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The Effect of Salinity and Temperature on Egestion in Mud Snails (Gastropoda: Hydrobiidae)

A Study on Niche Overlap

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Summary. A comparative study of egestion in three species of mud snails under controlled conditions of salinity ranging from 10 to 30‰, and temperatures ranging from 5 to 35° C, shows that *Hydrobia ulvae* has maximal egestion at the combination of high salinity (30‰) and high temperature (30° C). In *Hydrobia neglecta* a peak of egestion occurs at the combination of 25‰ salinity and 25° C. *Hydrobia ventrosa* shows a small maximum at 20‰ and 30° C. However, in contrast to the former two species the egestion is rather uniform over the range of salinities and temperatures tested.

Considering egestion as a measure of activity at combined temperature and salinity, there is a moderate degree of overlap of this niche axis. The often observed co-existence of the three species is discussed in relation to the present findings and other evidence illustrating the width of the niches. It is concluded that co-existence, in spite of interspecific competition, is possible provided the environment is sufficiently unpredictable.

Introduction

Muus (1967) showed that the three species *H. ulvae, H. neglecta* and *H. ventrosa* behaved differently in salinity gradients. Specific crawling pictures revealed that *H. ulvae* did not crawl into water with a salinity lower than 9‰. *H. ventrosa* revealed high activity at salinities down to 4‰ while *H. neglecta* occupied a position in between and did not crawl into water of less than 8‰ salinity.

Muus did the study at room temperature. However, it is well known that combinations of salinity and temperature affect the activity of marine animals in various ways. Among others interspecific competition, reproduction, and feeding are influenced by the combined factors of temperature and salinity (Brenko and Calabrese, 1969; Manzi, 1970; Tietjen and Lee, 1972; Dennert, 1974).

The purpose of this study is to estimate the role of temperature on egestion in mud snails when the salinity is constant and vice versa. Egestion is considered a measure of snail activity and quantification of this parameter can be used to judge the optimal conditions of a snail species at a certain combination of physical factors, *i.e.* within the fundamental niche of the species. In this study salinity and temperature effects are discussed in the sense of Levins (1968) who defines the fundamental niche as the part of the environment which an organism could exploit according to its physiology. Within the fundamental niche is a realised niche determined by the resistance of the environment in the form of among others interspecific competition and physical barriers to the organism.

In accordance with other experimental studies, *e.g.* Muus (1967) it is found that the fundamental niche of mud snails is very broad with a nearly complete overlap on a qualitative basis. However, on a quantitative basis there are optima of activity showing marked differences and reducing the degree of overlap within the fundamental niche. The purpose of this study is to estimate these differences and discuss them in the relation to the realised niche of the snails, *i.e.* the distribution of *Hydrobia* spp. in nature.

Materials and Methods

Hydrobia ulvae (Pennant), *Hydrobia neglecta* (Muus), and *Hydrobia ventrosa* (Montagu) used for experiments at the Rønbjerg Marine Laboratory were collected in the Limfjord at Lendrup and Aggersund. Snails for experiments at the University of Aarhus were collected in a brackish-water pool near Kalø Castle Ruin.

The experiments were carried out in steps of 5‰ salinity, starting at 10‰ and ending at 30‰. The temperature was controlled in steps of 5° C, starting at 5° C and ending at 35° C. All experiments were repeated four times, although some experiments, especially with *H. ulvae* were repeated ten times. The experiments with *H. ulvae* were all made at Rønbjerg where a few experiments with *H. ventrosa* and *H. neglecta* also were made in the period from April to July 1973. Most work, however, with the latter two species was made from September 1973 to February 1974 in Aarhus.

The snails at Rønbjerg were fed and kept at the salinity (about 25‰) and temperature of the running sea water between the experiments. The experiments with low temperatures were made in the spring and the higher temperatures were tested in the summer, resulting in some adaptation to temperature but not to salinity.

The snails used in Aarhus were transferred step-wise from low to high salinities and temperatures and fed and kept at room temperature between the experiments, resulting in some adaptation to salinity but not to temperature. However, no difference was found between the experiments at Rønbjerg and Aarhus with respect to feeding activity.

