Life Cycle and Production of *Hydrobia ventrosa* and *H. neglecta* (Mollusca: Prosobranchia)

Hans Redlef Siegismund

Institute of Ecology and Genetics, University of Aarhus, DK-8000 Aarhus C, Denmark

ABSTRACT: Life cycle, growth, and production of the mud snails *Hydrobia ventrosa* (Montagu) and *H. neglecta* Muus were studied in the Kysing Fjord estuary, Denmark. Recruitment of Age class 0 in summer revealed 2 maxima: July–August and September. The first recruited group reached a length of 2.3 mm in *H. neglecta* and 2.5 mm in *H. ventrosa* in November. After September, no growth was found in the last recruited group of both species; their mean length remained 1.3 mm. Both species have a life span of approximately 18 months. The annual production of *H. ventrosa* and *H. neglecta* was 8.40 and 5.86 g ash-free dry weight m⁻², respectively.

INTRODUCTION

The hydrobiid species *Hydrobia ventrosa* (Montagu), *H. neglecta* Muus, *H. ulvae* (Pennant), and *Potamopyrgus jenkinsi* (Smith) are important members of the shallow-water fauna in Denmark. They are found at most lenitic localities, except where the sediment consists of mud. The salinity preference varies among the species (Hylleberg, 1975), resulting in some differential habitat selection. However, their distributions along salinity gradients often show considerable overlap, leading to the co-existence of 2 or 3 of the species (Fenchel, 1975). The hydrobiids are deposit feeders with diatoms as their main food source (Fenchel and Kofoed, 1976; Jensen and Siegismund, 1980). The ingested diatoms are assimilated with a high efficiency (Kofoed, 1975a).

Where abundant, the population densities of the species are often in the range of 20 000 to 40 000 m⁻². Such high densities make the snail an important link in the estuarine food web, e.g. as a food resource for waders and ducks (Olney, 1965; Evans et al., 1979). However, an estimate of the annual production is needed in order to obtain a quantitative measure of the mud snails as consumers of the microflora and as a food resource for predators. This paper studies the production in populations of *Hydrobia ventrosa* and *H. neglecta* in the Kysing Fjord estuary. Life cycles of the 2 species are described and production is estimated from the knowledge of the age structure and density through time.

MATERIALS AND METHODS

Study Area

The study was carried out in Kysing Fjord, a small estuary on the east coast of Jutland, Denmark (Fig. 1). The estuary is shallow with a mean depth of 0.6 m, one third of the water mass is exchanged during each tide (Muus, 1967). An average salinity gradient from 12‰ S at the innermost part to 20‰ S at the mouth of the estuary was observed during the study period.

All 3 *Hydrobia* species are present in the estuary, with *H. ventrosa* and *H. neglecta* being the dominant species and *H. ulvae* only of minor importance. *H. neglecta* dominates at the mouth of the estuary; its population density decreases inwards, where *H. ventrosa* dominates in the middle part of the estuary. The zone of overlap between the 2 species extends through most of the estuary. In addition to the *Hydrobia* species mentioned, the hydrobiid *Potamopyrgus jenkinsi* is found in the innermost part of the estuary, where it dominates during summer.

While *Hydrobia ventrosa* and *H. neglecta* were studied at several stations in the estuary, this paper treats only a single station (Fig. 1); here the 2 species co-existed and reached high densities, allowing both of them to be studied in the same area. The distance of the station from the shoreline was about 50 m; the salinity varied from 10.5 to 22.5‰ S during the study period with a mean of 16‰ S.

