

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

II. Effects of temperature and salinity changes

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ABSTRACT: Ventilation and oxygen uptake of *Nereis virens*, *N. succinea* and *N. diversicolor* were monitored during changing temperatures (5.5 to 37.5 °C) and salinities (1.7 to 24.0 ‰ S). Measurements were performed using a direct flow sensing technique with worms in polyethylene tubes simulating natural conditions. Ventilation amplitude increased with temperature ($Q_{10} = 2.6$ to 2.9) for the 3 species, reaching well defined species specific upper limits. This is assumed to be the upper limit for *Nereis* ventilation capacity. At temperatures above 30 to 35 °C, but below the lethal limit, ventilation decreased and eventually ceased. Oxygen uptake during active periods appeared to increase with temperature over the range measured ($Q_{10} = 1.3$ to 2.2). Ventilation requirement (\dot{V}_{O_2}/\dot{V}_w) showed minimum values at species specific temperatures, suggesting optimum temperatures at the present acclimation level (*N. virens*, 11 to 20 °C; *N. succinea* 20 to 35 °C and, *N. diversicolor*, 5 to 16 °C). Reduction in salinity resulted in a decreased ventilation amplitude, possibly due to osmotic swelling of the worms. Oxygen uptake during active periods was quite unaffected by salinity changes. Ventilation requirement increased for all 3 species at low salinities and was most pronounced in the stenohaline *N. virens* and least in the euryhaline *N. diversicolor*. The observed responses to temperature and salinity changes are also related to distributional patterns of the 3 species in a Danish estuary.

INTRODUCTION

Annelid polychaetes of the genus *Nereis* are among the most common and abundant members of the Danish estuarine infauna. *Nereis virens* Sars, *N. succinea* (Frey & Leuckart) and *N. diversicolor* O. F. Müller each occupy distinct areas of estuaries (Muus, 1967; Rasmussen, 1973). These distributional patterns are thought to result from differences in tolerance limits to extreme and variable environmental conditions as well as from interspecific competition (Rasmussen, 1973; Kristensen, 1981a).

While there is a multitude of factors which can affect activity level and oxygen consumption of an animal, 2 of the most important environmental factors are temperature and salinity. Synergistic interactions between these factors can be expected to regulate the distribution and activity of many estuarine invertebrates. Within estuaries temperature and salinity conditions vary tidally and diurnally. The effects of each of these individual factors on simultaneously measured ventilation and oxygen uptake has been well documented for marine bivalves (McLusky, 1973; Widdows, 1973; Newell and Kofoed, 1977; for review see Remane and

Schlieper, 1971; Newell and Branch, 1980) and crustaceans (Halcrow and Boyd, 1967; Taylor, 1977; Taylor et al., 1977; Dyer and Uglow, 1980; for review see Kinne, 1970, 1971; Remane and Schlieper, 1971), but attempts to study this on polychaetes are scarce (Mangum and Sassaman, 1969). Comparative measurements of ventilation and oxygen consumption should reveal evidence useful in predicting distributional patterns of closely related species.

The current investigation on the respiratory physiology of *Nereis virens*, *N. succinea* and *N. diversicolor* attempts to assess the effects of temperature and salinity changes on simultaneously measured ventilation and oxygen uptake and to relate the interspecific differences to the distributional patterns of these species.

MATERIALS AND METHODS

Animals

Experimental animals were collected during April and May, 1982 in Kysing Fjord, Denmark. The estuary's water temperature and salinity showed consider-

able fluctuations due to solar radiation and tides (8 to 20 °C; 5 to 24 ‰ S). The worms were collected from the following habitats: *Nereis virens* in the outer part of the estuary on a sandflat of low to medium organic content; *N. succinea*, in the lower intertidal zone of the outer part of the estuary in sandy mud with dense growth of *Mytilus edulis*; *N. diversicolor*, in silty sand at the high intertidal of the middle part of the estuary. The areas were subjected to variable periods of submergence.

