

# Ventilation and oxygen uptake by three species of *Nereis* (Annelida: Polychaeta). I. Effects of hypoxia

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**ABSTRACT:** Oxygen consumption of *Nereis virens*, *N. succinea* and *N. diversicolor* were measured during gradually decreasing oxygen tensions. Two techniques were employed to determine the effect of muscular activity on oxygen consumption: (1) worms free in water, using respirometer; (2) worms in polyethylene tubes simulating natural conditions with additional measurements of ventilation, using a direct flow-sensing technique. For these polychaetes muscular movements of the entire body provided the basis for both motor and ventilatory activity. When free in water all 3 nereids showed conformity of oxygen consumption during lowered oxygen tension, exhibiting uncontrolled and variable motor activity. In tubes, the worms showed conformity at high oxygen tensions and variable degrees of regulation at intermediate tensions: *N. succinea* exhibited a wide range of regulation (30 to 140 mm Hg); *N. virens* was a weak regulator (30 to 70 mm Hg); *N. diversicolor* revealed intermediate regulatory abilities (30 to 90 mm Hg). Oxygen regulation at intermediate tensions was due to compensatory responses of ventilation (behavioural regulation) and oxygen extraction (physiological regulation). A correlation appeared to exist between regulatory ability of the species and reducing capacity of preferred sediment types; thus a good regulator (*N. succinea*) commonly is found living in muddy sediment of high organic content, whereas the weakest regulator (*N. virens*) prefers sandy sediments of low organic content.

## INTRODUCTION

Nereid polychaetes commonly live in large numbers in the intertidal zone of estuarine and brackish waters, normally in sediments of medium to high organic content (Muus, 1967). When buried in sediment, they depend on water pumped through the burrows for oxygen supply. Previous studies concerning ventilatory patterns in *Nereis* spp. have revealed that ventilatory activity is intermittent, interrupted by periods of rest (Wells and Dales, 1951; Scott et al., 1976; Kristensen, 1981b). Since oxygen penetrates to a depth of only a few mm below the surface of sediments (Revsbech et al., 1980), animals buried in the sediment commonly are exposed to very low oxygen tensions during periods of ventilatory rest. It is well known that nereids are able to switch from aerobic to anaerobic metabolism during periodic oxygen depletion (Beadle, 1961; Scott, 1976; Schöttler, 1978, 1979; Jørgensen and Kristensen, 1980).

The capacity of several marine invertebrate groups for partial regulation of oxygen consumption in water of reduced oxygen tension is well studied. Commonly,

a distinction is made between oxygen regulators which maintain a steady oxygen uptake over a wide range of ambient oxygen tensions, and oxygen conformers in which the amount of oxygen consumed is directly dependent on oxygen availability (Prosser, 1973). However, this does not hold in general since perfect regulation or conformity is very rare. More often the rates correspond to intermediate regulatory patterns (Mangum and Van Winkle, 1973).

Several reports concerning the regulatory ability of polychaetes have revealed contradictory results. Among the polychaetes that have been tested, regulation of oxygen uptake was found in *Nereis* spp. (Dam, 1937; Lindroth, 1938; Theede, 1973; Theede et al., 1973), *Ophelia bicornis* (Beis et al., 1980), *Lumbrineris zonata* (May, 1972) and conformity of oxygen uptake in *Nereis* spp., *Arenicola marina*, *Abarenicola assimilis*, *Glycera americana*, *Perineris nuntia* (Shumway, 1979), *Mesochaetopterus taylori* (Petersen and Johansen, 1967), *Abarenicola pacifica* (May, 1972), and *Cirriiformia tentaculata* (Dales and Warren, 1980). The measurements of oxygen uptake during such experiments may be affected by a variety of factors, such as previous

environmental history, nutritional state, size, and state of activity (Beis et al., 1980). In this paper a distinction is made between motor and ventilatory activity; muscular movements of the entire body of these polychaetes provide the basis for both forms of activity and will, as such, affect oxygen uptake.

The aim of the present work was to investigate responses of simultaneously measured ventilation and oxygen consumption in the polychaetes *Nereis virens* Sars, *N. succinea* (Frey & Leuckart) and *N. diversicolor* O. F. Müller in conditions of reduced oxygen. Earlier measurements on oxygen consumption of *Nereis* during hypoxia were made without consideration of ventilatory activity (Theede, 1973; Shumway, 1979). By using artificial tubes simulating the worms' natural burrows and by monitoring ventilatory activity, it was hoped that a better understanding of polychaete respiratory responses to hypoxia could be achieved.

## MATERIALS AND METHODS

### Animals

*Nereis virens*, *N. succinea* and *N. diversicolor* were collected during March and April, 1982 in the estuary, Kysing Fjord, close to Aarhus, Denmark (Muus, 1967). *N. virens* was collected on a sandflat of medium to low organic content; *N. succinea*, in sandy mud with dense growth of *Mytilus edulis*; *N. diversicolor*, in silty sand. Habitat temperature was 6 to 10 °C; mean salinity, ca. 20‰ S. The collection area was subjected to variable periods of submergence. Only intact worms were used for experiments.

