

DISTRIBUTION, DYNAMICS AND PRODUCTIVITY OF A COLONIZING  
 (*POLYDORA QUADRILOBATA*) AND AN ESTABLISHED (*P. LIGNI*) POLYDORID  
 POLYCHAETE IN LAKE GREVELINGEN: AN ENCLOSED ESTUARY IN  
 THE SW NETHERLANDS\*

R.H.D LAMBECK AND P. VALENTIJN

*Delta Institute for Hydrobiological Research, Vierstraat 28, 4401 EA YERSEKE, The Netherlands.*

ABSTRACT

The enclosure of the Grevelingen estuary in May 1971 (from then on saline Lake Grevelingen) did not result in an immediate population response of *Polydora ligni*, known as an opportunist. A large summer settlement (2 to 5000 ind·m<sup>-2</sup>) and a subsequent high mortality occurred at one station in the period 1972 to 1975; abundance fluctuations at a second station were much smaller. In 1977 densities were very low.

The congeneric *P. quadrilobata* (a species new to Dutch waters) was not observed in 1971-1975, but an average density of 760 ind·m<sup>-2</sup> (with a biomass of 0.1 g ADW·m<sup>-2</sup>) was found in the lake in April 1977. Its abundance was low in shallow water (<2.5 m); in the rest (54%) of the lake no preference for depth, substrate or species association could be detected. Seasonal maxima occurred in spring. These opposing population developments can be explained from the different life histories of the two polydorids in combination with a changed seasonal pattern in food supply.

The maximum life span of *P. quadrilobata* was 1 to 1½ years with one main cohort a year. Maximum values for its biomass and density at the stations were 1.42 g ADW·m<sup>-2</sup> and 6900 ind·m<sup>-2</sup>. Based on reconstructed survivorship curves, annual minimum and maximum values for production were calculated. The (conservative) estimates varied from 0.2 to 2.6 g ADW·m<sup>-2</sup>·a<sup>-1</sup> for different stations and years, with P/B values varying from 1.5 to 8.2.

1. INTRODUCTION

The Grevelingen used to be one of the estuarine branches of the rivers Rhine and Meuse in the so-called Dutch Delta area. The river influence was considerably reduced after the construction of a secondary dam in the eastern part (Fig. 1) in 1964. The estuary was turned into a saline lake in 1971 by the completion of a 6-km-long primary dam in the mouth, cutting off the connection with the North Sea.

One of the many consequences of the elimination of the tides was an overall decline in the number of macrozoobenthic species (LAMBECK, 1981). However, the changed environmental conditions provided new opportunities for other species that were scarce or even unknown in the former estuary (cf. LAMBECK, 1984). A special example of a successful colonizer is the spionid polychaete *Polydora quadrilobata*, new to the Dutch fauna (see Discussion). It gained a foothold in spite of the presence of a closely related congeneric *P. ligni*, the dominant *Polydora* species in the former estuary (WOLFF, 1973). The latter is a well-known species with a nearly world-wide distribution (HARTMANN-SCHRÖDER, 1971; GRASSLE & GRASSLE, 1974) and, moreover, known as a classic example of an opportunist (GRASSLE & GRASSLE, 1974; ZAJAC & WHITLACH, 1982): a species able to respond quickly to disturbed conditions (cf. WHITLACH & ZAJAC, 1985).

This paper compares the long-term and seasonal dynamics as well as the distribution characteristics of the two polydorids, with emphasis on niche differentiation and the relative

\* Communication no. 367 of the Delta Institute for Hydrobiological Research

success of life strategies under changing environmental conditions.

As *P. quadrilobata* became one of the abundant species in the lake, special attention has been paid to its productivity. This may contribute to the knowledge of the quantitative role of polychaetes in shallow marine ecosystems. Particularly in smaller species this knowledge is still limited, as pointed out by e.g. GARWOOD (1982) and OYENEKAM (1983).

## 2. MATERIAL AND METHODS

Lake Grevelingen ( $108 \text{ km}^2$ ) is characterized by deep channels (maximum depth 48 m) intersecting extensive shallow areas. The average depth is 5.3 m; 40% of it (often covered by eelgrass (*Zostera marina*)) is less than 2 m deep. The chlorinity of the water decreased slowly from about 17‰ immediately after the closure in 1971, to about 13‰ in 1978 and has, since 1979, been regulated at 16 to 16.5‰ with the aid of a new sluice in the North Sea dam (operated only in winter). Further details on water chemistry and sediments are provided by BANNINK *et al.* (1984) and KELDERMAN *et al.* (1984), respectively.

Long-term colonization studies —because they are typically not planned as such— require a recombination of data that inevitably involves some methodological heterogeneity. Population densities in the first years after the closure were

obtained from diversity studies at 4 permanent stations (A, B, C and G; Fig. 1). Environmental characteristics of the stations are compiled in Table 1 (see also LAMBECK, 1984). Station B was sampled 26 times from May 1971 to August 1975, station G 15 times from May 1971 to February 1973, and A plus C 13 times from February 1973 to February 1975. At stations B, C and G, 10 samples per sampling date were taken with a 0.1-m<sup>2</sup> van Veen grab. At the shallow station A, 10 corer samples of 0.01545 m<sup>2</sup> each were taken. Animals retained by a 1-mm sieve were preserved in seawater formalin. Sorting was done by stereomicroscopy. Because of frequent fragmentation, numbers in the samples were assessed by counting the heads.

Data on the distribution of numbers and biomass of the *Polydora* species came from a stratified random survey in April 1977. Within the depth range of 2 to 25 m, 70 samples were taken with a similar (0.093 m<sup>2</sup>) van Veen grab. Sieving and sorting were as above. After drying for ~3 days at 80°C, the ash-free dry weights (ADW) per sample were determined by incinerating at 580°C for two hours. The accuracy of the electronic balance was 0.1 mg.

For a better insight into the factors that might influence the distribution of *Polydora* numbers, individual macrobenthic species as well as entire samples were classified according to the TWINSPLAN-method (HILL, 1979). The analysis

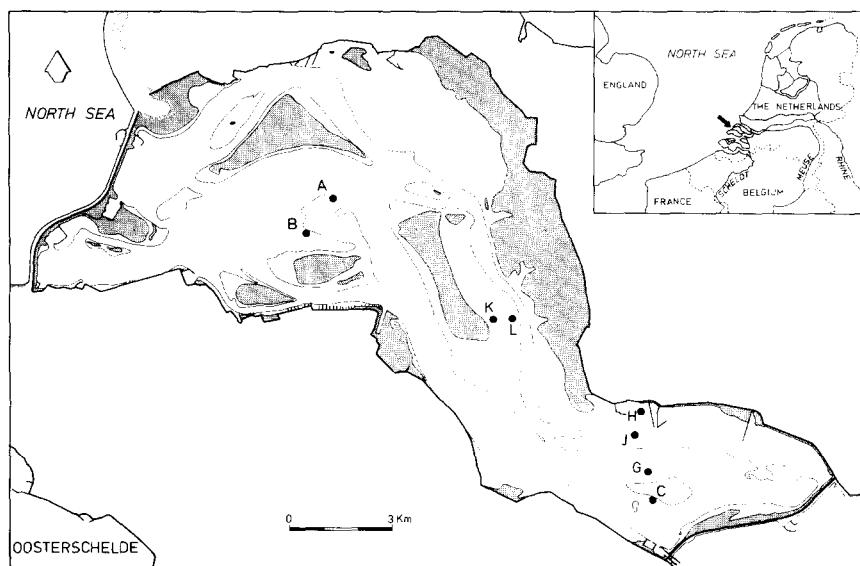


Fig. 1. Location of the sampling stations in Lake Grevelingen; permanent land since closure (shaded) and contour of 2-m water depth are indicated.

was further refined by distinguishing density categories, treated as so-called pseudo-species.

During the period March through October 1977 *Polydora* dynamics and growth were studied at the stations A, B and C. At roughly 6-weeks intervals, SCUBA divers with a 32.2-cm<sup>2</sup> perspex corer collected 10 samples of 64.4 cm<sup>2</sup> (2 cores combined). The top 5 cm was separated from the rest (15 to 20 cm) of the core. The top layers of each sample were preserved in formalin. In the laboratory they were washed through a 1.0 + 0.3 mm sieve combination. On the first sampling occasion the same procedure was applied to the remaining bottom layers as well. Since hardly any small polychaetes proved to be present below 5 cm, only a 1-mm sieve was used for these sections thereafter. To obtain a crude picture of changes in population composition, the body lengths (from the anterior of the prostomium to the end of the pygidium) of all intact animals (or a random sample in case of large numbers) were measured on millimeter paper. Biomass (in ADW) had to be determined for 5 or 10 samples combined. The 3 fractions (the 0.3 and 1.0-mm residue of the top layers plus the 1.0-mm residue of the bottom layers) were treated separately.

Between March 1980 and April 1981 a second data-set was collected at the 4 easterly shallow stations H, J, K and L (Fig. 1). Environmental characteristics are presented in Table 1. Stations H and J were situated in a dense eelgrass (*Zostera marina*) bed, and particularly H contained a high amount of detritus (350 g ADW·m<sup>-2</sup> in the upper 25 cm of the sediment, a value that was 2.2 times higher than at station J and 12 and 5 times higher than the stations K and L, respectively). Sampling frequency, procedure and sample treatments were identical with the 1977

study, except that length measurements were not carried out.

