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The Feeding Ecology of the Gastropod Batillaria attramentaria, Chuckanut Mudflat, Washington

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THE FEEDING ECOLOGY
OF THE GASTROPOD
BATILLARIA ATTRAMENTARIA,
CHUCKANUT MUDFLAT, WASHINGTON

A Thesis

Presented to

The Department of Biology

Western Washington University

In Partial Fulfillment

Of the Requirements for the Degree

Master of Science

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by

Karen Marie Mellema Steensma

May, 1985

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Advisory Council

Chairman

THE FEEDING ECOLOGY OF THE GASTROPOD BATILLARIA ATTRAMENTARIA, CHUCKANUT MUDFLAT, WASHINGTON

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ABSTRACT. - The deposit-feeding gastropod Batillaria attramentaria lives upon algal mat, mud, gravelly mud and gravelly sand substrates at Chuckanut Mudflat, Washington and upon homogeneous sand at Semiahmoo Spit, Washington. The efficiencies and rates of feeding by B. attramentaria on these substrates were studied in order to determine whether an optimal foraging strategy exists in this species.

Gut content analysis of snails taken from the various substrates revealed a fairly constant diet of sediment particles and diatoms, along with occasional animal fragments. Diatoms were ingested with efficiencies ranging from 38 to 51 percent; digestive efficiency increased with increasing availability of diatoms in sediments. Snail fecal pellets contained two to seven times more organic carbon than was contained in sediments. Carbon enrichment of pellets decreased with increasing availability of carbon in the sediments.

Gut residence times for materials ingested ranged from 260 to 400 minutes and varied inversely with the percentage of mud in the sediments. Pellet egestion rates increased with increasing percentage of mud in sediments, and ranged from 0.1 to 7.0 mg snail^{-1} hr^{-1}.

Results for gut content analysis, gut residence and egestion rate experiments supported the hypothesis that Batillaria attramentaria feeds selectively on mud and diatoms regardless of sediment type. Egestion rate, diatom digestion and carbon enrichment results pointed to an energy optimization strategy in this species.

ACKNOWLEDGEMENTS

My sincere thanks to Dr. David Schneider for sharing his ideas and materials through all aspects of my graduate work at Western Washington University. His unselfish aid on problems large and small went far beyond the call of duty of any major professor. Many thanks, also, to my committee members, Dr. June Ross and Dr. William Summers, who made helpful suggestions to improve this manuscript. I am grateful for initial advice from Dr. Meribeth Riffey and Dr. Charles Flora on design of the research project.

I appreciate instruction in the use of the carbon analyzer given by Dr. William Wilson and Mr. Clint Burgess; hints on sediment sieving procedure from Dr. Maurice Schwartz; aid in identification of algae from Dr. Maurice Dube. Mr. Doug Doolittle and Mr. Dennis Bohrer cheerfully met my most unreasonable equipment demands on short notice and Ms. Jane Friesen prepared this manuscript with exceptional speed and accuracy.

Last but not least I must thank my husband, John Steensma, who was temporarily compelled to focus on gastropod ecology rather than bovine ecology. As always, he has survived with dignity intact!

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INTRODUCTION

The deposit-feeding mud snail *Batillaria attramentaria* occurs throughout the Strait of Georgia and Puget Sound in Western Canada and Washington and in two California localities, Tomales Bay and Elkhorn Slough (Hanna, 1966). Introduced from Japan as early as 1930 (Bonnet, 1935), this gastropod is abundant on mudflats in many areas where the Japanese oyster *Crassostrea gigas* was planted (Quayle, 1964). It is the only representative of the genus known on the west coast of North America (Hanna, 1966). Though often found burrowed one to five centimeters during the winter, *B. attramentaria* is active during warmer months whenever even a thin film of water is present on the substrate surface (Whitlatch, 1974). The animals feed on soft substrate by pulling themselves over the surface and sweeping their mouths from side to side, ingesting the sediment in a vacuum-cleaner fashion (Driscoll, 1972).

Batillaria attramentaria is classified as a deposit-feeder because it ingests sediment or the film of material on the surface of the sediment (Whitlatch, 1974; Kozloff, 1983:300). Deposit-feeding gastropods are common in marine bottoms, salt marshes, estuaries and rivers (Levinton, 1972; Fenchel, 1975; Montague, *et al*, 1981). These animals generally predominate in fine-grained sediments, ingesting particles and organic debris and egesting fecal material consisting of particles which may be bound into pellets (Levinton, 1972; Levinton and Lopez, 1977). Deposit-feeders obtain their food through direct ingestion of diatoms, scraping diatoms and bacteria from sedimentary grains, digestion of microbes from ingested sedimentary particles, ingestion and digestion of detritus or digestion of microbes associated with detritus (see Newell, 1965; Fenchel and Kofoed, 1976; Levinton and Bianchi, 1981).

Gastropods in mud or salt marsh habitats have physical effects on the ecosystem both as consumers of organic materials and as regulators of microbial and algal communities through their grazing activities (Wetzel, 1977; Montague, *et al*, 1981). These animals help to regulate the flow of energy and materials in soft-substrate communities by cropping microalgae, reworking the sediment and packaging detritus into fecal pellets which may provide nutritive reward for other species. The effects of such gastropods are of potentially greatest importance on shores where there is no domination of community structure by large, active, generalist predators such as starfish (Underwood, 1979), which may often be the case in areas of fine sediment.

The diets of some fresh water deposit-feeding gastropods have been studied (Heywood and Edwards, 1962; Calow, 1975) and more recently attention has focused on the nutrition of the marine *Hydrobia* spp. (e.g., Levinton and Bianchi, 1981; Lopez and Cheng, 1983), the mud snail *Ilyanassa* (*Nassarius*) *obsoleta* (Wetzel, 1977; Bianchi and Levinton, 1981; Connor and Edgar, 1982) and the salt marsh gastropods *Cerithidea californica* (Whitlatch and Obrebski, 1980) and *Bittium varium* (Lopez, 1980). Work with these gastropods has shown a relationship between ingested particle size and nutrition and suggested the possibility of an optimal foraging strategy. Several mechanical properties of particles provide potential variation in deposit-feeder adaptations, the most obvious property being size; other important factors might include shape, density and surface smoothness (Levinton, 1980). A positive correlation exists between feeding on larger particles and increased body size. Where diatoms are an important food source, particle size selectivity by gastropods of different sizes has been described in terms of selection of diatoms of different sizes (see Fenchel and Kofoed, 1976). In *Batillaria attramentaria* diatom food size has been shown to increase with snail length (Whitlatch and Obrebski, 1980). Levinton (1980) in his review of particle feeding stated that ingestion as a function of particle size is probably most strongly regulated by mechanical constraints of the buccal apparatus.

Switches in foraging strategy, or optimization, can occur when a deposit-feeding gastropod which characteristically feeds on one grade of sediment finds itself upon another type of sediment. Lopez and Kofoed (1980) showed that _Hydrobia_ _ventrosa_, which occurs upon a variety of substrates, switches from ingestion of fine particles to an "epipsammic browsing" mode of feeding upon sediments composed of larger particles. Such an optimal foraging strategy is possible only if the animal possesses the morphologic and behavioral flexibility to permit the switch. The hydrobiids are apparently able to scrape diatoms from the surface of coarse grains when smaller, easily swallowed particles are not available. Sediments of differing textures may differ strongly in the relative proportions of swallowing vs. scraping (Levinton, 1980).

Batillaria _attramentaria_ has been documented and studied in California mud habitats (Whitlatch, 1974; Whitlatch and Obrebski, 1980) but its feeding biology has not been examined in relation to coarser substrates such as sand and gravel. Populations of _B_. _attramentaria_ exist upon a variety of substrates, including sand and gravel, at Chuckanut Mudflat and Semiahmoo Spit in Whatcom County, Washington. The objective of this study was to determine the mode, efficiency and rate of feeding by _B_. _attramentaria_ on these various substrates.

The following questions were posed:

1. Do the characteristics of gut contents and fecal pellets of _Batillaria_ _attramentaria_ vary between the different substrates?

2. Do the gut residence times of ingested material and the rates of egestion of pellets vary between the different substrates?
3. Does the mode of ingestion vary (i.e., does a switch in foraging strategy occur) between the different substrates?

Seven substudies were undertaken in an attempt to answer these questions: 1) grain size analysis of the various substrates; 2) density of snails upon the various substrates; 3) gut content analysis of snails taken from the various substrates; 4) measures of efficiency of digestion of diatoms by the snails; 5) measures of total organic carbon in sediments and pellets; 6) measures of gut residence times; 7) measures of egestion rates.

STUDY AREA

Chuckanut Mudflat (Fig. 1) is a section of Chuckanut Bay, which is located about one mile south of Bellingham, Washington. Huggins (1969) surveyed the mudflat and described its composition as varying from pure clay, mud, sand and gravel to combinations of these sediments. He categorized eight major substrate types and four tidal zones. *Batillaria attramentaria* (listed by Huggins as *Bittium eschrichtii*) was noted at the west end of the mudflat in a protected mud/sand area adjoining large boulders. Preliminary surveys of the mudflat from April 1983 through July 1984 showed *Batillaria attramentaria* continued to be concentrated in that location, though occasional animals were noted in immediately adjacent areas.

A transect line was established in the area of greatest density of the snails, running from the high intertidal zone to the low intertidal zone. The line included four major divisions of substrate which serve as common habitats for *Batillaria attramentaria*: 1) filamentous algal mats over mud, 2) mud, 3) gravelly mud and 4) gravelly sand. The algae comprising the mats was identified as belonging to the genus *Enteromorpha*, probably *E. clathrata*.

Semiahmoo Spit (Fig. 2), the only other major site of a *Batillaria attramentaria* population in Whatcom County (pers. obs.), is located on Drayton Harbor, adjacent to the city of Blaine. Much of Drayton Harbor lies exposed as mudflat during low tide. The snails are concentrated along the spit on the protected northwest side of the tideflats, upon a fairly homogeneous sand. The sand is intermediate in grain size in comparison to the substrates at Chuckanut Mudflat. A transect was placed through the tidal zone with the greatest density of snails.

Figure 1. Chuckanut Mudflat.

