Oecologia (1990) 83:53–61

F-4 For

Oecologia

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

Valery E. Forbes* and Glenn R. Lopez

Marine Sciences Research Center, State University of New York, Stony Brook, NY 11794, USA

Received August 20, 1989 / Received in revised form October 17, 1989 / Accepted December 13, 1989

Summary. 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.

Key words: 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 material 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).

---

* *Present address and address for offprint requests:* Biology Institute Odense University, Campusvej 55, DK-5230, Odense M., Denmark

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 (2-Jul-87), but under identical laboratory conditions, as for the other groups (17-Apr-87). 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 × 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-*a* 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-*a* values were higher at Setauket Harbor than Flax Pond, on two dates (Sep, Feb) Flax Pond values were higher, and on the remaining date (Jun), there was no difference between the two sites. Average values were: 0.043 µg/mg for Flax Pond; 0.052 µg/mg for Setauket Harbor; 0.011 µg/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/cm^2 for Flax Pond, 4.55 snails/cm^2 for Setauket Harbor, and 0.54 snails/cm^2 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 Fig. 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

Table 1. Field Measurements. Microalgal concentration of field sediments (µg chl-*a*·(mg dry wt sed)$^{-1}$ and densities of *H. truncata* (snails·cm^{-2}); 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-*a* 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-*a*	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-*a*	0.038 (0.0021,4)	0.068 (0.0066,4)	0.016 (0.0006,4)
	Density	2.21 (0.972,3)	0.76 (0.644,3)	0.03 (0.050,3)
Jun 87	Chl-*a*	0.071 (0.0107,4)	0.074 (0.0021,4)	0.007 (0.0002,4)
	Density	0.59 (0.453,3)	3.94 (1.809,3)	0.07 (0.017,3)
Aug 87	Chl-*a*	0.015 (0.0065,4)	0.036 (0.0026,4)	0.015 (0.0006,4)
	Density	6.68 (4.260,3)	11.61 (3.880,3)	0.44 (0.608,3)
Sep 87	Chl-*a*	0.047 (0.0049,4)	0.037 (0.0018,4)	0.007 (0.0005,4)
	Density	3.42 (0.652,3)	5.85 (1.336,3)	2.65 (0.422,3)
Feb 88	Chl-*a*	0.052 (0.0037,8)	0.037 (0.0020,6)	0.012 (0.0006,6)
	Density	2.03 (0.559,3)	4.42 (2.795,3)	0.07 (0.067,3)

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 (Fig. 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 (Fig. 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 (Fig. 5a, Table 6). Setauket Harbor snails laid more eggs on sand, and a greater percentage of eggs hatched on sand than on silt-clay (Fig. 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 (Fig. 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.

Table 5. Growth Experiment II. Microalgal concentration (μg chl-$a \cdot mg^{-1}$) 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 × 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		

lowing recruitment. The spring growth 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 epipfluorescence 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 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.

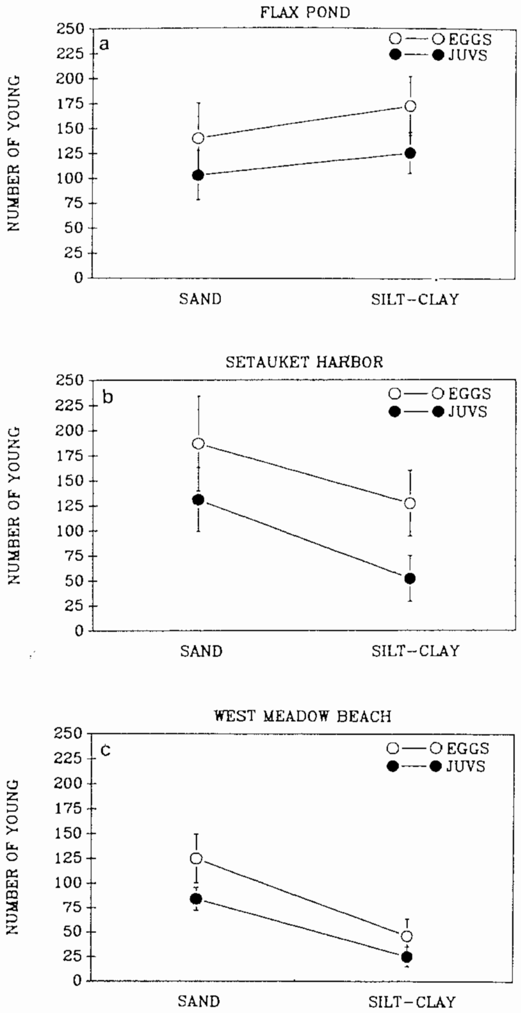

Fig. 5a–c. Laboratory Fecundity Experiment. The effect of sediment particle size on the number of eggs laid and the number of juveniles hatched (% hatch = juvs/eggs) for *H. truncata* from **a** Flax Pond, **b** Setauket Harbor, and **c** West Meadow Beach populations. Error bars indicate 95% confidence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

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, b), 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 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.

Acknowledgements. We thank D. Carey, R. Cerrato, R. Etter, T. Forbes, J. Levinton, A. Okubo, C. Peterson, and R. Whitlatch for helpful discussions and critical review of various drafts of this manuscript. G. Davis identified the snail populations and was invaluable for his knowledge of hydrobiid morphology and systematics. T. Forbes provided assistance in the field. Funding was provided by NSF grant OCE8501140 to G. Lopez.