An overall picture of the summer distribution in shallow water (0.4 to 2.2 m) was obtained from a survey during August 1980. At 20 locations a corer sample (84.4 cm<sup>2</sup>) was collected in an eelgrass area and in an adjacent bare area. Further treatment of the 40 samples was as described above.

Production values were computed according to the method described by CRISP (1971), which is based on growth-survivorship curves of separable age classes (cohorts).

### 3. RESULTS

#### 3.1. POLYDORA QUADRILOBATA

##### 3.1.1. DISTRIBUTION

*Polydora quadrilobata* was not found in the sampling period 1971 to 1975. In April 1977, however, it appeared to be widespread all over the lake: it was lacking in only 1 out of the 70 samples. The maximum density amounted to 7300 ind·m<sup>-2</sup>. A picture of the depth distribution was obtained by splitting the samples into 7 depth classes. Confidence intervals of the mean densities were wide, but the data did not indicate a consistent relationship between depth and density (Fig. 2). The average density in water deeper than 2.5 m was 1340 ind·m<sup>-2</sup>. Only in the 2 to 2.5 m depth class numbers were significantly reduced (~200·m<sup>-2</sup>). This corroborates the very low average density of 24 ind·m<sup>-2</sup> found in the 1980 survey of the 0.4 to 2.2 m zone and the low densities or even absence of *P. quadrilobata* at 4 out of the 5 shallow stations in 1980 (see 3.1.2.).

TABLE 1

Environmental characteristics of the sampling stations. Water depth is in meters. Median grain size and sorting coefficient are in phi-units; silt is expressed in % of dry weight. For details about methods see KELDERMAN *et al.* (1984).

Station	Depth (m)	Median grain size (ϕ units)	Sorting coefficient (ϕ units)	Silt (%)
A	1.1	1.9	0.35	1.5
B	3	2.1	0.4	4
C	3	2.5-3.0	~0.5	4.5-7
G	9	-	-	10
H	0.75	-	-	17
J	1.75	2.7	0.4	6
K	0.75	2.95	0.35	6
L	1.75	2.95	0.35	8

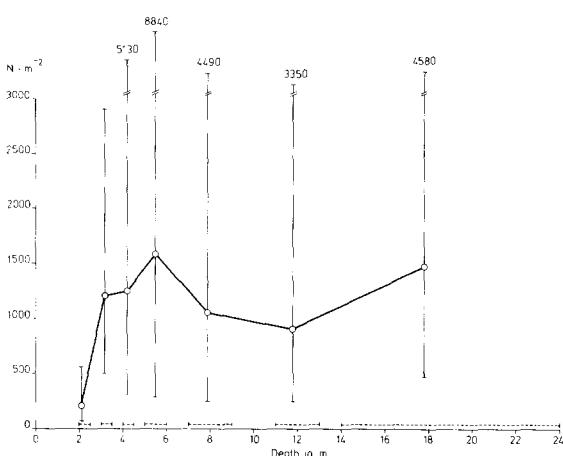


Fig. 2. Average density ( $N \cdot m^{-2}$ ) of *P. quadrilobata* in relation to water depth in Lake Grevelingen from the survey of April 1977. The ranges of each depth class and the 95% confidence intervals of the means are indicated.

No sediment data are available for the 1977 survey. KELDERMAN *et al.* (1984) showed that the composition of the lake sediment was very homogeneous over large areas and had hardly changed since the closure. Water depth appeared to be a key factor for the sediment distribution. Their extensive test of local inhomogeneities (sediment patchiness) at 4 stations produced only low coefficients of variation *viz.* ~1% for the median grain size and ~20% for silt and particulate organic carbon (POC) content. Therefore, the sediment data from 1981 (when nearly all survey locations were revisited) were used to detect general trends in the distribution of *P. quadrilobata* as determined in 1977.

No correlation (Spearman test,  $p < 0.1$ ) was found between the 3 above-mentioned sediment parameters and the density of the polychaetes, even if the analysis was refined by splitting the samples into categories with "lower" and "higher" silt (2 to 9%,  $n = 34$ , and 10 to 46%,  $n = 32$ , respectively) and POC figures (0 to 1%,  $n = 28$ , and 1.5 to 5%,  $n = 39$ , respectively). However, within the "low" categories of both silt and POC a highly significant (Spearman test,  $p < 0.001$ ) positive relation existed between water depth and density; this relationship was lacking in the "high" categories.

Sediment characteristics may affect the depth to which *Polydora* and its tube penetrates the bottom. In the very fine sand, rich in silt, of sta-

tion C the proportion of worms below 5 cm depth was negligible (0.3%), but it was higher at the clean sandy stations A (10%) and B (22%), poor in silt.

*P. quadrilobata* appears to occur quite independently of other species: no correlation was found between its numbers and the total macrozoobenthic biomass in a grab sample.

A TWINSPAN-analysis classified *P. quadrilobata* within a category of abundant species with only little differentiation in their distribution pattern. This also implies that *P. quadrilobata* hardly plays a part (indicated by so-called preferences) in the classification of samples. Only in a group of clean sandy samples, mostly characterized by dense stocks of *Hydrobia ulvae*, *Pygospio elegans*, *Arenicola marina*, *Capitella capitata*, *Cerastoderma edule* and *C. lamarcki*, did high densities of *P. quadrilobata* ( $> 1000 \cdot m^{-2}$ ) occur less frequently ( $\chi^2$  test,  $p < 0.05$ ).

There is no indication of a competitive exclusion between *P. quadrilobata* and the less abundant *P. ligni* (see 3.2.) in Lake Grevelingen: a correlation between their densities when they co-occur was absent (Spearman,  $p > 0.1$ ).

### 3.1.2. SEASONAL DYNAMICS AND POPULATION STRUCTURE

In 1977 as well as in 1980/81 *P. quadrilobata* showed a distinct seasonal pattern (Figs 3 and 4). Maximum numbers,  $7000 \cdot m^{-2}$  at station C in 1977 and 1300 and 1750 at station H in 1980 and 1981, respectively, were reached between late winter and late spring. Numbers decreased rapidly towards midsummer and were at a minimum in autumn/early winter.

No settlement was found at the stations K and L and at A, B and J settlement was limited, with maxima of 150 to 450  $ind \cdot m^{-2}$ . In these apparently suboptimal habitats the population (nearly) disappeared in autumn (Fig. 5).

Length measurements of worms from station C (Fig. 6) showed that in March 1977 the population was dominated by small juveniles. Their average length increased from 4.7 mm in March to 10.1 mm in April. Growth is further illustrated by a decrease in the share of the 0.3-mm sieve fraction from 72 to 6% of the numbers. The few adult (1976) worms had a mean length of 24 mm in April. Growth continued and in early June it was hardly feasible to distinguish between the two age-classes.

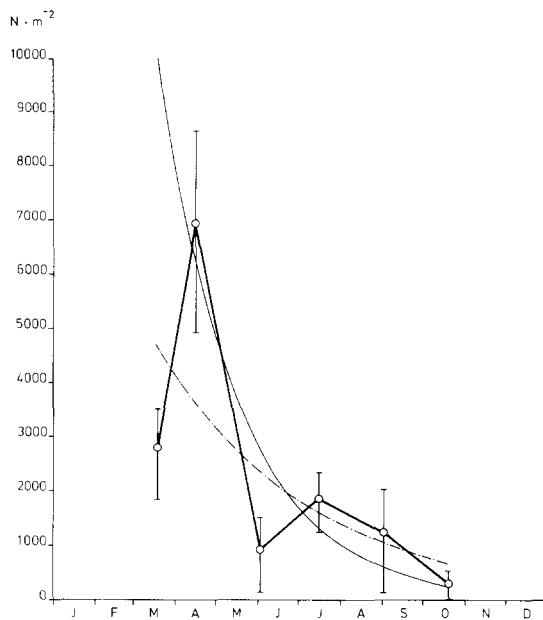


Fig. 3. Changes in the numerical density ( $N \cdot m^{-2}$ ; 95% confidence intervals of the means indicated) of *P. quadrilobata* at station C in 1977. Calculated exponential "maximum" (—) and "minimum" (--) survivorship curves (see 3.1.3.) also indicated.

July was characterized by a different situation: a maximum size of only 15 mm and, again, several very small animals. Although patchiness in growth performance may have existed in the rather heterogeneous environment at station C, a small second generation seems possible, con-

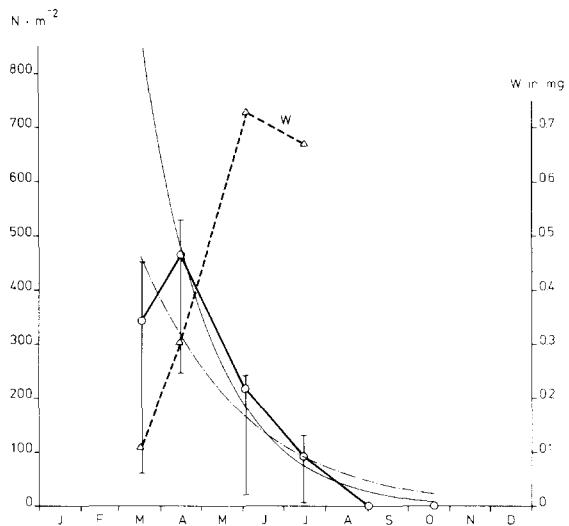


Fig. 5. Changes in numerical density ( $N \cdot m^{-2}$ ; 95% confidence intervals of the means indicated) and the mean individual weight (W in mg ADW;  $\Delta \cdots \Delta$ ) of *P. quadrilobata* at station B during 1977. Also indicated calculated exponential "maximum" (—) and "minimum" (--) survivorship curves.

