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Production of *Nereis diversicolor* O. F. Müller (Polychaeta) in a Shallow Brackish-water Pond

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A *Nereis diversicolor* population inhabiting a shallow and landlocked brackish-water pond in Belgium has been studied over one year to estimate its production. This population reproduces from May to December with a peak in August. Total numbers vary between 5000 and 17000 individuals/m^2, the total standing stock lies between 13 and 39 g dry weight per m^2, with a mean of 24 g dry wt m^{-2}.

Individuals grow linearly over long periods of time, although slower when they get larger. Production was calculated by determining the weight-specific growth-rate of the different size-classes in the population; production in the year 1975–1976 was equal to 61 g dry wt m^{-2} year^{-1}. The P/B-ratio was equal to 2·5. This value is compared with the value for other Polychaeta and is intermediate.

Introduction

The polychaete *Nereis diversicolor* O. F. Müller is a dominant organism in soft bottoms of brackish water habitats throughout Europe. It has been a favourite species of physiologists for a long time and there exists a large literature on its physiology, but it has been studied far less by ecologists, which is surprising considering the increasing interest in estuarine processes in general and the great importance of this species in estuarine food webs in particular, both as a predator of other benthic organisms and a scavenger, and as a food organism for fishes and birds. One of the main parameters in the evaluation of the trophic role of a population is its production, but when we started this study we were unaware of any paper reporting on this; in the mean time Chambers & Milne's (1975) paper appeared, but as conditions are quite different in the Scottish Ythan estuary it remains worthwhile to present our results in detail.

The reproduction of *Nereis diversicolor* has been studied by Dales (1950). The eggs are released by rupture of the body wall and the female nearly always dies after spawning. The larvae lack chaetae when they hatch but soon afterwards three pairs of chaetal sacs are formed simultaneously. Although the larvae can swim by means of the prototroch ciliary band, they do not enter the plankton but remain in the surface layer of the sediment or in the parental burrow. They do not feed for approximately two months, after which they become active at a stage when they have about ten chaetigerous segments and are about 2 mm long. When about 4 mm long they start to behave like adults and they construct the U-shaped burrow where they live (Green, 1968).

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Material and methods

The population of *Nereis diversicolor* which we studied inhabits a landlocked, shallow brackish water pond, called Dievengat (Map reference 51°21′30″N, 3°22′15″E), with a surface area of 1·5 ha and a maximum depth of about 50 cm. It is a tideless area, which according to salinity must be placed sometimes in the meso- and sometimes in the polyhaline region of the Venice system, this without much change in the community (Heip, 1976). Mean salinity during the period of investigation was 17·7‰*S*, coming from a mean value of 9·0‰*S* in 1968–1969. Values are considerably higher in summer than in winter: the extremes are 23·5‰*S* on 3 July 1975 and 8·0‰*S* on 3 December 1975. Temperature also shows strong fluctuations; mean temperature of two-week periods can be predicted from $T = 11{\cdot}2 + 8{\cdot}3 \sin(t - 116)$, in which T is temperature and t is time, with $t_0 = 1$ January (Heip & Smol, 1976). The mean temperature during our investigation was 12·6° C (mean of point estimates on sampling dates and therefore somewhat higher than predicted from the equation because all samples were taken around noon). The extremes were 27·6 °C on 13 August 1975 and 0·8 °C on 18 December 1975.

Every fortnight from 24 April 1975 till 22 April 1976 two samples were taken with a plastic core covering a surface area of 78·5 cm^2 and pushed 25 cm into the sediment. The material was sieved immediately on the spot, using a sieve with a mesh-size of 0·8 mm. Samples were fixed with 4% formaldehyde. To obtain density estimates of the smallest stages two additional cores covering a surface area of 6 cm^2 and pushed 10 cm into the sediment were taken, fixed and elutriated in the laboratory without sieving. Due to the maximum penetrable depth of 10 cm some small larvae inhabiting the parental burrow might have escaped, but their small weight makes the error in the production estimate negligible.

