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Life cycle, growth and production in estuarine populations of the polychaetes Nereis virens and N. diversicolor

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Life cycle, growth, mortality and production of the polychaetes *Nereis virens* and *N. diversicolor* were studied in Norsminde Fjord, Denmark. When 3 yr old, *N. virens* showed synchronous spawning induced at new moon in April when water temperature was 10-12°C. *Nereis diversicolor* showed a prolonged spawning during early spring and summer at an age of 12–18 months. Average weight-specific growth rate for *N. virens* and *N. diversicolor* were 0.0062 and 0.0050 d^{-1}, respectively; showing a reduced rate with age. Annual mortalities of 76–77% and 98%, respectively, reduced *N. virens* to 1.2–1.4% and *N. diversicolor* to 1.2–2.3% of the initial population at the time of spawning. Annual production of *N. virens* and *N. diversicolor* was 23.73 and 27.17 g AFDW m^{-2}, tantamount to an annual turnover (P/B) of 2.52 and 2.60, respectively.

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Introduction

The polychaetes *Nereis virens* Sars and *N. diversicolor* O. F. Müller are widely distributed inhabitants of the intertidal zone of marine and brackish waters throughout Europe. They are common in estuaries, where particularly *N. diversicolor* forms dense populations. Several attempts to describe the lifecycle of these animals have been made; *N. virens* (Brafield and Chapman 1967, Bass and Brafield 1972, Snow and Marsden 1974) and *N. diversicolor* (Dales 1950, 1951, Bogucki 1953, Chambers and Milne 1975, Olive and Garwood 1981, Mettam et al. 1982). However, no general agreement exists between these reports, and the discrepancies are so pronounced that further investigations have to be made. This study compares Danish estuarine populations with recent reports and thereby attempts to contribute to the knowledge of *Nereis* life cycle.

Production estimates of nereids are scarce (Kay and Brafield 1973, Chambers and Milne 1975, Heip and Herman 1979) considering the great importance of these species in estuarine food webs, both as predators and prey. For evaluation of the trophic role of a population, one of the main parameters is the production estimate. In the present investigation population parameters such as growth, mortality and production of Danish estuarine populations of *N. virens* and *N. diversicolor* are presented.

Materials and methods

Study area

Dense populations of *Nereis virens* and *N. diversicolor* inhabit the estuary Norsminde (Kysing) Fjord near Aarhus, Denmark. This shallow estuary has a mean depth of about 60 cm; one third of the watermass is exchanged during each tide (Muus 1967). Mean salinity during the investigation was 21‰ in summer and 14‰ in winter. Temperature extremes were 27°C in June-July and −0.5°C in January-February.

Sampling

Worms from the outer (*N. virens*) and middle part (*N. diversicolor*) of the estuary were collected monthly from June 1979 through August 1980, using a steel core covering a surface area of 143 cm^2 ($\frac{1}{70}$ m^2) pushed 25 cm into the sediment. Depending on density, 6 to 30 cores were taken for each species during the monthly collections. The sediment was sieved through a 1.5 mm mesh sieve on the location, except for the upper 5–10 cm which was taken to the laboratory for a closer examination, to obtain the smallest stages. Such separation was necessary since the smallest individuals, that only penetrated a few centimeters below the surface, were not retained on a 1.5 mm mesh sieve. Only individuals having a body length larger than 0.3 cm were included as the younger stages appeared very low in numbers throughout the year. No distinction was made between sexes.

Size determinations

For both species total body length of worms fixed in 4% formalin (formalin-length, l_F) was used as an estimate of size, measured to the nearest 0.5 cm. The advantage of using formalin-length in preference of live-length (l_L), was the achievement of an equal fixation of body muscles of all individuals. When nereid worms are placed in 4% formalin the body muscles contract and the animals die in an equal state of contraction. A group of 19 individuals of each species was narcotized with $MgCl_2$ (Lincoln and Sheals 1979) and the length in this state was compared with the formalin-length of the same individuals. The following conversions were obtained: *N. virens*, $l_L = 1.35 \times l_F$; and *N. diversicolor*, $l_L = 1.27 \times l_F$.

When worms were sampled as fragments, the following relationship between formalin-length (l_F) in cm and width of the third setigerous segment (W) in mm was used to obtain an estimate of body length:

N. virens $l_F = 1.384 \times W^{0.640}$,
                $n = 194, r^2 = 0.962$;
N. diversicolor $l_F = 1.116 \times W^{0.705}$,
                $n = 156, r^2 = 0.933$.

Age classes were separated by the method of Harding (1949) dissolving the polymodal size-frequency distributions in gaussian components, assuming the frequency distributions of each age class to be normally distributed (the young age classes appeared slightly truncated). The proportion and average body length of each age class were estimated from cumulative plots of the size-frequency distributions on probability paper.

Growth and mortality

In order to obtain the individual body weight for estimating the weight-specific growth rate and production, a

Tab. 1. Conversions between ashfree dry weight (AFDW), dry weight (dw), and wet weight (ww) for *N. virens* and *N. diversicolor*.

	N. virens	*N. diversicolor*
AFDW/dw	0.855 ± 0.028	0.889 ± 0.027
dw/ww	0.130 ± 0.012	0.133 ± 0.017

relationship between formalin length in cm and mg ashfree dry weight (AFDW) was necessary:

N. virens $AFDW = 0.668 \times l_F^{2.307}$,
                $n = 68, r^2 = 0.967$;
N. diversicolor $AFDW = 0.695 \times l_F^{2.081}$,
                $n = 65, r^2 = 0.911$.