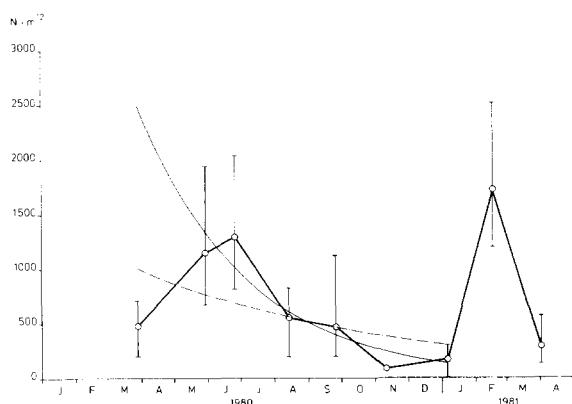


Fig. 4. Changes in the numerical density ( $N \cdot m^{-2}$ ; 95% confidence intervals of the means indicated) of *P. quadrilobata* at station H in 1980/81. Also indicated the calculated exponential "maximum" (—) and "minimum" (--) survivorship curves for the 1980 population.

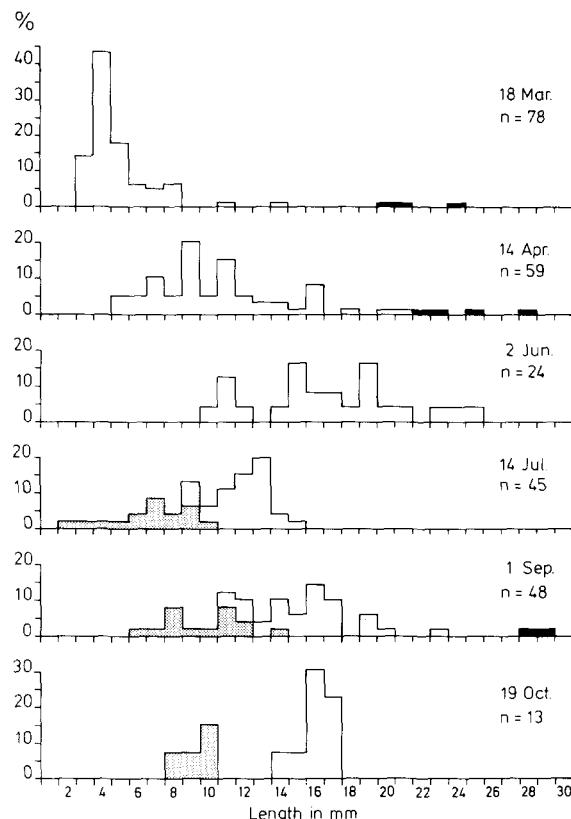
sidering the size distribution at the two consecutive sampling dates. The developments in the size distribution suggest, furthermore, a high mortality for the larger size-classes. The maximum life span of the worms is presumably 1 to 1½ years.

The small population at station B does not indicate a slower weight increase (Fig. 5, cf. Table 2) than at station C. Older animals were absent. The disappearance of the worms in autumn 1977 also showed the inability of *P. quadrilobata* to maintain a permanent stock at station B.

Data on the population structure are lacking for station H. But patterns in numbers (Fig. 4) and mean weight (Table 3) do not provide evidence for a second cohort of any importance.

### 3.1.3. BIOMASS AND PRODUCTIVITY

The relationship between water depth and biomass in the 1977 survey was rather pronounced. By far the lowest amount,  $0.019 \text{ g ADW} \cdot m^{-2}$ , was found in the 2 to 2.5 m samples, and a maximum,  $0.28 \text{ g ADW} \cdot m^{-2}$  was reached in the 5 to 6 m zone (Fig. 7). The highest value that occurred in one sample was  $1.59 \text{ g} \cdot m^{-2}$  (at a depth of 3 m).



This pattern parallels a similar relationship between mean individual weight and water depth (Fig. 7). Although size frequencies are not available for this survey, the large variation in mean weight per sample, even between samples with several hundred worms, suggests that the bigger-sized older worms were not homogeneously distributed. They are presumably underrepresented both in very shallow and in deeper water (Fig. 7).

By dividing the lake into 4 depth strata, 0 to 2.5 m (supposing the 9 samples from 2 to 2.5 m depth to be representative also of shallower water), 3 to 6 m ( $n = 34$ ), 6.5 to 13.5 m ( $n = 18$ ) and  $\geq 14$  m ( $n = 9$ ), a weighted mean value for biomass of  $0.10 \text{ g ADW} \cdot \text{m}^{-2}$  (95% conf. interval 0.07 to 0.15) and a corresponding density value of  $760 \text{ ind} \cdot \text{m}^{-2}$  (conf. interval 460 to 1250) were determined. Biomass values at station C in 1977 ranged from  $0.14 \text{ g ADW} \cdot \text{m}^{-2}$  in October to  $1.42 \text{ g}$  in April, and at station H in 1980 from  $0.03 \text{ g}$  in

Fig. 6. Length-frequency distributions of *P. quadrilobata* at station C at 6 consecutive sampling dates in 1977. Presumed 1976 (black), 1977-I (open) and 1977-II (shaded) worms and numbers of individuals measured indicated.

TABLE 2

Population parameters for the *P. quadrilobata* population at station C in 1977. A) All worms combined.  $N_o$  = average density  $\cdot \text{m}^{-2}$  found,  $N_-$  and  $N_+$  are, respectively, the recalculated "minimum" (based on all dates) and "maximum" (excluding first date) survivorship (see 3.1.3.); B) is the average biomass in  $\text{g ADW} \cdot \text{m}^{-2}$  and  $W$  the mean individual weight in mg ADW. B) Estimated values of density, biomass and mean weight for the presumed 1977-I and 1977-II cohorts.  $N_{I-}$  and  $N_{I+}$  are, respectively, the recalculated "minimum" and "maximum" survivorship for the presumed 1977-I cohort.

A)

Date	$N_o$	B	W	$N_-$	$N_+$
18-3	2795	0.26	0.093	4690	10 134
14-4	6925	1.42	0.205	3644	6284
2-6	916	0.47	0.514	2365	2770
14-7	1863	0.36	0.194	1605	1330
1-9	1242	0.66	0.534	1042	586
19-10	280	0.14	0.500	676	258

B)

Date	$N_I$	$B_I$	$W_I$	$N_{I-}$	$N_{I+}$	$N_{II}$	$B_{II}$	$W_{II}$
18-3	2686	0.08	0.029	4490	11013	-	-	-
14-4	6444	0.85	0.132	3218	6056	-	-	-
2-6	885	0.47	0.514	1976	2173	-	-	-
14-7	1196	0.32	0.285	1242	867	668	0.04	0.058
1-9	807	0.45	0.552	739	311	388	0.06	0.143
19-10	186	0.13	0.692	440	112	93	0.01	0.117

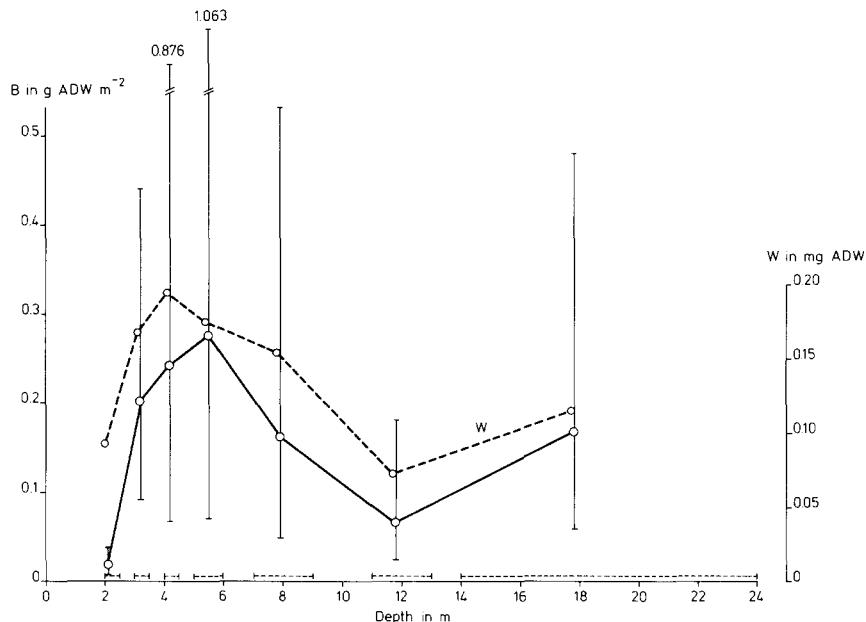


Fig. 7. Average biomass ( $B$  in  $\text{g ADW}\cdot\text{m}^{-2}$ , solid line; 95% confidence intervals of the means indicated) and individual weight ( $W$  in  $\text{mg ADW}$ , broken line) of *P. quadrilobata* in relation to water depth in the lake survey of April 1977. Ranges of each depth class are indicated.