Worms for both temperature and salinity experiments were allowed to acclimate to 20 °C and 19 ‰ S for at least 7 d in natural sediment. Before experiments, the experimental animals were transferred to Petri dishes, provided with polyethylene tubing for artificial burrows, and maintained for 2 d, during which time they voided their guts.

Measurements of ventilation and oxygen uptake

The experiments were performed with worms inhabiting polyethylene tubes. To prevent errors due to microbial oxygen uptake, the tubes employed were cleaned before measurements (Kristensen, 1983).

Ventilation was determined with an electromagnetic flowmeter (Kristensen, 1981b, 1983) and measured as ventilation amplitude (\dot{V}_w) computed as the mean flow rate during periods of active ventilation. The results are expressed as ml min⁻¹, standardized to a 0.5 g wet wt. individual, using the relationship reported by Kristensen (1981b).

Oxygen extraction during active periods was recorded continuously by a Radiometer P_{O₂}-electrode (Kristensen, 1983), and oxygen consumption (\dot{V}_{O_2}) was calculated as, $\dot{V}_{O_2} = \dot{V}_w \times \text{Extr.}$, expressed as μg O₂ g⁻¹ h⁻¹ standardized to a 0.5 g wet wt. individual.

Effects of temperature changes

In order to establish the effects of temperature changes on ventilation and oxygen consumption at full air saturation, the worms were exposed to temperatures from 5.5 to 37.5 °C. Measurements were made for 4 to 5 individuals of each species at temperature steps above acclimation level: 20.0, 25.0, 30.0, 35.0 and 37.5 °C; 4 to 5 individuals of the same sizes were measured at temperature steps decreasing from acclimation temperature: 20.0, 16.0, 11.0 and 5.5 °C. After each temperature step the worms were allowed to acclimate for 24 h before monitoring in order to reduce the acute temperature responses commonly exhibited by marine invertebrates (Kinne, 1963, 1970; Prosser, 1973; Newell and Branch, 1980). Each individual was

monitored for about 1 h. A constant salinity of 19 ‰ S was maintained during experiments. The size ranges used were: *N. virens*, 0.5 to 1.9 g; *N. succinea*, 0.5 to 1.6 g; *N. diversicolor*, 0.2 to 0.7 g wet wt.

Effects of salinity changes

To study the effects of decreasing salinity on ventilation and oxygen uptake at full air saturation, 4 individuals of each species were measured at stepwise, decreasing salinities from 24.0 to 1.7 ‰ S. The salinities chosen were: 24.0, 18.0, 13.2, 8.1 and 1.7 ‰ S. Before the start of experiments, the 19 ‰ S acclimated worms were exposed for 24 h to the initial salinity (24 ‰ S), chosen because this is the maximum value reported from the collection area (Muus, 1967). At each salinity, acclimation was allowed for the same time length before monitoring. The size ranges used were: *N. virens*, 0.7 to 2.0 g; *N. succinea*, 0.5 to 1.0 g; and *N. diversicolor*, 0.3 to 0.5 g wet wt. Each individual was monitored for about 1 h. Temperature was kept constant at 20 °C during experiments.

RESULTS

Effects of temperature changes

Fig. 1A illustrates the relationship between ventilation amplitude (\dot{V}_w) and temperature in the range 5.5 to 37.5 °C for the 3 nereids. For all 3 species, \dot{V}_w increased directly with temperature reaching a well defined maximum level at 20 and 16 °C for *Nereis virens* and *N. diversicolor* and at 25 °C for *N. succinea*. The temperature coefficient (Q_{10}) was very similar for the 3 species, 2.61 to 2.91 (Table 1). The worms maintained the \dot{V}_w maximum for a further 10 °C increase in temperature ($Q_{10} = 1.00$ to 1.06), suggesting that the upper limits of ventilation capacity were reached. At temperatures above 30 °C, both *N. virens* and *N. diversicolor* ceased ventilation; possibly due to heat stress, but they survived 35 °C for at least 24 h. For *N. succinea* ventilation decreased at temperatures above 35 °C (Fig. 1A), suggesting the onset of thermal stress. \dot{V}_w for *N. diversicolor* was 2 to 3 times that of *N. virens* over the entire range of temperatures ($p < 0.05$). *N. succinea* ventilation was intermediate to that of the other 2 species below 20.0 °C, but above that temperature \dot{V}_w for *N. succinea* exceeded that of *N. diversicolor* (1.3 to 1.6 times).