For comparison of the present results with data from the literature Tab. 1 gives the conversions between wet weight (ww), dry weight (dw) and ashfree dry weight (AFDW).

The weight-specific growth rate (G_i) of each age class i, defined as $G_i = d(\ln AFDW)/dt$ (Crisp 1971), was determined as the slope of the growth equation: $\ln AFDW_t = \ln AFDW_0 + Gt$, where $AFDW_t$ is the weight at time t and $AFDW_0$ the initial weight. As growth during a whole lifespan commonly is sigmoid, the growth equation will not be linear, and as a consequence G_i was estimated for discrete time-intervals, $\Delta t = t_2 - t_1 \sim 1$ month, as:

$$G_i = (\ln AFDW_{t2} - \ln AFDW_{t1})/\Delta t$$

Survival of an age class for the nereids studied here was assumed to decline exponentially: $N_t = N_0 \times e^{-dt}$, where N_t is age class density at time t and N_0 the initial density. The age-specific mortality Z can then be determined as the slope of a logarithmic transformation of the survival equation: $\ln N_t = \ln N_0 + Zt$, and is defined, using the annual mortality (M), as, $-d, = Z = d(\ln M)/dt$ (Crisp 1971), which can be approximated to

$$Z = (\ln N_{t2} - \ln N_{t1})/\Delta t.$$

The annual mortality will be

$$M = (N_1 - N_0)/N_1 1 - e^{-Z},$$

where N_1 is the density after 1 yr, and N_0 the initial density.

Production

Production was estimated according to the method of Crisp (1971) as:

$$P = \sum_s^t \sum_s^n G_i N_i w_i \Delta t$$

where G_i is the weight-specific growth rate of size i, w_i is the average weight of an individual in size class i, and N_i
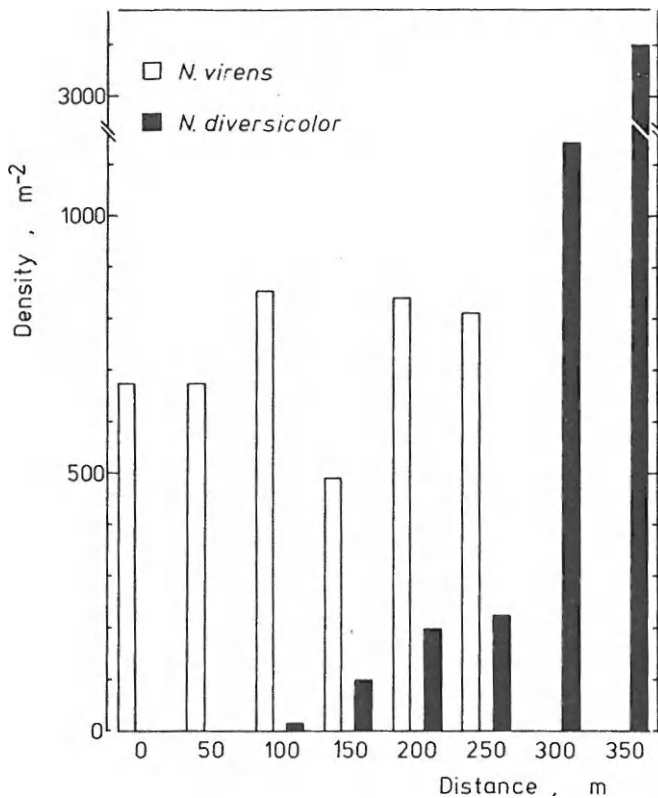
Fig. 1. Density of *Nereis virens* and *N. diversicolor* along a transect from the mouth and 350 m into Norsminde Fjord in September 1979.

is the average number of individuals in class i during the time interval Δt. As the increase in weight for the individuals in each age class during time Δt approximates the growth rate, $G = d\bar{w}/dt$, the production will be:

$$P = \sum_S \sum_S^t \bar{N}^n \ d\bar{w}/dt \ \times \ \Delta t \sum_S \sum_S^t \bar{N}^n \ \Delta \bar{w}.$$

According to Siegismund (1982) this method will underestimate the production of an age class during a period of increasing density. He suggested a better approximation would be simply to measure the difference between biomass at the time of highest density and initial biomass. This modification still underestimates production as it neglects the production of individuals recruited and later dead during the period of increasing density, but this estimate is considered closer to the actual production than the method of Crisp.

Results

The two species of *Nereis* occupied separate parts of the estuary (Fig. 1). *N. virens* dominated near the mouth of the estuary, forming a dense and continuous population. *N. diversicolor* was dominating in the middle and innermost parts, reaching very high densities.

Age distribution, growth and mortality

Nereis virens

The size-frequency distributions of *N. virens* are shown in Fig. 2A. This clearly shows the arrival of recruits in August 1979 (I) and July 1980 (0) with mean lengths of 1.3 and 0.9 cm, respectively (Fig. 3A). The class I, that was followed throughout the sampling period, reached a size in July 1980 of about 4 cm. This corresponded to the age class II in August 1979 (size 4.2 cm). In July 1980 the class II had reached a size of 9 cm, equivalent to the class III in 1979 (length in August, 11 cm). It was not possible to follow the age class III after August 1979, presumably due to low density associated with an apparent ability of these larger sized animals to dig deep during autumn and winter, reaching a more insulated sediment (Muus 1967). The sampling technique employed was not adequate to collect such worms quantitatively.

