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# Feeding, growth and respiration in the polychaetes *Nereis diversicolor* (facultative filter-feeder) and *N. virens* (omnivorous) — a comparative study

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ABSTRACT: The polychaetes *Nereis diversicolor* and *N. virens* were fed various amounts of shrimp meat in laboratory experiments and linear relationships between specific growth rate and specific respiration rates were found. From this relation the energy cost of growth ('specific dynamic action', SDA) was found to be 20 to 26% of the growth. The starvation respiration rate (maintenance) ($R_m$, µl $O_2$ $h^{-1}$ $ind.^{-1}$) as a function of body mass ($W$, g dry wt) was: $R_m = 1306 W^{1.2}$ and $R_m = 704 W^{1.0}$ for *N. diversicolor* and *N. virens*, respectively. For worms fed shrimp meat the maximum specific growth rate was 7% $d^{-1}$ in *N. diversicolor* and 5.9% $d^{-1}$ in *N. virens*. In filter-feeding *N. diversicolor* fed algal cells (6.2 µm diameter *Rhodomonas* sp.) there was a strong correlation between ingestion rate and growth rate, the maximum specific growth rate being 3% $d^{-1}$. No functional response was seen even at the highest algal concentration of $2 \times 10^4$ cells $ml^{-1}$. It is possible that filter-feeding in *N. diversicolor* is a relatively recent adaptation which has resulted in a broader fundamental niche compared to that of the closely related *N. virens*. This filter-feeding adaptation may possibly explain the coexistence of the 2 polychaetes in certain brackish water areas.

KEY WORDS: Feeding · Growth · Respiration · Costs of growth · Specific dynamic action (SDA) · Net growth efficiency · Filter-feeding

## INTRODUCTION

The closely related polychaetes *Nereis diversicolor* and *N. virens* are commonly found in shallow brackish soft-bottoms in the temperate zone of the northern hemisphere (Bass & Brafield 1972, Kristensen 1984). Both species live in U-shaped burrows in the sediment, and they both utilize 2 different foraging strategies. They use their powerful jaws as predators or scavengers (Gross 1921, Copeland & Wieman 1924, Goerke 1971, Tenore & Gopalan 1974, Heip & Herman 1979, Rönn et al. 1988), or obtain nourishment by swallowing the uppermost sediment layer with its content of detritus and microbenthic algae (Wells & Dales 1951, Goerke 1971). The 2 worm species differ from each other in several ways. As regards salinity tolerance, *N. diversicolor* is euryhaline, adult individuals resisting salinities (S) down to 2–3‰, while *N. virens* is seldom found below 15‰ S (Jørgensen & Dales 1957, Hartmann-Schröder 1971, Oglesby et al. 1982, Kristensen 1988). The different abilities of the 2 species to detoxify sulfide in pore water have also been suggested to play a role in determining their distribution when they are living in the same area (Miron & Kristensen 1993). However, the most conspicuous difference between the 2 otherwise omnivorous polychaetes is the unique ability of *N. diversicolor* to obtain nourishment as a facultative filter-feeder (Goerke 1966, Riisgård 1991b, Riisgård et al. 1992, Vedel & Riisgård 1993, Vedel et al. 1994). It has recently been discovered that *N. diversicolor*, just like a typical obligate filter-feeder, may satisfy its metabolic requirements from a diet of phytoplankton. If the phytoplankton concentration is sufficiently high, *N. diversicolor* shifts from predatory/

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surface deposit-feeding to suspension-feeding. The worm spins a funnel-shaped mucous net-bag and pumps water through the net by vigorously undulating body movements. After a period of pumping the worm moves forward to swallow the net-bag with entrapped food particles. This feeding behaviour is maintained as long as the phytoplankton concentration is above the 'trigger' level of 1 to 3 µg chlorophyll $a\ l^{-1}$ (for a review, see Riisgård 1994).

In individuals of comparable size there are no conspicuous morphological differences between *Nereis virens* and *N. diversicolor*, and filter-feeding is probably a relatively recent adaptation in the latter (see also Riisgård & Larsen 1994). In the present study we investigated the biological significance of the adaptation of *N. diversicolor* to filter-feeding. The maximum specific growth rates of the 2 species feeding on meat (i.e. predatory living) were compared with the specific growth rate of *N. diversicolor* feeding on suspended algal cells (i.e. filter-feeding). As a complementary evaluation the specific respiration rate, the respiratory energy cost of growth (specific dynamic action, SDA), and the net growth efficiency obtained in feeding experiments were compared. The overall aim of the experiments was to reveal adaptations originating from possible interspecific competition and niche differentiation.

## MATERIALS AND METHODS

The polychaetes *Nereis diversicolor* and *N. virens* were collected from mud flats in the inner part of the shallow cove Kertinge Nor (14 to 22‰ S), Denmark.

Population investigations were made from September 1992 to August 1993 by taking samples (n = 10) at each of 8 evenly distributed stations located in the southernmost part of Kertinge Nor. The stations covered a total area of about 1 $km^2$, corresponding to the locality covered by Stns 1 to 6 in the work of Miron & Kristensen (1993). The polychaetes were sampled at water depths of 0.5 m from randomly chosen sediment cores (143 $cm^2$, 25 cm deep) which were sieved (1 mm mesh size). The worms were brought to the nearby Fjord Biological Laboratory, Kerteminde, and individually weighed (wet weight) to determine the population size distribution and density.

