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## The Distribution of Hydrobiids and the Effects of Sediment Characteristics on the Population Dynamics of *Hydrobia ventrosa* in a Coastal Region of the Southern Baltic

*key words:* Hydrobiidae, *Hydrobia ventrosa*, Baltic Sea, reproduction, distribution

### Abstract

The composition of the hydrobiid fauna in a coastal water of the southern Baltic was studied in 1990/91 at three stations with different sediment characteristics (grain size, organic content). Four species were found (*Hydrobia ventrosa*, *H. ulvae*, *H. neglecta* and *Potamopyrgus jenkinsi*). *H. ventrosa* was dominant at all stations. The mean hydrobiid abundances were 4,000 (stn. C), 18,000 (stn. B) and 40,000 (stn. A) ind./m<sup>2</sup> respectively. Abundance was found to correlate with the organic content of the sediment. The reproduction and growth of *H. ventrosa* was studied. Two reproduction phases were observed, one in summer and the other in late autumn. The autumn reproduction peaks were staggered owing to the different growth rates at the various stations. Possible correlations between the differences in shell size of *H. ventrosa* at the various stations and both sediment characteristics and abundance are discussed.

### 1. Introduction

Hydrobiids are among the characteristic species of European coasts and are particularly numerous in tidal waddens and shallow inland coastal waters. Owing to their ubiquity, sometimes huge abundances and the sympatric occurrence of closely related species, they are popular subjects of marine ecological and taxonomic studies. The influence of hydrographic factors on the distribution of the species has been described several times (MUUS, 1967; LASSEN and HYLLEBERG, 1978; HYLLEBERG, 1986; HYLLEBERG and SIEGISMUND, 1987; LAPPALAINEN, 1979). Observed differences between the shell sizes of allopatric and sympatric populations led to some controversy concerning "character displacement" (FENCHEL, 1975 a, b, 1988; FENCHEL and KOFOED, 1976; CHERRILL, 1987, 1988; CHERRILL and JAMES, 1987). The discussion proved to be a fruitful starting point for various detailed studies into the effects of abiotic factors and intraspecific interactions on reproduction, growth and behaviour (ANDERSON, 1971; LASSEN and CLARK, 1979; BARNES, 1988; MANDRACCHIA and RUBER, 1990; MORRISEY, 1990). Interspecific interactions with other substrate feeders have also been investigated (MORRISEY, 1987, 1988). Many studies have been undertaken in British and Danish waters, but information concerning the distribution and ecology of hydrobiids in the South Baltic is relatively sparse although they are also among the most important representatives of the macrozoobenthos in this area (JAGNOW and GOSSELCK, 1987; Prena, 1987). The purpose of our investigation was to elucidate the observed hydrobiid distribution pattern in the study region and discover the causes of the varying abundances in shallow Baltic coastal waters.

## 2. Materials and Methods

The investigation area is an almost tideless coastal water in the Mecklenburger Bucht (South Baltic) (Fig. 1). Samples were collected at monthly intervals, the temperature and salinity being measured at the same time. Sediment samples were also taken on each occasion to determine the mean grain size, water content and organic matter content. To compensate for the natural variability in the distribution of hydrobiids, four cores (2.83 cm<sup>2</sup> each) were pooled each time to yield a haul with a total area of 11.34 cm<sup>2</sup>. At least three hauls (i.e. 12 cores altogether) were collected at each station on each occasion. This relatively small sample volume was sufficient in view of the high abundances.

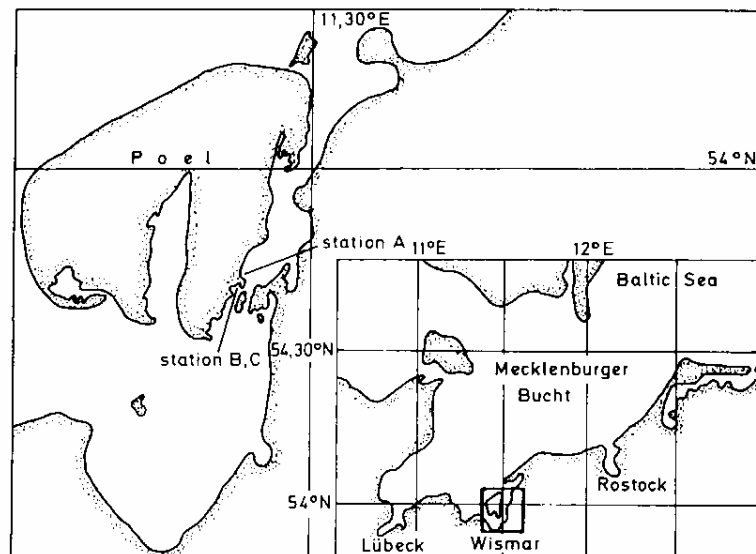


Figure 1: Study area in the Mecklenburger Bucht, southern Baltic.