March to 1.22 g in May. The maximum biomass at station B was  $0.16 \text{ g}\cdot\text{m}^{-2}$ .

Assuming the population to represent one cohort, the production of *P. quadrilobata* at station H in 1980 would amount to only  $0.14 \text{ g ADW}\cdot\text{m}^{-2}$ , far below the maximum biomass figure. Productivity will be seriously underestimated if the decrease in mean weight after May (Table 3) is due to selective mortality: assuming zero growth in that period would increase the figure to 0.86 g.

The Crisp method cannot be applied correctly, however, because the only growth observed (March to May 1980, Table 3) took place while

numbers were still increasing. To assess at least the potential range of production, two assumptions have been made: 1) all settlement took place around the first sampling date (most of the worms being still too small to be retained by a 0.3-mm sieve) and 2) the mortality rate was constant. Survivorship (according to  $N_t = N_0 \cdot e^{-b \cdot t}$ ) has been reconstructed by an iteration procedure, presuming a "minimum" (based on all sampling dates) and a "maximum" (excluding the first sampling date) situation (Fig. 4). Annual production (=biomass in March + production March-January), calculated on the basis of 1) the original mean weight data and 2) a zero-growth

TABLE 3  
Population parameters for *P. quadrilobata* at station H in 1980/1981. For units see Table 2A.

Date	$N_0$	$B$	$W$	$N_-$	$N_+$
28-3	478	0.02	0.07	1014	2495
29-5	1150	1.22	1.06	781	1331
25-6	1292	0.95	0.73	697	1013
13-8	549	0.25	0.46	567	616
25-9	478	0.18	0.38	473	399
10-11	88	0.04	0.47	389	250
5-1	177	0.06	0.33	308	142

after May (see above), would then range between 0.49 and 2.06 g ADW·m<sup>-2</sup>, with resultant P/B ratios of 1.5 to 6.2 (Table 4).

The data of station C have been treated in the same way (Fig. 3). The "zero-variant" in the production figures (Table 2) assumes selective mortality without production between June and July, while the weight increase towards August (Table 2) would reflect growth of the remaining worms. The annual productivity at station C was roughly twice as high as at station H (Table 4).

The one-cohort assumption for station C is a simplification, however. In a second approach, numbers were split over 3 cohorts (1976, 1977-I and 1977-II) on the basis of the length-frequency distributions presented (Fig. 6). Assuming that the width of the worm increases proportionally with its length and that the specific weight remains constant during growth, a third power relationship would exist between weight and length, as was, indeed, found for e.g. *Nephtys hombergii* (WARWICK & PRICE, 1975) and *Pectinaria koreni* (KIRKEGAARD, 1971). Given the total weight of all animals and the length distribution, biomass can be divided over these 3 cohorts.

The density of the 1976 worms was low and there was no distinct trend in their (high) mean weights. Therefore, their productivity in 1977 has been set at zero. The survivorship of the numerically dominant 1977-I cohort was again reconstructed for a "minimum" and "maximum" (omitting the March value) abundance (Table 2B). The production of the 1977-II cohort, only present on the last 3 sampling dates, was small: ~0.1 g ADW·m<sup>-2</sup>. Estimates for the total annual production for all 1977 worms ranged from ~1.6 g to 2.9 g, with resultant P/B ratios of 4.9 to 9.1 (Table 4).

The productivity at station B, again based on a reconstructed "minimum" and "maximum" survivorship (Fig. 5), was low but the P/B ratio of this

small non-permanent population approached that of station C (Table 4).

A crude estimate of the 1977 productivity of *P. quadrilobata* in the whole lake was obtained by dividing the annual production figures of stations B and C by the average biomass between the March and April sampling dates (the survey was held halfway!) and applying this turnover ratio to the survey biomass data. It was, furthermore, assumed that the samples from 2 to 6 m water depth were also representative of the extensive shallow areas of the lake not sampled in this survey. Using the "minimum" and "maximum" approaches would give an estimated production for the lake of 0.3 to 0.5 g ADW·m<sup>-2</sup>·a<sup>-1</sup>. Limiting the estimation to the area deeper than 1.5 m (65% of the lake) would increase this range to 0.4 to 0.7 g·m<sup>-2</sup>·a<sup>-1</sup>.

### 3.2. POLYDORA LIGNI

In the period 1971 to 1975 no taxonomic distinction was made between *Polydora ligni* and *P. ciliata*. In a few test samples *P. ciliata* was absent, however (W.J. Wolff, pers. comm.). From the results of subsequent studies it may be concluded that the data almost entirely concern *P. ligni*: with a share of 98% ( $n=752$ ) this species outnumbered by far *P. ciliata* in the 1977 survey and, moreover, no *P. ciliata* were found during the station studies of 1977 and 1980/81.

The absence of *P. ligni* at the channel station G and a low density at station B (Fig. 8) indicate that in 1971, immediately after the closure of the estuary, the abundance of this species was insignificant. In June 1972 a small stock (150 ind·m<sup>-2</sup>) settled at station G. Mass settlement in 1972, with a peak value of 5100 ind·m<sup>-2</sup> in August, took place at station B. However, 90% of these animals disappeared within two months (Fig. 8). With somewhat lower maxima the same

TABLE 4

The average annual biomass B (in g ADW·m<sup>-2</sup>), the production P (in g ADW·m<sup>-2</sup>·a<sup>-1</sup>) calculated according to 4 procedures (see text) and the calculated P/B ratios of *P. quadrilobata* at 3 permanent stations.

Procedure:	Minimum			Minimum-Zero		Maximum		Maximum-Zero	
	B	P	P/B	P	P/B	P	P/B	P	P/B
Station/year									
H, 1980	0.33	0.49	1.5	0.96	2.9	1.42	4.3	2.06	6.2
B, 1977	0.06	0.22	3.9	-	-	0.35	6.1	-	-
C, 1977 (total population)	0.45	1.60	3.6	2.25	5.0	2.92	6.5	3.57	7.9
(1977 worms)	0.32	1.58	4.9	1.91	5.5	2.63	8.2	2.92	9.1

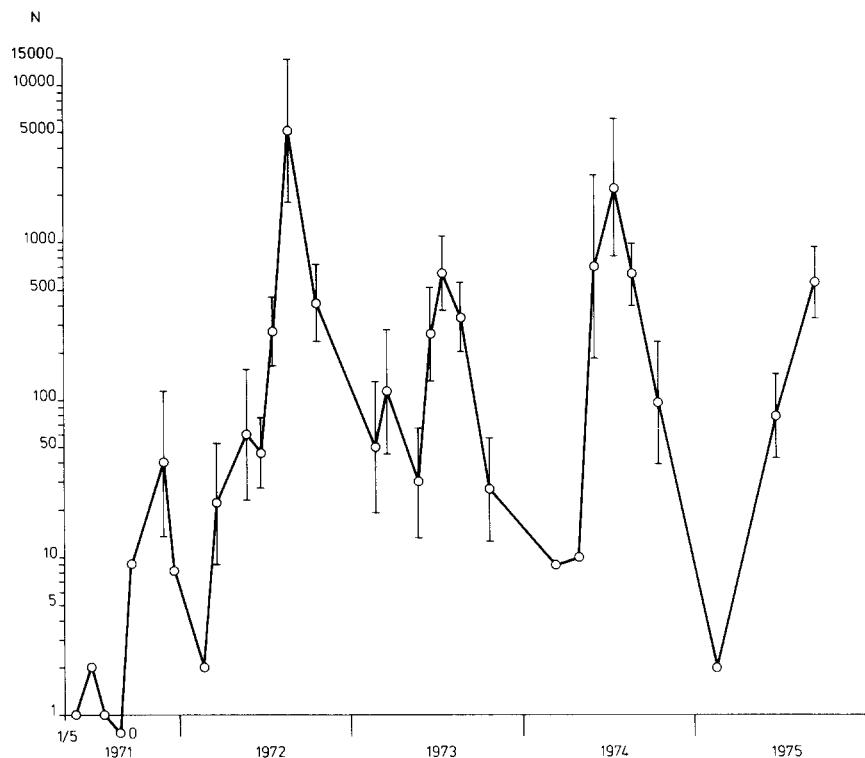


Fig. 8. Changes in the numerical density ( $N \cdot m^{-2}$ ; 95% confidence intervals of the means indicated) of *P. ligni* at station B from May 1971 (directly after the closure of the Grevelingen estuary) to September 1975.

pattern was repeated here in 1973 and 1974; also the incomplete data of 1975 point to a summer peak. In all these years only a very small stock survived the winters (Fig. 8).

Maximum density at station C amounted to  $835 \cdot m^{-2}$  in June 1974. Numerical fluctuations (Fig. 9) here appear to be smaller than at station B.