Laboratory feeding and growth experiments using shrimp meat were performed with *Nereis diversicolor* and *N. virens* of 30 to 92 and 34 to 109 mg body dry weight respectively. The worms were transferred to U-formed glass tubes as described by Vedel & Riisgård (1993) and acclimatized to the experimental conditions (15‰ S, 15°C) for 3 d. Ten glass tubes were mounted on a rack maintaining the tubes in an upright position at 2 cm intervals and the rack was placed in an aerated aquarium (20 l) with seawater filtered by the mussel *Mytilus edulis*. Every day the seawater was changed and the aquarium cleaned. *N. diversicolor* and *N. virens* were fed a known amount of shrimp meat. The daily meat ration was determined on the basis of previously measured maximum ingestion rates for worms fed with surplus shrimp meat for 2 wk. Small pieces of shrimp meat were individually fed to the worms twice a day during the experimental period (4 to 14 d). Before each meal all shrimp meat remains from the previous feeding were carefully removed from the glass tubes and weighed to calculate the individual ingestion rate. The effects of different salinities (5, 10, 15, 20 and 25‰) on the growth rate were studied in additional growth experiments performed with worms fed on surplus shrimp meat.

The flagellate *Rhodomonas* sp. (mean diameter 6 2 µm) from a continuous culture (constant light, pH and dilution rate) was used in feeding and growth experiments with *Nereis diversicolor* (n = 10). Different algal concentrations (3, 5, 7, 10, 15 and $20 \times 10^3$ cells $ml^{-1}$) were maintained in the growth aquarium (same set-up as described above) by continuous addition of *Rhodomonas* sp. cells. Throughout the experimental period (7 to 10 d) the algal concentration in the growth aquarium was checked twice a day. The pumping activity (defined as the percentage of worms actively filter-feeding) and stroke frequency (i.e. waving body motion for pumping water) were determined by inspection (10 min periods) 2 or 3 times a day.

During each growth experiment with *Nereis diversicolor* fed algae, the filtration rate was measured daily. The algal supply was turned off while the filtration rate ($F$, defined as clearance of 100% efficiently retained particles = pumping rate) was measured according to Riisgård (1991b) by using the equation:

$$F = V/(tn) \times \ln(C_0/C_t) \quad (1)$$

where $C_0$ and $C_t$ are algal concentration at time 0 and time $t$ respectively; $V$ is water volume in the aquarium; $n$ is the number of actively filtering worms. The algal concentration in the growth aquarium was measured by means of an electronic particle counter (Elzone 80 XY).

Initial and final wet weights of worms in growth experiments were determined after 24 h of starvation to empty the gut and 2 min drainage on filter paper. The dry weight was determined after drying for 24 h at 105°C.

The specific growth rate ($\mu$, $d^{-1}$) of *Nereis diversicolor* and *N. virens* was calculated according to Jørgensen (1990) by using the equation:

$$\mu = \ln(W_t/W_0)t^{-1} \quad (2)$$

where $W_0$ and $W_t$ are mean body mass (wet weight) of the polychaetes on Day 0 and Day $t$ respectively.

Oxygen consumption was repeatedly measured in *Nereis diversicolor* and *N. virens* throughout the growth experiments by using either a 'closed' or an 'open' system for respiration measurements.

**'Closed' respiratory system.** All measurements were made approximately 30 min after feeding. The worms were transferred to straight glass tubes with the same diameter. Either 2 or 3 tubes were placed in a respiration chamber consisting of a plexiglass tube (length = 20 cm, inner diameter = 21 mm) with one end permanently closed and the other end tightened with a plexiglass collar with an oxygen electrode inserted into the chamber and connected to an oxygen monitor (WTW, microprocessor based oximeter, OXI 196) and a recorder (Servogor S). A magnetic stirrer (Oximeter-RZ 90) was mounted close to the membrane of the electrode. In the other end of the respiration chamber was placed a small coated magnet, and both stirrers were coupled to an outside rotating magnet. The temperature was held constant (15°C) by placing the respiration chamber in a water bath. All measurements were conducted at 15‰ S. During each respiration measurement (approximately 30 min) the decreasing dissolved oxygen tension was continously monitored. Control measurements without worms were performed between every second respiration measurement. The oxygen uptake rate was calculated from the decrease of dissolved oxygen tension taking temperature, salinity and pressure into consideration. Comparison of oxygen uptake rates requires similar pumping activity of the worms and the body stroke frequency was measured twice during each measurement.

**'Open' respiratory system.** Measurements of respiration rate were performed in a special computer-controlled apparatus which will be described in detail elsewhere (Eriksen & Iversen unpubl.). Briefly, a thermostated measuring chamber was equipped with a galvanic oxygen electrode (Mackereth 1964). The chamber was designed to exclude air bubbles completely from the liquid phase. Oxygen dissolved in air-saturated water was added to the system using solenoid valves. Recording the amount of air-saturated water required to maintain constant dissolved oxygen tensions in the measuring chamber allowed on-line determination of respiration rate of the specimen. Temperature and salinity were kept constant (15°C, 15‰ S), and the different steady-state values of dissolved oxygen tension were maintained for about 8 h. Previous to respiration measurements the polychaetes (n = ca 7) were transferred to transparent silicone rubber tubes, with dimensions corresponding to the glass tubes and mounted in the respiration chamber. Worms in growth experiments were fed approximately 11 h before the beginning of the measurements. The activity, measured in a single experiment, was determined as the number of ventilation pumping periods as well as the number of head to tail turns of the worms.

**Calculation of energetic parameters.** By simultaneous measurements of respiration and growth in specimens with body mass $W$ the relationship between total respiration rate ($R$) and growth rate ($\mu W$) may be described according to Kiørboe et al. (1987):

$$R = R_m + n\mu W$$

or

$$R/W^b = a + n\mu W^{1-b} \quad (3)$$

where $R_m = aW^b$ is the maintenance (measured as starvation respiration rate) and $n$ is the energy cost per unit of growth. In the present work the energy cost of growth was estimated from experimentally determined values of $R_m$, $R$ and $\mu$ which enables the identification of $n$ (i.e. slope of regression line for $R/W^b$ as a function of $\mu W^{1-b}$).

