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# Filter-feeding in the polychaete *Nereis diversicolor*: growth and bioenergetics

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ABSTRACT: Field studies in Danish waters (Odense Fjord and Fyns Hoved) showed that the facultatively filter-feeding polychaete *Nereis diversicolor*, kept in U-shaped glass tubes elevated 15 cm above the bottom, is able to grow on phytoplankton as the sole food source. The greatest increase in body weight, corresponding to an instantaneous specific growth rate of $\mu = 0.039\ d^{-1}$ or 3.9 % $d^{-1}$, was measured in worms from the eutrophicated Odense Fjord. Negative growth was observed for *N. diversicolor* in Kertinge Nor (Denmark), possibly a consequence of a high cyanobacteria biomass which was not ingested by the worms. When fed in the laboratory on a diet of monocultural suspended algal cells, the worms (kept in glass tubes) attained growth rates ($\mu = 0.031\ d^{-1}$) comparable to those found in the wild. The growth rate of worms fed algal cells (*Rhodomonas* spp.) was estimated from an energy budget based on estimated ingestion rate, assimilation efficiency and metabolic rate. At 1700 cells $ml^{-1}$ the estimated growth rate was 0.25 mg $d^{-1}$ and in good agreement with the actual growth rate of 0.23 mg $d^{-1}$. At algal concentrations greater than 1700 cells $ml^{-1}$ the agreement between estimated and actual growth was less satisfactory. Population filtration capacities of 9.5 and 4.6 $m^3\ d^{-1}\ m^{-2}$ respectively estimated for *N. diversicolor* from Odense Fjord and Fyns Hoved corresponded to volumes 30 and 15 times greater than that of the water column of these 2 areas.

## INTRODUCTION

The facultatively filter-feeding polychaete *Nereis diversicolor* is able to filter-feed by pumping large volumes of water through a filter-net secreted at the entrance of its U-shaped burrow in the sediment (Riisgård 1991). The energetic cost to *N. diversicolor* of such pumping has been assessed and compared to that of obligate suspension-feeding marine invertebrates (Riisgård et al. 1992). *N. diversicolor* changes from predatory or surface deposit-feeding behaviour to a filter-feeding mode in the presence of sufficient numbers of suspended algal cells. The energetic expense of such 'pump work' is comparable to values estimated for obligate suspension-feeders in that the pump power output represents only a few percent of the total metabolic output (Riisgård et al. 1992).

To assess the ecological role of *Nereis diversicolor* in the consumption of phytoplankton in shallow brackish-water areas it is necessary to know how frequently filter-feeding is utilized and to assess to what extent the worm is able to grow on phytoplankton when this is the sole food source. The present study has examined the ability of *N. diversicolor* to grow on a sole diet of phytoplankton in field and laboratory situations. Predictions of growths rates of *N. diversicolor* when filter-feeding were made using an energy budget based on estimated ingestion rate, assimilation efficiency and metabolic rate, and the values obtained were compared to actual growth rates.

## MATERIALS AND METHODS

**Growth experiments.** Field and laboratory growth experiments were made using *Nereis diversicolor* O. F. Müller of 47 to 71 mg dry wt, described as 'standard' worms. Worms were collected from mud flats at water depths of ca 0.5 m by taking sediment samples which were sieved (1 mm mesh size). Standard worms retained by the sieve were transferred to U-shaped glass tubes (22 cm length, 4.0 mm internal diameter). Twenty-five such tubes were mounted on a rack that maintained them in an upright position with 1.5 cm

between tubes. Initial and final weights (after 24 h starvation to empty the gut) were determined as wet weight (after 2 min drainage on filter paper; uncertainty less than 1% when reweighed). Dry weight was determined after drying for 24 h at 105 °C. In the growth experiments chlorophyll *a* was used to assess the phytoplankton biomass. Chlorophyll *a* was measured according to standard procedures (Arvola 1981) and based on filtration (Whatman GF/C filter) of 0.5 to 5 l water samples (the volume of water used depending on algal concentration). The absorption of extracted (96% ethanol, within 1 to 3 h after sampling) chlorophyll *a* was measured at 665 nm on a Perkin-Elmer model 554 spectrophotometer. Carbon analysis was made using a Hewlett-Packard 185 B CHN-analyzer.

**Field experiments.** Growth of *Nereis diversicolor* was measured during the summer of 1992 at 3 localities in the northern part of Fyn, Denmark (Fig. 1): Odense Fjord, Fyns Hoved (Pughavn) and Kertinge Nor. Standard worms were collected from each area and transferred to U-shaped glass tubes (which were painted black to avoid light stress). One rack of worms was set up at each of 5 stations at Odense Fjord and Fyns Hoved (125 worms at each locality), or at 1 station at Kertinge Nor (25 worms) (see Fig. 1). The racks were positioned so that the openings of the glass tubes were ca 15 cm above the bottom so that the worms could only obtain food by suspension feeding At the end of the study period (14 d), an average of 72% (range 60 to 92%) of the worms remained. During the 14 d growth period water samples for chlorophyll *a* measurements were taken every second or third day at each station, and the water temperature was measured.