The samples were fixed with borax buffered 4% formaldehyde and, to permit juvenile snails to be taken into account, initially sorted in the laboratory on a fine sieve (0.1 mm mesh). The samples were analyzed at a magnification of X15 to X20. All representatives of the macrozoobenthos were counted in order to calculate the hydrobiid dominances. The three hauls were pooled for determination of the wet weight so that one biomass value per month was available for each station.

The hydrobiids were identified at a magnification of X20 using shell features, proboscis and tentacle pigmentation and penis shape as characters. The shell height was measured with an accuracy of 0.1 mm at a magnification of X15, and groups of 10-20 animals of the same size class were weighed together to calculate the relationship between shell height and biomass. Only hydrobiids larger than 1.1 mm could be sexed reliably, and smaller animals were therefore regarded as juveniles.

The organic matter content of the sediment was determined by roasting (4 h at 550°C). The mean grain size was calculated after wet sieving through a set of sieves (1.0, 0.5, 0.2, 0.1 and 0.063 mm mesh).

## 3. Results

The water temperature and salinity were the same at all three stations, the temperature varying between 0 and 24°C in the course of the year and the salinity between 10.5‰ in summer and 16.5‰ in winter. However, the stations differed considerably in

degree of exposure and, therefore, with respect to sediment quality (Table 1). The most exposed station was stn. A, where considerable changes were recorded between 1984 and 1992, possibly as a result of shifting currents. The organic matter content of the sediment was particularly high at stn. C. The stations also differed with regard to water depth, the mean water depths being 0.6 m, 0.4 m and 0.2 m at stn. A, B and C respectively.

Table 1: Sediment characteristics at site A, B, C in 1984–1991. Data for organic matter are given as % dry weight.

sediment parameter		1984 × (sd)	1985 × (sd)	1988 × (sd)	1989 × (sd)	1990 × (sd)	1991 × (sd)
stn A	org. matter (%)	1,97 (0,69)	1,56 (0,63)	1,11 (0,37)	0,83 (0,26)	0,71 (0,19)	0,97 (0,19)
	medium grain size (mm)	0,161 (0,065)	0,176 (0,038)	0,253 (0,039)	0,280 (0,028)	0,271 (0,030)	0,233 (0,047)
stn B	org. matter (%)	-	-	-	1,57 (0,62)	1,85 (0,51)	2,04 (0,47)
	medium grain size (mm)	-	-	-	0,166 (0,015)	0,168 (0,028)	0,163 (0,040)
stn C	org. matter (%)	-	-	4,24 (1,76)	4,98 (1,68)	4,71 (1,60)	5,66 (1,39)
	medium grain size (mm)	-	-	0,134 (0,038)	0,144 (0,022)	0,145 (0,020)	0,131 (0,056)

Four hydrobiid species were found during the investigation period: *Hydrobia neglecta* MUUS 1963, *H. ulvae* (PENNANT 1777), *H. ventrosa* (MONTAGU 1803) and *Potamopyrgus jenkinsi* (SMITH 1889).

The dominances and abundances at the three stations differed considerably in parallel to sediment organic matter content. Abundances were highest at stn. A (Fig. 2), where the highest densities of 77 ind./10 cm<sup>2</sup> (77,030 ind./m<sup>2</sup>) were found in March, 1989. The abundance at this station for the period 1988–1992 was around 40 ind./10 cm<sup>2</sup>. It is interesting to compare these figures with results obtained at the same station in 1984/85 (Fig. 3): the abundance exceeded 30 ind./10 cm<sup>2</sup> on only one occasion (September 1985), and the mean abundance for the period was only 13 ind./10 cm<sup>2</sup>.

