

Influence of Temperature and Salinity on Food Conversion and Growth of Different *Nereis* Species (Polychaeta, Annelida)*

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ABSTRACT: Feeding experiments in 15 and 30‰ salinity reveal similar food conversion rates of *Nereis succinea* and *N. diversicolor* at high temperature (15 °C). At low temperature (5 °C) food conversion of *N. diversicolor* is more efficient. A salinity increase from 15 to 30‰ S facilitates better food conversion in both species leading to an increased energy content (exception: *N. succinea* at 5 °C and 30‰ S). *N. diversicolor* exhibits better food conversion at low temperature, generally higher production rates, lower gross energy demand for production and a lower maintenance metabolism at 15‰ S in comparison with *N. succinea*. This suggests that *N. diversicolor* is better fitted to the specific environmental conditions of the Baltic Sea than *N. succinea*. A comparison of assimilation efficiencies and gross growth efficiencies of different species showed an increase in the sequence *N. succinea*, *N. diversicolor* and *N. virens*.

INTRODUCTION

Nereis species are known to serve as food organisms, for example for cod and plaice (Kinne, 1954; Muus, 1967). Some of these species are stenohaline; others are euryhaline and show quite different salinity preferences ranging from fresh water to marine environments (Smith, 1970). *Nereis* species of Kiel Bay prefer shallow waters and, therefore, are exposed to seasonally changing temperatures. Both temperature and salinity are known to influence functional and structural properties (Kinne, 1964, 1970b, 1971b). They might affect body components and growth parameters as well and cause qualitative and quantitative changes. To quantify these changes, individuals of the omnivorous *N. diversicolor* and the detritus-feeding *N. succinea* from the same habitat in Kiel harbour (Baltic Sea) were fed under various temperature and salinity combinations. A comparison with data from the literature for the omnivorous *N. virens* should permit the evaluation of species-specific differences of productivity parameters and ecological pretensions.

MATERIAL AND METHODS

The two examined *Nereis* species are free-living and tolerate a wide range from euhaline to oligohaline

salinities, temporarily even fresh water (Hartmann-Schroeder, 1971). In Kiel harbour, *N. succinea* is abundant in a sapropel habitat at a depth of 5 m (near Bellevue Bridge) feeding on substrate and detritus particles. The omnivorous *N. diversicolor* is also found in this habitat but prefers a shallower sand biotope down to 2 m depth (for feeding preferences consult Goerke, 1966, 1971a; and Hartmann-Schroeder, 1971).

During the feeding experiments the worms were kept in a darkened box containing 25 l sea water, allowing at least 1 l per animal. At a pumping rate of 180 l h⁻¹ the sea water was cleaned by filtering through a charcoal filter. In addition, the whole water content was renewed once a week. Each worm lived in a Petri dish of 5-cm diameter and two opposing chimney-like glass tubes 7.5 cm long with inner diameters varying from 3 to 7 mm according to the animal's size (Fig. 1). Worms which had left their dish were identified by distinguishing marks and weight. Animals were fed once a day but only when they had eaten up their last ration. Food portions ranged from 0.05 to 0.2 g_{ww} and were placed into the Petri dishes.

For experiments under marine conditions, the worms were gradually adapted to 30‰ S, whereby the Baltic-

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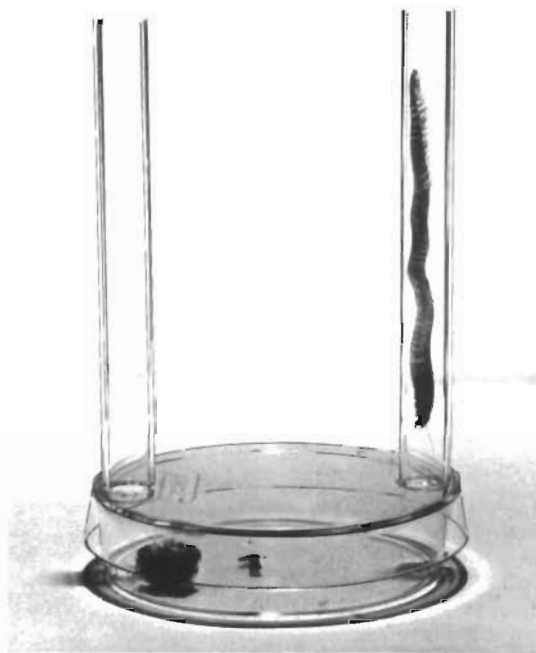


Fig. 1. *Nereis succinea*. A test individual in its housing. Petri dish (Polystyrene) \varnothing 5 cm; glass tubes \varnothing 3–7 mm, depending on worm size; food cube

Sea salinity was increased in 3 ‰ steps over a period of 10 days. For the same period the animals were not fed in order to clear their gut. The subsequent feeding period lasted for 28 days.