To estimate the potential grazing impact of the local populations of *Nereis diversicolor* and to evaluate the growth conditions at the different stations, the density and size distribution of worms were determined. At each station 6 randomly chosen sediment core samples (143 $cm^2$ × 25 cm deep) were taken, and all worms retained by a sieve (1 mm mesh size) retained. In the laboratory these worms were counted and individually weighed (wet wt) to determine the density and size distribution at each station and to allow calculation of the population filtration rate according to Riisgård (1991).

**Laboratory experiments.** *Nereis diversicolor* were collected from mud flats in the innermost part of the shallow brackish Odense Fjord (mean depth 0.8 m, 10‰ S) during January to March and in September 1992. Worms were transferred to glass tubes as described previously and acclimated to experimental conditions (22‰ S, 15 °C) for 2 d before use.

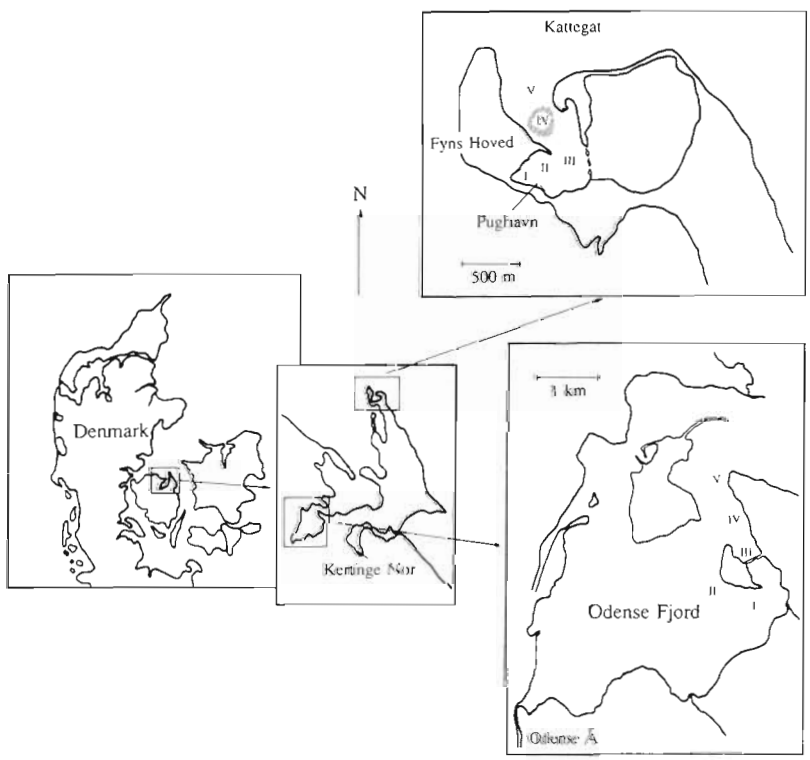


Fig. 1. Study area. Kertinge Nor, Stn I. Odense Fjord, Stns I to V. Fyns Hoved (Pughavn), Stns I to V (location of a mussel bed is shown in the hatched area). Shaded areas show 'high densities' (> 1000 ind $m^{-2}$) of *Nereis diversicolor*

Worms were fed *Rhodomonas* spp. cells (mean diameter 6.2 µm) from a chemostat culture (constant light and pH regulated by means of NaOH and $CO_2$) and algal concentration in the growth aquaria was checked at least twice a day during the growth period. Filtration rate ($F$) was estimated from the clearance of 100% retained *Rhodomonas* cells in an aerated aquarium according to Riisgård (1991) by means of the formula:

$$F = V/tn \times \ln(C_0/C_t),$$

where $C_0$ and $C_t$ = algal concentration at time = 0 and time = $t$ respectively; $V$ = water volume in the aquarium; $n$ = number of actively filtering worms. The algal concentration was measured by means of an electronic particle counter (Elzone-80XY with a 76 µm orifice tube).

Growth experiments were made in 2 types of experimental design: a flow system and a closed system.

***Flow-system:*** This system consisted of aquaria (10 l) containing through-flowing seawater prefiltered using

*Mytilus edulis* as a bio-filter. Each aquarium held 25 worms (1 rack). Constant quantities of *Rhodomonas* spp. cells were continously added to each aquarium by means of a peristaltic pump to maintain a constant (steady-state) algal concentration. Throughout the experimental period (14 or 21 d) the percentage of the worms actively filter-feeding was determined by inspection (10 min periods) 2 to 4 times daily. The population filtration rate was assessed by means of the clearance method, by periodically (2 to 3 d intervals) stopping the flow (1 to 2 h) and following the subsequent exponential reduction in algal concentrations. Faeces on the bottom of the aquaria were quantitatively collected (by pipette) every 3 to 4 d and centrifuged (3000 rpm, 3 min), and the remaining material was dried (105 °C, 24 h). After determining dry weight a sub-sample was used for carbon analysis.