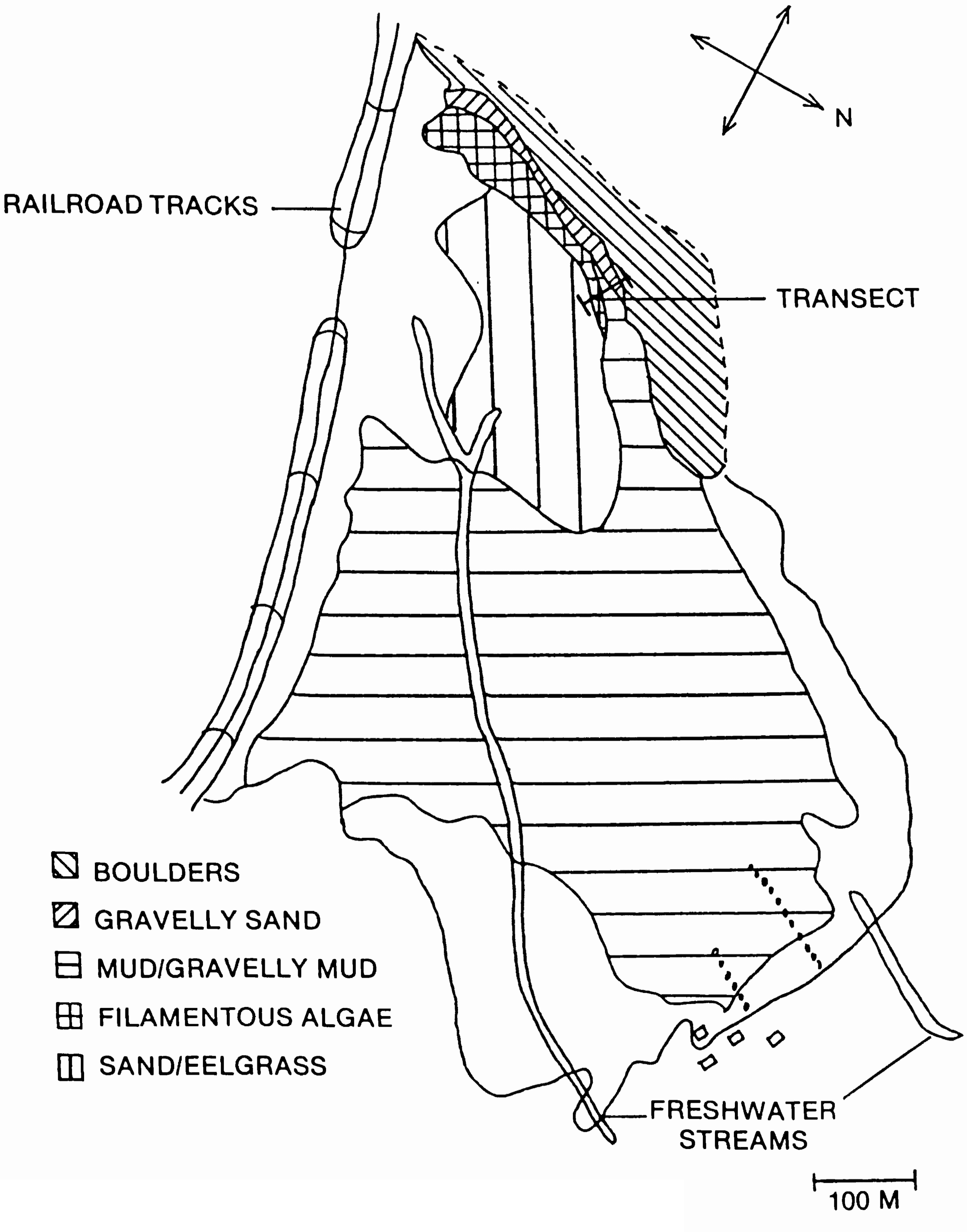
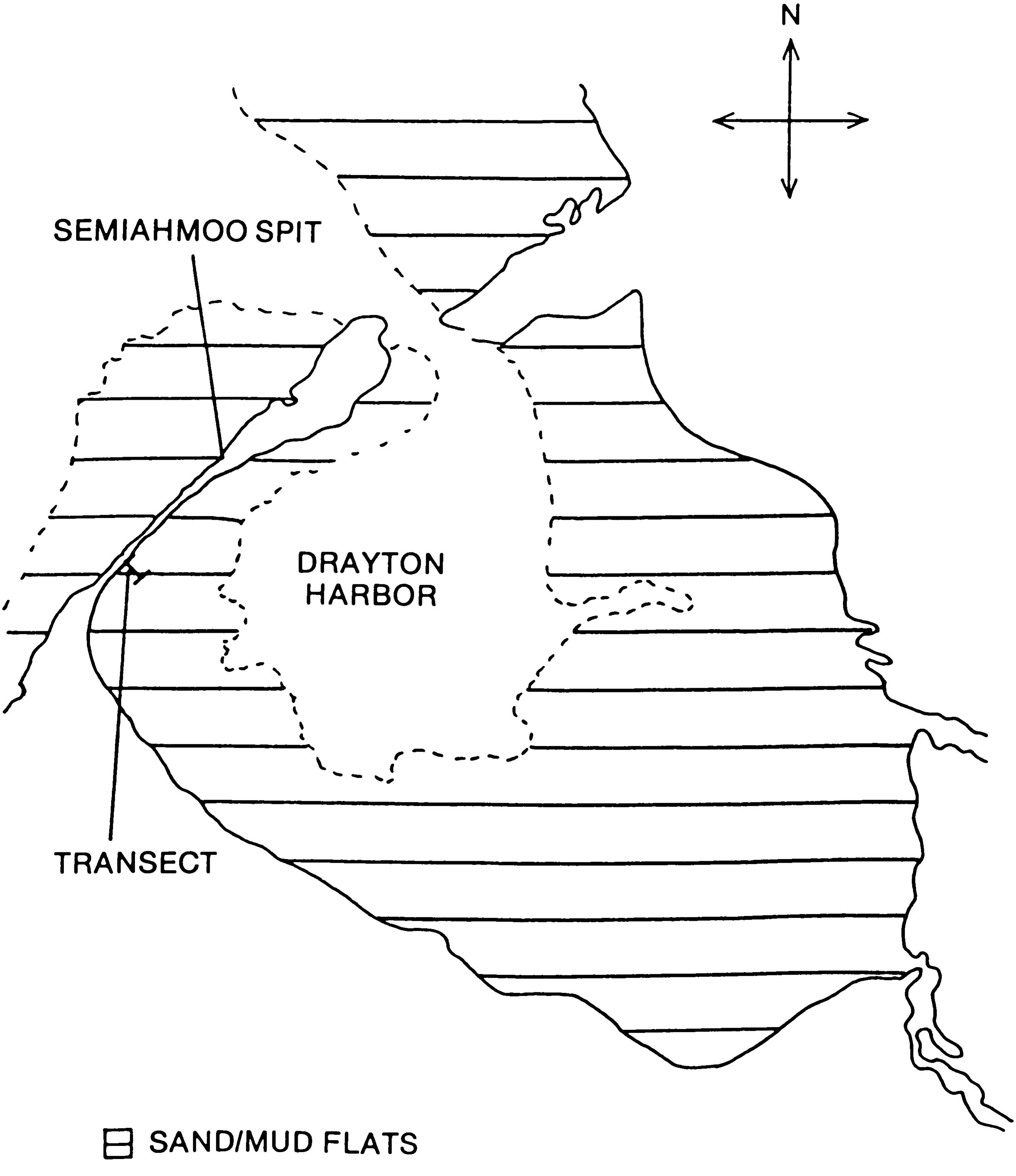

N
RAILROAD TRACKS
TRANSECT
▧ BOULDERS
▨ GRAVELLY SAND
⊟ MUD/GRAVELLY MUD
⊞ FILAMENTOUS ALGAE
◫ SAND/EELGRASS
FRESHWATER STREAMS
100 M

Figure 2. Semiahmoo Spit.


N
SEMIAHMOO SPIT
DRAYTON HARBOR
TRANSECT
SAND/MUD FLATS
500 M

METHODS

Preliminary observations had shown that Batillaria attramentaria populations at Chuckanut Mudflat and Semiahmoo Spit remained inactive and burrowed under sediment throughout the winter and indeed were difficult to locate from October through April. Thus all laboratory studies requiring active snails and fresh sediments and all field work were performed in August and early September, 1984. Materials which could be frozen and examined later were also collected during this time, so that all results would be consistent with any seasonal aspect of snail activity and sediment characteristics.

Grain size analysis

Sediments for grain size analysis were collected from each substrate type to a depth of two or three cm (adequate since snails ingest only the top few mm) using a flat spatula of area 96 cm^2. Three replicate samples, randomly located, were collected for each substrate; macroscopic algae and other organic materials were removed and grain size was analyzed through dry sieving. Particle diameters larger than 2 mm were considered gravel; those from 0.0625 to 2 mm, sand; those smaller than 0.0625 mm, mud (Folk, 1974:25-35). Textural classifications were made based upon proportions of mud, sand and gravel in the samples. Sorting coefficients were determined using the Inclusive Graphic Standard Deviation (Gray, 1981:11-15).

Snail density

Snail density was measured by counting the number of snails in 0.1 m^2 sampling quadrats (McIntyre, 1971:4-9). Ten quadrats, randomly located, were counted for each substrate type. Snails counted were assigned to three size classes: those smaller than 20 mm in length, those greater than 20 mm in length and those of length 20 mm. Since snails of length 20 mm were present in large numbers on all substrate types, this size class was used for all of the feeding studies. The length 20 mm corresponds to an age of 10 years for southern British Columbia habitats (Behrens Yamada, 1982) and is also about the minimum size in which it is feasible to work with gut contents and fecal pellets.

Gut content analysis

Snails collected for gut content analysis were placed on ice in the field and transferred to a freezer within 30 minutes of collection. At the time of processing specimens were thawed and shells were carefully cracked. Gut contents were removed with a Pasteur pipette, mixed with a small amount of distilled water and gently disaggregated. This material was then viewed on a Sedgwick Rafter cell (McAlice, 1971) under 200x magnification, and frequency of occurrence of identifiable items was estimated using random transects across the slide. Ten snails were collected from each substrate and 100 items were counted per snail.

Efficiency of diatom digestion

The presence of chlorophyllose pigment in diatom frustules was used as an indication of living vs. non-living diatoms. The proportion of living diatoms in the sediments was compared to the proportion of living diatoms in fecal pellets as a measure of the snails' efficiency in digesting the diatoms ingested. Ten sediment samples from each substrate type were collected as for grain size analysis, placed on ice in the field and transferred to a freezer until processing. Ten snails from each substrate type were collected and placed on ice in the field; within 90 minutes of collection these animals were transferred to individual plastic compartments secured with fiberglass mesh. The compartments were placed in Instant Ocean aquaria equipped with fluorescent lights and maintained at 20°C (a temperature previously found to be optimal for producing activity levels close to those seen in the field; see also Yamada and Sankurathri, 1977). The snails were allowed to produce pellets for one hour, after which pellets were collected and frozen until processing. For enumeration of living diatoms, sediment samples and fecal pellets were thawed and placed on a Sedgwick Rafter cell as for gut content analysis. The proportion of live diatoms was estimated by examining the first 100 diatoms encountered in random transects across the slide.

Total organic carbon in sediments and pellets

Carbon in sediments and pellets was measured with an Oceanography International Total Carbon Analyzer. Ten sediment samples and ten fecal pellet samples were collected and frozen for each substrate type, using the methods outlined for diatom counts. Previous to the time of processing, samples were thawed, dried for 24 hours at 80°C and weighed on an analytical balance to the nearest 0.0001 g. The sample used in carbon analysis depends upon the carbon concentration of the sample; 50 to 100 μg of carbon is desirable. Thus, weights of sediment samples ranged from 0.01 g for the most carbon-rich sediments to 0.07 g for the least carbon-rich sediments. Fecal pellet weights, limited by the amount of material produced by each snail (pellets from individual snails were not pooled), ranged from 0.0001 g to 0.006 g. Each sample, along with 1.0 ml of 6% phosphoric acid, 0.2 g potassium persulfate and 4.0 ml distilled water, was placed in a pre-combusted glass ampule, purged of inorganic carbon for eight minutes with a purging unit and sealed with a microburner. Sealed ampules were autoclaved at 130°C for a minimum of 20 hours before analysis with the total organic carbon IR analyzer. The amount of carbon dioxide in each sample was given in a unitless integrator count, which was converted to μg carbon per mg sediment using a calibration curve prepared with standardized carbon (potassium biphthalate) samples. A few samples were lost during the sealing, autoclaving and analyzing processes due to ampule breakage.

Gut residence times

Gut residence time for material ingested by the snails was measured by marking substrates with colored material, allowing snails to feed on the substrates and noting the first appearance of color in the fecal pellets. Snails were starved for 24 hours, allowed to feed on unmarked sediment for one hour, on carmine-marked sediment for the second hour and on methylene blue-marked sediment for the third hour. Snails were then placed upon unmarked sediment again until the appearance of the bright red carmine (minimum residence time) and the methylene blue (maximum residence time) was noted in the pellets. Except for the periods in which the snails were actually feeding on the dyed sediments, they were kept at 20°C in Instant Ocean aquaria. The animals were separated from each other in compartmentalized plastic boxes and pellets were periodically collected with an eyedropper and examined under a dissecting microscope for red and/or blue colors.

Twenty snails were initially used for each substrate type. However, not all snails would feed on the altered substrates and some would feed only on the red or only on the blue. To test for the effect the colored markers might have upon the percentage of snails feeding on the substrate, twenty snails were placed upon unaltered Semiahmoo sand for one hour and twenty snails were placed upon marked Semiahmoo sand for one hour. The number of snails which had fed after one hour (the number which had moved from their original positions since Driscoll (1972) found the snails feed whenever they move) was 13 for the unmarked sediment and 14 for the marked sediment. Thus refusal to feed was not considered to be a result of the markers.

To test for any effect the colored markers might have upon the pellet egestion rate, the egestion rate of snails which had fed on Semiahmoo sand marked with carmine and methylene blue was compared with the egestion rate of snails which had fed on unmarked Semiahmoo sand. Egestion rate for the marked sand was 2.69 mg/snail/hour and egestion rate for unmarked sand was 2.40 mg/snail/hour. Analysis of variance at the 0.05 significance level showed no significant difference between these two values.

The Chuckanut algae substrate did not mix well with methylene blue although it did mix with carmine. As a result, pellets from the snails which had fed on the marked Chuckanut algae showed red but not blue coloration. Since blue was used to note maximum gut residence time, maximum gut residence values were not obtained for ingested Chuckanut algae.

Egestion rates

Fecal pellet egestion rates of snails were measured by placing twenty previously starved snails upon a substrate in an Instant Ocean aquarium at 20°C for 24 hours, removing snails to individual compartments empty of sediment and then collecting the fecal pellets from the compartments after one hour. Previous attempts to keep the snails feeding on the substrate during pellet collection had eliminated the effect that one hour of not eating might have on the egestion rate. However, this resulted in much destruction of pellet material during separation of pellets from sediments. Since the snails do continue to produce pellets for some time after they have been removed from their food, pellets were collected for one hour immediately following a 24-hour feeding. During this hour the snails were closely observed to ensure that they did not re-ingest the pellets they were producing.

Pellets were removed from compartments with an eyedropper, rinsed briefly with distilled water to dissolve ocean salts and collected upon pre-weighed glass fiber filter paper using a Sartorius membrane filtration apparatus. Dried filters were weighed to the nearest 0.0001 g on an analytical balance to obtain mg of pellets/snail/hour.

Statistical analysis

The research was designed so that all statistical inferences made in the study could be based on linear regression analysis or on a completely randomized design, analysis of variance and Student-Newman-Keuls multiple range test, with the significance level chosen at 5% before analysis. Where raw data were expressed in percentage values, arcsin transformations of the values were used in statistical analysis.