The Petri dishes of two worms per experiment were cleaned every second day, collecting food residues, faeces and the thin mucous layer with which inhabited parts of the housings were often coated. The wastes were deep frozen (-28°C) for later analysis. Their total energy value was subtracted from the total energy value of the food consumed, thus revealing the value of the food assimilated. Due to the normally inseparable mucous component, this value can be slightly underestimated.

Biochemical criteria like glycogen, lipid and protein contents were determined according to methods of Lowry et al. (1951), Zöllner and Kirsch (1962) and Handel (1965). Energy contents were determined according to Phillipson (1964) and a manual of Gentry Instruments. For details see Neuhoff (1979).

The food used in these experiments was composed of 1 part Agar Agar, 20 parts freeze-dried and ground *Mytilus* tissue and 100 parts water. The preparation was done as follows: Water was heated until boiling and Agar Agar added. While stirring, the solution was cooled to 60°C . The lyophilized and ground *Mytilus* tissue was then added. While stirring, the pulp was cooled to 30°C and then poured into Petri dishes.

RESULTS

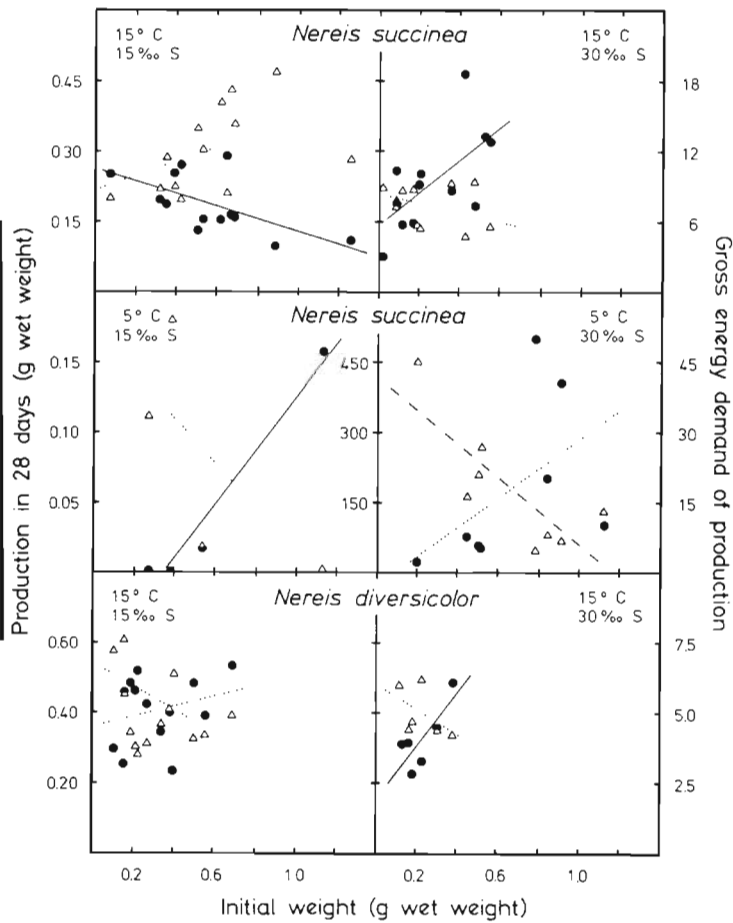
Results of feeding experiments whether they refer to body components or to growth responses must be comparable. For this reason results of this study are normally given for a standard worm containing 0.0962 g organic substance (= ash free dry weight). This represents the mean value of 290 *Nereis succinea* derived from samples collected during 18 successive months. Where necessary, values were also calculated for a standard worm containing 0.015 g organic substance.