Fig. 1. Kysing Fjord estuary showing sampling station (encircled cross)
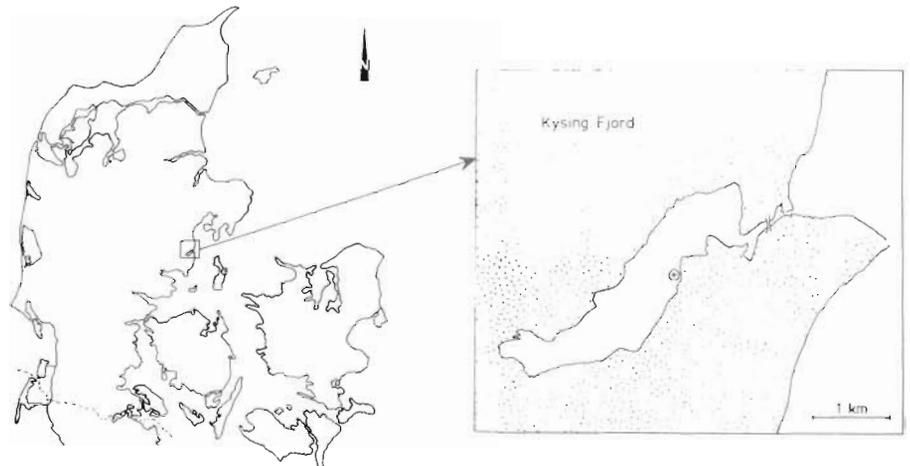
Sampling

Snails were collected from April 21, 1978 to February 21, 1979. Samples of the sediment were taken with Plexiglas tubes (inner diameter 2.6 cm). The sediment was sieved through a 0.5 mm sieve and the snails were subsequently removed from the remaining sediment material with a dissecting microscope. Snail length was measured from apex to anterior margin of the aperture with an ocular micrometer at $12 \times$ magnification.

Age classes were separated according to Harding (1949), assuming that size-frequency distributions of the age classes were normally distributed. The proportion of each age class, average length, and standard deviation were estimated from a plot of the size-frequency distribution on probability paper. The density of an age class was calculated as the product of total density and proportion of the given age class.

Length-Weight Relationship

The average weight (W) of individuals from a given age class was estimated from the average length (L) of the age class, using

$$W = aL^b$$

The parameters a and b were estimated by a regression of the logarithm of the ash-free dry weight on the logarithm of length. The ash-free dry weight was measured as weight loss after 8 h of incineration at 550 °C of snails dried at 105 °C for 24 h.

Production Measurement

The different age classes of both species were regarded as separate cohorts, and production was calculated separately for each of these cohorts. The

production of a cohort which declines in density from time t to time $t + \Delta t$ can be calculated as

$$\Delta P = \frac{N(t) + N(t + \Delta t)}{2} \times \{W(t + \Delta t) - W(t)\}$$

where $N(t)$ and $W(t)$ are density of the cohort and average weight at time t, respectively (Crisp, 1971). The expression $\{N(t) + N(t + \Delta t)\}/2$ approximates the mean density of the cohort that occurs during the time interval Δt, and $W(t + \Delta t) - W(t)$ measures the weight gain during this period. Total production of the cohort is calculated as sum of the production increments over all time intervals.

According to Crisp (1971), this method can also be applied to an age class with a prolonged period of recruitment in which the density increases until the recruitment is finished. Crisp's method, however, seems to underestimate the production of the cohort during periods of increasing density. The survivors of a cohort at time $t + \Delta t$ would have a production of $N(t + \Delta t) \times \{W(t + \Delta t) - W(t)\}$ which is larger than $\{N(t) + N(t + \Delta t)\}/2 \times \{W(t + \Delta t) - W(t)\}$ because $N(t + \Delta t) > N(t)$. A better approximation of the production of the cohort during a period of increasing density would, therefore, be simply to measure the difference between biomass at the time of highest density and initial biomass. In the present paper, the biomass of hatched larvae was ignored.

The modification of Crisp's method still underestimates production, as it neglects the production of individuals recruited during the period of increasing density, and eliminated before observation at the end of the period. However, this estimate is closer to the actual production than an estimate following Crisp's method. From the time when density decreases, the production can be measured by Crisp's method.

