

Effects of Seasonally Varying Factors on a *Nereis succinea* Population (Polychaeta, Annelida)*

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ABSTRACT: *Nereis succinea* populations of the Kiel Fjord (Baltic Sea) show marked annual changes in energy content and main body components (glycogen, lipid, protein). Maximum values of body components and energy content were recorded in spring and early autumn, when food supply and other environmental circumstances are favourable. During the first half of the year the food value of the worm (determined as energy content of fresh weight) is higher than during the second half. Biomass values reveal a similar dynamic pattern. They are markedly influenced by spawning.

INTRODUCTION

Benthic polychaetes represent a major food reservoir for marine demersal fishes. Among the polychaete species of shallow coastal areas members of the genus *Nereis* have been studied under different ecological aspects (Brand, 1927; Dales, 1951; Kinne, 1954a, b; Goerke, 1971a, b; Bass and Brafield, 1972; Kay and Brafield, 1973; Chambers and Milne, 1975). In the Kiel Fjord both abundance and nutritive value of *N. succinea* change continuously due to fluctuations in abiotic and biotic factors, such as temperature, salinity and food supply. I have investigated the correlations between these factors and annual changes in population strength as well as changes in the main body components and energy content. The results obtained facilitate a better evaluation of *N. succinea* as a food organism for demersal fishes.

MATERIALS AND METHODS

The free-living *Nereis succinea* tolerates euhaline or oligohaline salinity conditions, temporarily even fresh water (Hartmann-Schroeder, 1971). In Kiel harbour it is abundant at a depth of 5 m (near Bellevue Bridge) where it occupies a sapropel habitat. The species feeds on substrate and detritus particles (Goerke, 1971a). According to Hartmann-Schroeder, *N. succinea* lives

in U-shaped passages that are lined with mucus. I have often found individuals living in the sludge-filled shells of dead *Mytilus edulis*.

A 0.1-m² van Veen grab was used for sampling. For the analysis, the adhering water was dried off and the worms' fresh weight determined. To obtain their dry weight, the worms were deep frozen and lyophilized. This procedure was followed by oven drying at 105 °C until weight constancy. For further analysis, each worm was separately powdered. Only individuals with less than 60 mg dry substance were pooled. The monthly analysis data presented are based on 15 individuals in each case.

Glycogen content was determined according to Handel (1965) with some modifications: 4 mg sample powder were boiled with 0.5 ml KOH (30 %) for 30 min. The dissolved glycogen was then precipitated with 2 ml ethanol (96 %) and 0.05 ml saturated Na₂SO₄. To allow bigger aggregates to form, the samples were stored in a refrigerator overnight. After centrifugation (4200 g) the supernatant ethanol was discarded and the glycogen redissolved with 1 ml trichloroacetic acid (TCA: 15 %). Precipitating proteins were centrifuged; the TCA-dissolved glycogen was quantitatively transferred into a clean test tube and precipitated with 5 ml ethanol and some grains of KCl (Giese, 1967). The overnight refrigerated samples were centrifuged, the supernatant ethanol was discarded and the glycogen dissolved in distilled water (10 to 15 ml). In an ice bath 2 ml Anthrone reagent (2 mg Anthrone per ml H₂SO₄, d = 1.84) were added to 1 ml glycogen solution. The mixture was heated for 20 min at 90 °C, cooled and measured at 620 nm using a 1-cm cuvette. The calibra-

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tion straight line was determined with commercial glycogen.

Lipid content determination was carried out with a test kit for total lipids*. The method, described by Zöllner and Kirsch (1962), was originally developed for determination of serum lipids. Barnes and Blackstock (1973) tested its suitability for analysing tissues of marine animals. As the sulphophospho-vanillin-reaction is not sensitive to interfering substances, 3 mg dry substance were directly dissolved by adding 2 ml H_2SO_4 ($d = 1.84$) and boiling the mixture for 10 min in a water bath. Then the dissolved substance was analysed according to the test kit's manual.