The energy balance of a polychaete can be expressed as:

$$I = P + R + E \quad (4)$$

where $I$ is ingestion, $P$ is production (growth), $R$ is respiration, and $E$ is excretion. Further, assimilation, $A = P + R$, and the net growth efficiency, $NGE = P/A$. In the present work $NGE$ was calculated according to Hamburger et al. (1983):

$$NGE = P/A = P/(P + R) = W_D\mu/(W_D\mu + R) = \mu/(\mu + R_s) \quad (5)$$

where $W_D$ = body dry weight and $R_s = R/W_D$.

**Conversion factors.** Dry weight ($W_D$, mg) was found to correlate with wet weight ($W_W$, mg) of *Nereis diversicolor* and *N. virens* according to the equations: $W_D = 0.124 W_W$ ($r^2 = 0.98$, n = 65, range 25 to 100 mg dry wt) and $W_D = 0.119 W_W$ ($r^2 = 0.97$, n = 65, range 25 to 100 mg $W_D$) respectively. The following equivalencies were used: 1 mg dry wt worm = 8 mg wet wt = 18.4 J (Chambers & Milne 1975); 1 ml $O_2$ = 19.88 J. The following relationship between *Rhodomonas* sp. and energy content was used: 2.25 µJ cell$^{-1}$ (Vedel & Riisgård 1993). 1 mg wet wt shrimp meat = 3.3 J (data from Royal Greenland, Aalborg, Denmark).

## RESULTS

Population size and distribution of *Nereis diversicolor* and *N. virens* in the shallow cove of Kertinge Nor are shown in Fig. 1. The 2 species coexist and are widely distributed in the investigated area. The maximum worm population densities (>500 ind. m$^{-2}$) and biomass values (>50 g $W_W$ m$^{-2}$) were found in summer though no general growth pattern could be seen.

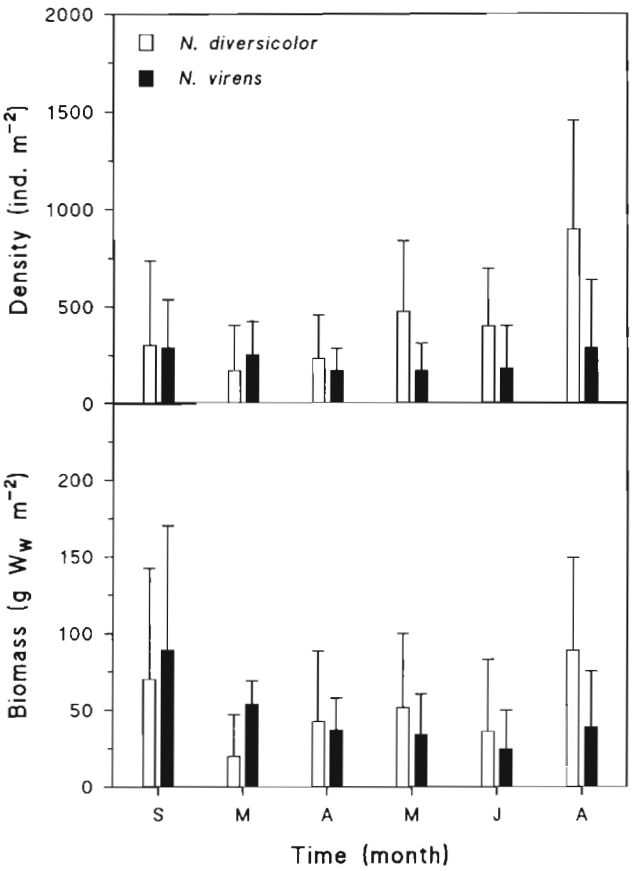


Fig. 1. *Nereis diversicolor* and *N. virens*. Population density and biomass of worms collected in the southernmost part of Kertinge Nor, Denmark, in the months: S: September 1992; M–J: March to June 1993; A: August 1993. Mean (n = 80) and standard deviation are shown

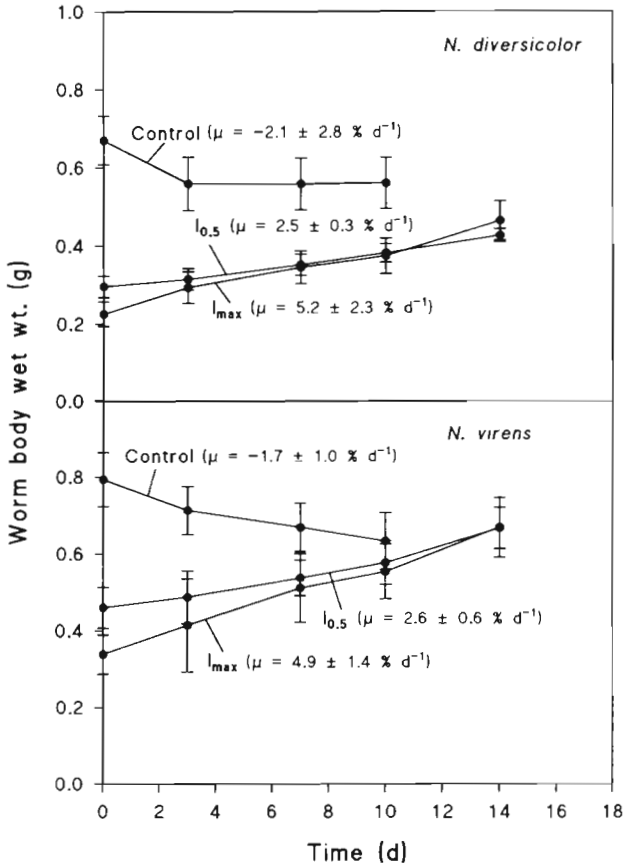


Fig. 2. *Nereis diversicolor* and *N. virens*. Mean (± SD) body wet weight as a function of time for worms (n = 8) fed different shrimp meat rations in growth experiments. $I_{max}$: maximum food ration; $I_{0.5}$: half maximum food ration; control: starved worms. Mean (± SD) specific growth rates ($\mu_{mean}$) for the total period are given in parenthesis

The laboratory growth experiments suggest that different salinity tolerance may be a decisive factor in the distribution of the 2 polychaete species in brackish and marine waters (Table 1) because *Nereis virens* is inhibited at low salinities (<15‰) but seems to be more competitive at higher salinities (>20‰). At salinities of 15 to 20‰ both *N. diversicolor* and *N. virens* achieve high and near identical maximum specific growth rates (Table 1) indicating that different salinity preferences may not be crucial for their distribution in the Kertinge Nor which has a mean salinity of approximately 18‰.

