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Size of mudsnails, *Hydrobia ulvae* (Pennant) and *H. ventrosa* (Montagu), in allopatry and sympatry: conclusions from field distributions and laboratory growth experiments

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Abstract

In most areas, sizes of the two mudsnails Hydrobia ulvae and H. ventrosa diverge when their distributions overlap, while in allopatry they are about equally large. This has been suggested as an example of character displacement, although later studies suggest alternative interpretations. In this study, distribution and snail size of both species was assessed in 30 localities on the Swedish West coast, both allopatric sites of each species and sympatric sites. Overall, mean sizes varied considerably among populations; in H. ulvae mean size range was 2.0-4.5 mm and in H. ventrosa 2.2–3.6 mm. Mean sizes in allopatry were roughly similar, while in sympatry H. ulvae was always larger than H. ventrosa. In the field, snail size of both species increased with increasing silt content of the sediment. However, silt content alone seemed unable to explain the character displacementlike pattern as growth in the laboratory was not differently affected by sandy or silty sediments. In the laboratory, however, snails of both species grew at various rates over sediments from different bays, suggesting environmental effects other than grain size. Furthermore, H. ulvae constantly grew at about 150% the rate of H. ventrosa when grown under the same conditions. This suggests that the divergence in size in sympatric sites is due to intrinsic growth rate differences, which persist over a range of environments. The similar sizes in allopatric sites may be explained by phenotypic adjustments to environmental factors. Our results reject inherited differences in growth rate among populations as an explanation of the character displacement-like pattern of size variation. We also argue that differences in recruitment time seems an unlikely explanation. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Character displacement; Environmental effects; Growth rate; Size differences

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1. Introduction

Where they occur alone, the two marine gastropods *Hydrobia ulvae* and *H. ventrosa* have more similar size ranges than in sites where both species occur; here *H. ulvae* is always larger than *H. ventrosa* (Fenchel, 1975b; Cherril and James, 1987; Saloniemi, 1993, however, see Hylleberg (1986) for a different result). The shell size divergence in sympatry is suggested to be a consequence of interspecific competition for a common food resource (Fenchel, 1975a,b; Fenchel and Kofoed, 1976). Indeed, this has been considered a classical example of character displacement (e.g. Arthur, 1982; Barnes and Hughes, 1982; Levinton, 1982). The suggested mechanism was competition for food-particles (mostly diatoms) between the two species which led to selection for traits reducing the overlap in resource requirements (Fenchel, 1975b). At sympatric sites where *H. ulvae* is larger, on average, than *H. ventrosa*, the former presumably eats larger food particles than the latter, and this supports a model of character displacement (Fenchel, 1975b).

The hypothesis that size variation in *Hydrobia* is a result of character displacement has, however, been challenged. Recent studies have, for example, observed that snail size and abundance are correlated with environmental factors (Cherril and James, 1987; Saloniemi, 1993). Hylleberg (1986), analysing Danish populations, found the same size ratios between *H. ulvae* and *H. ventrosa* in allopatry as in sympatry and suggested that environmental factors cause the intraspecific size variation between populations. Several studies suggest a coupling between sediment type and snail size. Chatfield (1972); Fish and Fish (1974) and Morrisey (1990) all found *H. ulvae* was larger in muddy than in sandy sites. However, Barnes (1988) proposed water movements rather than sediment composition being important, noting that other factors, such as predation and parasitism, cannot be ruled out. These studies all suggest that snail size and distribution of *H. ulvae* and *H. ventrosa* are direct effects of environmental conditions rather than inherited effects of evolutionary processes.

It is very important to stress the assumption of the character displacement model that the intraspecific differences between allopatric and sympatric populations should be inherited (Brown and Wilson, 1956; Connell, 1980). As stressed by Arthur (1982), the assumption of inheritance has not been adequately tested in *Hydrobia*. If, for example, populations of *Hydrobia* have inherited differences in snail growth rate or in time of recruitment, these differences may result in differences in snail size among populations established by evolution. Alternatively, different snail sizes may be explained as environmentally induced non-genetic differences among populations.