The worms were acclimated to experimental conditions, 16 °C and 20 ‰ S, for at least 7 d in a recirculating seawater aquarium partially filled with natural sediment. Two d prior to use, the worms were placed in polyethylene tubes of appropriate sizes, and stored in petri dishes to void their guts.

### Ventilation measurements

Experiments were performed in a 12 l darkened aquarium thermostatted at 16 °C. The tubes containing the worms were placed in V-shaped Plexiglas tubes, simulating the natural position of the worms in the sediment (Fig. 1).

Ventilation was determined with an electromagnetic flowmeter (Micron Instr. Corp.) and continuously recorded by a Hewlett-Packard 7132A recorder (Kristensen, 1981b).

Ventilation amplitude was measured as average water flow computed as mean flow rate during periods

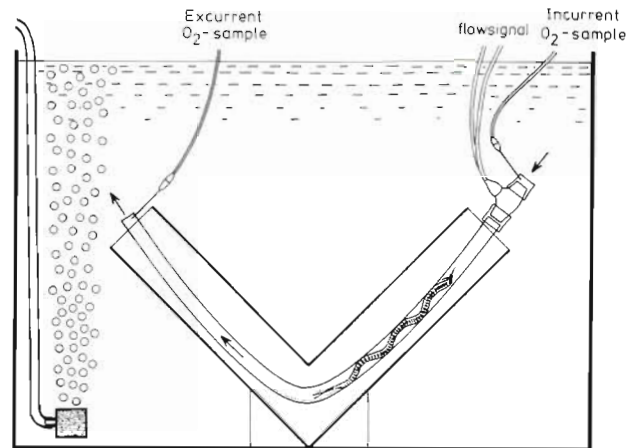


Fig. 1. Experimental set-up for measuring *Nereis* ventilation and oxygen uptake. Cables for flow signal are connected to an electromagnetic flowmeter. Tubes for O<sub>2</sub>-samples are connected to a Radiometer P<sub>O<sub>2</sub></sub>-electrode

of active ventilation ( $\dot{V}_w$ ). Measurements for each individual were carried out over 1 h intervals. During ventilation periods the water flow was integrated and averaged. Ventilation was expressed as ml min<sup>-1</sup>, standardized to a 0.5 g wet wt. individual of each species, according to the weight relationship reported by Kristensen (1981b). Ventilation activity was determined both as ventilation amplitude ( $\dot{V}_w$ ) and as average duration of ventilation periods, determined as percent of total measured time ( $D_v$ ).

### Measurements of oxygen uptake

#### During active ventilation

Oxygen uptake during active ventilation was determined by measuring the water flow as described; simultaneously, inspiratory and expiratory water samples were taken from the tube for oxygen analysis with Radiometer P<sub>O<sub>2</sub></sub>-electrodes (Kristensen, 1981b). Incurrent and excurrent water samples from the tube passed the P<sub>O<sub>2</sub></sub>-electrodes at a constant rate (ca. 1 ml min<sup>-1</sup>). Oxygen extraction was recorded continuously (Fig. 2). For each species 4 to 6 individuals were used (weight range: *N. virens*, 0.8 to 1.5 g; *N. succinea*, 0.4 to 0.9 g; *N. diversicolor*, 0.2 to 0.5 g wet wt.). P<sub>O<sub>2</sub></sub> was reduced in steps of ca. 20 mm Hg, from 155 to 10 mm Hg by bubbling nitrogen through the water. Ventilation and oxygen extraction were recorded immediately after each step for ca. 1 h for each individual.

Oxygen consumption ( $\dot{V}_{O_2}$ ) was calculated as:

$$\dot{V}_{O_2} = (C_{iO_2} - C_{eO_2}) \cdot \dot{V}_w$$

where  $C_{iO_2}$  and  $C_{eO_2}$  = incurrent and excurrent oxygen

concentrations.  $\dot{V}_{O_2}$  was expressed as  $\mu\text{g O}_2 \text{ g}^{-1} \text{ h}^{-1}$  standardized to a 0.5 g wet wt. individual, according to Kristensen (1981b). A 2.5 g *N. virens* that showed great variations in  $\dot{V}_w$  was used to determine the relationship between  $\dot{V}_w$  and  $\dot{V}_{O_2}$  (or oxygen extraction).

#### Worms free in water

Oxygen uptake determinations of worms removed from the tubes were performed in a closed 27 ml respirometer thermostatted at 16 °C. Oxygen tension was measured by a Radiometer P<sub>O<sub>2</sub></sub>-electrode. A magnetic stirrer assured sufficient mixing of the medium. In experiments change of P<sub>O<sub>2</sub></sub> was recorded continuously. The worms were allowed to reduce P<sub>O<sub>2</sub></sub> from 155 to 20 mm Hg. Four individuals of each species were used, and  $\dot{V}_{O_2}$  was standardized to a 0.5 g wet wt. individual for comparison.

#### Role of microbial oxygen uptake

When a nereid inhabits a clean polyethylene tube, it will quickly line the inner surface of the tube with mucus. This mucus may serve as a rich substrate for microbial growth (Aller and Yingst, 1978).