***Closed-system:*** This system consisted of a large (300 l) aquarium in which the seawater was strongly agitated and changed every fifth day. To restrict the growth of ciliates the water was UV-sterilized prior to addition. Algal cells were added to the aquarium to produce the desired concentration, which remained relatively stable over several days due to the large water volume relative to the number of worms (50 worms in 2 racks). Additional algae were pumped into the aquaria at low rates to compensate for those eaten or sedimented during the experiment. The algal concentration was measured every day in order to establish the mean algal concentration during the experiment (15 d). To evaluate the filtration activity 2 worms were continuously monitored over a 24 h period by means of a phototransducer-technique (Riisgård et al. 1992). At the start and end of the experiment the total filtration rate of the 50 worms was measured by means of the previously described clearance method after transfering the racks containing the worms to two 10 l aquaria (1 tube rack in each).

**Conversion factors.** The following conversion factors were used to establish energy budgets. Dry weight (*dw*, mg) of *Nereis diversicolor* was found to correlate with wet weight (*ww*, mg) according to the equation $dw = 0.170 + 0.157\,ww$ ($r^2 = 0.899$, n = 77, range 1 to 122 mg dry wt). A 1 mg dry wt *N. diversicolor* = 4.4 ± 0.3 cal $mg^{-1}$ dry wt (Chambers & Milne 1974) = 18.4 J $mg^{-1}$ dry wt. The relationship between *Rhodomonas* spp. cell concentration (*C*, cells $ml^{-1}$) and chlorophyll *a* (chl *a*, $\mu g\ l^{-1}$) was found by: chl $a = 1.251 \times 10^{-3} \times C$ (5 algal concentrations, and 3 determinations on each sample, range = 2 to $30 \times 10^3$ cells $ml^{-1}$, $r^2 = 0.998$). The energy content of *Rhodomonas* spp. was determined as follows: a known volume of algal culture with known cell concentration was centrifuged (3000 rpm, 10 min). After drying (105 °C, 24 h) the dry weight of the remaining pellet was determined, and samples analyzed for carbon (Hewlett-Packard 185 B CHN-analyzer). The carbon content was found to be 40.2% of the dry weight, equivalent to $117 \times 10^{-12}$ g C $cell^{-1} \times 40.2\%$ C = $47.17 \times 10^{-12}$ g C $cell^{-1}$. Assuming 1 mg C = 11.40 cal (Platt & Irwin 1973) = 47.7 J, the energy content was found to be 2.25 μJ $cell^{-1}$.

## RESULTS

### Field experiments

The field experiments show that *Nereis diversicolor* is able to grown on phytoplankton as the sole food source. The mean growth rate of the worm is shown in Table 1. The growth rates as related to chlorophyll *a* concentration at the different stations in the 3 areas are shown in Fig. 2. Generally, there was an increase in growth rate with increasing chlorophyll *a* concentration, with a maximal observed growth rate of 3 mg dry wt $d^{-1}$ at chlorophyll *a* concentrations of 11 $\mu g\ l^{-1}$. However, at the extremely high chlorophyll *a* concentration of 44 $\mu g\ l^{-1}$ in Kertinge Nor, growth was negative. The worm population densities and population filtration potential at the different stations are given in Table 2. It is seen that the maximal population density (>3000 ind. $m^{-2}$) and maximal filtration capacity was found at station OF-I in the eutrophicated Odense Fjord (9.5 $m^3\ d^{-1}$).

Table 1. *Nereis diversicolor.* Mean (± SD) individual daily increase in body dry weight in field experiments with 25 worms. Mean ± SD chlorophyll *a* values in surface water are shown for each station (see Fig. 1). Experiments were performed in 1992 in Odense Fjord (OF), 18 May to 1 June, in Pughavn at Fyns Hoved (FH), 13 to 27 June, and Kertinge Nor (KN), 3 to 17 September. Mean water temperatures ± SD during the experimental periods were 21.3 ± 1.2, 19.0 ± 2.0 and 15.0 ± 1.0 respectively for the 3 areas