Table 1. *Nereis diversicolor* and *N. virens*. Mean specific growth rate ($\mu$) of worms (n = 8) fed maximum shrimp meat rations in 4 to 14 d growth experiments at different salinities

| Species | Body wet wt (mg) Initial | Final | Growth period (d) | Salinity (‰) | Specific growth rate, $\mu$ (% d$^{-1}$) |
|---|---|---|---|---|---|
| *N. diversicolor* | 247 ± 10 | 253 ± 7 | 5 | 5 | 0.4 |
| | 474 ± 6 | 535 ± 6 | 11 | 10 | 1.1 |
| | 243 ± 10 | 549 ± 13 | 14 | 15 | 5.8 |
| | 254 ± 5 | 546 ± 8 | 14 | 20 | 5.4 |
| | 275 ± 5 | 472 ± 7 | 14 | 25 | 3.8 |
| *N. virens* | 380 ± 11 | 294 ± 14 | 4 | 5 | −6.5 |
| | 293 ± 8 | 237 ± 9 | 4 | 10 | −5.3 |
| | 284 ± 8 | 515 ± 11 | 10 | 15 | 5.9 |
| | 333 ± 14 | 685 ± 15 | 14 | 20 | 5.1 |
| | 221 ± 7 | 357 ± 10 | 10 | 25 | 4.7 |

Laboratory growth experiments performed at 15‰ S show that *Nereis diversicolor* and *N. virens* are able to grow on shrimp meat as the only food source (Fig. 2). The maximum specific growth rates obtained, representing the growth potential on a shrimp meat diet, were 7 and 5.9% d$^{-1}$ for *N. diversicolor* and *N. virens*, respectively (see Tables 1 & 2). The growth of worms

was strongly correlated with ingestion rates as apparent from Fig. 3 and Table 2. Maximum observed specific growth rates were obtained at mean ingestion rates of 42 and 50 mg shrimp meat ind.$^{-1}$ d$^{-1}$, eqivalent to 139 and 165 J ind.$^{-1}$ d$^{-1}$ for *N. diversicolor* and *N. virens*, respectively. *N. diversicolor* grew on a pure diet of suspended algal cells (*Rhodomonas* sp.), but the maximum specific growth rate attained was lower than that obtained on a pure shrimp meat diet (Fig. 3). The maximum specific growth rate on algal cells was 3% d$^{-1}$ at $2 \times 10^4$ cells ml$^{-1}$ corresponding to 288 J ind.$^{-1}$ d$^{-1}$ (Fig. 3, Table 2).

In the algal growth experiments with *Nereis diversicolor* approximately 75% of the worms were actively filter-feeding (mean stroke freqency = 61 ± 4 strokes min$^{-1}$). It is notable that the filtration rate of 5.76 to 6.40 l ind.$^{-1}$ d$^{-1}$ was independent of the algal concentration, without indication of a 'functional response' or of a reduced activity due to saturation/overloading of the digestive system (Table 2).

The maintenance respiration rate ($R_m$, µl $O_2$ h$^{-1}$) of starved worms (10 to 14 d starvation) was directly proportional to body mass ($W$, g dry wt) for worms with same ventilation pumping activity, and the relationship can be expressed as $R_m = 1306 W^{1.2}$ and $R_m = 704 W^{1.0}$ for *Nereis diversicolor* and *N. virens*, respectively (Fig. 4).

Table 2. *Nereis diversicolor* and *N. virens*. Mean (±SD) algal cell concentration (*Rhodomonas* sp.), filtration rate, ingestion rate and specific growth rate ($\mu$) of worms (n = 10) during 7 to 14 d growth experiments

**Algae as food (for *Nereis diversicolor*)**

| Algal conc. (× $10^3$ cells ml$^{-1}$) | Filtration rate (l ind.$^{-1}$ d$^{-1}$) | Ingestion rate (×$10^6$ cells ind.$^{-1}$ d$^{-1}$) | Growth, $\mu$ (% d$^{-1}$) |
|---|---|---|---|
| 3 ± 0.2 | 5.8 | 17.3 | 0.4 |
| 5 ± 0.4 | 6.0 | 31.2 | 0.7 |
| 7 ± 0.4 | 6.0 | 41.7 | 1.5 |
| 10 ± 0.7 | 6.1 | 61.0 | 2.2 |
| 15 ± 0.8 | 5.8 | 87.0 | 2.7 |
| 20 ± 1.2 | 6.4 | 128.0 | 3.0 |