To test possible interference of microbial oxygen uptake on measurements of *Nereis* oxygen uptake, a tube (20 cm long, 0.5 cm diameter) was used that had previously been occupied by 1 *Nereis virens* for 4 d. Gradually increasing water flow (1.4 to 8.0 ml min<sup>-1</sup>) was produced through the tube by a peristaltic pump. Water flow and microbial oxygen extraction were measured as described earlier. The tube was then cleaned by a pipecleaner and washed in warm water (60 °C), and the procedure was repeated.

## RESULTS

### Effects of reduced oxygen tension on ventilation

Ventilation in the 3 species of *Nereis* was intermittent, with alternations between periods of rest and bursts of ventilatory activity (Fig. 2), in agreement with reports of Wells and Dales (1951), Scott et al. (1976) and Kristensen (1981b).

As P<sub>O<sub>2</sub></sub> declined, average duration of bursts of ventilation ( $D_v$ ) increased for all 3 species (Fig. 3A).  $D_v$  for *Nereis virens* and *N. diversicolor* showed an increase of about 40 % as P<sub>O<sub>2</sub></sub> was reduced from air saturation down to 10 to 30 mm Hg. These 2 species appeared very much alike regarding  $D_v$ , and at air saturation  $D_v$  was ca. 60 % for both. *N. succinea*, in contrast, showed

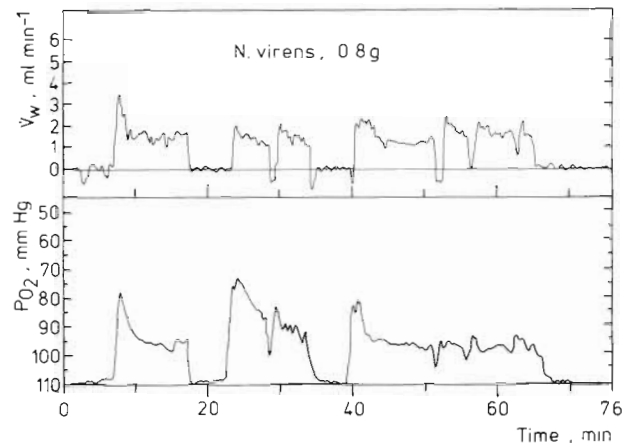


Fig. 2. *Nereis virens*. Ventilation and excurrent oxygen tension of a 0.8 g individual. Duration of recording 76 min. Incurrent P<sub>O<sub>2</sub></sub> = 110 mm Hg

a constant  $D_v$  of 25 % down to about 100 mm Hg, followed by an increase at lower tensions ( $p < 0.05$ ). At 10 mm Hg,  $D_v$  for this species reached the same level as the other 2 (~80 %).

Ventilation amplitude ( $\dot{V}_w$ ) appeared almost constant for all 3 species at P<sub>O<sub>2</sub></sub> below 100 mm Hg (Fig. 3B).  $\dot{V}_w$  for *Nereis virens* and *N. diversicolor* showed the same pattern, except that  $\dot{V}_w$  for the latter was about twice that of the former ( $p < 0.05$ ). Both species showed a decrease of about 40 % ( $p < 0.05$ ) when P<sub>O<sub>2</sub></sub> decreased to about 100 to 110 mm Hg. At lower tensions  $\dot{V}_w$  was fairly constant. In contrast,  $\dot{V}_w$  for *N. succinea* was nearly constant over the whole range of P<sub>O<sub>2</sub></sub>, at a level noticeably higher than *N. diversicolor* and about 2 to 2½ times higher than *N. virens* ( $p < 0.05$ ).

The 3 species of *Nereis* showed much the same pattern for the total volume of water passing the tubes per unit time ( $\dot{V}_w \times D_v$ ): a decrease to a minimum at 80 to 100 mm Hg was followed by an increase at lower tensions (Fig. 3C). On the other hand the volume of water and the magnitude of the changes was quite different. *N. virens* and *N. succinea* ventilated nearly identical volumes down to 100 mm Hg, but at lower tensions the latter showed a more rapid increase than the former. *N. succinea* eventually reached the level of *N. diversicolor* at 30 mm Hg, where these 2 species ventilated at a rate approximately 2 times that of *N. virens*.

### Effects of reduced tension on oxygen uptake

#### Worms free in water

When *Nereis* spp. were removed from the tubes,  $\dot{V}_{O_2}$  appeared highly dependent on external P<sub>O<sub>2</sub></sub> over the