| Locality/ Stn no. | Body dry weight on Day 0 (mg) | Body dry weight on Day 14 (mg) | Daily growth rate (mg $d^{-1}$) | Chl *a* ($\mu g\ l^{-1}$) |
|---|---|---|---|---|
| OF-I | 58.3 ± 7.2 | 65.8 ± 26.2 | 0.54 | 8.0 ± 5.3 |
| OF-II | 58.0 ± 6.9 | 78.8 ± 16.6 | 1.49 | 13.2 ± 7.9 |
| OF-III | 57.6 ± 7.5 | 84.9 ± 11.9 | 1.95 | 15.0 ± 6.8 |
| OF-IV | 58.3 ± 6.9 | 77.9 ± 9.1 | 1.40 | 8.5 ± 8.8 |
| OF-V | 58.5 ± 7.3 | 100.5 ± 13.4 | 3.00 | 11.4 ± 8.3 |
| FH-I | 62.0 ± 5.4 | 78.2 ± 11.1 | 1.16 | 2.5 ± 0.9 |
| FH-II | 59.3 ± 5.2 | 67.2 ± 6.9 | 0.56 | 1.5 ± 0.7 |
| FH-III | 60.6 ± 5.4 | 79.9 ± 9.2 | 1.38 | 1.4 ± 0.5 |
| FH-IV | 60.6 ± 5.4 | 58.3 ± 12.0 | −0.16 | 1.0 ± 0.3 |
| FH-V | 61.6 ± 5.8 | 65.2 ± 11.4 | 0.26 | 1.2 ± 0.4 |
| KN-I | 55.4 ± 5.1 | 50.8 ± 8.3 | −0.33 | 44.5 ± 14.4 |

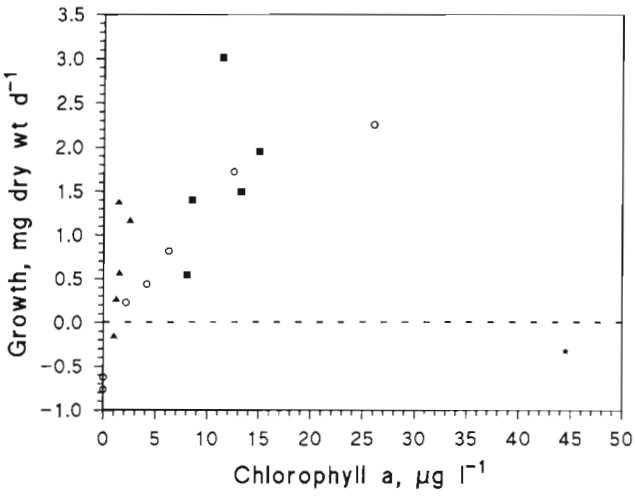


Fig. 2. *Nereis diversicolor*. Mean growth rates of worms (n = ca 20) as a function of chlorophyll *a* concentration: (■) in Odense Fjord; (▲) Pughavn, Fyns Hoved; and (•) in Kertinge Nor. Growth rates from laboratory experiments (○) are shown for comparison

## Laboratory experiments

The laboratory experiments with suspensions of monocultural algal cells show that *Nereis diversicolor* is able to attain growth rates comparable to those in the field and that the growth rates may be explained on the basis of the energy budget.

### Growth experiments

The mean growth rates of *Nereis diversicolor* in flow-system and closed-system experiments are shown in Table 3 and Fig. 3. The growth rate is strongly correlated with algal cell concentration, and a maximal growth rate of 2.253 mg dry wt $d^{-1}$ was achieved at $2 \times 10^4$ cells $ml^{-1}$ equivalent to a chlorophyll *a* concentration of 26 µg $l^{-1}$.

### Energy budgets

The estimated growth in the flow-system experiments is shown in Table 4. The values were calculated using: (1) the measured total volume of water filtered per day at the different algal concentrations; (2) the negative growth in the experiment without algal cells (i.e. starvation = −0.624 mg $d^{-1}$) as a measurement of metabolism ($R$); (3) the estimated assimilation efficiencies in Table 5; and (4) assuming that the filtration activity was 70% of the total time in all experiments (based on observation, and monitoring by means of the phototransducer technique).

Table 2. *Nereis diversicolor*. Size distribution, population density and estimated population pumping rate of worms at different stations (see Fig. 1), in Odense Fjord (OF), Pughavn at Fyns Hoved (FH), and Kertinge Nor (KN)

