NUMBERS, GROWTH, BIOMASS AND PRODUCTION OF ORGANIC AND CALCAREOUS MATTER OF HYDROBIA ULVAE (GASTROPODA: PROSOBRANCHIA) IN THE WESTERN DUTCH WADDEN SEA

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NUMBERS, GROWTH, BIOMASS AND PRODUCTION OF ORGANIC AND CALCAREOUS MATTER OF HYDROBIA ULVAE (GASTROPODA: PROSOBRANCHIA) IN THE WESTERN DUTCH WADDEN SEA*

door

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CONTENTS

I. SUMMARY

In the Western Dutch Wadden Sea, populations of *Hydrobia ulvae* (Pennant) at two tidal flat areas, the Mok and Balgzand, were observed during the period March-October 1978. Data on population density, growth, biomass and production of organic

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and calcareous matter were collected. A method to separate the soft parts of the animals from the shells is described.

At the Mok station, *H. ulvae* reached a maximum age of 1 year and 2 months, while at the Balgzand the maximum age was 2½ years. At the Mok the animals reached a density of about 180,000 individuals/m^2, an estimated average annual biomass of the soft parts of 8.4 g/m^2 ash free dry weight(ADW), a production of organic matter of about 35.5 g/m^2/yr of soft parts, 3.9 g/m^2/yr of conchine and 0.5 g/m^2/yr of egg-capsules, a production of calcareous matter of 120.3 g/m^2/yr and a P/B-ratio of 4.5 for the O-group and 1.1 for the I-group. At the Balgzand-location the situation was more complex, because of the absence of spatfall at the sampling stations and the almost continuous arrival of 1 year old animals. The maximum density, reached by October, amounted to 16,500 individuals/m^2. The average annual biomass of the soft parts along a transect of 4 stations was estimated at 2.8 g/m^2 ADW. The production of soft parts was about 2.0 g/m^2/yr, of conchine 0.4 g/m^2/yr, of egg-capsules 0.6 g/m^2/yr, and the production of calcareous matter was about 10.8 g/m^2/yr. The P/B-ratio was 0.7 for both the I-group and the II-group. The possible influences of migration, availability of food and sediment properties on polulation composition, spatfall and densities are discussed.

II. INTRODUCTION

Hydrobia ulvae (Pennant 1777), a small prosobranch mollusc, is common on the higher and more or less silty tidal flats of the Dutch Wadden Sea. With an average density of 866 individuals/m^2 (BEUKEMA, 1976), it is one of the most numerous macrobenthic animals in the Dutch Wadden Sea. However, due to the low individual weights, its share in the total quantity of biomass of benthic invertebrates of the Wadden Sea will be only minor.

So far, biomass nor production of *H. ulvae* have been estimated for the Wadden Sea. In the past, data published by BEUKEMA on biomass of *H. ulvae* in the Dutch Wadden Sea were only approximations, as they were based on the assumption that the average individual weight of the soft parts would be about 0.2 mg ash-free dryweight (BEUKEMA, pers. comm.). In the whole Western Dutch Wadden Sea the average biomass of *H. ulvae* , as estimated in this way, showed an increase from 0.2 g/m^2ADW in 1971/1972 to 0.5 g/m ADW in 1977 (BEUKEMA et al. 1978).

Individual weights are difficult to determine, for there are no easy methods to separate the soft parts of the animal from the shell. The shells are covered with a periostracum, a thin conchinous layer. This layer of organic matter has no part in the weight of organic matter of the soft parts of the animal.

Outside the Wadden Sea, data on biomass and production of *H. ulvae* are available from the Grevelingen estuary in the Netherlands (WOLFF & DE WOLF, 1977) and from the Firth of Forth in Scotland (ELLIOTT, 1977, cited from MCLUSKY & BERRY, 1977, p. 203). At the Grevelingen estuary WOLFF & DE WOLF found average annual biomass values ranging from 4.06 g/m^2 to 9.37 g/m^2 ADW, and annual productions ranging from 7.23 $g/m^2/yr$ to 12.79 $g/m^2/yr$. P/B-ratios varied between 1.24 and 1.78. ELLIOTT, at the Firth of Forth, found an annual average biomass of 2.328 g/m^2 ADW, an annual production of 5.99 $g/m^2/yr$, and a corresponding P/B-ratio of 2.57. The values for the average individual weight (soft parts + organic shell material) at the end of the growing season, given by WOLFF & DE WOLF, are about 0.3 mg ADW for the 0-year animals and about 0.8 mg for the 1-year animals. It is likely, that the approximations of BEUKEMA (0.2 mgADW for the soft parts) for the average individual weight is an underestimation. A method to separate soft parts from the shell is developed, to obtain a separate estimate of the weight of the soft parts.

The main purpose of this investigation was to estimate the annual biomass and production of organic and calcareous matter on the basis of a detailed study of some populations of *Hydrobia ulvae* in the Western Dutch Wadden Sea

III. METHODS

Two sampling locations were chosen: one station on a tidal flat at the Mok, a bay in the southernmost part of the Island of Texel, and 4 stations along a transect at Balgzand, a tidal flat area south-east of Den Helder (Fig. 1). Station 1 was at a distance of 200 m from the mainland, station 2, 3 and 4 were at 600 m, 800 m and 1000 m, respectively. This transect is identical to a transect used by BEUKEMA for his macrobenthos investigations (BEUKEMA, 1974: transect 6 in Fig. 1). Some characteristics of the sampling stations are given in Table I. The periods of immersion were obtained by determining the levels of the stations at a soundings-map, and plotting these values at a graph of the tide-curve of Den Helder. For sediment characteristics samples of the upper 1 cm of the sediment were taken. In the laboratory these samples were silted off until clear supernatants were obtained. The silt fractions and sand fractions were dried and weighed, and from the sand fractions median grain sizes were determined.