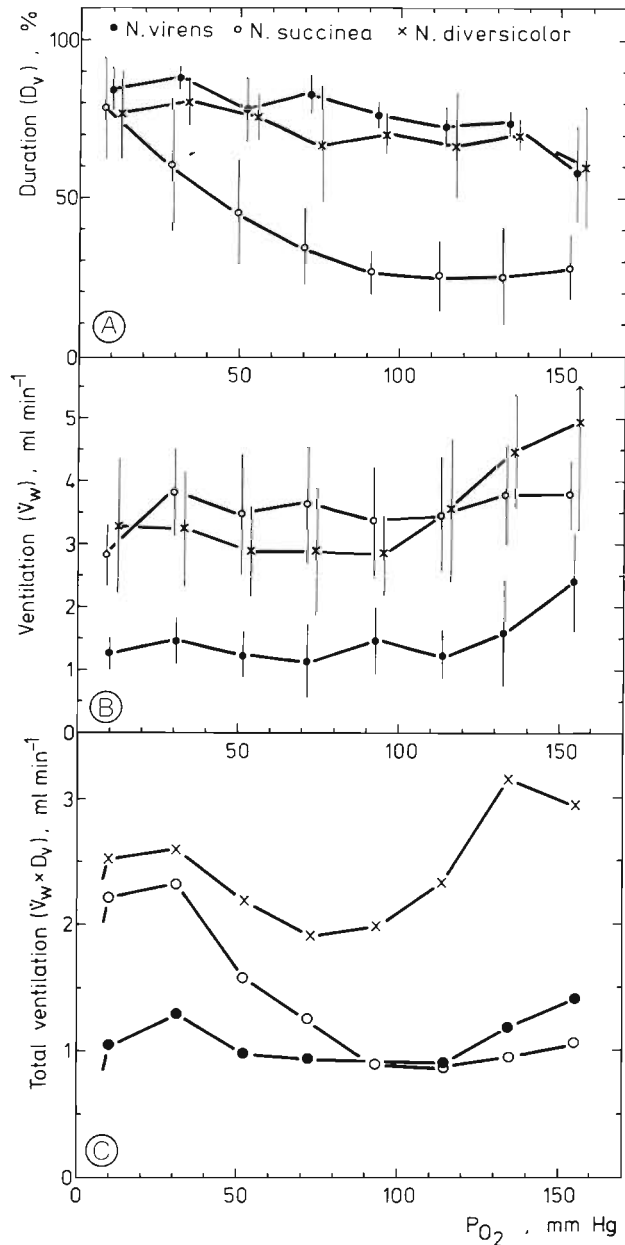


Fig. 3. *Nereis virens*, *N. succinea*, *N. diversicolor*. (A) Duration of ventilation (% of total measured time [ $D_v$ ]) during decreasing oxygen tension ( $P_{O_2}$ ). (B) Ventilation amplitude ( $\dot{V}_w$ ) during decreasing oxygen tension ( $P_{O_2}$ ) for 0.5 g wet wt. standard individuals. (C) Total volume of water ventilated per unit time ( $\dot{V}_w \times D_v$ ) for standard individuals. Results in (A) and (B) given as mean  $\pm$  S.D. for ca. 1 h recordings of 4 to 6 individuals

range from 155 to 20 mm Hg (Fig. 4). The values for the 3 species did not differ over the major part of the  $P_{O_2}$  range studied. The rates presented here for tubeless worms seem higher than earlier reported resting rates (Kristensen, 1981b). This agrees with direct observations during the experiments. The worms exhibited a relatively high level of motor activity; possibly they

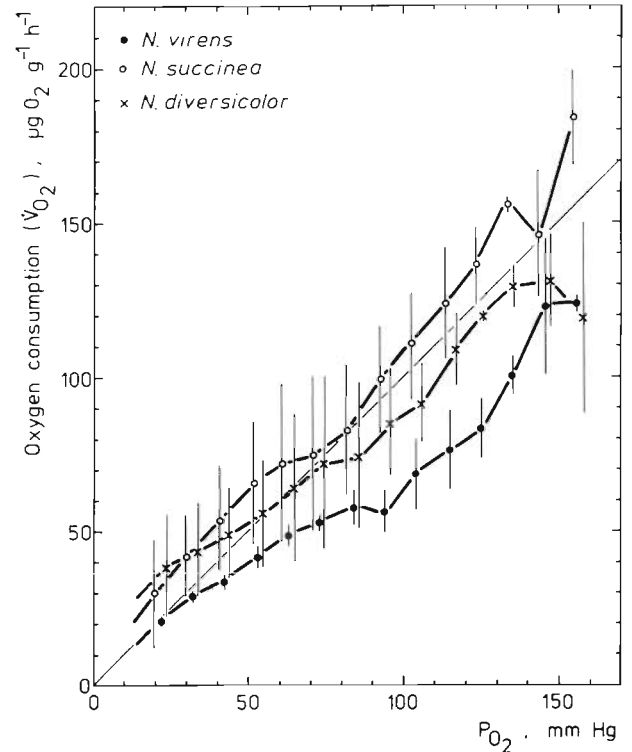


Fig. 4. *Nereis virens*, *N. succinea*, *N. diversicolor*. Oxygen consumption by 0.5 g wet wt. standard individuals, free in water, during declining oxygen tension. Results given as mean  $\pm$  S.D. for 4 individuals as indicated by error bars

were disturbed by the magnetic stirrer or activity was related to searching for a suitable place to construct a burrow.

#### Active worms in tubes

Each ventilation burst started with a peak of both ventilation amplitude and oxygen extraction (Fig. 2). Nereids commonly start a burst of ventilatory activity with a peak of  $\dot{V}_w$ , followed by a more or less constant amplitude. This ventilation peak caused a fast renewal of tube water, presumably a mechanism for rapid removal of metabolic wastes and oxygen deficient water. The observed peak in oxygen extraction was a consequence of the previous resting period, where the worm had more or less exhausted the oxygen available in the tube. As for  $\dot{V}_w$ , the peak of oxygen extraction was followed by a period of constant extraction.  $\dot{V}_{O_2}$  was computed from these constant periods.