The duration of ventilation periods (D_v) increased in all 3 species with temperature (Fig. 1B), but pattern and magnitude of the increase were different. *N. diversicolor* appeared to be quite unaffected by temperature

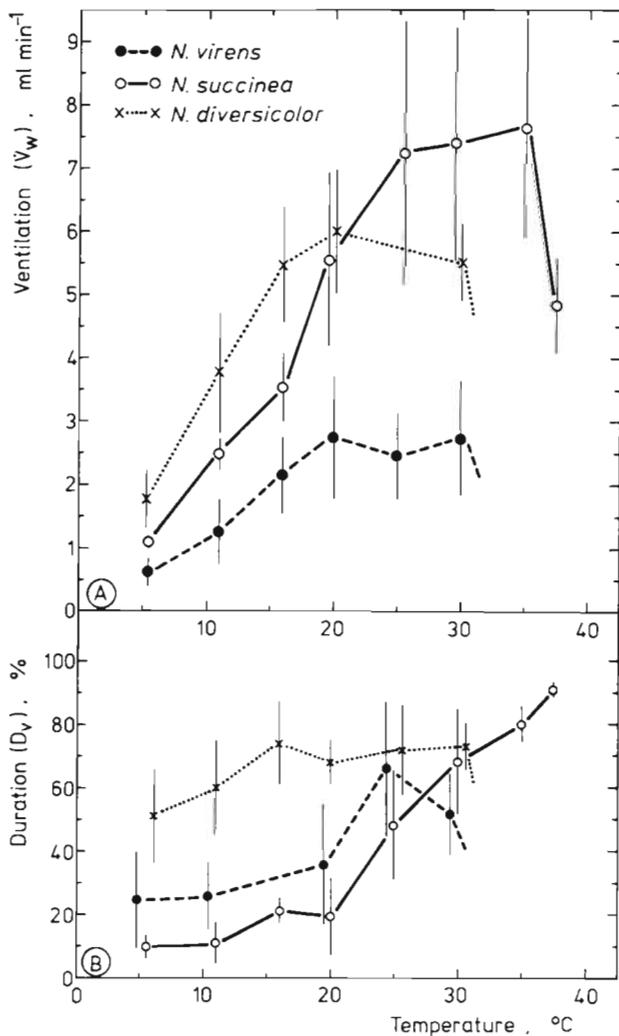


Fig. 1. *Nereis virens*, *N. succinea*, *N. diversicolor*. (A) Ventilation amplitude (\dot{V}_w) in ml min⁻¹ during increasing temperature (t °C) for 0.5 g wet wt. standard individuals. (B) Duration of ventilation in % of the total measured time (D_v) during increasing temperature. Results given as mean \pm S.D. of ca. 1 h recordings of 4 to 5 individuals

Table 1. *Nereis virens*, *N. succinea*, *N. diversicolor*. Q_{10} values of \dot{V}_w , D_v and \dot{V}_{O_2} in low and high temperature intervals

Species	Δt °C	\dot{V}_w	Q_{10} D_v	\dot{V}_{O_2}
<i>N. virens</i>	5.5–20.0	2.82	1.29	1.84
<i>N. succinea</i>	5.5–25.0	2.61	1.57*	1.64
<i>N. diversicolor</i>	5.5–16.0	2.91	1.42	2.20
<i>N. virens</i>	20.0–30.0	1.00	1.43	1.47
<i>N. succinea</i>	25.0–35.0	1.06	1.65	1.25
<i>N. diversicolor</i>	16.0–30.0	1.01	0.99	1.80

* 5.5–20.0 °C

over the range measured, showing only a slight increase ($Q_{10} = 1.13$); *N. virens* and *N. succinea* exhibited a similar response below 20.0 °C ($Q_{10} = 1.29$ to 1.57) (Fig. 1B, Table 1). Above 20.0 °C, when the upper limit of \dot{V}_w was reached, D_v for these 2 species increased markedly, suggesting a compensatory response.