The mode of reproduction differs between the two species of *Hydrobia*. While *H. ulvae* has a planktotrophic larval development *H ventrosa* lays egg-masses which hatch directly into young crawl-away stages. This suggests gene-flow among populations of *H. ulvae* is probably much more frequent than among populations of *H. ventrosa*. An effective gene flow largely prevents genetically based differentiation on a local scale, as is evident from allozyme studies of intraspecific differentiation in other genera of prosobranch gastropods (e.g. Janson, 1987; Johannesson, 1992; Reid, 1996). That is, genetically based differences in size, as predicted from a model of character displacement, would be much more likely in *H. ventrosa* than in *H. ulvae*.

Arthur (1982) lists four criteria for a conclusive demonstration of character displacement between two species. Rejecting one of these criteria is enough to question the conclusion of character displacement. In this study we test two of Arthur's criteria.

One criterion is that the character should not change state smoothly when going from allopatric to sympatric sites, and thus what happens in the sympatric sites should not simply be a predicted consequence of variation over allopatric sites (Arthur, 1982). If, for example, snail size is correlated with sediment grain-size among allopatric localities, the changes between allopatric and sympatric sites must be more than expected from mere grain-size changes between allopatric and sympatric sites.

In this study we assess snail size distributions in habitats of different sediment type. These sites contain different proportions of the two species of *Hydrobia*. A gradual change in snail size over different sediment qualities (grain-size), without any systematic shifts going from allopatry to sympatry, challenges the character displacement hypothesis.

A second criterion which we examine is that of heritability. Arthur (1982) claims that 'if the character-difference under study has a low or unknown heritability then an evolutionary explanation such as character displacement is suspect'. Thus, in our study we test if the variation in size among different populations is due to genetic differences in growth rate among populations. A purely non-genetic variation in growth rate is incompatible with a model of character displacement for the studied populations.

2. Materials and methods

2.1. Size distributions and relative abundance in sites of different sediment type

The study area, the northern part of the Swedish west coast, is an atidal area (tidal amplitude ≤ 0.3 m) although altering wind directions and atmospheric pressures impose water level changes of more than a meter. Surface salinity is variable and influenced by the outflow of brackish water from the Baltic, as well as fresh-water runoffs from the near-by river Glomma. However, the variation is temporal rather than spatial, with surface salinities of 15–30‰, or even more.

In June 1993 we randomly chose 30 small bays among a larger number of bays inhabited by *Hydrobia*, over 30 km of coastline. The bays are differently influenced by water movements and have, as expected, a range of sediment structures. Coarse grained, sandy, sediment dominates in wave-affected bays while in more wave-protected bays the sediment is fine grained (silty).

In each bay, we took five samples of sediment with snails from shallow depths (<50 cm). The sampling area was either 0.008 m² or 0.04 m²; the larger area being used in sites with low densities of snails. All *Hydrobia ulvae* and *H. ventrosa* from each sample were gathered by firstly picking all snails emerging from the sediment when left undisturbed for some hours. Thereafter, the sediment was sieved using a 0.5-mm mesh size; a sufficient mesh size as no individuals smaller than 1 mm was found among the picked snails, and snails still buried in the sediment were caught. The size of each snail

(the distance from the apex to the anterior margin of the aperture) was measured to the nearest 0.04 mm with an ocular micrometer.

As the sampling was made in June before expected time of recruitment, and as populations of *Hydrobia* at these latitudes only have one period of recruitment per year (Lassen and Clark, 1979), the snails of a sample picked in June ought to be at least about 1 year old. Furthermore, most individuals die before the end of their second year (Barnes, 1990; Sola, 1996), which implies that most snails belong to the cohort of 1 year old snails.

The grain-size in each bay was determined from a sample of the uppermost 0.5 cm of the sediment which was sieved and weighed following Buchanan (1984). The size-fraction smaller than 64 μ m, which contained silt and clay, was not further separated. The silt-clay fraction divided by the weight of all fractions smaller than 1 mm was taken as the proportion of silt.

To assess the temporal variation in abundance and size distribution we compared the results from June 1993 with data from ten, four and six of the same localities sampled in October 1989, July 1996 and July 1997, respectively.