The percentage extraction of oxygen removed from water passing through the gills during declining  $P_{O_2}$  often reflects the ability of marine invertebrates to regulate  $\dot{V}_{O_2}$  (Bayne, 1971). In water fully saturated with oxygen, extraction was rather low; there was a significant difference ( $p < 0.05$ ) between *Nereis diversicolor* (5.5 %) and the other 2 *Nereis* spp. (11 to 12 %)

(Fig. 5). During a decline in P<sub>O<sub>2</sub></sub> below 100 mm Hg, oxygen extraction showed a rapid increase, reaching 27 % for *N. diversicolor* and 35 % for *N. virens* and *N. succinea* at 10 mm Hg. This suggests that *Nereis* spp. physiologically regulate oxygen uptake to some extent at low tensions.

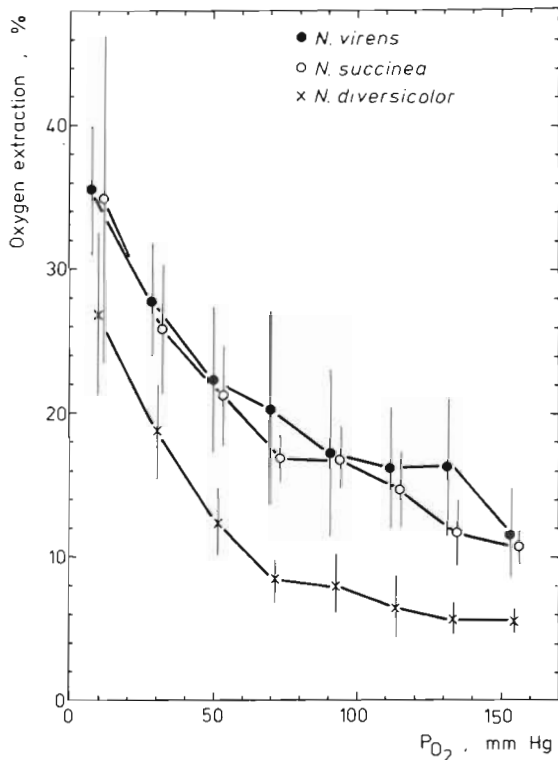


Fig. 5. *Nereis virens*, *N. succinea*, *N. diversicolor*. Fractional extraction of oxygen from water passing the tube during decreasing oxygen tension. Results given as mean  $\pm$  S.D. for ca. 1 h recordings of 4 to 6 individuals

Oxygen consumption rates during periods of active ventilation were clearly influenced by ventilatory activity. For the 2.5 g *N. virens* tested, a first-order relationship ( $\dot{V}_{O_2} = b + a \times \dot{V}_w$ ) was evident between ventilation activity expressed as ventilation amplitude ( $\dot{V}_w$ ) and oxygen consumption ( $\dot{V}_{O_2}$ ) (Fig. 6). Similar relationships have been shown for other marine invertebrates (Halcrow and Boyd, 1967; Hamwi and Haskin, 1969; Thompson and Bayne, 1972; Newell and Kofoed, 1977). A decrease in  $\dot{V}_w$  during declining P<sub>O<sub>2</sub></sub> would then produce changes in measured  $\dot{V}_{O_2}$ , which is not directly an effect of hypoxial conditions.

During active ventilation periods,  $\dot{V}_{O_2}$  was clearly influenced by external P<sub>O<sub>2</sub></sub> (Fig. 7). For *Nereis virens* and *N. diversicolor* a high degree of dependence on P<sub>O<sub>2</sub></sub> was found.  $\dot{V}_{O_2}$  for these species did not differ significantly ( $p > 0.10$ ). *N. succinea*, in contrast, showed moderate independence during active ventilation periods, reaching uptake rates twice those for the

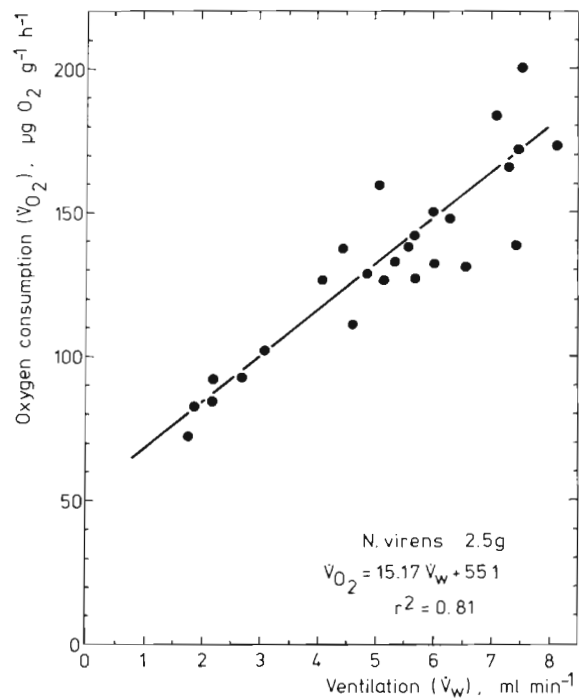


Fig. 6. *Nereis virens*. Oxygen consumption ( $\dot{V}_{O_2}$ ) by 1 individual plotted against ventilation amplitude ( $\dot{V}_w$ ). Line fitted by equation:  $\dot{V}_{O_2} = a \cdot \dot{V}_w + b$