| Range of wet wt (mg) | Individual clearance (µl $s^{-1}$) | Density (ind. $m^{-2}$) OF I | OF II | OF III | OF IV | OF V | FH I | FH II | FH III | FH IV | FH V | KN I |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| <50 | 7 | 1801 | 944 | 997 | 507 | 227 | 1032 | 1364 | 245 | 420 | 35 | 98 |
| 50–100 | 17 | 297 | 280 | 192 | 192 | 35 | 262 | 122 | 105 | | | 112 |
| 100–150 | 37 | 280 | 227 | 175 | 175 | | 175 | 70 | 17 | 35 | | 112 |
| 150–200 | 57 | 245 | 175 | 87 | 157 | 87 | 87 | 87 | 35 | | | 70 |
| 200–250 | 77 | 210 | 52 | 70 | 35 | | 53 | | 17 | 17 | | 56 |
| 250–300 | 97 | 175 | 17 | 52 | 35 | | 17 | 87 | | 17 | | 28 |
| 300–350 | 117 | 105 | 35 | | 17 | | 35 | 35 | 17 | | | 70 |
| 350–400 | 137 | 105 | | | | | | | | 35 | | 70 |
| 400–450 | 157 | 87 | | | 17 | | 52 | 35 | | | | 14 |
| 450–500 | 177 | | | | | | 35 | | | | | 56 |
| 500–550 | 197 | | | | | | 17 | | 17 | | | |
| 550–600 | 217 | | | | | | 17 | 17 | | 17 | | 28 |
| 600–650 | 237 | 52 | | | | | 35 | 17 | | | | 28 |
| 650–700 | 257 | | | | | | | | | | | 14 |
| 700–750 | 277 | | | | | | | | | | | |
| 750–800 | 297 | | | | | | | 17 | | | | |
| 800–850 | 317 | | | | | | | | | | | 14 |
| 850–900 | 337 | | | | | | | | | | | 14 |
| 900–950 | 357 | | | | | | | | | | | 14 |
| Pop. density (ind. $m^{-2}$) | | 3357 | 1730 | 1573 | 1135 | 349 | 1817 | 1851 | 453 | 541 | 35 | 798 |
| Filtration capacity ($m^3$ $d^{-1}$) | | 9.5 | 2.9 | 2.3 | 2.4 | 0.5 | 4.6 | 3.7 | 0.9 | 1.1 | ≈0 | 5.8 |
| Water depth (cm) | | 30 | 55 | 65 | 55 | 80 | 30 | 40 | 45 | 50 | 70 | 50 |

Table 3. *Nereis diversicolor*. Individual increase in mean body dry weight during 14 to 21 d growth experiments at defined *Rhodomonas* spp. concentrations

| Expt | Duration (d) | Algal cell conc. ($\times 10^3$ ml$^{-1}$) | Chl *a* conc. ($\mu$g l$^{-1}$) | Weight on Day 0 (mg) | Weight on last day (mg) | Daily growth rate (mg d$^{-1}$) |
|---|---|---|---|---|---|---|
| I-flow | 14 | 1.7 ± 0.2 | 2.13 ± 0.25 | 55.7 ± 4.9 | 58.9 ± 6.9 | 0.229 |
| II-flow | 21 | 3.3 ± 0.5 | 4.13 ± 0.63 | 55.4 ± 5.7 | 64.6 ± 9.3 | 0.438 |
| IIb-flow | 21 | 0 | 0 | 64.6 ± 9.3 | 51.5 ± 8.6 | −0.624 |
| III-flow | 14 | 5.0 ± 0.5 | 6.26 ± 0.63 | 55.3 ± 6.3 | 66.7 ± 10.8 | 0.814 |
| IV | 15 | 10.0 ± 0.8 | 12.51 ± 1.00 | 58.1 ± 6.8 | 83.9 ± 10.9 | 1.720 |
| VI | 15 | 20.8 ± 1.4 | 26.02 ± 1.75 | 56.5 ± 6.5 | 90.3 ± 9.8 | 2.253 |
| VIb | 15 | 0 | 0 | 90.3 ± 9.8 | 78.8 ± 12.7 | −0.766 |

From the data shown in Table 1 it was possible to calculate the instantaneous specific growth rate $\mu = \ln(W_t/W_0)\ t^{-1}$. In the eutrophicated Odense Fjord the mean specific growth rate of worms was 0.024 ± 0.010 d$^{-1}$ at a mean chlorophyll *a* concentration of 11.2 ± 2.7 $\mu$g l$^{-1}$. The maximal growth rate of 0.039 d$^{-1}$ or 3.9% d$^{-1}$ was found at Stn OF-V (see Fig. 1). In the unpolluted Pughavn at Fyns Hoved (i.e. Stns FH-I, FH-II & FH-III, see Fig. 1) the mean instantaneous specific growth rate was 0.015 ± 0.005 d$^{-1}$ at a mean chlorophyll *a* concentration of 1.8 ± 0.5 $\mu$g l$^{-1}$.

Fig. 4 showns 2 series of laboratory clearance experiments performed at high algal (*Rhodomonas* spp.) concentrations (mean concentration of 4 to 6 × $10^4$ cells ml$^{-1}$ or ca 50 $\mu$g chl *a* l$^{-1}$), maintained over 9 h by new algal additions (arrows). About 85% of the worms were actively filtering, and it is notable that the clearance rate (evaluated from the straight-line decrease of algal concentration in the semi-log plot; see Fig. 4) was high and constant, without any indication of a functional response or a saturation/overloading of the digestive system leading to reduced clearance rate.