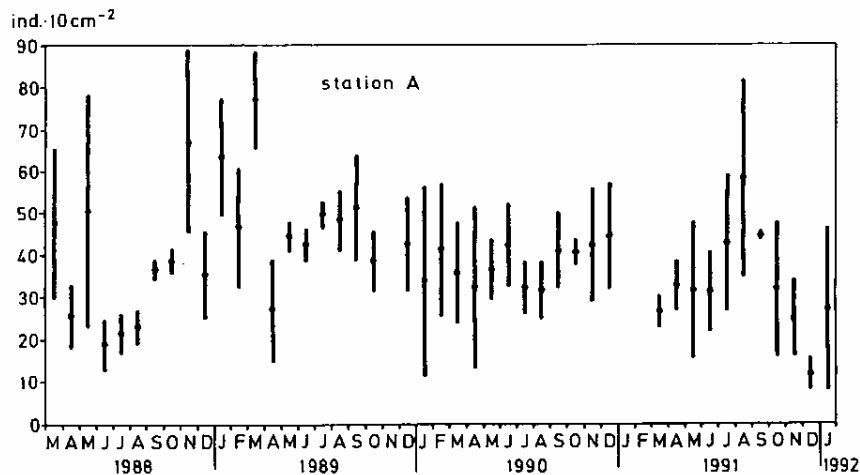


Figure 2: Abundance of hydrobiids at site A 1988–1992 (× ± sd).

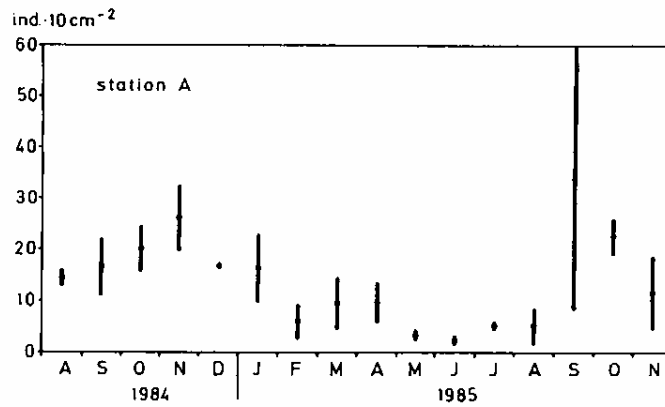


Figure 3: Abundance of hydrobiids at site A 1984-1985 ( $\times \pm$  sd).

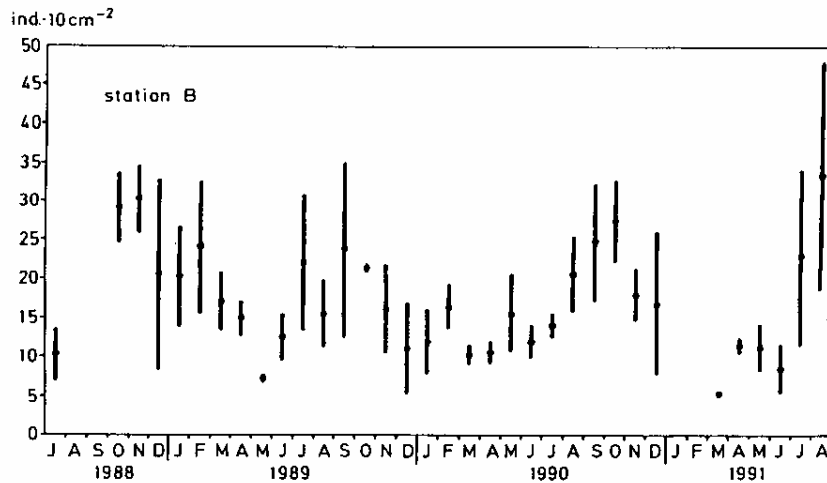


Figure 4: Abundance of hydrobiids at site B 1988-1991 ( $\times \pm$  sd).

The sediment at stn. B was similar to that recorded for stn. A studied in 1984/85 (Table 1), and the abundances found during the present study also were similar. The mean value of 18 ind./10 cm<sup>2</sup> was only slightly higher than recorded at stn. A during the former study (Fig. 4). The mean wet weights at these two stations in 1990 were  $43 \pm 15$  mg/10 cm<sup>2</sup> and  $38 \pm 14$  mg/10 cm<sup>2</sup> for stn. A and B respectively.

Hydrobiids obviously found stn. C less attractive (Fig. 5). This was almost certainly due to the not only high organic content and relatively small grain size, but also to the shallowness of the water and the occasional exposure of the bottom to the air. The long term mean abundance at this station was only 4 ind./10 cm<sup>2</sup>, and the biomass,  $9 \pm 4$  mg/10 cm<sup>2</sup>, was correspondingly low.