other 2 species at all P<sub>O<sub>2</sub></sub>'s ( $p < 0.01$ ) (Fig. 7). By considering the duration of bursts of ventilation ( $D_v$ ) (Fig. 3 A), the amount of oxygen consumed per unit time was very similar at intermediate oxygen tensions for the 3 species (Fig. 8). Corrected for  $D_v$ , the curves for the 3 species are more or less S-shaped; dependent uptake at high oxygen tensions, independence at intermediate, and dependent uptake at low tensions. The weakest regulator, *N. virens*, showed dependence down to about 70 mm Hg, followed by independence to 30 mm Hg; for *N. diversicolor*, independence occurred in the range 30 to 90 mm Hg; the strongest regulator, *N. succinea*, was independent of ambient P<sub>O<sub>2</sub></sub> in the range 30 to 140 mm Hg.

### Microbial oxygen uptake

It proved important to clean the polyethylene tubes before measurements of *Nereis* oxygen uptake. The mucus-lined tube showed considerable oxygen uptake (Fig. 9 A) of the same order of magnitude as that for the worm itself. Changes in water current through the tube produced only slight changes in the measured microbial oxygen uptake. This background microbial uptake could be a serious source of error in experiments of this kind if no cleaning procedure was employed. The cleaning procedure used proved to be sufficient, since

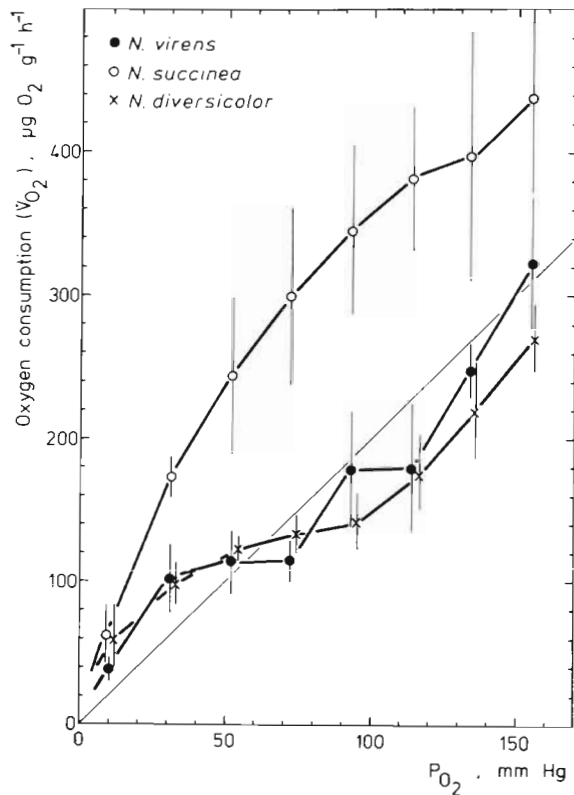


Fig. 7. *Nereis virens*, *N. succinea*, *N. diversicolor*. Oxygen consumption during active ventilation periods at declining oxygen tension; 0.5 g wet wt. standard individuals. Results given as mean  $\pm$  S.D. for ca. 1 h recordings of 4 to 6 individuals

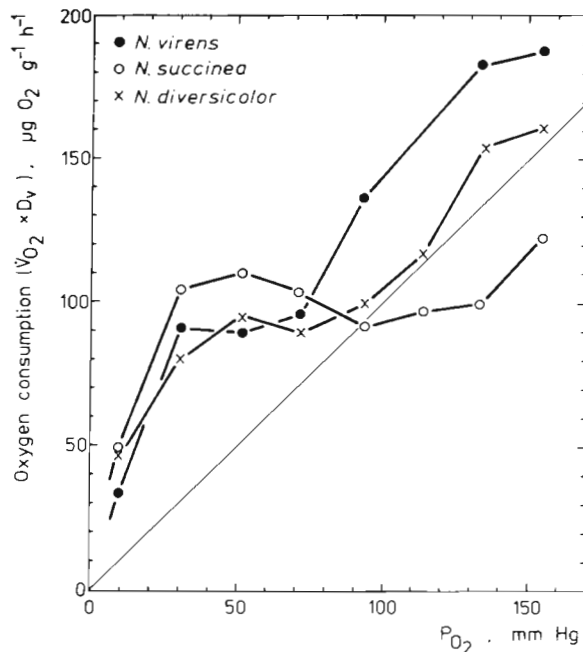


Fig. 8. *Nereis virens*, *N. succinea* and *N. diversicolor*. Oxygen consumption by 0.5 g wet wt. standard individuals, integrated over total measured time ( $D_v \times \dot{V}_{O_2}$ ) at each oxygen tension from 155 to 10 mm Hg