RESULTS

Grain size analysis

Sediment profiles for each of the five substrates studied are presented in Figures 3 through 7. The Chuckanut mud substrate (Fig. 3) and the Chuckanut algae substrate (Fig. 4) showed profiles generally similar in appearance; distinguishing these two sediment types in the field was virtually impossible except during the season when the algal mat was present. The Chuckanut gravelly mud substrate (Fig. 5) presented a profile in which the most obvious difference from the previous two substrates was the increased amount of material between 2 and 4 mm in diameter and the decreased amount of material between 0.062 and 0.25 mm in diameter. The Semiahmoo sand substrate profile (Fig. 6) was dramatically different from all other substrates in that it contained sediment grain sizes from a narrower range (covering only five sieve mesh sizes) and was the only substrate in which a single size fraction (the fraction between 0.50 and 0.25 mm) composed greater than 50 percent of the material in the sediment. Nearly 50 percent of the Chuckanut gravelly sand substrate (Fig. 7) was composed of material larger than 4 mm, a size category which was not observed in any of the other substrate types.

The percentages of mud in the various substrates (Table 1), when listed in decreasing order, reflect the position of these sediments on the shore from low in the intertidal zone to high in the intertidal zone. Though the Semiahmoo sand came from a different site, it could conveniently be placed between the Chuckanut gravelly mud and the Chuckanut gravelly sand in terms of percentage composition of mud. Textural classifications of these sediments are a verbal expression of the sediment profile histograms and show again that the Chuckanut algae substrate and the

Figure 3. Grain size distribution of Chuckanut mud substrate.

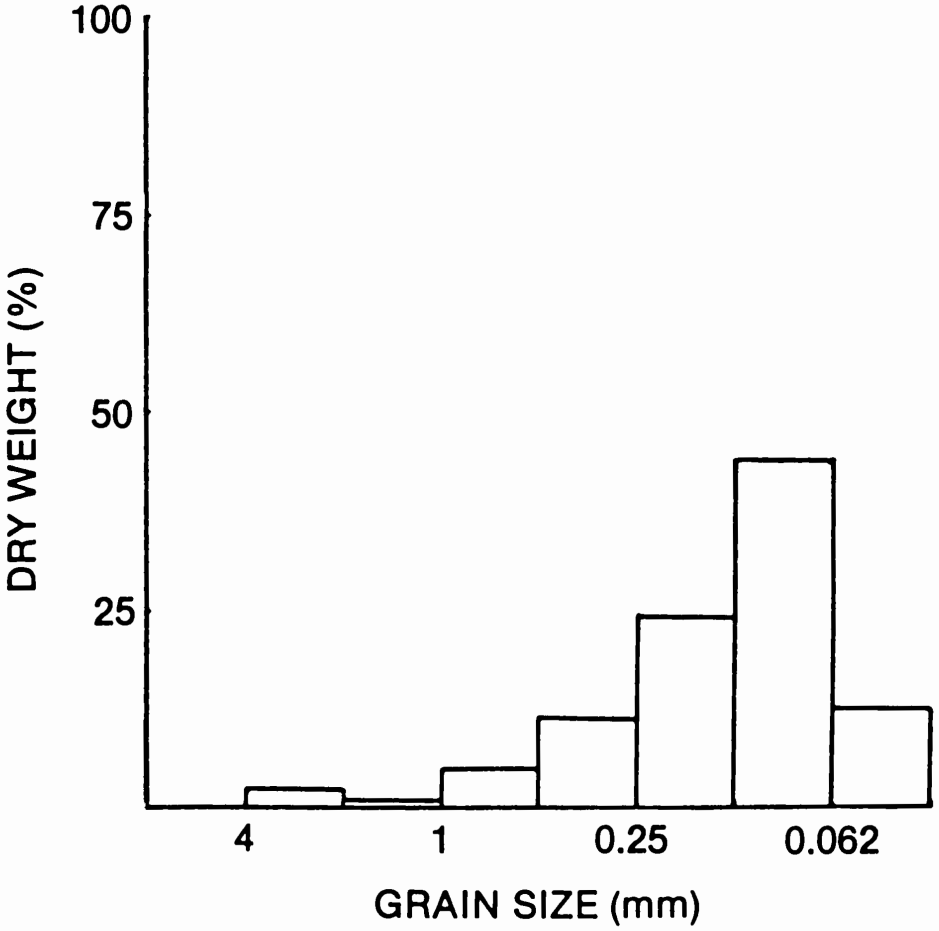

100
75
50
25
DRY WEIGHT (%)
4
1
0.25
0.062
GRAIN SIZE (mm)

Figure 4. Grain size distribution of Chuckanut algae substrate.

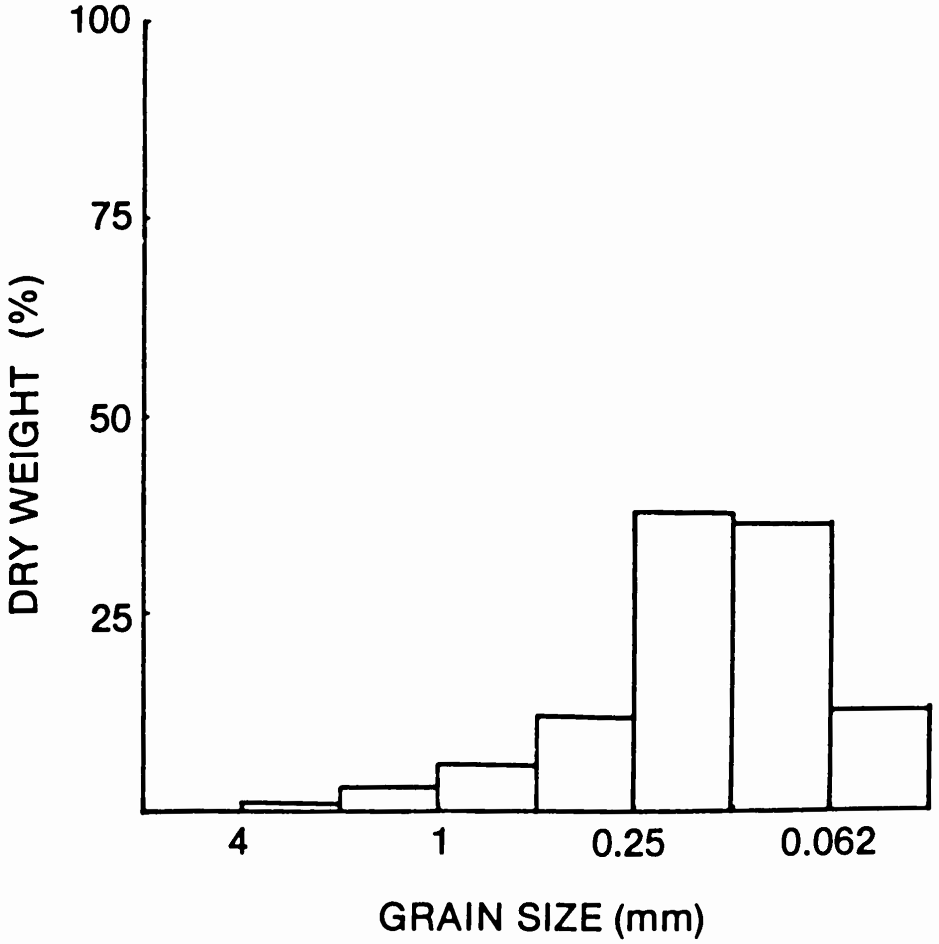
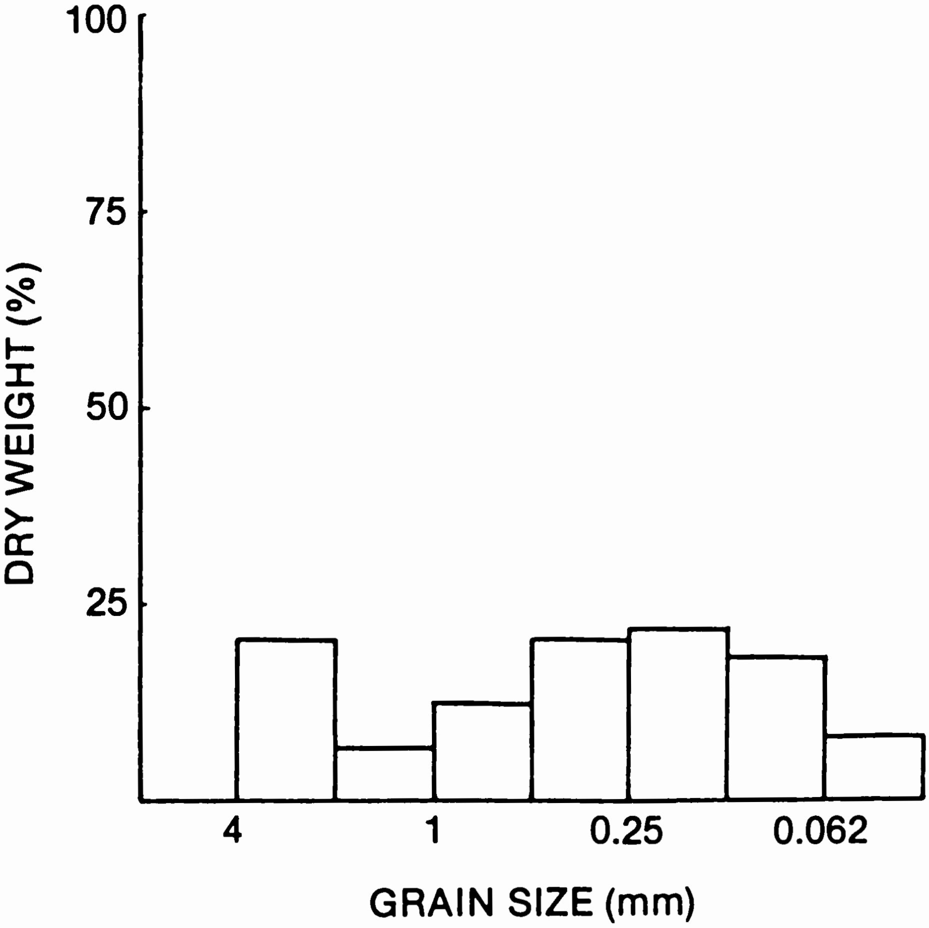
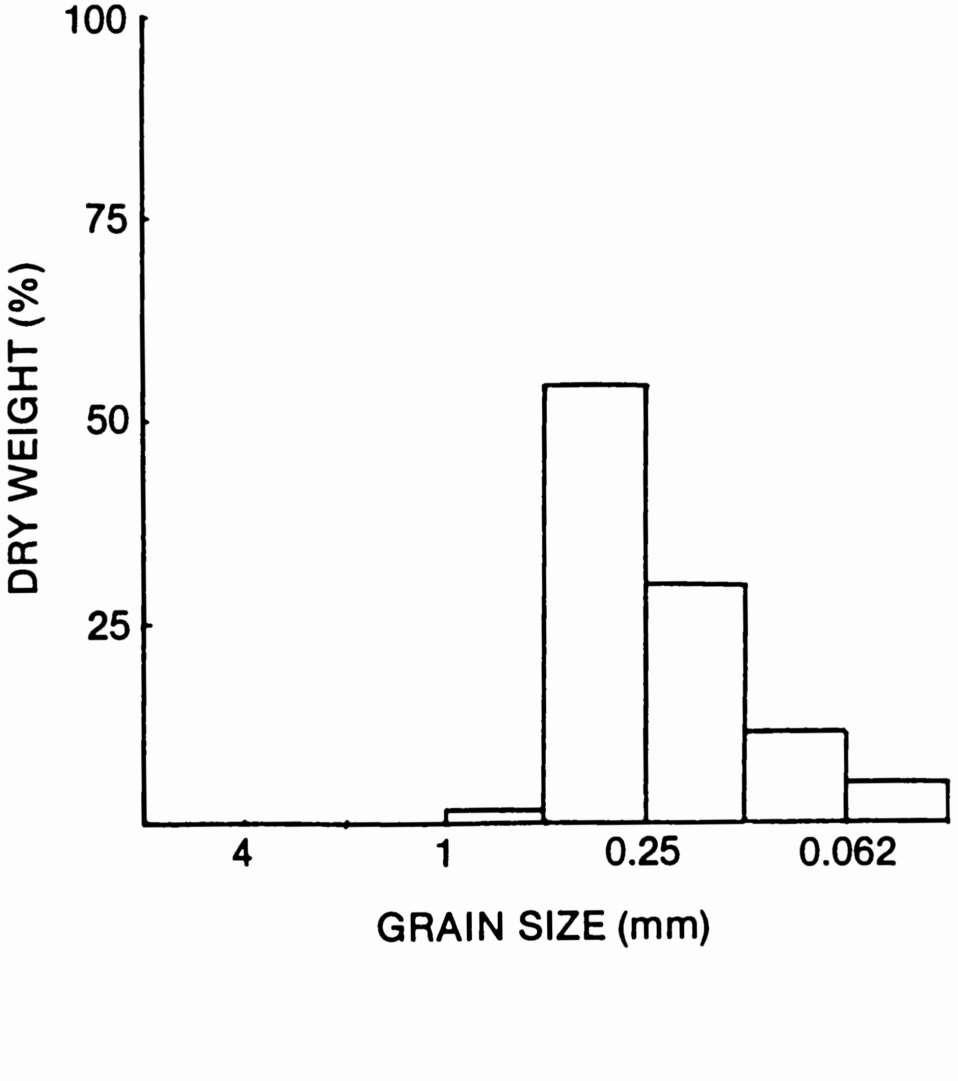

100
75
50
25
DRY WEIGHT (%)
4
1
0.25
0.062
GRAIN SIZE (mm)

Figure 5. Grain size distribution of Chuckanut gravelly mud substrate.