2.2. Growth rates on different sediments

Growth of young individuals of both species over 2 months was measured in the laboratory. We used two different sediment qualities; 'sandy' with maximum 4.3% silt-clay, and 'silty' with at least 22.9% silt-clay, each represented by sediment from three bays. Snails were from both sympatric and allopatric sites, five with small average adult snail sizes and five with large adult snail sizes. The populations and sediments used were from the following localities (see Table 1): *H. ulvae* populations: 3, 4, 6, 7, 8, 10, 14, 15, 17, 21, *H. ventrosa* populations: 7, 10, 12, 14, 15, 21, 22, 23, 29, 30, sandy sediments: 12, 14, 15, and silty sediments: 21, 22, 30. All snails living naturally on the sediments were removed before the experimental snails were introduced.

Each experimental snail was marked with paint and put in a separate plastic cup with a 1-cm layer of sediment covered by salt water (20‰). The bottom area of the container was 13 cm² corresponding to a population density of 770 m⁻². The water was changed once during the 2 months experiment, but distilled water was added several times to compensate for evaporation. The cups were put in randomized order at a controlled temperature of 15°C in light intervals of 16:8-h light/dark cycle. The experiment started on the 15 August 1994 and was terminated 2 months later. To estimate growth, we measured the length (as described above), before and after the experiment. The increase in shell length was used as an estimate of growth.

2.3. Statistical analysis

Growth in the laboratory of snails of the two species and on different sediment types were analysed using a four-factor analysis of variance (ANOVA). The four factors analysed were two orthogonal factors, species (SP); a fixed factor with two levels (H. *ulvae* and H. *ventrosa*), and sediment type (SE); a fixed factor with two levels (sandy and silty). Each of these factors had one nested factor; population (P), a random factor

Table 1

Proportion of *Hydrobia ventrosa* in samples of *H. ventrosa* and *H. ulvae*, mean shell sizes (\pm S.D.) and densities of both species, in 30 localities on the north part of the Swedish west coast

Site	Proportion of <i>H. ventrosa</i> (%)	Silt	H. ulvae			H. ventrosa	H. ventrosa		
		(%)	Size (mm)	п	Density (ind./m ²)	Size (mm)	п	Density (ind./m ²)	
1	0.0	2.2	2.35 ± 0.38	27	324		0	0	
2	0.0	2.9	2.00 ± 0.56	38	182		0	0	
3	0.0	4.7	1.94 ± 0.44	160	768		0	0	
4	0.0	6.1	2.23 ± 0.68	136	653		0	0	
5	0.0	6.9	2.54 ± 0.50	43	1032		0	0	
6	0.3	12.2	3.14 ± 0.50	391	9385	2.56	1	24	
7	3.7	4.5	2.34 ± 0.45	336	8065	2.32 ± 0.41	13	312	
8	11.9	90.9	3.45 ± 0.50	229	5497	2.75 ± 0.33	31	744	
9	13.9	5.4	2.45 ± 0.48	62	1488	2.51 ± 0.27	10	240	
10	19.0	74.3	3.43 ± 0.49	315	7561	2.52 ± 0.34	74	1776	
11	20.4	9.5	2.51 ± 0.45	242	5809	2.53 ± 0.35	62	1488	
12	22.6	4.3	$2.89 {\pm} 0.68$	65	1560	2.45 ± 0.39	19	456	
13	24.4	14.5	2.79 ± 0.42	609	7309	2.52 ± 0.21	197	2364	
14	29.2	3.5	2.67 ± 0.55	525	6301	2.15 ± 0.28	217	2604	
15	35.9	2.7	2.45 ± 0.66	152	730	2.32 ± 0.34	85	408	
16	49.3	4.0	2.74 ± 0.37	171	4105	$2.54 {\pm} 0.28$	166	3984	
17	49.6	34.2	2.99 ± 0.60	335	4021	2.73 ± 0.32	330	3960	
18	60.0	22.2	2.91 ± 0.53	12	288	2.60 ± 0.53	18	432	
19	69.5	69.7	3.81 ± 0.62	18	432	2.66 ± 0.34	41	984	
20	73.7	29.4	4.50 ± 0.43	5	120	$2.86 {\pm} 0.38$	14	336	
21	76.8	49.9	3.59 ± 0.68	33	792	3.13 ± 0.46	109	2616	
22	81.2	22.9	$3.58 {\pm} 0.56$	24	576	3.05 ± 0.43	104	2496	
23	83.8	57.5.	3.86 ± 0.72	36	864	3.22 ± 0.40	186	4465	
24	88.9	74.1	4.27 ± 0.46	34	816	3.45 ± 0.47	273	6553	
25	92.1	43.6	4.10 ± 0.45	8	192	$3.58 {\pm} 0.61$	93	2232	
26	92.7	51.4	$3.86 {\pm} 0.78$	14	336	2.82 ± 0.43	177	4249	
27	93.5	51.9	2.81 ± 0.41	4	96	2.92 ± 0.31	58	1392	
28	98.7	9.3	3.46 ± 1.00	4	96	$2.19 {\pm} 0.52$	185	4441	
29	100	18.8		0	0	2.90 ± 0.43	224	5377	
30	100	31.6		0	0	3.15 ± 0.43	249	5977	