As only small amounts of dry substance were available, the following method was used to determine the protein content: 3 mg dry substance were successively washed with 1 ml absolute ethanol and 1 ml diethyl ether to eliminate lipids. After each wash the sample was centrifuged (4200 g). Washing solutions had to be decanted very cautiously. The remaining substance was filled up with 5 ml 1 n NaOH; the test tubes were tightly stoppered and shaken in a horizontal position for 19 h. This period proved sufficient to dissolve even very resistant sample contents. The solution was then analysed according to Lowry et al. (1951). The calibration graph was measured from 60 to 300×10^{-6} g protein using the protein standard of Merckotest Total Protein**.

A Phillipson Microbomb Calorimeter was used to determine tissue energy content. A detailed description of the equipment's working modus was given by Phillipson (1964) and in the Gentry Instruments manual. Benzoic acid*** was used for calibration. Combustion conditions were 30 atm O_2 and room temperature. The energy content was determined as the mean of 3 runs per sample with pills weighing between 5 and 8 mg.

Ash content was determined by heating the combusted calorimetry samples to 500 °C in a muffle furnace to eliminate organic residues. This method sometimes gives slight underestimations of ash content. Samples, however, were often too small to allow separate ash determination.

RESULTS

Information on quantitative changes of the *Nereis succinea* population studied during one year was obtained from regular biomass examinations (Fig. 1; for sample sizes consult Table 1). In 1975, from January until May,

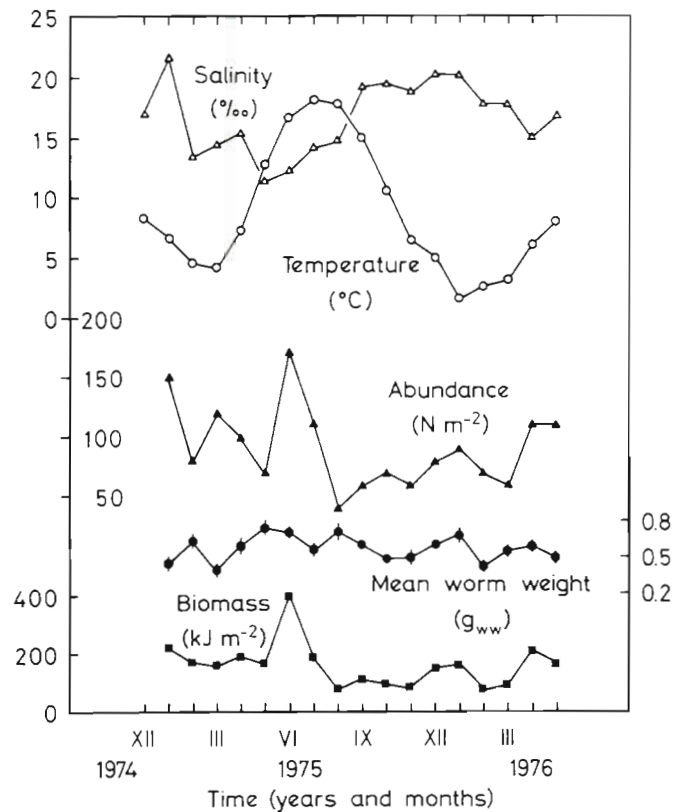


Fig. 1. *Nereis succinea*. Annual fluctuations recorded in a Kiel Fjord population and changes in temperature and salinity. Fw: wet weight. Vertical bars: standard deviation of the means ($s_{\bar{x}}$). Abundance values rounded to the closest ten. Biomass values given as product of abundance, mean worm weight and mean energy content of fresh weight

Table 1 *Nereis succinea*. Sample sizes and worm numbers. These data provide the basis for estimating abundance fluctuations of a Kiel Fjord population

Month/Year	Number of grabs	Number of worms
1/75	4	59
2	4	32
3	4	46
4	3	30
5	6	42
6	7	120
7	5	53
8	11	39
9	16	90
10	9	67
11	5	29
12	11	91
1/76	5	45
2	5	33
3	5	29
4	6	68
5	5	53

* Merck No. 3321.