100
75
50
25
DRY WEIGHT (%)
4
1
0.25
0.062
GRAIN SIZE (mm)

Figure 6. Grain size distribution of Semiahmoo sand substrate.



100
75
50
25
DRY WEIGHT (%)
4
1
0.25
0.062
GRAIN SIZE (mm)

Figure 7. Grain size distribution of Chuckanut gravelly sand substrate.

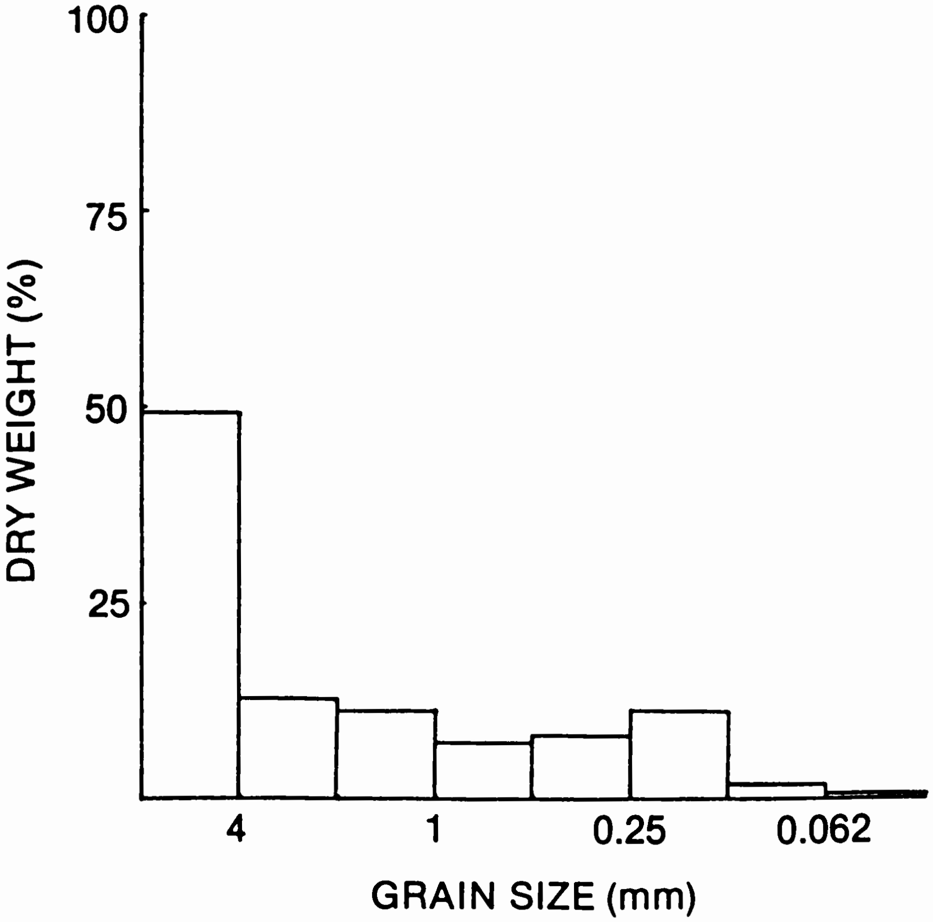

100
75
50
25
DRY WEIGHT (%)
4
1
0.25
0.062
GRAIN SIZE (mm)

Table 1. Sediment characteristics of *Batillaria attramentaria* habitats at Chuckanut Mudflat and Semiahmoo Spit

	Chuckanut mud	Chuckanut algae	Chuckanut gravelly mud	Semiahmoo sand	Chuckanut gravelly sand
% mud	12.3*	10.0*+	7.2+	4.2	0.5
sorting coefficient	1.16 (poor)	1.04 (poor)	2.41 (very poor)	0.82 (moderate)	2.15 (very poor)
textural classification	slightly granular, very fine sand	slightly granular, muddy, fine sand	granular, muddy, fine sand	well-sorted, medium sand	sandy pebble gravel

*, + = values not significantly different (ANOVA done on % mud only; MRT in Appendix I).

Chuckanut mud substrate were nearly indistinguishable when the algal mat was not considered. Sorting coefficients for the Chuckanut mud substrate and the Chuckanut algae substrate were also similar. All of the Chuckanut substrates had fairly high sorting coefficients compared to the Semiahmoo sand.

Snail density

Results of the snail density counts are presented in Table 2. No analysis of variance was done for the individual size classes due to high variability in the counts and to the lack of precision in counting snails less than 20 mm in length, which were more easily seen on some sediments than on others. The high variability probably relates to a qualitative observation of extremely patchy distribution of the snails. An ANOVA on the total numbers of snails showed no significant difference in snail density between any of the substrates at Chuckanut Mudflat. Only the density at Semiahmoo Spit was significantly different from the other substrates.

Gut content analysis

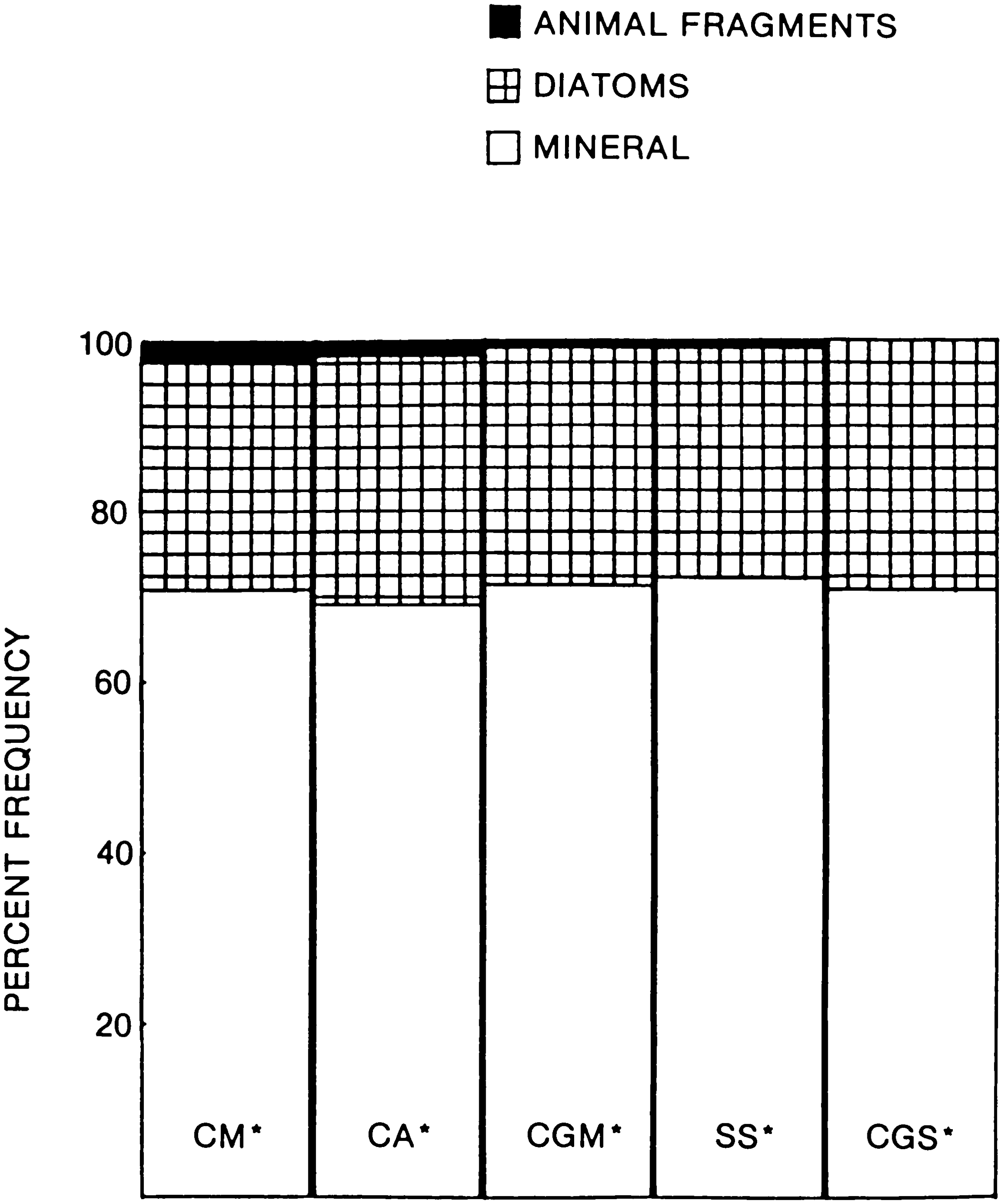
The results of the gut content analysis are presented in Figure 8. The only identifiable items in the gut were sediment particles (listed as mineral), diatoms and animal fragments. No significant difference was seen between the various substrates in relative proportions of these materials. A few fragments of vascular plant material were also seen in some of the guts but the proportions of plant material were not significantly different from zero and must be considered coincidental. No empty guts were found amongst the 50 snails dissected.

Table 2. Density of Batillaria attramentaria upon substrates at Chuckanut Mudflat and Semiahmoo Spit (number of snails per 0.1 m^2)

snail size class	Chuckanut mud	Chuckanut algae	Chuckanut gravelly mud	Semiahmoo sand	Chuckanut gravelly sand
<20 mm length	1.6	0.1	3.0	9.9	2.8
20 mm length	1.6	1.7	1.8	4.5	2.4
>20 mm length	2.3	2.0	0.6	0.6	0.3
TOTAL all size classes	5.5*	3.8*	5.4*	15.0	5.5*

*values not significantly different (ANOVA done on totals only; MRT in Appendix II).

Figure 8. Gut contents of Batillaria attramentaria specimens collected from five different substrates at Chuckanut Mudflat and Semiahmoo Spit. CM, Chuckanut mud; CA, Chuckanut algae; CGM, Chuckanut gravelly mud; SS, Semiahmoo sand; CGS, Chuckanut gravelly sand. * values not significantly different.


ANIMAL FRAGMENTS
DIATOMS
MINERAL
100
80
60
40
20
PERCENT FREQUENCY
CM*
CA*
CGM*
SS*
CGS*

Efficiency of diatom digestion

The proportion of living vs. non-living diatoms in the various substrates was not significantly different between any of the substrates except the Chuckanut algae (Table 3). The digestive efficiencies of the snails on diatoms in the various substrates likewise showed no significant difference except in the case of the Chuckanut algae. None of the substrates showed a significant difference in the proportion of live diatoms in the pellets. There was a significant linear relationship between the digestive efficiency upon diatoms and the percentage of living diatoms in the sediment (Fig. 9). Digestive efficiency upon diatoms increased 0.71% for each percentage point increase in the amount of living vs. non-living diatoms in the sediment.

Though the lengths of diatoms seen in sediments, guts and pellets were not measured, it was generally observed that diatoms in the Semiahmoo sediments were about twice the size of most of the diatoms in materials from Chuckanut Mudflat. A greater diversity of diatom species was also seen in the Semiahmoo sand, though again, no quantitative observations were made.

Total organic carbon in sediments and pellets

The results of total organic carbon analysis for sediments and pellets are presented in Table 4. For all substrates, fecal pellets were enriched in carbon compared to the sediments on which the snails had been feeding. This enrichment of pellets is shown as a calculated ratio of pellet carbon to sediment carbon. There was a significant linear relationship between the total organic carbon in the sediment and the percentage of mud in the sediment (Fig. 10). The amount of carbon in the sediment increased at a rate of 0.089 μg per mg of sediment for each percentage increase in the

Table 3. Efficiency of diatom digestion by *Batillaria attramentaria* feeding on substrates from Chuckanut Mudflat and Semiahmoo Spit

	percentage of living diatoms in sediment	percentage of living diatoms in pellets	digestive efficiency (%)
Chuckanut mud	58.34*	32.90^{+}	43.61$^{\wedge}$
Chuckanut algae	70.02	34.55^{+}	50.66
Chuckanut gravelly mud	57.65*	33.39^{+}	42.08$^{\wedge}$
Semiahmoo sand	54.18*	33.06^{+}	38.98$^{\wedge}$
Chuckanut gravelly sand	55.92*	32.41^{+}	42.04$^{\wedge}$

*, $^{+}$, $^{\wedge}$ = values not significantly different (MRT in Appendix III).