The mean abundances achieved by hydrobiids at stn. A and B were 49% and 19% of the total macrofauna respectively. Hydrobiids were therefore the dominant macrozoobenthos representatives at these two stations. At stn. C, in contrast, they rarely accounted for more than 10% of the macrofauna.

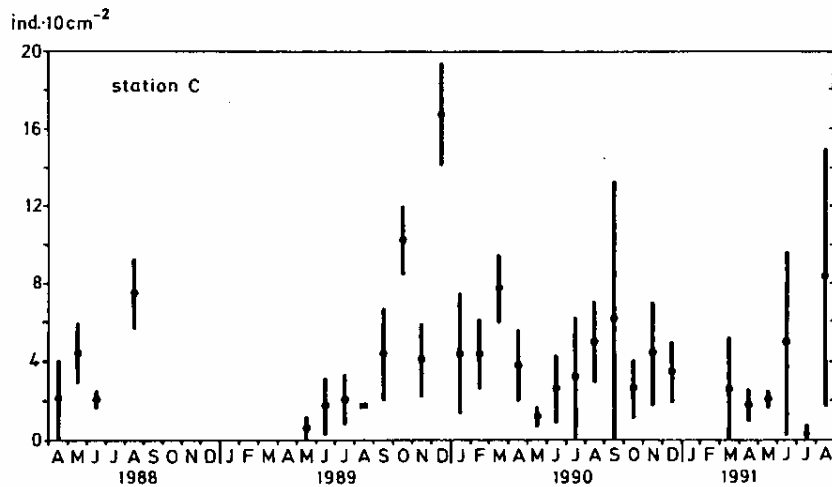


Figure 5: Abundance of hydrobiids at site C 1988-1991 ( $\times \pm$  sd).

Abundances peaked in late summer or autumn at all stations, and at stn. B it was particularly evident that this fluctuation was caused by reproductive activity (Fig. 4).

The relative abundance of the four hydrobiids during the investigation period is shown in Fig. 6. *H. ventrosa* was the dominant species at all stations. At stn. A, *H. ulvae* was almost always subdominant, accounting for 2-5% of the individuals. *P. jenkinsi* was rarely found at stn. A, but at stn. B it achieved dominances of up to 20%. *H. ulvae* was also a subdominant for at least part of the time. In view of the low hydrobiid abundances recorded at stn. C, it would probably be wrong to attach too much value to the high dominances of *H. ulvae* and the considerable fluctuations in the species composition.

Juveniles (snails smaller than 1.1 mm) were found in all samples (Fig. 7 and 8), but they were particularly numerous from June to September. At stn. A they accounted for almost 50% of the hydrobiids from July to August, and they were also unusually abundant at stn. B at that time (26 and 32% in July and August respectively). The slight increase in the number of juveniles in November/December at stn. A and October at stn. B suggests a second period of reproductive activity. The size distribution scarcely changed in January and February, and the overall abundance did not decrease appreciably during this period (Fig. 2 and 4). Growth of the smaller classes started in March and continued until the summer. From March until April/May, this growth was accompanied by a decrease in total abundance.

The variation in shell size, which we used as a measure for age determination, is shown in Fig. 9. The curve showing the mean shell height of female *H. ventrosa* is identical for stn. A and B. There were evidently two growth phases. The first started in February/March and ended in June. This part of the curve describes the growth of animals that had wintered up to the reproduction period. The mean size then decreased due to the appearance of juveniles and mortality among the adults, and then increases again from August until October/November. Growth was obviously interrupted in winter. The growth curve for males was similar.

On the average, females were about 0.5 mm smaller at stn. A in 1990 than at stn. B (Fig. 9). A similar difference was found between the mean sizes of the males (stn. A:  $1.98 \pm 0.06$  mm; stn. B:  $2.38 \pm 0.18$  mm).

