

OXYGEN CONSUMPTION AND FEEDING RATES OF THE SABELLID POLYCHAETE, *MYXICOLA INFUNDIBULUM* (RENIER)

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Abstract—1. Rates of respiration and feeding were measured for the sabellid polychaete, *Myxicola infundibulum*.

2. Basal rates of respiration were 1.5 times lower than routine rates.

3. Clearance and irrigation rates were independent of cell type when the worms were fed on monocultures of algae; however, preferential selection was seen when the algal species were offered simultaneously.

4. Calculations indicate that this species can meet its energetic needs at rather low cell densities.

5. It is suggested that these low energy requirements, coupled with the capacity for high pumping/clearing rates may be of adaptive significance in reducing competition for food resources.

INTRODUCTION

The sabellid polychaete, *Myxicola infundibulum* (Renier) is a subtidal species, commonly occurring in cold waters at depths of 1–20 m, although they have been reported as deep as 500 m (Hartmann-Schroder, 1971). They are found living in colonies amongst rubble or mussel beds and are cosmopolitan (MacKay, 1977a). Optimum temperature and salinity for this species are 8–10°C and 30–33‰, respectively. MacKay has suggested that the worms may accept and utilize detritus and pointed out that the species occurs where suitable substrate and topographic configurations tend to concentrate plankton and organic debris.

Like other sabellids, *M. infundibulum* is a tubicolous polychaete with a prostomium and peristomium modified into a tentacular crown. This crown is utilized for respiration, feeding or both (Fauchald and Jumars, 1979). Most studies assign the crown as both a respiratory and feeding organ in this species (Wells, 1952). Little work has been done on either the respiratory or feeding biology of this species (see Wells, 1952; Dales, 1957).

M. infundibulum has recently become an important species in medical research and is of considerable economic importance. These worms possess a single, large central nerve cord which has been shown to be a suitable substitute for the squid in the application of space-voltage clamp and provides stable, reliable determinations of the absolute membrane potential (Binstock and Goldman, 1969a,b, 1971). Since then, the species has become the basis of a diverse range of research efforts and is supplied commercially to research workers.

The worms are difficult to collect as they occur subtidally, often in cracks and crevices of ledge and rocks. For this reason, recent efforts have centered on the reproductive biology of these worms in an effort to propagate the species in the laboratory (Dean *et al.*, 1987).

The present investigation was undertaken to provide basic information on the energetic requirements of the adult worms. Data are presented for both the routine and basal rates of oxygen consumption, feeding rates and preferences, filtration rates and clearance rates. These data will provide a basis for establishing the energy requirements of the adult worms which need to be maintained in the laboratory as breeding stocks.

MATERIALS AND METHODS

Specimens of the sabellid polychaete, *M. infundibulum* (Renier) were supplied from the Ira C. Darling Center, University of Maine. Worms were maintained in temperature-controlled tanks at 10°C and were held for at least 1 week prior to use in experiments. Each worm was housed in its own test tube to simulate its natural environment. Similar methods for holding polychaetes have been used by Wells (1952) and Kristensen (1981, 1983). Worms ranged from 0.1 to 0.5 g dry tissue weight.

Algal food cultures were prepared just prior to the feeding experiments. Algal species used and their dimensions are given in Table 1. Algal cultures were supplied by the Provosolli-Guillard Culture Center for Marine Phytoplankton (Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, Maine 04575, USA). Cultures were grown in F/2 media at 10°C with a 14:10 photoperiod. In the first series of feeding experiments, worms were fed on monocultures of three different species: 3H, 3C and TISO. Worms were placed in individual containers containing 1 liter of algal solution at a concentration of $1.0\text{--}3.5 \times 10^4$ cells/ml. Animals were left to feed for 1 hr after which cell concentrations were monitored using a Coulter Counter Model ZM. Each beaker was gently aerated and held in an incubator at 10°C.