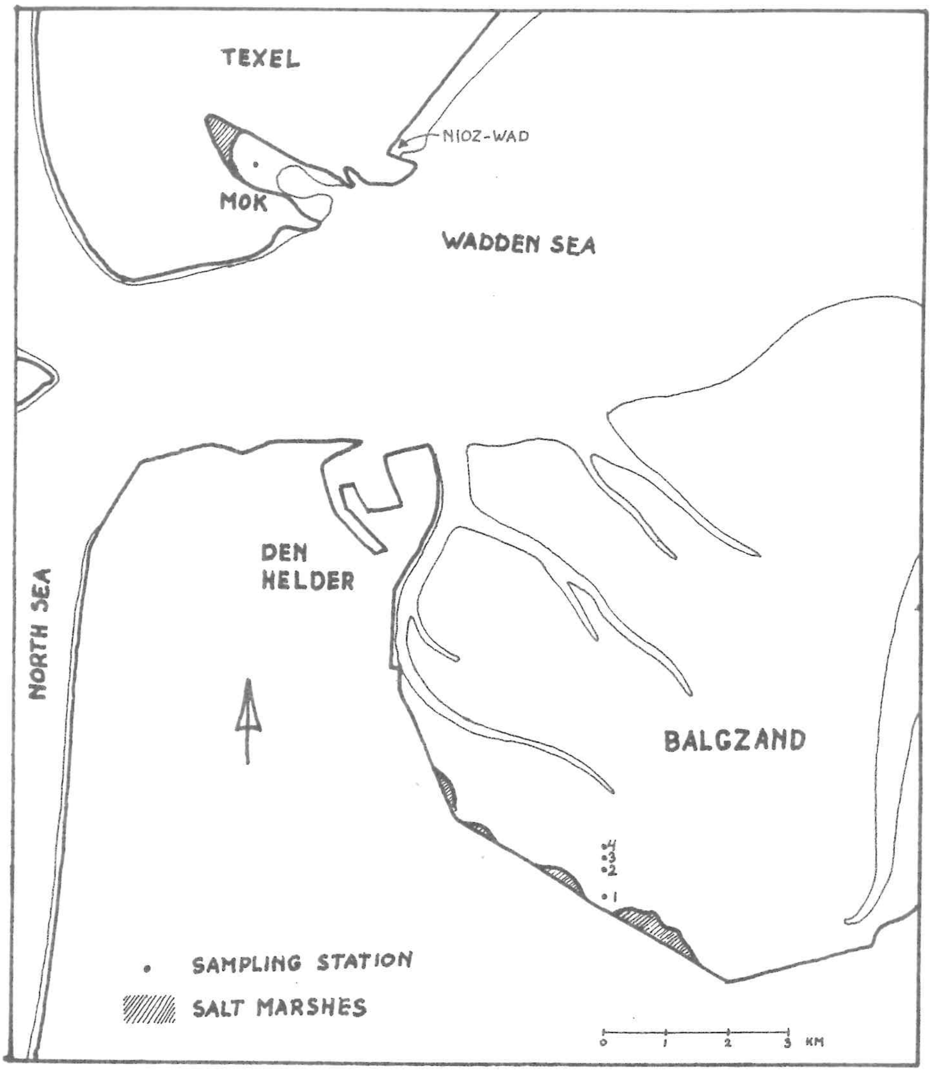

Fig. 1. Map of the south-westernmost part of the Dutch Wadden Sea. The spots denote the sampling stations.

Table I

Sediment characteristics and tidal heights of the Mok station and the Balgzand stations.

Station	Mok	Bz 1	Bz 2	Bz 3	Bz 4
Period of immersion	66 %	46 %	50 %	52 %	55 %
Silt content	60.9 %	43.3 %	25.3 %	15.8 %	11.5 %
Median grain size	145 μ	110 μ	135 μ	145 μ	160 μ

Samples were obtained by means of circular PVC-cores covering areas of 27 cm^2 and 90 cm^2, depending on the density of *H. ulvae* at the sampling stations. Sampling depth was approximately 3 cm. At the Mok location each sample consisted of 20 subsamples, while at the Balgzand location, for practical reasons, each sample consisted of only 6 subsamples. The sampling period lasted from March 1978 up to and including October 1978. Samples were taken once per month.

Samples were taken to the laboratory and washed there over 1000 μ and 300 μ mesh sieves. Egg-capsules, when present on the shells, were removed, counted and collected for biomass determination. The snails were counted and divided into length-classes. In nearly all samples year-classes could be separated from the frequency distributions of lengths. Especially in spring and early summer, a growth-ring could be observed between the newly grown parts of the shell with an unaffected periostractum and the elder weathered parts of the shell. Lateron, this ring became indistinct, as also the new parts of the periostractum became affected. Moreover, in many cases the whole shell became overgrown with a thin layer of green algae.

The snails of each length-class were divided into two groups: one group was dried for total organic weight determination, the animals of the other group were squashed with a pestle and put into a beakerglass containing a solution of the enzym collagenase (Sigma C-6885 Collagenase Type II) in order to separate the soft parts of the animals from the shells. After a 24 hour period in a 35 °C water bath, the soft-part remnants were removed by decantation until a clear supernatant was obtained. The clean shell fragments, which contained only calcareous matter and organic matter in the form of nearly undigestible conchine, were also dried for weight determinations. The snails and shells were dried during 3-4 days at 60 °C in a well-ventilated stove, weighed, placed in an incinerator for 2 hours at 450 °C (higher temperatures were avoided to prevent loss of calcareous matter) and weighed again. The weight loss at incineration was considered to be the ash-free dry weight and was used as a measure for organic matter. The difference between the total individual organic weight and the individual organic weight of the shell of each length-class was considered to be the individual organic weight of the soft parts. Biomass of the egg-capsules was obtained in the same way.

Numbers of snails per m^2 (N_i) and average weights ($\bar{W}_i$) of individuals of each year-class on each date i were plotted on on graphs, and from these graphs the biomass (B = N x W) and production (P) per m^2 per year were calculated as described by CRISP (1971). Because of the complex situation at Balgzand, where numbers of *H. ulvae* almost continuously increased, the usual production-formula (CRISP, 1971) had to be modified. The formula used for the present production-calculations is based on two items: 1) at the beginning of the sampling period of each year-class N_1 animals were present with an average individual weight W_1. At the end of the growing season (i = n) these originally present animals will have produced $(\bar{W}_n - \bar{W}_1) \times N_1$ g/m^2. It is assumed that their growth rates equaled those of the immigrants, and that their death rate was negligible; 2) the animals arriving at the stations later in the year of course produced less than $\bar{W}_n - \bar{W}_1$ each. It is assumed that the animals that arrived between two sampling dates, had a mean individual weight equal to the average of the individual mean weights at these two sampling dates. The number of snails arriving during that period was $N_{i+1} - N_i$ with an average individual weight of $\frac{1}{2}(\bar{W}_{i+1} + \bar{W}_i)$. The contributions of these immigrants to the production of the sampling station will have been:

$$\sum_{i=1}^{n} \left[(N_{i+1} - N_i) \times \left\{ \bar{W}_n - \tfrac{1}{2} (\bar{W}_{i+1} + \bar{W}_i) \right\} \right].$$

The total production, therefore, amounts to:

$$P = \sum_{y=1}^{m} \left[(\bar{W}_n - \bar{W}_1) \times N_1 + \sum_{i=1}^{n} \left\{ (N_{i+1} - N_i) \times \left[\bar{W}_n - \tfrac{1}{2}(\bar{W}_{i+1} + \bar{W}_i) \right] \right\} \right]$$

The sum of the productions of year-classes (y=0,1,..,m) equals the total annual production. The share of the originally present population will have been overestimated (as they will have shown some mortality), but that of the immigrants is an underestimation, because $(N_{i+1} - N_i)$ is in fact the net result of immigration minus mortality and the animals that died between two sampling dates will have had a positive production during that period. It is assumed that both biases cancel each other.