The influence of temperature change on the oxygen consumption (\dot{V}_{O_2}) by *Nereis* spp. during ventilation periods is illustrated in Fig. 2. \dot{V}_{O_2} increased with

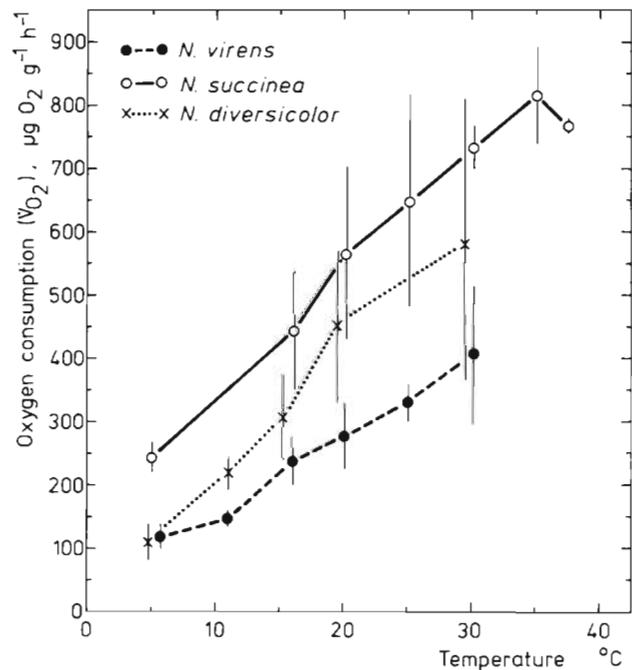


Fig. 2. *Nereis virens*, *N. succinea*, *N. diversicolor*. Oxygen uptake during active periods by 0.5 g wet wt. standard individuals during increasing temperature. Results given as mean \pm S.D. of ca. 1 h recordings of 4 to 5 individuals

temperature in all 3 species, exhibiting a steeper increase at temperatures below 20.0 °C ($Q_{10} = 1.64$ to 2.20) than above ($Q_{10} = 1.25$ to 1.80). \dot{V}_{O_2} for *N. virens* and *N. succinea* was significantly different over the measured range of temperatures ($p < 0.05$), the latter species consuming twice that of the former. \dot{V}_{O_2} of *N. diversicolor* generally was intermediate to the other species.

Effects of salinity changes

Fig. 3A illustrates the effect of declining salinity on \dot{V}_w of 0.5 g individuals of *Nereis* spp. All 3 species responded to low salinity conditions with a reduction in \dot{V}_w . For *N. virens*, \dot{V}_w decreased below 13.2‰ S. At 3.1‰ S all individuals of *N. virens* died within 24 h. *N. succinea* and *N. diversicolor* demonstrated similar pat-