In a second set of feeding experiments, worms were placed in individual beakers and maintained as above. In these experiments, a mixture of algal cells was used as the food source: ISO, PLATY 1 and 3C. These experiments were designed to ascertain whether or not the worms exhibited any tendencies/capabilities for particle selection. At the end of the feeding period, cells were analysed by differences in

Table 1. Algal species used in feeding experiments

Species	Clone	Size (μm)
<i>Chroomonas salina</i> (Wisilouch) Butcher	3C	6.25–7.5 \times 8.75–12.5
<i>Isochrysis galbana</i> Parke	ISO	5 \times 6 \times 2–4.0
<i>Isochrysis</i> sp. Parke (Tahitian strain)	TISO	3.25 \times 5.75
<i>Tetraselmis levis</i> T. Hori	PLATY 1	10 \times 12 \times 6–10.0
<i>Thalassiosira pseudonana</i> (Hustedt) Hasle <i>et</i> Heimdal	3H	3.5–4.0

Table 2. Weight-specific clearance rates and irrigation rates (\dot{V}_w) for *Myxicola infundibulum* fed on monocultures of the three algal clones, 3H, 3C and TISO

Algal clone	Ration (cells/ml $\times 10^4$)	Clearance rate (cells/hr/g $\times 10^7$)	Irrigation rate (ml/hr/g $\times 10^3$)
3H	1.7	3.25 \pm 1.91	2.8 \pm 1.64
3C	2.4	3.25 \pm 2.07	1.34 \pm 0.81
TISO	3.5	3.76 \pm 2.22	1.04 \pm 0.62

Table 3. Weight-specific clearance and irrigation rates for each of the algal clones when fed simultaneously to *M. infundibulum*. 100% retention efficiency is assumed

Algal clone	Ration (cells/ml $\times 10^3$)	Clearance (cells/hr/g $\times 10^7$)	Irrigation (ml/hr/g $\times 10^3$)
ISO	8.3	2.57 \pm 0.43	3.06 \pm 1.04
3C	5.2	1.65 \pm 0.26	3.11 \pm 1.01
PLATY 1	6.4	3.27 \pm 0.38	5.25 \pm 1.48
Σ	1.99 $\times 10^4$	7.49	

their fluorescing intensities and size using a FACS Analyzer. Experimental animals were maintained in filtered (0.4 μm) sea-water for a minimum of 24 hr prior to experimentation to ensure that the guts were cleared.

Filtration rate (\dot{V}_w) was calculated using the formula of Coughlan (1969):

$$\dot{V}_w = M/n \cdot t \left(\log_e \frac{\text{conc}_o}{\text{conc}_f} \right)$$

where M is the volume of the experimental chamber, conc_o and conc_f are the original and final concentration of algae, respectively, n is the number of individuals per container (in this case, 1) and t is the length of time spent feeding.

Respiration rates were measured using either a Radiometer oxygen electrode in a closed system (Shumway, 1981) or a micro Winkler titration (Burke, 1969). Both routine and basal rates were measured. A number of animals were starved for a period of three weeks after which $\dot{V}\text{O}_2$ was measured (basal metabolic rate). Dry tissue weights were determined after oven drying at 70°C for 24 hr.

Carbon requirements were calculated using a conversion factor of 22.4 $\mu\text{l O}_2 = 12 \mu\text{g C}$.

RESULTS

The relationship between oxygen consumption rates (both routine and basal) and tissue dry weight for *M. infundibulum* is given in Fig. 1. Linear regression equations are given in Fig. 1. Routine metabolic rate was found to be approximately 1.5 times greater than the basal rate. The difference was significant ($P < 0.001$). There was no significant difference between slopes of the two lines.

One difficulty with estimates of the clearance rate of particles from a fixed volume of medium is that the experimental animal is likely to be subject to a continuous decline in particle concentration with time, depending on the clearance rate and the volume of medium used (see Shumway *et al.*, 1985, for discussion). In the present study, the problem was minimized by using a relatively large volume of suspension medium, such that a reduction in cell concentration with time could be estimated over a short period of time.