Besides calculations on biomass and production of digestible organic matter, calculations are made on production of calcareous matter of the shell. The same formula as mentioned above is used, on the understanding that $\bar{W}_i$ and $\bar{W}_n$ are shell-weights.

IV. RESULTS

a. Population composition

1. At station "Mok"

The numerical densities of *H. ulvae* observed during 1978 at the Mok were highly variable (Fig. 2). In springtime only 1-year old animals were present (Fig. 3). Their shell-heights did not exceed 4 mm. Egg-capsule production was already found in March, and reached its maximum during May. After the reproduction period most of the 1-year animals disappeared. During

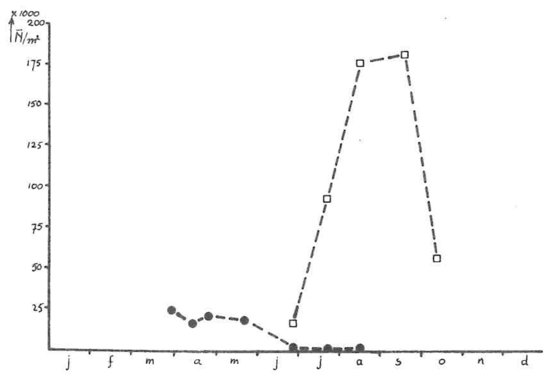

Fig. 2. Average numbers of individuals per m^2 observed during 1978 at the Mok station, belonging to the year-classes born in 1977 (●) and 1978 (□).

late June and July spat settled on the tidal flats in tremendous densities, upto about 180,000 individuals per m^2. By October a dramatic decrease of numbers occurred, probably due to predation by migratory birds, mainly Shelduck (*Tadorna tadorna*), as bird-faeces contained lots of *Hydrobia* shell-fragments at the Mok location.

By October, the average shell-height of 0-year animals was nearly equal to that of the 1-year animals observed in March (Fig. 3). Thus, there will be no growth during the winter-period between October and March.

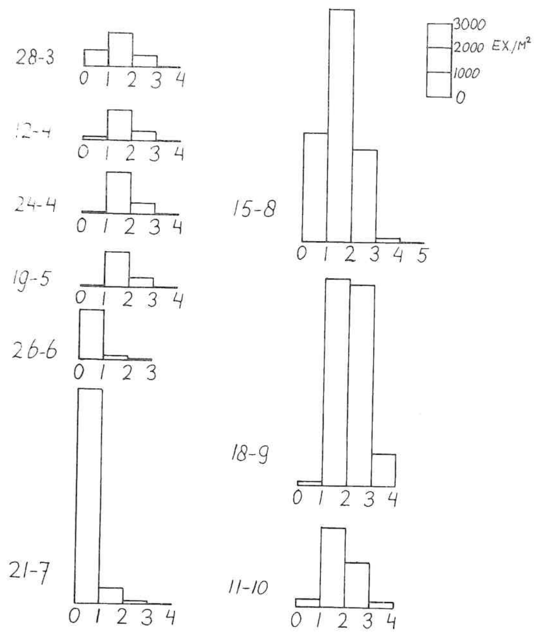

Fig. 3. Length frequency distributionsobserved at 9 dates during 1978 at the Mok station.

2. At the Balgzand stations

Numbers per m^2 of *H. ulvae* at the 4 Balgzand stations generally increased gradually during 1978 (Fig. 4). The division into length-classes (Fig. 5) shows the age distribution. The numbers were dominated by 1-year old animals (yearclass-1977). They increased consistently at most sampling stations (except at station 2) during the growing season. Undoubtedly, immigration was responsible for this phenomenon. Even more remarkable is the time at which and the numbers in which the spat (ycl-1978) appeared at the Balgzand locations. In spite of the large numbers of egg-capsules, produced during springtime (see below), no settlement was observed during late June and July. Not before August the first juvenile animals appeared, having already a length of about 1 mm. The numbers of these juveniles

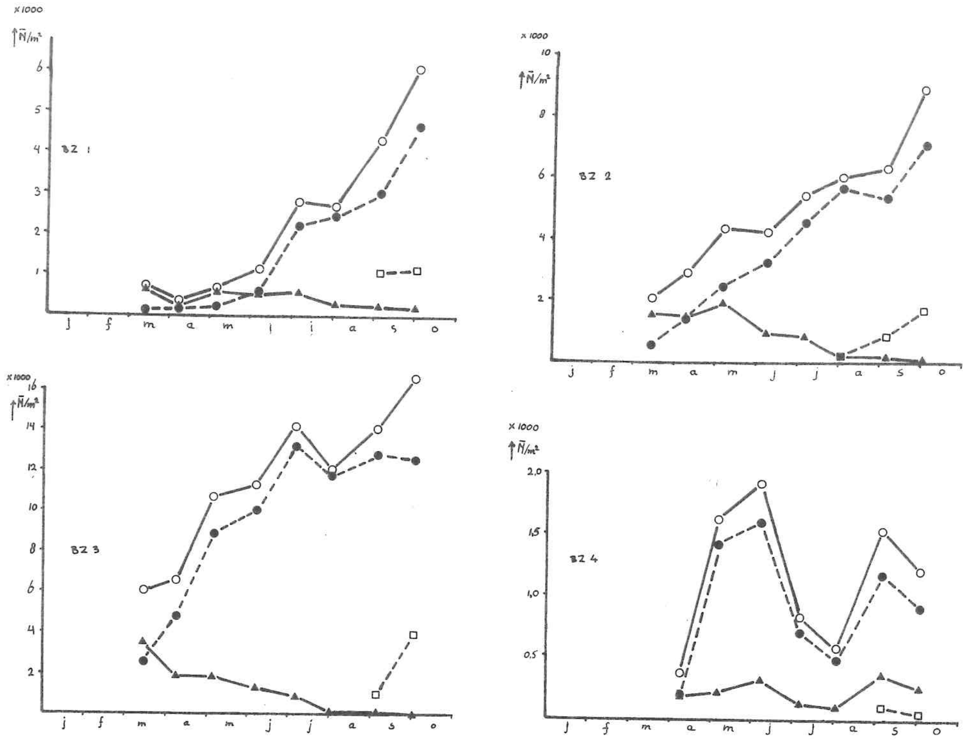

Fig. 4. Average numbers of individuals per m^2 observed during 1978 at 4 Balgzand stations, belonging to the year-classes born in 1976 (▲), 1977 (●) and 1978 (□). Totals indicated by (O).

were low and increased only slowly.