For comparison, production of the snails was measured by both Crisp's method and by its modification described.
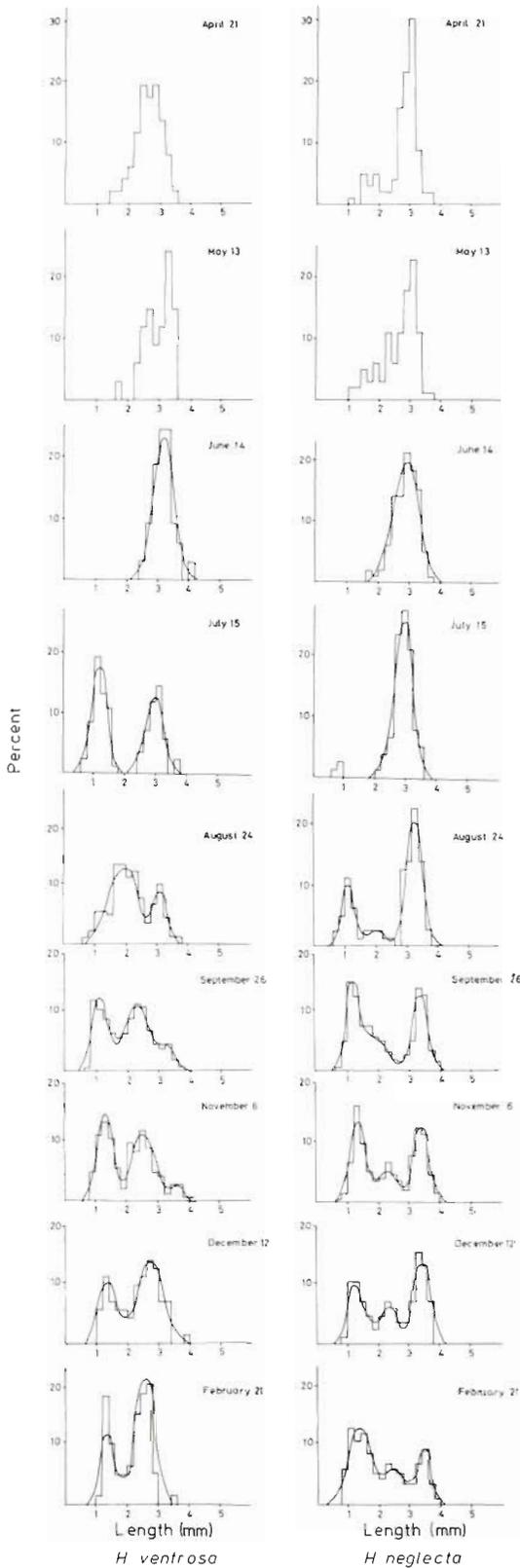
Fig. 2. *Hydrobia ventrosa* and *Hydrobia neglecta*. Length frequency distribution from April 1978 to February 1979. Sums of fitted normal distributions drawn from June on

RESULTS

Growth and Life Cycle

In both *Hydrobia ventrosa* and *H. neglecta*, the initial Age class I consisted of large individuals with an unimodal size distribution in July when the recruitment of Age class 0 started (Fig. 2). Therefore, offspring classes could easily be distinguished at the beginning of the recruitment. In both species Age class 0 was recruited in separate groups during summer.

Age class 0 of the *Hydrobia ventrosa* population was recruited twice during summer: in July (0–1 group) and in September (0–2 group) (Fig. 2). The first recruited group attained a size of 2.50 mm in November when growth ceased. The second group did not grow after it had been observed in September, and mean length did not exceed 1.50 mm (Fig. 3). Age class I of the *H. ventrosa* population started to grow in April
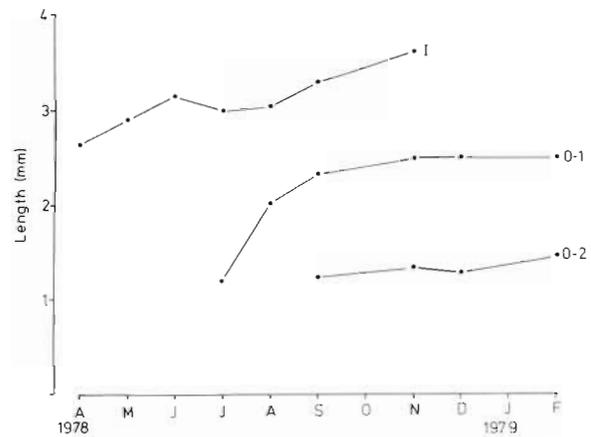