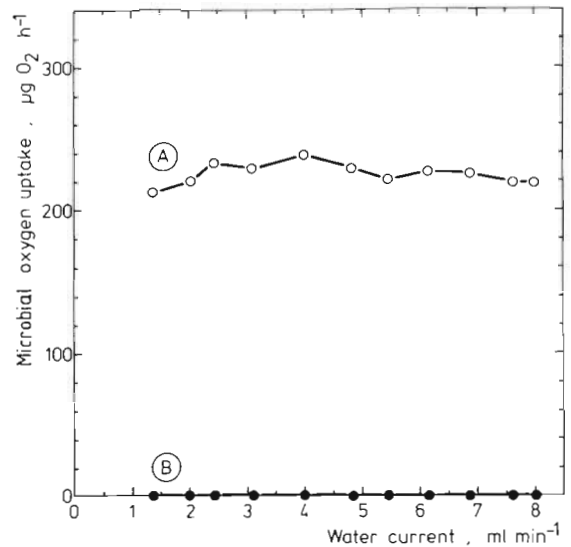


Fig. 9. Microbial oxygen consumption in empty polyethylene tubes, plotted against water current passing the tube. (A) Polyethylene tube occupied for 4 d by 1 *Nereis virens* before measurements. (B) Same tube cleaned by pipecleaner and washed in warm water

no measurable microbial oxygen uptake was observed after the treatment (Fig. 9B).

## DISCUSSION

Investigations of oxygen consumption with declining tension in several marine invertebrates have indicated that oxygen uptake is regulated behaviourally by increasing ventilation as in *Mytilus perna* (Bayne, 1967) and *Hyalinoecia tubicola* (Dales et al., 1970), or regulated physiologically by maintaining a constant ventilation and increasing the fractional extraction of oxygen from the ventilatory current as in *M. edulis* (Bayne, 1971). *Nereis* spp. appeared capable of regulating oxygen uptake by combining both mechanisms. During a decline in oxygen tension, oxygen extraction increased markedly for the three species (Fig. 5); simultaneously, ventilation volume remained constant or decreased at tensions from 155 to 100 mm Hg (Fig. 3C). At lower tensions ( $P_{O_2} < 80$  to 100 mm Hg) ventilation periods were longer thereby increasing the volume of water pumped, although  $\dot{V}_w$  was fairly constant (Fig. 3).

Under well-oxygenated conditions, oxygen extraction in the 3 nereid polychaetes was 6 to 12 % which is considerable lower than reported for these species earlier: *Nereis virens*, 20 to 75 % (Dam, 1937; Lindroth, 1938), 20 % (Mangum and Burnett, 1975). Other polychaetes, especially sedentary species with well developed gills – like *Thelepus crispus*, *Eupolytnia heterobranchia*, *Neoamphitrite robusta* (Dales, 1961)

and *Amphitrite ornata* (Mangum and Burnett, 1975) – are reported to extract 40 to 60 %. The generally lower rate of extraction found in the non-sedentary species such as *Nereis* might be explained by the possession of respiratory organs with smaller surface areas. Some annelids, including nereids, lack special respiratory organs but have localized structures, i.e. parapodia, which increase the surface area of the animals. The dorsal lamellae of *Nereis* parapodia are believed to be a major site of gas exchange, since these organs are highly vascularized (Mangum et al., 1980). The segmented 'gills' (parapodia) of *Nereis* spp. undoubtedly represent the more primitive condition. *N. diversicolor* extracts only about 5.5 % of the available oxygen at high tensions, while *N. virens* and *N. succinea* extract 11 to 12 %. This difference can be explained by the size of the parapodia (Fig. 10). The dorsal parapodia

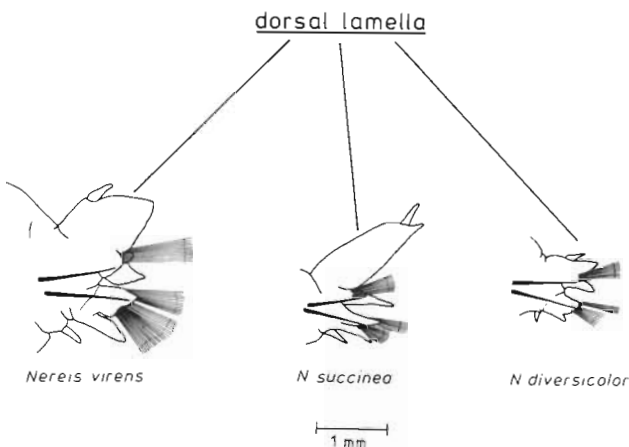


Fig. 10. *Nereis* spp. Parapodia from posterior third of body showing the dorsal lamella

lamellae of the posterior segments of both *N. virens* and *N. succinea* are large and leaf-shaped, while *N. diversicolor* has very small lamellae.

Experiments with tubeless worms suggest conformity of oxygen consumption (Fig. 4) in agreement with Shumway (1979) in *N. virens* and *N. diversicolor*. However, Theede (1973) and Theede et al. (1973) suggested a high degree of regulation for *N. diversicolor* and *N. pelagica* down to 30 to 40 mm Hg. Commonly, such experiments are performed with the worms free (i.e. tubeless) in the respirometer chamber. Results of such investigation may be misleading: it is impossible in those tests to determine the level of motor activity, which is known to have a substantial influence on oxygen uptake (Fig. 8; Dales, 1961; Newell and Northcroft, 1967; Mangum and Sassaman, 1969; Kristensen, 1981b). In the present investigation, rates of oxygen uptake for worms free in water greatly exceeded the rates reported by Shumway (1979), Cammen (1980),

and Kristensen (1981b) for resting individuals. This suggests that when free in the water, worms may demonstrate an uncontrolled and high motor activity, which should be considered in such experiments. Moreover, respiratory independence can be modified by body size, temperature and physiological conditions (Bayne, 1971).