Numbers of 2-year animals (ycl-1976) showed a steady decrease until they were nearly extinct in late summer and autumn. The 2-year animals attained a shell-height of maximally 9 mm. In many cases animals of 6 mm height and more showed shells with more swollen and irregular whorls than normal type *H. ulvae* does. These differences in growth may be caused by infection with cercariae, i.e. larval Trematodes (ROTHSCHILD, 1936). These cercariae affect and finally destroy the gonads, so that no energy is used for reproduction, but only for growth.

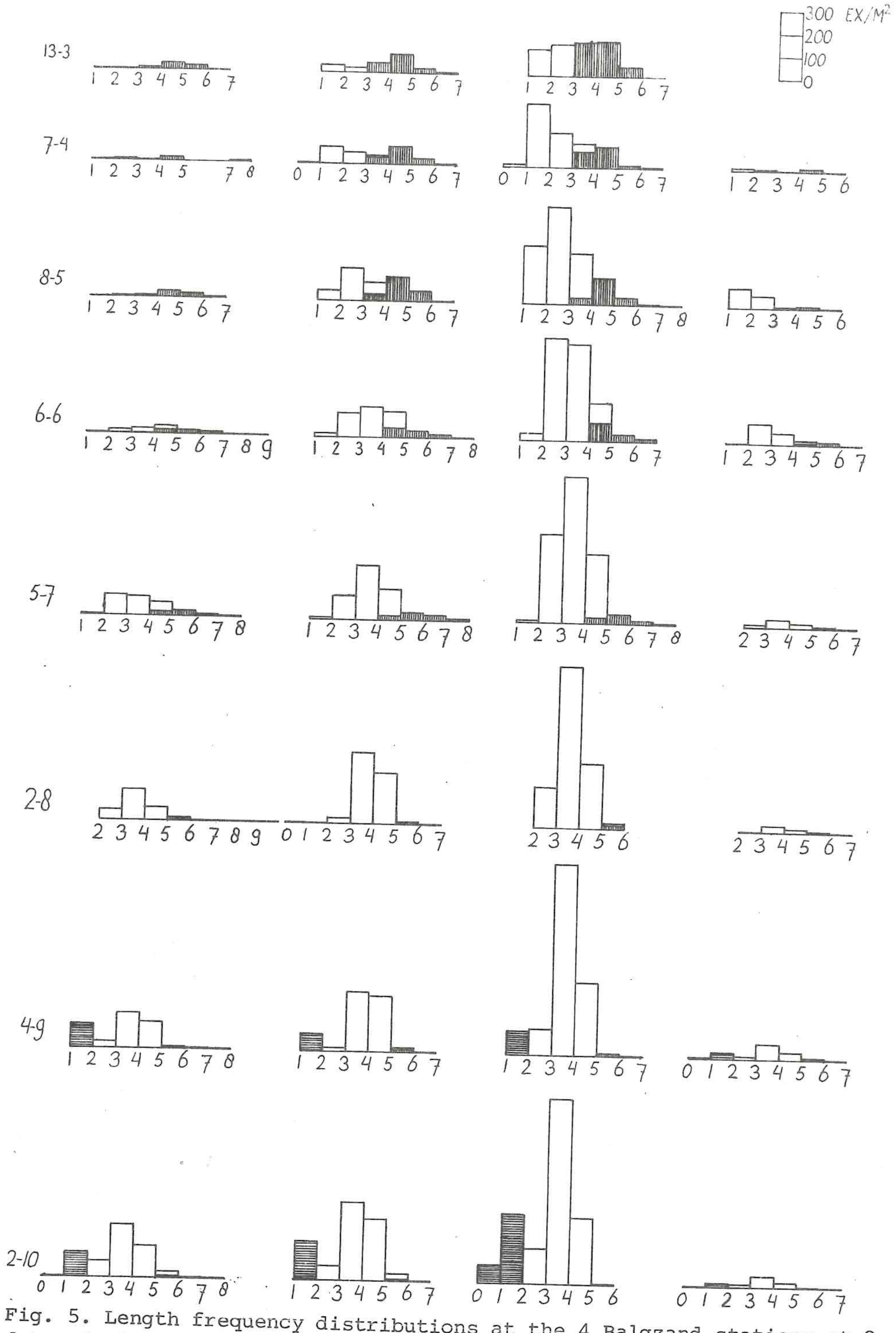

Fig. 5. Length frequency distributions at the 4 Balgzand stations at 8 dates during 1978.

b. Individual weights

1. Organic matter

Figure 6 showes the individual increases of weight of organic matter included in the soft parts of the animals of every year-class present at the sampling stations. At the Mok, 0-year animals showed an average growth of about 0.2 mg, while the 1-year animals showed a growth of about 0.3 mg. The share of the organic matter of the shell was only about 10 % of the total organic matter. This percentage was nearly constant for all length-classes at the Mok. At the Balgzand stations the situation was very different. The 0-year animals showed hardly any growth because of their late arrival; the 1-year animals produced about 0.4 mg per individual, and the 2-year animals showed a weight grain of soft parts of about 0.7 mg. The latter is only a rough estimate because of the capricious courses of the graphs for the 2-year animals at the 4 Balgzand stations. At these stations the share of the conchine to the total individual organic weight was about 15 % for all length-classes.

2. Shell lime

The average individual weights of calcareous matter of the shells at the Mok and Balgzand were based on weight determinations of calcareous matter on October 11th at the Mok and July 5th and October 2th at Balgzand (Table II). It is assumed that there was a constant relation between shell-height and weight of calcareous matter throughout the year.

At the Mok, 1-year animals added about 1.5 mg to their individual weight during the growing season, and the 0-year animals about 0.5 mg (Fig. 7). At Balgzand 1-year animals added about 2 mg, and 2-year animals about 4 mg to their