Surface sediment from the sampling localities was sieved (wet) in 25‰ sea water and the fraction of sediment smaller than 63 μm added to Erlenmeyer flasks with 100 ml water adjusted to the desired value. Low salinity was obtained with demineralized water and high salinities by addition of sea water concentrated by evaporation. The flasks with 50 snails added per flask were immersed in a constant temperature bath for 24 hrs. Then the snails were sampled, dryed on blotting paper and weighed. The sediment and feces mixture was sieved wet in 25‰ sea water by use of a 80 μm sieve which retained the fecal pellets. In demineralized water, the pellets fell apart during the sieving. This was avoided in sea water.

The uneaten sediment and the separated pellets were transferred to tubes centrifuged and the supernatant sucked off. The samples were washed with demineralized water, centrifuged and the particulate material transferred to crucibles and dryed at 105° C for 18 to 24 hrs. The crucibles were cooled in a desiccator, weighed and the content ignited at 480° C for 12 hrs. After cooling in a dessicator the loss on ignition was estimated on a micro-balance.

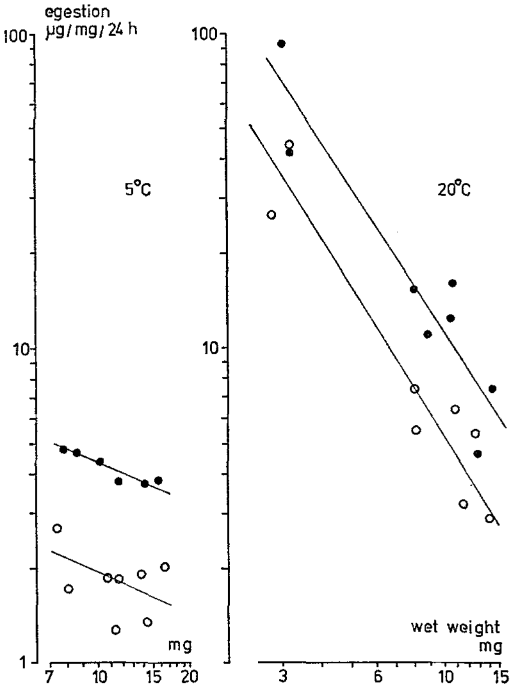
The salinity was measured on a conductivity meter (Radiometer, Copenhagen) calibrated with standard sea water (Charlottenlund, Denmark).

Results

1. Egestion in *Hydrobia ulvae*

Three size classes of *H. ulvae* were studied, viz. large individuals with a wet weight of 15–17 mg, medium sized (10–13 mg) and small sized (7–9 mg) individuals. One sample of juvenile snails (about 3 mg) was tested at 20° C at salinities from 10 to 25‰.

Egestion is calculated as loss on ignition because this value showed less variation than the total amount of feces, including inorganic particles. Fig. 1 shows that the egestion at 20° C calculated as μg ash free organic matter per mg per 24 hrs was about 14 times higher in the juveniles compared with the large snails. However,



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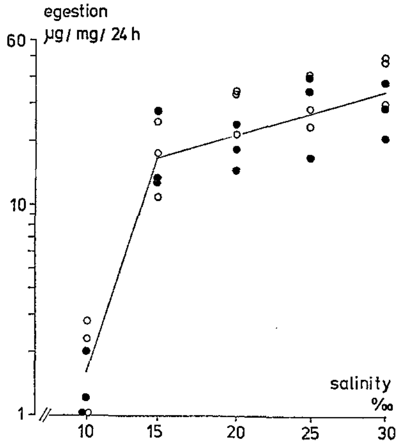

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Fig. 1. Egestion rates per unit weight of *Hydrobia ulvae* in relation to the size of the snails. Measurements at two salinities: $15\,^0/_{00}$ (open circles) and $25\,^0/_{00}$ (filled circles) at constant temperatures of 5 and 20° C

Fig. 2. Egestion rates per unit weight of *Hydrobia ulvae* at 30° C and five salinities. Individual measurements of snails with an average wet weight of 8 mg (open circles) and 10 mg (filled circles

the egestion rate in relation to body size depended much on the temperature and to a lesser degree on the salinity. At 5° C the egestion per mg wet weight was 25% higher in a 7 mg individual compared to a 15 mg individual. At 20° C the difference was 86% over the same weight range.

