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The role of sediment type in growth and fecundity of mud snails (*Hydrobiidae*)

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Abstract

We test the hypothesis that body size and population density of the deposit-feeding gastropod, *Hydrobia truncata*, are greater in muddy than in sandy habitats as a result of faster growth on fine- compared to coarse-grained sediments. We refute this hypothesis using a combination of field measurements and laboratory experiments. Three out of three populations tested had higher maximal growth rates and two of three populations approached their asymptotic size more quickly on sand than on silt-clay fractions of natural sediment. Growth decreased with increasing snail density and was as high or higher on sand as on silt-clay at all densities. Two populations were more fecund on sand than on silt-clay, and fecundity of the third population was not affected by sediment type. We show that the smaller body sizes observed in snails from the sandiest habitat result from late recruitment of these snails, relative to the other populations.

Keywords: Deposit feeder, Population dynamics, Intraspecific variation



Sediment grade has been considered of primary importance in controlling the distribution and abundance of deposit feeder populations. Deposit feeders are generally most numerous in fine-grained, organic-rich sediment (Sanders 1958; Newell 1965). Conditions that result in the deposition of small sediment particles tend to enhance the accumulation of low-density organic material (Mayer et al. 1985). Furthermore, the high surface-to-volume ratio of small particles provides relatively more area for the attachment of microbes and organic coatings (Zobell 1938; Newell 1965; Yamamoto and Lopez 1985; but see Cammen 1982; Whitlatch and Weinberg 1982; DeFlaun and Mayer 1983). Since deposit feeders utilize some combination of organic detrital ma-

terial and living microbes for food, it has been widely held that sediment particle size limits food availability for populations of deposit feeders (Lopez and Levinton 1987, for review). Correlations between deposit feeder abundance and various measures related to sedimentary food value and results of direct density manipulations provide convincing evidence that populations of deposit feeders are often food-limited (Newell 1965; Longbottom 1970; Levinton 1972, 1977; Fenchel and Kofoed 1976; Levinton and Bianchi 1981; Bianchi and Levinton 1984; Olafsson 1986).

Body size and population density of hydrobiid gastropods have been positively correlated with silt-clay content of the sediment (Newell 1965; Chatfield 1972; Fish and Fish 1974). The larger body sizes observed have been hypothesized to be the result of faster growth on muddy sediments (Fish and Fish 1974). Our purpose was to test the hypothesis that larger body sizes and densities of *Hydrobia truncata* populations from Long Island Sound (NY, USA) occur in muddy relative to sandy habitats as a result of faster growth on fine- compared to coarse-grained sediments. We combined field measurements of body size and population density with laboratory estimates of growth, mortality, and fecundity in order to determine the role of sediment type in controlling field distributions of this species.

Materials and methods

Habitat characteristics

The locations of the three study sites are shown in Figure 1. Flax Pond, a *Spartina* salt marsh, is a protected, low energy, intertidal habitat. The sediment is poorly sorted, and modal particle size is 125–250 μm . The sediment consists of approximately 12% silt-clay and has a total organic content of 2.7% by weight (Forbes 1988).

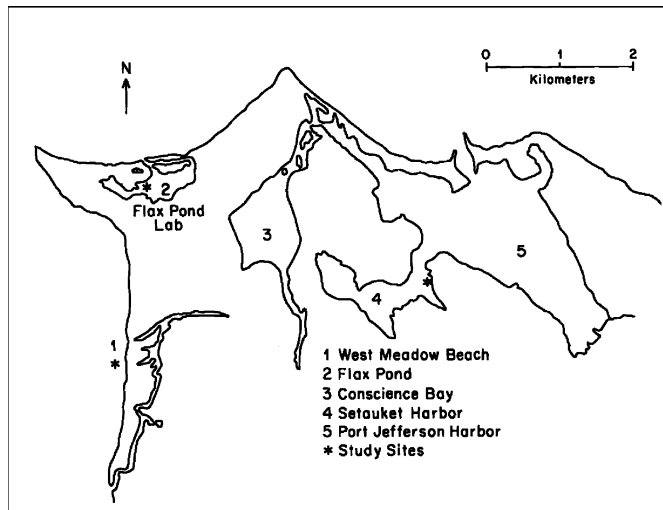


Figure 1. Map of the study sites

The Setauket Harbor site is a moderately protected, intertidal-sand flat. The sediment is poorly sorted, and the percentage of fine particles increases away from shore. Modal particle size is 125-250 μm with 2% silt-clay and an organic content of 1.4% (Forbes 1988).

West Meadow Beach is the most exposed of the three intertidal habitats. It is open to Long Island Sound and is subject to frequent sediment transport events, particularly during the winter months. Modal particle size is 297-420 μm ; there are no particles < 125 μm . Total organic content is approximately 0.5% by weight (Forbes 1988).

The temperature of surface sediment and overlying water was measured weekly at low tide to the nearest 0.5 $^{\circ}\text{C}$. There was no consistent difference in sediment or water temperature among sites. Temperatures were highest during July and August and lowest in February. Salinity was similar at the three sites and generally varied between 25-30‰ (Forbes 1988).