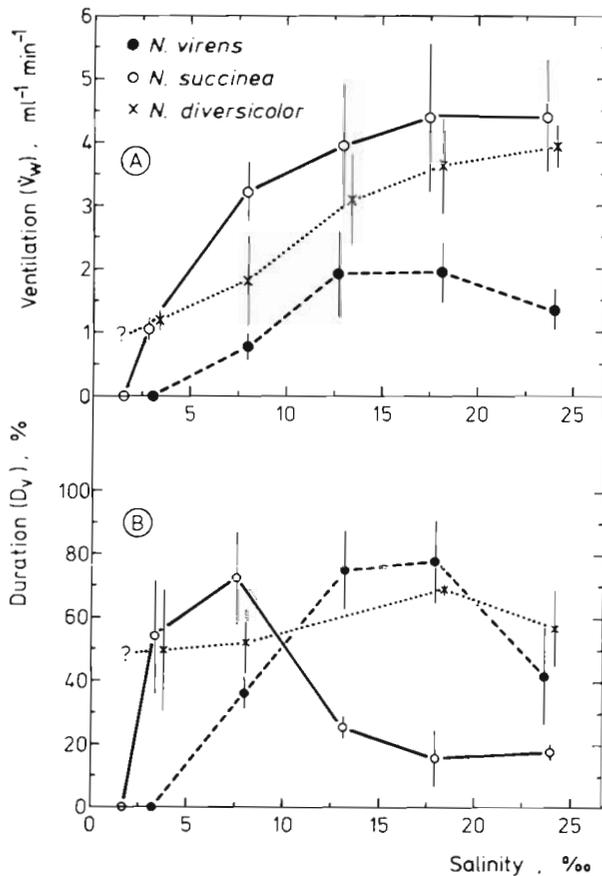


Fig. 3. *Nereis virens*, *N. succinea* and *N. diversicolor*. (A) Ventilation amplitude (\dot{V}_w) in ml min⁻¹ during decreasing ambient salinity for 0.5 g wet wt. standard individuals. (B) Duration of ventilation in % of the total measured time (D_v) during decreasing salinity. Results given as mean \pm S.D. of ca. 1 h recordings of 4 individuals

terns of decrease in \dot{V}_w during a salinity reduction from 24.0 to 8.1 ‰ S. Below 8.1 ‰ S the former exhibited a swifter decrease in \dot{V}_w than the latter, and at 1.7 ‰ S all *N. succinea* died within 24 h. Due to failure in flowmeter equipment, no measurements were performed at 1.7 ‰ S, but all *N. diversicolor* survived this salinity for more than 24 h; by direct observation, ventilation activity could be detected but not quantified. \dot{V}_w for *N. succinea* was 2 to 4 times that of *N. virens* at all salinities ($p < 0.05$). \dot{V}_w of *N. diversicolor* was intermediate to the other species.

D_v for *Nereis diversicolor* appeared to be quite unaffected by decreasing salinity, remaining fairly constant over the entire range ($D_v = 50$ to 70 %) (Fig. 3B). For *N. succinea*, no significant changes were observed in D_v down to 13.2 ‰ S ($D_v = 15$ to 25 %), but below that salinity D_v showed a rapid increase, reaching 70 % at 8.1 ‰ S. A similar increase was observed for *N. virens* from 24.0 to 18.0 ‰ S, suggesting a higher sensitivity to low salinity conditions for this species. For both *N.*

virens and *N. succinea*, D_v decreased at lower salinities, below 13.2 and 3.2 ‰ S, respectively.

A reduction in salinity from 24.0 to 3.1 ‰ S caused no significant changes in active \dot{V}_{O_2} for *N. succinea* and *N. diversicolor* (Fig. 4); this contrasted the response in \dot{V}_w . The mean \dot{V}_{O_2} of *N. virens* apparently increased about 100 % from 18.0 to 8.1 ‰ S, due to variability in the data this increase was not significant ($p > 0.05$).

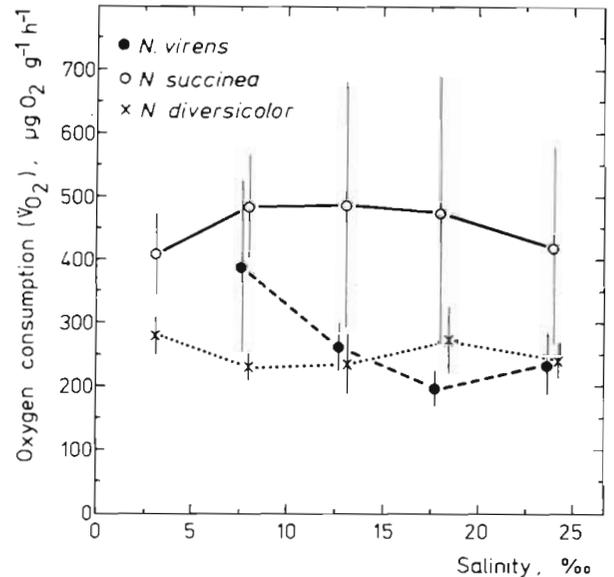


Fig. 4. *Nereis virens*, *N. succinea* and *N. diversicolor*. Oxygen uptake during active periods by 0.5 g wet wt. standard individuals during decreasing salinity. Results given as mean \pm S.D. of ca. 1 h recordings of 4 individuals

