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Authors: Kim, Dongsung, and Shirayama, Yoshihisa

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Respiration Rates of Free-Living Marine Nematodes in the Subtidal Coarse-Sand Habitat of Otsuchi Bay, Northeastern Honshu, Japan

Dongsung Kim¹ and Yoshihisa Shirayama^{2*}

¹Marine Biology Division, Korea Ocean Research & Development Institute, Ansan P. O. Box 29, Seoul 425-600, Korea,

²Seto Marine Biological Laboratory, Graduate School of Science, Kyoto University, Shirahama-cho, Wakayama Prefecture 649-2211, Japan

ABSTRACT—Respiration rates of six free-living nematode species dominant in the subtidal coarse-sand habitat of Otsuchi Bay, Northeastern Honshu, Japan, were measured discriminating sex and adult or juvenile. To measure the respiration rate, each nematode was put in a temperature-controlled microchamber of 45 μ l in volume, and the dissolved oxygen concentration of the seawater was monitored for more than 3 hrs. Measurements were done at 5, 10, 15, and 20°C, covering the yearly temperature range of the habitat. Metabolic intensities (*M.I.*) of these species at 20°C were within the range of values previously reported for other nematode species. Juveniles of *Mesacanthion* sp. had the highest *M.I.* among the species measured, reflecting the carnivorous nature of the species. For *Polygastrophora* sp., *Mesacanthion* sp., *Metachromadora* sp. and *Monoposthia* sp., *M.I.* decreased at lower temperature, and the Q_{10} value was close to 2. On the other hand, *M.I.* values of *Symplocostoma* sp. and *Theristus* sp. were independent of the change of temperature and the Q_{10} value was close to 1. For *Symplocostoma* sp., *Polygastrophora* sp. and *Mesacanthion* sp., *M.I.* of male was higher than that of female. Males of all these species were rare and may need to be more active than females, to copulate with many females.

INTRODUCTION

Meiofauna is an important component of the marine benthic ecosystem, especially from the view point of energetics because smaller organisms are more active than larger ones at per biomass basis (Gerlach, 1971). Among meiofauna, nematodes are almost always the most dominant group of Metazoa, usually occupying more than 80% of total meiofauna (Heip *et al.*, 1985). They thus can be considered to play a key role in the energy flow through the meiofauna.

Since 1992, we have been studying ecology of meiofauna in very coarse sediment in the subtidal area of Otsuchi Bay, Northeastern Honshu, Japan (Kim and Shirayama, 1996). In this habitat, harpacticoid copepods exceptionally predominated over nematodes, though the nematodes were also abundant, and its biomass reaches to 0.49 g m⁻² in summer (Kim and Shirayama, 1996). The present nematode assemblage is simple in the structure as characterized by low species diversity (37 species) and a few dominant species in each season. These characteristics have made it possible to estimate the energy budget of nematodes in the habitat on the community level by summing up the figures of the dominant species. In the present study, we measured respiration rates as a repre-

sentative of the energy consumption for the dominant species and examine the metabolic activity of the nematode assemblage in the subtidal coarse-sand habitat.

MATERIALS AND METHODS

Nematodes were collected from subtidal zone at a depth of 4 m in Otsuchi Bay (Fig. 1). The sediment was sampled using a Smith-McIntyre grab sampler, and sent to the laboratory in Tokyo keeping the temperature cool. In the laboratory, the sediment was kept at the ambient temperature, and illuminated to enhance the growth of benthic algae, which are considered as the main food source for most nematodes of the area.

To measure the respiration rate of nematodes, individuals were kept in a microchamber with a room of 45 μ l in volume. The seawater aerated well in advance was placed in the chamber and the oxygen concentration of the seawater was monitored for more than 3 hr using an oxygen microelectrode (Model 1302, Strathkelvin Instruments) placed at the bottom of the chamber. The temperature of the seawater in the chamber was kept constant by shielding the chamber with running water. The temperature fluctuation of the running water was controlled using Coolnics (CTE-22A) with the precision less than 0.1°C. Such a precise control was necessary because the oxygen electrode is sensitive to the change of temperature.