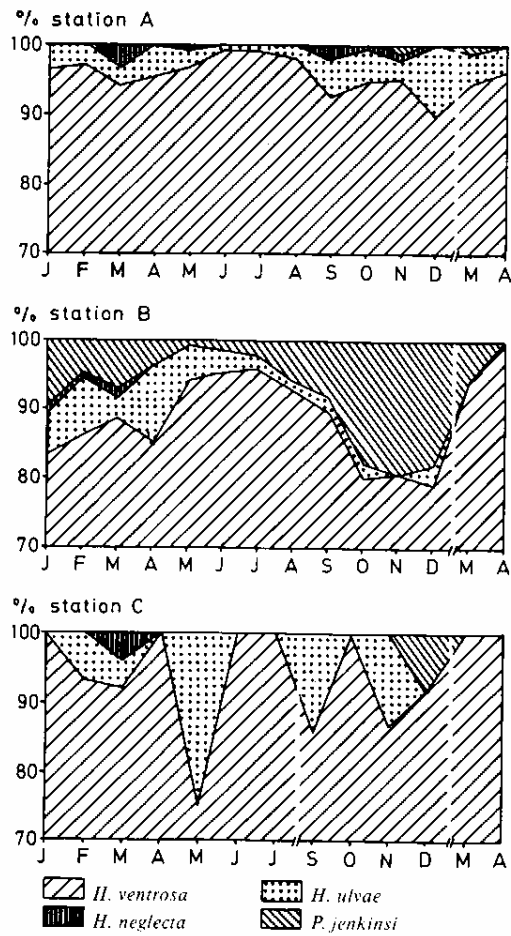


Figure 6: Dominance of the 4 observed species of hydrobiids in 1990/1991.

Almost all samples from stn. A contained more females than males, the mean sex ratio being 1.7 : 1, but in August females were five times as numerous as males. The sex ratio was almost balanced only in March. Females usually predominated at stn. B as well, but the ratio of 1.3 : 1 was somewhat more balanced. However, males predominated with a ratio of 1.3 : 1 at this station in November/December 1990 and March 1991.