Figure 9. Batillaria attramentaria efficiency in digesting diatoms vs. percentage of living diatoms in sediments. $r^2 = 0.44$, slope = 0.71, y-intercept = 1.16.

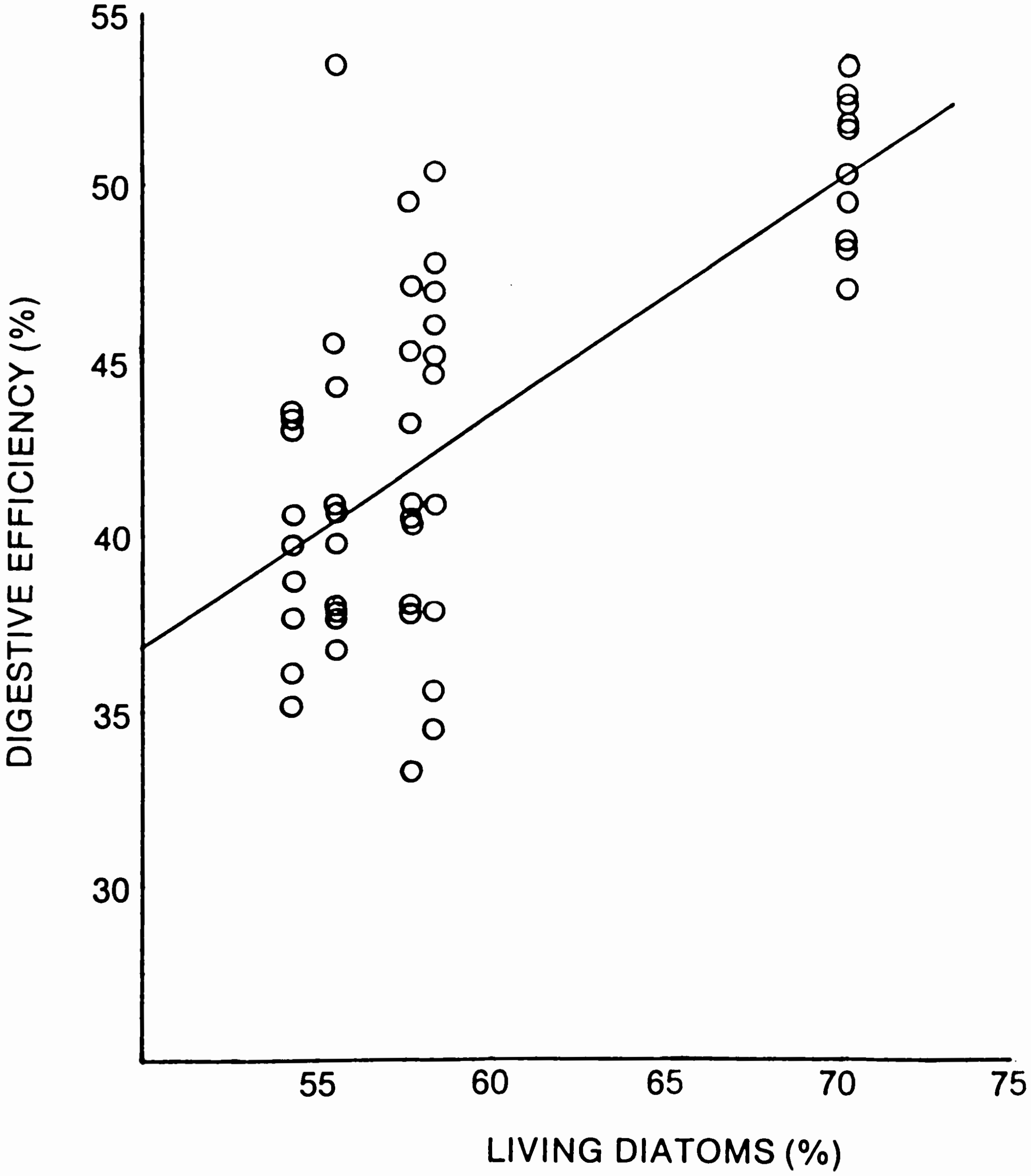

55
50
45
40
35
30
DIGESTIVE EFFICIENCY (%)
55
60
65
70
75
LIVING DIATOMS (%)

Table 4. Ratio of carbon in <u>Batillaria</u> <u>attramentaria</u> fecal pellets to carbon in sediments

	total organic carbon in sediment (μg C mg^{-1})	total organic carbon in fecal pellets (μg C mg^{-1})	pellet carbon: sediment carbon
Chuckanut mud	1.547^{+}	5.854^{++**}	3.784
Chuckanut algae	1.504^{+}	3.557^{++}	2.365$^{\wedge}$
Chuckanut gravelly mud	2.163	5.807^{++**}	2.685$^{\wedge}$
Semiahmoo sand	0.906*	6.101**	6.734$^{\wedge\wedge}$
Chuckanut gravelly sand	0.680*	3.946^{++}	5.803$^{\wedge\wedge}$

+, ++, *, **, ^, ^^ = values not significantly different (MRT in Appendices IV through VI).

Figure 10. Total organic carbon in sediments vs. percentage of mud in sediments for substrates from Chuckanut Mudflat and Semiahmoo Spit. $r^2 = 0.34$, slope = 0.09, y-intercept = 0.80.

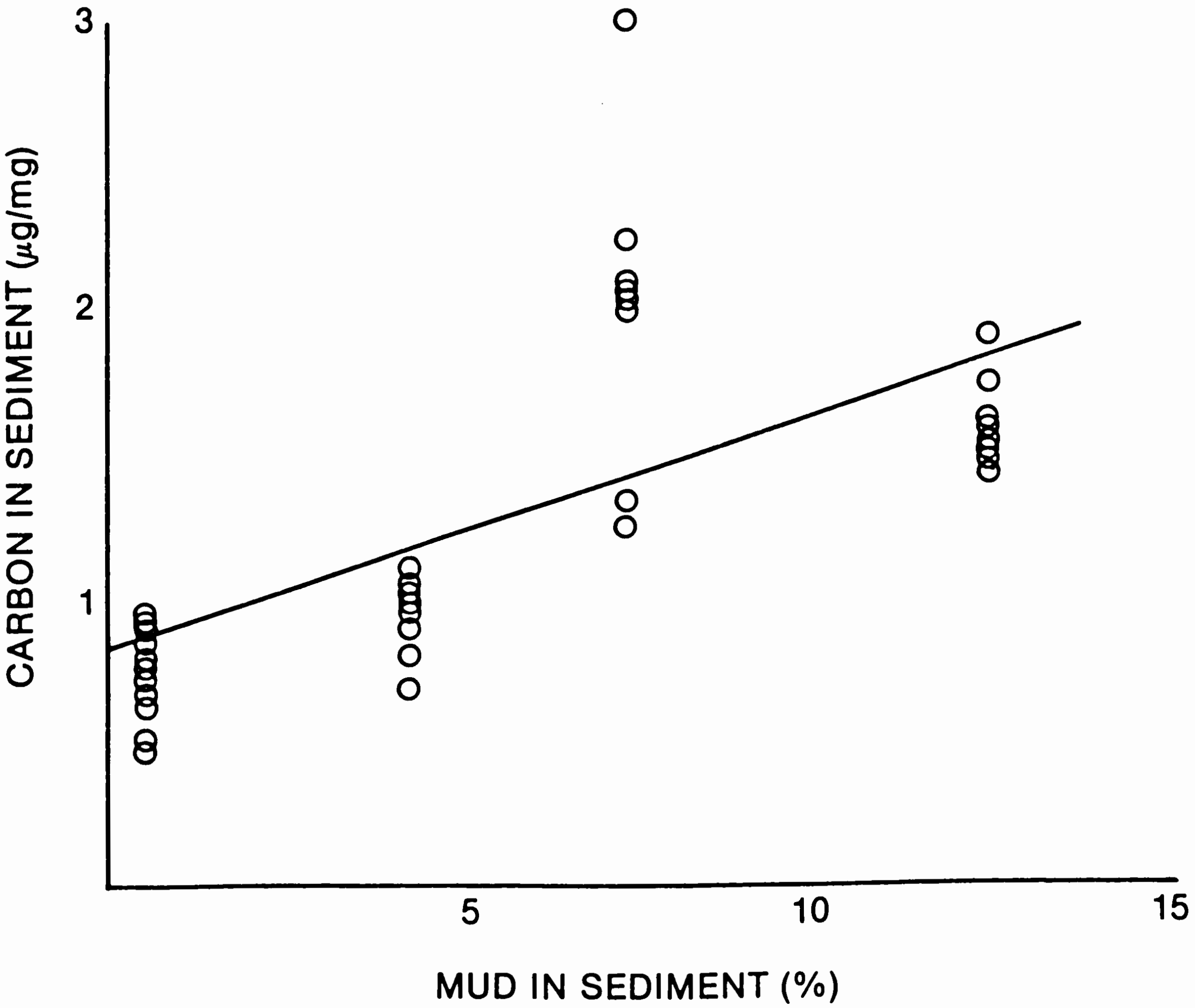

CARBON IN SEDIMENT (µg/mg)
3
2
1
MUD IN SEDIMENT (%)
5
10
15

Figure 11. Ratio of *Batillaria attramentaria* pellet carbon to sediment carbon vs. total organic carbon in sediments. $r^2 = 0.64$, slope = -2.56, y-intercept = 8.23.

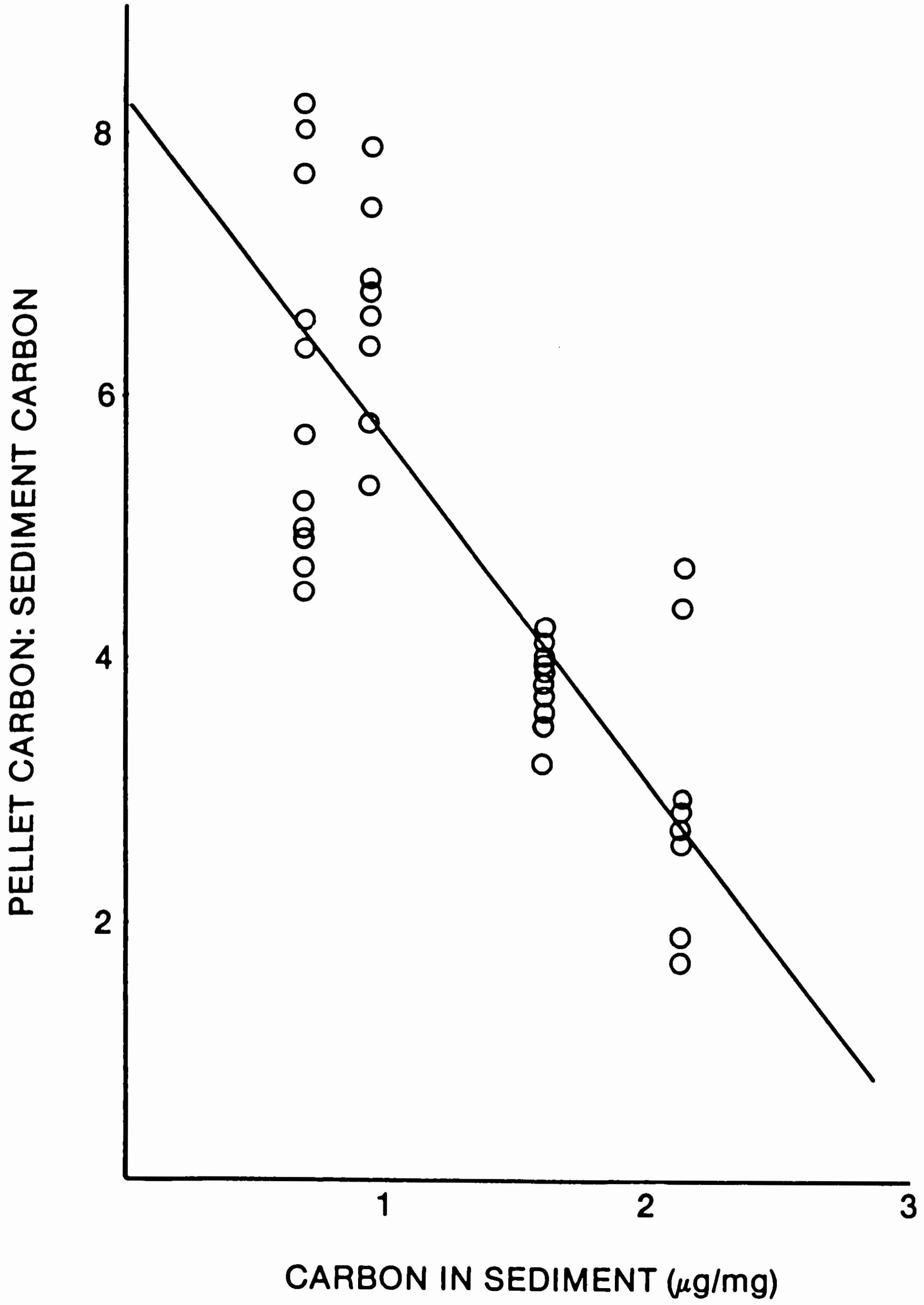

PELLET CARBON: SEDIMENT CARBON
8
6
4
2
1
2
3
CARBON IN SEDIMENT (µg/mg)

Figure 12. Gut residence times of material ingested by _Batillaria attramentaria_ feeding on substrates from Chuckanut Mudflat and Semiahmoo Spit. CM, Chuckanut mud; CA, Chuckanut algae; CGM, Chuckanut gravelly mud; SS, Semiahmoo sand; CGS, Chuckanut gravelly sand. CA maximum estimate was not obtained. *, $^{+}$ = values not significantly different (MRT in Appendix VII).