Ventilation requirement

The ratio ml water ventilated/ μl oxygen consumed (\dot{V}_w/\dot{V}_{O_2}) (Jørgensen, 1952) is commonly used to estimate the concentration of available organic matter needed in order to meet the maintenance requirements of bivalve molluscs (for review see Newell and Branch, 1980). This index might also be used as a basis for comparison between organisms under different environmental conditions. For tube-dwelling polychaetes, the inverse ratio, μl oxygen consumed/ml water ventilated (\dot{V}_{O_2}/\dot{V}_w , 'ventilation requirement', appear more appropriate to use as an index for comparing effects of changing environmental conditions.

During changing temperatures, the ventilation requirement (\dot{V}_{O_2}/\dot{V}_w) for the 3 species of *Nereis* studied showed considerable interspecific differences (Fig. 5). For all 3, minimum ratios were observed over a 10 to 15° range, i.e. between 5 and 15 °C for *N. diversicolor* and between 20 and 35 °C for *N. succinea*, suggesting this range as the optimum at the present acclimation temperature (20 °C). \dot{V}_{O_2}/\dot{V}_w was lowest for

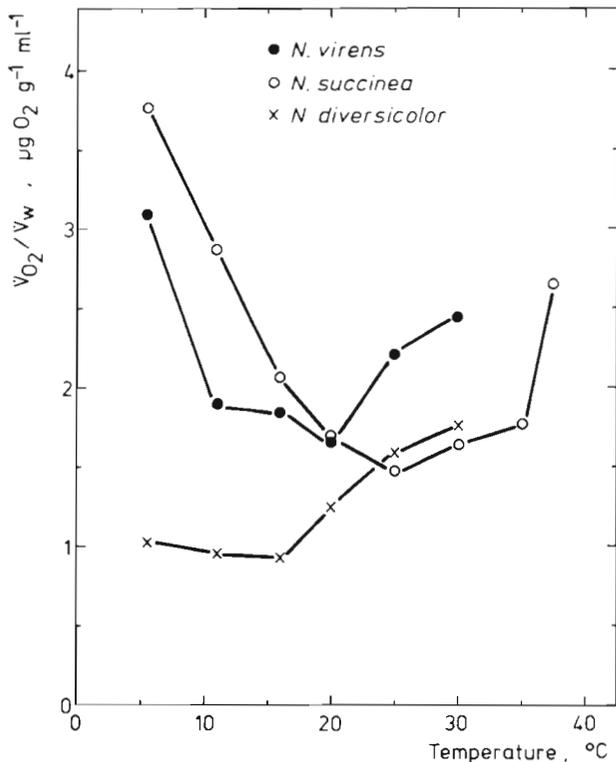


Fig. 5. *Nereis virens*, *N. succinea*, *N. diversicolor*. Ventilation requirement (\dot{V}_{O_2}/\dot{V}_w) during changing temperatures

N. diversicolor at temperatures below the acclimation level, *N. virens* reached minimum values below and at the acclimation temperature, and *N. succinea* showed the lowest figures above that temperature.

Decreasing salinities from 24.0 to 13.2‰ S affected the ventilation requirement for the 3 species only slightly. *N. virens* showed a drastic increase from 13.2 to 8.1‰ S. A similar increase appeared for *N. succinea* below 8.1‰ S (Fig. 6). For *N. diversicolor* no such sharp increase was observed; the ratio \dot{V}_{O_2}/\dot{V}_w only showed a gradually increase during lowered salinity, indicating no clearcut lower limit in contrast to the other species.