The silt content (as percent silt) of each locality is indicated.

with ten levels nested under species, and bay (B), a random factor with three levels nested under sediment type. Hence, the model of the ANOVA was:

$$x_{ijklm} = \mu + SP_i + P(SP)_{j(i)} + SE_k + B(SE)_{l(k)} + SP \times SE_{ik} + SP \times B_{il(k)} + P$$
$$\times SE_{j(i)k} + P \times B_{j(i)l(k)} + e_{ijklm}$$

where x_{ijklm} is growth of a specific individual, μ is the growth averaged over all treatments, and e_{ijklm} is the residual.

We used five replications of each treatment, that is, five snails with the same combination of factors. To obtain appropriate interactions (Hurlbert and White, 1993), and to reduce the heterogeneity of variances to a non-significant level (Cochran's test), we used the logarithm of growth $(\ln(\text{growth}+1))$ in the analysis. Degrees of freedom and expected mean sums of squares were calculated according to Underwood (1997) (p. 364–369). To obtain a balanced analysis, dead snails were replaced with the average growth of the survivors within the same treatment. This reduced the degrees of freedom in the residual of the ANOVA correspondingly (see Underwood (1997), p. 382). The design of the ANOVA model does not permit direct tests of the effects of species (*SP*), sediment type (*SE*), and the interaction $SP \times SE$. Valid tests were, however, obtained by pooling all non-significant interactions (P > 0.25) with the residual (Underwood, 1997, p. 375–377). We furthermore used a post-hoc test (Student–Newman–Keul's) to unveil differences among the levels of the significant factors.

3. Results

3.1. Size distributions and relative abundance of species

The proportion of silt-clay in the sediments varied between 0.02 and 0.91 (Table 1). Except for site 12, sediments with a silt-clay proportion less than 0.15 were all compact and sandy. Most sites which had silt-clay proportions higher than 0.15, and site 12, had black silty sediments with a high water content. The exceptions were sites 24 and 27, which had a sediment of compact grey clay.

There were large differences among localities in relative snail abundances and average body size of the two species (Table 1). The size distribution of each species at single sites (for sites with N>100) were all with a single peak, indicating that average size and standard deviation are good descriptors of size at the time of sampling. As expected, small snails (<1 mm) were absent in all samples, and thus all snails were 1 year or older.

Mean snail size was regressed on the habitat factor (% silt) for each of the two species, and both showed a positive relationship to habitat with 31 and 50% of the variation in mean size being 'explained' by the variation in silt concentration (Fig. 1). Mean snail size of *H. ulvae* was also regressed on % *ventrosa* in each sample (Fig. 2), and mean snail size of *H. ventrosa* was regressed on % *ulvae* (Fig. 3). These regressions indicated that mean size of *H. ulvae* increased with increasing proportion of *H. ventrosa* at a site, while *H. ventrosa* decreased in size when *H. ulvae* became more frequent. Moreover, % *ventrosa* and % silt were positively correlated (r=0.435, df=28, P<0.05, Fig. 4). Thus, *H. ulvae* generally dominated the sandy sites, with two exceptions, while *H. ventrosa* was the most numerous species in most silty sediments (Fig. 4).

Thus, in summary, sizes of both species increased with increasing silt content of the sediment. At the same time, the proportion of *H. ventrosa* was positively correlated with silt content. Thus, the increase in size of *H. ulvae* with increasing proportion of *H. ventrosa* could either be an effect of competition, or, an effect of a more silty sediment. Likewise, the decrease in size of *H. ventrosa* with increasing proportion of *H. ulvae* could be a result of inter-specific competition, or, a result of an increasingly sandy sediment which possibly disfavours growth of both species.