Both the weight-specific clearance rates and irrigation rates for *M. infundibulum*, fed on monocultures of the three algal clones, 3H, 3C and TISO, are given in Table 2. There were no significant differences between either the clearance rates or the irrigation rates for any of the algal clones, i.e. the clearance and irrigation rates were independent of cell type offered. Table 3 shows the weight specific clearance and irrigation rates for each of the algal clones, ISO, 3C and PLATY 1 when fed simultaneously to *M. infundibulum*. In contrast to the rates obtained when fed monocultures, there were significant differences between algal species when fed simultaneously. The cells were cleared preferentially

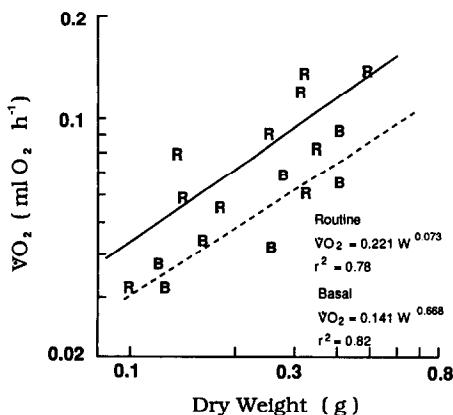


Fig. 1. Basal (B) and routine (R) metabolic rates for the polychaete, *Myxicola infundibulum*.

Table 4. The energy requirements of *M. infundibulum* of 1 g dry tissue weight

	$\dot{V}O_2$ (ml/hr)	\dot{V}_w (ml/hr)	$\mu\text{g C}$	calories	Joules
Basal	0.141	2780	151.1	0.68	2.80
Routine	0.221	2780	236.8	1.06	4.45

Assuming an oxycaloric equivalent of 4.8 cal/ml (Crisp, 1971).

as follows: PLATY 1, ISO, 3C. ($P < 0.05$ for each comparison).

No feces or pseudofeces were produced during the experiments, and therefore no estimates can be made of any potential for preferential digestion. It appears that pre-ingestive selection of PLATY 1 takes place, i.e. these cells are cleared at a faster rate than the other two species, ISO and 3C. While PLATY 1 is somewhat larger than the other two species used in the experiments, all of the cells offered were of a size range likely to be encountered by the worms in their natural habitat. Furthermore, the cells were sufficiently similar in size, so as to reduce the likelihood of an obvious selection on the basis of particle size.

DISCUSSION

The rates of oxygen consumption by *M. infundibulum* are similar to those reported for other species of polychaetes (Shumway, 1979) and support the theory that sedentary species of polychaetes have a respiratory rate approximately 2.4 times lower than errant species (Shumway, 1979).

There is little information available on the quantitative aspects of filter feeding in the sabellid worms. Dales (1957) reported that particles are caught in the pinnules and become entangled in mucus. He suggested that the majority of suitable particles would be ingested such that the filtering rate becomes equivalent to the feeding rates. Dales fed *M. infundibulum* on graphite particles (Aquadag) almost entirely in the 1–2 μm size range. He reported rates of approximately 0.286 l/hr/animal for a worm of approximately 2.7 g wet weight. Assuming 22% dry weight (this study), this is a worm of approximately 0.6 g dry weight. This gives a value of 0.48 l/hr/g dry weight, which is approximately an order of magnitude lower than the irrigation rates reported in the present study. The differences observed in the two studies are probably due to the presence of inert particles rather than the particle size. No information is given by Dales (1957) regarding the production of pseudofeces. Dales further suggested that free-swimming algae escape through the crown and that only inert particles down to 1–2 μm are retained, implying that fan worms depend on suspended detritus alone as a food source. It was also suggested that *M. infundibulum* is less efficient than other suspension-feeding invertebrates, both in the volume of water they are capable of straining and in the kind of particles which can be retained. Clearly this is not the case. In the present study, five different species of unicellular algae were presented to *M. infundibulum* and all were cleared from suspension with considerable efficiency. Furthermore, the rates of particle clearance recorded in the present study are higher than those of similar

sized species of bivalve molluscs (see Bayne and Newell, 1984).