All experiments were preceded by a 10 d period without feeding. This was necessary in order to clear the animals' gut and to adapt them to a higher salinity (30‰ S) where required. Thus all individuals had equal starting conditions at the beginning of an experiment. During this time the worms had to maintain their metabolism at the expense of their own body substance. When exposed to habitat salinity (15‰ S , 15°C), *Nereis diversicolor* showed a smaller energy loss during this starvation period than *N. succinea* (Table 1). When in the course of this period the worms were adapted to 30‰ S their energy loss was generally higher, with energy loss of *N. diversicolor* surpassing that of *N. succinea*.

Table 1. *Nereis succinea* and *N. diversicolor*. Energy requirements for maintenance metabolism of standard worms (0.0962 g organic substance) during starvation period of 10 d at 15°C and 15 or 30‰ S

Salinity (‰)	WW* (g)	Loss of body substance (%)	WW** (g)	Energy loss (J/d)	Additional energy loss (J/d)
<i>N. succinea</i>					
15	0.7273	– 20.7	0.5767	41.5	
30	0.7273	– 31.4	0.4989	62.8	21.3
<i>N. diversicolor</i>					
15	0.6789	– 11.4	0.6015	24.3	
30	0.6789	– 35.2	0.4399	75.0	50.7

* Calculated initial wet weight of a standard worm.
** Calculated wet weight at end of 10-day starvation period.



Growth parameters are calculated for a standard worm containing 0.0962 g organic substance (Table 2). In addition to the 28-d production rate and the gross energy demand for production (C/P), both presented in Figure 2, they give the net energy demand of production (A/P), gross and net growth efficiency (P/C and P/A) as well as assimilation efficiency (A/C) in percent. The latter three show what percentage of the consumed (or assimilated) food is used for production and what percentage of the consumed food is assimilated.

In standard experiments with *Nereis succinea* (15 °C, 15 or 30‰ S) the worms showed two distinct reaction types: fast- and slowly-growing animals (Type A and B) were clearly discernible by a discrimination analysis (Table 2). Both types showed decreasing production rates with increasing worm weight at 15‰ S. The gross energy demand for production (C/P), however, increased, thus indicating that older worms convert food less effectively. The 30‰-salinity experiment revealed inverse relations: production rate increased

Fig. 2. *Nereis succinea* (Type A) and *N. diversicolor*. Size dependence of production rate (P) and gross energy demand for production (C/P). Individuals were fed for 28 d at different temperatures and salinities. — Regression of production rate on initial weight; values correlated at $\leq 5\%$ significance. ··· Regression of production rate on initial weight; values not correlated. --- Regression of gross energy demand of production on initial weight; values correlated at $\leq 5\%$ significance. - - - Regression of gross energy demand of production on initial weight; values not correlated

Table 2. *Nereis succinea* and *N. diversicolor*. Growth parameters of standard worms after feeding period of 28 d under different abiotic conditions. P : production rate; L : rate of substance loss; C/P : gross energy demand of production; A/P : net energy demand of production; P/C : gross growth efficiency; P/A : net growth efficiency; A/C : assimilation efficiency

t °C	S (‰)	Type	Initial weight (g)	$P/28$ d (g)	n_p	L	n_l	C/P (kJ)	A/P (kJ)	P/C (%)	P/A (%)	A/C (%)
<i>Nereis succinea</i>												
15	15	A	0.544*	0.190 ± 0.052	13			9.9 ± 3.7	7.3 ± 2.1	10.1	13.7	60.9
15	30	A	0.511*	0.320 ± 0.083	12	-0.069 ± 0.028	8	6.3 ± 1.8	4.2 ± 1.2	15.9	23.8	67.4
15	15	B	0.591*	0.020 ± 0.032	13			72.5 ± 15.5	44.1 ± 9.4	1.4	2.3	60.9
15	30	B	0.493*	0.079 ± 0.031	8			18.4 ± 49.2	12.4 ± 33.5	5.4	8.1	67.4
5	15		0.677*	0.062 ± 0.018	4	-0.037 ± 0.019	19	190.0 ± 210.6	152.6 ± 169.1	0.5	0.7	80.3
5	30		0.578*	0.050 ± 0.055	8	-0.060 ± 0.026	12	21.0 ± 8.8	17.8 ± 7.5	4.8	5.6	84.7
<i>Nereis diversicolor</i>												
15	15		0.666*	0.457 ± 0.099	13			4.2 ± 1.3	3.4 ± 1.1	23.8	31.3	80.8
15	30		0.553*	0.568 ± 0.062	6			3.5 ± 0.8	2.9 ± 0.7	28.6	34.5	84.1
<i>Nereis diversicolor</i>												
15	15		0.123**	0.378 ± 0.099	13			5.5 ± 1.3	4.5 ± 1.1	20.0	22.2	80.8
15	30		0.107**	0.233 ± 0.062	6			5.6 ± 0.8	4.7 ± 0.7	17.9	21.3	84.1
5	15		0.114**	0.032 ± 0.014	12	-0.002 ± 0.005	6	14.8 ± 12.6		6.8		
5	30		0.096**	0.041 ± 0.015	4	-0.014 ± 0.009	4	13.3 ± 7.6		7.5		