Six species of nematodes dominant in the subtidal sediment in Otsuchi Bay (Kim and Shirayama, 1996) were used for measurement of respiration rates. *Symplocostoma* sp., *Polygastrophora* sp. and *Mesacanthion* sp. were large and active enough to measure their respiration individually. However, *Metachromadora* sp., *Theristus* sp. and

* Corresponding author: Tel. 0739-42-3515;
FAX. 0739-42-4518.

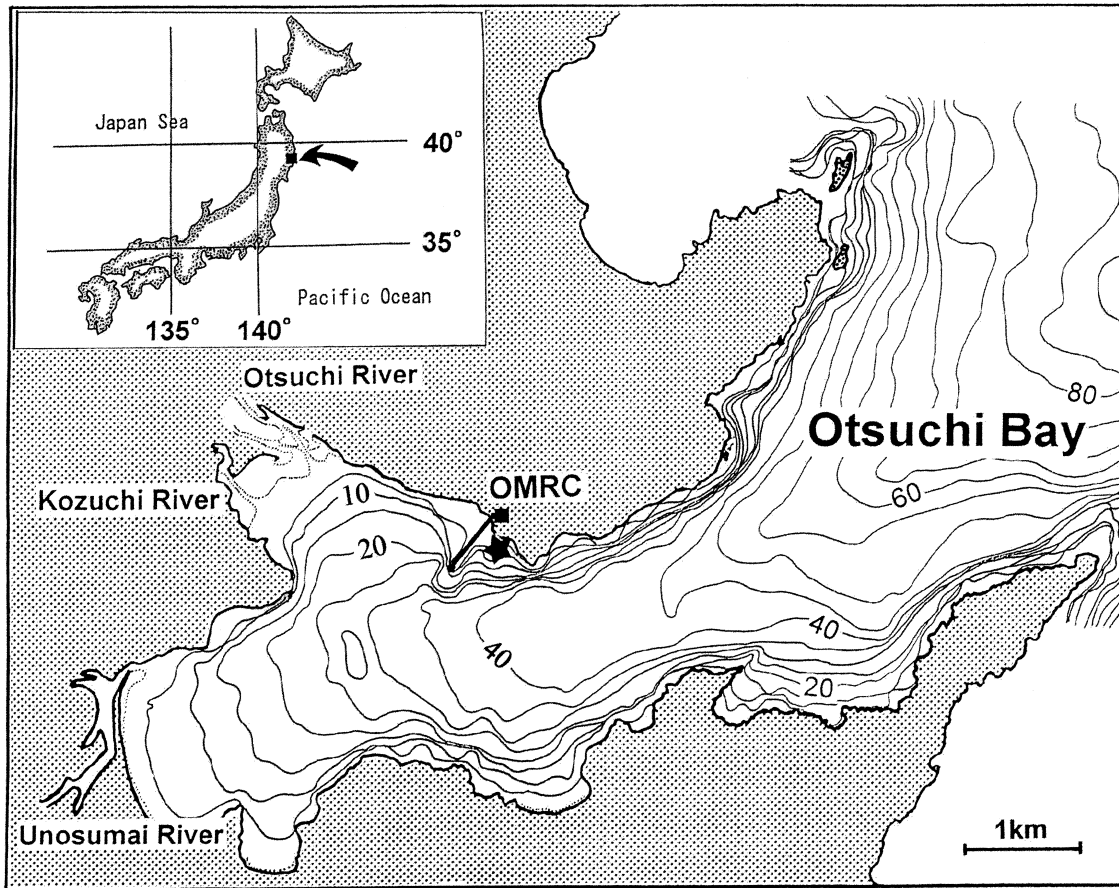


Fig. 1. Location of the study site in Otsuchi Bay, northeastern of Honshu, Japan. (○ sampling site; OMRC, Otsuchi Marine Research Center)

Monoposthia sp. were too small in body size to measure their respiration individually. Respiration rates of these species were determined by applying 5, 5 and 30 individuals into the chamber, respectively.