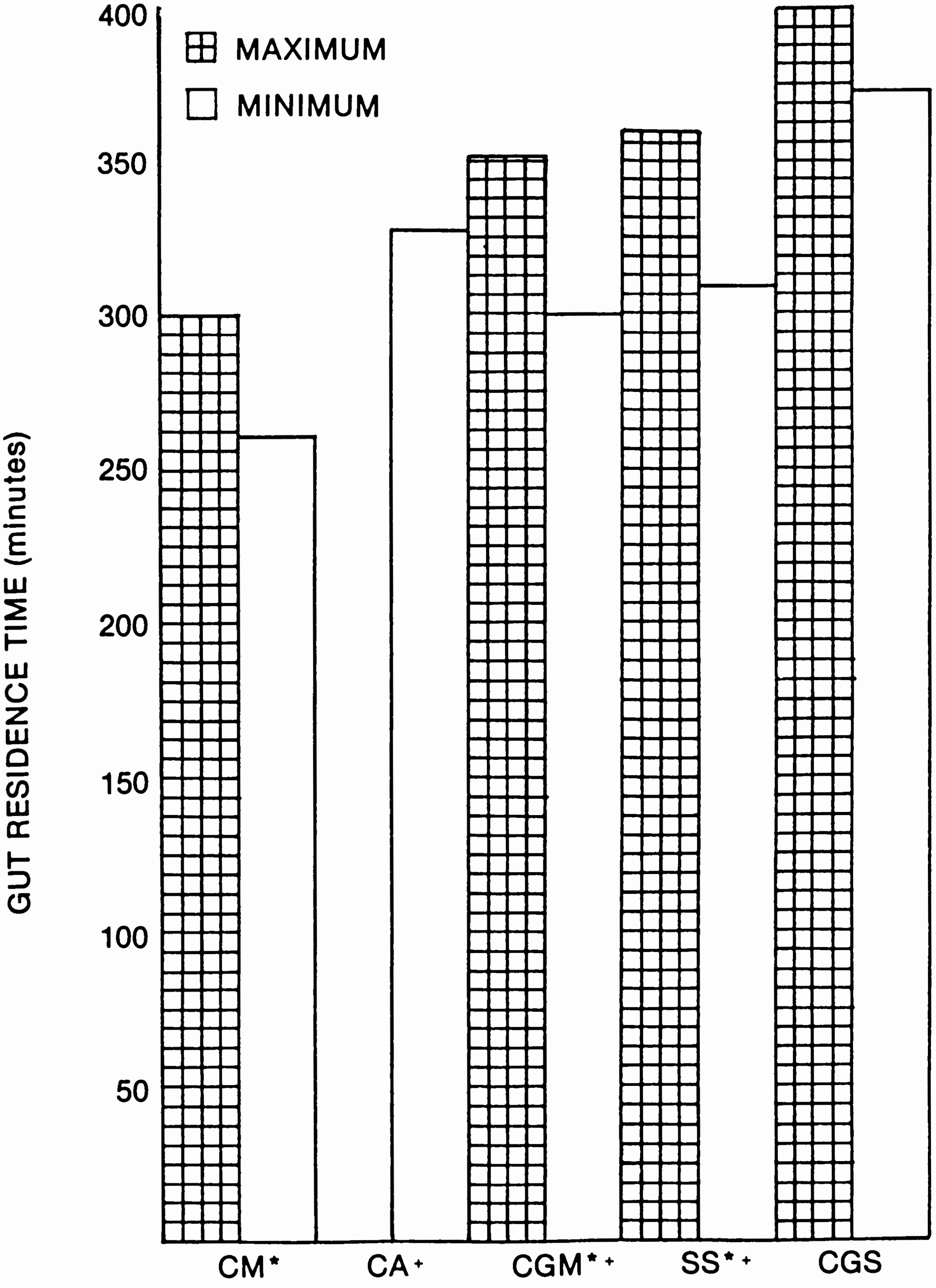
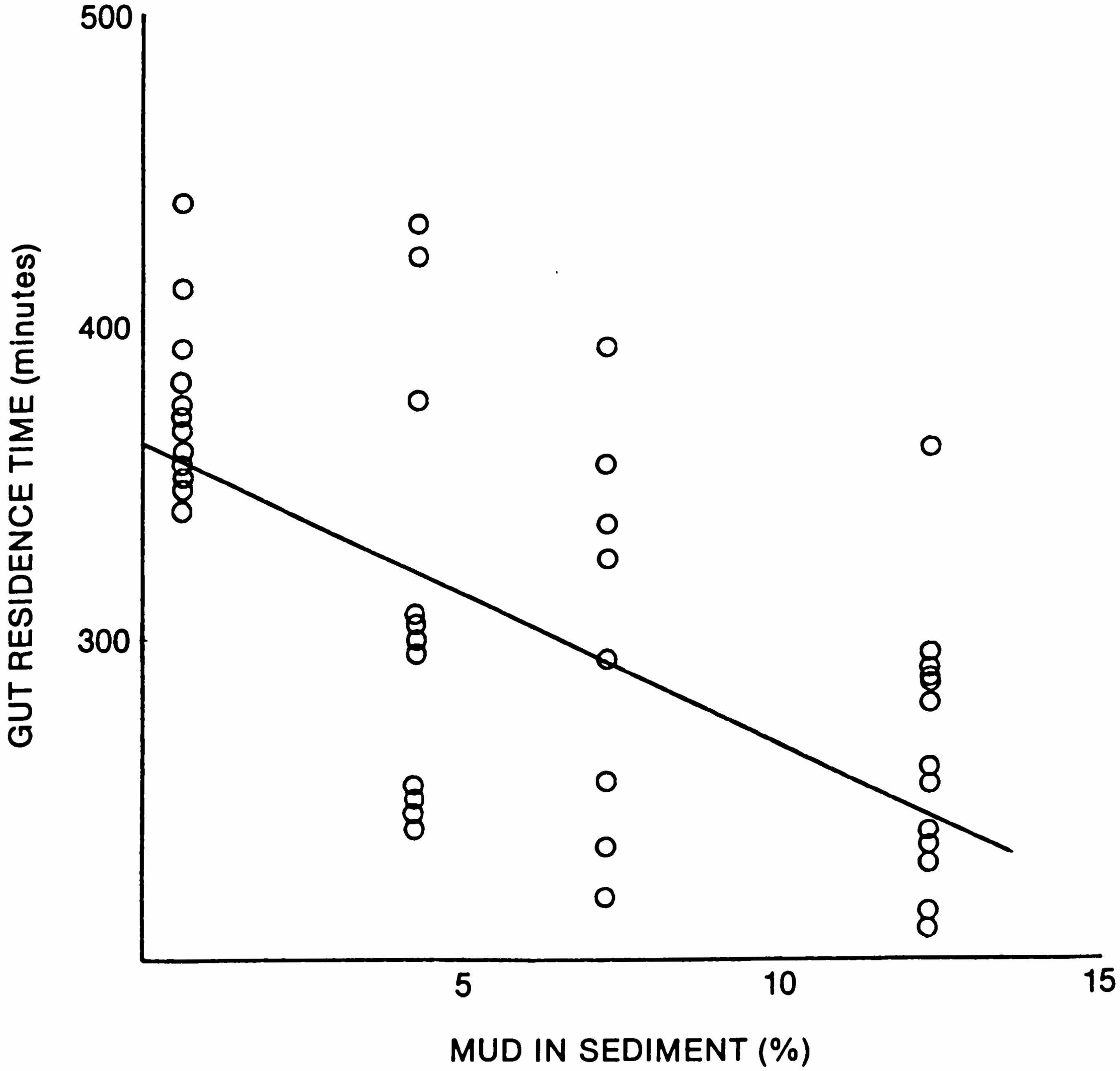

GUT RESIDENCE TIME (minutes)
400
350
300
250
200
150
100
50
⊞ MAXIMUM
☐ MINIMUM
CM*
CA+
CGM*+
SS*+
CGS

Figure 13. Batillaria attramentaria gut residence times vs. percentage of mud in sediments. $r^2 = 0.39$, slope = -8.54, y-intercept = 363.7.



500
400
300
GUT RESIDENCE TIME (minutes)
5
10
15
MUD IN SEDIMENT (%)

the mat, percentage of mud in the sediment would not be expected to have a significant effect on the gut residence time.

Egestion rates

Egestion rates for the snails ranged from less than 0.1 mg per snail per hour for the Chuckanut algae substrate to nearly 5 mg per snail per hour for the Chuckanut mud substrate (Fig. 14). Snails feeding on the Chuckanut mud and Chuckanut gravelly mud substrates showed egestion rates which, while not significantly different from each other, were nearly twice the rates of the snails feeding on the Semiahmoo sand and Chuckanut gravelly sand substrates. There was a significant linear relationship between the egestion rate and the percentage of mud in the sediment (Fig. 15). Egestion rates increased by 0.24 mg per hour for each percentage point increase in the amount of mud in the sediment. Once again the linear regression analysis for Figure 15 did not include data for the Chuckanut algae substrate since the percentage of mud in the sediment under an algal mat would not be expected to have a significant effect on the egestion rates of snails feeding on the mat.

Figure 14. Egestion rates of Batillaria attramentaria feeding on substrates from Chuckanut Mudflat and Semiahmoo Spit. CM, Chuckanut mud; CA, Chuckanut algae; CGM, Chuckanut gravelly mud; SS, Semiahmoo sand; CGS, Chuckanut gravelly sand. *, + = values not significantly different (MRT in Appendix VIII).