n_p Number of worms producing body substance.
 n_l Number of worms losing body substance in spite of being fed.
 * Calculated for 0.0962 g organic substance.
 ** Calculated for 0.0150 g organic substance.

with rising initial weight and the ratio C/P decreased. In all four cases initial weight and production rate were correlated on a 5% level of significance.

High salinity not only caused an inversion of the size dependence of the production rate but also a lower gross energy demand for production (C/P), a higher gross growth efficiency (P/C) and assimilation efficiency (A/C), as shown by a comparison of corresponding reaction types at 15 °C and 15 or 30 ‰ S (Table 2).

Low temperature experiments with *Nereis succinea* (5 °C; 15 or 30 ‰ S) were first of all marked by numerous worms which lost weight although they were fed (Table 2). Far more worms were able to grow at a salinity of 30 ‰ than at 15 ‰ S. Both experiments documented increasing production rates with increasing initial weight (Fig. 2). Values for standard worms were of similarly low magnitude (Table 2). The energy demand for production decreased with body weight. In contrast to a similar magnitude of production rates in both experiments a standard worm at 15 ‰ S needed nine times more energy for production than at 30 ‰ S. The observed substance losses of fed worms were higher in the high salinity experiment. They were lower, however, than comparable values at 15 °C (Table 2).

Growth reactions of *Nereis diversicolor* were examined at temperatures of 5 °C and 15 °C and salinities of 15 and 30 ‰ S. In all cases production rates increased, and gross energy demands for production decreased with increasing initial weight (Fig. 2). However, the values showed a very high variability so that a statistical correlation between body size and the growth parameters investigated was only found for the production rate at 15 °C, 30 ‰ S (5% level of significance).

Growth parameters of 5 °C experiments had to be calculated for a smaller standard worm with 0.015 g organic substance. In the case of these experiments wastes were too small for determining assimilation values. At 5 °C the gross energy demand for production (C/P) was about three times higher than at 15 °C. Correspondingly, a far smaller production rate was found at 5 °C. A higher salinity of 30 ‰ produced higher growth rates regardless of whether temperature was high or low.

Production rates of *Nereis diversicolor* at 15 °C and in both salinities were about twice as high as those of *N. succinea* under the same conditions. Correspondingly, the gross energy demand of *N. diversicolor* for production (C/P) was lower. In contrast to *N. succinea*, most *N. diversicolor* were able to grow at 5 °C.

Some difficulties, often reducing the number of evaluable worms, arose in metamorphosing individuals or worms with quite variable response patterns ranging from high (Type A) over low (Type B) to negative

growth rates, or due to mortality and handling damages incurred during experiments.

Size dependence of body components of individuals of a *Nereis succinea* field population is shown in Figure 3 and can be described by regression lines. Glycogen and lipid contents of *in situ* worms normally increased, while the protein content decreased with increasing body size. Energy content often seemed to be size independent.

Low temperature influenced feeding in *Nereis succinea* (Fig. 4, worms fed for 28 days) in the following way: The glycogen and lipid levels were lower at 5 °C than at 15 °C. Corresponding contents of a field individual, however, reached higher values at the lower

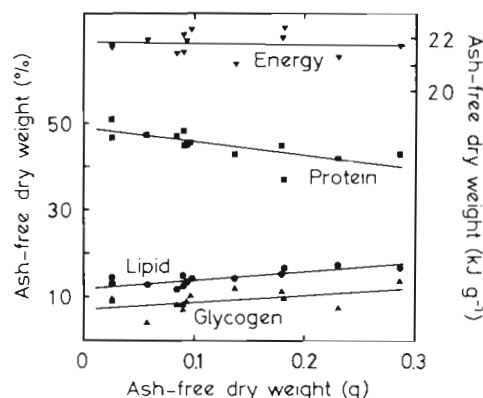


Fig. 3. *Nereis succinea*. Size dependence of some body parameters

temperature. Protein contents were similar at both temperatures with slightly elevated values at 5 °C. Low temperature experiments produced lower energy contents which were very similar to those of field individuals.