Fig. 3. *Hydrobia ventrosa*. Growth of Age classes I, 0–1, and 0–2
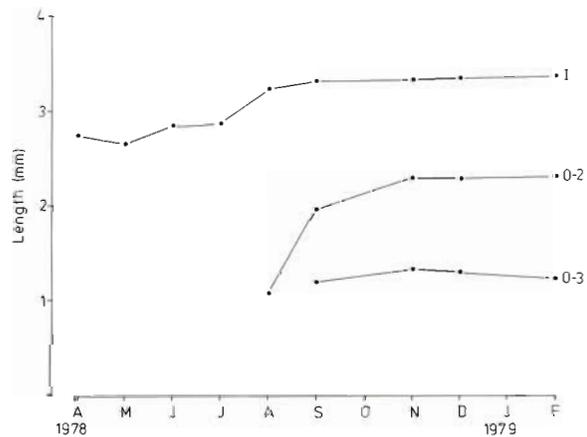

Fig. 4. *Hydrobia neglecta*. Growth of Age classes I, 0–2, and 0–3

and reached a length of 3.6 mm in November right before it vanished.

Age class 0 in the *Hydrobia neglecta* population was recruited in 3 groups. The first recruitment group (0–1) was observed in July at a low density. It reached maximum density of 1600 m^{-2} in August; from September on, it could not be distinguished from Group I and the second recruited group. Age class 0–2 was the first larger recruitment in the *H. neglecta* population (Fig. 2). It was observed in August and attained a length of 2.3 mm in November when it ceased to grow (Fig. 4). The third recruited group, 0–3, was observed in September. Its mean length (1.3 mm) did not change during the observation period. Age class I in the *H. neglecta* population started to grow from May and attained a size of 3.4 mm in November. This age class survived the winter, but its density decreased from 7700 m^{-2} in November to 2800 m^{-2} in February (Table 1).

Length-Weight Relationship

Ash-free dry weight (µg) as a function of length (mm) in *Hydrobia ventrosa* and *H. neglecta* is illustrated in Figs. 5 and 6. The functions are:

H. ventrosa:
$$W = 0.0417L^{2.279} \quad (r^2 = 0.93, \; n = 57)$$
H. neglecta:
$$W = 0.0290L^{2.521} \quad (r^2 = 0.97, \; n = 53)$$

Production

In the *Hydrobia ventrosa* population the major production took place in Age class 0. In this age class, a production of 5.21 g ash-free dry weight m^{-2} of a total of 6.34 g ash-free dry weight m^{-2} was achieved by the first recruited group (Table 2). Production of the 0 group mainly occurred before November, when growth

Table 1. *Hydrobia neglecta*. Production of different age classes of the population studied from April 1978 to February 1979

Sampling date	Age class	Density (1000 m^{-2})	Mean length (mm)	Mean ash-free dry weight (mg)	Biomass (g m^{-2})	Production[*] (g m^{-2})	Production[**] (g m^{-2})
21/4 78	I	20.6	2.78	0.383	7.89		
13/5 78	I	20.4	2.64	0.336	6.85	−0.96	−0.96
14/6 78	I	19.8	2.86	0.412	8.16	1.53	1.53
15/7 78	I	14.8	2.90	0.426	6.31	0.24	0.24
24/8 78	I	10.4	3.24	0.564	5.87	1.74	1.74
26/9 78	I	12.6	3.34	0.609	7.67	0.52	0.52
6/11 78	I	7.7	3.37	0.623	4.80	0.14	0.14
12/12 78	I	8.4	3.35	0.614	5.16	−0.07	−0.07
21/2 79	I	2.8	3.38	0.628	1.76	0.08	0.08
Total production of Age class I						3.22	3.22
15/7 78	0–1	0.6	0.84	0.019	0.01		
24/8 78	0–1	1.6	2.03	0.173	0.28	0.17	0.28
Total production of Age class 0–1						0.17	0.28
24/8 78	0–2	4.2	1.09	0.036	0.15		
26/9 78	0–2	7.4	1.97	0.161	1.19	0.73	1.19
6/11 78	0–2	4.4	2.30	0.237	1.04	0.45	0.45
12/12 78	0–2	3.8	2.30	0.237	0.90	0	0
21/2 79	0–2	2.8	2.32	0.243	0.68	0.02	0.02
Total production of Age class 0–2						1.20	1.66
26/9 78	0–3	13.0	1.21	0.047	0.61		0.61
6/11 78	0–3	7.7	1.35	0.062	0.48	0.16	0.16
12/12 78	0–3	5.8	1.32	0.058	0.34	−0.03	−0.03
21/2 79	0–3	6.1	1.26	0.052	0.32	−0.04	−0.04
Total production of Age class 0–3						0.09	0.70