**Shrimp meat as food**

| Species | Ingestion rate (mg ind.$^{-1}$ d$^{-1}$) | Growth, $\mu$ (% d$^{-1}$) |
|---|---|---|
| *N. diversicolor* | 2.8 ± 0.5 | 0.7 |
| | 8.7 ± 1.2 | 2.4 |
| | 10.4 ± 1.1 | 2.9 |
| | 15.8 ± 2.6 | 3.6 |
| | 21.3 ± 4.9 | 4.3 |
| | 37.6 ± 5.2 | 6.3 |
| | 40.4 ± 4.3 | 6.7 |
| | 42.0 ± 5.6 | 7.0 |
| *N. virens* | 12.3 ± 1.6 | 2.0 |
| | 13.0 ± 1.4 | 2.1 |
| | 15.1 ± 1.6 | 2.6 |
| | 19.9 ± 1.7 | 3.5 |
| | 22.6 ± 0.9 | 4.0 |
| | 37.7 ± 3.1 | 5.0 |
| | 46.6 ± 4.8 | 5.3 |
| | 50.0 ± 5.2 | 5.6 |

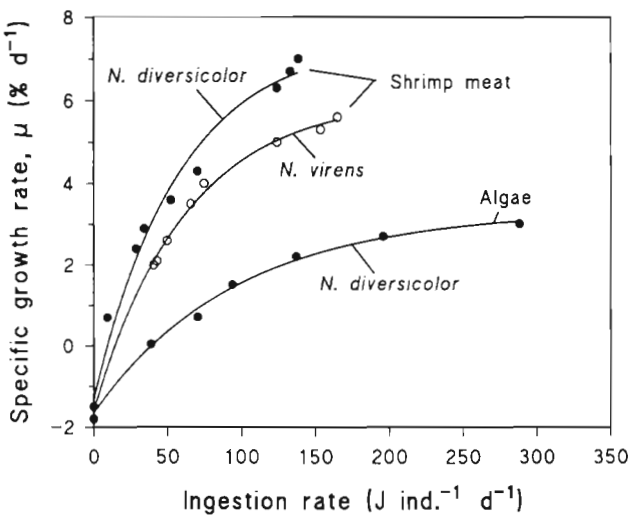


Fig. 3. *Nereis diversicolor* and *N. virens*. Mean specific growth rate ($\mu$) as a function of ingestion rate for worms (n = ca 10) fed algae (*Rhodomonas* sp.) and shrimp meat. Curves fitted by eye

Fig. 5 shows the specific respiration rate for *Nereis diversicolor* and *N. virens* fed a maximum shrimp meat ration during the first 14 d and then starved during the remaining experimental period of 28 d. It is seen that the specific respiration rate increased during the whole feeding period (Days 0 to 14) followed by a decrease to approach the original level after a few days of starvation. The total increase of the specific respiration rate at the end of the feeding period (Day 14) was 46 and 50% for *N. diversicolor* and *N. virens*, respectively.

In the present work the exponent $b \approx 1$ (cf. Fig. 4), so Eq. (3) reduces to $R = n\mu + a$. From Fig. 6 it appears that the relationship between total specific respiration rate ($R_t$) and specific growth rate ($\mu$) may be expressed by this linear function, where $n$ is the slope of the regression line and $a$ is the specific respiration rate ($R_m$) at zero growth rate. As $n$ expresses the energy cost per unit of growth, cf. Eq. (3), it is seen that the energy cost of growth constituted 26% and 20% of the growth for *Nereis diversicolor* and *N. virens*, respectively (when the respiration measurements were performed within

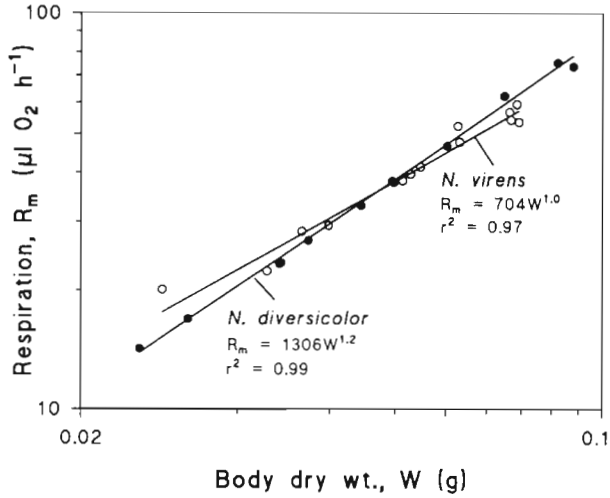


Fig. 4. *Nereis diversicolor* and *N. virens*. Mean starvation respiration rate ($R_m$) as a function of body dry weight ($W$) for worms with similar ventilation activities. Regression lines and their equations are shown

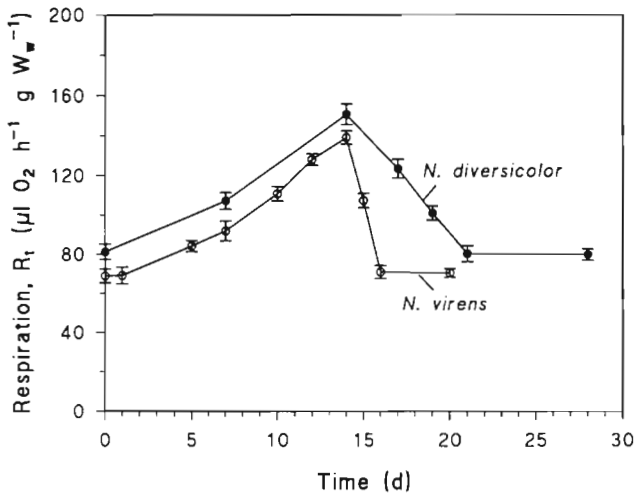


Fig. 5. *Nereis diversicolor* and *N. virens*. Mean (±SD) specific respiration rate ($R_t$) as a function of time for worms (n = 8) fed daily maximum shrimp meat rations. Feeding started at Day 0 and ceased at Day 14

30 min of starvation; Fig. 6A, C). When, however, the respiration rate was measured after 11 h of starvation (Fig. 6B, D) the slope of the lines was reduced considerably (i.e. $n$ = 8 to 11%) in agreement with the decrease of respiration rates after starvation (Fig. 5).