DISCUSSION

The great majority of data on the effects of changing environmental conditions on polychaete oxygen uptake were recorded without independent consideration of motor and ventilatory activity (Mangum, 1972; Ivleva, 1973; Young and Anderson, 1974; Mangum, 1978; Beis et al., 1980; Ferraris and Trivelpiece, 1980; McMahon and Russel-Hunter, 1980). The present study revealed that ventilation and oxygen uptake of *Nereis* spp. increased markedly with temperature from 5.5 °C to 16 to 25 °C (Figs 1 A; 2). The Q_{10} values in this

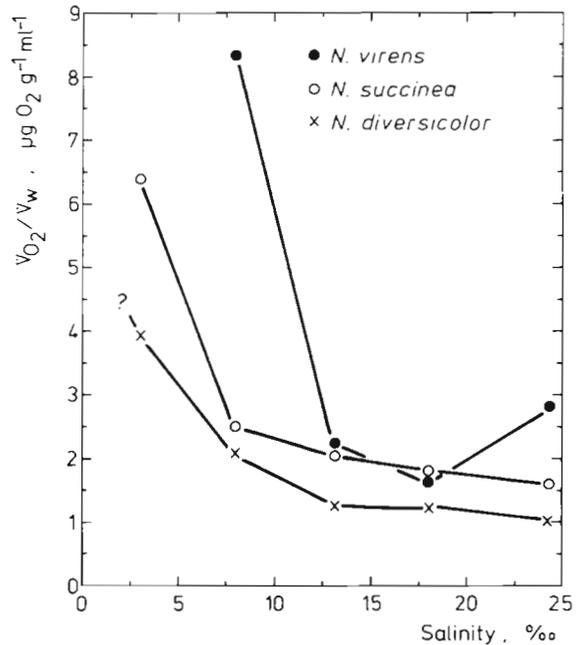


Fig. 6. *Nereis virens*, *N. succinea*, *N. diversicolor*. Ventilation requirement (\dot{V}_{O_2}/\dot{V}_w) during decreasing salinity

temperature range were higher for \dot{V}_w (2.61 to 2.91) than for \dot{V}_{O_2} (1.64 to 2.20) and D_v (1.29 to 1.57) (Table 1). Previous reports on ventilation of other polychaete species revealed Q_{10} values somewhat lower than for the \dot{V}_w obtained here, i.e. *Arenicola marina*, $Q_{10} = 2.14$ (6 to 20 °C) (Baumfalk, 1979) or 1.17 (12.25 to 14.45 °C) (Seymour, 1972); and for *Diopatra cuprea*, $Q_{10} = 1.60$ to 1.88 (12.5 to 27.5 °C) (Mangum and Sassaman, 1969). The values of Seymour and of Mangum and Sassaman were not based on \dot{V}_w , but ventilation frequency, which is comparable to D_v . The Q_{10} for \dot{V}_{O_2} reported here agree with earlier studies on polychaetes, i.e. for *Diopatra cuprea*, $Q_{10} = 1.77$ (17.5 to 27.5 °C) (Mangum and Sassaman, 1969); *Glycera dibranchiata*, $Q_{10} = 1.91$ to 2.30 (Coyer and Mangum, 1973). Despite constancy in \dot{V}_w at temperatures from 16 to 25 °C to 30 to 35 °C ($Q_{10} = 1.00$ to 1.06), \dot{V}_{O_2} continued to increase ($Q_{10} = 1.25$ to 1.80). With a further increase in temperature, heat coma sets in at the critical temperature maximum (Kinne, 1971), between 30 and 35 °C for *N. virens* and *N. diversicolor*, and above 37.5 °C for *N. succinea*. The cessation of ventilation by *Nereis* at high temperatures, but below the lethal limit, might be due to an internal mechanism that reduces or stops ventilation activity when the surface water is in some way noxious for the animals (Wells and Albrecht, 1951). The critical temperature maxima, reported here for nereids previously acclimated to 20 °C, are probably not fixed for these species, since thermal tolerance for marine invertebrates will tend to show translation of temperature curves following acclimation temperature

(Newell and Bayne, 1973; Mangum, 1978; Newell and Branch, 1980).