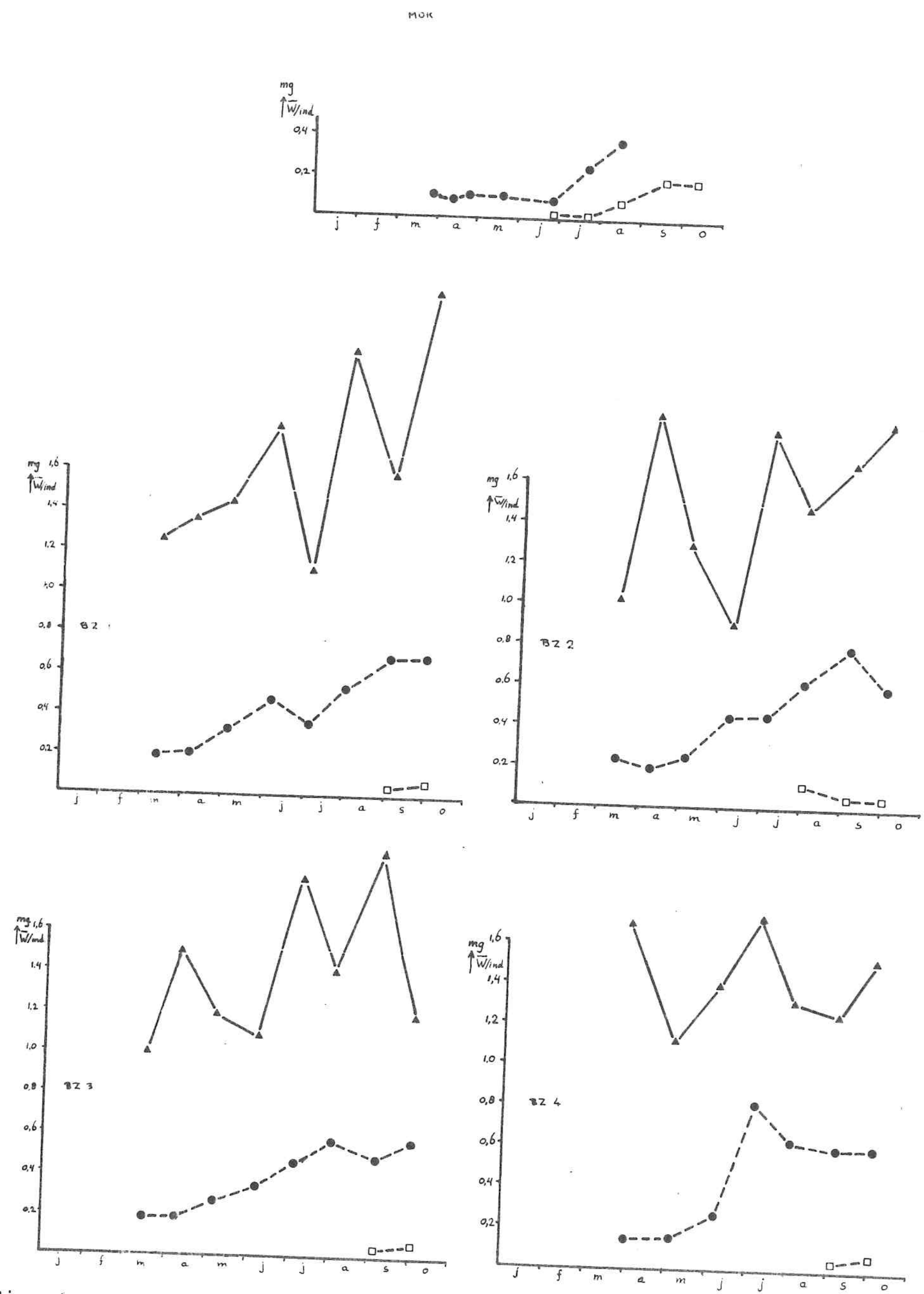

Fig. 6. Mean individual weights of soft parts (in mg ash-free dry weight) at the Mok and at the 4 Balgzand stations, observed during 1978 for *Hydrobia* belonging to the various year-classes (animals born in 1976: ▲, in 1977: ● and in 1978: □).

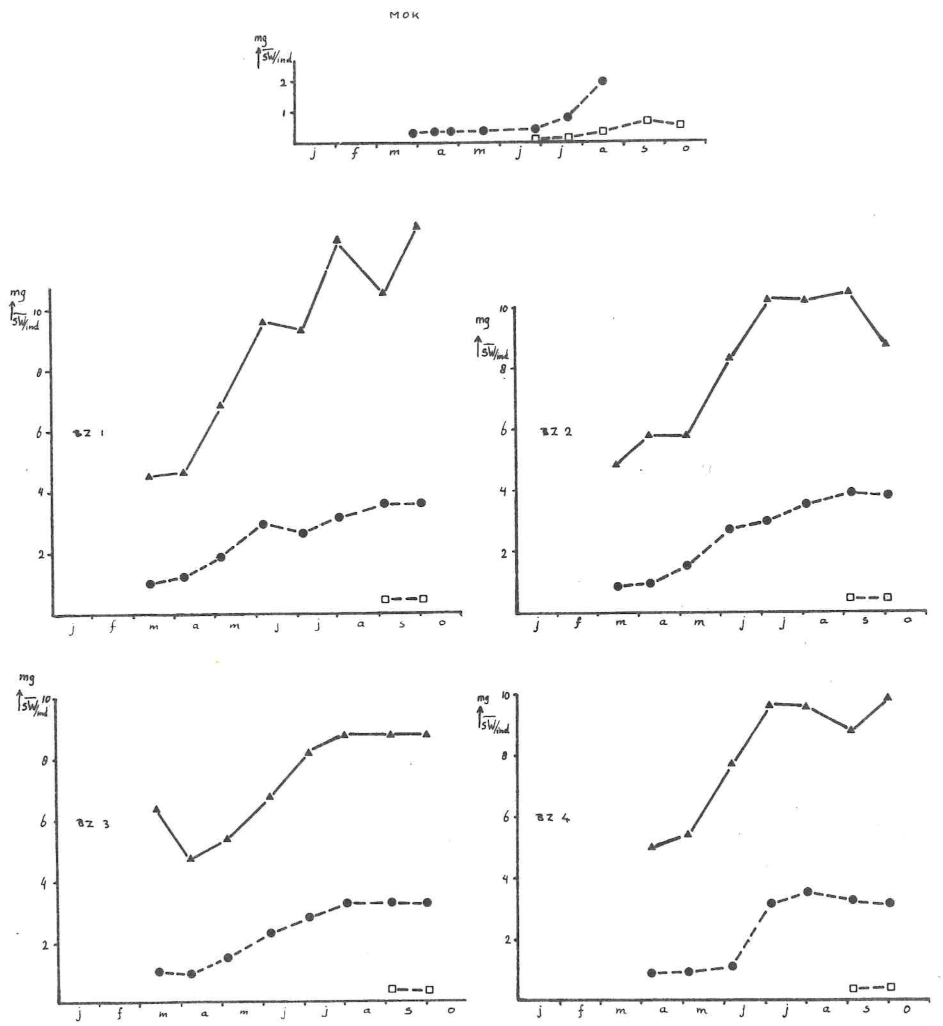

Fig. 7. Mean individuals weights of shells (in mg calcareous matter) at the Mok and at the 4 Balgzand stations, observed during 1978. Symbols as in Fig. 6.

average individual weight of calcareous matter.

Organic shell matter amounted to only about 3 % of total shell weight at all places.

Table II

Average individual weights of calcareous matter of the shells in mg at Balgzand (dates 5-7 and 2-10) and at the Mok (date 11-10).