With maxima of 60 and  $200 \cdot m^{-2}$ , respectively, numbers at stations B and C were considerably lower in 1977. On the contrary, a small stock with a maximum of  $450 \text{ ind} \cdot m^{-2}$  in early September was present at station A where *P. ligni* was absent in the period 1973 to 1975.

The survey of April 1977 produced an overall density of  $122 \text{ ind} \cdot m^{-2}$  (95% conf. interval 79 to 187). The extensive shallow areas were not sampled, however. The abundance in the area deeper than 1.5 m (65% of the lake) was only  $96 \text{ ind} \cdot m^{-2}$  (95% c.i. 77 to 138) with a negligible biomass of  $0.03 \text{ g ADW} \cdot m^{-2}$ . This reduction can be ascribed to the near absence of *P. ligni* below 7 m depth.

In the 2 to 7 m zone, the density was positively correlated with the total macrobenthic biomass in a sample (Spearman test,  $p < 0.01$ ). Relatively high numbers occurred particularly in samples with a dense stock of older mussels (*Mytilus edulis*) with barnacles (*Balanus crenatus*). The highest density in a sample corresponded with  $2000 \text{ ind} \cdot m^{-2}$  and a biomass value of  $0.46 \text{ g ADW} \cdot m^{-2}$ .

At the 4 shallow stations studied in 1980/81, *P. ligni* was absent until September, when low numbers ( $< 500 \text{ ind} \cdot m^{-2}$ ) settled at 3 of them. The worms disappeared again from J and K; only at L was the density maintained through the winter.

The tendency towards reduced numbers in shallow water was confirmed by the survey of August in 1980. In the depth range of 0.4 to 2.2 m, a mean density as low as  $30 \cdot m^{-2}$  was found.

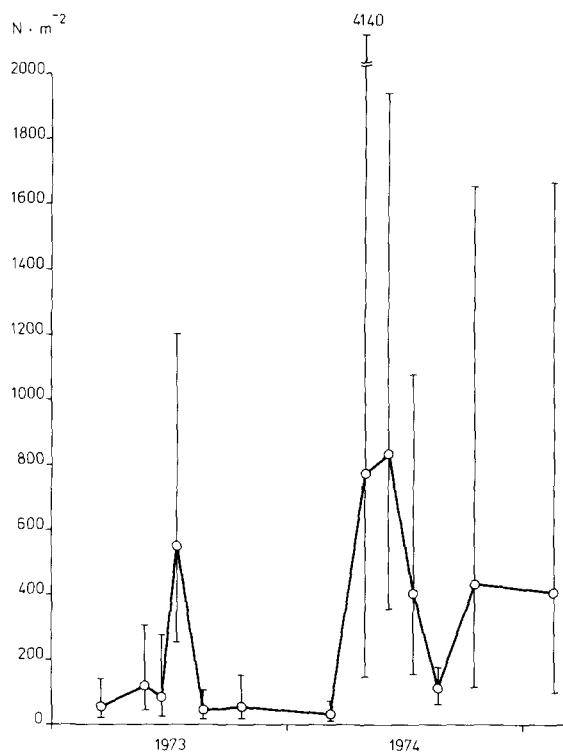


Fig. 9. Changes in the numerical density ( $\text{N} \cdot \text{m}^{-2}$ ; 95% confidence intervals of the means indicated) of *P. ligni* at station C in the period March 1973 to February 1975.

#### 4. DISCUSSION

##### 4.1. *P. LIGNI/CILIATA* DISCRIMINATION

The validity of taxonomic differences between *P. ligni* and *P. ciliata* has been amply discussed by SMIDT (1951), HANNERZ (1956), RASMUSSEN (1973), MICHAELIS (1978) and RAMBERG & SCHRAM (1983). The problems may be enhanced by the considerable morphological variation in *P. ligni* and *P. ciliata* (RICE & SIMON, 1980; MUSTAQUM, 1986). In Lake Grevelingen *P. ligni* was quite common, but some *P. ciliata* have been found too. The animals clearly fit the descriptions given by HARTMANN-SCHRÖDER (1971). The very low abundance of *P. ciliata* is not surprising considering the soft-bottom character of the sampling locations: *P. ciliata* is predominantly a borer in calcareous substrates, stiff clay banks etc. (e.g. HEMPEL, 1957b; DORSETT, 1961; RAMBERG & SCHRAM, 1983), while *P. ligni* mostly builds its tubes into soft sediments (HEMPPEL, 1957b; MICHAELIS, 1978; see also RASMUSSEN, 1973).

#### 4.2. POPULATION DEVELOPMENTS AND ENVIRONMENTAL CHANGES

In the former Grevelingen estuary 3 *Polydora* species occurred: *P. ligni*, *P. ciliata* and *Pseudopolydora pulchra*. In surveys held in 1962/63 and 1967 only *P. ligni* was rather common, mainly in intertidal areas (WOLFF, 1973).

The abrupt change from a tidal estuary to a stagnant lake implied a severe disturbance. Although *P. ligni* is widely known as an opportunist (cf. GRASSLE & GRASSLE, 1974), data of 1971 do not indicate a quick mass settlement. Contrary to the experiments of ZAJAC & WHITLACH (1982) or ARNTZ & RUMOHR (1982), who created a local disturbance, in Lake Grevelingen the whole ecosystem changed. Populations in the former upper intertidal (now permanently land) and in deeper water (temporary oxygen deficiency) were eliminated (cf. LAMBECK, 1981), and there may have been a detrimental interference with spawning in the remaining stock and/or with the survival of planktonic larvae, e.g. by an initially heavy sedimentation of particles. In fact molluscs such as *Mytilus edulis* (WOLFF *et al.*, 1977) behaved more "opportunistically" than *P. ligni*, the latter requiring 14 months after the closure for widespread settlement.

Maximum densities were similar to those reported by MUUS (1967) and DAUER & CONNER (1980), but remained far below the 40 to 100 000  $\text{m}^{-2}$  observed to occur in dense banks (e.g. SMIDT, 1951; HEMPEL, 1957b; GRAY, 1976). The pattern of large settlement and subsequent high mortality was repeated 3 more years at station B. In contrast, station C contained lower, but also more stable numbers. This difference is in agreement with the described declines of opportunists to a background position in more "mature" ecosystems (GRASSLE & GRASSLE, 1974; ARNTZ & RUMOHR, 1982; CHESNEY, 1985). In the former estuary, station B was a nearly bare area where after 1971 a benthic community gradually developed (WOLFF *et al.*, 1977). The more sheltered station C was already a rich benthic community before the closure.

As shown for intertidal flats (REISE, 1978), predators may structure benthic communities. After a 3-month experiment in Lake Grevelingen in the summer of 1975, the mid-September density of *P. ligni* within a protecting cage was indeed 4 times higher than outside the cage ( $p < 0.01$ , unpubl. results). Competition for food, space etc. may also play a part. However, the "predictable"

decline of *P. ligni*, very distinct in 1971, when the total benthic biomass in the lake had increased by 160% (LAMBECK, 1985), is in sharp contrast with the success of *P. quadrilobata*, a closely related species.

The latter was not found in the 1971 to 1975 study. Considering its quite different appearance, even a limited occurrence cannot easily be overlooked. The summer peaks in density during that period (Fig. 8) exclude, moreover, any mistake since *P. quadrilobata* is a spring species in Lake Grevelingen. In 1976 *P. quadrilobata* was already widespread in the lake and more abundant than *P. ligni*, as shown by VOLCKAERT (1979), who studied the polychaetes in meiofauna samples. All evidence indicates that mass colonization had taken place by 1976, which would imply that, at least locally, significant populations settled as early as 1975.

Nothing is known about the origin of the colonizers. Before its discovery in Lake Grevelingen *P. quadrilobata* was unknown in the Netherlands. In NW Europe this boreal species, with a distribution in the Arctic, North Pacific and North Atlantic (HARTMANN-SCHRÖDER, 1971), was reported in a tidal bay in the northern German Wadden Sea (HEMPPEL, 1957a), and in non-tidal areas in Denmark (RASMUSSEN, 1973) and along the German Baltic coast (HEMPPEL, 1957a; ROGAL *et al.*, 1978). More recent Dutch finds came from a silty intertidal dead-end branch of the Oosterschelde, near the eastern dam of Lake Grevelingen, where a small stock (<50 ind·m<sup>-2</sup>) was present during 3 successive autumn surveys in the period 1978 to 1980 (COOSEN & VAN DEN DOOL, 1983; *P. quadrilobata* was absent in other investigated tidal and subtidal Oosterschelde areas).

Few other quantitative data on *P. quadrilobata* appear to be available. A summer value of 4000 ind·m<sup>-2</sup> in an "optimal" habitat on Sylt (HEMPPEL, 1957a) and values of 80 to 480 ind·m<sup>-2</sup> in summer surveys from Lübeck Bay (ROGAL *et al.*, 1978), suggest that the densities observed in Lake Grevelingen are relatively high. Favourable conditions in 1977 are also reflected by size data. The largest intact formalin-preserved worm at the stations measured 29 mm, while in the April survey an incomplete worm of 35 mm was found. In contrast, RASMUSSEN (1973) mentions a maximum length of 30 mm for a live specimen, and HARTMANN-SCHRÖDER (1971) 25 mm, presumably for a preserved one.