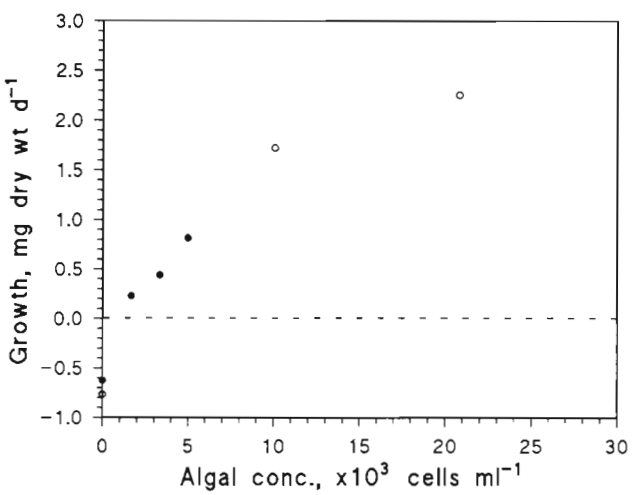


Fig. 3. *Nereis diversicolor*. Mean growth rates of worms (n = ca 20) as a function of algal concentration in laboratory experiments: (●) 'flow-system'; (○) 'closed-system'

## DISCUSSION

The present work shows that the facultative filter-feeding *Nereis diversicolor* is able to grow on phytoplankton when this is the sole food source in field situations, and when fed in the laboratory on a diet of monoculture suspended algal cells, worms are able to obtain growth rates comparable to those in the wild. The growth experiments clearly demonstrate that *N. diversicolor* has the ability to live as a true suspension-feeder.

It is notable that the estimated growth (0.35 mg d$^{-1}$) at the low algal concentration (1.7 × $10^3$ cells ml$^{-1}$; see Table 4) was in reasonably good agreement with the actual growth rate (0.23 mg d$^{-1}$, see Table 3). But at the high algal concentration of 5000 cells ml$^{-1}$ there was a less satisfactory agreement which may be due to an over-estimation of the assimilation efficiency (which apparently decreases above 5000 cells ml$^{-1}$ as evident from the high carbon content in faeces, Table 5).

From Table 2 it can be seen that the density and population filtration rate vary between stations in the same area. At present we cannot interpret the distribution of *Nereis diversicolor*. But from estimates of the potential ability of the worms to filter the entire overlying water column (up to 10 to 20 times per day), and from the measured chlorophyll *a* concentrations it is clear that the worms may exert a heavy grazing impact on the phytoplankton. However, it is also evident that the worms are not – probably due to insufficient vertical mixing – able to reduce the phytoplankton completely. A very thin (a few cm) boundary layer of water directly above the worms may inevitably result in the worms refiltering the same water many times, giving rise to strong intraspecific competition for food and consequently reduced growth. The observed high growth rates of *N. diversicolor* elevated just 15 cm above the bottom (Table 1) supports the existence of inefficient

Table 4. *Nereis diversicolor*. Daily individual energy budgets and estimated growth when fed different concentrations of *Rhodomonas* spp. in laboratory growth experiments. Metabolism was estimated by using negative growth in the experiment without algal cells (i.e. starvation = -0.624 mg $d^{-1}$, Table 3). Calculations of assimilated energy are based on values from Table 5. The clearance values have been reduced to 70%, to match actual filtering activity

| Expt | Duration (d) | Algal cell conc. ($C$) ($\times 10^{-3}$ ml $l^{-1}$) | Chl *a* conc. ($\mu$g $l^{-1}$) | Volume of water filtered ($V$) ($l^{-1}$ $d^{-1}$) | No. of cells ingested ($C \times V$) ($\times 10^{6}$ $d^{-1}$) | Energy ingested (J $d^{-1}$) | Assimilated energy ($A$) (J $d^{-1}$) | Respiration ($R$) (J $d^{-1}$) | Estimated growth ($A - R$) (J $d^{-1}$) | Estimated daily growth rate (mg $d^{-1}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| I-flow | 14 | 1.7 ± 0.2 | 2.13 ± 0.25 | 5.54 | 9.42 | 21 | 18 | 11.5 | 6.5 | 0.35 |
| II-flow | 21 | 3.3 ± 0.5 | 4.13 ± 0.63 | 6.31 | 20.81 | 47 | 42 | 11.5 | 30.5 | 1.66 |
| IIb-flow | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 11.5 | 11.5 | -0.62 |
| III-flow | 14 | 5.0 ± 0.5 | 6.26 ± 0.63 | 5.98 | 29.89 | 67 | 60 | 11.5 | 48.5 | 2.64 |
| IV | 15 | 10.0 ± 0.8 | 12.51 ± 1.00 | 7.49 | 74.90 | 169 | - | - | - | - |
| VI | 15 | 20.8 ± 1.4 | 26.02 ± 1.75 | 8.00 | 166.42 | 375 | - | - | - | - |

vertical mixing and intraspecific competition. Worms transferred to Stn FH-4, in the middle of a large mussel bed, showed negative growth due to competition with the mussels. The negative growth in Kertinge Nor was undoubtedly due to the extremely high concentration (44.5 $\mu$g chl *a* $l^{-1}$) of cyanobacteria which completely dominated the phytoplankton during the late summer and autumn of 1992. This interpretation is supported by a laboratory test with water from Kertinge Nor. Starved worms from Odense Fjord promptly started filtering the water but ceased after a few hours. Small clots of cyanobacteria wrapped in mucous and spread both within and outside the tubes showed that the trapped bacteria were not ingested. The unwillingness of the worms to ingest cyanobacteria was probably not due to overloading or saturation of the digestive system.