In addition to temperature, food conversion of *Nereis succinea* was influenced by salinity. Protein contents were higher at 30 ‰ S regardless of whether experimental temperatures were 5° or 15 °C. Energy content showed salinity-elevated values at 15 °C. Glycogen and lipid contents were generally lower than those at 15 ‰ S (Fig. 4).

Experiments under standard conditions (15 °C; 15 or 30 ‰ S) were also carried out with *Nereis diversicolor* (Fig. 4). Salinity influence on food conversion was largely the same as for *N. succinea*. In comparison with this species, however, much higher glycogen contents were found while lipid and protein contents showed lower values. Energy levels of both species were very much alike under these conditions.

To compare the results of 5 °C feeding experiments on *Nereis diversicolor* with those of other experiments, all values had to be calculated for a standard worm

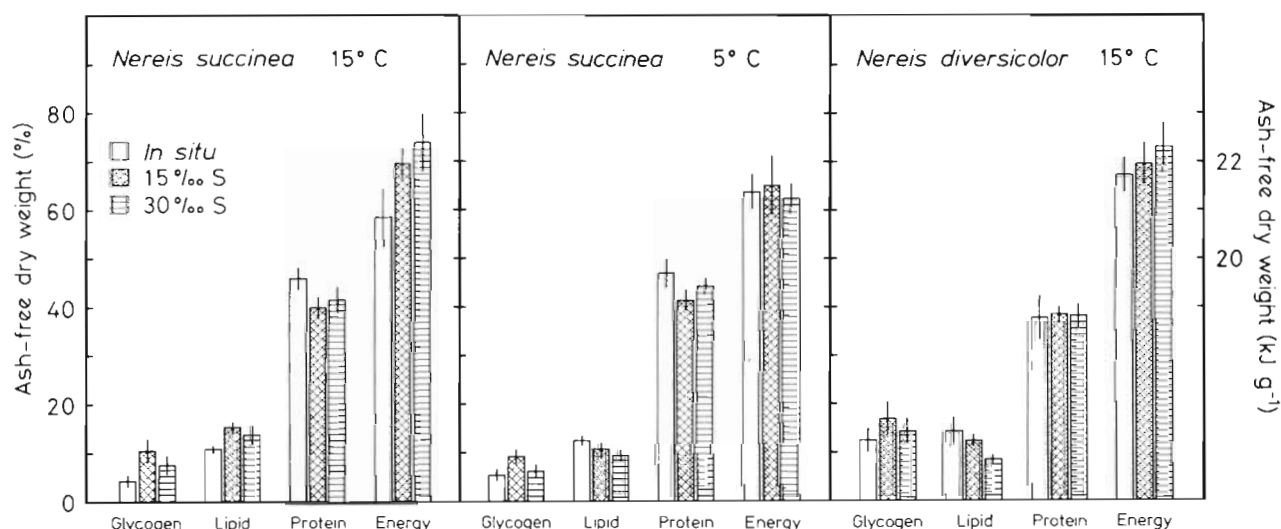


Fig. 4. *Nereis succinea* and *N. diversicolor*. Biochemical parameters of standard worms (0.0962 g organic substance) fed for 28 d at 15 °C in different salinities. Values calculated via regression equation; vertical bars: standard error of the estimate ($s_{y,x}$)

containing 0.015 g organic matter (Table 3) as only small individuals were available for these experiments. Similar to corresponding experiments with *N. succinea* glycogen contents of *N. diversicolor* decreased with decreasing temperature. Lipid, protein and energy contents, however, increased.

Compared with a *Nereis succinea* worm of the same size (0.015 g organic matter), *N. diversicolor* showed higher glycogen and – in contrast to the experiments conducted at 15 °C – also higher lipid and much higher energy levels. Although the standard field animal already showed a relatively high energy level, this value could be increased by feeding in the 30‰ S experiment irrespective of the low temperature. The corresponding experiment with *N. succinea* showed no similar effect (Table 3).