References

Bianchi TS, Levinton JS (1984) The importance of microalgae, bacteria and particulate organic matter in the somatic growth of *Hydrobia totteni*. J Mar Res 42:431–443

Cammen LM (1982) Effect of particle size on organic content and microbial abundance within four marine sediments. Mar Ecol Prog Ser 9:273–280

Chatfield JE (1972) Studies on variation and life history in the prosobranch *Hydrobia ulvae*. J Conch 27:463–473

Deflaun MF, Mayer LM (1983) Relationships between bacteria and grain surfaces in intertidal sediments. Limnol Oceanogr 28:873–881

Eltringham SK (1971) Life in mud and sand. The English Universities Press, LTD., London, p 218

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

Fenchel T, Kofoed LH, Lappalainen A (1975) Particle size-selection of two deposit feeders: the amphipod *Corophium volutator* and the prosobranch *Hydrobia ulvae*. Mar Biol 30:119–128

Fish JD, Fish S (1974) The breeding cycle and growth of *Hydrobia ulvae* in the Dovey Estuary. J Mar Biol Ass UK 54:685–697

Forbes VE (1988) Intraspecific variation among populations of the deposit-feeding gastropod, *Hydrobia truncata:* the effect of sediment particle size on physiological energetics. Ph. D. Dissertation, State University of New York, Stony Brook, New York

Forbes VE, Lopez GR (1989a) The role of sediment particle size in the nutritional energetics of a surface deposit feeder. I. Ingestion and absorption of sedimentary microalgae by *Hydrobia truncata* (Vanatta). J Exp Mar Biol Ecol 126:181–192

Forbes VE, Lopez GR (1989b) The role of sediment particle size in the nutritional energetics of a surface deposit feeder. II. Metabolic cost estimated as ^{14}C-loss from uniformly-labeled *Hydrobia truncata* (Vanatta). J Exp Mar Biol Ecol 126:193–202

Hylleberg J (1986) Distribution of hydrobiid snails in relation to salinity, with emphasis on shell size and co-existence of the species. Ophelia 4:85–100

Jensen KT, Siegismund HR (1980) The importance of diatoms and bacteria in the diet of *Hydrobia*-species. Ophelia 1:193–199

Kaufmann KW (1981) Fitting and using growth curves. Oecologia 49:293–299

Kofoed LH (1975) The feeding biology of *Hydrobia ventrosa* (Montagu). I. The assimilation of different components of the food. J Exp Mar Biol Ecol 19:233–241

Levinton JS (1972) Stability and trophic structure in deposit-feeding and suspension-feeding communities. Am Nat 106:472–486

Levinton JS (1977) The ecology of deposit-feeding communities: Quisset Harbor, Massachusetts. In: Coull BC (ed) Ecology of marine benthos. University of South Carolina Press, Columbia, South Carolina, pp 191–228

Levinton JS (1982) The body size-prey size hypothesis: the adequacy of body size as a vehicle for character displacement. Ecology 63:869–872

Levinton JS (1985) Complex interactions of a deposit feeder with its resources: roles of density, a competitor, and detrital addition in the growth and survival of the mudsnail *Hydrobia totteni*. Mar Ecol Prog Ser 22:31–40

Levinton JS, Bianchi TS (1981) Nutrition and food limitation of deposit-feeders. I. The role of microbes in the growth of mud snails (Hydrobiidae). J Mar Res 39:531–545

Longbottom MR (1970) The distribution of *Arenicola marina* (L.) with particular reference to the effects of particle size and organic matter of the sediments. J Exp Mar Biol Ecol 5:138–157

Lopez GR, Kofoed LH (1980) Epipsammic browsing and deposit-feeding in mud snails (Hydrobiidae). J Mar Res 38:585–599

Lopez GR, Levinton JS (1978) The availability of microorganisms attached to sediment particles as food for *Hydrobia ventrosa* Montagu (Gastropoda: Prosobranchia). Oecologia 32:263–275

Lopez GR, Levinton JS (1987) Ecology of deposit-feeding animals in marine sediments. Quart Rev Biol 62:235–260

Mayer LM, Rahaim PT, Guerin W, Macko SA, Watling L, Anderson FE (1985) Biological and granulometric controls on sedimentary organic matter of an intertidal mudflat. Est Coast Shelf Sci 20:491–503

Morrisey DJ (1987) Effect of population density and presence of a potential competitor on the growth rate of the mud snail *Hydrobia ulvae* (Pennant). J Exp Mar Biol Ecol 108:275–295

Morrisey DJ (1988) Differences in effects of grazing by deposit-feeders *Hydrobia ulvae* (Pennant) (Gastropoda: Prosobranchia) and *Corophium arenarium* Crawford (Amphipoda) on sediment microalgal populations. II. Quantitative effects. J Exp Biol Ecol 118:43–53

Newell RC (1965) The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. Proc Zool Soc Lond 144:25–45

Olafsson EB (1986) Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica:* a field experiment. J Anim Ecol 55:517–526

Sanders HL (1958) Benthic studies in Buzzards Bay. I. Animal-sediment relationships. Limnol Oceanogr 3:245–258

Sokal RR, Rohlf FJ (1981) Biometry, second edition. W.H. Freeman and Company, San Francisco, California, p 859

Strickland JDH, Parsons TR (1972) A practical handbook of seawater analysis. Fish Res Bd Can Bull 167, 2nd ed., p 310

Whitlatch RB, Weinberg JR (1982) Factors influencing particle selection and feeding rate in the polychaete *Cistenides* (*Pectinaria*) *gouldii*. Mar Biol 71:33–40

Wilkinson L (1986) SYSTAT. SYSTAT, Inc., Evanston, Illinois

Yamamoto N, Lopez GR (1985) Bacterial abundance in relation to surface area and organic content of marine sediments. J Exp Mar Biol Ecol 90:209–220

Zobell CE (1938) Studies on the bacterial flora of marine bottom sediments. J Sed Petrol 8:10–18