The maximal increase of 72% in body mass during 14 d found in Odense Fjord (Stn OF-V in Table 1) corresponds to an instantaneous specific growth rate of $\mu = 0.039$ $d^{-1}$, which may be compared to the maximal value of $\mu = 0.031$ $d^{-1}$ obtained in the laboratory experiments. A maximal specific growth rate, representing the growth potential, of $\mu_{max} = 0.04$ $d^{-1}$ seems to apply for the standard size class (47 to 71 mg dry wt) of worms used. In experiments with *Nereis diversicolor* fed on a surplus of Tetramin (a freeze-dried flaked fish food substrate) as an artificial food, Esnault et al. (1990) found maximal growth rates corresponding to $\mu_{max} = 0.04$ to 0.06 $d^{-1}$ for 3 to 5 mg dry wt worms. The mean $\mu$ for worms at Odense Fjord and at Fyns Hoved (Pughavn) was 0.024 and 0.015 $d^{-1}$ respectively. This difference in growth can be explained by a generally higher algal concentration (6 times) in Odense Fjord, though it is not obvious how to interpret the modest difference in growth rates between the 2 localities. Differences in water depth, vertical mixing, current flow at the bottom, and intraspecific competition may all be factors of importance for the chlorophyll *a* concentration in surface water samples which may not always reflect the near-bottom concentrations.

The presence of many particularly large *Nereis diversicolor* in Kertinge Nor (Table 2) may be explained by observed high concentrations of especially diatoms (*Skeletonema costatum* and *Stephanodiscus hantzschii*), presumably with a high nutritive value, dominating the phytoplankton during spring until the cyanobacteria took over in June.

The specific growth rates measured in the present work can be compared with growth rates measured in the Ythan Estuary, Scotland, where a cohort of *Nereis diversicolor* (5 to 22 mg dry wt) had a specific growth

Table 5. *Nereis diversicolor*. Carbon content in faeces and assimilation efficiency in laboratory experiments

| Expt | Algal cell conc. (± SD) ($\times 10^{3}$ ml $l^{-1}$) | Dry wt of ingested cells (mg $d^{-1}$) | Dry wt of $C$ in ingested cells ($I$) ($\mu$g $d^{-1}$) | Faeces dry wt (mg $d^{-1}$) | $C$ content in faeces (%) | Dry wt of $C$ in faeces ($F$) ($\mu$g $d^{-1}$) | Assimilation efficiency $(I - F)/I$ (%) |
|---|---|---|---|---|---|---|---|
| I-flow | 1.7 ± 0.2 | 1.11 | 444.2 | 0.70 | 8.40 | 58.8 | 86.8 |
| II-flow | 3.3 ± 0.5 | 2.38 | 981.6 | 1.16 | 9.12 | 105.8 | 89.2 |
| III-flow | 5.0 ± 0.5 | 3.51 | 1409.9 | 2.07 | 6.88 | 142.4 | 89.9 |
| IV | 10.0 ± 0.8 | - | - | - | 12.39 | - | - |
| VI | 20.8 ± 1.4 | - | - | - | 14.62 | - | - |