DISCUSSION

Changes in environmental conditions, e.g. fluctuations in temperature and salinity, can affect metabolic activities and cause changes in growth rates and chemical composition of marine animals. For reviews consult 'Marine Ecology', Volume I: Kinne, 1970a, b, 1971a, b.

In this study individuals of *Nereis succinea* and *N. diversicolor* were fed at different combinations of temperature (5 and 15 °C) and salinity (15 and 30‰ S). Growth experiments with *N. succinea* and *N. diversicolor* generally show an inverse size dependence of production rate (P) and gross energy demand for production (C/P). At 15 °C and 15‰ S, the production rate of *N. succinea* decreases while the gross energy

Table 3. *Nereis diversicolor* and *N. succinea*. Biochemical composition of standard worms (containing 0.015 g organic substance) after a feeding period of 28 d under different abiotic conditions. dw, af: Dry weight, ash free

Time of experiment	t °C	S (‰)	Glycogen (dw, af; %)	Lipid (dw, af; %)	Protein (dw, af; %)	Energy (dw, af; kJ g ⁻¹)
<i>Nereis diversicolor</i>						
September	<i>in situ</i>		7.3 ± 2.6	15.6 ± 2.9	53.8 ± 4.5	21.194 ± 0.367
	15	15	14.4 ± 3.4	12.9 ± 1.2	39.2 ± 1.7	22.203 ± 0.425
	15	30	9.2 ± 2.6	8.4 ± 1.0	41.6 ± 2.4	21.500 ± 0.514
February	<i>in situ</i>		4.1 ± 1.0	13.4 ± 0.5	43.6 ± 7.7	22.105 ± 0.339
	5	15	9.6 ± 1.9	14.5 ± 1.6	45.5 ± 3.1	22.180 ± 0.310
	5	30	5.6	14.0	44.0	22.456
<i>Nereis succinea</i>						
December	<i>in situ</i>		2.9 ± 1.3	9.9 ± 1.1	50.0 ± 3.0	20.995 ± 0.361
	5	15	6.8 ± 1.6	9.0 ± 1.2	42.8 ± 2.3	21.385 ± 0.614
	5	30	4.3 ± 1.6	6.7 ± 1.2	48.6 ± 1.5	20.899 ± 0.324

demand for production increases with increasing body size. Small worms show high productivity combined with a low gross energy demand for production. When the temperature is lowered or the salinity increased, inverse relations prevail: The larger worms then exhibit higher productivity values. According to Goerke (1971b), high and low temperature experiments (8° and 16 °C) with *N. virens* in brackish water (20 ‰ S) produced the same response pattern. However, the production rate of *N. diversicolor*, irrespective of temperature and salinity, always increases with body size.

Nereis succinea, *N. diversicolor* (this paper) and *N. virens* (Goerke, 1971b) perform high growth rates at temperatures near 15 °C. At lower temperatures, however, only very small growth rates were found. Accordingly, all three species may reduce or even cease growth during winter.

Feeding experiments with adequate food produce gross and net growth efficiencies increasing in the sequence *Nereis succinea*, *N. diversicolor*, *N. virens* (Table 4). The values of the latter species are by far the highest. Consequences in nature may be found in regard to differences in final weight. Both *N. succinea* and *N. diversicolor* have a life span of about two years (Dales, 1951; Chambers and Milne, 1975; Neuhoff, 1977). The largest individuals of both species observed in Kiel harbour suggest that a final weight may be reached in the range of 2 g_{ww}. *N. virens*, with a maximum life span of three years, can reach about 15 g_{ww} in two years (Kay and Brafield, 1973). Different assimilation efficiencies may be an expression of specific

modes of nutrition. The omnivorous *N. diversicolor* and *N. virens*, for instance, show assimilation efficiencies of about 80 ‰, whereas in the detritus-feeding *N. succinea* a range of only 60 ‰ is found (Table 4). Higher assimilation efficiencies of *N. succinea* at 5 °C may be caused by temperature-induced slower gut passage of the food. The low gross-growth efficiencies found for *N. virens* feeding on biodeposits (Tenore and Gopalan, 1974) suggest an influence of food quality. But even the high-grade food offered by the authors gave poor results, in contrast to the gross-growth efficiency reported by Kay and Brafield (1973).