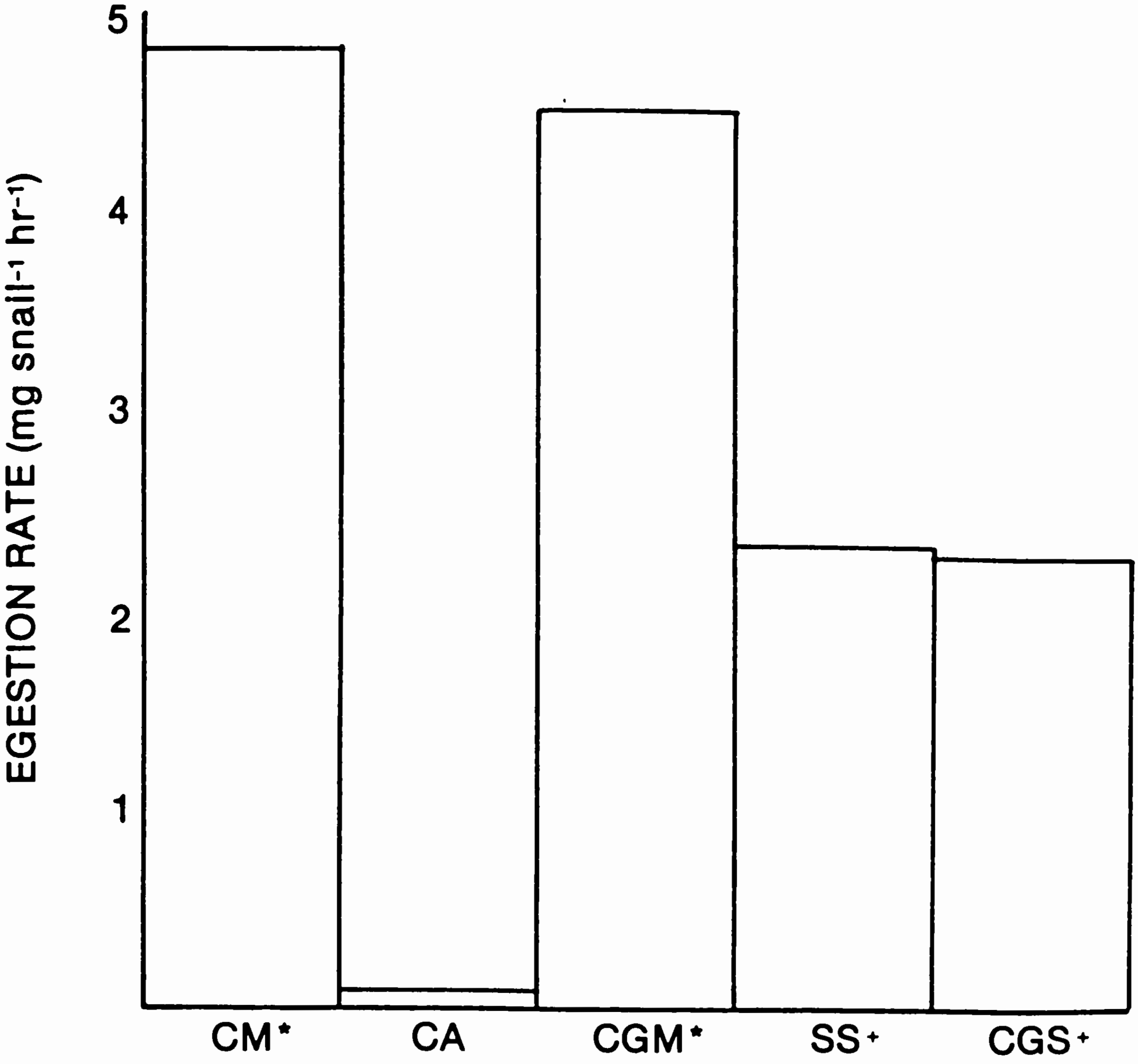
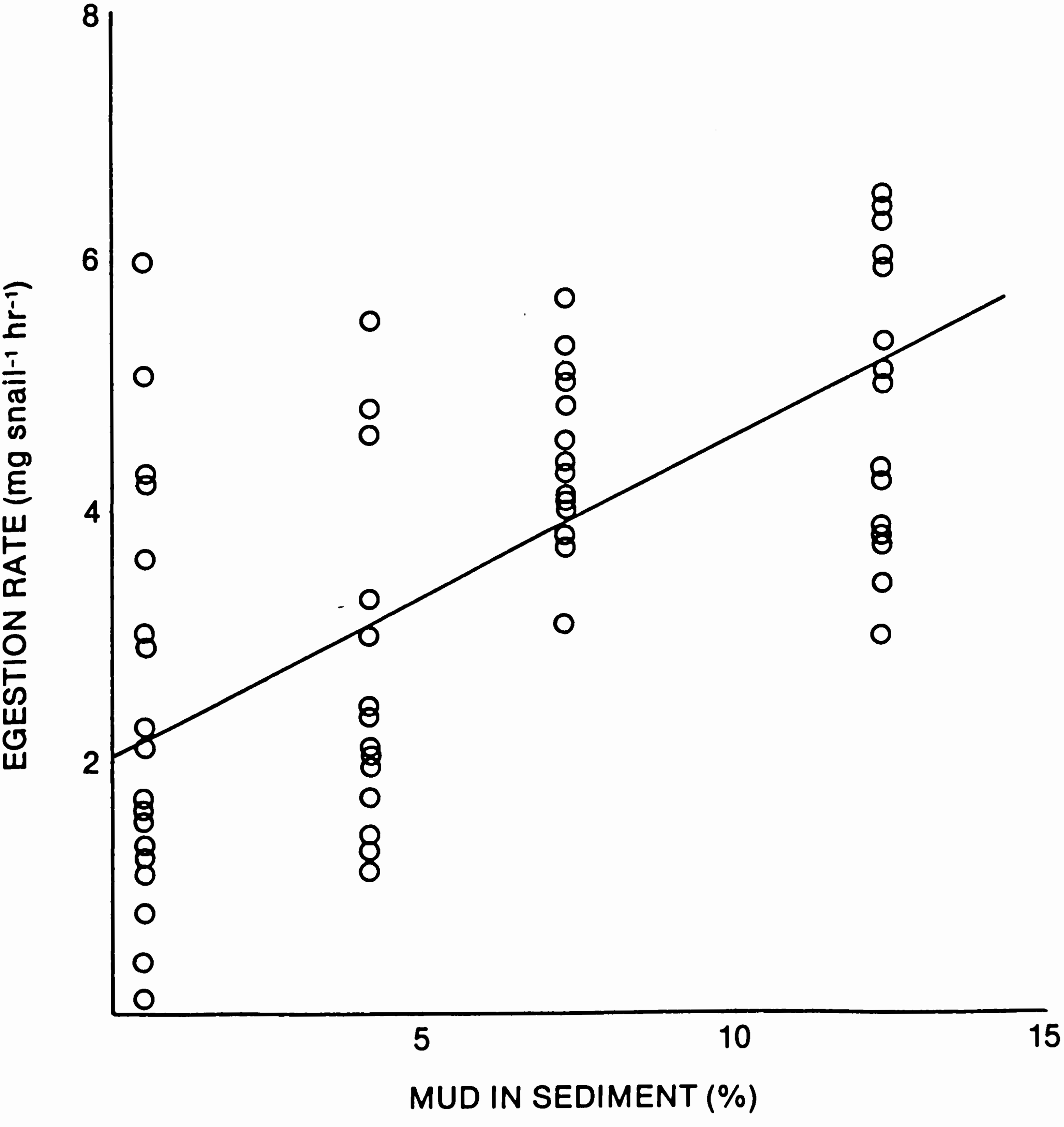

EGESTION RATE (mg snail-1 hr-1)
5
4
3
2
1
CM*
CA
CGM*
SS+
CGS+

Figure 15. *Batillaria attramentaria* egestion rates vs. percentage of mud in sediments. $r^2 = 0.38$, slope = 0.24, y-intercept = 2.09.


EGESTION RATE (mg snail⁻¹ hr⁻¹)
8
6
4
2
5
10
15
MUD IN SEDIMENT (%)

DISCUSSION

Substrate characteristics

The grain size distributions for the four substrates studied at Chuckanut Mudflat show variations in the amount of coarse sediment which are typical of a marine beach. Gray (1981:11-15) noted that the coarsest particles usually lie at the top of a beach, with a gradation to finer particles lower on the beach. The poor sorting of the Chuckanut Mudflat substrates is indicative of the low wave activity at the protected site. The Semiahmoo site is less protected, with a little more wave activity, leading to more homogeneous, better-sorted sediment.

Greater amounts of organic carbon in fine substrates is usual in marine sediment analysis (Gray, 1981:11-15). The increased surface area of fine mud as opposed to coarser sediment allows for more adherence of organic material. Muddier areas have been shown to support larger numbers of deposit-feeders in benthic communities (Sanders, 1958). The patchy distribution of *Batillaria attramentaria* and the resultant high variability in density counts preclude any conclusions about the relationship of snail density to muddiness in this study. A comprehensive distribution study was not the purpose here; however, Whitlatch (1972) and Behrens Yamada (1982), who studied the patchy distribution of *B. attramentaria*, felt that distribution of this species was related to factors other than the percentage of mud (such as length of atmospheric exposure). A related snail, *Cerithidea cingulata*, has been found to prefer mixed composition substrate over fine mud; distribution was not correlated with organic matter per se (Rao and Sukumar, 1981).

The proportion of living vs. non-living diatoms did not vary significantly between the substrates studied, except in the case of the

Chuckanut algae substrate, which had a much higher proportion of live diatoms than the other substrates. The algal mat bloom on this substrate would be expected to support a corresponding bloom of epiphytic diatoms. Obvious, though unquantified, differences in sizes and species composition of the Semiahmoo microalgae vs. the Chuckanut microalgae did not seem to relate to the percentage of mud or organic carbon in sediments. According to Levinton (1982:179), larger sizes and greater diversity of diatoms may represent the second successional stage in a phytoplankton bloom. Why such a rich assemblage of diatoms should occur at Semiahmoo Spit and not at Chuckanut Mudflat was beyond the scope of this study but it is interesting to note that highest densities of _Batillaria attramentaria_ were also seen at Semiahmoo Spit.

Characteristics of ingested material

The types and proportions of material contained in the guts of the snails remained constant for all the substrates examined. By virtue of their sheer numbers in the gut and the demonstrated efficiency of _Batillaria attramentaria_ in digesting them, diatoms seem to be the major nutrition source for these snails. Diatoms and mud-sized sediment particles have been the primary materials found in _B. attramentaria_ gut content analyses performed by Whitlatch (1972) and Whitlatch and Obrebski (1980). Diatoms are believed to be an important food source for other deposit-feeding gastropods, including the hydrobiids (Kofoed, 1975a; Fenchel and Kofoed, 1976; Levinton and Lopez, 1977; Lopez and Levinton, 1978; Levinton and Bianchi, 1981; Lopez and Cheng, 1983), _Ilyanassa obsoleta_ (Scheltema, 1964; Wetzel, 1977), _Bittium varium_ (Lopez, 1980) and _Cerithidea californica_ (Whitlatch and Obrebski, 1980).

Though the proportion of sediment found in guts of snails removed from the Chuckanut algae substrate was smaller than that seen for the other substrates, the lack of a statistically significant difference from the other substrates poses a problem in understanding the role of the algal mat in the diet of *Batillaria attramentaria*. Snails feeding on the mat would not be expected to ingest much sediment and apparently were not ingesting the filamentous mat itself. Gut contents would thus be expected to show a higher proportion of epiphytic diatoms. Several experimental design factors could explain why this did not occur: 1) Snails taken from the algal mat in the field, which was interspersed with mud areas, could have been feeding on mud just a short time before collection. 2) Egestion rates of snails were lowest for the algal mat and gut residence times were high. This would compound problem one (1) in keeping the previously consumed mud in the gut even longer. 3) Egestion rates and gut residence times were based upon feedings on pieces of algal mat which had been removed from the sediment. The handling of the mat in setting up these feedings probably caused further loss of incorporated sediment, leading to a substrate different from the natural situation. Gut content analysis for snails fed this "artificial" substrate might well have shown a low proportion of sediment.

Digestive efficiencies of 40 to 50 percent upon diatoms, such as those seen here for *Batillaria attramentaria*, are common in deposit-feeding gastropods. Such values have been found for *Hydrobia ventrosa* (Lopez and Levinton, 1978), *H. totteni* (Lopez and Cheng, 1983) and *Ilyanassa obsoleta* (Wetzel, 1977). Values seen here were, however, lower than the 66 percent efficiency found for *B. attramentaria* by Whitlatch and Obrebski (1980), whose results were based upon only six snails. Kofoed (1975a) found values of 60 to 71 percent digestive efficiency for *H. ventrosa* fed pure cultures of diatoms in the absence of natural sediment.

Animal fragments have not been documented in the gut of *Batillaria attramentaria* before now, though Whitlatch and Obrebski (1980) noted that meiofauna were abundant in sediments fed on by *B. attramentaria* in California. Among other deposit-feeding gastropods, only *Ilyanassa obsoleta* is considered a carrion feeder (Scheltema, 1964). Both *I. obsoleta* and *B. attramentaria* possess crystalline styles, which are unique to the microherbivorous members of the Gastropoda and to some bivalves (Owen, 1966). The styles function in extracellular digestion of carbohydrates and fats. Yonge (1930) was the first to point out that because the crystalline style is protein in composition, a carnivorous mollusc cannot normally possess a style. Since the carnivorous habit usually demands the presence of an enzyme (or enzymes) capable of breaking the flesh of prey down to soluble polypeptides and amino acids, the protein style could not exist in the gut of a carnivore. The possession of a crystalline style by the omnivore *I. obsoleta* has been attributed to the ability of this gastropod to dissolve and re-form the style on a daily basis. Curtis (1980) found that styles were low in frequency just after dawn and when snails were fed meat but were present when snails fed on algae. Further study of sediments, gut contents and digestive enzymes would be necessary to substantiate the role of *B. attramentaria* as an omnivore.

Besides microalgae and dead animal tissue, carbon (*sensu lato*) is available to *Batillaria attramentaria* in the form of live vascular plants, dead plants, bacteria, macroalgae and feces. Evidence is accumulating against significant, direct use of live vascular plants by any salt marsh or estuarine invertebrate (Montague, *et al.*, 1981). However, some use of dead vascular plant material (i.e., detritus minus the associated bacteria) has been shown in *Hydrobia ventrosa* (Kofoed, 1975b), *Bittium varium* (Adams and Angelovic, 1970), *Potamopyrgus jenkinsi* (Heywood and Edwards, 1962) and the pulmonate *Planorbis contortus* (Calow, 1975). Even very low assimilation efficiencies for detritus may be important since deposit-feeders can take advantage of an abundance of detritus by rapidly feeding and passing large quantities of material through the alimentary tract in order to secure the necessary intake of assimilable carbon (Hylleberg Kristensen, 1972; Levinton and Bianchi, 1981). The lack of significant amounts of vascular plant material in the guts of Chuckanut Mudflat and Semiahmoo Spit populations of *Batillaria attramentaria* may be due to the position of the snails on the shore. At both sites snails were located above eelgrass zones which could provide substantial amounts of plant detritus. *B. attramentaria* live within eelgrass beds at Padilla Bay, Washington (pers. obs.) and work with this population might reveal larger amounts of vascular plant material in gut contents.

Bacteria have been shown to be efficiently digested by hydrobiid snails and other deposit-feeders, but their actual contribution to growth in *Hydrobia* spp. is questionable (Levinton and Bianchi, 1981). Likewise, dietary importance of fecal material is not clear for deposit-feeding snails; reports of coprophagy conflict. Some areas in *Hydrobia* habitats are highly pelletized (Levinton and Lopez, 1977) but hydrobiids will ingest fecal pellets only after pellets are disaggregated. Fecal pellets are often enriched in organic carbon compared to sediments, as was the case here for *Batillaria attramentaria*. With reinvasion by bacteria, feces could provide a rich and renewable food source (Newell, 1965; Levinton and Lopez, 1977). Pelletized areas were not noticeable at Chuckanut Mudflat and Semiahmoo Spit sites, however, and the importance of bacteria and fecal material in the diet of B. attramentaria remains unknown.

