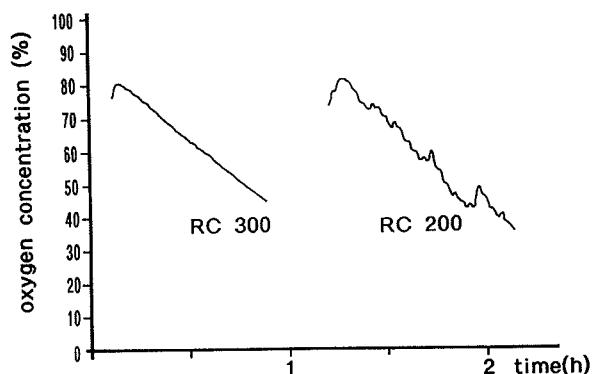


Fig. 4. The respiration profiles obtained for a single nematode sample with the RC 300 (left) and the RC 200 (right), respectively.

vial, the respiration pattern obtained with the RC 200 was usually more irregular and deviant from a linear slope than that obtained when using the RC 300 (Fig. 4). We compared data sets on nematode respiration obtained using the RC 200 and RC 300, and found that respiration rates obtained with the RC 300 were, on average, significantly higher ($P < 0.05$, post hoc test). A likely explanation for this phenomenon is the absence of stirring in the RC 200; movement of the nematodes does not suffice for an adequate O_2 diffusion. It is possible to provide a stirring facility in the RC 200, by positioning the vial top-down over a magnetic plate. However, even then, respiration rates determined with the RC 200 were dependent upon the sample volume, and the recorder signal remained much more irregular than when the RC 300 was used. As a consequence, all subsequently reported measurements were performed using the RC 300 respiration vial.

Fig. 5 shows an inverse linear relationship between the number of nematodes (*C. elegans*) in a sample and the sample respiration. The minimum numbers necessary for accurate and highly reproducible measurements differed from species to species (Fig. 6), primarily as a consequence of the species-specific respiratory activity, but also in relation to the physiological homogeneity of animals within one sample. The relatively large variation in *P. marina* respiration rates, even at higher numbers of experimental animals, is probably due to the fact that *P. marina* from our cultures reproduces partly ovoviviparously; the presence or the absence of a few juvenile-containing females (there may be tens of juveniles in a gravid female) may cause significant differences in respiration between subsamples.

Data from our experiments and from Cartesian diver respirometry were highly comparable (Table 3). Moreover, the respiration of axenic *C. elegans* as determined in our experiments was 63% of that of monoxenic nematodes, which corresponds well with an activity ratio of 5:3 for monoxenic to axenic *C. elegans* (Johnson, 1985).

4. Discussion

Respiration measurements with polarographic electrodes face bias mainly in two

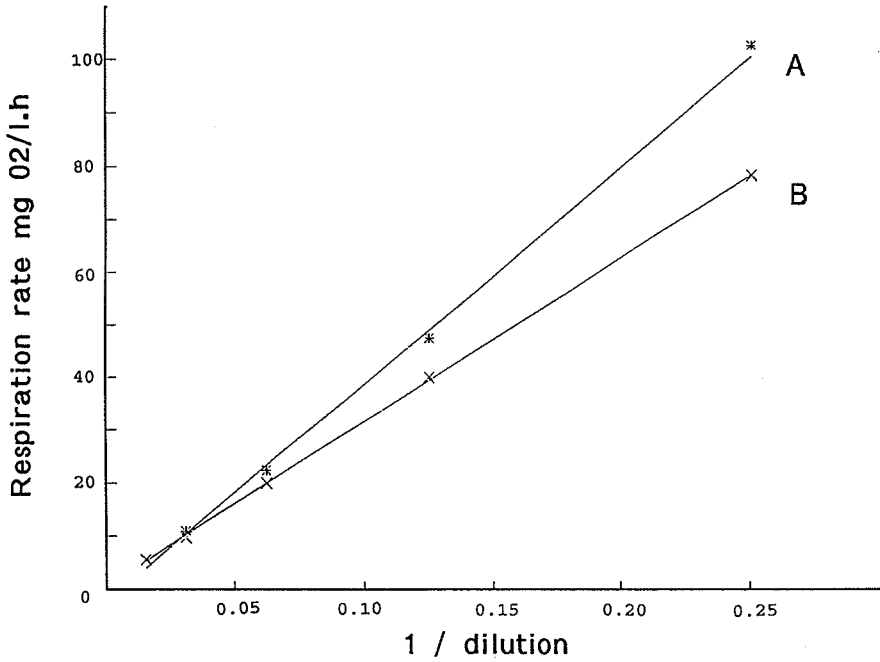


Fig. 5. The respiration as a function of the nematode numbers. A and B represent samples with adults only and a mixture of adults and J4-juveniles, respectively.