From Fig. 6B it is seen that the specific respiration rate of *N. diversicolor* is apparently independent of the food item used (algal cells or shrimp meat) though this observation does not harmonize with the finding that the maximum specific growth rate is considerably

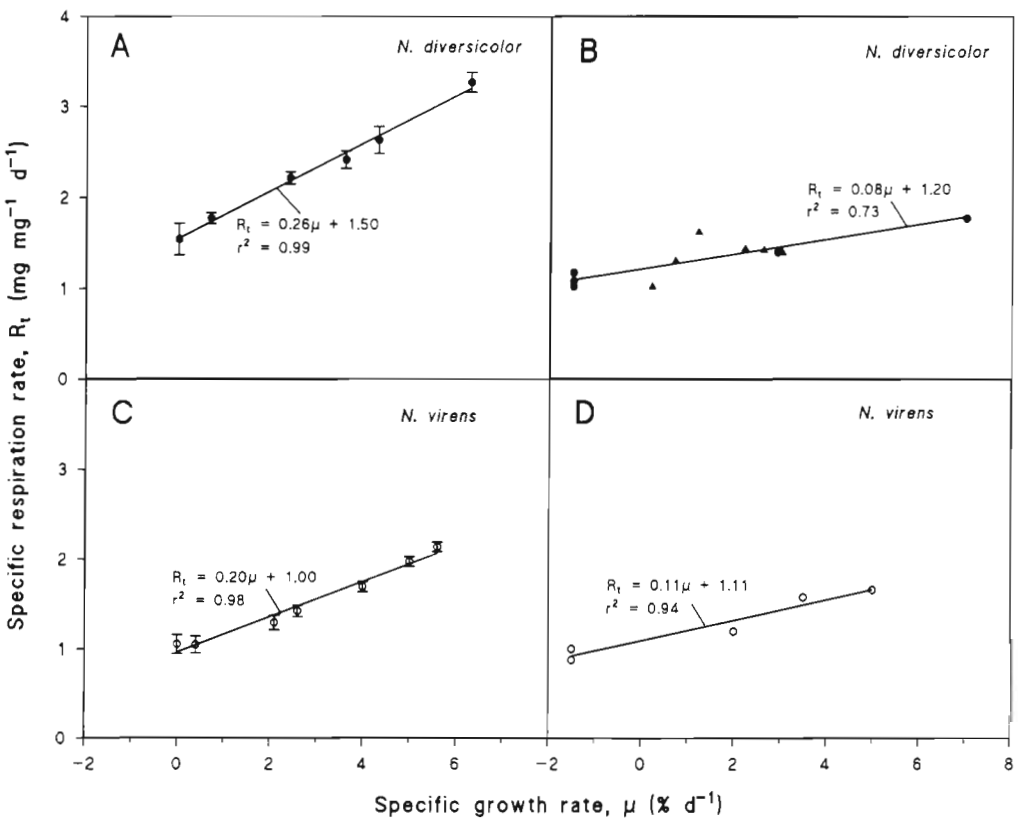


Fig. 6. *Nereis diversicolor* and *N. virens*. Specific respiration rate ($R_t$) as a function of specific growth rate ($\mu$) of worms (n = 10) fed shrimp meat (●/○) and algal cells (▲). (A, C) Measured within 30 min after feeding in the 'closed' system. (D, B) Measured 11 h after feeding in the 'open' system. Respiration expressed in 'worm wet wt equivalents' Regression lines and their equations are shown

lower on a diet of algae than on a diet of shrimp meat (Fig. 3).

Fig. 7 shows the relationship between the specific growth rate ($\mu$) and net growth efficiency (*NGE*) in *Nereis diversicolor* and *N. virens* fed shrimp meat (based on data in Table 3). It is seen that the maximum *NGE* approaches 70% for *N. virens* whereas *NGE* is lower for *N. diversicolor* at all specific growth rates. It is noteworthy that the specific growth rate may be far from fully exploited even at relatively high *NGE*. A high *NGE* of 50%, corresponding to about two-thirds of the maximum *NGE*, was obtained at only one-third of the maximum specific growth rate.

Simultaneous measurements of specific respiration rates and ventilation pumping activities at different dissolved oxygen tensions show that *Nereis diversicolor* apparently reacts to decreasing dissolved oxygen tensions by a compensatory response in the ventilation pumping activity (Fig. 8). The specific respiration rate was constant (70 to 80 µl $O_2$ $h^{-1}$ $g^{-1}$ $W_W$) at dissolved oxygen tensions of 20 to 70% saturation, but decreased below 20% saturation to 30 µl $O_2$ $h^{-1}$ $g^{-1}$ $W_W$ at the lowest dissolved oxygen tension of 7%, corresponding to a 63% reduction of the specific respiration rate. Correspondingly, *N. diversicolor* showed the highest ventilation pumping activity (67%) near the 'critical' dissolved oxygen tension, i.e. about 20% saturation. The turning freqency of the worms in their tubes showed a similar pattern, but there were no turns below 15% dissolved oxygen tension and the freqency seemed more or less constant at dissolved oxygen tensions above 25%.