Dependency of metabolic activity on the ambient temperature is well known for poikilothermal organisms (Price and Warwick, 1980). The temperature in Otsuchi Bay fluctuates from 6.1 to 20.4°C. To figure out annual nematode community respiration, it is necessary to estimate respiration at the temperature of each season. For this purpose, we measured respiration rate of nematodes at 5, 10, 15, and 20°C to cover the range of temperature fluctuation in Otsuchi Bay.

Sex ratios of three species, *Mesacanthion* sp., *Symplocostoma* sp., and *Polygastrophora* sp., dominant in the study site are extremely biased to female, and males are rare (Kim, 1996). In addition, the latter two species show distinct sexual dimorphism, namely the stoma of male is small whereas those of female or juvenile are armed with strong dorsal and subventral teeth. We thus measured respiration rate of these species discriminating male, female and juvenile because such unusual population structure or morphological characteristics may reflect differences in metabolic activities.

After the measurement of respiration rates, nematodes were fixed with 5% formalin in seawater, transferred into anhydrous glycerol, and their body volume was measured after the method of Warwick and Price (1979).

To compare the metabolic activities interspecifically, respiration rates were analyzed by standardizing the individual body size as reviewed in Heip *et al.* (1985) and applying the metabolic intensity (*M.I.*) as follows:

$$\log R = M.I. + 0.75 \log V \quad (1)$$

where *R* is respiration rate ($\text{nIO}_2 \text{ h}^{-1}$) per individual, and *V* body volume (nl). The equation (1) gives the *M.I.* as the estimated *R* at *V* = 1.

RESULTS

The respiration rates per individual increased with body volume and the inclination of the regression line between them was not different significantly from 0.75; e.g., 0.72 for *Mesacanthion* sp. (Fig. 2). This result confirmed that the equa-

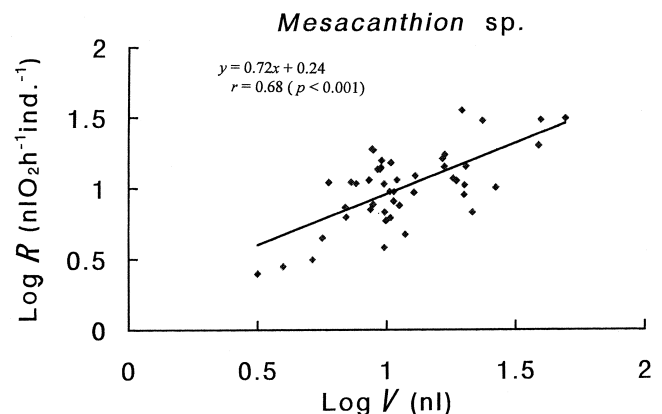


Fig. 2. The relationships between the body volume and respiration rates for *Mesacanthion* sp.

Table 1. Metabolic intensity (*M.I.*) measured at 20°C and *Q*₁₀ values of six dominant nematode species in Otsuchi Bay. M, male; F, female; J, juvenile.

Species		<i>M.I.</i>	<i>Q</i> ₁₀
<i>Symplocostoma</i> sp.	M	0.090	1.08
	F	0.115	1.07
	J	0.172	1.03
<i>Polygastrophora</i> sp.	M	0.414	2.45
	F	0.243	1.53
	J	0.145	1.93
<i>Mesacanthion</i> sp.	M	0.329	1.64
	F	0.177	1.56
	J	0.762	2.34
<i>Metachromadora</i> sp.		0.043	1.87
<i>Monoposthia</i> sp.		0.175	1.88
<i>Theristus</i> sp.		0.062	0.99

tion (1) was applicable to estimate *M.I.* for the nematodes in the present study.

Table 1 shows respiration rates (*M.I.*) measured at 20°C and *Q*₁₀ values for six major nematode species in Otsuchi Bay. Within species that we could measure their *M.I.* discriminating males, females and juveniles, *M.I.* value was the highest for juveniles of *Mesacanthion* sp. (0.762), and the lowest for males of *Symplocostoma* sp. (0.090). The *M.I.* values of *Methchromadora* sp. (0.043) and *Theristus* sp. (0.062) were even lower, though these values were obtained using 5 and 30 individuals collectively. Respiration rates of *Polygastrophora* sp., *Mesacanthion* sp., *Metachromadora* sp. and *Monoposthia* sp. increased significantly with temperature (Fig. 3). On the other hand, *M.I.* of *Symplocostoma* sp. and *Theristus* sp. remained constant regardless of temperature (Fig. 4). Reflecting such difference, *Q*₁₀ values of *Symplocostoma* sp. and *Theristus* sp. were close to 1, whereas these of the remaining four species to 2.