Field measurements

Sedimentary food content was estimated by chlorophyll-*a* concentration since benthic microalgae are the most important food source for *Hydrobia* species (Fenchel et al. 1975; Kofoed 1975; Fenchel and Kofoed 1976; Jensen and Siegismund 1980; Levinton and Bianchi 1981; Bianchi and Levinton 1984). Chlorophyll-*a* concentration ($\mu\text{g}/\text{mg}$ sediment dry weight) was estimated by fluorometric analysis (Turner Designs Fluorometer) following extraction with 90% acetone for 15-20 h, and was corrected for phaeopigment (Strickland and Parsons 1972).

Seasonal variation in snail density was estimated by taking three (5 cm depth \times 34.5 cm²) cores at each site. Cores were sieved to 500 μm and sorted under a dissecting microscope immediately upon return to the laboratory, and the total number of live snails was counted.

To obtain estimates of body size, snails were collected weekly at each site from July 1985 through July 1987 by filling a 1 L container with (unsieved) surface sediment. Shell lengths of the first one hundred snails encountered were measured under a dissecting microscope to obtain a mean for each site. In several of the samples collected during the winter at West Meadow Beach, fewer than 100 snails were obtained. Therefore for these samples mean shell lengths were based on fewer individuals. Measurements of shell length were made at 12 \times (for snails \geq 2 mm) or 20 \times (for snails < 2 mm) with an ocular micrometer, to the nearest 0.04 mm or 0.025 mm respectively.

Laboratory growth experiment I

This experiment was designed to investigate the effect of sediment type on growth rate. Snails from Flax Pond, Setauket Harbor and West Meadow Beach populations were grown individually in 35 mm diameter polystyrene culture dishes (0.10 snails/cm²) for 11 months, beginning in July, 1985. The cultures were kept at room temperature (approximately 21 $^{\circ}\text{C}$). No attempt was made to regulate light conditions; however, fresh sediment (ca. 3.5 gm dry weight) and seawater (ca. 5 mL) were replaced weekly. Seawater (28‰) used in all laboratory experiments was glass fiber filtered. The <63 μm fraction of sediment from Flax Pond and the 300-600 μm fraction of sediment from West Meadow Beach comprised the two sediment treatments used in all growth and fecundity experiments. The fractions were chosen from separate sites so that the natural diatom assemblages associated with each sediment type would be represented. Each week, snails were blotted dry and weighed on a Cahn (model 26) electrobalance. Blotted weight is an excellent indicator of shell dimensions (Levinton and Bianchi 1981) and is correlated with dry tissue weight (\log_{10} (dry wt) = 1.465 + 2.3421 \log_{10} (shell length); $N = 1124$; $r = 0.93$; Forbes, unpublished). Twelve replicates were used for each combination of sediment type and population (2 sediment types \times 3 populations).

Specific growth rates (SGR) were calculated as

$$\text{SGR} = (\log_e W_2 - \log_e W_1) / t$$

where W_1 and W_2 are weights at times t_1 and t_2 respectively, and t is in days (Kaufmann 1981). SGR was plotted against geometric mean size, $W = (W_2 \times W_1)^{1/2}$, and the data were fitted to several standard growth curves. Standard least squares regression was used to obtain the parameters of the model equation. The Gompertz curve, in which $\text{SGR} = b - a \ln(W)$, gave the highest correlation coefficient in 4 of 6 cases, as well as in field growth estimates for this species (Forbes, unpublished) and was therefore used in all further growth analyses. The parameter 'b' is the maximum growth rate; 'a' is a measure of the growth schedule or rate at which an animal approaches its asymptotic size (i.e., the rate of change of the size specific growth rate with increasing size). Residual analysis was used to detect outliers and points with high leverage. Any point that fit both of these criteria was deleted from the analysis (Sokal and Rohlf 1981). A maximum of 7 out of 139 points in a single regression was deleted using these criteria. Average shell lengths were calculated from a regression against blotted wet weight to facilitate comparison with field data.

Laboratory growth experiment II

In this experiment we examined the combined effects of sediment type and snail density on growth rate of *H. truncata*. Snails were cultured for 31 days (September 7 to October 9, 1987) at three densities: 0.10, 1.04, and 2.10 snails/cm² for Flax Pond and Setauket Harbor populations, and 0.10, 1.04, and 3.10 snails/cm² for the West Meadow Beach population. There were two replicates for each combination of population, sediment type, and density (with the exception of the high density West Meadow groups which were not replicated due to difficulty in obtaining enough animals) giving a total of 34 groups (2 sediment types \times 3 density levels \times 3 populations).

The snails were maintained in 35 mm diameter polystyrene culture dishes (1, 10, and 20 (or 30) snails/dish) at 17 $^{\circ}\text{C}$. Seawater (ca. 5 mL) and 2.5 mL sediment slurry (ca. 3.5 gm dry weight) were added to each dish. Seawater was changed weekly; sediment was not changed, but the cultures were maintained on a 14L:10D light cycle to permit microalgal growth. At the beginning and end of the experiment, the snails in each dish were blotted dry and weighed to the nearest 0.001 mg. Growth rate (mg/snail) was calculated as an average based on the weight gain of the entire group. At the conclusion of the experiment, sediment chlorophyll-*a* concentrations were measured by fluorometry as described above.