Some of the growth results (Table 2) reported are characterized by high standard errors of the estimate ($s_{y,x}$), e.g. the values of the slowly growing B-Type *Nereis succinea*, all 5 °C results, and whenever worms lost weight in spite of being fed. This suggests that either the abiotic conditions were unfavourable or the worms themselves might not have been in a normal, healthy condition.

Feeding experiments with *Nereis succinea* and *N. diversicolor* at different combinations of temperature and salinity (with the exception of *N. succinea* at 5 °C, 30 ‰ S) always produced higher energy contents than in comparable *in situ* individuals, thus indicating the suitability of the food supplied.

Low temperature has a far greater effect on *Nereis succinea* than on *N. diversicolor*. Compared with results at higher temperature (15 °C) *N. diversicolor* at 5 °C shows only a reduced glycogen content while lipid values as well as energy levels increase

Table 4. Gross growth efficiency (P/C), net growth efficiency (P/A) and assimilation efficiency (A/C) of three *Nereis* species

Species	Author	Food	t (°C)	S (‰)	Size (g _{ww})	P/C (%)	P/A (%)	A/C (%)
<i>N. succinea</i>	1	<i>Mytilus edulis</i>	15	15	0.5	10	14	61
			15	30	0.5	16	24	67
<i>N. diversicolor</i>	1	<i>Mytilus edulis</i>	15	15	0.7	25	31	81
			15	30	0.6	29	35	84
	1	<i>Mytilus edulis</i>	15	15	0.1	20	22	81
			15	30	0.1	18	21	84
	2	<i>Enchytraeus albidus</i>	15	18	0.1-0.2	35	70	59
<i>N. virens</i>	3	<i>Lanice conchilega</i>	8/16	20	0.5-8.0	35-50		
	4	<i>Nephtys hombergii</i>	15		1.5-4.0	44	52	85
	5	Biodeposits	20		0.6	7	29	
Clamtissue		20		0.5	23	77		
1 Neuhoff (this study).			4 Kay and Brafield (1973).					
2 Ivleva (1970).			5 Tenore and Gopalan (1974).					
3 Goerke (1971b).								

(30 ‰ S) or remain unaffected (15 ‰ S). Compared with *N. succinea*, the reserve and energy contents of *N. diversicolor* are higher at 5 °C. This indicates that *N. diversicolor* is better fitted to low temperature conditions than is *N. succinea*. *N. succinea* reduces or even ceases feeding at low temperatures. This fact agrees with observations of Mangum (1969) who reported that *N. succinea* from York River Estuary exhibited no feeding response to chemical stimulation at temperatures below 10 °C.

An influence of salinity on metabolism is demonstrated by markedly lower amounts of reserves in fed individuals and by higher energy losses of starving worms tested at 30 ‰ S, compared with those at 15 ‰ S. This effect may be explained on the basis of the model given by Hochachka and Somero (1973) who discuss a Na⁺ or Cl⁻ induced activation of enzymatic glutamate catalysis as a base for the production of amino acids needed for cell-volume regulations necessary to cope with external salinity increase.

The lower energy loss of *Nereis diversicolor* during starvation at 15 ‰ S in comparison with *N. succinea* indicates a better adaptation of this species to brackish water conditions. At high salinity (30 ‰ S) the reverse relation prevailed indicating that *N. succinea* prefers higher salinities.

In summary *Nereis virens*, the largest species tested here, has by far the fastest and most efficient growth (Goerke, 1971b; Kay and Brafield, 1973). This species tolerates euhaline and oligohaline conditions but prefers habitats with higher salinities (Hartmann-Schroeder, 1971). *N. diversicolor* from the Baltic Sea combines fast growth and efficient food conversion with an ability to inhabit biotopes with low salinities and temperatures. This omnivorous species is able to grow even at low temperatures. Ivleva (1970) reports that gonads of adult individuals ripen even at 5 °C. Baltic Sea *N. succinea* grow slower and show less efficient food conversion. The salinity range of the detritus-feeding worms is similar to that of *N. diversicolor*. *N. succinea*, however, requires higher temperatures for growth. The ability to live at low salinities and to produce even at low temperatures predestinates *N. diversicolor* for the specific environmental conditions prevailing in the Baltic Sea, including its eastern parts which are rather cold in winter. My results on growth and food conversion in *N. succinea*, however, suggest that this species prefers distinctly higher salinities and temperatures.

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