Fig. 2 shows the variation in egestion measured in 6 replicates at 30° C, *i.e.* the optimum temperature in this species. There was a marked jump in egestion when the salinity rose from 10—$15\,^0/_{00}$. At increasing salinities the egestion increased but there was a high degree of scatter of the measurements at each salinity tested. The maximal output at $15\,^0/_{00}$ exceeded the minimal output at $30\,^0/_{00}$ salinity. The scatter is due to small differences in size of the 50 pooled individuals (*cf.* Fig. 1). The sieving procedure, variations in substrate quality and among the snails of course also contributed to the scatter. Mortality during the experimental period of 24 hrs did not contribute. Only at the lowest salinity of $10\,^0/_{00}$, especially in combination with the highest temperature of 35° C was mortality observed, influencing the calculated rates of egestion.

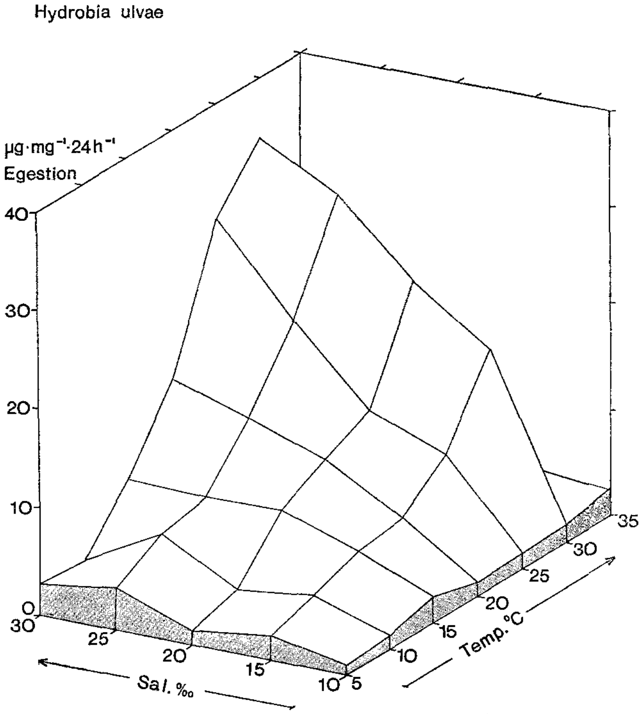

Fig. 3. Perspective plot of egestion in *Hydrobia ulvae* at 35 combinations of salinity and temperature

Fig. 3 summarizes the average egestion values obtained at 35 combinations of salinity and temperature in snails ranging from 7—17 mg wet weight. When the temperature was low (5–10° C) the egestion was low (0.9–4.1 μg/mg/24 hrs) at all salinities tested. The egestion increased with increasing temperature as well as salinity and the maximal output of feces occurred at 30° C and 30 ‰ salinity (35 μg/mg/24 hrs). At a temperature of 35° C the egestion dropped markedly at all salinities and the egestion was roughly the same (3–14 μg/mg/24 hrs) as found at 20° C.

A temperature of 35° C is hardly experienced in nature and 30° C is rare although experienced for shorter periods. The optimal salinity of 30 ‰ is normally not found in the natural habitat of the specimens used in this study. However, as pointed out by Jansson (1962) the conception of euryhalinity does not exclude a preference for a certain part of the salinity scale.

2. Egestion in *H. neglecta*

The output of organic matter in the feces of *H. neglecta* was significantly higher than in *H. ulvae* when calculated per mg snail as shown in Fig. 4. This was partly due to the smaller size of *H. neglecta*, viz. 2.3 mg per individual and a selection for organic matter in the sediment (Hylleberg, in prep.).