Laboratory fecundity experiment

This experiment determined the effects of sediment type on the number of eggs laid and percent hatch. Adult snails were collected at the onset of egg production in the field. Since the West Meadow Beach population recruited approximately 1.5 months later than the other populations, fecundity estimates for this population commenced at a later time (July 2, 1987), but under identical laboratory conditions, as for the other groups (April 17, 1987). One female was placed in each of 72 culture dishes (35 mm diameter). A male was added to each dish to ensure fertilization. Seawater (changed weekly) and 2.5 mL sediment slurry (ca. 3.5 gm) were added to each culture. Twelve replicates were used in each combination of sediment type and population (2 sediment types \times 3 populations). The cultures were maintained at 17 °C under a 14L:10D light cycle to permit microalgal growth. Shell lengths of the adults were measured prior to and following the experiment. Cultures were examined microscopically every other day for the presence of newly hatched juveniles. Once eggs began to hatch, juveniles were removed from the sediment and preserved in 70% ethanol and stained with Rose Bengal. The experiment was terminated 18 days after the first eggs hatched. By this time the rate of hatching had slowed considerably. At the conclusion of the experiment, the sediments containing unhatched eggs were preserved and all juveniles and eggs counted.

Statistical analyses of field and laboratory data, detailed in the results, were performed using SYSTAT (Wilkinson 1986).

Results

Field measurements

With the exception of the August sampling date, chlorophyll- α values were consistently lower at West Meadow Beach than at either of the other two sites (Table 1). On three of six sampling dates (Mar, May, Aug), chlorophyll- α values were higher at Setauket Harbor than Flax Pond, on two dates (Sept., Feb.) Flax Pond values were higher, and on the remaining date (June), there was no difference between the two sites. Average values were: 0.043 $\mu\text{g}/\text{mg}$ for Flax Pond; 0.052 $\mu\text{g}/\text{mg}$ for Setauket Harbor; 0.011 $\mu\text{g}/\text{mg}$ for West Meadow Beach.

Snail densities at West Meadow Beach were generally lower than at the other two sites (Table 1). In March, May, August, and February, densities were lower at West Meadow Beach than at Flax Pond; in March, June, August, September and February, West Meadow Beach densities were lower than those at Setauket Harbor. In March and May densities were lower at Setauket Harbor than at Flax Pond. In June and September, densities were lower at Flax Pond than at Setauket Harbor. On the remaining dates, there were no significant differences in density among sites. Average snail densities at each site were 2.98 snails/cm² for Flax Pond, 4.55 snails/cm² for Setauket Harbor, and 0.54 snails/cm² for West Meadow Beach. Low densities following recruitment (June for Flax Pond and Setauket Harbor; August for West Meadow Beach) were due to newly hatched juveniles passing through the 500 μm collection sieve. The new recruits first appeared in the August collection at Flax Pond and Setauket Harbor and in the September collection at West Meadow Beach.

Average shell lengths of the 1986 cohort of snails from each habitat are shown in Figure 2. (Similar curves were obtained for the 1985 year class (Forbes 1988)). Snails from West Meadow Beach were smaller than Flax Pond and Setauket Harbor snails throughout the year. Flax Pond and Setauket Harbor populations were indistinguishable in size for the first 3 months following recruitment. After this time, the average size of Flax Pond snails was approximately 0.2 mm greater than Setauket Harbor snails.

For Flax Pond and Setauket Harbor populations, the most rapid increase in length occurred during the first three months following recruitment (June, July, and August). By September, these populations reached sexual maturity (determined by whorl number and egg laying behavior when brought into the laboratory) and showed little additional growth. At West Meadow Beach, recruitment occurred 1.5 months later than at the other sites and was followed by approximately 7 weeks of rapid growth. Average body size changed very little over the fall and winter months for

Table 1. Field Measurements. Microalgal concentration of field sediments ($\mu\text{g chl-}\alpha/(\text{mg dry wt sed})$) and densities of *H. truncata* (snails/cm²); Mean (SD, N). Data were log transformed to reduce heterogeneity of variances prior to ANOVA. Separate ANOVA's (and planned comparisons among means, Sokal and Rohlf, 1981) for population effect on chlorophyll- α and snail density were calculated for each date; all were significant at $P < 0.01$. Solid lines join means that were not significantly different ($P > 0.05$)