The abundance of recruits in July suggested that spawning had occurred in spring, which is in agreement with observations of swarming males at new moon on 15 April 1980, at a temperature of 10–12°C. Neither age class I nor II showed any marked decrease in density during spring 1980, indicating that none of these age classes participated in spawning that year. The age class III, however, was not observed later than August 1979. This suggests that *N. virens* in Kysing Fjord reproduces at an age of 3 yr.

The weight-specific growth rate (G) for age class I and II during the sampling period is shown in Fig. 4. Not unexpectedly, a maximal growth rate was observed during summer for both age classes. The average growth rate during the sampling period was: class I, G = 0.0078 d^{-1}; class II, G = 0.0046 d^{-1}, age class II showing a growth only 59% of class I.

The density of *N. virens* reached a maximum during July-October, when the new recruits had arrived, and a minimum after spawning in spring (Fig. 5A). The density increased from 152 m^{-2} in June 1979 to 809 m^{-2} in October 1979. Annual mean density was 534 m^{-2} (Tab. 2). The decline in density from October to April was due to mortality, primarily through predation and severe winter conditions. The age-specific mortality of age class I and II was very similar; thus Z = 1.47 and 1.41 yr^{-1} (Fig. 6). This suggests constant mortality over the whole lifetime of this species, except during spawning. The annual mortality for class I and II was 77 and 76%. Assuming a constant mortality from hatching until reproduction, an age class of *N. virens* will be reduced to 1.2–1.4% of the initial number 3 yr after hatching.

Nereis diversicolor

The size-frequency distributions of *N. diversicolor*, shown in Fig. 2B, suggest one age class during most of the year, with recruits appearing in two displaced groups; one appearing in March-May and another in July-August. The age class 0 was first recognized during
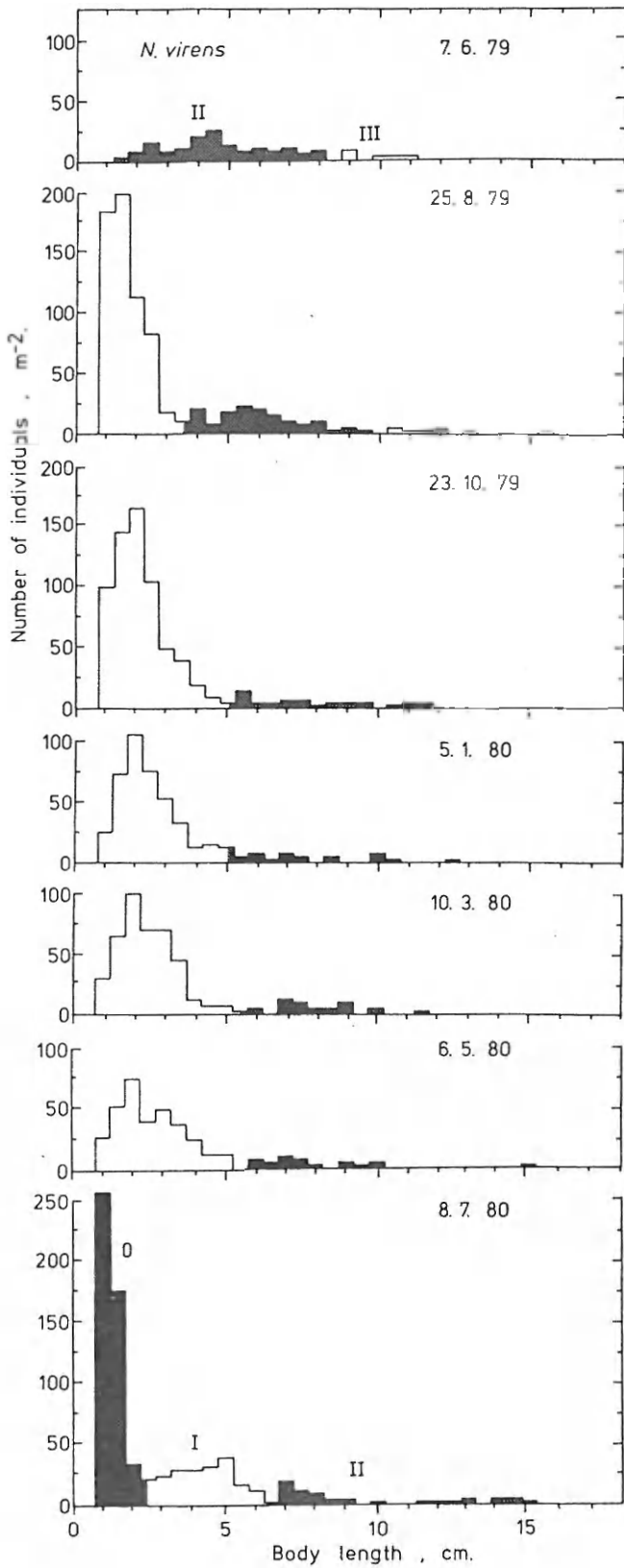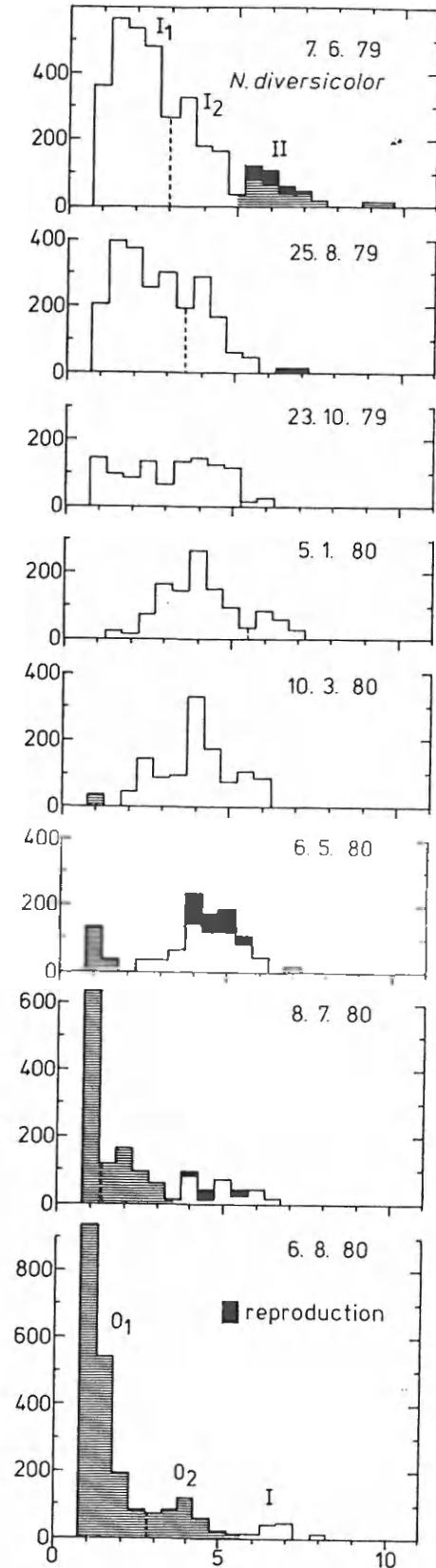
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A