** Merck No. 3327

*** BDH Chemicals Ltd, Poole, England; No. 27334.

the biomass showed an average of 175 kJ m⁻². In June the energy content per m² rose to 400 kJ. In July it declined to 190 kJ m⁻², followed by an average value of 100 kJ m⁻² until November. This level was clearly below the biomass values of the first half of the year. The abundance showed similar changes; however, the monthly average worm weight varied less. The sudden rise in the number of individuals in June was remarkable. As the worms' reproductive phase begins in June at temperatures above 14 °C (Kinne, 1954b), new recruits cannot be the cause of this change in abundance. Another important piece of evidence against the appearance of young individuals is that the mean body weight remains at its high level. Hence the high abundance in June must have been due to immigration of mature worms from surrounding areas. Immigration into the population's main area, not only when reproduction begins, has also been reported for *N. virens* (Kay and Brafield, 1973).

The marked changes in biomass are strongly influenced by timing and duration of reproduction. This seems to be a common phenomenon in the genus, as

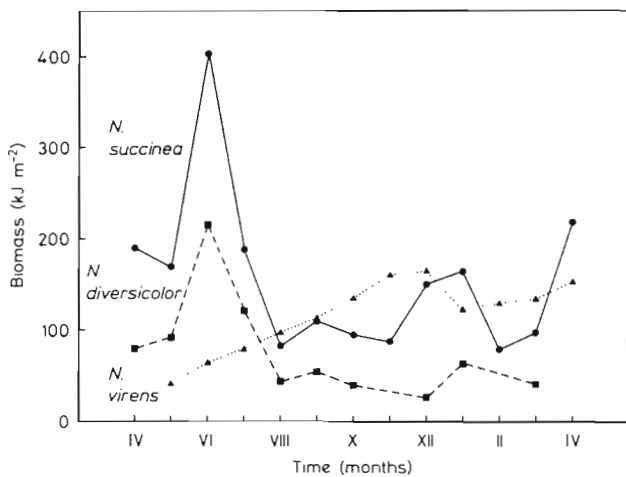


Fig. 2. Typical annual biomass dynamics of three *Nereis* species: *N. succinea* from Kiel Fjord (this study); *N. diversicolor* from Ythan estuary (Chambers and Milne, 1975); *N. virens* from Thames estuary (Kay and Brafield, 1973)

shown by a comparison of standing-stock biomasses of *N. diversicolor* and *N. virens* (Fig. 2). Maximum biomass values are attained at the beginning of the spawning period (*N. succinea*: June to September; *N. diversicolor*: June to August; *N. virens*: April/May). Minimum biomass values are found during or at the end of the spawning period. From then on they increase again – slowly but steadily in *N. virens*, with a small increase at the beginning of winter and with a sudden increase immediately preceding spring spawning in *N. succinea* and *N. diversicolor*. In *N. diversicolor* this might be due, in part, to a possible second spawning period (Chambers and Milne, 1975).