Date		Flax Pond	Setauket Harbor	W. Meadow Beach
Mar 87	Chl- α	0.036 (0.0012,4)	0.057 (0.0017,4)	0.008 (0.0025,4)
	Density	2.95 (0.349,3)	0.73 (0.622,3)	0.00 (0.000,3)
May 87	Chl- α	0.038 (0.0021,4)	0.068 (0.0066,4)	0.016 (0.0006,4)
	Density	2.21 (0.972,3)	<u>0.76 (0.644,3)</u>	<u>0.03 (0.050,3)</u>
Jun 87	Chl- α	<u>0.071 (0.0107,4)</u>	<u>0.074 (0.0021,4)</u>	0.007 (0.0002,4)
	Density	<u>0.59 (0.453,3)</u>	3.94 (1.809,3)	<u>0.07 (0.017,3)</u>
Aug 87	Chl- α	<u>0.015 (0.0065,4)</u>	0.036 (0.0026,4)	<u>0.015 (0.0006,4)</u>
	Density	<u>6.68 (4.260,3)</u>	<u>11.61 (3.880,3)</u>	0.44 (0.608,3)
Sep 87	Chl- α	0.047 (0.0049,4)	0.037 (0.0018,4)	0.007 (0.0005,4)
	Density	<u>3.42 (0.652,3)</u>	5.85 (1.336,3)	<u>2.65 (0.422,3)</u>
Feb 88	Chl- α	0.052 (0.0037,8)	0.037 (0.0020,6)	0.012 (0.0006,6)
	Density	<u>2.03 (0.559,3)</u>	<u>4.42 (2.795,3)</u>	<u>0.07 (0.067,3)</u>

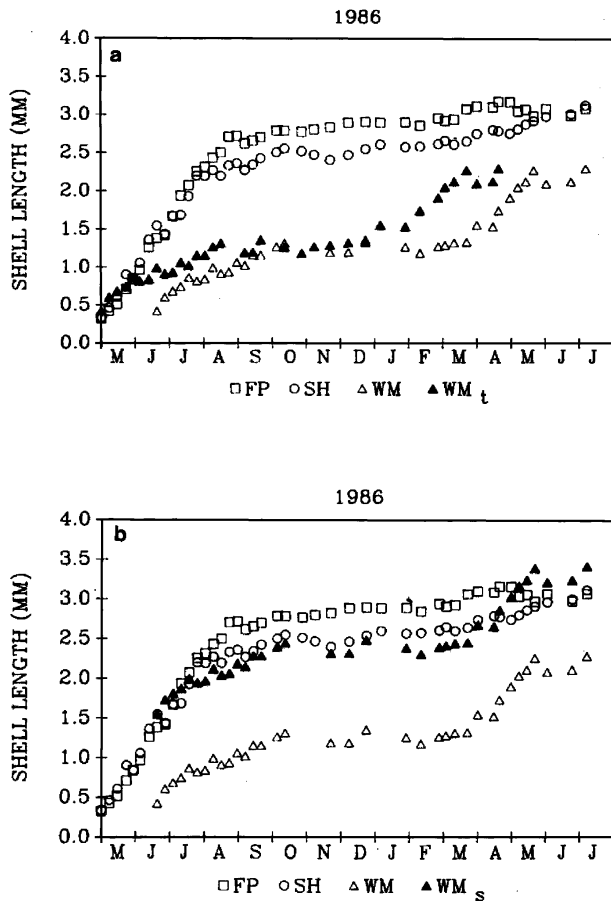


Figure 2. Average shell length of *Hydrobia truncata* from three populations. FP = Flax Pond, SH = Setauket Harbor, WM = West Meadow Beach. **a)** WM_t = average size of West Meadow Beach snails adjusted for the difference in recruitment timing. **b)** WM_s = average size of West Meadow Beach snails adjusted for the size difference at recruitment.

all populations, but in the spring a second period of rapid growth was observed in the West Meadow Beach population prior to snails reaching sexual maturity. When individuals from West Meadow recruited, in mid-July, the Flax Pond and Setauket Harbor juveniles were approximately 1.5 mm in length. By adjusting the West Meadow curve for the time difference in recruitment (WM_t , Figure 2a) we can compare size-specific growth rates among populations. During the first 7 weeks following recruitment, growth rates were similar among the 3 populations. After this period, West Meadow Beach snails appeared to decrease their growth relative to the other populations. In Figure 2b, we retain the real time axes but adjust the West Meadow curves for the initial size lag (by addition of the size difference between Setauket Harbor and West Meadow snails at the time of the latter's recruitment; WM_s). The similarity in shape of WM_s to the Flax Pond and Setauket Harbor size curves indicates that environmental constraints on growth outweigh size-specific factors in the West Meadow Beach population and suggests that the smaller size of West Meadow Beach snails occurs primarily as a result of the recruitment time lag interacting with environmental constraints on growth.