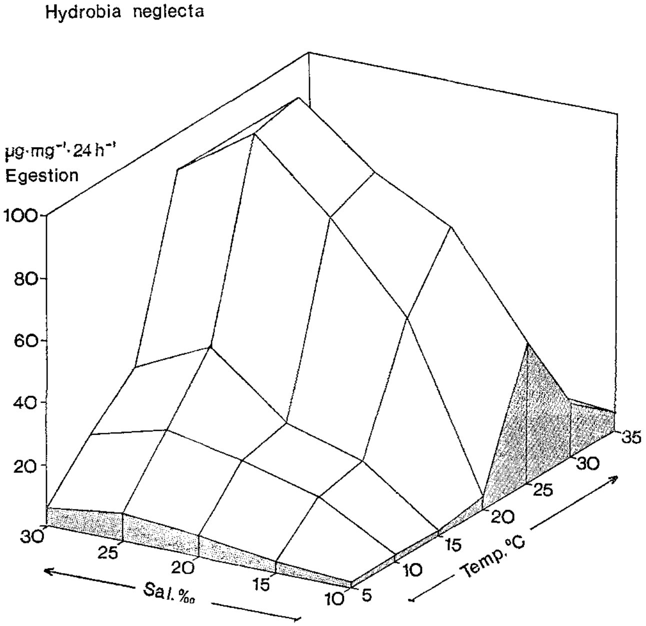

Fig. 4. Perspective plot of egestion in *Hydrobia neglecta* at 35 combinations of salinity and temperature

Like in *H. ulvae* the feeding activity was very low at low salinities (10–15 ‰) and low temperature (5–15° C). At increasing temperature (20–30° C) the egestion increased significantly. The maximum output of organic matter in feces occurred at 25 ‰ salinity and 25° C (103 µg/mg/24 hrs). At 35° C the egestion was similar to the egestion at 5° C, viz. about 5 µg/mg/24 hrs.

3. Egestion in *H. ventrosa*

The size of *H. ventrosa* was 2–3 mg, *i.e.* comparable to *H. neglecta*. With respect to the quantity of organic matter in the feces, *H. ventrosa* occupied a position in between the former two species. However, in contrast to those *H. ventrosa* increased feeding activity at lower salinities. An egestion of 40–60 µg/mg/24 hrs was maintained over the range of salinities from 10–30 ‰ and temperatures from 10–25° C (Fig. 5). The maximum activity (77 µg/mg/24 hrs) occurred at 20 ‰ salinity and 30° C. At 35° C the egestion was similar to what was found at 5° C.

Relative Egestion Rates

Due to size differences among the species and variable selectivity in feeding with respect to organic matter the patterns of egestion are easier to compare if calculated on a relative basis.

For each species of *Hydrobia* the highest egestion measured at a constant temperature is considered equal to 100% and the egestions over the salinity range

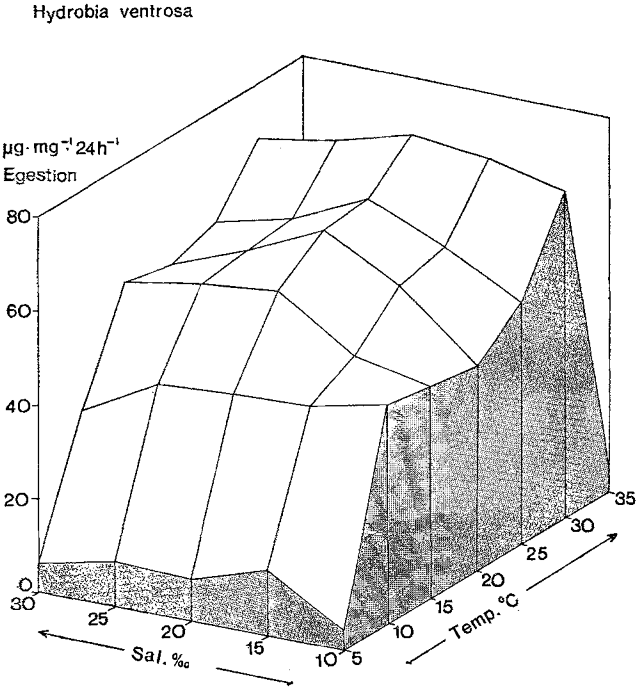

Fig. 5. Perspective plot of egestion in *Hydrobia ventrosa* at 35 combinations of salinity and temperature

calculated relative to this value. An example is shown in Fig. 6. However, the relative values at low temperatures must be interpreted with som reservation because of the small absolute amounts of feces (*cf.* Figs. 3–5).