Some evidence, though not unequivocal, is presented here for preferential removal of algal cells of different types from mixed suspensions. Previous evidence has been presented for particle selection in the sabellids. Fitzsimons (1965) showed that *Sabellastarte magnifica* could separate the filtered particles into three size fractions. The smaller fractions (3–5 μm in small worms; 6–8 μm for larger worms) consist of food particles. The larger fractions were either used in tube building or rejected. It was suggested that sabellids select particles exclusively based on size; no evidence for selection based on other particle characteristics has as yet been presented (Fauchald and Jumars, 1979).

The algal cells used in the present study would seem to be close enough to the same as to eliminate the possibility of selection based on size alone. The mechanism of particle collection/entrapment was described in detail by Nicol (1930). Briefly, it can be summarized as follows: a double row of ciliated pinnules on the inner surfaces of each filament of the branchial plume cause water currents to be drawn past the filaments; particles are strained from the water by cilia on the pinnules; the particles are then forwarded along ciliated tracts on the inner surfaces of the filaments to the mouth where ingestion occurs. For purposes of discussion, we can assume 50% absorption efficiency, even though no feces was produced here and efficiency is likely to be much higher.

Minimum carbon requirements for respiration are calculated using the following equation (Lucas *et al.*, 1987):

$$\text{O}_2 \text{ consumption } (\mu\text{l O}_2/\text{g/hr}) \times \frac{12 \mu\text{g C}}{22.4 \mu\text{l O}_2} \times \text{absorption efficiency } (\%).$$

Carbon requirements for respiration ($\mu\text{g C/g/hr}$), where $22.4 \mu\text{l O}_2 = \mu\text{g C}$.

Thus, the carbon requirements are:

$$141 \times 12/22.4 \times 100/50 = 151.07 \mu\text{g C/g/hr} \quad (\text{basal})$$

$$221 \times 12/22.4 \times 100/50 = 236.79 \mu\text{g C/g/hr} \quad (\text{routine}).$$

The filtration rate of a 1 g dry tissue weight *M. infundibulum* is approximately $2.78 \text{ ml/hr/g} \times 10^3$ (average value, this study) depending on the cell type being filtered. This means that each 2780 ml of water filtered by the worm must therefore contain at least 151.1 $\mu\text{g C}$ (basal) or 236.8 $\mu\text{g C}$ (routine) to sustain the animal.

Table 4 summarizes the requirements of *M. infundibulum* in terms of carbon, calories and Joules. Since 10×10^6 cells is approximately equal to 1 cal (Malouf, 1977), 6.8×10^6 cells are required to maintain basal metabolic rate and 1.1×10^7 cells for routine metabolic rate. At a filtration rate of 2780 ml/hr, this requirement could be met by a cell concentration of $0.68/2780 \times 10^6 = 243.5$ cells/ml (basal) and 3.81×10^3 cells/ml (routine). These correspond with rather low cell densities such as might be

encountered in comparatively nonproductive areas or areas of high competition for food resources.

Populations of *M. infundibulum* occur in areas differing markedly in the concentrations of potential food. MacKay (1977) associated high abundance of *M. infundibulum* with areas high in suspended matter concentration and sparse abundance (of *M. infundibulum*) with areas of high water clarity. *M. infundibulum* are also commonly found in association with other filter-feeding invertebrates, e.g. with sponges and horse mussels (*Modiolus modiolus*) at less than 30 m depth (MacKay, 1977) and with giant scallops (*Placopecten magellanicus*). R. S. Steneck (personal communication) recently has noted extensive beds of *M. infundibulum* in the Gulf of Maine at densities of 100/m² at depths *ca* 73 m.

The low energy requirements of *M. infundibulum* coupled with their capacity for high pumping/clearing rates and possible particle selection may be of adaptive significance in reducing the competition for food resources between *M. infundibulum* and co-existing species. The possible role of bacteria as a potential food source cannot be ruled out. *M. infundibulum* appears to be adapted to exploit habitats where the concentrations of phytoplankton and natural seston may be low and/or to avoid competition for food resources by utilizing low levels of particles not utilized by coexisting species whose filtration efficiencies are greatly reduced at low particle sizes (e.g. *P. magellanicus*).

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