Fig. 1. Mean snail size (shell height, mm) of natural populations of *H. ulvae* and *H. ventrosa* in sites with different silt content of the sediment. Both regressions deviate from zero slope; *H. ulvae*: a = 0.0182b + 2.56, P < 0.001, $r^2 = 0.50$, and *H. ventrosa*: a = 0.00779b + 2.49, P < 0.01, $r^2 = 0.31$.

3.2. Temporal variation

Proportions of the two species in ten localities did not change between 1989 and 1993, as indicated by a positive correlation between counts of the same sites in both years $(n=10, r^2=0.56, P=0.01)$. In one locality, however, there was a shift in the proportion of *H. ventrosa* from 0.15 in 1989 to 1.00 in 1993. This was mainly caused by large numbers of *H. ulvae* in 1989. If this locality is excluded, the correlation in proportions between the years is almost perfect $(n=9, r^2=0.94, P<0.0001)$. The correlations between the proportions in 1993, and in 1996 and 1997, were also positive (1993–1996: $n=4, r^2=0.94, P=0.03; 1993-1997: n=6, r^2=0.94, P<0.01)$. Thus, the proportions of the two species are mostly stable through time, although rarely, sites may be affected by radical shifts.

3.3. Growth in the laboratory

The laboratory growth experiment was set up to assess the effects of two factors; species (SP) and type of sediment (SE), and their interaction, on growth rate of a snail using snails from different populations (P) and sediments from different bays (B) (see Section 2 for the complete linear model). Initial sizes of the two species, averaged over all individuals from all populations, were very similar at start of the growth experiment



Fig. 2. Mean snail size of *H. ulvae* in populations with different proportions of *H. ventrosa* and *H. ulvae*. The regression deviates from zero slope: a = 0.0147b + 2.43, P < 0.001, $r^2 = 0.57$.

(*H. ulvae* x = 1.49 mm, s = 0.18 mm and *H. ventrosa* x = 1.50, s = 0.17 mm). An insignificant number of snails (5.6%) were lost during the experiment, which suggests the results are not to any large extent affected by differential mortality.

The original ANOVA showed no significant interactions, not even at P < 0.25, and thus we were able to pool three of the four interactions into the residual (interactions; $SP \times B(SE)$, $SE \times P(SP)$, $P(SP) \times B(SE)$) (Table 2). After pooling we performed tests of all the main factors and the Species×Sediment interaction (Table 3). This ANOVA indicated that snail growth in the laboratory was significantly dependent on Species (SP), Population (P), and Bay (B) (Table 3). Growth rate were, however, neither affected by the Species×Sediment interaction nor by the Sediment factor alone. This suggested that the two sediment types we used (sandy and silty) did not affect growth rate differently, although the test was performed with only three replicates which gives low statistical power. On the other hand, we found significant growth rate differences among snails grown on sediments from different bays. This thus suggests that some component of the sediment other than grain size affects growth.

Growth differed between the two species, but it was also influenced by the origin of the snails. Thus the factor population had a significant effect on growth rate (Table 3), but there was still no tendency, in either species, for snails from populations with large snail sizes in the field to grow faster than did snails from populations with small snail sizes in the field (Fig. 5). Thus, we got no support for genetic differences in growth rate in the way predicted by the character displacement model.



Fig. 3. Mean snail size of *H. ventrosa* in populations with different proportions of *H. ulvae* and *H. ventrosa*. The regression deviates from zero slope: a = -0.0068b + 3.04, P < 0.001, $r^2 = 0.40$.

The most consistent pattern of variation in growth rate was that, independent of origin, snails of *H. ulvae* grew, on average, about 150% the rate of *H. ventrosa* when grown on replicate samples of the same sediment (Fig. 6).

4. Discussion

Independent of the mechanisms of the differences in growth rate and size distribution of different populations of *H. ventrosa* and *H. ulvae*, the results may be adaptive in the way that size divergence of sympatric populations may decrease the interspecific competition for food as a limiting resource, as suggested by Fenchel (1975b). However, the basic assumption of interspecific competition over a common food source, has been challenged (Levinton, 1987; Levinton and DeWitt, 1989). Furthermore, to conclude that the observed size distributions are a result of character displacement, we must find support for the criteria of inherited differences, and unpredicted character variation, as explained by Arthur (1982).