The calculations show that at 5° C, *H. ventrosa* had the highest feeding activity at a salinity of $15^{0}/_{00}$. Compared to this value the egestion dropped to 30%, respectively 41% at 10 and $30^{0}/_{00}$ salinity. When the temperature increased these patterns were somewhat altered. In *H. ventrosa* the maximum at 10° C was observed at $10^{0}/_{00}$ salinity while at 15° C it shifted to $20^{0}/_{00}$ where it remained all the way up to 35° C (Fig. 6).

At 5° C *H. neglecta* increased its egestion steadily as salinity increased from 10–$25^{0}/_{00}$ where the maximum was found. At $30^{0}/_{00}$ the egestion dropped to 63% of the maximum egestion at this temperature (Fig. 6). The feeding activity at a given temperature was very salinity dependent, especially at temperatures below 20° C where the activity dropped to between 1 and 15% of the maximal value always found at $25^{0}/_{00}$ salinity.

In *H. ulvae* the maximum at 5–10° C also occurred at $25^{0}/_{00}$ salinity. At 15° C the peak covered 20–$30^{0}/_{00}$. At 20–35° C the salinity effect was very pronounced (Fig. 6). The egestion increased steadily with increasing salinity with a maximum at $30^{0}/_{00}$ salinity.

In summary it is concluded that *H. ventrosa* is the generalist among the three species with regard to the abiotic factors tested. Although a small maximum was

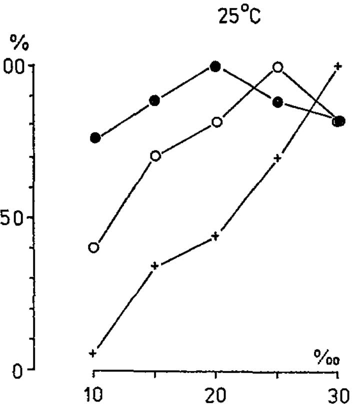

Fig. 6. Relative egestion rates in *Hydrobia ventrosa* (filled circles), *Hydrobia neglecta* (open circles) and *Hydrobia ulvae* (crosses). Calculated at 25° C and five salinities

found at 20 ‰ salinity, *H. ventrosa* maintained a high feeding activity (more than 50 %) over the range of salinities from 10–30 ‰. The egestion at these salinities was dependent on the temperature but the effect was moderate, *i.e.* more than 50% activity was maintained at temperatures ranging from 10–30° C. Only in cold water (5° C) and very warm water (35° C) the activity of *H. ventrosa* significantly decreased.

H. neglecta is a specialist, being very sensitive to the salinity as well as the temperature. The optimum salinity was 25 ‰ and the activity decreased rapidly with decreasing salinity, especially below 15 ‰. The optimum temperature was from 20–25° C. Above and below this narrow range a rapid decrease in activity took place.

H. ulvae was also sensitive to the salinity but the activity at low salinity (10 ‰) was relatively high as long as the water was cool (5–15° C). With increasing temperature the activity increased along with increasing salinity, showing that *H. ulvae* is favoured by the combination of high salinity and temperature. In consequence, *H. ulvae* can be characterized as a moderate specialist. The activity of this species was less affected by low salinities (10 ‰) than was *H. neglecta*. It is noted that the absolute amount of feces was low at low salinity in all three species (*cf.* Figs. 3–5).

Discussion

Niche Overlap and Interspecific Competition

The early definition of the competitive exclusion principle has been stated as follows: Two species cannot co-exist if they occupy the same niche. This definition has proved unacceptable to many ecologists because of difficulties in defining the term niche since it encompasses virtually all facets of the existence of a species (Jaeger, 1974). Some of these facets are discussed in the following.