B

Fig. 2. (A) Size-frequency distributions of *N. virens*. Symbols 0, I, II, III represents each recognized age class. (B) Size-frequency distributions of *N. diversicolor*. Symbols 0, I, II represents each recognized age class. Dotted lines in (B) separate the early (I₂ and 0₂) and late (I₁ and 0₁) recruited groups of each age class. Distributions are given bimonthly for simplicity.
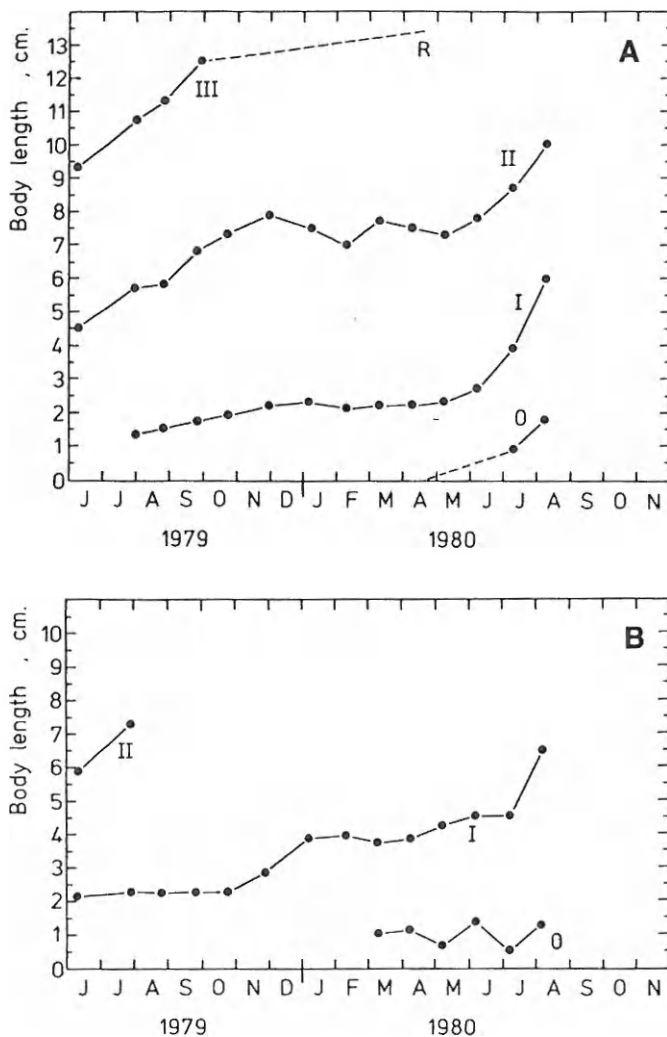
Fig. 3. (A) Average body length of *N. virens* age classes during the sampling period. Symbol R indicate time of reproduction. (B) Average body length of *N. diversicolor* age classes during the sampling period.