In tubes, *Nereis* spp. showed conformity (*N. virens* and *N. diversicolor*) or moderate regulation (*N. succinea*) during active ventilation periods (Fig. 7). Active oxygen uptake exceeded the uptake of tubeless worms by more than 100 %. A totally different picture emerged when oxygen uptake during ventilation was integrated over the total measured time (i.e. corrected for duration of ventilation,  $D_v$ ) (Fig. 8). This resulted in conformity at high tensions and a good regulatory ability at intermediate tensions; *N. succinea* was the best regulator and *N. virens* the poorest, indicating a compensatory ventilation response, as reported for *Cancer pagurus* (Bradford and Taylor, 1982). Mangum and Burnett (1975) reported that during a reduction in environmental oxygen level the terebellid polychaete *Amphitrite ornata* showed only slight increases in ventilation. This response, in contrast to *Nereis* spp., was achieved by an increase in the amplitude of muscular movements rather than a change in parameters of the spontaneous rhythm itself. Mangum and Burnett concluded that there was no mechanism that increased the ventilation at low oxygen levels in *Amphitrite*. This is in agreement with *Nereis* only at oxygen levels above 50 %. The form of the curves in Fig. 8 at high oxygen tensions might be a consequence of a decrease in  $\dot{V}_w$  during a lowering from air saturation to about 100 mm Hg (Fig. 3B). Such a decrease (especially for *N. virens* and *N. diversicolor*) will affect oxygen consumption as depicted in Fig. 6. At high tensions the worms possibly need no regulation since the blood with a half-saturation tension of 4.0 mm Hg at 15 °C (Weber, 1978) is likely to become fully oxygenated at these tensions. However, at lower tensions regulation becomes necessary. The oxygen uptake during active periods, corrected for  $D_v$ , showed a critical tension  $P_c$  at about 30 to 40 mm Hg for all 3 species (Fig. 8), below which the uptake rate decreased rapidly and ventilation tended to decrease (Fig. 3C).

Scott (1976) has shown that, during ventilatory rest periods, *Nereis virens* respire anaerobically, accumulating small amounts of lactic acid. Later, during ventilation periods, the oxygen debt is repaid. This might explain the high oxygen uptake of *N. succinea* during active ventilation periods compared to the other 2 species (Fig. 7). In *N. succinea*, ventilation pauses generally are longer than in the other species, generating a greater oxygen debt. Accordingly, and because of a shorter duration of ventilation periods, *N. succinea*

consequently must exhibit a higher rate of oxygen uptake.

Hyman (1932) demonstrated that *Nereis virens*, when free in water, showed conformity of oxygen uptake; this agrees with the majority of reported cases. But she found that when in tubes, *N. virens* was predominantly an oxy-regulator, consuming 40 % less oxygen at air saturation than when free in water. Both of Hyman's experiments were performed in respirometers, which would not permit the measurement of level of muscular activity (neither motor nor ventilatory activity) of the worms. The results of Hyman are supported by the present study even though the interpretation is somewhat different. She believed that when natural conditions were simulated by enclosing the worms in tubes, some internal mechanism made oxygen regulation possible. When free in water a number of unknown factors other than muscular activity could be responsible for the loss of the regulatory ability. The present study reveals that increased regulation within tubes is achieved partly by a compensatory response of ventilation (behavioural regulation) and partly by increased oxygen extraction (physiological regulation) at low tensions, whereas the missing ventilatory current is believed responsible for the apparent loss of regulatory ability when the worms are free in water.

It is tempting to assume that regulation reflected in an independent type of respiration is an adaptation necessary for life at low oxygen levels. However, the facts do not generally support such an assumption, since several tube-living intertidal polychaetes have been shown to be oxy-conformers, e.g. *Mesochaetopterus taylori* (Petersen and Johansen, 1967), *Glycera dibranchiata* (Mangum, 1970), *Arenicola marina*, *Abarenicola assimilis*, *Glycera americana* and *Perineris nuntia* (Shumway, 1979). The findings for the 3 species of *Nereis* tested here, on the other hand, suggest a correlation between regulatory ability and preferred sediment type. *N. succinea*, which showed the best regulatory ability, has a preference for mud flats among lumps of *Mytilus edulis* (Rasmussen, 1973; Kristensen, 1981a). Conditions in such sediment types are highly reducing and low oxygen might be normal in the burrows of *N. succinea*. *N. virens*, showing the least regulatory ability, prefers sandy substrate of low organic content and is never found in pure mud flats (Rasmussen, 1973; Kristensen, 1981a). *N. diversicolor* is intermediate to the other 2 species, both in regulatory ability and sediment preference (Kristensen, 1981a).

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