Due to the difference in dependency on temperature, *M.I.* of *Symplocostoma* sp. and *Theristus* sp. were significantly higher than the rest four species at the lowest temperature (5°C; Table 2). At modest temperatures (10 and 15°C),

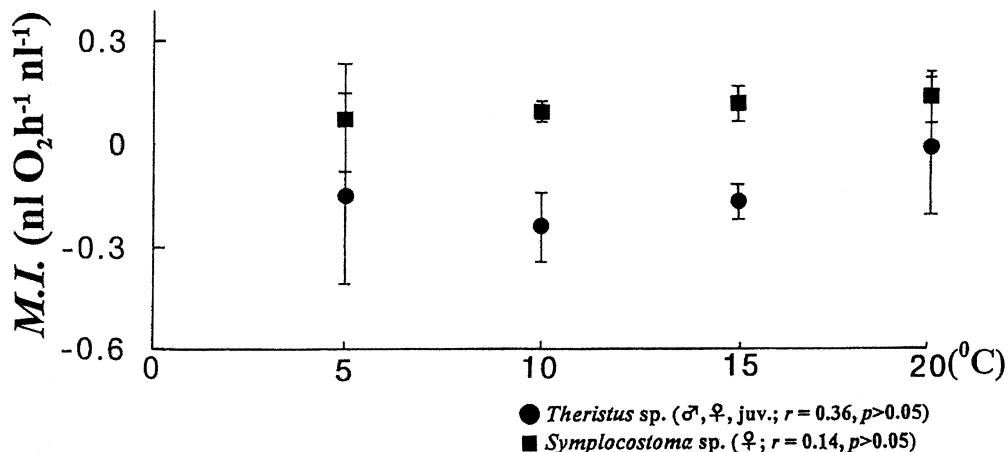


Fig. 4. The relationships between metabolic intensity and temperature for *Symplocostoma* sp., and *Theristus* sp. The *M.I.* of these species are constant regardless of the change of temperature.

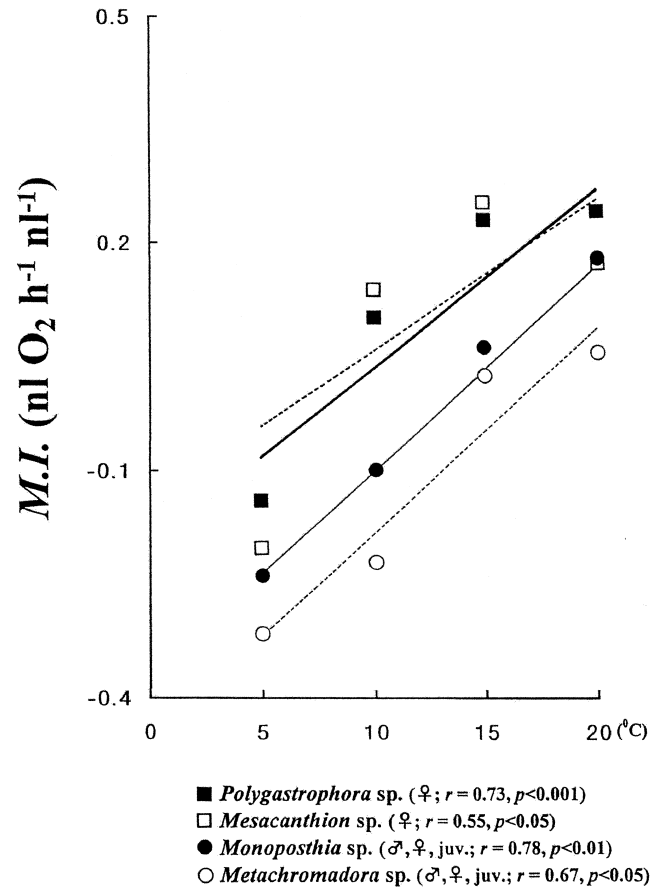


Fig. 3. The relationship between metabolic intensity and temperature for *Polygastrophora* sp., *Mesacanthion* sp., *Monoposthia* sp. and *Metachromadora* sp. The *M.I.* of these four species significantly increased with temperature.