Shell-height (mm)	Balgzand	Mok
0-1		0.106
1-2	0.420	0.249
2-3	1.512	0.891
3-4	2.779	1.954
4-5	5.072	
5-6	8.724	
6-7	13.042	
7-8	18.871	

c. Egg-capsule production

Hydrobia ulvae deposits its egg-capsules on firm substrates as shell, stones etc. It shows a preference for laying egg-capsules on shells of living individuals of the own species (FISH & FISH, 1974). At the Mok and Balgzand stations there were hardly any firm objects in the upper 1 cm of the sediment. Therefore,the egg-capsules present on live *H. ulvae* shells were considered to be all the egg-capsules deposited during the preceding 16 days. The time for development of the eggs to veliger larvae is about 16 days (PILKINGTON, 1971). At hatching time the egg-capsules (consisting of sand grains and mucus) are already partially affected by bacteria, so the veliger larvae easily can leave the capsules. After that the capsules soon decay entirely by bacterial activity. The numbers of egg-capsules observed during the sampling period are shown in Fig. 8. The estimated total numbers of egg-capsules produced are listed in Table III.

The average weight of an individual egg-capsule at the Mok and at Balgzand was 17.3 µg ADW. The total production in

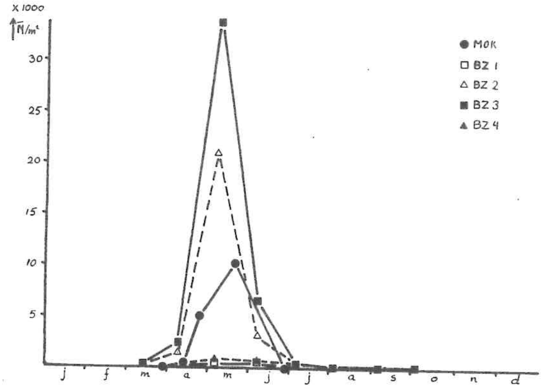

Fig. 8. Mean numbers of egg-capsules observed per m^2 at the various sampling stations during spring 1978.

the form of egg-capsules was calculated from the total number per m^2 x 17.3 µg and listed in Table III. The average production at the whole Balgzand transection in the form of capsules was estimated at 0.574 g/m^2/yr.

Table III

Estimated total numbers (in 1000 per m^2) of egg-capsules deposited, maximal number of veligers hatched (ANDERSON, 1971) and production of organic matter (ADW) of the egg-capsules.

Station	Mok	Bz 1	Bz 2	Bz 3	Bz 4
Capsules	27	2	51	85	3
Veligers	207	17	395	666	24
Production (g/m^2/yr)	0.458	0.035	0.873	1.476	0.054

d. Biomass

The courses of the biomass values for the soft parts (Fig. 9 for Mok and Fig. 10 for Balgzand) show much similarity with those of the numbers (Fig. 2 and 4, respectively). Of course, the older year-classes have a relatively greater share in the total biomass of each station. Average biomass values for the

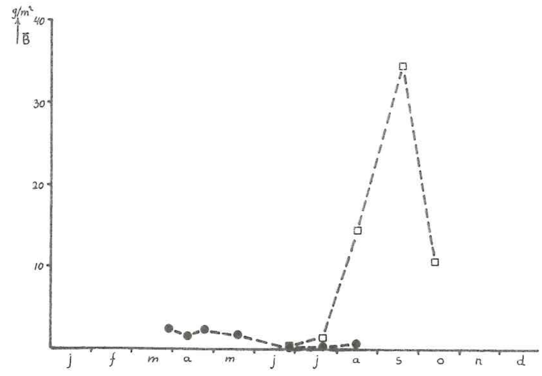

Fig. 9. Average values for biomass (in g ash-free dry weight per m^2) of soft parts of *Hydrobia* observed at the Mok station in the course of 1978. Symbols as in Fig. 2.

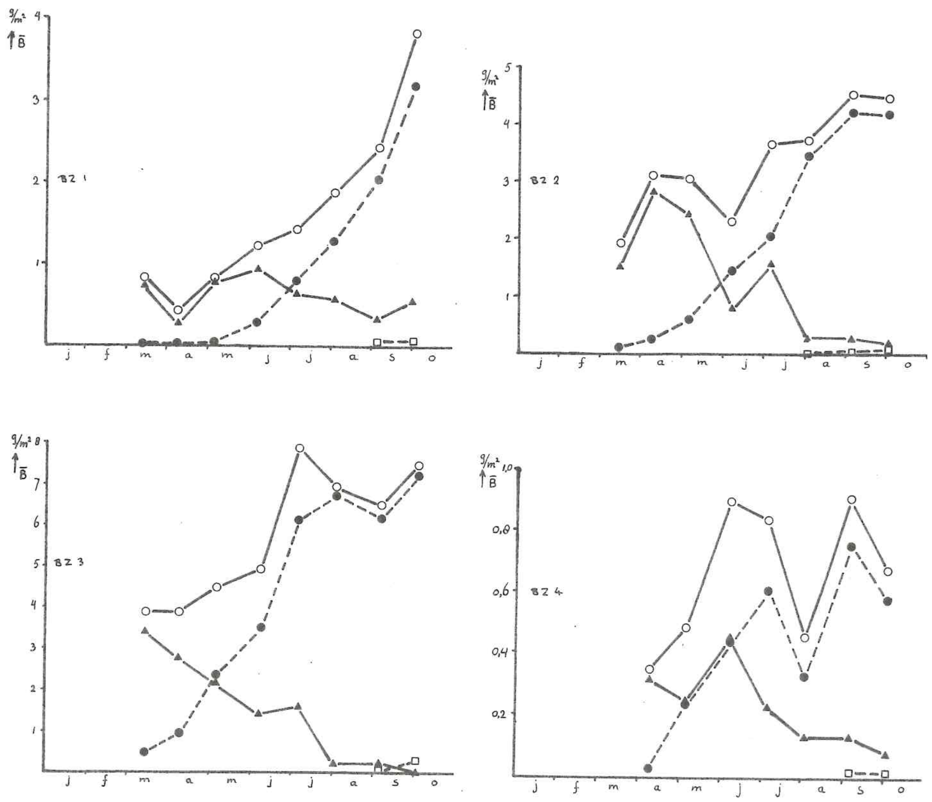

Fig. 10. Average values for biomass (in g ash-free dry weight per m^2) of soft parts of *Hydrobia* observed at the 4 Balgzand stations in the course of 1978. Symbols as in Fig. 4.

whole year were obtained by estimating roughly the course of the winter values of the biomass at each station, supposing that there is a considerable decrease in numbers and biomass during October and November, viz. to the same level as that of the foregoing year-class observed in spring. The annual values are listed in Table IV. The average annual biomass of the whole Balgzand transect is estimated at 2.534 g/m^2.