[*] Calculated according to Crisp (1971)
[**] Calculated according to a modification of Crisp's method (see text)

Table 2. *Hydrobia ventrosa*. Production of different age classes of the population studied from April 1978 to February 1979

Sampling date	Age class	Density (1000 m^{-2})	Mean length (mm)	Mean ash-free dry weight (mg)	Biomass (g m^{-2})	Production[*] (g m^{-2})	Production[**] (g m^{-2})
21/4 78	I	10.6	2.65	0.385	4.08		
13/5 78	I	6.8	2.92	0.480	3.26	0.83	0.83
14/6 78	I	6.4	3.16	0.574	3.67	0.62	0.62
15/7 78	I	7.6	2.98	0.503	3.83	−0.50	−0.50
24/8 78	I	5.0	3.05	0.530	2.65	0.17	0.17
26/9 78	I	4.0	3.32	0.643	2.57	0.51	0.51
6/11 78	I	2.2	3.62	0.783	1.72	0.43	0.43
12/12 78	I	0	−	−	−	−	−
21/2 79	I	0	−	−	−	−	−
Total production of Age class I						2.06	2.06
15/7 78	0–1	9.2	1.19	0.062	0.57		
24/8 78	0–1	10.9	2.00	0.202	2.20	1.41	
26/9 78	0–1	15.5	2.30	0.278	4.31	1.00	4.31
6/11 78	0–1	15.0	2.50	0.337	5.06	0.90	0.90
12/12 78	0–1	10.2	2.50	0.337	3.44	0	0
21/2 79	0–1	4.1	2.50	0.337	1.38	0	0
Total production of Age class 0–1						3.31	5.21
26/9 78	0–2	13.7	1.25	0.069	0.95		0.95
6/11 78	0–2	12.8	1.33	0.080	1.02	0.15	0.15
12/12 78	0–2	4.4	1.28	0.073	0.32	−0.06	−0.06
21/2 79	0–2	2.2	1.47	0.10	0.22	0.09	0.09
Total production of Age class 0–2						0.18	1.13

[*] Calculated according to Crisp (1971)
[**] Calculated according to a modification of Crisp's method (see text)

ceased. During winter, production was zero in the 0–1 group and partly negative in the 0–2 group (Table 2). Production of Age class I amounted to 2.06 g ash-free dry weight m^{-2} (Table 2). During summer, negative production was found from June to July in this age class due to decline in length from 3.26 to 2.98 mm.

Total production from April 1978 to February 1979 in the *Hydrobia ventrosa* population amounted to 8.40 g ash-free dry weight m^{-2} (Table 3). An estimate according to Crisp's method, 5.55 g ash-free dry weight m^{-2}, is 34 % lower.

The major production in the *Hydrobia neglecta* population took place in Age class I. The production of this age class amounted 3.22 g ash-free dry weight m^{-2}. As in the *H. ventrosa* population, a negative production was observed in this age class from April to May. During winter, production of Age class I declined and was approximately zero from November 1978 to February 1979. The production of Group 0 amounted to 2.64 g ash-free dry weight m^{-2}, of which the major part was caused by the production of the 0–2 group (1.66 g ash-free dry weight m^{-2}). As in Group I, the production

of Group 0 was negligible during winter. Total production of the *H. neglecta* population amounted to 5.86 g ash-free dry weight m^{-2} (Table 3). Calculation according to Crisp's method yields 4.68 g ash-free dry weight, i. e. a 20 % smaller value.

The total production of *Hydrobia ventrosa* and *H. neglecta* from April 1978 to February 1979 yielded 14.26 g ash-free dry weight m^{-2} at this locality.