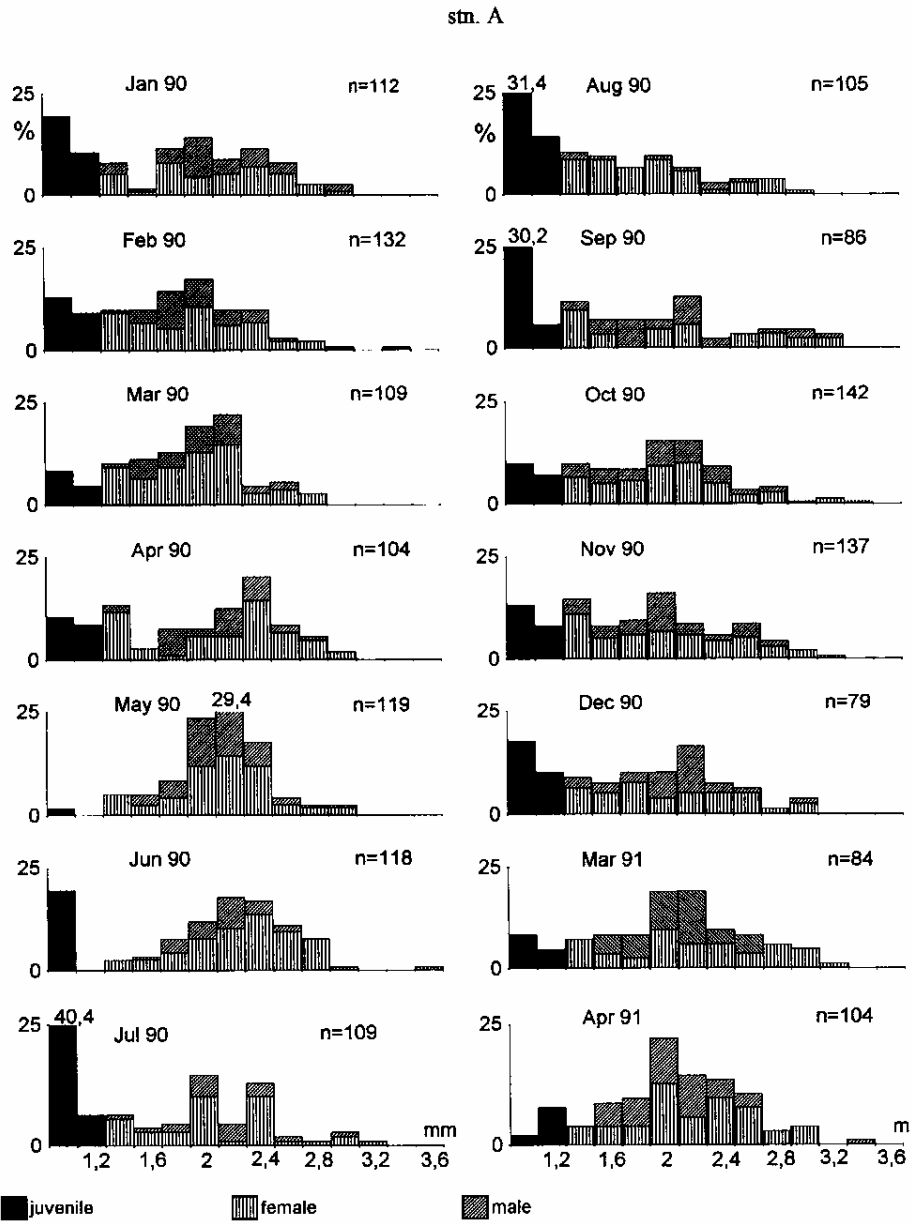


Figure 7: Size-frequency distribution of *H. ventrosa* at site A in 1990/1991.

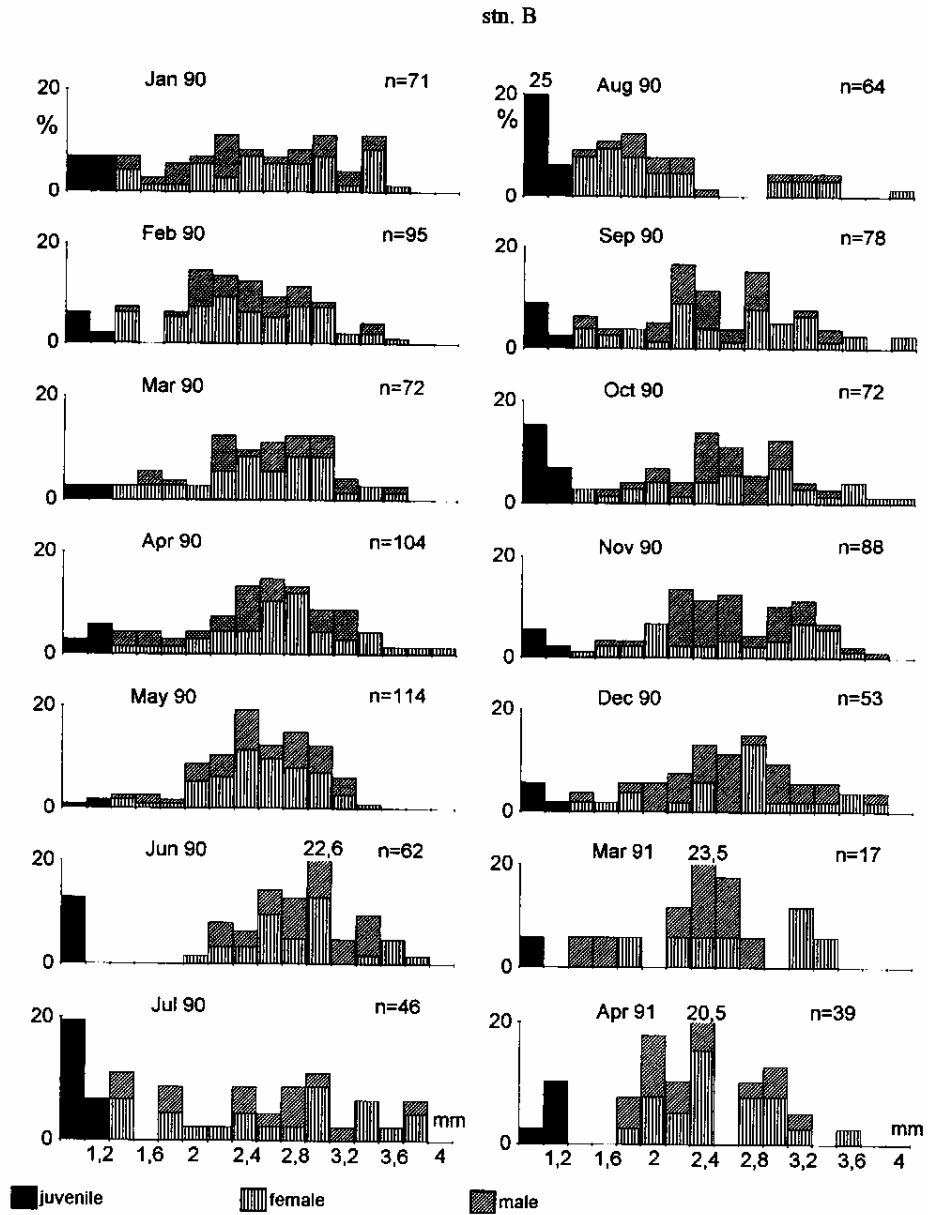


Figure 8: Size-frequency distribution of *H. ventrosa* at site B in 1990/1991.