Production was calculated using the method described by Crisp (1971) for populations where cohorts are not easily distinguished. In this method total production is obtained from summation over time of the production of all size-classes as:

$$P = \sum_t \sum_i G_i f_i w_i \Delta_t \qquad (1)$$

in which f_i is the mean number of individuals in class i during Δt and w_i is the mean individual weight of an individual in size-class i. G_i is the weight specific growth rate of size-class i and can be calculated, when growth during $t = t_2 - t_1$ can be considered as being exponential, as:

$$G_i = \frac{\ln w_{i,2} - \ln w_{i,1}}{t_2 - t_1} \qquad (2)$$

in which $w_{i,2}$ and $w_{i,1}$ are the weights of an individual of size class i at t_2 and t_1 respectively.

Calculation of production according to (1) requires knowledge of three parameters for each size-class and implies that constant values can be attributed to these parameters during the time interval considered, which therefore has to be sufficiently small. These parameters are density, mean weight and specific growth rate. Density was estimated from the large and small cores. As the core-size in both cases is rather small the importance of spatial variability could be marked. It was decided to apply a data-smoothing technique (Velleman, 1977) where unsupported values are first eliminated and then a weighted running mean is calculated over three adjacent values. This is an uncommon procedure in ecological work (but see Heip, 1976) but it has been used widely in other fields and offers considerable advantages when the aim is to detect pattern in time series in which the data are subject to measurement error and other noise. However, all trendline-values obtained in this way will be compared to values obtained from the raw data.

In order to obtain the mean individual weight per size-class, 150 animals were measured for length, width of the tenth segment, wet (wwt) and dry weight (dwt). As correlation was better between wet weight and length ($r = 0{\cdot}985$) than between dry weight and length ($r = 0{\cdot}862$) all calculations were performed using wet weights and converted to dry weights using the grand mean of dwt = 0·154 wwt, which is nearly the same value as found by Lappalainen & Kangas (1975) for *Nereis diversicolor* populations in Finland (0·157). The regression is $\ln \text{wwt} = (-3{\cdot}31 \pm 0{\cdot}12) + (2{\cdot}16 \pm 0{\cdot}04) \ln l$ (3). When the animals were broken the regression between width of the tenth segment b and length $l = 15{\cdot}5\ b^{1{\cdot}41}$ ($r = 0{\cdot}997$) was used.

The weight-specific growth-rate G_i of each size-class i was determined using the average time it takes an individual from that size-class to grow over a length equal to the size-class-width, taken at 5 mm, in the field. To determine this time the cross-correlation-functions (*ccf*) between all pairs of time-series representing the densities of successive size-classes (14 pairs) were calculated for 13 time lags from 0 to 24 weeks with increments of 2 weeks, the sampling interval; i.e. the 13*ccf*'s between the density of the 0–5 mm class and the density of the 5–10 mm class, the 13 *ccf*'s between the density of the 5–10 mm class and the 10–15 mm class, and so on. This was done for both the raw and the smoothed data. In words, the calculation of these *ccf*'s consists of gliding one series of data alongside the other until maximum correspondence is found. The rationale of this method and the mathematics can be found in Platt & Denman (1975). The time-lag yielding the maximum *ccf* [the maximum-correspondence-lag from Figure 2(a)] was considered to represent the time necessary to grow from the lower size-class to the next higher one. The maximum lag of 24 weeks used in the calculations of the *ccf* may be too high as only 52 weeks of data are available, but a maximum *ccf* was found for lags varying from 6 to 14 weeks, i.e. mostly in the lower range, where results are more substantial.

The time-lag yielding a maximum value of the *ccf* increases slowly with size [Figure 2(a)] and two linear regressions were calculated to express this relationship. For the smallest classes $\Delta t = -0{\cdot}4\,l + 11{\cdot}3$ ($r^2 = 0{\cdot}76$) (4); for the larger classes $\Delta t = 0{\cdot}165\,l + 4{\cdot}14$ ($r^2 = 0{\cdot}83$) (4′). Values obtained from these regression equations were used in the calculation of G_i according to (1). These calculations were done on 5 mm class-intervals; only for the smallest class the 1–4 mm class was taken, as of course $\ln 0 = -\infty$. The weights were calculated from (3) for the class-boundaries. The time-interval was calculated from (4) or (4′) for the midpoint. Values of G_i are shown in Figure 2(b) and Table 1.