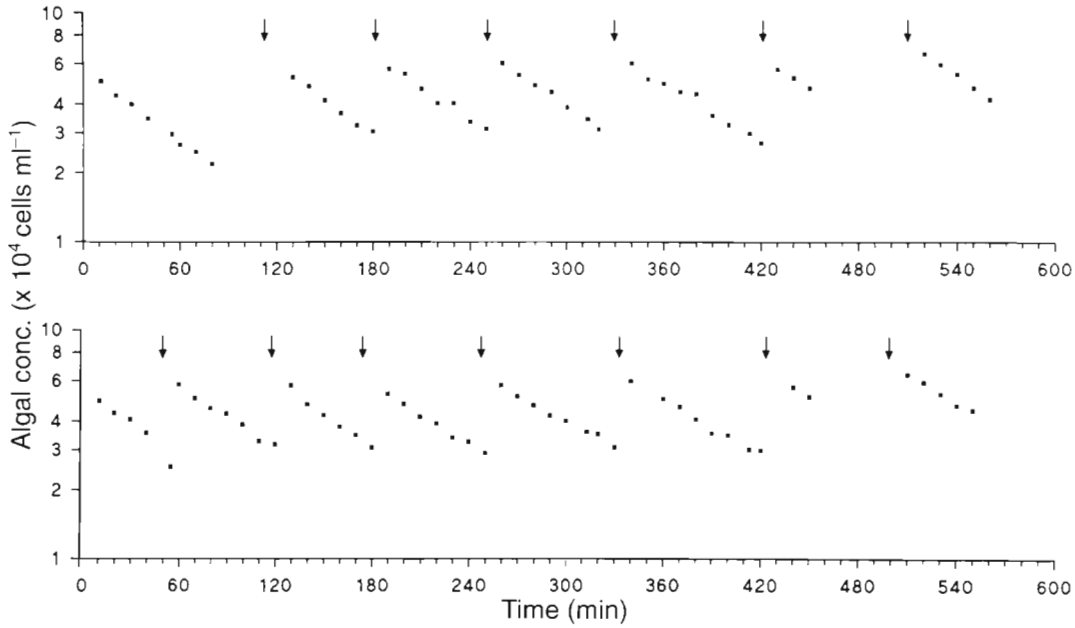


Fig. 4. *Nereis diversicolor*. Reduction in algal cell concentration due to grazing by 2 groups of worms (n = 25). Arrows indicate additions of algal suspension to the aquaria (volume = 10 l)

rate of approximately 0.015 $d^{-1}$ (Chambers & Milne 1975). In Norsminde Fjord, Denmark, a mean specific growth rate of 0.005 $d^{-1}$ can be calculated from data presented in Kristensen (1984), while worms in a comparable size-class (55 to 65 mg dry wt) grew at a rate of 0.0008 $d^{-1}$ in a shallow brackish-water pond in Belgium (Heip & Herman 1979). From the above considerations it may be concluded that (exclusively) suspension feeding *N. diversicolor* kept in glass tubes are able to attain growth rates comparable to those of worms living in natural sediment tubes in nature or grown on a surplus diet of animal matter (e.g. Tetramin). However, the maximal specific growth rate of *N. diversicolor* is smaller than $\mu_{max}$ = 0.09 $d^{-1}$ found for the obligate suspension-feeding mussel *Mytilus edulis* grown in net bags suspended in the Limfjorden, Denmark (Riisgård & Poulsen 1981) or grown under otherwise optimal conditions (Jørgensen 1990). Another feature by which *N. diversicolor* differs from obligate suspension feeders is the lack of a 'functional response' (or reduction in filtration rate due to overloading/saturation of the digestive system) (Fig. 4), as found in, for example, *M. edulis* (Riisgård 1991), in the suspension feeding polychaete *Sabella penicillus* (Riisgård & Ivarsson 1990), and in the ascidian *Ciona intestinalis* (Petersen & Riisgård 1992). The mechanism of this difference between obligate filter-feeders and the facultatively filter-feeding *N. diversicolor* remains unknown.

The estimated growth of the worms of 0.35 mg $d^{-1}$ at 1700 cells $ml^{-1}$ (Table 4) is in reasonably good agreement with the actual growth of 0.23 mg $d^{-1}$, but the energy budget is less satisfactory at the high algal concentrations. The negative growth (−0.624 mg $d^{-1}$ = 11.5 J $d^{-1}$) in the laboratory experiment without algal addition (IIb-flow in Table 3) was used as a measure for metabolism in the present work. This measure of metabolism is probably an underestimate because respiration may decrease in starved worms, as found for *Nereis virens*, where the oxygen uptake decreased 50% during a period of 5 d starvation (Kristensen 1989). Furthermore, the estimate of metabolism used did not take into consideration the extra metabolic costs of growth. Uncertainty in the estimation of the assimilation efficiency (Table 5), due to difficulties in making accurate quantitative collections of faeces, remains another factor influencing the reliability of the energy budget (Table 4). In growth experiments with the facultative suspension-feeder *Lanice conchilega*, Buhr (1976) found assimilation efficiencies of 70 to 77% which were lower (and probably more realistic) than the 87 to 90% shown in Table 5 for the animals in this study.

The water depth and population filtration capacities for worms from the different areas are shown in Table 2. From this it is clear that the grazing impact of *Nereis diversicolor* may be pronounced, especially if the water column is well mixed by the wind action. In Odense Fjord (Stn OF-I) and Fyns Hoved (Stn FH-I) the maximal estimated population filtration capacities of 9.5 and 4.6 $m^3$ $d^{-1}$ $m^{-2}$ respectively correspond to volumes of 30 and 15 times greater than the water column at these 2 sites. As a consequence *N. diversi-*

*color* may experience periods when low phytoplankton concentrations prevent filter-feeding activity. It is thus of considerable ecological importance to document the percentage of total time used for suspension-feeding by *N. diversicolor* in nature – as well as the time spent resting (passive) or on alternative ways of feeding (surface deposit-feeding, predation).

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