March 1980, by the low density 0_2 group, having an average body length of 1.0 cm (Fig. 3B). The 0_1 group that appeared in July 1980 outnumbered the 0_2 group. The average body length of age class 0 reached 1.3 cm in August 1980, but varied much during spring and summer due to new recruits arriving. This class is equivalent to class I recruited in 1979. Age class I, with an average size of 2.2 cm in August 1979, was apparently composed of two groups; I_2, recruited in the spring, and I_1, recruited during the summer (Fig. 2B). This age class (I) spawned from April to August 1980 at a length of 4.0–6.5 cm. Spawning was recognized by the appearance of grass-green reproducing individuals. Apparently some individuals of this age class (group I_2) started spawning earlier (February), since recruitment of the offspring, the 0_2 group, was recognized as early as March, although no spawning individuals of class I were observed at that time. Age class II reproduced in June-July 1979 at an average size of 5.9–7.2 cm, and disappeared in August 1979. The 1979 spawning and larval develop-

ment were apparently more successful than in 1980, since the recruits in 1979 were larger and more abundant. *N. diversicolor* in Norsminde Fjord showed one age class composed of an early and a late recruited group per year. The lifespan appeared to vary from 12 to 18 months.

The weight-specific growth rate for *N. diversicolor* did not show any marked seasonal pattern, except a slight tendency for faster growth during winter than during summer. This may be due to a differential mortality of the youngest individuals during winter, producing a high apparent growth rate. Recruitment of young individuals produced the observed slower growth during summer. The annual mean growth rate for age class I was, $G = 0.0050$ d^{-1}.

The density of *N. diversicolor* reached a maximum during summer 1979, as new recruits of the I_1 group appeared (Fig. 5B). During autumn and winter the density decreased gradually, presumably due to predation and high winter mortality, reaching minimum density in spring. A marked reduction in density was observed from April to June 1980, presumably caused by dying out of summer spawning individuals. After June 1980 new recruits were responsible for a huge increase in density. The recruits of 1979 were more abundant than those of 1980; maximum density in June 1979 was 3250
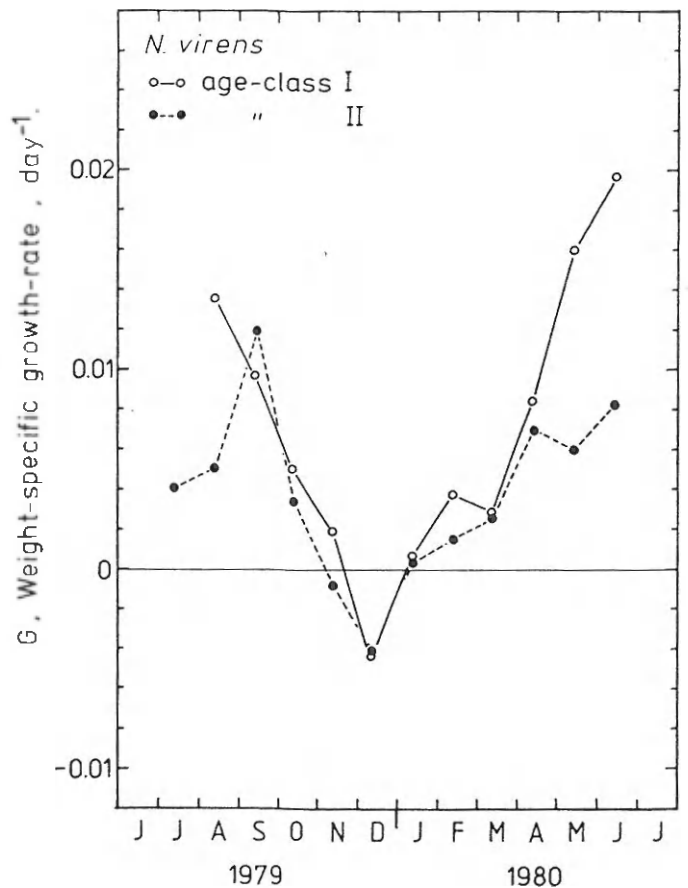

Fig. 4. Estimated weight-specific growth rate for age class I and II of *N. virens* during the sampling period.
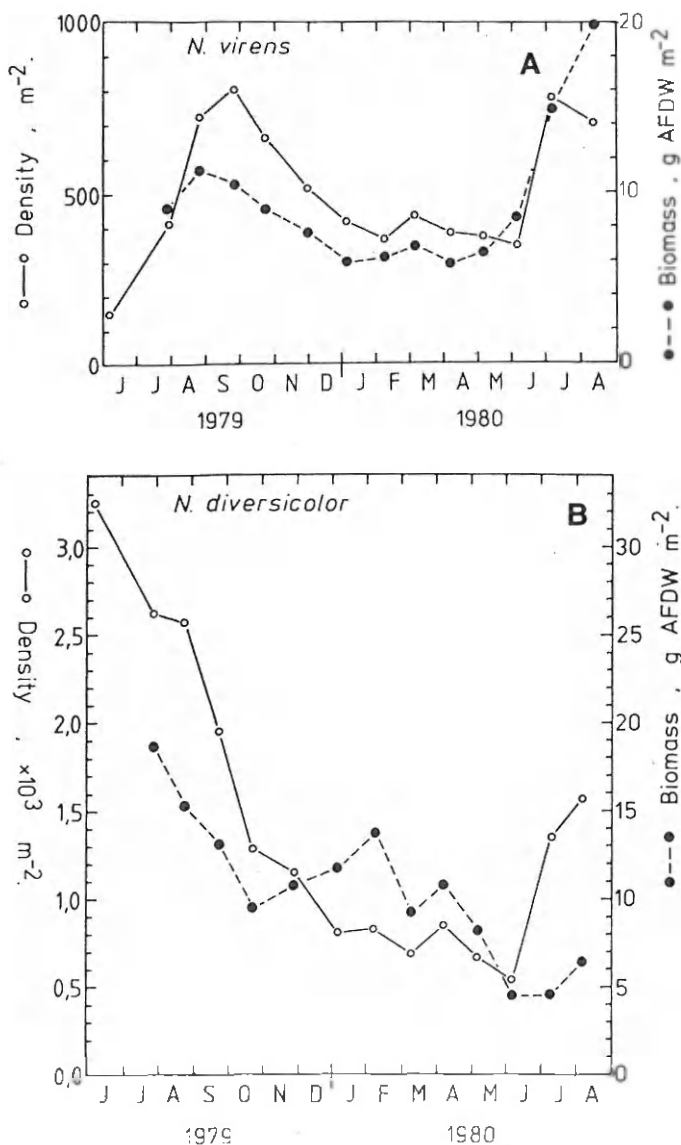
Fig. 5. (A) Total density and biomass of *N. virens* during the sampling period. (B) Total density and biomass of *N. diversicolor* during the sampling period.