The distribution of the two species in the field were related to silt content in the sediment. In general, *H. ventrosa* was more numerous on silty sediments, while *H. ulvae* dominated sandy sediments. We found, however, two exceptions to this; two silty sites dominated by *H. ulvae*. Both these localities had, however, on other occasions been observed to have a dominance of *H. ventrosa*. Occasional switches away from the fairly



Fig. 4. Proportions of *H. ventrosa* in samples of *H. ulvae* and *H. ventrosa* from natural sites with different silt contents. Dominance of one or the other of the two species is indicated.

stable numerical relationship between the two species in a site seems a possibility, due to the broadcasting of pelagic larvae in *H. ulvae*. Thus, our results support those of Saloniemi (1993) in that the relative distribution of the two species is habitat-dependent. Furthermore, we found mean sizes of both species in the field to increase from sandy to

Table 2

Factor	SS	df	MS	F-ratio versus	F	Р
Species (SP)	7.783	1	7.783	No test		
Population $P(SP)$	2.470	18	0.137	_		
Sediment type (SE)	1.966	1	1.966	No test		
Bay $B(SE)$	6.776	4	1.694	-		
$SP \times SE$	0.004	1	0.004	No test		
$SP \times B(SE)$	0.119	4	0.030	$P(SP) \times B(SE)$	0.81	0.52
$SE \times P(SP)$	0.556	18	0.031	$P(SP) \times B(SE)$	0.85	0.64
$P(SP) \times B(SE)$	2.627	72	0.036	Residual	0.98	0.53
Residual	16.703	446	0.037			
Total	39.004	565				

The effects of four factors on growth rate of *Hydrobia ulvae* and *H. ventrosa* in the laboratory as tested by an analysis of variance

Growth rates were transformed using ln(x+1). The interaction Species × Sediment, and the factors Species and Sediment, have no valid test. However, as none of the three remaining interactions were significant they could be pooled into the residual and the test repeated (see Table 3).

Table 3

The effects of four factors on growth rate of *H. ulvae* and *H. ventrosa* in the laboratory as tested by an analysis of variance

Factor	SS	df	MS	F-ratio versus	F	Р
Species (SP)	7.783	1	7.783	P(SP)	56.73	< 0.0001
Population $P(SP)$	2.470	18	0.137	Residual	3.71	< 0.0001
Sediment type (SE)	1.966	1	1.966	B(SE)	1.16	0.34
Bay $B(SE)$	6.776	4	1.694	Residual	45.78	< 0.0001
$SP \times SE$	0.004	1	0.004	Residual	0.11	0.74
Residual	20.005	540	0.037			
Total	39.004	565				

Growth rates were transformed using $\ln(x+1)$. The interactions $SP \times B(SE)$, $SE \times P(SP)$, and $P(SP) \times B(SE)$ are all non-significant and pooled with the residual (see Table 2).

silty sites, although no effect of sediment on growth rate was evident in the laboratory experiments.

Sites having higher frequencies of *H. ventrosa*, also had *H. ulvae* with larger shell sizes (Fig. 2). This correlation was also described by Saloniemi (1993). The frequency of *H. ulvae*, on the other hand, was negatively correlated to shell size of *H. ventrosa* (Fig. 3). This pattern is predicted from the character displacement model suggesting that *H. ulvae* increases its mean size when competition from *H. ventrosa* becomes more intense, while the reverse would be true for *H. ventrosa*. As however, frequency of *H. ventrosa* and silt content were correlated in our study, this pattern of variation might equally well be explained by size variation caused by a habitat gradient (e.g. % silt). The field data of mean sizes are thus inconclusive and we could neither support nor reject the first Arthur (1982) criteria; that character alterations going from allopatry to sympatry should not be a predicted consequence of changes among allopatric sites.



Fig. 5. Mean growth of snails in a laboratory environment (n=30) in relation to mean snail size of the field populations from which the laboratory reared snails derived (varying sample sizes, see Table 1). Filled symbols represents allopatric localities (rare morph <5%), while open symbols are sympatric ones.