Table 3. *Hydrobia ventrosa* and the *Hydrobia neglecta*. Production of populations studied from April 1978 to February 1979

	Production[*] (g ash-free dry weight m^{-2})	Production[**] (g ash-free dry weight m^{-2})
H. ventrosa	5.55	8.40
H. neglecta	4.68	5.86

[*] Calculated according to Crisp (1971)
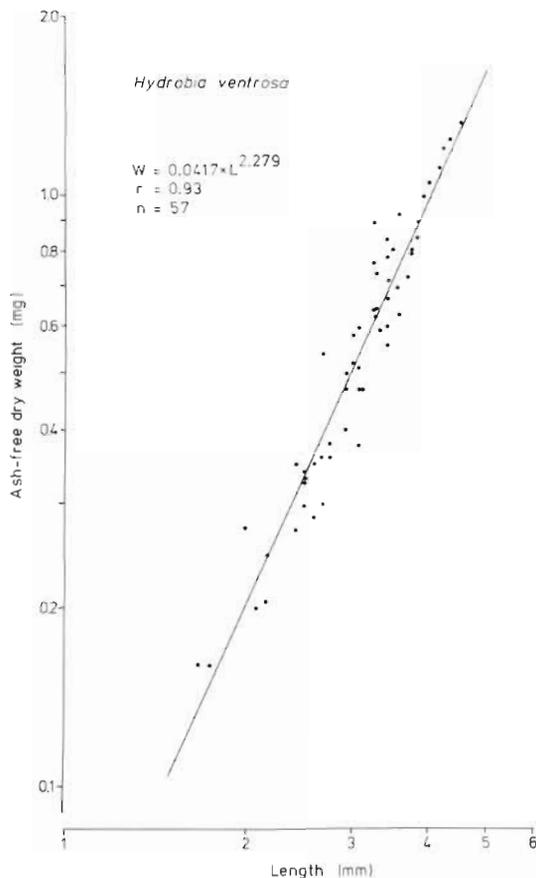[**] Calculated according to a modification of Crisp's method (see text)

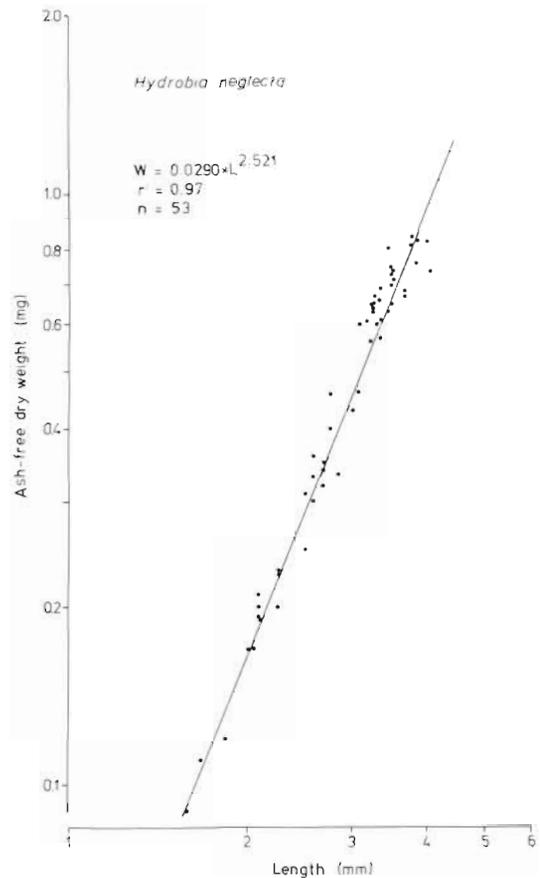Fig. 5. *Hydrobia ventrosa*. Regression of ash-free dry weight on body length

Fig. 6. *Hydrobia neglecta*. Regression of ash-free dry weight on body length

DISCUSSION

Life Cycle

Age class 0 of the *Hydrobia ventrosa* population was recruited from 2 groups, whereas recruitment of this age class was observed 3 times in *H. neglecta* (the first one being of minor importance). The first major recruitment in *H. neglecta* was displaced 1 mo compared with the first recruitment in *H. ventrosa*. This displacement was found only at the reference station in Kysing Fjord. At other stations where the 2 species co-existed, the recruitment was simultaneous (unpubl. own results).