Due to the extremely high numbers of young *Hydrobia* at the Mok (Fig. 2: hundred thousands per m^2), biomass at this station reached tens of grams per m^2 (Fig. 9) with an annual average of 8.390 g/m^2 (Table IV).

Table IV

Biomass, production of organic and calcareous matter and P/B-ratios at at the Mok and Balgzand (biomass in g/m^2, production in $g/m^2/yr$).

		Mok	Bz 1	Bz 2	Bz 3	Bz 4	Bz (mean)
Soft parts							
av. biomass	ycl 76	-	0.409	0.765	0.867	0.139	0.553
"	ycl 77	0.683	1.253	2.194	4.146	0.335	1.930
"	ycl 78	7.707	0.046	0.084	0.028	0.015	0.048
"	total	8.390	1.689	3.008	5.126	0.483	2.534
production	ycl 76	-	0.485	0.465	0.364	<0.1	0.358
"	ycl 77	0.723	0.745	1.592	4.084	0.374	1.593
"	ycl 78	34.739	0.026	<0.01	0.020	0.008	0.013
"	total	35.462	1.259	2.057	4.468	0.382	1.965
P/B-ratio	ycl 76	-	1.185	0.608	0.420	-	0.647
"	ycl 77	1.059	0.594	0.726	0.985	1.118	0.825
"	ycl 78	4.507	-	<0.01	0.706	0.497	0.271
Conchine							
production	total	3.940	0.222	0.363	0.788	0.067	0.347
Calcareous matter							
production	ycl 76	-	2.652	6.294	2.922	<0.1	3.268
"	ycl 77	2.453	2.504	10.525	21.815	1.980	8.668
"	ycl 78	117.878	0.109	<0.1	0.111	0.042	0.063
"	total	120.331	5.265	16.819	24.848	2.022	11.999
Egg-capsules							
production	total	0.458	0.035	0.873	1.476	0.054	0.578

e. Production of organic matter

The production of soft parts at the Mok location was almost limited to the yearclass born in 1978. A minimal estimate for the production of ycl. '78 will be the maximal amount of organic matter present in September, i.e. 34.7 g/m^2. The production of ycl. '77 is estimated at only 0.7 $g/m^2/yr$. The total production, thus, was at least 35.5 $g/m^2/yr$ (Table IV). This is an underestimation of the total production, as the production of animals that died before September should be added.

At the Balgzand stations the production of soft parts was calculated with the formula as mentioned on page 8. The average production for the whole Balgzand transect was estimated at almost 2 $g/m^2/yr$. Detailed production data are shown in Table IV.

The production of conchine at the Mok is estimated at 10 % of the total production of organic matter. At the Balgzand stations this percentage of the total production was 15 %. Detailed data on conchine production are listed in Table IV. The estimated conchine production at the whole Balgzand transect is estimated at 0.35 $g/m^2/yr$.

f. Production of calcareous matter

Total production of calcareous shell parts and the production for the various year-classes are listed in Table IV. The average production of calcareous matter at the whole Balgzand transect is estimated at 12 $g/m^2/yr$.

g. P/B-ratios

The P/B-ratios of all sampling stations, separated into year-classes, are given in Table IV. The highest P/B-ratio is found at the Mok, where the maximum age of *H. ulvae* is only a little more than one year. The average P/B-ratio at the whole Balgzand transect is only 0.7, due to the high share of old animals. This is an underestimate for the population value, as the major part of P has been produced in other area's at a low value of B.

V. DISCUSSION

a. Population dynamics and migration

Several authors who investigated population of *Hydrobia ulvae* give data for maximum age in different areas. CHATFIELD (1972) states a maximum age of 1 year and 3 months for animals on tidal flats and 2 years for animals on salt marshes. WOLFF & DE WOLF (1977) give for various tidal stations slightly more than 1 year and nearly 2 years, while FISH & FISH (1974) give maximum ages of 2½-3 years. My own observations are within this range: 1 year and 2 months for animals at the Mok station, and 2½ years for the Balgzand animals.

The population density of *H. ulvae* at the Balgzand location does not show great differences with other data from the Dutch coast (BEUKEMA, 1976; WOLFF & DE WOLF, 1977). However, the population density of the animals at the Mok is extremely high and similar only to data from ANDERSON (1971) from the Ythan estuary (50.000 per m^2).

Data collected by BEUKEMA at the same transect at Balgzand as used for this investigation, showed consistently lower density values, probably as a consequence of incomplete countings (Fig. 11). Especially during summer (early September), when *H. ulvae* are small, BEUKEMA will have underestimated the numbers in his samples (Fig. 11b).

Both in my and BEUKEMA's data lowest densities were observed at the start and the end of the transect. The location

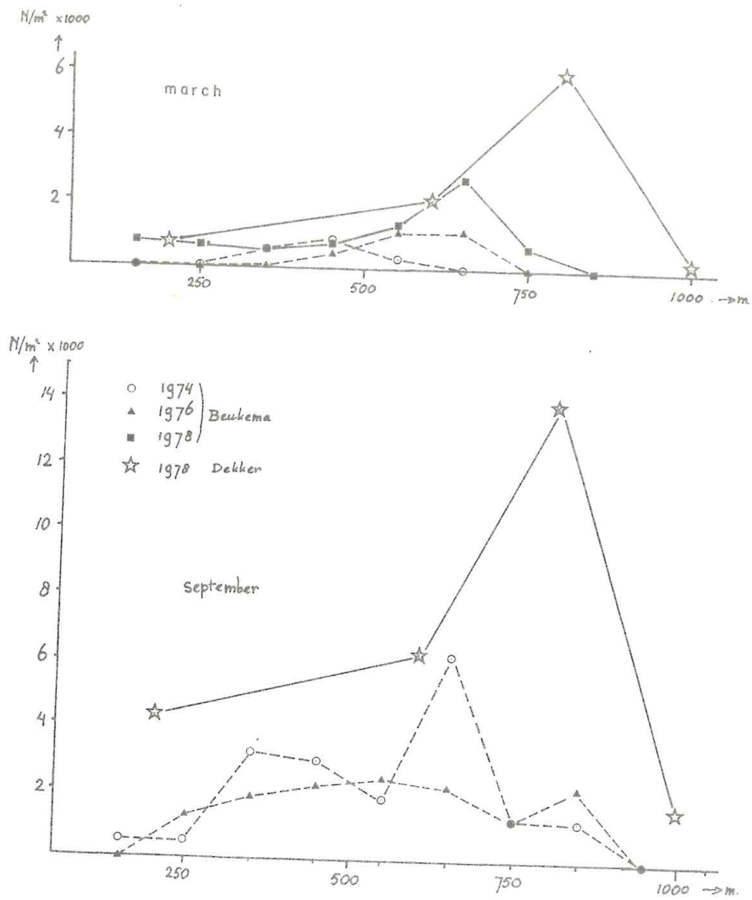

Fig. 11. Numerical densities of *Hydrobia* as observed by BEUKEMA (1974, 1976 and 1978) and DEKKER (1978: asteriks) at the same transect on Balgzand during spring (a) and late-summer (b).

of the maximal density appears to be slightly different, viz. at 800 m in my observations, and at 700 m in the samples of BEUKEMA during the same period. (And at even shorter distances during foregoing years).