Results

The population of *Nereis diversicolor* in the Dievengat contains some small juveniles throughout the year [Figure 1(a)], but whether this is due to a constant low reproduction or to other reasons such as delayed development is not known. As judged from the number of smallest juveniles, reproduction starts in May and reaches a peak in August, then declines gradually until the beginning of December. Total numbers in the population vary between 5000 per m^2 in February and 17000 per m^2 in August (trendline-values), with nearly 12000 individuals per m^2 being smaller than 1 cm at the later date. From these data it appears that the main variation in density is due to the appearance of the smallest juveniles and that the older individuals constitute a more stable population.

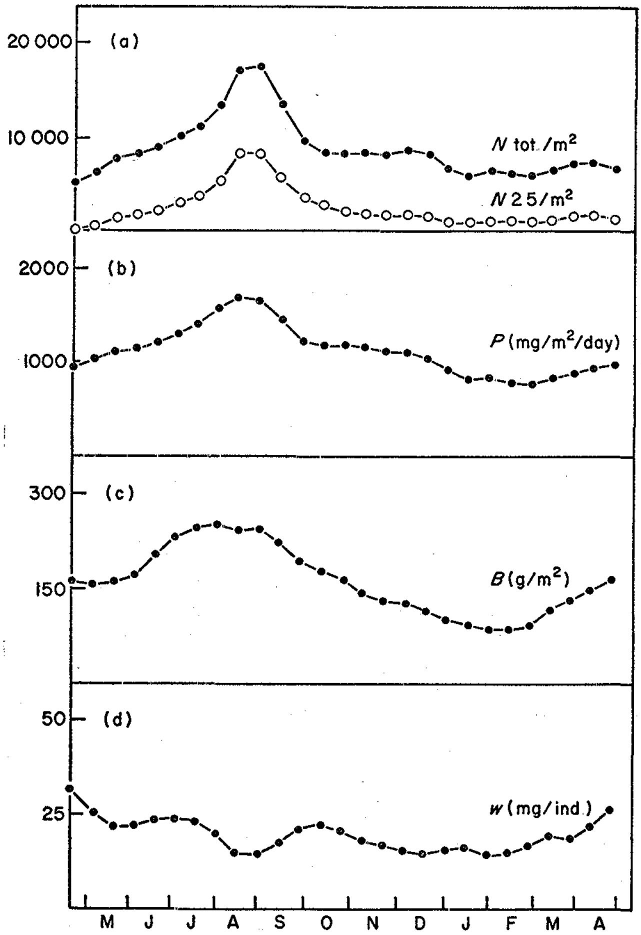

Figure 1. *Nereis diversicolor*: total numbers and number of size-class 0–5 mm per m^2 (a); production in mg wwt m^{-2} day^{-1} (b); biomass in g wwt m^{-2} (c); individual weight in mg wwt individual. All values are trendline-values.

Total standing stock varies between 84 g wwt m^{-2} in February and 250 g wwt m^{-2} in August; the corresponding dry weight figures are 12·9 g dwt m^{-2} and 38·5 g dwt m^{-2} [Figure 1(c)]. Mean biomass over the year is 158 g wwt m^{-2} or 24·3 g dwt m^{-2}. The corresponding figure for the raw data is 171 g wwt m^{-2} or 26·3 g dwt m^{-2}.

Individual weight varies between 13·9 mg wwt/individual and 31·4 mg wwt/individual, rather irregularly due to overlapping of the cohorts, but with a trend of increasing from a minimum in May to a maximum in early July, from a minimum in August to a maximum in October and from a minimum in January to a maximum in April. As it is irrelevant to our discussion, we will not go into the significance of these trends.

The time needed to grow 5 mm (the class-width) in the field is a linear function of size, but is higher for the smallest juveniles [Figure 2(a)]. As it is known that these smallest juveniles do not feed, we accepted this higher time as real and calculated a different regression for these data.