Although limited to shallow water, the 1980/1981 data suggest that *P. quadrilobata*

maintained its dominant position in comparison with *P. ligni* in the years following the colonization of Lake Grevelingen. Three partly interrelated factors, *viz.* a) distribution differences, b) food supply and c) life history, may play a part in this *P. ligni*-*P. quadrilobata* shift.

#### 4.3. DISTRIBUTION DIFFERENCES

*P. quadrilobata* showed no preference for a particular type of sediment, which is in agreement with HEMPEL(1957a). None of the limited data for *P. ligni* points to a distinct preference. According to HEMPEL (1957a) and ZAJAC & WHITLACH (1982), *P. ligni* inhabits a wide range of sediments, although SMIDT (1951), MUUS (1967) and WOLFF (1973) mention a preference for muddier types of sediment. The two species were scarce in the shallow areas of Lake Grevelingen that are mostly composed of relatively clean sand. This explains the positive relationship between water depth and *P. quadrilobata* density within the category of 1977 survey samples with a "low" content of silt or POC.

Mud and detritus, especially abundant in the tubes of *P. quadrilobata*, may be a prerequisite for successful tube building (*cf.* HEMPEL, 1957b). Population density may also be low because the fine sand bottoms in shallow areas are too unstable during gales. Of all shallow stations only H, with a high clay content (Table 1), supported a significant population. The higher penetration depth of *P. quadrilobata* at the exposed 3-m station B, in comparison with the sheltered station C that has a less loosely packed sediment (Table 1), may also be functional in this respect.

Biotic interactions may be involved too. WEINBERG (1984) showed that the density of *P. ligni* was negatively affected by a deep-burrowing, sediment-eating polychaete. In Lake Grevelingen that category is represented by *Arenicola marina*, which is abundant in sandy shallow areas. Finally, food conditions in shallow water may be limiting (see 4.4).

HEMPPEL (1957a) mentions the avoidance by *P. ligni* of areas with H<sub>2</sub>S. This may explain its absence in the deeper waters of Lake Grevelingen, which are rich in silt and detritus. *P. quadrilobata* is apparently more tolerant. Moreover, oxygen conditions in early spring, when this species has its highest abundance, are much more favourable than in summer when on windless days anoxia in the channel sediments even affects the overlying water (LINDEBOOM *et*

*et al.*, 1984). The rather low individual weights in deep water point to a high share of juveniles, and hence to a low survival. This suggests that the unstable environmental conditions in the channels also affect *P. quadrilobata*.

#### 4.4. FOOD SUPPLY

Data on feeding are not available for Lake Grevelingen. According to HEMPEL (1957a) *Polydora* mainly catch particles (phytoplankton, zooplankton, detritus) from the water with their palps. Scraping off the mud with the palps was the normal way of feeding in a Belgian area (DARO & POLK, 1973). RASMUSSEN (1973) called *P. ciliata* (including *P. ligni*) both a deposit and a suspension feeder, a conclusion confirmed for *P. ligni* by DAUER *et al.* (1981). Predation on small macrofauna (*cf.* WEINBERG, 1984) and meiofauna, as well as carrion consumption (DARO & POLK, 1973) also occur. Microphytobenthos is probably not an important food source for polydorids. Although diatoms were found in the intestine, DARO & POLK (1973) called their deposit-feeding *P. ciliata* "essentially detritivorous". In Lake Grevelingen the deep channels were able to sustain a high density of *P. quadrilobata*, while *Polydora* abundance was low in shallow water, where the main stock of microphytobenthos is concentrated (NIENHUIS & DE BREE, 1984). With a rich food supply an extensive settlement would be expected, even if temporary, harsh physical conditions prevent the maintenance of a permanent population.

However, the flux of suspended matter can strongly influence the feeding behaviour, as shown by TAGHON *et al.* (1980) and DAUER *et al.* (1981), suggesting that suspension feeding may be the first choice. Out of 6 species of spionid polychaetes studied, *P. ligni* had the largest repertoire of water-orientated feeding-techniques (DAUER *et al.*, 1981).

As a consequence of the increased transparency since the closure, phytoplankton productivity in the Lake begins in February, much earlier than under estuarine conditions (VEGTER & DE VISSCHER, 1984). In the Baltic, a non-tidal brackish sea, an important part of the spring bloom sinks to the bottom. This material has a high nutritive value (BONSDORFF & ÖSTERMAN, 1985; GRAF *et al.*, 1982). The share of refractory components quickly increases with time, however. The importance of the spring bloom for benthic suspension and deposit-feeders has

been demonstrated by CHRISTENSEN & KAN-NEWORFF (1985).

The summer biomass of phytoplankton in Lake Grevelingen is lower than in spring and is, moreover, lower than in the former estuary (BAKKER & DE VRIES, 1984). This can be ascribed to the increased impact of benthic filter feeders: they can now filter the entire lake volume every 4 days (DE VRIES, 1984). Their activity is temperature-dependent and hence maximal in summer (*cf.* NEWELL & BAYNE, 1980; Fig. 10).

Increased mineralization rates (LINDEBOOM *et al.*, 1984) further reduce the availability of easily consumable particles in summer. The locally large amounts of detritus in the sediment have a refractory character (DE VRIES, 1984).

An early spring species such as *P. quadrilobata* can profit from a temporarily high food supply, allowing even an opportunistic type of population response (*cf.* BONSDORFF & ÖSTERMAN, 1985; CHESNEY, 1985). The coincidence in spring 1980 of an unusually late start of the phytoplankton productivity (VEGTER & DE VISSCHER, 1984) and the retarded population increase at station H may be illustrative (see also 4.5). The "classical" opportunist *P. ligni*, however, is presumably confronted with a food shortage. Food conditions in summer 1977 were less favourable due to a combination of a low phytoplankton productivity (VEGTER & DE VISSCHER, 1984) and an unusually dense stock of filter-feeding molluscs (LAMBECK, 1985). Under food limitation a species that has to pick individual particles out of the water or from the bottom may be a weak competitor as compared to species filtering large amounts of water.

These observations are not in conflict with the

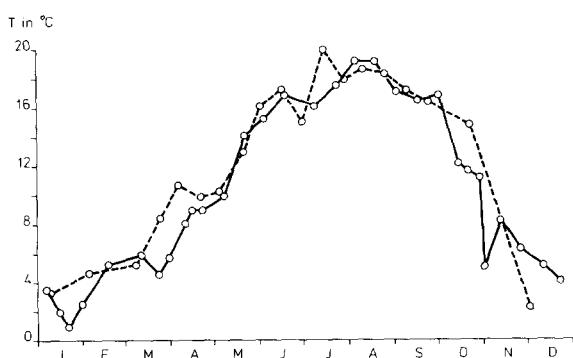


Fig. 10. Seasonal pattern in water temperature during 1980 (—) and 1981 (---). Data provided by G. Doornbos and C. Bakker.

positive correlation between *P. ligni* density and local benthic biomass. Relatively high numbers of *P. ligni* were often found in dense beds of older mussels, situated at places with an wind-driven inflow of water from the channels, which is rich in food (VERHAGEN, 1983). Shells, barnacles etc. are used as a substrate for the tubes. An epibiotic way of life, also mentioned by RAMBERG & SCHRAM (1983), presumably enhances feeding opportunities over an infaunal one. The lack of such a correlation in *P. quadrilobata* suggests that deposit-feeding on sedimented planktonic particles is of more importance in this species.

In the well-mixed water of Lake Grevelingen the phytoplankton production per m<sup>2</sup> is directly related with water depth. In combination with the prevailing water circulation patterns (cf. VERHAGEN, 1983), this results in less favourable food conditions in shallow water, which also may contribute to the low densities of *P. quadrilobata* and particularly *P. ligni*.

#### 4.5. LIFE HISTORY

Besides the timing of larval settlement, the mode of reproduction may differ between the two species, although few direct data are available. In the period 1976 to 1980, densities of polychaetous larvae in the plankton were low during January/February (30 ind·dm<sup>-3</sup>), increasing to 500 to 1000 in April. Qualitative observations in 1976 showed a dominance of *Pygospio elegans* up to April, when *Polydora* took over (C. Bakker, unpubl. data). Hence, there is no evidence for an abundant *P. quadrilobata* larval stock in late winter. Considering, moreover, the slow rates of development at low temperatures (BLAKE, 1969), the late spring-summer abundance of *Polydora* is likely to be made up of *P. ligni*, which fits the observations of many *P. ligni* with egg capsules during the survey in early April 1977 and spring observations elsewhere (e.g. SMIDT, 1951; BLAKE, 1969; HARTMANN-SCHRÖDER, 1971). In contrast, a *P. quadrilobata* with eggs was an exception.

BLAKE (1969) distinguished two allopatric larval developmental modes in *P. quadrilobata* populations in Maine (USA). Larvae of type I develop slowly before being released in late winter. Type II larvae depend on higher water temperatures and are released in the spring plankton at a much earlier developmental stage. Although BLAKE (l.c.) presumes a short

planktonic phase in type I, he failed to find pelagic larvae. Lake Grevelingen worms fit the type I pattern; the plankton data strongly suggest that the released *P. quadrilobata*-I larvae settle directly, which may explain the absence of pelagic larvae in Blake's study and also in that of HANNERZ (1956) in a Swedish fjord.