m⁻², about twice the number in August 1980 of 1550 m⁻². Minimum density of about 50 m⁻² appeared in June 1980. The annual mean density was 1305 m⁻².

The age-specific mortality of *N. diversicolor* appeared quite high compared to *N. virens*; thus $Z = 3.79$ yr⁻¹ for age class I. This equals an annual mortality of 98%. Assuming a lifespan for *N. diversicolor* of 12–18 months, only 1.2–2.3% of a newly hatched age class would survive until spawning.

Production

The biomass followed the pattern of density throughout the year for both *N. virens* and *N. diversicolor* (Fig. 5). For *N. virens* maximum biomass was observed in August 1979 and 1980, when the majority of recruits were included, reaching values of 11.32 g AFDW m⁻² and

20.34 g AFDW m⁻², respectively, and a minimum of about 6 g AFDW m⁻² was observed during winter and spring. The annual mean biomass ($\bar{B}$) for this species was 9.34 g AFDW m⁻² (Tab. 2). *N. diversicolor* showed a maximum biomass of 18.75 g AFDW m⁻² in July 1979, and a mimimum of 4.56 g AFDW m⁻² in June-July 1980. The annual mean biomass ($\bar{B}$) of *N. diversicolor* was 10.46 g AFDW m⁻².

The estimated annual production (P) for *N. virens* and *N. diversicolor* were 23.73 g AFDW m⁻² and 27.17 g AFDW m⁻². By considering biomass ($\bar{B}$), annual turnover P/$\bar{B}$ for the two populations was 2.52 and 2.60, respectively.

The two methods for determining production of a newly recruited age class that increases in number showed quite different results. Tab. 3 summarizes the production of the increasing age class I for *N. virens* and class 0 for *N. diversicolor* determined by the methods of Siegismund (1982) and Crisp (1971). The underestimate by the method of Crisp was in the range of 48–85%, which is about 5.7–6.0% of the total annual production.

Discussion

Recent reports on reproduction of *N. virens* have revealed that timing of spawning and triggering stimuli are quite universal. Spawning occurs in spring during new moon when water temperature is about 8–10°C (Brafield and Chapman 1967, Bass and Brafield 1972, Rasmussen 1973) and lasts for only one or two days, indicating a spawning synchronized by lunar period cycles for this epitokous species. This is in agreement with the present observations; *N. virens* in Norsminde Fjord
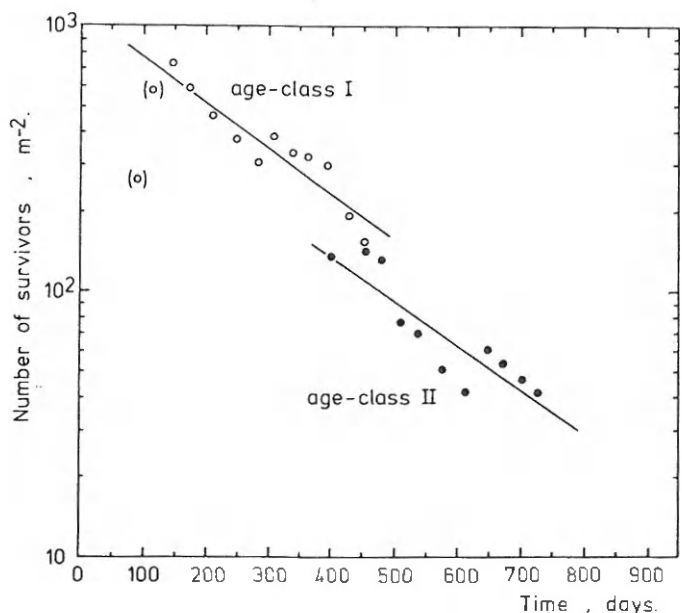

Fig. 6. Survivorship curves for age classe I and II of *N. virens*. Time 0 was chosen as new moon in April 1979 and 1978, respectively, where reproduction was assumed to occur.

Tab. 2. Annual mean density and biomass ("standing crop"), annual production and turnover (P/B) for populations of *N. virens* and *N. diversicolor*.