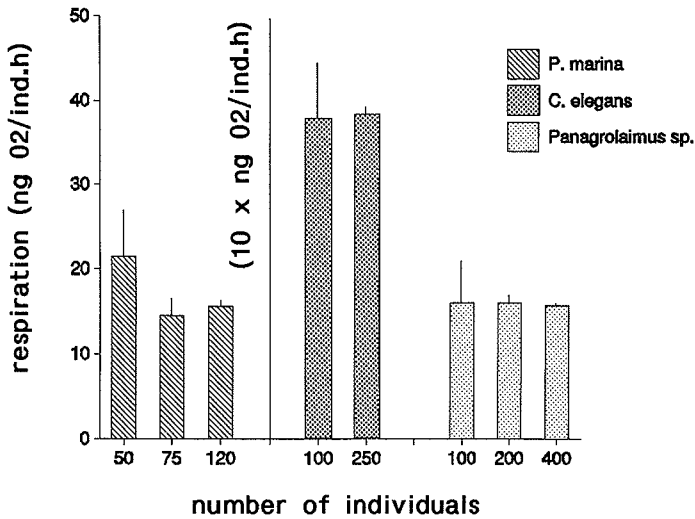


Fig. 6. The respiration as a function of the nematode numbers in 3 species of rhabditid nematodes. The average and the maximum of 2 replicate values are shown.

Table 3

Respiration of axenically and monoxenically cultured *C. elegans*: comparison between data from electrode measurements (our experiments) and from Cartesian diver respirometry

Culture	Age	Respiration (ng oxygen/h per ind)	
		Electrode	Cartesian Diver
monoxenic	adult	5.74±0.56	5.64±0.69 ^a
axenic	adult	3.65±0.35	3.39±0.41 ^b
axenic	J4/adult	2.35±0.33	2.30±0.32 ^b

Shown are data±SD.

^a The value for monoxenic respiration was calculated from De Cuyper and Vanfleteren (1982), taking into account the ratio of respiration of monoxenically to axenically cultured *C. elegans*, as proposed by Johnson (1985). The second axenic value was calculated, assuming a 50/50 ratio of J4 to adults. Our measurements were performed with 250 nematodes per replica.

^b Data from De Cuyper and Vanfleteren (1982).

ways: through O₂ consumption by the electrode and through O₂ diffusion into the respiration chamber. O₂ consumption by the Strathkelvin electrode is proportional to O₂ concentration, and averages about 0.5% of full scale in 20 min, with a range from 0–1%. O₂ diffusion into the respiration chamber is probably negligible for most applications proposed in this paper. However, at low pO₂ this aspect should be carefully considered.

The Strathkelvin respirometer provides conditions ideally suited for measurements of respiration under varying environmental parameters, such as temperature, salinity and O₂ tension.

The sensitivity of the presently described method can be determined using data shown for *Panagrolaimus* sp. (Fig. 6). A 5% accuracy level can be reached with O₂ consumption rates down to 200 nl O₂ h⁻¹. This matches the conclusions of Holter and Zeuthen (1966) that a consumption of 100 nl h⁻¹ is a minimum value for reaching this accuracy level. This inevitably puts some constraints on measurements with smaller juveniles or species, since a high number of individuals is then still needed for sufficiently accurate experiments. The lower limit for detection of O₂ consumption may in part be set by the ability of the materials in contact with the sample to absorb and release small volumes of O₂ (Atkinson and Smith, 1973; Haller et al., 1994). As such, using Viton instead of neoprene in the 'O'-ring may further improve the sensitivity of the presently described equipment.

Clearly, the amount of O₂ consumed is not the only parameter influencing variance. Physiological status (similar body volume, age, sex, etc.) will importantly influence the minimum number of individuals necessary for adequately reproducible measurements. Prolonging the duration of the measurements may further reduce nematode numbers needed, but we prefer short experimental incubation times, since longer measurements are likely to increase stress to the animals. Furthermore, when working in closed respiration chambers, prolonged measurements imply intrapolation of respiration rate over a timescale during which incubation conditions (e.g., O₂ tension) may significantly change (Gnaiger, 1983b; Moens et al., unpublished data).