Fig. 6. Growth of *H. ulvae* and *H. ventrosa* in the laboratory on replicates of six different sediments. The correlation is highly significant (P < 0.001, $r^2 = 0.94$).

Fish and Fish (1974) and Chatfield (1972) found snails of *H. ulvae* to be larger, on average, on silty as compared to sandy sediments. If silt content of the sediment has an effect on growth rate this would be evident from our laboratory experiment. In these experiments, however, we did not find clear evidences for a direct effect of silt content on individual growth rate. Forbes and Lopez (1990) reached the same conclusion when investigating growth of the congeneric species *H. totteni* on sand and silt. They found that growth did not differ, although body size was larger on silt.

In our study, the factor bay had a significant effect, which means that sediments of the same type (sandy or silty), but from different bays, affected growth in a significant way. An interpretation of this is that some environmental factor other than grain size affects growth rate, and that this factor in our experiments varied independently of sediment type. Morrisey (1990), who transplanted individuals of *H. ulvae* between field sites of different sediment type, concluded that sediment type was of some importance, but that other, unknown, factors were involved as well.

According to the Arthur (1982) second criteria, the model of character displacement predicts inherited variation in size between allopatric and sympatric populations. Our data does not support this. That is, we did not find snails from field populations with

larger mean sizes to grow larger in the laboratory experiment (Fig. 5). Rothschild and Rothschild (1939) got similar results as us; when growing *H. ulvae* from a large-sized and a small-sized population in the laboratory no size differences were evident after 1 year.

A somewhat puzzling finding is the significant effect of population in our laboratory experiment, possibly suggesting genetic differences in growth rate among populations. However, these differences, if real, are independent of whether the populations are allopatric or sympatric, and they could thus not explain the character displacement-like pattern in the field. Furthermore, even if genetic differences among populations seems a possibility for the direct developing species *H. ventrosa*, it seems less likely that *H. ulvae*, which has planktotrophic larvae, would be genetically structured at a scale of kilometers. The population effects on growth rate in the laboratory may alternatively be non-genetic effects persisting from influences of earlier favourable or unfavourable environments. Such effects would, however, have been correlated with mean sizes of field populations, which was not the case.

One possibility is that size differences among populations may reflect differences in mean ages due to different recruitment times, or different age-specific mortality rates. Forbes and Lopez (1990) showed that differences in body size of *Hydrobia truncata* between sandy and silty sites was caused by later recruitment to the sandy site. Likewise Fenchel (1975b) suggested recruitment time to differ between allopatric and sympatric sites of *H. ventrosa* and *H. ulvae*. Barnes (1990), (1996), however, proposed recruitment failure of some cohorts or size-dependent death rates as an explanation for the size differences among populations.

Different recruitment times seem, however, a poor explanation for the similarity of mean sizes among populations of the two species living in allopatric sites. The reason is that if comparing allopatric *H. ulvae* and *H. ventrosa* cohorts of similar sizes, a model of different recruitment times suggests *H. ventrosa* to be the oldest of the two, as this species grow more slowly. However, the life-span of *H. ventrosa* is probably shorter than that of *H. ulvae* (Fish and Fish, 1974; Siegismund, 1982; Barnes, 1990). Failure of recruitment of, for example, *H. ulvae*, may contribute to allopatric populations of this species being similar in mean size to *H. ventrosa*. But such a phenomenon must by necessity be temporary and can not explain the general observation of similar mean shell sizes when allopatric populations are compared (Fenchel, 1975b; Saloniemi, 1993; this study).

Yet, we have no obvious suggestion of a mechanism which may explain the similar size ranges in allopatric sites of the two species, size differences in sympatry may easily be explained as a general interspecific difference in growth rate. The very strong positive correlation between growth rates of *H. ventrosa* and *H. ulvae*, in the laboratory, when grown on different sediments (Fig. 6), indicates that although growth rate vary a lot over the six different sediments, *H. ulvae* always grew about 150% the rate of *H. ventrosa* on replicates of the same sediment, independent of snail origin. That is, body sizes at sympatric localities reflects an intrinsic difference in growth between the species, rather than a genetic difference between sympatric and allopatric populations within the species.

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