Species are per definition genetically distinct and in consequence species are exposed to differing selective criteria which again implicates that related species normally display superiority at opposite ends of environmental gradients. In

Hydrobiids this has been found in laboratory experiments at room temperature for 17 months. *Hydrobia ventrosa* showed a feeding optimum in the brackish part of the saline spectrum but it grew only slightly better at $7^0/_{00}$ salinity compared to $25^0/_{00}$. In contrast the mortality was significantly lower at $7^0/_{00}$ compared to $25^0/_{00}$. *Hydrobia ulvae* grew significantly better at $25^0/_{00}$ than at $7^0/_{00}$ and it also survived better at $25^0/_{00}$ (Fenchel, personal communication). In agreement *H. ulvae* had feeding optimum in the saline end of the studied range. However, in habitats intermediate with respect to the fresh water and sea water ends, co-existence is common between two or three *Hydrobia* spp. In general co-existence of congeneric marine invertebrates is quite common and the number of sympatric species may be high. For example, I have found four species of benthic clams (*Macoma* spp.) within one square meter of intertidal mud in the Pacific North West of US.

If all dimensions of the niche of a species are measured in order to describe the fundamental niche as defined by Hutchinson (1957) (the niche is a set of points in an n-dimensional space where the n-dimensions are environmental parameters), it is likely that no or only little overlap will be found between the niches of related species since the species are genetically different. It follows from this consideration that co-existing species will have different niches and according to the early definition of niche it can be stated, by circular reasoning, that since the species are different they may co-exist.

Although the *Hydrobia* species actually are very different, *i.e.* with a moderate degree of overlap in all dimensions studied so far there is no doubt that competition among *Hydrobia* spp. occurs in natural habitats. The situation is comparable to *e.g.* mussels (Harger, 1972). In the laboratory, exclusion or severe competition among *Hydrobia* species having limited resources is easily demonstrated (Fenchel, personal communication). Other examples are the classic experiments with fluor beetles.

An important question is therefore: How different must species be in order to be sufficiently different to co-exist in spite of competitive interactions between the species? The present study shows that at a certain combination of salinity and temperature the three species of mud snails have distinct optima of feeding activity, *i.e.* utilization of a common food resource. However, at other combinations of physical factors, the optima either completely overlap or they are even more widely separated. MacArthur (1972) states that the co-existence of two or more competitors become rapidly more precarious as the distance between their resource mean values approaches $\sqrt{2}$ times their standard deviation. In the present study calculation of resource utilization functions cannot be made from the data shown in Fig. 6 by plotting egestion versus salinity because the functions are not normal and because of the shift in position of the optima mentioned above, so I see no simple answer to the question raised. Fenchel (1975b) treats the problem from other view points.

The Niche in Relation to Distribution and Growth

The width of the niche is determined by the overall genetic constitution of the organism so genetic diversity often determines niche width (MacNaughton and Wolf, 1970). The *Hydrobia* species seem to be in accordance with this concept judged on basis of isoenzymes (Lassen, personal communication). As pointed out by Levins (1968) the width of the niche is usually associated with the abundance of the organism. He concludes that a broad niche is optimal in an environment which is uncertain. In agreement the abundant *H. ventrosa* and *H. ulvae* have a significant width of their niches as found in the present study while *H. neglecta* is rarer (Fenchel, 1975a) and has a narrow niche.

The natural habitats of Hydrobiids are characterized by fluctuating environmental factors, *e.g.* salinity (Muus, 1967; Fenchel, 1975a). With respect to salinity *H. ventrosa* is "jack of all trades" (MacArthur, 1972). However, because *H. ventrosa* is capable of propagating over a wide range of salinities it must compromise its efficiency at each salinity. In agreement the species is slow growing at all salinities compared to the more specialized *H. ulvae* and especially *H. neglecta.* High efficiency at certain salinities involves reduced efficiency at other salinities since a premium usually is put on efficiency (MacArthur, 1972). In agreement *H. ulvae* and *H. neglecta* grows rapidly given optimal conditions and show reduced growth at decreased salinities (Hylleberg, unpublished).