interspecific differences were not significant in any combination. At the highest temperature studied (20°C), *M.I.* of *Symplocostoma* sp. was significantly lower than that of *Monoposthia* sp., again because the *Q*₁₀ of the former is around 1 whereas that of the latter is close to 2.

Table 2. Metabolic intensity (*M.I.*) measured at 5, 10, 15 and 20°C for six dominant nematode species in Otsuchi Bay.

Species	Temperature (°C)			
	5	10	15	20
<i>Mesacanthion</i> sp.	-0.025±0.241	0.225±0.114	0.367±0.198 **	0.316±0.220 ***
<i>Symplocostoma</i> sp.	0.124±0.129	0.224±0.114	0.138±0.085	0.121±0.140
<i>Polygastrophora</i> sp.	-0.143±0.217	0.143±0.156 ***	0.285±0.097 *	0.309±0.158
<i>Metachromadora</i> sp.	-0.312±0.185	-0.224±0.220 **	0.027±0.124 *	0.043±0.255
<i>Monoposthia</i> sp.	-0.236±0.146	-0.101±0.332 ***	0.040±0.098 ***	0.175±0.073
<i>Theristus</i> sp.	-0.135±0.404	0.167±0.017	-0.149±0.025	0.062±0.205

In the comparisons between male and female, males of three species we measured were more active than female at certain temperatures (Fig. 5). For example, male of *Mesacanthion* sp. was more active than female at all temperatures studied. In the case of *Symplocostoma* sp., the *M.I.* value of males exceeded over the female significantly at lower temperatures (5 and 10°C). On the other hand, males of *Polygastrophora* sp. were more active than females at higher (15 and 20°C) temperatures. It was also noteworthy that in *Mesacanthion* sp., *M.I.* of juveniles at 20°C were 2 and 4 times higher than those of male and female, respectively.

DISCUSSION

The literatures measured nematode respirations prior to 1979 were reviewed by Warwick and Price (1979) with new data of their own, and further review was done by Heip *et al.* (1985). The values of metabolic intensity summarized in these reviews were very large in range, namely on a logarithmic basis, from 0.386 for *Oncholaimus campyloceroides* to -1.081 for *Spirinia gnaigeri*, i.e. from 2.43 to 0.08 nO₂ h⁻¹ nL⁻¹ on a linear scale. In other words, the highest figure is 30 times larger than the lowest. Because of such a huge range of previously reported data, all *M.I.* measured in the present study (*Symplocostoma* sp. (0.09–0.17), *Polygastrophora* sp. (0.14–0.41), *Mesacanthion* sp. (0.18–0.76), *Metachromadora* sp. (0.22), *Monoposthia* sp. (0.35) and *Theristus* sp. (0.36)) were within the range so far reported. A variety of Cartesian diver methods (e.g., Hamburger, 1981; Shirayama, 1992) have been used in the previous measurements of the respiration rates of nematodes. Though the method is so accurate as to measure the respiration rate of down to 0.1 nO₂ h⁻¹, it is not very easy to carry out. In the present study, we tried a recently devised microelectrode with a small chamber. This method is easy to use and yet still possible to measure the oxygen consumption down to 0.7 nO₂h⁻¹. Because our results fell within the range of previously reported values, it was confirmed that the microelectrode technique was also accurate enough to measure respiration rates of free-living marine nematodes.