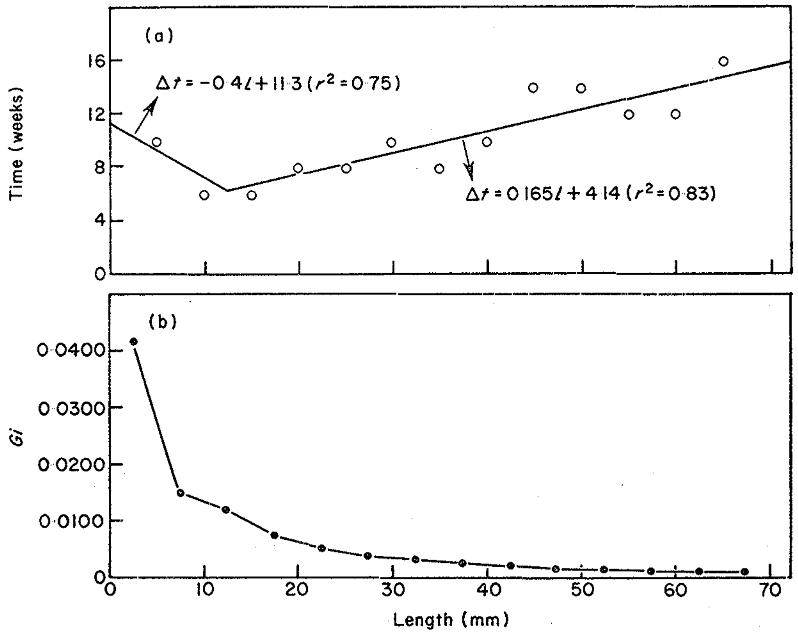

Figure 2. (a) The relationship between the lag yielding a maximum cross-correlation-function between two successive size-classes and size. (b) The relationship between the weight-specific growth-rate G_l and size.

Values of G_l, the weight-specific growth-rate, as calculated from (2) using the linear regressions between the maximum-correspondence-lag and size, are shown in Figure 2(b). As $G = (1/w)\,(\mathrm{d}w/\mathrm{d}t)$ and introducing the relationship $w = al^b$ between weight and length we obtain:

$$G = \frac{1}{a}\, l^{-b} a\, b\, l^{1-b}\, \frac{\mathrm{d}l}{\mathrm{d}t} = \frac{b}{l}\, \frac{\mathrm{d}l}{\mathrm{d}t} \tag{5}$$

and from (3) $G = 2{\cdot}16\ \frac{1}{l}\ \frac{\mathrm{d}l}{\mathrm{d}t}$; the weight-specific growth-rate is slightly more than two times higher than the length-specific growth-rate.

The relationship between G_l and l is approximately hyperbolic [Figure 2(b)] and can be represented by the equation:

$$G\, l = 0{\cdot}1062\ (r^2 = 0{\cdot}988) \tag{6}$$

(r^2 is shown here as a measure for goodness of fit, not as a correlation coefficient). Introducing a hyperbolic relationship $Gl = c$ into (4) we obtain:

$$\frac{\mathrm{d}l}{\mathrm{d}t} = \frac{c}{b} \tag{7}$$

and, as b and c are constants with values given by (3) and (6):

$$\frac{\Delta l}{\Delta t} = \frac{c}{b} = \frac{0{\cdot}1062}{2{\cdot}1583} = 0{\cdot}05 \text{ mm day}^{-1} \tag{8}$$

TABLE 1. Length-growth dl/dt and weight-specific growth-rate G_i of each size-class i

Size-class (mm)	$\Delta l/\Delta t$ (mm day^{-1})	G_i (per day)
2·5	0·069	0·0415
7·5	0·086	0·0151
12·5	0·113	0·0118
17·5	0·102	0·0075
22·5	0·091	0·0052
27·5	0·082	0·0039
32·5	0·075	0·0030
37·5	0·069	0·0024
42·5	0·064	0·0020
47·5	0·060	0·0016
52·5	0·056	0·0014
57·5	0·052	0·0012
62·5	0·049	0·0010
67·5	0·047	0·0009
72·5	0·044	0·0008

In other words, providing the hyperbolic relationship holds, length growth of *Nereis diversicolor* is linear over the entire range and equal to 0·05 mm day^{-1}.