	N. virens	*N. diversicolor*
N, mean density (ind. m⁻²)	534	1305
B̄, mean biomass (g AFDW m⁻²)	9.34	10.46
P, annual production (g AFDW m⁻²)	23.71	27.17
Annual turnover, P/B	2.52	2.60

spawned on 15 April 1980 at new moon, when water temperature was 10–12°C.

Some confusion exists concerning age distribution and lifespan of *N. virens*. Several reports conclude that spawning occurs after 2 yr of somatic growth in the Thames Estuary (Brafield and Chapman 1967, Bass and Brafield 1972, Kay and Brafield 1973), but Snow and Marsden (1974) proposed from size-distributions that a New Brunswick population of *N. virens* initiates spawning after 4–6 yr. The Norsminde Fjord population apparently reached maturity and spawned after 3 yr but the results do not exclude that a few individuals spawned after 2 or 4 yr. Most likely, spawning of *N. virens* from marine environments of high salinity occurs after 2 yr. The apparent deviation in the Norsminde Fjord population may be due to the fact that gamete maturation is not simply related to age. The hormonal control of gamete maturation is probably related to the size of the animals (Olive and Clark 1978). It is known that marine species living in brackish water show depauperization, i.e. a reduced growth compared to populations in marine environments (Remane and Schlieper 1971). The salinity range of 14–21‰ in Norsminde Fjord is near the lower limit of *N. virens* tolerance (Rasmussen 1973), and consequently the slower growth resulted in a later development of gametes, giving a 3 yr lifespan.

Timing of spawning and life cycle of *N. diversicolor* vary in different geographical regions and with vertical distribution on the shore (Dales 1950, Muus 1967, Mettam 1971). This is believed to be a consequence of different local temperature regimes, since the inducing

Tab. 3. Comparison between the method of Siegismund (1982) and the method of Crisp (1971) for estimating the production of an age class that increases in numbers. Figures are given as g AFDW m⁻² month⁻¹.

	N. virens	*N. diversicolor*
Age class	1	0
Siegismund	2.96	1.81
Crisp	1.54	0.27

stimulus was reported to be a sharp temperature rise (Dales 1950). No synchronized spawning induced by lunar cycles occurred in this atokous species. Apparently two annual spawning periods occurred in Norsminde Fjord; one in February and a second in April-July. Spawning was only observed during April-July, but the recruits appearing in March-April may be offspring of an early spawning in February. As no spawning was observed in the sampling area during February, the early recruits could be immigrants from adjacent parts of the estuary. Similarly, Chambers and Milne (1975) reported two reproductive periods in the Ythan Estuary – one from January to March and a second one from June to August. Herpin (1925) found that *N. diversicolor* at Cherbourg spawned during every month of the year. In contrast, others have proposed only one spawning period in the spring; February in the Thames Estuary (Dales 1950), April in the Blyth Estuary (Olive and Garwood 1981), May in the Severn Estuary (Mettam et al. 1982).

From the present study it must be concluded that *N. diversicolor* living in temperature and salinity regimes of the Norsminde Fjord normally spawns after 12–18 months, in agreement with Dales (1950). Chambers and Milne (1975), however, found 18–24 months, Mettam et al. (1982) believed 24–36 months, and Olive and Garwood (1981) reported 33–42 months.

Nereis virens and *N. diversicolor*, with an average lifespan of 36 and 12–18 months, respectively, showed weight-specific growth rates of the same order of magnitude: 0.0046–0.0078 and 0.0050 d⁻¹, respectively. Heip and Herman (1979) estimated the weight-specific growth rate of a population of *N. diversicolor* in Dievengat, Belgium. They found a reduced growth for larger individuals. The growth rate ranged from 0.0415 d⁻¹ for juveniles to 0.0008 d⁻¹ for mature individuals, with an average of 0.0066 d⁻¹, which is in the range of the Norsminde Fjord animals. *Nereis virens* in Norsminde Fjord commonly reached sizes more than twice that of *N. diversicolor*. This difference apparently was a consequence of a longer lifespan in the former, rather than a faster growth, since the growth rates of both species appeared similar. Marine populations of *N. virens*, however, show a faster growth than the Norsminde Fjord population as the latter may be depauperized.

The negative growth observed for *N. virens* during winter was apparently due to a cessation of growth and worms moving deep down the sediment to avoid low temperatures (Muus 1967); the corer (25 cm) would undersample large individuals. For *N. diversicolor* no negative growth was observed during winter, possibly due to the presence of a compact layer of empty *Cardium*-shells at a depth of 6–8 cm in this habitat and due to high winter mortality of the youngest individuals.

The age-specific mortality of the two species was quite different; annual mortality of *N. virens* was 76–77%, whereas *N. diversicolor* showed 98%. As the former has a lifespan more than twice the latter, it needs

to be better protected against predation than *N. diversicolor*. At spawning almost identical fractions of an age class survived; 1.2–1.4% and 1.2–2.3%, respectively. The major mortality was probably caused by predation by benthic macro-invertebrates (including cannibalism), fish and birds, and by severe winter conditions. Peer (1970) reported that a population of the polychaete *Pectinaria hyperborea* at Nova Scotia had an annual mortality of 89.5%, which reduced this species, having a lifespan of 2 yr, to 1.1% at spawning. Of this mortality 80% was due to predation. Available information suggests that only 1–2% of an age class in semelparous polychaetes survives for reproduction, but further investigations are necessary before any final conclusions can be drawn.