Two maxima of reproduction were also reported by Fenchel (1975b) for *Hydrobia ventrosa* and *H. ulvae* populations in the Limfjord, Denmark, and by Fish and Fish (1974) for *H. ulvae* populations in the Dovey Estuary, Great Britain. In both cases, egg deposition occurred in spring and late summer. However, Muus (1967) and Lassen and Clark (1979) observed in several populations of the 3 *Hydrobia* species continuous

reproduction throughout the summer usually with a single peak in the recruitment. These variations in recruitments are probably caused by climatic changes. The differences in size distributions in April 1978 and February 1979 (Fig. 2) suggest that the recruitment in 1977 might have had a single peak in the *H. ventrosa* population because of unimodal size distribution in April 1978, while the recruitment of the *H. neglecta* population might have had a small second peak in 1977, as its size distribution in April 1978 is skewed to the left.

In late autumn, the first recruited group of *Hydrobia ventrosa* (0–1) and the first major recruitment of *H. neglecta* (0–2) had grown from a size of 0.2 mm at hatching (Muus, 1967) to a size of 2.5 and 2.3 mm, respectively. The last recruited groups (0–3 in *H. neglecta* and 0–2 in *H. ventrosa*) did not show any growth after they had been observed in September. This absence of growth may be due to high intra- and interspecific competition for food. The 2 groups had approximately the same size (1.3 mm), hence they are expected to have an almost complete overlap in their

resource niche (Fenchel, 1975b). Furthermore, the sum of their densities was high, 26700 m⁻², and the primary production of their main food, diatoms, decreased during that period (Grøntved, 1960).

The parental age classes, I, were about 1 yr old at their first reproduction. In *Hydrobia ventrosa* this age class disappeared in autumn, whereas in *H. neglecta* a small number of this age class survived the winter. The resulting life span of about 18 mo in both species is in agreement with Muus (1967).

The observed body sizes of both species is in line with the ranges previously reported (Muus, 1967; Fenchel, 1976; Hylleberg, 1978).

Production

The average weight of an individual of a given age class was calculated from the average length of the age class as

$$W = a \left(\sum_i p_i L_i \right)^b,$$

where p_i is the frequency of the size group with a median length of L_i within the age class. This causes a minor underestimation of weight (and therefore of production) due to the convexity of the function $W = aL^b$ when b is larger than 1. The average weight ought to be calculated as the average of the weights of the size groups in the age class,

$$W = \sum_i p_i \left(aL_i^b \right).$$

Calculations indicate that the average underestimate is about 3 % with the size frequencies in the present populations.

The production calculated by Crisp's (1971) method underestimates the production in *Hydrobia ventrosa* by 34 % and in *H. neglecta* by 20 %. Crisp's method has been used by serveral workers; this may have resulted in similarly low estimates. From the works of Buchanan and Warwick (1974) and Warwick and Price (1975) the production of age classes with a prolonged recruitment was calculated with the modified method and compared with their own estimates based on Crisp's method. Buchanan and Warwick (1974), investigating a population of the polychaete *Heteromastus filiformis*, underestimated the production of the Year class 0 by 53 %; Warwick and Price (1975), investigating the polychaete *Nephtys hombergi*, underestimated the production of the Year class 0 by 10 %. The suggested modification still underestimates the actual production during a period of increasing density, because the calculated production ignores the production of individuals being recruited and eliminated within the period of observation. The modified method

still appears to provide a better estimate of the actual production.

The total production of *Hydrobia ventrosa* and *H. neglecta* from April 1978 to February 1979 amounted to 14.26 g ash-free dry weight m⁻². Although determined for only 10 mo, this probably approximates the total annual production due to the negligible growth in early spring. The sum of the production of both species is similar to that reported by Wolff and de Wolf (1977) for allopatric *H. ulvae* populations on tidal flats in the Grevelingen estuary, The Netherlands.

The importance of hydrobiid snails in the estuarine food chain can be evaluated by comparing their production with the production of their food resource, benthic diatoms. Grøntved (1960) measured the annual benthic primary production to be 116 g C m⁻², an average value for some Danish fjords. In the form of glucose this would correspond to 4.539 MJ m⁻². The calorific value of aquatic invertebrates has a mean of 23.44 kJ g⁻¹ ash-free dry weight (Winberg, 1971), rendering the production of *Hydrobia ventrosa* and *H. neglecta* 334.3 kJ m⁻² yr⁻¹. This value neither includes the production of gametes nor excreted organic matter. The latter may be significant at least for *H. ventrosa* (Kofoed, 1975b). Kofoed (1975b) showed that about 20 % of the consumption of a relatively protein-rich diet were used for production. With this value the total consumption of *H. ventrosa* and *H. neglecta* amounts to 1.672 MJ m⁻² yr⁻¹, i. e. these snails would consume about 40 % of the annual primary production of the benthic microflora. This evaluation is crude, but it suggests the *Hydrobia* species studied to be most important consumers of benthic microalgae.