However, length-growth can be calculated directly from the maximum-correspondence-lag as well, and here the linearity over the whole range disappears (Table 1). A maximum is reached for the 12·5 mm size-class, with 0·11 mm/day, decreasing to a nearly constant value of 0·05 mm/day for 55 mm and higher. Linear growth as found in (8) seems to be a good representation of what really happens for the older stages, as already for 35 mm the growth-rate is only 0·07 mm day^{-1}.

Production per m^2 and per day of the *Nereis diversicolor* population as calculated from (1) is given in Figure 1(b). Total production as calculated from trendline-values is 398 g wwt m^{-2} year^{-1} or 61·3 g dwt m^{-2} year^{-1}, as calculated from the raw data total production amounts to 417 g wwt m^{-2} year^{-1} or 64·2 g dwt m^{-2} year^{-1}. As the mean standing stocks over the year are 158 g wwt m^{-2} and 171 g wwt m^{-2} respectively, the production/biomass (P/B) ratios are equal to P/B = 2·51 (trendline-values) and P/B = 2·44 (raw data). This close correspondence shows that the effect of spatial variability on our production estimate obtained from raw data is small.

The extensive tables representing numbers, biomass and production of all size-classes over the period of investigation are not reproduced, but are available from the authors on request.

Discussion

The Dievengat population of *Nereis diversicolor* has a very high standing stock when compared to other populations. Numbers found elsewhere are often one order of magnitude lower and range from 10 to 200 individuals/m^2 in the polluted Tees estuary (Gray, 1976) and 55–300 individuals/m^2 in the Thames at Chalkwell (Dales, 1951) to maxima of 5000 m^2 in Danish estuaries (Muus, 1967), 6800/m^2 in the Severn (Boyden & Little, 1973) and 10000/m^2 in the Medway (Wharfe, 1977). Of particular interest to us is the figure found by Govaere (1969) in the Zwin salt marsh, because prior to reclamation in 1872 of the polder

TABLE 2. *P/B* ratio for Polychaeta

Ampharete acutifrons	5·5	Warwick & Price (1975)
Ampharete acutifrons	4·6	Richards & Riley (1967)
Pectinaria hyperborea	4·6	Peer (1970)
Pectinaria californiensis	4·3	Nichols (1975)
Harmothoë imbricata	2·6	Zaika (1971)
Nereis diversicolor	2·5	This study
Nephtys incisa	2·2	Sanders (1956)
Cistenoides gouldii	1·9	Sanders (1956)
Nephtys hombergii	1·9	Warwick & Price (1975)
Nereis diversicolor	1·8	Chambers & Milne (1975)
Nereis virens	1·6	Kay & Bradfield (1973)
Spiophanes kroyeri	1·4	Buchanan & Warwick (1974)
Lumbrineris fragilis	1·3	
Chaetozone setosa	1·3	
Heteromastus filiformis	1·0	
Glycera rouxi	0·4	

where it is now situated, the Dievengat was a part of this salt marsh; this author found between 230 and 2000 $/m^2$.

These differences are obviously reflected in biomass differences as well. In the Tees estuary the standing stock is very low, about 0·7 g dwt m^{-2} (Gray, 1976) maximum, and this is also true for the Ythan estuary, where Chambers & Milne (1975) found 4·2 g dwt m^{-2} on the average. In the Zwin salt marsh standing stock normally lies between 2·2 and 5·2 g dwt m^{-2}, but a maximum of 15·7 g dwt m^{-2} was recorded in September (Govaere, 1969). This maximum is somewhat later than the maximum of 38·2 g dwt m^{-2} (trendline-value) found in August in the Dievengat which can be explained as water temperatures in the North Sea are highest in September, later than in the landlocked and shallow Dievengat where water temperatures will follow air temperatures more closely and where the maximum temperature is predicted for 25 July. In Niva Bay in Denmark, a habitat which is comparable to the Dievengat in many ways, Muus, (1967) found a mean biomass of 13·75 g dwt m^{-2} and a maximum of 18·0 g dwt m^{-2}. It is clear from these comparisons that the standing stock of *Nereis diversicolor* in the Dievengat is the highest recorded up to now.