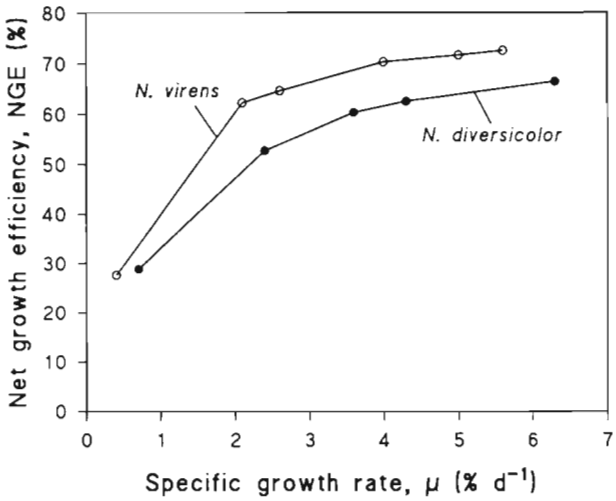


Fig. 7. *Nereis diversicolor* and *N. virens*. Relation between net growth efficiency (*NGE*) and specific growth rate ($\mu$) for worms (n = 8) fed shrimp meat

## DISCUSSION

There is a strong linear relationship between specific growth rate and specific respiration rate in both *Nereis diversicolor* and *N. virens* (Fig. 6). This increase of the specific respiration rate in response to feeding, also termed 'specific dynamic action' (SDA), amounted to 20 to 26% of the growth (Fig. 6A, C). Thus, SDA (i.e. mainly energy costs of biosynthesis; cf. Jørgensen 1990) constitutes a substantial proportion of the total energy released by respiration in worms growing at

Table 3. *Nereis diversicolor* and *N. virens*. Wet weight ($W_W$), dry weight ($W_D$), body stroke frequency ($S$), ventilation pumping period in percent of total time ($A$), total respiration rate ($R$), specific respiration rate ($R_s$) and net growth efficiency (*NGE*) for worms fed shrimp meat. Mean (±SD) (n = 8) given

| Species | Body weight (mg) | | Ventilation activity | | Respiration rate | | Growth | |
|---|---|---|---|---|---|---|---|---|
| | $W_W$ | $W_D$ | $S$ (strokes $min^{-1}$) | $A$ (%) | $R$ (µl $O_2$ $h^{-1}$) | $R_s$ (µl $O_2$ $h^{-1}$ $g^{-1}$ $W_D$) | $\mu$ (% $d^{-1}$) | *NGE* (%) |
| *N. diversicolor* | 490 ± 6.4 | 62.6 ± 5.1 | 35 ± 2 | 70 | 34.1 | 54.5 | −1.5 | – |
| | 415 ± 8.6 | 53.4 ± 4.1 | 34 ± 1 | 75 | 34.8 | 65.2 | −1.8 | – |
| | 432 ± 11.3 | 55.5 ± 3.4 | 34 ± 2 | 80 | 36.8 | 66.3 | 0.7 | 28.8 |
| | 402 ± 7.5 | 51.9 ± 2.9 | 33 ± 3 | 70 | 42.8 | 82.5 | 2.4 | 52.7 |
| | 496 ± 9.1 | 63.5 ± 2.1 | 31 ± 2 | 80 | 57.6 | 90.7 | 3.6 | 60.3 |
| | 517 ± 12.1 | 66.1 ± 4.1 | 36 ± 1 | 80 | 65.4 | 98.9 | 4.3 | 62.5 |
| | 455 ± 8.2 | 58.4 ± 3.3 | 32 ± 3 | 75 | 71.4 | 122.3 | 6.3 | 66.4 |
| *N. virens* | 623 ± 3.7 | 79.1 ± 2.1 | 29 ± 2 | 70 | 32.9 | 41.6 | −1.3 | – |
| | 545 ± 5.3 | 69.7 ± 3.8 | 25 ± 3 | 80 | 33.5 | 48.1 | −1.8 | – |
| | 675 ± 4.6 | 85.2 ± 2.7 | 22 ± 2 | 65 | 34.3 | 40.3 | 0.4 | 27.6 |
| | 533 ± 10.3 | 68.3 ± 5.4 | 30 ± 1 | 80 | 33.4 | 48.9 | 2.1 | 62.2 |
| | 706 ± 6.6 | 88.9 ± 3.3 | 23 ± 2 | 75 | 48.6 | 54.7 | 2.6 | 64.6 |
| | 647 ± 4.8 | 81.9 ± 2.4 | 26 ± 3 | 70 | 53.2 | 65.0 | 4.0 | 70.3 |
| | 740 ± 5.8 | 93.0 ± 3.1 | 24 ± 2 | 80 | 70.8 | 76.1 | 5.0 | 71.6 |
| | 583 ± 4.7 | 74.3 ± 2.3 | 25 ± 3 | 65 | 60.3 | 81.2 | 5.6 | 72.5 |

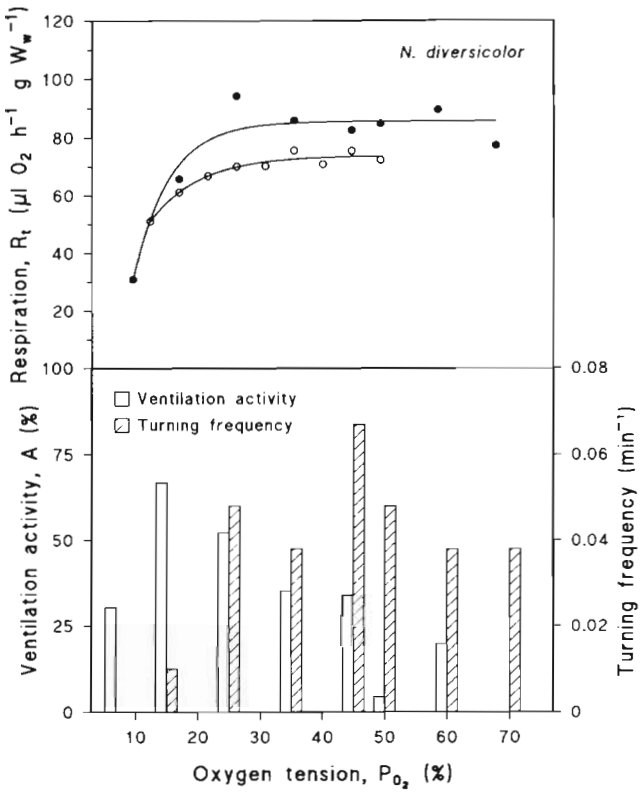


Fig. 8. *Nereis diversicolor*. Specific respiration rate ($R_t$) as a function of steady-state dissolved oxygen tension ($P_{O_2}$) in non-fed worms (n = 7) measured in the 'open' respiratory system. (o) Expt 1; (●) Expt 2. Expts 1 & 2 were performed with the same individuals but at different times. The relationship between ventilation activity (A), turning frequency ($min^{-1}$) and dissolved oxygen tension, measured in Expt 1 (o), is also given. Pumping activity and turning frequency were measured as ventilation pumping period (in percent of total time) and head to tail turns (ind.$^{-1}$ $min^{-1}$)