Density and biomass as well as annual production (Tab. 3) were intermediate to values reported earlier for *N. virens* and *N. diversicolor*. Kay and Brafield (1973) found production of *N. virens* in the Thames Estuary to be 8.4 g AFDW m^{-2} yr^{-1}, which is about ⅓ of the production in Norsminde Fjord. For *N. diversicolor* Heip and Herman (1979) estimated the production in Dievengat to be 54.28 g AFDW m^{-2} yr^{-1}, whereas Chambers and Milne (1975) found 11.36 g AFDW m^{-2} yr^{-1} in the Ythan Estuary. It is inadequate to compare the production figures for different populations, since environmental factors such as food resource quality and quantity can influence population size and production. However, it is important to include the biomass or "standing crop" of a population in production reports. The ratio of production and biomass (P/B) expresses the annual turnover of a population, and is more informative than either production or biomass alone. *N. virens* in Norsminde Fjord showed a turnover of 2.52. Kay and Brafield (1973) found only 1.62 for this species in the Thames Estuary, but their estimate was based on relatively large individuals excluding the small ones, which contribute much to production but little to biomass. For *N. diversicolor* in Norsminde Fjord turnover was 2.60, very close to the values obtained in Dievengat (Heip and Herman 1979) and the Ythan Estuary (Chambers and Milne 1975) of 2.50 and 3.03, respectively.

References

Bass, N. R. and Brafield, A. E. 1972. The life-cycle of the polychaete *Nereis virens*. – J. mar. biol. Ass. U.K. 52: 701–726.

Bogucki, M. 1953. The reproduction and the development of *Nereis diversicolor* (O. F. Müller) in the Baltic. – Pol. Arch. Hydrobiol. 14: 251–270.

Brafield, A. E. and Chapman, G. 1967. Gametogenesis and breeding in a natural population of *Nereis virens*. – J. mar. biol. Ass. U.K. 47: 619–627.

Chambers, M. R. and Milne, H. 1975. Life cycle and production of *Nereis diversicolor* O. F. Müller in the Ythan Estuary, Scotland. – Estuar. Coast. Mar. Sci. 3: 133–144.

Crisp, D. J. 1971. Energy flow measurements. – In: Holme, N. A. and McIntyre, A. D. (eds). Methods for the study of marine benthos, IBP Handbook No. 16. Blackwell Scientific Publications, Oxford and Edinburgh, pp. 197–280.

Dales, R. P. 1950. The reproduction and larval development of *Nereis diversicolor* O. F. Müller. – J. mar. biol. Ass. U.K. 29: 321–360.

– 1951. An annual history of a population of *Nereis diversicolor* O. F. Müller. – Biol. Bull. 101: 131–137.

Harding, J. P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. – J. mar. biol. Ass. U.K. 28: 141–153.

Heip, C. and Herman, R. 1979. Production of *Nereis diversicolor* O. F. Müller (Polychaeta) in a shallow brackish-water pond. – Estuar. Coast. Mar. Sci. 8: 297–305.

Herpin, R. 1925. Recherches biologiques sur la reproduction et le développement de quelques annélides polychétes. – Bull. Soc. sci. nat. l'ouest France (sér. 4) 5: 1–250.

Kay, D. G. and Brafield, A. E. 1973. The energy relations of the polychaete *Neanthes* (= *Nereis*) *virens* (Sars). – J. Anim. Ecol. 42: 673–692.

Lincoln, R. J. and Sheals, J. G. 1979. Invertebrate animals – collection and preservation. – British Museum (Natural History), Cambridge University Press.

Mettam, C. 1981. Survival strategies in estuarine nereids. – In: Jones, N. and Wolff, W. J. (eds). Feeding and survival strategies of estuarine organisms. Marine Science Vol. 15, pp. 65–77. Plenum Press.

– , Santhanam, V. and Havard, M. S. C. 1982. The oogenic cycle of *Nereis diversicolor* under natural conditions. – J. mar. biol. Ass. U.K. 62: 637–645.

Muus, B. J. 1967. The fauna of danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. – Medd. Danm. Fisk. Havunders. ny ser. 5: 3–316.

Olive, P. J. W. and Clark, R. B. 1978. Physiology of reproduction. – In: Mill, P. J. (ed.). Physiology of annelids. Academic Press, London, pp. 271–369.

– and Garwood, P. R. 1981. Gametogenic cycle and population structure of *Nereis* (*Hediste*) *diversicolor* and *Nereis* (*Nereis*) *pelagica* from Northeast England. – J. mar. biol. Ass. U.K. 61: 193–213.

Peer, D. L. 1970. Relation between biomass, productivity, and loss to predators in a population of a marine benthic polychaete, *Pectinaria hyperborea*. – J. Fish. Res. Bd Can. 27: 2143–2153.

Rasmussen, E. 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). – Ophelia 11: 1–507.

Remane, A. and Schlieper, C. 1971. Biology of brackish water. 2 ed. – Wiley, New York.

Siegismund, H. R. 1982. Life cycle and production of *Hydrobia ventrosa* and *H. neglecta* (Mollusca: Prosobranchia). – Mar. Ecol. Prog. Ser. 7: 75–82.

Snow, D. R. and Marsden, J. R. 1974. Life cycle, weight and possible age distribution in a population of *Nereis virens* (Sars) from New Brunswick. – J. nat. Hist. 8: 513–527.