To observe the influence of seasonally changing

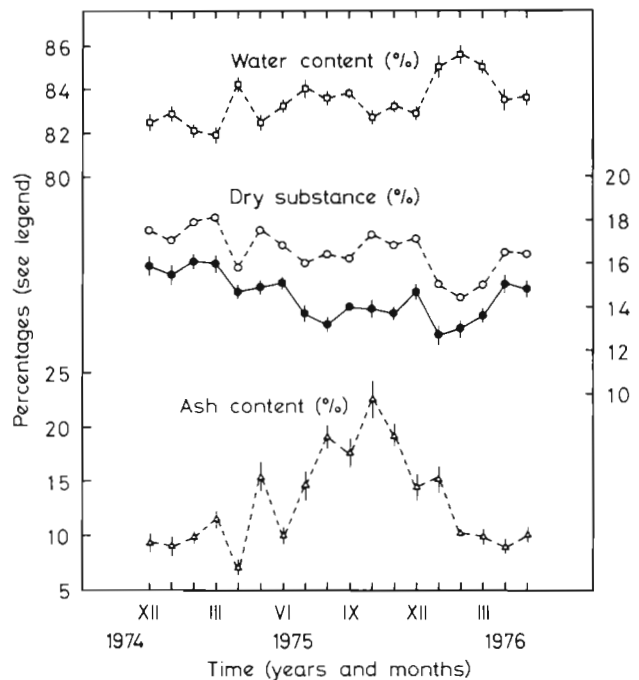


Fig. 3. *Nereis succinea*. Changing biochemical composition in a Kiel Fjord population. Water content and dry substance (broken lines: ash fraction; solid lines: ash-free fraction) are expressed as percentages of fresh weight, ash content as a percentage of dry weight. Vertical bars: standard deviations of the means ($s_{\bar{x}}$)

Table 2. *Nereis succinea*. Annual extremes and mean values of main body components

Components	Maximum	Month	Minimum	Month	Annual mean value (1975)
Ash	226 ± 17 mg g ⁻¹ _{dw}	X	71 ± 5 mg g ⁻¹ _{dw}	IV	139 ± 13 mg g ⁻¹ _{dw}
Glycogen	116 ± 8 mg g ⁻¹ _{dw,af}	IV	40 ± 3 mg g ⁻¹ _{dw,af}	X	70 ± 7 mg g ⁻¹ _{dw,af}
Lipid	154 ± 6 mg g ⁻¹ _{dw,af}	VI	91 ± 5 mg g ⁻¹ _{dw,af}	XI	125 ± 5 mg g ⁻¹ _{dw,af}
Protein	481 ± 8 mg g ⁻¹ _{dw,af}	I	403 ± 8 mg g ⁻¹ _{dw,af}	VIII	458 ± 7 mg g ⁻¹ _{dw,af}
Energy	22.57 ± 0.14 kJ g ⁻¹ _{dw,af}	VI	20.88 ± 0.18 kJ g ⁻¹ _{dw,af}	X	21.69 ± 0.14 kJ g ⁻¹ _{dw,af}

dw: dry weight.
 dw, af: dry weight, ash free.
 Extremes represent mean values for 15 individuals ± standard deviation of the mean ($s_{\bar{x}}$).

environmental factors on the worms' main body components, a sample of 15 individuals was analysed every month. The mean values of the analyses are presented in Figures 3 and 4. Water content did not vary much throughout the year (820 to 840 mg g⁻¹ fresh weight, 1975). Dry weight changed complementarily with a maximum of 181 mg g⁻¹ fresh weight in March and a minimum of 158 mg g⁻¹ in April. Correcting the dry weight for its ash fraction results in totally different extreme values, I found a maximum of the organic matter (ash-free dry weight) in February (161 mg g⁻¹ fresh weight) and a minimum in August (132 mg g⁻¹). The ash content, responsible for this shifting, rose in zig-zag shape until October, when it reached a value of 226 mg g⁻¹ dry weight, and then decreased again. The smallest amount was found in April (71 mg g⁻¹ dry weight).