The dynamics of *Nereis diversicolor* populations appear to show local characteristics. The reproductive activity of this species can be limited to a short period in spring, as in the Thames (Dales, 1950) or the Medway (Wharfe, 1977) or can extend over the whole year (Herpin, 1925). Populations of the Zwin salt marsh reproduce from spring till autumn (Govaere, 1969), as does the Dievengat population, which is derived from them, and the Ythan estuary population shows two peaks, one in June–August coinciding with the main peak in the Dievengat, and one in January–March, which has no counterpart in the Dievengat. Levins (1975) shows how dynamics of similar populations can differ according to the local environment and the different evolutionary responses of populations to selective pressures from it. Heip (1976) described the dynamics of the ostracod *Cyprideis torosa* in the Dievengat and its dependence on the local temperature regime; he suggested how these dynamics might be different in another environment. Muus (1967) suggested the existence of different physiological races in *Nereis diversicolor* and the variability of morphological characters as the number of teeth on the paragnaths in this species is well documented.

Linear growth of polychaetes has been observed previously by Zaika (1971) using Smidt's (1951) data on *Nereis diversicolor* and by Nichols (1975) for older stages of *Pectinaria californiensis*. We can compare our values with those obtained by Dales (1950) and Chambers

& Milne (1975). Between 0–30 mm, the mean growth-rate is 0·09 per day, for the larger classes it is 0·06 mm day^{-1}. Values found by Dales (l.c.) vary from 0·11 mm day^{-1} for the 0–1 cm class to 0·06 mm day^{-1} for the 4–5 cm class, with an average of 0·08 mm day^{-1}. Values found by Chambers & Milne (1975) are very erratic, with a low of 0·03 mm day^{-1} for the 0–1 cm class and a high of 0·30 mm day^{-1} for the 3–4 cm class. They found an average of 0·13 mm day^{-1} for all classes. Smidt (1951) found 0·09 mm day^{-1} for the smaller juveniles in the Wadden Sea from May till October in 1946 but 0·20 mm day^{-1} from June till October 1947, and attributed the difference to higher water temperatures in 1947. The close correspondence between our values and those of Dales (l.c.) and Smidt in 1946 contrasts with the extremely low values for the smallest juveniles in the Ythan estuary, where according to Chambers & Milne (l.c.) it takes these juveniles nearly 11 months to grow up to a length of 1 cm, whereas Smidt (l.c.) found a 3 cm long juvenile after only 3 months' growth.

The $P/B = 2{\cdot}5$ which we found in this investigation for the *Nereis diversicolor* population of the Dievengat is compared to other values in Table 2. This value fits into the series of previously reported values and is about the same as those reported for *Nephtys incisa*, *Nephtys hombergii* and *Harmothoë imbricata*; this is reasonable taking the unknown but existing error on P/B and the relationship between P/B and body size into account. The lower value obtained by Chambers & Milne (1975) for the Ythan estuary (when their estimate of gamete production is subtracted) is of particular interest, as it shows that the P/B-ratio does not necessarily decrease with increasing standing stock. The lower value for the Ythan estuary can only partly be explained by a possible underestimation of the growth-rate of the smallest juveniles but may also be attributed to the shorter reproductive period of this population.

The limitations of the P/B-ratio as a tool in assessing energy-flow have been discussed adequately by Kay & Bradfield (1973) and by Chambers & Milne (1975). One additional remark is justified: as argued by these authors much of the mortality of adults in this and related species might not be due to predatory activity. However, this does not mean that this production would be totally unavailable to higher levels in the food web. Meiofauna, feeding directly on dead bodies or on the bacteria associated with them, may in fact be a link in this transfer and serve as a food source to vertebrate and invertebrate predators, including *Nereis diversicolor* itself.

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