the maximum rate. This value of SDA may be compared with those reported for other invertebrates: 20% of the growth in the blue mussel *Mytilus edulis* (Jørgensen 1990), 19% in the copepod *Acartia tonsa* (Kiørboe et al. 1985) and 40% in the sea star *Asterias rubens* (Vahl 1984). The reduction of SDA (from 20–26 to 8–11%) after 11 h starvation (Fig. 6B, D) and the 50% reduction of the specific respiration rate in *N. diversicolor* and *N. virens* during a starvation period of 2 to 7 d (Fig. 5) is in agreement with the results of Kristensen (1989) who observed similar reductions in *N. virens* during a period of 6 d of starvation. This response, including a relatively fast decrease in body mass within the first 3 d of starvation (see controls in Fig. 2), underlines the often neglected fact that respiration and growth are integrated through the energetic costs of growth.

The values for starvation-specific respiration rates of *Nereis diversicolor* and *N. virens* in the present work are in good agreement with the values of Shumway (1979), but substantially higher than measured in *N. diversicolor* by Riisgård (1989). From Fig. 6 it is seen that the specific respiration rate at zero growth for both worm species is almost identical, independent of the 2 methods used for respiration measurements.

*Nereis diversicolor* reacts to decreasing dissolved oxygen tensions by a compensatory response with an increase of the ventilation pumping activity (Fig. 8) as previously reported (Kristensen 1983). The underlying function of such a regulatory response, at the level of the whole organism, could be to minimize the development of a diffusive boundary layer at the interface between the body surface and the ventilatory water current (Jørgensen et al. 1986).

Filter-feeding *Nereis diversicolor* grew on a diet of suspended algal cells, but the maximum specific growth rate was lower than in the feeding experiments with shrimp meat (Fig. 3, Table 2). The highest specific growth rate in feeding experiments with algae (3% $d^{-1}$) was obtained at the highest algal concentration used (i.e. $2 \times 10^4$ cells $ml^{-1}$, resulting in an ingestion rate of 288 J ind.$^{-1}$ $d^{-1}$). When fed a diet of surplus shrimp meat the maximum specific growth rate was more than twice as high (7% $d^{-1}$). The lower specific growth rate on algae may partly be due to the extra energy costs of pumping (filter-feeding), and partly due to a lower assimilation efficiency of algal cells compared to shrimp meat.

The specific growth rates measured in this study can be compared with specific growth rates of 4 to 6% $d^{-1}$ for *Nereis diversicolor* (3 to 5 mg dry wt) fed Tetramin (Esnault et al. 1990). Studies performed by Vedel & Riisgård (1993) showed that *N. diversicolor* fed algal cells (*Rhodomonas* sp.) obtained specific growth rates of 3.1% $d^{-1}$ comparable to 3.9% $d^{-1}$ measured in worms in glass tubes placed 15 cm above the bottom in the eutrophicated Odense Fjord. A cohort of *N. diversicolor* (5 to 22 mg dry wt) in the Ythan Estuary, Scotland, UK, obtained a specific growth rate of 1.5% $d^{-1}$ (Chambers & Milne 1975) and *N. diversicolor* and *N. virens* (55 to 65 mg dry wt) in Norsminde Fjord, Denmark, achieved mean specific growth rates of 0.8 and 0.5% $d^{-1}$, respectively (Kristensen 1984). However, the maximum specific growth rate of the facultative *N. diversicolor* fed algae is lower than 9% $d^{-1}$ found for the obligate suspension-feeding blue mussel *Mytilus edulis* grown in nature in net bags (Riisgård & Poulsen 1981). From Table 2 and previous studies (Vedel & Riisgård 1993) it is seen that *N. diversicolor* lacks a 'functional response' or reduction of filtration rate due to overloading of the digestive system. This is, for unknown reasons, in contrast to observations on obligate suspension-feeders such as *M. edulis* (Riisgård 1991a), the polychaete *Sabella penicillus* (Riisgård &

Ivarsson 1990), and the ascidian *Ciona intestinalis* (Petersen & Riisgård 1992). In other ways, in terms of particle retention efficiency and pumping capacity, *N. diversicolor* competes well with obligate filter-feeders (Riisgård 1991b, Riisgård & Larsen 1994).

It is tempting to consider filter-feeding in *Nereis diversicolor* to be a relatively recent adaptation which has resulted in a broader fundamental niche compared to that of the closely related *N. virens*. To what extent this supplementary possibility of filter-feeding has actually led to a niche diversification is unknown at the present, but theoretically it may explain the coexistence of the 2 polychaetes in Kertinge Nor (Fig. 1). This interpretation is an alternative to that proposed by Miron & Kristensen (1993) who suggested that differential sulfide tolerance could be a decisive factor controlling the distribution of *Nereis* species in soft-bottom communities. However, further comparative studies are necessary to clarify the extent of niche diversification in *N. diversicolor* and *N. virens*, for example of the overlap of feeding methods which are at the disposal of the 2 polychaetes and time allocated by the worms to the different types of feeding in nature.

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