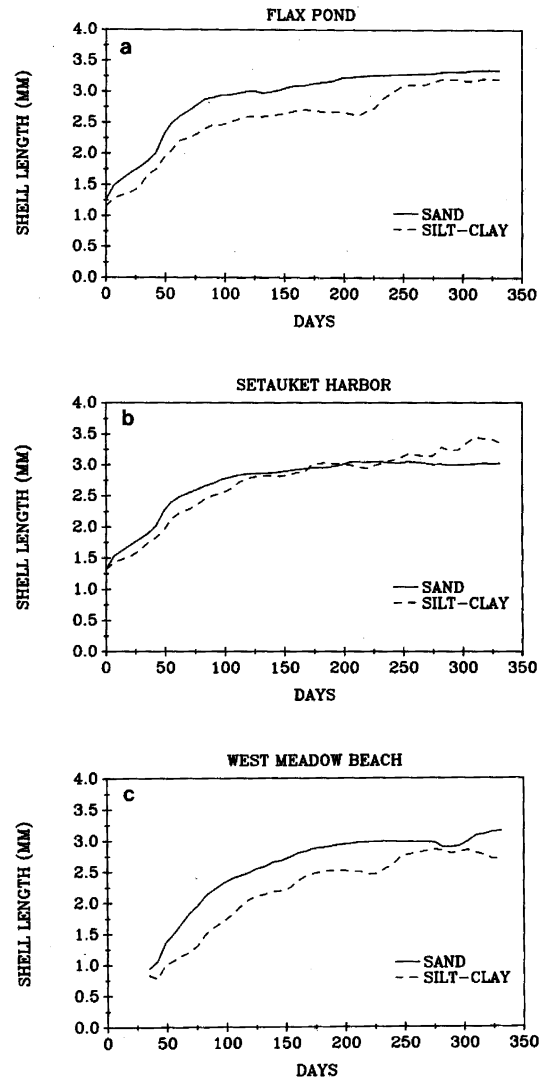


Figure 3. Laboratory Growth Experiment I. Average shell length of **a)** Flax Pond, **b)** Setauket Harbor, and **c)** West Meadow Beach snails as a function of time and sediment type. Shell lengths were calculated from a regression against wet weight to facilitate comparison with field data.

Laboratory growth experiment I

Average snail size versus time for three populations and two sediment treatments is shown in Figure 3. Specific growth rate regression parameters are provided in Table 2. Growth schedules (i.e., slopes) of individual Flax Pond snails were similar between sediment treatments, however, snails from this population had higher initial growth rates (i.e. y-intercepts) on sand compared to silt-clay (Table 3). Setauket Harbor and West Meadow Beach snails approached their asymptotic size more rapidly and had higher initial growth rates on sand than on silt-clay (Table 3).

The number of days to reach 50% mortality was 98 for Flax Pond snails on sand, 154 for Flax Pond snails on silt-clay, 283 for Setauket Harbor snails on sand, 255 for Setauket Harbor snails on silt-clay, 261 for West Meadow Beach snails on sand, and 14 for West Meadow Beach snails on silt-clay.

Table 2. Growth Experiment I. Regression parameters estimated by fitting data to Gompertz growth model (see text for equation). Regression equations for all groups were significant at $p < 0.00001$. FP = Flax Pond, SH = Setauket Harbor, WM = West Meadow Beach, SA = Sand, SC = Silt-Clay

Population	Sediment	Slope (SE)	Y-Intercept (SE)	n	r
FP	SA	1.404 (0.0886)	2.743 (0.1297)	275	0.693
FP	SC	1.174 (0.0984)	1.939 (0.1152)	268	0.590
SH	SA	1.762 (0.0725)	2.990 (0.1004)	435	0.760
SH	SC	1.093 (0.0776)	2.020 (0.1021)	360	0.597
WM	SA	1.477 (0.0766)	2.309 (0.0852)	387	0.701
WM	SC	1.139 (0.1177)	1.534 (0.1111)	139	0.639

Table 3. Growth Experiment I. Results of ANCOVA of shell length and sediment effects on specific growth rate (calculated using regression equations shown in Table 2) for Flax Pond, Setauket Harbor, and West Meadow Beach populations

I. Flax Pond					
Source	SS	DF	MS	F-Ratio	P
Size	435.35	1	435.35	374.46	<0.001
Sediment	23.67	1	23.67	20.36	<0.001
Size × Sed	3.51	1	3.51	3.02	0.083
Error	630.16	540	1.17		
II. Setauket Harbor					
Source	SS	DF	MS	F-Ratio	P
Size	594.41	1	594.41	720.35	<0.001
Sediment	37.39	1	37.39	45.31	<0.001
Size × Sed	32.66	1	32.66	39.58	<0.001
Error	652.71	791	0.83		
III. West Meadow Beach					
Source	SS	DF	MS	F-Ratio	P
Size	423.66	1	423.66	356.27	<0.001
Sediment	37.28	1	37.28	31.35	<0.001
Size × Sed	7.06	1	7.06	5.93	0.015
Error	620.73	522	1.19		

Laboratory growth experiment II

Growth rate in the three populations of *Hydrobia truncata* decreased with increasing snail density (Figure 4). Sediment type had no effect on growth rate of Flax Pond and Setauket Harbor snails (Table 4). West Meadow Beach snails grew more on sand than on silt-clay at all densities; the difference in growth between sediment fractions was greatest at the lowest snail density (Figure 4c). Sediment chlorophyll-*a* was not affected by snail density or population, but was much lower on sand than on silt-clay; there was no significant interaction between snail density and sediment type on chlorophyll-*a* concentration (Table 5).