LITERATURE CITED

Buchanan, J. B., Warwick, R. M. (1974). An estimate of benthic macrofaunal production in the offshore mud of the Northumberland coast. J. mar. biol. Ass. U. K. 54: 197–222

Crisp, D. J. (1971). Energy flow measurements. In: Holme, N. A., McIntyre, A. D. (eds.) Methods for the study of marine benthos. Blackwell, Oxford, pp. 197–279

Evans, P. R., Herdson, D. M., Knights, P. J., Pienkowski, M. W. (1979). Short-term effects of reclamation of part of Seal Sands, Teesmouth, on wintering waders and shelduck. Oecologia (Berl.) 41: 183–206

Fenchel, T. (1975a). Factors determining the distribution patterns of mud snails (Hydrobiidae). Oecologia (Berl.) 20: 1–17

Fenchel, T. (1975b). Character displacement and coexistence in mud snails (Hydrobiidae). Oecologia (Berl.) 20: 19–32

Fenchel, T., Kofoed, L. H. (1976). Evidence for exploitative interspecific competition in mud snails (Hydrobiidae). Oikos 27: 367–376

Fish, J. D., Fish, S. (1974). The breeding cycle and growth of
    Hydrobia ulvae in the Dovey estuary. J. mar. biol. Ass.
    U. K. 54: 685–697
Grøntved, J. (1960). On the productivity of microbenthos and
    phytoplankton in some Danish fjords. Medd. Danm. Fisk.
    Havunders. N. S. 3: 1–17
Harding, J. P. (1949). The use of probability paper for the
    graphical analysis of polymodal frequency distributions.
    J. mar. biol. Ass. U. K. 28: 141–153
Hylleberg, J. (1975). The effect of salinity and temperature on
    egestion in mud snails (Gastropoda: Hydrobiidae).
    Oecologia (Berl.) 21: 279–289
Hylleberg, J. (1978). Mud snails on Åland II: a study of
    potential competition in term of snail sizes and spacial
    segregation. (Swedish; Engl. summary). Husö biol. stat.
    Medd. 20: 31–49
Jensen, K. T., Siegismund, H. R. (1980). The importance of
    diatoms and bacteria in the diet of *Hydrobia*-species.
    Ophelia 1 (Suppl.): 193–199
Kofoed, L. H. (1975a). The feeding biology of *Hydrobia ven-
    trosa* (Montagu). I. The assimilation of different compo-
    nents of the food. J. exp. mar. Biol. Ecol. 19: 233–241

Kofoed, L. H. (1975b). The feeding biology of *Hydrobia ven-
    trosa* (Montagu). II. Allocation of the components of the
    carbon-budget and the significance of the secretion of
    dissolved organic matter J. exp. mar. Biol. Ecol. 19:
    243–256
Lassen, H. H., Clark, M. E. (1979). Comparative fecundity in
    three Danish mudsnails (Hydrobiidae). Ophelia 18:
    171–178
Muus, B. J. (1967). The fauna of Danish estuaries and lagoons.
    Medd. Danm. Fisk. Havunders. N. S. 5: 1–316
Olney, P. J. S. (1965). The food and feeding habits of shelduck
    Tadorna tadorna. Ibis 107: 527–532
Warwick, R. M. and Price, R. (1975). Macrofauna production
    in an estuarine mud-flat. J. mar. biol. Ass. U. K. 55: 1–18
Winberg, G. G. (1971). Methods for the estimation of produc-
    tion of aquatic animals, Academic Press, London, New
    York
Wolff, W. J., de Wolf, L. (1977). Biomass and production of
    zoobenthos in the Grevelingen estuary, The Netherlands.
    Estuar coast. mar. Sci. 5: 1–24