One of the most important questions raised by this investigation is: what may be the cause of the significant differences in population composition between the Mok and the Balgzand location. This question breaks up into two parts: 1) Why does spatfall only occur at the Mok and not at the Balgzand location, and 2) what governs the observed changes in density of the 1-year animals, disappearing at the Mok and increasing in numbers at Balgzand.

At the Mok *H. ulvae* lives on and in very silty sediments. This does not mean, that spatfall occurs on all silty places where adults are found. At the most silty stations on the Balgzand transect no spatfall was observed, in spite of the presence of silty sediments near the mainland (Balgzand -1). On the other hand, spatfall also occurs at sites with sandy sediments. At the NIOZ-wad (Fig. 1), many 0-year *H. ulvae* with a shell height of 1-1.5 mm were observed on sandy sediments with a median grain size of about 300 µ and silt content of only 5 % (VAN MOORSEL, pers. comm.). Many of them were seen floating on the water surface when the tide was out.

In the southernmost part of Balgzand there is an area low in the intertidal zone with very soft and silty sediments where *H. ulvae* may be living in great densities. It is possible that spatfall at Balgzand is concentrated to this special area. High densities of young *H. ulvae* have been observed also on sandy parts of Balgzand (BEUKEMA, pers. comm.). Apparently, spatfall is restricted to small parts of the Wadden Sea.

If there is really such an area at Balgzand, then the second question could be answered. After settlement the 0-year animals could gradually colonise the other suitable parts of Balgzand, actively by crawling over the mud surface, or passively by floating on the water surface. This process of gradual dispersal would last at least one year, for otherwise the gradual increase of the numbers of 1-year animals at the Balgzand stations could not be explained.

Such migration could also explain the decline of numbers of 1-year animals at the Mok, as this station may have been part of an area delivering *H. ulvae* to areas without spatfall. Migration of adult *H. ulvae* will occur more or less frequently in the Dutch Wadden Sea. Unpublished data of the NIOZ on van Veen-grab bottom samples from deeper tidal channels in the Western Dutch Wadden Sea sometimes show large numbers of living *H. ulvae* sampled at depths between 6 m and 20 m, mostly in the month July. Probably these have been floating animals, sunk of by vigorous wave action, and washed together to quiet sites on the bottom of these tidal channels.

Details on these migration are not known. It is possible that animals migrate after having deposited egg-capsules. On the other hand it is quite probable that migration is a response to unsuitable environmental conditions (viz. the floating behaviour of the 0-year animals at the coarse grained NIOZ-wad). HOLME (1949) supposed that the floating behaviour plays an important rol in the dispersal of *H. ulvae*. However, floating behaviour as a part of a more complex behaviour as described by NEWELL (1962) could never be observed. Anyhow, the increasing numbers of both 0 and 1-year animals at the Balgzand stations must be due to immigration. From the rapidly decreasing numbers at the Mok station, it may be concluded, that this was an emigration station, delivering animals to such stations as the Balgzand ones.

b. Biomass and production

The individual weights of *H. ulvae* at Balgzand as well as at the Mok were lower than those of comparable year-classes at the Grevelingen estuary (WOLFF & DE WOLF, 1977). At the Grevelingen estuary 0-year animals reached an average individual weight of 0.3 mg in the autumn, and 1-year animals a individual weight of 0.8 mg. At the Mok these values were 0.2 and 0.4 mg, respectively, while at Balgzand 1-year animals reached a weight of 0.6 mg. These differences may be caused partly by differences in treatment of the animals in the laboratory: 1) WOLFF & DE WOLF incinerated their animals at higher temperatures, i.e. 570 °C as compared to 450 °C in the present observations, and 2) They incinerated the whole animals, including shells containing 10-15 % of the weight of the total organic matter of the whole animals. Therefore, ash-free dryweights of only the soft parts will have been about 0.7 mg for the 1-year animals at the Grevelingen estuary, close to my values of about 0.6 mg for the Balgzand (Fig. 6).

The production of organic matter at Balgzand stations is relatively low because of the absence of highly productive 0-year animals. At the Mok the situation is just opposite: a high production caused by large numbers of 0-year animals. That means rather divergent average values for the P/B-ratios at the Mok and the Balgzand stations. Between these divergent P/B-ratios values, data of ELLIOTT (1977) and WOLFF & DE WOLF (Table V) occupy more intermediate positions.

The production of organic matter in the form of egg-capsules was very different for the stations. At the Mok, the egg-capsule production was only 1.1 % of the total production of organic matter. At the Balgzand stations these percentages were higher, so it is likely that the 2-year animals at Balgzand contribute the largest share of the egg-capsule production. The production of organic matter of the egg-capsules of the 2-year animals at some Balgzand station (2 and 3, see Table IV) may even exceed the production of soft parts of these animals.

Table V

Biomass and production of *Hydrobia ulvae* at the Grevelingen estuary (WOLFF & DE WOLF, 1977).

Station	Period of immersion	Sediment characteristic	Biomass (g/m^2)	Production ($g/m^2/yr$)	P/B-ratio
A	33 %	very fine sand	4.06	7.23	1.78
B	54 %	very fine sand	7.12	8.80	1.24
C	68 %	very fine sand with mud	9.37	12.79	1.36

c. Relation to available food and the sediment

It is generally believed, that the food of various *Hydrobia*-species consists mainly of micro-algae and bacteria, attached to sand grains and particulate organic matter. At Balgzand the benthic microflora and accumulated organic matter have been studied by CADÉE & HEGEMAN (1977). At the same transect as investigated for this study, they found chlorophyll-a contents of the sediment decreasing from 10 µg/g.sediment at station 1 to 4 µg/g.sediment at station 4. The densities of *H. ulvae* do not show any correllation with these data. This may be caused by a reduction of the availability of bacteria, attached to the organic matter at the stations 1 and 2 (LOPEZ & LEVINTON, 1978). These authors studied the closely related species *Hydrobia ventrosa* (Montagu), which food demands may be similar to those of *H. ulvae*.

At Balgzand the greatest densities of *H. ulvae* were found at station 3. Median grain size of the sand in the sediment was 145 µ. The same median grain size value is found at the Mok, where *H. ulvae* is even occuring in greater densities. This similarity may be only accidental, for the silt content of the sediment may be of greater importance for the occurrence and density of *H. ulvae* than the grain size of the sand.

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