The influence of the ash fraction on the biochemical parameters measured is illustrated for the energy content in Figure 4. The broken line includes the ash fraction, revealing a pronounced maximum in April, whereas the organic matter curve (solid line) indicates

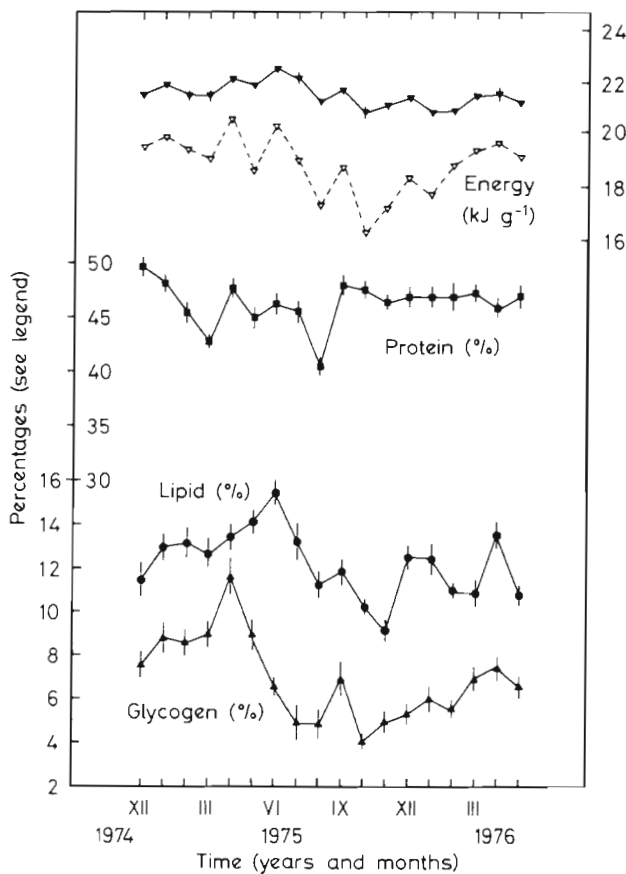


Fig. 4. *Nereis succinea*. Changing biochemical composition in a Kiel Fjord population. Solid lines: ash-free fraction; broken lines: ash fraction. Vertical bars: standard deviations of the means ($s_{\bar{x}}$)

the highest energy content in June. This shifting of the energy maximum depending on whether values are based on dry weight or ash free dry weight, prompted me to compare the body components measured on the basis of organic matter alone.

With the exception of the lipid and energy content, for which the spring maximum is retarded until June, the other components examined in 1975 show a main maximum in April and an autumn maximum in September.

Minima of glycogen and energy content were found in October. The absolute minimum of the lipid content, however, was measured in November. The protein content attained an absolute minimum in August.

Regarding the significance of *Nereis succinea* as a food organism for fishes (Fig. 5), it must be remembered here that the results refer only to immature

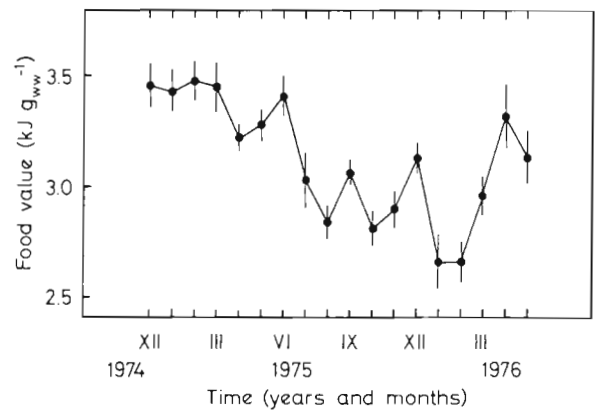


Fig. 5. *Nereis succinea*. Seasonally changing food values. ww: wet weight. Vertical bars: standard deviations of the means ($s_{\bar{x}}$)

ground-dwelling stages. The worms' food value is expressed as energy content in relation to body fresh weight; it showed higher values from December to June than during the rest of the year.

Interestingly, the food-value maxima coincide with those of the ash-corrected lipid content. A correlation analysis assures a correlation of both values with an error probability of 1%. The energy content of the organic matter and the ash-corrected lipid content are correlated with an even smaller error probability of only 0.1%. Glycogen and protein, however, showed no correlation with the energy content of the organic matter examined.