The ventilation requirement (\dot{V}_{O_2}/\dot{V}_w) changed with altered temperatures, and reached minimum values at species specific temperatures (Fig. 5). These changes might be due to the fact that the ventilation requirement includes a variety of energy consuming processes other than muscular activity itself (Newell and Kofoed, 1977). The temperature range of minimum ventilation requirement, where maximal ventilation efficiency was obtained, is assumed to be the optimum temperatures for these nereids. The interspecific differences in ventilation requirement suggested adaptation to low ambient temperatures in *Nereis diversicolor* and *N. virens*, and adaptation to higher temperatures in *N. succinea*. These adjustments may be considered genetic adaptations of metabolic rates, since the 3 species were preacclimated to the same temperature for a period of at least 9 d, as reported for the polychaetes *Clymenella* spp. and *Diopatra* sp. (Mangum, 1963). Smith (1963) reported that *N. succinea* in the early 1950's was extending its range northward in Europe. In Denmark the first adult specimens of this species were collected in 1953 (Rasmussen, 1973). These points of evidence suggest that, genetically, *N. succinea* is a warm-water species.

Nereis spp. respond to lowered salinities with a decreased \dot{V}_w , but not with an altered \dot{V}_{O_2} (Figs. 3A; 4). Several reports on ventilatory response to lowered salinities in marine invertebrates have revealed different results. Commonly crustaceans increase ventilation and muscular activity at low salinities (Taylor, 1977; Taylor et al., 1977; Dyer and Uglow, 1980). This is believed primarily to be the result of an increased locomotor activity associated with an escape reaction from water of unfavourable salinity (Taylor, 1977). For marine bivalves (Theede, 1963) and polychaetes (Wells and Ledingham, 1940; Shumway and Davenport, 1977) any marked decrease of salinity in the external medium result in a slowing down or inhibition of ventilation. Decreasing salinity is known to produce a swelling of the body of polychaetes, due to osmotic influx of water through the soft body walls (Sayles, 1935; Jørgensen and Dales, 1957; Oglesby, 1978). Beadle (1931) reported that the weight of *Perinereis cultrifera* and *Nereis diversicolor* rose after transfer to low salinity, and after several hours volume regulation, they both appeared very expanded and especially the former was capable of only very slight movements. This might inhibit peristaltic body movements, which occur during ventilation and explain the gradual decrease in \dot{V}_w at decreasing salinities found presently for the 3 species of *Nereis*.

Ventilation requirement, especially of *Nereis virens* and *N. succinea*, showed a dramatic increase (300 to

400%) at salinities below 10 to 15‰ S (Fig. 6). The least euryhaline *N. virens* shows a much greater body swelling at low salinities than does the more euryhaline *N. diversicolor* (Beadle, 1931; Oglesby, 1978). This is in accord with, and might be responsible for, the greater increase in ventilation requirement observed for *N. virens* and *N. succinea* at low salinities than for *N. diversicolor*. Several reports reveal that the onset of hyperosmotic and hyperionic regulation of *Nereis* spp. occurs at salinities below 10 to 12‰ S (Oglesby et al., 1982; Quinn and Bashor, 1982), but the increased ventilation requirement cannot solely be due to increased demands for active ion transport. Potts (1954) showed that the energetic cost of ionic and osmotic regulation is low, accounting for only a small part of the observed oxygen consumption in marine invertebrates.

The interspecific differences shown here in ventilation requirement at different temperatures and salinities provides some evidence for explaining the distributional patterns of nereids in estuaries. Due primarily to its weak tolerance of low salinities, *Nereis virens* is never found in areas of low and fluctuating salinity, but always outside and in the mouth of estuaries (Muus, 1967; Rasmussen, 1973; Kristensen, 1981a). Both *N. succinea* and *N. diversicolor* can live at low salinities; the latter can even endure nearly fresh-water conditions. However, *N. succinea* are never found in the upper intertidal and inner low salinity areas of estuaries (Muus, 1967; Kristensen, 1981a); these areas are always occupied by *N. diversicolor*. This might be due to the different thermal tolerances of these species. Possibly, the warm-water species *N. succinea* cannot survive the heavy ice-cover and low temperatures that develop during winter in the upper intertidal and inner parts of Danish estuaries. Of course, tolerance limits of temperature and salinity cannot explain fully the distributional patterns of these nereids, since a high degree of interspecific competition apparently exists among these species (Kristensen, 1981a).

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