Larval development rates are enhanced by higher temperatures (BLAKE, 1969). That may be a second proximate factor besides food supply in the timing of juvenile release. The very early abundance of juveniles at station H in 1981 did coincide with relatively high water temperatures in comparison with 1980 (Fig. 10). The *P. quadrilobata* larvae are released to the bottom in a period with presumably abundant food, while those of *P. ligni* are released in the water and subjected to extra predation and competition, not only with the now fully developed zooplankton community but also with benthic species.

In the Danish Isefjord (RASMUSSEN, 1973) and the German Wadden Sea (HEMPPEL, 1957b) *P. quadrilobata* breeds in summer. Its apparent broad temperature range in reproduction, probably related to its boreal distribution, has given to *P. quadrilobata* a great selective advantage over *P. ligni* in the Lake Grevelingen situation.

#### 4.6. PRODUCTIVITY AND SIGNIFICANCE IN THE BENTHIC ECOSYSTEM

The 1977 density data and biomass values for the whole lake, based on grab samples washed through a 1-mm sieve on board, are certainly underestimates. In the cautious laboratory procedure, 75% of the worms in the cores from station C were not retained by the 1-mm sieve in March; the loss decreased to 6% in mid-April. Expressed in biomass values these proportions were 16 and 2%, respectively.

Formalin preservation negatively influences annelid biomass. HOWMILLER (1972) found a decrease of 23% in oligochaete dry weight, similar to our own preliminary data for 4 large polychaete species (25% in ADW). The factors mentioned suggest that values for biomass and production as given here should be increased by roughly one third.

Most of the somatic growth took place within a short period. Hence a six-week sampling interval appears to be inadequate to obtain detailed production estimates, but the approach chosen may yield the most likely range of productivity

values.

The P/B ratios observed for *P. quadrilobata* are in the upper range of published values for polychaetes (see ROBERTSON, 1979). They are similar to the value of 4.86 for the small spionid *Spiophanes bombyx* in the Bristol Channel (WARWICK *et al.*, 1978), the values of 3.26 and 11.6 for two populations of the opportunist *Capitella capitata* in polluted areas near Southampton (OYENKAM, 1983), and the values of 4.00 to 5.47 found in the Lynher estuary for *Ampharete acutifrons*, resembling *P. quadrilobata* with one cohort in its 1-year lifespan. This 5-year range of P/B values for *Ampharete* was relatively small, in spite of large fluctuations in biomass between years (PRICE & WARWICK, 1980).

The perhaps best studied species, *Nereis diversicolor*, with a lifespan of 1½ to 2 and sometimes 3 years, has an annual P/B ratio of 2.5 to 3.0 (CHAMBERS & MILNE, 1975; HEIP & HERMAN, 1979; KRISTENSEN, 1984). MÖLLER (1985) stressed the importance of juvenile *Nereis*, reaching a P/B ratio (May-December) of 4.8.

Large polychaetes, as e.g. *Nephtys hombergii* and *Arenicola marina*, with lifespans of 3 years and more, relatively low and stable densities but with a high biomass, show P/B ratios around 1 (WOLFF & DE WOLF, 1977; BEUKEMA & DE VLAS, 1979; PRICE & WARWICK, 1980). These ratios approach the values observed in several species of bivalves (ROBERTSON, 1979).

With an average share of 0.3% in April 1977, *P. quadrilobata* was not a major component of the Lake Grevelingen macrobenthic biomass. On an annual basis, its biomass represented less than 1% at station C. However, in the April survey *P. quadrilobata* comprised 3.3% of the 5.1 g ADW·m<sup>-2</sup> in the deeper channels. On the annual basis, its constituted 4% of the 13.1 g ADW·m<sup>-2</sup> at station H and even 8.2% at its peak density. Owing to its high turnover rate, production values of 1 to 3 g ADW·m<sup>-2</sup>·y<sup>-1</sup> appear in several areas. Hence, locally and seasonally *P. quadrilobata* could play an important role in the benthic ecosystem.

The results of this study support the view that biomass values alone underestimate the significance of, particularly, small polychaetes.

**Acknowledgements.**—We are much indebted to A.J.J. Sandee, who did the sorting of the 1971 to 1975 samples (part of a study initiated by W.J. Wolff), and to Edith G. Alkema, who carried out a major part of a study into the relationship be-

tween eelgrass and macrozoobenthos, from which the 1980/1981 *Polydora* data were derived. Marjolein Eijgenraam and Emiel B.M. Brummelhuis also contributed to the latter data set. We thank the SCUBA divers of the Delta Institute, R.H. Bogaards, P. de Kooyer, A.J.J. Sandee and J.C.M. Weststrate-Rijk, for taking the corer samples at the stations. W.R. Rozing, A.J.J. Sandee and L. de Wolf assisted in the grab-sampling programmes, as did the crews of R.V. "Jan Verwey" (C.M. de Rooy and J.A. van Sprundel) and R.V. "Maris Stella" (W.J.L. Röber and P. de Koeijer).

J. van der Meer (Rijkswaterstaat, Middelburg) was of great help during the TWINSPAN computer runs. Comments by P.H. Nienhuis considerably improved the manuscript. We wish to express our gratitude to W.G. Beeftink, R.H. Drent, F.H. Nichols, W.J. Wolff and an anonymous reviewer for critically reading the final draft.

## 5. REFERENCES

- ARNTZ, W.E. & H. RUMOHR, 1982. An experimental study of macrobenthic colonization and succession, and the importance of seasonal variation in temperate latitudes.—J. exp. mar. Biol. Ecol. **64**: 17-45.
- BAKKER, C. & I. DE VRIES, 1984. Phytoplankton and nutrient dynamics in saline Lake Grevelingen (SW Netherlands) under different hydrodynamical conditions in 1978-1980.—Neth. J. Sea Res. **18**: 191-220.
- BANNINK, B.A., J.H.M. VAN DER MEULEN & P.H. NIENHUIS, 1984. Lake Grevelingen: from an estuary to a saline lake. An introduction.—Neth. J. Sea Res. **18**: 179-190.
- BEUKEMA, J.J. & J. DE VLAS, 1979. Population parameters of the lugworm, *Arenicola marina*, living on tidal flats in the Dutch Wadden Sea.—Neth. J. Sea Res. **13**: 331-353.
- BLAKE, J.A., 1969. Reproduction and larval development of *Polydora* from northern New England (Polychaeta: Spionidae).—Ophelia **7**: 1-63.
- BONDORFF, E. & C.-S. ÖSTERMAN, 1985. The establishment, succession and dynamics of a zoobenthic community, an experimental study. In: P.E. GIBBS. Proc. 19 Europ. Mar. Biol. Symp., Cambridge University Press: 287-297.
- CHAMBERS, M.R. & H. MILNE, 1975. Life cycle and production of *Nereis diversicolor* A.F. Müller in the Ythan estuary, Scotland.—Estuar. Coast. Mar. Sci. **3**: 133-144.
- CHESNEY, E.J., 1985. Succession in soft-bottom benthic environments: are pioneering species really outcompeted? In: P.E. GIBBS. Proc. 19 Eur. Mar. Biol. Symp., Cambridge University Press: 277-286.