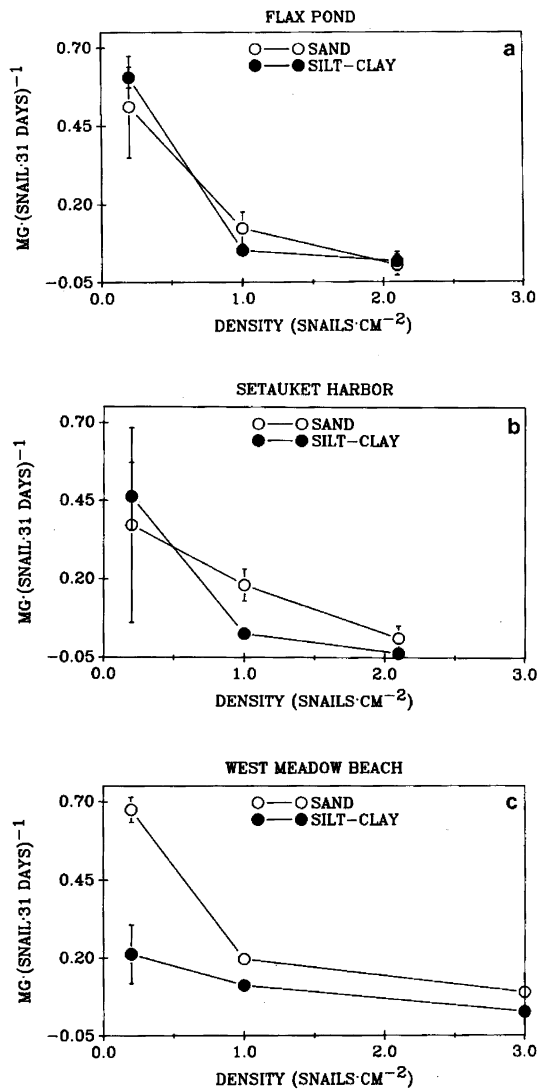
Laboratory fecundity experiment

Sediment type had no effect on the number of eggs laid by Flax Pond *H. truncata* or on the percentage of those eggs that hatched over an 18 day period (Figure 5 a, Table 6). Setauket Harbor snails laid more eggs on sand, and a greater percentage of eggs hatched on sand than on silt-clay (Fig-

ure 5b, Table 6). Percent hatch on West Meadow Beach snails was not affected by sediment type, but snails from this population laid more eggs on sand (Figure 5c, Table 6). Also, the West Meadow Beach adults grew more on sand so that by the end of the experiment, shell lengths of the adults were significantly greater on sand than on silt-clay (t-statistic = 2.577, $P = 0.017$).

Discussion

Given observations of the predominance of deposit feeders in fine-grained, organic-rich sediments (Sanders 1958; Newell 1965) and evidence for food limitation of natural populations of deposit feeders (Levinton 1972, 1977; Fenchel and Kofoed 1976; Levinton and Bianchi 1981; Bianchi and Levinton 1984; Olafsson 1986), we hypothesized that larger body sizes and densities of *Hydrobia truncata* from muddy habitats in Long Island Sound resulted from faster growth on fine- compared to coarse-grained sediments. Our results clearly refute this hypothesis.



Maximum sizes attained by snails in the field were approximately 3–3.5 for Flax Pond snails, 3.0 for Setauket Harbor snails and 2–2.25 for West Meadow Beach snails. West Meadow Beach snails recruited 1.5 months later than the other populations and reproduced at a smaller size. Differences in maximum size among populations reared in the laboratory were less than in the field. In the laboratory, Flax Pond and Setauket Harbor snails attained a maximum size of 3–3.5 mm; West Meadow Beach snails reached 2.75–3.0 mm. Growth patterns exhibited by laboratory-grown snails were also similar among the three populations (Figure 3). In the field, however, growth rates of West Meadow snails decreased at a smaller body size but at the same time (i.e., early autumn) as the other populations (Figure 2), suggesting that environmental constraints may limit growth during autumn and winter. As a result, West Meadow Beach snails overwintered at a much smaller size than the other populations. Pronounced growth bands, separating pre-from post-winter growth, are present in the majority of West Meadow Beach snails in the spring (Forbes, pers. obs.), suggesting that the second growth spurt observed in field collected-snails is due to growth and not migration. Observations of size at sexual maturity (G. Davis, pers. comm.), as well as egg laying behavior of field-collected animals, suggest that Flax Pond and Setauket Harbor, but not West Meadow Beach, populations reach sexual maturity approximately 3 months following recruitment. The spring growth

Figure 4: a–c. Laboratory Growth Experiment II. Average weight gain of *H. truncata* from a) Flax Pond, b) Setauket Harbor, and c) West Meadow Beach populations as a function of snail density and sediment particle size. Error bars indicate 95% confidence limits around the mean.