H. neglecta is especially interesting in this context because of an obvious specialization in spite of its occurrence in fluctuating environments. With respect to feeding activity and digestive enzyme activities *H. neglecta* is sandwiched in between the two other species studied. In consequence, Fenchel (1975a) refers to it as a fugitive species. This may be the case in the region of overlap with one or two congeneric species but in its region of environmental optima it is certainly not a fugitive species (see "Note Added in Proof").

Prediction of Hydrobiid Distribution

Muus (1967), Rasmussen (1973) and Fenchel (1975a) show that the distribution of *Hydrobia* spp. is related to environmental factors, above all salinity. However, in order to secure a better understanding of the distribution of mud snails, the food availability must be studied further, in addition to interspecific competition which may be brought about by formation of fecal pellets, excluding potential food items from the diet of another species. Other possibilities are excretion of metabolites increasing mortality of co-existing species and retarding growth as found in mosquitoes (Moore and Fisher, 1969). This will be potentially significant in pools and other areas with limited water exchange. The significance of parasites and predation is also untreated in any detail. In accordance with Smidt (1951) I have found mud snails very sensitive to predation, especially by Crustaceans. As a matter of fact I find it a challenging question why Hydrobiids are absent from large areas harbouring all the species associated with Hydrobiids where these are abundant. The patchy occurrence of mud snails may well be caused by predators. Laboratory experiments have shown that it is not due to lack of food items in the sediment and migration cannot explain the absence either. No physical barriers prevent migration from nearby areas with dense populations. Where *Hydrobia* spp. occur, fresh water often seeps out and may influence the presence of predators, especially the common shore crab.

As previously mentioned *H. ventrosa* is slow growing under all conditions but as it obviously maintains its feeding activity over a wide range of salinities and temperatures, it may grow to nearly the same size as *H. neglecta* where they live sympatrically. This has been found in the three localities examined so far and agrees with Fenchel (1975b) *H. ventrosa* is rather sensitive to environmental stress, especially drying out (Muus, 1967; Hylleberg and Lassen, in prep.). Under unfavourable conditions populations are likely to go extinct. This may be one reason why *H. ventrosa* is often replaced by *H. ulvae* at low salinities where *H. ventrosa*, according to the present study should be competitively superior. Fenchel (1975a) discusses other view points.

On an overall basis *H. ulvae* seems to be the most tolerant of the three mud snails with respect to environmental stress, so the species can be expected to be present in most localities allowing the existence of *Hydrobia* spp. However, due to extreme tolerance towards environmental stress the species will survive under sub-optimal conditions like coarse sediment and/or reduced salinity but the individuals will grow to a smaller size and the population density will be low compared to more saline and fine grade deposit areas (Newell, 1965).

In summary the present study and the results in preparation indicate that the niche overlap of the three species is moderate and co-existence should be possible for two or three species in meso- and polyhaline areas. The obvious existence of interspecific competition need not necessarily lead to competitive exclusion (Miller, 1967), but co-existence presupposes that the environment is sufficiently unpredictable and complex, so that the advantages can fluctuate between the congeneric species both in space and time. No doubt, co-existence depends on historical events like extinction and immigration but it also strongly depends on environmental factors due to superior capacities of individual species in exploiting the resources at opposite ends of environmental gradients. When the environment is predictable only one species is really successful so along with the predictability goes the probability of allopatric occurrence of only one species.

Note Added in Proof. Studies on the distribution of Hydrobiids in the Kattegat between Grenaa and Horsens from May-August 1975 show that *Hydrobia neglecta* is the dominating species making 70% of the 10000 individuals examined from 50 localities. *H. ventrosa* makes 29% and *H. ulvae* the remaining 1% of the individuals. The Hydrobiids live sympatrically in 43 of the localities, usually *H. neglecta* together with *H. ventrosa*. The study is continued together with H. Heidemann Lassen.

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