The relevance of the respiration rates obtained under laboratory circumstances may be questioned in view of the stress conditions resulting from differences with the in situ

conditions of the animals. Overestimations or underestimations could be a consequence of metabolic adaptations to experimental stress, i.e., stirring and floating of benthic animals in water, without contact with a substrate. However, any mechanical damage caused by stirring can simply be assessed by determining mortality after measurements. An important influence of stirring is unlikely in view of the very similar respiration rates obtained with Cartesian diver respirometry (no stirring) and with the presently described procedure. Furthermore, our observations show that nematodes may change their behaviour in reaction to floating, either by remaining quite immobile (e.g., *Viscosia*, *Daptonema*), or in contrast by increased activity (vigorous body shaking or active swimming, the latter behaviour especially in monhysterids). The impact of motility rather than metabolic activity on experimentally obtained respiration rates still remains uncertain. However, experiments with a non-motile mutant of the terrestrial *C. elegans* indicate that metabolism largely dominates motility in respiration (J. Vanfleteren, personal communication), and even extreme movement would probably cause less than a doubling of O_2 consumption. This is further supported by studies cited in Schiemer (1987).

At present, experiments are in progress to determine the degree to which several meiobenthic representatives, and in particular dominant nematode genera, partake in total sediment respiration. From the results presented in this paper, it is clear that the respiratory activity of at least the dominant nematode genera can be derived from determinations of numbers and biomass on the one hand, and from laboratory measurements of respiration with batches of animals, collected from sediment samples, on the other. If sufficient numbers, i.e., from some tens to a few hundred, in contrast with the “as few as 5000 individuals” (for nematodes, Marks and Sørensen, 1971) — are available, similar experiments can be performed with other representatives of the meiobenthos, like harpacticoid copepods and oligochaetes. Preliminary experiments on harpacticoids and individual amphipods, as well as many previous reports of electrode measurements of respiration in a variety of small invertebrate organisms, indicate the present and the related electrode-based methods to be applicable in much wider a field than nematology. The aim of this paper, therefore, is not to hint at any superiority of the presently used equipment over similar devices from other companies, but rather to enhance the use of O_2 electrodes in unravelling meiobenthic respiration rates.

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Life Strategies in Two Bacterivorous Marine Nematodes: Preliminary Results

TOM MOENS, ANDY VIERSTRAETE & MAGDA VINCX

University of Gent, Zoology Institute, Marine Biology Section, K. L. Ledeganckstraat 35, B-9000 Gent, Belgium.

With 8 figures and 1 table

Key words: Nematodes, feeding, respiration, life strategies.

Abstract. Temperature dependence of sex ratio and maximal densities of the estuarine, deposit-feeding nematodes *Pellioiditis marina* (Rhabditiidae) and *Diplolaimelloides meyli* (Monhysteridae) were investigated *in vitro*. Both species are characteristic for organically enriched habitats. Data from competition culture experiments with both species are integrated with information from respiration measurements at different temperatures, and from observations on the influence of temperature and bacterial density on uptake rates.

Sex ratio was significantly influenced by temperature in both species, with the highest relative numbers of males at the highest temperatures. Total numbers attained fluctuated only moderately in the 10 to 20 °C interval, but increased and decreased highly significantly at 25 °C for *D. meyli* and *P. marina*, respectively.

Respiration at temperatures from 5 °C to 30 °C was measured with nematodes from monospecific cultures using a modified Clark electrode procedure. Respiration was dependent upon temperature in the entire range for *P. marina*, but not for *D. meyli*, where only at 25 °C a clear respiratory acceleration was observed.

Feeding experiments with *P. marina* showed a dominant influence of bacterial density on uptake rates, with a lower but still significant temperature effect.

These data are discussed in relation to the overall life strategies of both species.

Problem

Several studies have suggested a role for nematodes in the mineralization of organic matter and nutrient turnover (review in SCHIEMER, 1987; recent data in FINDLAY & TENORE, 1982; RIEPER-KIRCHNER, 1989; TIETJEN & ALONGI, 1990; ALKEMADE *et al.*, 1992 a, b). It is generally believed that nematodes exert their influence through stimulation of bacterial growth by one or a combination of the following processes: (a) direct grazing, whereby bacterial populations could be kept in a prolonged log phase of growth, (b) increasing available surface for microbial degradation processes through mucus secretion (RIEMANN & SCHRAGE, 1978) and/or tube building (NEHRING *et al.*, 1990; NEHRING, 1991), and (c) increasing O₂-diffusion by bioturbation (CULLEN, 1973; ALKEMADE *et al.*, 1992 b).

Pellioiditis marina (BASTIAN, 1865) ANDRASSY, 1983 and *Diplolaimelloides meyli* TIMM, 1966 are brackish-water nematodes characteristic for organically enriched habitats. Both species are generally considered to be deposit feeders and to