- CHRISTENSEN, H. & E. KANNEWORFF, 1985. Sedimentating phytoplankton as major food source for suspension and deposit feeders in the Øresund.—*Opelia* **24**: 223-244.
- COOSEN, J. & A. VAN DEN DOOL, 1983. Macrozoobenthos van het Krammer-Keeten-Volkerak estuarium. Verspreiding der soorten, aantallen en biomassa in relatie met het zoutgehalte. Eindrapportage project ZACHTSUB. Delta Instituut voor Hydrobiologisch Onderzoek, Yerseke/Deltadienst Rijkswaterstaat, Middelburg: 1-131.
- CRISP, D.J., 1971. Energy flow measurements. In: N.A. HOLME & A.D. MCINTYRE. Methods for the study of marine benthos. Blackwell, Oxford: 197-279.
- DARO, M.H. & P. POLK, 1973. The autecology of *Polydora ciliata* along the Belgian coast.—*Neth. J. Sea Res.* **6**: 130-140.
- DAUER, D.M. & W.G. CONNER, 1980. Effects of moderate sewage input on benthic polychaete populations.—*Estuar. Coast. Mar. Sci.* **10**: 335-346.
- DAUER, D.M., C.A. MAYBURY & R.M. EWING, 1981. Feeding behavior and general ecology of several spionid polychaetes from the Chesapeake Bay.—*J. exp. mar. Biol. Ecol.* **54**: 21-38.
- DORSETT, D.A., 1961. The reproduction and maintenance of *Polydora ciliata* (Johnston) at Whitstable.—*J. mar. biol. Ass. U.K.* **41**: 383-396.
- GARWOOD, P.R., 1982. The life-cycle and population dynamics of *Streptosyllis websteri* (Polychaeta: Syllidae) from a Northumberland beach.—*J. mar. biol. Ass. U.K.* **62**: 783-798.
- GRAF, G., W. BENGSSON, U. DIESNER, R. SCHULZ & H. THEEDE, 1982. Benthic response to sedimentation of a spring phytoplankton bloom: process and budget.—*Mar. Biol.* **67**: 201-208.
- GRASSLE, J.F. & J.P. GRASSLE, 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes.—*J. Mar. Res.* **32**: 253-284.
- GRAY, J.S., 1976. The fauna of the polluted river Tees estuary.—*Estuar. Coast. Mar. Sci.* **4**: 653-676.
- HANNERZ, L., 1956. Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil, and Poecilochaetidae n. fam. in the Gullmar Fjord (Sweden).—*Zool. Bidrag Uppsala* **31**: 1-204.
- HARTMANN-SCHRÖDER, G., 1971. Annelida, Borstenwürmer, Polychaeta.—*Tierwelt Deutschlands* **58**: 1-594.
- HEIP, C. & R. HERMAN, 1979. Production of *Nereis diversicolor* O.F. Müller (Polychaeta) in a shallow brackish-water pond.—*Estuar. Coast. Mar. Sci.* **8**: 297-305.
- HEMPEL, C., 1957a. Über den Röhrenbau und die Nahrungsaufnahme einiger Spioniden der deutschen Küsten.—*Helgoländer wiss. Meeresunters.* **6**: 100-135.
- , 1957b. Zur Ökologie einiger Spioniden der deutschen Küsten.—*Kieler Meeresforsch.* **13**: 275-288.
- HILL, M.O., 1979. TWINSPLAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Ecology and Systematics Section, Cornell University, Ithaca, New York: 1-90.
- HOWMILLER, R.P., 1972. Effects of preservatives on weights of some common macrobenthic invertebrates.—*Trans. Amer. Fish. Soc.* **101**: 743-746.
- KELDERMAN, P., J. NIEUWENHUIZE, A.M. MEERMAN-VAN DE REPE & J.M. VAN LIERE, 1984. Changes of sediment distribution patterns in Lake Grevelingen, an enclosed estuary in the SW Netherlands.—*Neth. J. Sea Res.* **18**: 273-285.
- KIRKEGAARD, J.B., 1971. Settling, growth and life span of some common polychaetes from Danish waters.—*Meddr Danm. Fisk.- og Havunders. N.S.* **7**: 447-496.
- KRISTENSEN, E., 1984. Life cycle, growth and production in estuarine populations of the polychaetes *Nereis virens* and *N. diversicolor*.—*Holarctic Ecol.* **7**: 249-256.
- LAMBECK, R.H.D., 1981. Effects of closure of the Grevelingen estuary on survival and development of macrozoobenthos. In: N.V. JONES & W.J. WOLFF. Feeding and survival strategies of estuarine organisms. Plenum Press, New York: 153-158.
- , 1984. Dynamics, migration and growth of *Nassarius reticulatus* (Mollusca: Prosobranchia) colonizing saline Lake Grevelingen (SW Netherlands).—*Neth. J. Sea Res.* **18**: 395-417.
- , 1985. Leven zonder getij.—*Natuur & Techniek* **53**: 916-931.
- LINDEBOOM, H.J., H.A.J. DE KLERK & A.J.J. SANDEE, 1984. Mineralization of organic carbon on and in the sediment of Lake Grevelingen.—*Neth. J. Sea Res.* **18**: 492-510.
- MICHAELIS, H., 1978. Zur Morphologie und Ökologie von *Polydora ciliata* und *P. ligni* (Polychaeta, Spionidae).—*Helgoländer wiss. Meeresunters.* **31**: 102-116.
- MÖLLER, P., 1985. Production and abundance of juvenile *Nereis diversicolor*, and oogenetic cycle of adults in shallow waters of western Sweden.—*J. mar. biol. Ass. U.K.* **65**: 603-616.
- MUSTAQIM, J., 1986. Morphological variation in *Polydora ciliata* complex (Polychaeta: Annelida).—*Zool. J. Linn. Soc.* **86**: 75-88.
- MUUS, B.J., 1967. The fauna of Danish estuaries and lagoons.—*Meddr Danm. Fisk.- og Havunders. N.S.* **5**: 1-316.
- NEWELL, R.I.E. & B.L. BAYNE, 1980. Seasonal variation in the physiology, reproductive condition and carbohydrate content of the cockle *Cardium* (= *Cerastoderma*) *edule* (Bivalvia: Cardidae).—*Mar. Biol.* **56**: 11-19.
- NIENHUIS, P.H. & B.H.H. DE BREE, 1984. Carbon fixation and chlorophyll in bottom sediments of brackish Lake Grevelingen, The Netherlands.—*Neth. J. Sea Research.* **18**: 337-359.
- OYENKAM, J.A., 1983. Production and population dynamics of *Capitella capitata*.—*Arch. Hydrobiol.* **98**: 115-126.
- PRICE, R. & R.W. WARWICK, 1980. Temporal variation in annual production and biomass in estuarine population of two polychaetes, *Nephtys hombergii* and *Ampharete acutifrons*.—*J. mar. biol. Ass. U.K.* **60**: 481-487.

- RAMBERG, P. & T.A. SCHRAM, 1983. A systematic review of the Oslofjord species of *Polydora* Bosc. and *Pseudopolydora* Czerniawsky with some new biological and ecological data (Polychaeta: Spionidae).—*Sarsia* **68**: 233-247.
- RASMUSSEN, E., 1973. Systematics and ecology of the Isefjord marine fauna (Denmark).—*Ophelia* **11**: 1-507.
- REISE, K., 1978. Experiments on epibenthic predation in the Wadden Sea.—*Helgoländer wiss. Meeresunters.* **31**: 55-101.
- RICE, S.A. & J.L. SIMON, 1980. Intraspecific variation in the pollution indicator polychaete *Polydora ligni* (Spionidae).—*Ophelia* **19**: 79-115.
- ROBERTSEN, A.I., 1979. The relationship between annual production: biomass ratios and lifespans for marine macrobenthos.—*Oecologia* **38**: 193-202.
- ROGAL, U., K. ANGER, G. SCHRIEVER & C. VALENTIN, 1978. In-situ investigations on small-scale local and short-term changes of sublittoral macrobenthos in Lübeck Bay (western Baltic Sea).—*Helgoländer wiss. Meeresunters.* **31**: 303-313.
- SMIDT, E.L.B., 1951. Annual production in the Wadden Sea.—*Meddr Danm. Fisk. -og Havunders. Ser. Fisk.* **11**: 1-151.
- TAGHON, G.L., A.R.M. NOWELL & P.A. JUMARS, 1980. Induction of suspension feeding in spionid polychaetes by high particulate fluxes.—*Science* **210**: 562-564.
- VEGTER, F. & P.R.M. DE VISSCHER, 1984. Phytoplankton primary production in brackish Lake Grevelingen (SW Netherlands) during 1976-1981.—*Neth. J. Sea Res.* **18**: 246-259.
- VERHAGEN, J.A., 1983. A distribution and population model of the mussel *Mytilus edulis* in Lake Grevelingen. In: W.K. LAUENROTH, G.V. SKOGERBOE & M. FLUG. Analysis of ecological systems: state-of-the-art in ecological modelling. Elsevier, Amsterdam: 373-383.
- VOLCKAERT, F., 1979. Oecologische studie van de meiobenthische polychaetenfauna van de Grevelingen (Nederland). Licentiaatsverhandeling Rijksuniversiteit Gent (Belgium): 1-96.
- VRIES, I. DE, 1984. The carbon balance of a saline lake (Lake Grevelingen, The Netherlands).—*Neth. J. Sea Res.* **18**: 511-528.
- WARWICK, R.M., C.L. GEORGE & J.R. DAVIES, 1978. Annual macrofauna production in a *Venus* community.—*Estuar. Coast. Mar. Sci.* **7**: 215-241.
- WARWICK, R.M. & R. PRICE, 1975. Macrofauna production in an estuarine mud-flat.—*J. mar. biol. Ass. U.K.* **55**: 1-18.
- WEINBERG, J.R., 1984. Interactions between functional groups in soft-substrata: do species differences matter?—*J. exp. mar. Biol. Ecol.* **80**: 11-28.
- WHITLACH, R.B. & R.N. ZAJAC, 1985. Biotic interactions among estuarine infaunal opportunistic species.—*Mar. Ecol. Progr. Ser.* **21**: 299-311.
- WOLFF, W.J., 1973. The estuary as a habitat.—*Zool. Verhand. (Leiden)* **126**: 1-242.
- WOLFF, W.J. & L. DE WOLF, 1977. Biomass and production of zoobenthos in the Grevelingen Estuary, The Netherlands.—*Estuar. Coast. Mar. Sci.* **5**: 1-24.
- WOLFF, W.J., A.J.J. SANDEE & L. DE WOLF, 1977. The development of a benthic ecosystem.—*Hydrobiologia* **52**: 107-115.
- ZAJAC, R.N. & R.B. WHITLACH, 1982. Responses of estuarine fauna to disturbance. I. Spatial and temporal variation of initial recolonization.—*Mar. Ecol. Progr. Ser.* **10**: 1-14.

(received 21-11-1986, revised 18-3-1987)