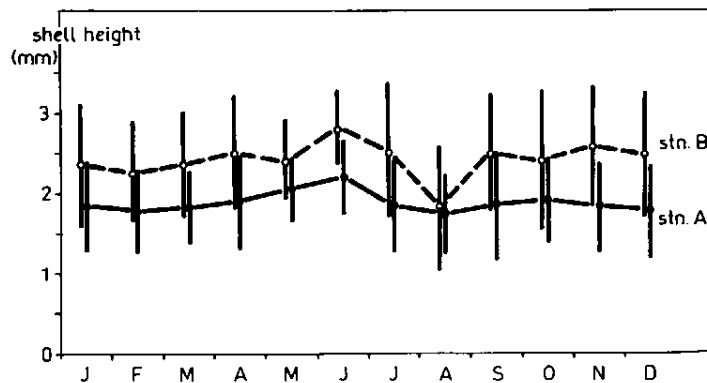


Figure 9: Medium shell height of female *H. ventrosa* at site A and B in 1990 ( $\times \pm$  sd).

#### 4. Discussion

In view of their abundances and dominances, hydrobiids can be considered a dominant group in the eulittoral community of the investigation area. Similarly high abundances of 20 to 40,000 ind./m<sup>2</sup> have been reported for Danish and English waters, for instance by SIEGISMUND (1982) and MORRISEY (1990). REISE (1987) even observed mean abundances of up to 84,000 ind./m<sup>2</sup> (up to 663,000 ind./m<sup>2</sup> in the case of juveniles) in the North Sea waddens. The wet weights of about 40 g/m<sup>2</sup> at stn. A and B in 1990 also indicate the importance of these snails for shallow water communities and benthophagous organisms (e.g. fish and waders).

The clear dominance of *H. ventrosa* among the hydrobiids we found was not surprising. This species is a typical inhabitant of lenitic tideless brackish waters (LASSEN and HYLLEBERG, 1978; HYLLEBERG, 1986). In contrast, *H. ulvae* prefers regions with higher salinities and greater exposure (MUUS, 1967; HYLLEBERG, 1986) and is consequently found in the deeper (brackish submersal) and lotic regions of the Baltic Sea (SCHÜLER, 1984). *H. neglecta* also requires higher salinities and was therefore rare in our study area. *P. jenkinsi* is a freshwater species which often penetrates into brackish regions. However, since it can not tolerate low temperatures in a brackish water environment (HYLLEBERG and SIEGISMUND, 1987), it suffers from high mortality in winter.

The differences in abundance shown by our studies must be considered in connection with sediment quality at the different stations. This becomes particularly apparent if the abundances and dominances are considered in relation to the organic content of the sediments. The highest abundances during the period from 1988 to 1991 were recorded at stn. A with a mean organic content of the sediment of 1.0% dw (Table 1). Even a reduction to 0.6% dw in the winter of 1991 reduced the abundance at this station (Fig. 2). An increase in the organic content by about 0.7–1.1% to a total of 1.6–2.0% dw at stn. B (and at stn. A in 1984/85) also led to a lower abundance. FORBES and LOPEZ (1990) have shown that *H. truncata* also prefers a certain sediment type. They found that abundances were highest (4,550 ind./m<sup>2</sup>) at an organic content of 1.4%. Higher and lower organic contents led to distinctly lower population densities.

Experiments with *H. ulvae* revealed that the optimum density with corresponding sediment parameters was about 10,000 ind./m<sup>2</sup>. Higher densities led to behavioural changes such as emigration, climbing and coprophagy (LOPEZ-FIGUERA and NIELL, 1987). It has been pointed out, however, that the "optimal" densities in the laboratory are considerably lower than observed in natural biotopes (MORRISEY, 1987).

Physical factors such as currents or wave exposure may also affect population densities in the area we investigated. The relatively large mean grain diameter at stn. A indicates fairly strong water movements, and it is therefore possible that drifting individuals accumulate there.