Table 4. Growth Experiment II. Results of 2-way ANOVA of sediment and density effects on weight gain of *H. truncata* from Flax Pond, Setauket Harbor, and West Meadow Beach populations. Homogeneity of variances was tested using Bartlett's Test; $P > 0.05$. The sediment \times density interaction term was omitted from the West Meadow Beach ANOVA due to non-replication of the high density treatment

I. Flax Pond					
Source	SS	DF	MS	F-Ratio	P
Sediment	<0.001	1	<0.001	0.038	0.852
Density	0.702	2	0.351	31.803	0.001
Sed \times Den	0.014	2	0.007	0.624	0.567
Error	0.066	6	0.011		
II. Setauket Harbor					
Source	SS	DF	MS	F-Ratio	P
Sediment	0.004	1	0.004	0.113	0.749
Density	0.395	2	0.197	5.222	0.049
Sed \times Den	0.030	2	0.015	0.401	0.686
Error	0.227	6	0.038		
III. West Meadow Beach					
Source	SS	DF	MS	F-Ratio	P
Sediment	0.134	1	0.134	7.293	0.036
Density	0.261	2	0.131	7.108	0.026
Error	0.110	6	0.018		

Table 5. Growth Experiment II. Microalgal concentration ($\mu\text{g Chl-}a/\text{mg}$) of experimental sediments and results of 2-way ANOVA of the effect of sediment type and snail density on Chl- a concentration of experimental sediments. Data are pooled among populations since population had no effect on Chl- a (based on initial 3-way ANOVA of population, sediment, and density effects). Sediment \times density interaction term is omitted since each sediment type had a single control treatment. * = no SE since $n = 1$ for controls.

	Snail Density	Mean	SE	n	
Sand	0.00	0.0043	*	(1)	
	0.10	0.0044	(0.00025)	(6)	
	1.04	0.0047	(0.00054)	(6)	
	2.10	0.0047	(0.00051)	(5)	
Silt-Clay	0.00	0.161	*	(1)	
	0.10	0.143	(0.0130)	(6)	
	1.04	0.143	(0.0075)	(6)	
	2.10	0.139	(0.0046)	(5)	
Source	SS	DF	MS	F-Ratio	P
Sediment	0.1718	1	0.17183	714.907	<0.001
Density	0.0002	3	0.00007	0.277	0.842
Error	0.0074	31	0.00024		

spurt may be necessary for the West Meadow Beach snails to reach a minimum size for reproduction. The annual, semelparous life history of these populations prevents late reproducing snails from catching up and will act to maintain the lag in recruitment once initiated.

Population density of *H. truncata* was lowest at West Meadow Beach, which had the lowest average sedimentary chlorophyll- a content of the three habitats. Although conditions favoring high standing stocks of benthic microalgae also favor large sizes and densities of *Hydrobia truncata*, our results indicate that sediment type does not directly control growth and fecundity in field populations. For a given sediment size fraction, growth of *Hydrobia* species is limited by microalgal standing stock (Levinton and Bianchi 1981; Bianchi and Levinton 1984). Comparisons of food availability between sediment fractions are confounded by the ability of snails to browse particle surfaces. Browsing is an effective technique for food-particle selection and results in greater ingestion rates than expected on the basis of bulk estimates of sediment microalgal concentration (Lopez and Kofoed 1980).

We found no density-dependent reduction in sedimentary microalgal concentration (Table 5), although snail growth was strongly and negatively related to density. There was a trend toward decreasing chlorophyll- a concentration with increasing density on silt-clay, but this trend was not significant. Levinton (1982; 1985) and Morrisey (1987; 1988) also found depressed growth with increasing *Hydrobia* density, however, both authors found that increasing snail density decreased diatom standing stock (estimated by epifluorescence counts). We suggest several explanations to explain this discrepancy: 1) chlorophyll- a concentration did not adequately reflect food availability (e.g., grazing by snails may select for smaller or less digestible diatom species which might negatively influence growth rate, but not be reflected in bulk estimates of

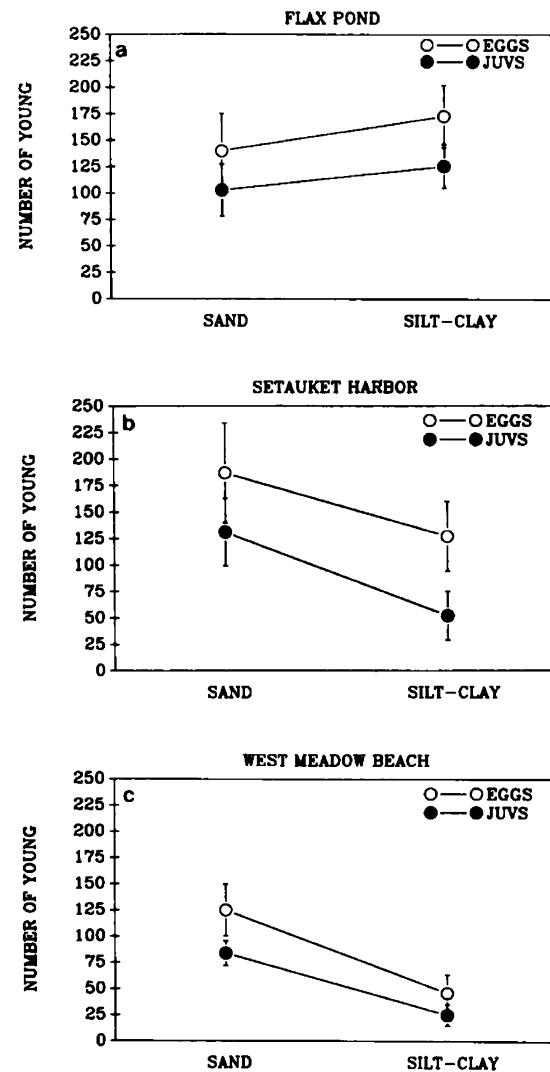


Figure 5: a-c. Laboratory Fecundity Experiment. The effect of sediment particle size on the number of eggs laid and the number of juveniles hatched (% hatch = juvs/eggs) for *H. truncata* from a) Flax Pond, b) Setauket Harbor, and c) West Meadow Beach populations. Error bars indicate 95% confidence limits around the mean.