DISCUSSION

Annual changes in biomass values of the standing stock of a *Nereis succinea* population are determined by timing and duration of the spawning period. Maxi-

imum standing stock values are indicative of the forthcoming spawning period. As the worms die after spawning (Hartmann-Schroeder, 1971), this period is marked by heavy losses and minimum biomass values. A comparison with other *Nereis* species shows that the short reproductive period of *N. virens* in early spring facilitates a more or less steady biomass production until the next reproduction phase begins. However, *N. succinea* and *N. diversicolor*, which both have extended spawning periods, seem to exhibit their highest productivity just prior to reproduction. Laboratory experiments revealed an enormous growth capacity of *N. succinea* in spring. Increasing mean body weights in spring suggest the existence of similar capacities in *N. succinea* and *N. diversicolor* (Fig. 1; see also Chambers and Milne, 1975). Combined with a supposed immigration of mature(?) worms into the population's main area both species reach very high biomass values just before spawning begins.

As it feeds on detritus, *Nereis succinea* is a link in the decomposer food chain, eliminating the residues of primary and secondary production of pelagial and benthic. Its swarming heteronereis stages even transport benthic secondary energy into the water column where this energy can be used by pelagic predators. Biomass values of the standing stock of the reproductive summer population were found to be an average of 75 kJ m⁻² lower as compared with the non-reproductive winter population. Since large numbers of swarming heteronereis can be seen in summer nights, most of the losses may be due to reproductive activities rather than to a predatory decimation of immature ground-dwelling stages.

To estimate the worms' seasonally changing nutritive value and state, their body composition and energy content were determined. Considerable changes in ash content (Fig. 3) made it necessary to correct all readings for the ash fraction, except when referring to the energy equivalent for the nutritive value of living worms. The latter is related to the fresh weight and, therefore, comprises ash plus water content.

Spring and autumn maxima of body components and energy content are correlated with food supply. Boje (1965) and Kölmel (1977) found two maxima of seston sedimentation with a higher maximum in spring/summer and a lower one in late summer/autumn. According to Boje, 12% of the spring and 4% of the summer/autumn seston consists of organic detritus. Corresponding to this, body components and energy content exhibit maximum values from April to June and a smaller peak in September. Chambers and Milne (1975) describe similar dynamics in energy content for *Nereis diversicolor* from the Scottish border with maxima in March and September.

The lowest energy content was found in August and

October but not, as might have been expected, in winter with its low temperatures. Marked oxygen deficiency (values < 1 ml O₂ l⁻¹), combined with H₂S production in the sediment (Reimers, 1976; Kölmel, 1977), may cause a drastic deterioration of the worms' living conditions (Theede et al. 1969, 1973). Concomitant high ash contents suggest a low food supply, not enough to cover the worms' requirements. As detritus feeders utilize microorganisms associated with detritus rather than the detrital particles themselves (e.g. Fenchel, 1972), a low food supply may not result from lack of organic detritus but could be caused by a breakdown of aerobic microbial populations as a consequence of oxygen deficiency.

While the organic body components change considerably with the season, the energy content of the worms varies within relatively narrow limits. The food value of *Nereis succinea*, comprising all organic and inorganic components, is markedly influenced by the lipid content. This is based on a strong correlation of lipid and energy content. Inorganic components influencing the food value are water and ash content. It seems to be due to these factors that, in 1975, the highest food values of *N. succinea* were found from January to March. A year later at the same time a lower food value was caused by a high water content. This coincided with rather low environmental temperatures.

As most of the predators of *Nereis succinea* reduce or cease food intake in winter, the worms' food value from March to December is more important. It shows an average of 3.1 kJ g⁻¹ fresh weight with peaks corresponding to the lipid maxima. Hence, to provide a rough estimation of seasonally changing food values for immature stages of *Nereis succinea* it might be sufficient to measure their lipid content. In the future, it would be worthwhile, to learn something about the food value of swarming heteronereis stages. They are far more accessible to predatory fishes and, therefore, under higher predatory pressure.

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