The effect of temperature on the rate of respiration was studied by Wieser and Schiemer (1977) for *Trefusia schiemeri* and *Trichotheristus floridanus* and by Price and Warwick (1980) for *Sphaerolaimus hirsutus*. In the latter study, *Q*₁₀ was found to be as low as 1.17, meaning that the respiration rate of the species was only slightly affected by temperature over the range normally experienced by the species in the field (Heip *et al.*, 1985). In the present study, respiration rates of *Polygastrophora* sp., *Mesacanthion* sp., *Metachromadora* sp. and *Monoposthia* sp. increased with temperature but those of *Symplocostoma* sp. and *Theristus* sp. were constant in the range of temperature studied. Price and Warwick (1980) tentatively proposed that animals living in habitats where food supply was stable tended to have low *Q*₁₀ values around 1,

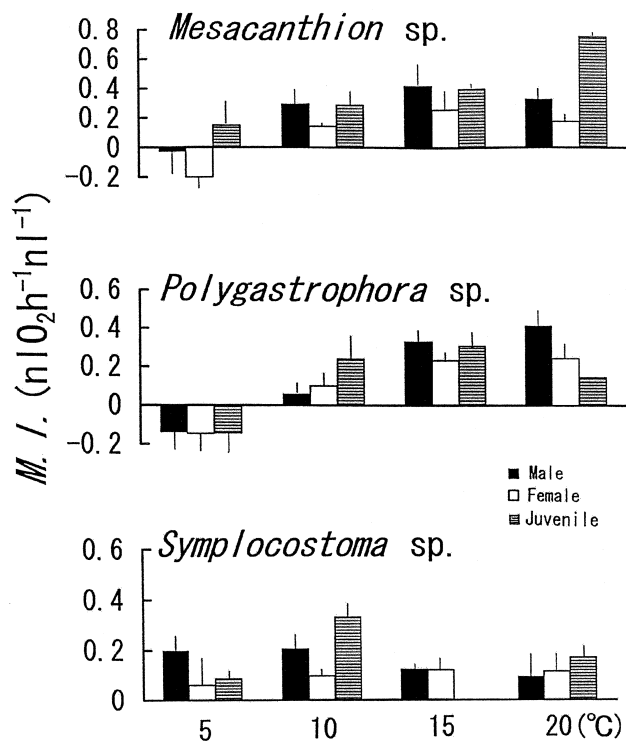


Fig. 5. The *M.I.* values of male, female and juvenile for *Mesacanthion* sp., *Polygastrophora* sp. and *Symplocostoma* sp. measured at 5, 10, 15 and 20°C.

whereas those in habitats of seasonally variable food supply possibly had Q_{10} of around 2. Their idea however was not applicable in the present result, because Q_{10} of *Symplocostoma* sp. was 1.0 whereas that of *Polygastrophora* sp. was 2.0, though both species feed on the same food item of diatoms (Kim, 1996).

For *Symplocostoma* sp., *Polygastrophora* sp. and *Mesacanthion* sp., males were more active than females. Sex ratio of these species were extremely biased (100:1) to females and their males were rare (Kim and Shirayama, 1996). In such a population structure, a male should copulate with more than 100 females to send more of its own gene set to the next generation than other males. Thus males may need to be more active than females, and consequently respiration rates of males were expected to be higher than those of females. Actually, we could notice that males of *Symplocostoma* sp. bended their body more frequently and more strongly than females.

The *M.I.* of male *Symplocostoma* sp. drastically decreased at 15 and 20°C (Fig. 5). The life span of this species is long, i.e. about 1 year, and the field census in the previous study (Kim and Shirayama, 1996) has shown that the adult males were present only in winter and spring. Their physiological characteristics (i.e. not active in summer) are therefore in accordance with its potential for seasonal activity.

The *M.I.* value of juvenile *Mesacanthion* sp. at 20°C was the highest amongst the species studied here. This species was the most abundant in summer and the juveniles accounted for 76% of the total density (Kim and Shirayama, 1996). It is considered that optimal temperature condition for the juveniles of *Mesacanthion* sp. is found in summer, when the temperature is high.

In the present study, we found that physiological characteristics of free-living nematodes are unique from species to species. To understand the comprehensive figure of the energy flow in the meiobenthic community at a certain site, thus, it is necessary to accumulate data on the respiration

rates of variety of free-living nematode species dominant at each site.

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