The differences in shell height of the dominant species, *H. ventrosa*, at stn. A and B must also be considered in connection with the abundance figures (Fig. 9). The males and females at stn. B are 0.5 (23%) and 0.4 (17%) millimetres larger than at stn. A. Differences in shell height between specimens of sympatric or allopatric hydrobiid have often been reported and sparked off the "character displacement" controversy (FENCHEL, 1975 a, b, 1988; CHERRILL, 1988; CHERRILL and JAMES, 1987). Our results show that sediment quality and, perhaps, abundance seem to influence the shell height of *H. ventrosa*. In other words, the size of the snails is not governed by interspecific competition alone, growth and size obviously being affected by other factors besides. It seems possible that the higher organic content and the consequently better food potential of stn. B played some role in enhancing growth at this station. Our results certainly show that individual biomasses of *H. ventrosa* are higher on sediments with a high organic content. The relation between the length and weight of animals larger than 1.2 mm is  $WW \text{ (in mg)} = -2.144 + 1.921 * L \text{ (in mm)}$  ( $n = 213$ ,  $R^2 = 0.98$ ) at stn. A and  $WW \text{ (in mg)} = -2.514 + 2.142 * L \text{ (in mm)}$  ( $n = 266$ ,  $R^2 = 0.98$ ) at stn. B. MORRISEY (1990) reported that the mean biomass of *H. ulvae* specimens living on a fine mud substrate was higher than that of specimens living on muddy sand. On the other hand, the more intense intraspecific competition resulting from the high abundances at stn. A might also inhibit growth. Probably both factors are involved. We found no sign of differences in parasite infestation, which can also cause affect in growth rates (ROTHSCHILD and ROTHSCCHILD, 1936; MORRISEY, 1990). According to FORBES and LOPEZ (1990), different growth rates and population densities can also result from differences in the time of juvenile recruitment. The first juveniles were found in June at both stations in 1990, so that differences due to this factor can be ruled out in our case. However, strikingly more juveniles were found at stn. A (about 15,000 ind./m<sup>2</sup>) than at stn. B (4,000 ind./m<sup>2</sup>) in July, 1990. The higher abundance at stn. A might well cause greater competition for food among juveniles and could, therefore, possibly account for the lower growth rate.

At stn. B, the first generation (June/July) had grown to about 2.5 mm (Fig. 8) by September, whereas at stn. A they were only 2.1 mm high (Fig. 7). The later onset of the second reproduction phase in autumn at stn. A supports the hypothesis of slower growth at this station. According to LASSEN and CLARCK (1979), *H. ventrosa* takes 13 weeks to achieve sexual maturity. An increase in the proportion of juveniles was recorded at stn. B in October, i.e. 16 weeks after the first recruitment period (Fig. 7), but no similar increase was observed at stn. A until December (Fig. 8).

Owing to the lower abundance, but higher individual biomass, at stn. B, the mean wet weight was similarly high at both stations (about 38 g/m<sup>2</sup> at stn. B and 43 g/m<sup>2</sup> at stn. A). This indicates that the given potential of the biotope is expressed in terms of a certain biomass. This biomass is obviously achieved either by high abundance or high individual biomass.

When seeking the factors causing differences in abundance and shell height among hydrobiids, it would be wrong to consider only sediment quality and the intra- and interspecific competition without taking the remainder of the benthic community into account. *Corophium volutator* and *Amphichaeta sannio*, both of which are also substrate and diatom feeders, achieved abundances of up to 55,000 ind./m<sup>2</sup> and 350,000 ind./m<sup>2</sup> at stn. A. In view of these enormous individual densities, interactions with hydrobiids must be regarded as very probable.

### Summary

The hydrobiids regarded as character species in European coastal waters were studied at three stations in a shallow tideless water on the south coast of the Baltic Sea. The three stations differed mainly in terms of sediment quality.

Four hydrobiid species were found: *Hydrobia ventrosa*, *H. ulvae*, *H. neglecta* and *Potamopyrgus jenkinsi*. A distinct relationship was found between sediment parameters and both abundance/dominance and shell height. The abundance was highest (40,000 ind./m<sup>2</sup>) at stn. A, where the organic content of the sediment was lowest and the mean grain size largest. The abundance was lowest (4,000 ind./m<sup>2</sup>) at stn. C, the station with the highest organic content and smallest mean grain size. *H. ventrosa* was clearly the dominant species at all three stations. A negative correlation was found between abundance and shell size of this species. The females and males at stn. B (about 18,000 ind./m<sup>2</sup>) were on the average 23% and 17% larger respectively than at stn. A (about 40,000 ind./m<sup>2</sup>).

Slower growth of the summer population at stn. A delayed the second reproduction phase by 6 to 8 weeks relative to stn. B. This was probably due to interspecific competition. The sex ratio in the *H. ventrosa* population was 1.3–1.7:1 (females:males) at both stn. A and B.

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