chlorophyll- a (Lopez and Levinton 1978; Kofoed, pers. comm.), 2) reduction in growth in our experiments at high densities was caused by interference competition (Levinton 1985), 3) differences in chlorophyll- a were not statistically discernible due to the small sample size of our data.

The fact that growth rates in laboratory experiments were as high or higher on coarse compared to fine-grained sediments is consistent with carbon absorption and loss estimates (Forbes and Lopez 1989a, 1989b), which demonstrated that net carbon gain on coarse-grained sediment is at least equal to, and often greater than, that on fine-grained sediment. Calculations of net carbon intake and snail growth, combined with estimates of field microalgal concentration and snail density, suggest that population density of *Hydrobia truncata* at West Meadow Beach is below that at which food limitation is likely to occur (Forbes and Lopez 1989a).

Table 6. Fecundity Experiment. Results of 1-way ANOVA of the effect of sediment type on the number of eggs laid and the percent hatch for snails from Flax Pond, Setauket Harbor, and West Meadow Beach populations. Homogeneity of variances was tested using Bartlett's Test; $P > 0.05$.

Source	SS	DF	MS	F-Ratio	P
I. Flax Pond					
Dependent Variable: Eggs					
Sediment	6733.50	1	6733.50	2.56	0.124
Error	57788.33	66	2626.74		
Dependent Variable: Percent Hatch					
Sediment	1.26	1	1.26	0.003	0.954
Error	8270.68	22	375.94		
II. Setauket Harbor					
Dependent Variable: Eggs					
Sediment	21540.04	1	21540.04	5.24	0.032
Error	90366.92	22	4107.59		
Dependent Variable: Percent Hatch					
Sediment	3484.86	1	3484.86	5.55	0.028
Error	13819.68	22	628.17		
III. West Meadow Beach					
Dependent Variable: Eggs					
Sediment	37052.04	1	37052.04	32.21	<0.001
Error	25303.58	22	1150.16		
Dependent Variable: Percent Hatch					
Sediment	858.01	1	858.01	2.52	0.127
Error	7506.40	22	341.20		

Due to the small size of this species, it was impractical to mark and recapture individuals to estimate growth rates. Growth rate comparisons among populations using mean size will be biased if the degree of size-dependent mortality or migration vary among habitats. Casual inspection indicated that the abundance of crabs, shore-birds and juvenile fish, likely predators of *Hydrobia* species (Fish and Fish 1974; Hylleberg 1986), is highest in the muddy salt-marsh habitat. Predation therefore does not appear a likely explanation for the small sizes and low densities observed at West Meadow Beach. Size-dependent mortality or removal may result from factors other than predation (i.e., due to transport by water currents) and may contribute to size differences among populations.

Sediment grade may influence the time available for feeding in intertidal habitats due to its effect on sediment porosity and drainage. *H. truncata* will feed when exposed to air, but as the sediment loses moisture the snails will eventually retreat into their shells (Forbes 1988). The greater porosity of sandy sediments may result in decreased feeding activity, compared to muddy habitats, during low tide. Thus the West Meadow Beach population may have had a lower average foraging time relative to the other populations. The smaller size of snails from Setauket Harbor (2% silt-clay) compared to those from Flax Pond (12% silt-clay) might also be related to differences in sediment water content at low tide.

Sediment grade in aquatic habitats is generally a function of the degree of water flow. Muddy sediments tend to accumulate in quiescent areas, whereas sandy sediments are often indicative of energetic conditions (Eltringham 1971). Sed-

iment transport events are common at West Meadow Beach, and such disturbance may have negative effects on survival and available foraging time for snails in this habitat. If wave energy, and not sediment grade, primarily controls size and abundance of *H. truncata*, then large and dense populations of *Hydrobia* species should occur in sandy but quiescent habitats. Such populations have been observed around Cape Cod, Massachusetts where a lack of availability of fine sedimentary material results in an abundance of low-energy habitats having sediment grades and sedimentary chlorophyll-*a* values similar to those at West Meadow Beach (D. Carey pers. comm.; V. Forbes unpublished).

In conclusion, the larger body sizes and population densities of *H. truncata* occupying muddy habitats can not be attributed to faster growth afforded by greater food availability on fine-grained sediment. Differences in body size due to variability in the timing of recruitment may be augmented by environmental constraints on growth. The resulting differences in population dynamics among conspecifics from different habitats may be of particular importance in annual, semelparous species.

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