Foraging strategy

Comparisons of Batillaria attramentaria gut contents, digestive efficiencies, gut residence times and egestion rates, in relation to the various substrates at Chuckanut Mudflat and Semiahmoo Spit, present evidence for particle selectivity and energy optimization strategies in these snails. Levinton (1980) states that particle selection by benthic animals is dependent upon ingestion rate, food quality, physical characteristics of the particles and depth/mobility of the animals in the sediment. The carbon enrichment of fecal pellets when compared to the substrates from which they were derived strongly suggests that B. attramentaria can select particles on the basis of size or quality. This enrichment was greatest for coarse, carbon-poor sediments but also occurred in fine, carbon-rich sediments. The enrichment of the pellets may have been somewhat distorted by two problems in experimental design:

1) Sediment samples were taken to two cm depth, while it is unlikely that snails, at least on the finest sediments, consume much of the material below five mm depth. The top centimeter of substrate was probably richer in carbon and nitrogen than the deeper layers (Connor and Edgar, 1982).

2) Weights of some fecal pellet samples were so small that weighing error could have been introduced. However, pellet carbon values two to seven times the original sediment carbon values are well within the range found by other workers. Connor and Edgar (1982) found the mud snail Ilyanassa obsoleta to produce pellets five to seven times richer than the sediments in carbon. Fecal pellets which are richer in organic compounds than were the original sediments may be more of a rule than an exception for deposit-feeders. Among the many other deposit-feeders found to concentrate organic

matter in the feces are the marsh snail *Littorina irrorata* (Montague, *et al*., 1981), the bivalve *Macoma nasuta* (Hylleberg and Gallucci, 1975) and the tubificid oligochaetes *Tubifex tubifex* and *Limnodrilus hoffmeisteri* (Brinkhurst, *et al*., 1972).

Increases in gut residence times with sediments containing less fine material (and corresponding decreases in egestion rates; these two measures being inversely proportional) also point toward selectivity in *Batillaria attramentaria*. If, due to physical constraints of the buccal apparatus, snails are selecting a particular size fraction (in this case mud) it would be expected that they would not be able to put as much material through the gut as rapidly on coarse sediment as on fine sediment. If snails are selecting for food quality, with quality or amount of food being directly proportional to surface area available in the sediment, slower gut residence times would again be expected on coarser sediment. Lopez and Kofoed (1980) found egestion rates of *Hydrobia ventrosa* to be greatest for fine sediments, paralleling the results for *B. attramentaria* in this study. The fact that the proportions of materials in the gut and the size ranges of these materials (qualitative observation) remained constant for substrates varying widely in composition suggests that particle selection in *B. attramentaria* may be strongly regulated by physical constraints rather than any behavioral ability. The idea that particle size chosen is strictly a function of an animal's body size has been supported by work with polychaetes, amphipods, bivalves and holothurians (Taghon, *et al*., 1982) as well as with snails (Whitlatch, 1974; Fenchel, 1975).

Optimal foraging theory, an approach to predicting and explaining the food choice of animals, assumes that animals seek out and eat those food items which result in maximum energy gain and that the animals also maximize their fitness by doing so (Taghon and Jumars, 1984). Emlen (1966) and MacArthur and Pianka (1966) did early work regarding the way in which animals exploit the food available to them. Particle feeding and optimal foraging models have been developed for deposit-feeders (Taghon, et al., 1978; Levinton, 1980). However, these models focused strictly on choice of food items. Taghon (1982) pointed out that other components of an animal's feeding biology, such as regulation of ingestion rate and digestive process, may be important in foraging strategy of less selective animals. Cammen (1980) formulated an egestion rate model based on work with polychaetes, bivalves and decapod crustaceans which predicted that ingestion rate would vary inversely with organic content of food. He assumed that feeding was totally non-selective for these animals. Batillaria attramentaria does appear to be selective and, in fact, shows a greater egestion rate (which can be considered an indirect measure of ingestion rate) with fine sediment containing more organic matter. This situation is in keeping with the models of Lehman (1976) and Taghon (1981), which predicted that in order to maximize energy gain, ingestion rate would increase as the energetic value of the food increases. Such models were supported by a study in which polychaetes fed artificial sediments varying only in protein content (i.e., food value) showed increased ingestion rates with increased food value (Taghon and Jumars, 1984). Though the use of natural sediments in the current study of B. attramentaria could not be as carefully controlled for food value, the egestion rates do support an energy maximization model. In addition, the increased digestive efficiency of B. attramentaria on diatoms when more diatoms were available and the decreased carbon enrichment of pellets when sediments were carbon-rich also support this type of model.

Low egestion rates seen on the Chuckanut algae do not, however, fit a model of increased ingestion with increased food value. Though experimental design factors (mentioned previously) could have distorted egestion rates and gut residence times for this substrate, snails feeding on the energy-rich algal mat would be expected to show higher egestion rates. The epiphytic diatom film could make the algal mat the richest potential carbon source of all the substrates studied. In such a case of extreme energy richness the snails may be able to afford to keep ingestion rates low and still show a net rate of energy gain. This element of the feeding strategy of *Batillaria attramentaria* may well fit with Cammen's (1980) idea that at low ingestion rates, the decreased energetic costs of feeding enhance the energetic gain derived from the organic matter.

Effects on the soft-substrate community

The food of soft-bottom, deposit-feeding communities is a limiting resource (Levinton, 1972). Bacteria are probably the rate-controlling step in the utilization of organic matter in soft sediments. Levinton (1972) compared deposit-feeding and suspension-feeding communities and hypothesized that deposit-feeders exploit a relatively predictable food supply. The production of detritus and the transport of it are less strictly limited to a certain season of the year than the production of phytoplankton (an important food source for suspension-feeders). Organic matter resides in the sediment as a "sink," buffering the deposit-feeders against fluctuations in abundance of organic matter in the overlying water. Recycling of this organic matter is extremely important.

Though deposit-feeding gastropods may account for little of the total ecosystem production, they do contribute to the recycling of material and the energy flow (Montague, *et al.*, 1981). These animals assimilate organic material and egest material which serves as food for other organisms. In the case of *Batillaria attramentaria*, extrapolation of egestion rates and carbon in pellets using the conservative density of 50 snails per square meter seen at Chuckanut Mudflat gives a value of 435.6 g reworked sediment per square meter per year (snails are assumed to be active only during the daytime, five months per year). In terms of organic carbon output, this value converts to 2.55 g carbon packaged and excreted per square meter per year. Numbers for comparison with other deposit-feeding gastropods are unavailable but sediment reworking rates have been estimated for bivalves and polychaetes. *Yoldia limatula* in Buzzards Bay, Massachusetts reworked 5-6 liters of sediment per square meter per year and in Long Island Sound, 23-51 liters per square meter per year (Rhoads, 1963). Gordon (1966) projected that *Pectinaria gouldii* would completely work all sediment in the 6-cm thick surface layer of the flat at Barnstable Harbor, Massachusetts once every 15 years.

Underwood (1979) noted that differences in grazing patterns of gastropods at different areas on the shore and variability in the intensity of grazing between shore locales will lead to patchiness in distribution of occupiers of the grazed space. Swinbanks (1970) documented the presence of *Batillaria attramentaria* on the Fraser River delta tidal flats in British Columbia. Though he did not study the snails' feeding biology, he noted an algal mat similar to the one at Chuckanut Mudflat and postulated a probable limiting of the algal mat zone by the grazing activities of *B. attramentaria*. Such a role for this species does not seem probable at Chuckanut Mudflat since snails do not appear to ingest the mat itself. Removal of snails from a portion of a natural community and elucidation of a complete carbon budget would greatly aid in an understanding of the deposit-feeding role of *B. attramentaria*.

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APPENDIX I

Multiple range test for percentage of mud in sediments.

SE = 1.168 Error df = 10

treatment:	CGS	SS	CGM	CA	CM
rank:	1	2	3	4	5
value:	3.803	11.600	15.447	18.460	20.520

Comparison	Difference	q_{calc}	Range	q_{table}	Decision
5-1	16.717	14.313	5	4.654	SD
5-2	8.920	7.637	4	4.327	SD
5-3	5.073	4.343	3	3.877	SD
5-4	2.060	1.764	2	3.151	NSD
4-1	14.657	12.549	4	4.327	SD
4-2	6.860	5.873	3	3.877	SD
4-3	3.013	2.580	2	3.151	NSD
3-1	11.644	9.969	3	3.877	SD
3-2	3.847	3.294	2	3.151	SD
2-1	7.797	6.676	2	3.151	SD

APPENDIX II

Multiple range test for snail density (No. snails 0.1 m^{-2})

SE = 1.690 Error df = 45

treatment:	CA	CGM	CM	CGS	SS
rank:	1	2	3	4	5
value:	3.8	5.4	5.5	5.5	15.0

Comparison	Difference	q_{calc}	Range	q_{table}	Decision
5-1	11.2	6.627	5	4.039	SD
5-2	9.6	5.681	4	3.791	SD
5-3	9.5	5.621	3	3.442	SD
5-4	9.5	5.621	2	2.858	SD
4-1	1.7	1.006	4	3.791	NSD
4-2	0.1	0.059	3	3.442	NSD
4-3	0.0	0.000	2	2.858	NSD
3-1	1.7	1.006	3	3.442	NSD
3-2	0.1	0.059	2	2.858	NSD
2-1	1.6	0.947	2	2.858	NSD

APPENDIX III

Multiple range test for efficiency of diatom digestion by *Batillaria attramentaria* (%).

SE = .8600   Error df = 45

treatment:	SS	CGS	CGM	CM	CA
rank:	1	2	3	4	5
value:	38.379	40.122	40.196	40.951	45.308

Comparison	Difference	q_{calc}	Range	q_{table}	Decision
5-1	6.929	8.057	5	4.039	SD
5-2	5.186	6.030	4	3.791	SD
5-3	5.112	5.944	3	3.442	SD
5-4	4.357	5.066	2	2.858	SD
4-1	2.572	2.991	4	3.791	NSD
4-2	0.829	0.963	3	3.442	NSD
4-3	0.756	0.879	2	2.858	NSD
3-1	1.817	2.113	3	3.442	NSD
3-2	0.074	0.086	2	2.858	NSD
2-1	1.743	2.027	2	2.858	NSD

APPENDIX IV

Multiple range test for total organic carbon in sediment (μg C mg^{-1})

Error df = 47

treatment:	CGS	SS	CA	CM	CGM
rank:	1	2	3	4	5
value:	0.680	0.906	1.504	1.547	2.163

Comparison	Difference	SE	q_{calc}	Range	q_{table}	Decision
5-1	1.483	0.104	14.260	5	4.039	SD
5-2	1.257	0.110	11.427	4	3.791	SD
5-3	0.659	0.107	6.159	3	3.442	SD
5-4	0.616	0.104	5.923	2	2.858	SD
4-1	0.867	0.104	8.337	4	3.791	SD
4-2	0.641	0.110	5.827	3	3.442	SD
4-3	0.043	0.107	0.402	2	2.858	NSD
3-1	0.824	0.107	7.701	3	3.442	SD
3-2	0.598	0.112	5.339	2	2.858	SD
2-1	0.226	0.110	2.055	2	2.858	NSD

APPENDIX V

Multiple range test for total organic carbon in fecal pellets ($\mu g\ C\ mg^{-1}$)

Error df = 39

treatment:	CA	CGS	CGM	CM	SS
rank:	1	2	3	4	5
value:	3.557	3.946	5.807	5.854	6.101

Comparison	Difference	SE	q_{calc}	Range	q_{table}	Decision
5-1	2.544	0.603	4.219	5	4.039	SD
5-2	2.155	0.550	3.918	4	3.791	SD
5-3	0.294	0.550	0.535	3	3.442	NSD
5-4	0.247	0.582	0.424	2	2.858	NSD
4-1	2.297	0.620	3.705	4	3.791	NSD
4-2	1.908	0.568	3.359	3	3.442	NSD
4-3	0.047	0.568	0.083	2	2.858	NSD
3-1	2.250	0.590	3.814	3	3.442	NSD
3-2	1.861	0.535	3.479	2	2.858	NSD
2-1	0.389	0.590	0.659	2	2.858	NSD

APPENDIX VI

Multiple range test for the ratio of pellet carbon to sediment carbon (unitless)

Error df = 47

treatment:	CA	CGM	CM	CGS	SS
rank:	1	2	3	4	5
value:	2.458	2.907	3.807	6.078	6.890

Comparison	Difference	SE	q_{calc}	Range	q_{table}	Decision
5-1	4.432	0.302	14.676	5	4.039	SD
5-2	3.983	0.296	13.456	4	3.791	SD
5-3	3.083	0.296	10.416	3	3.442	SD
5-4	0.812	0.296	2.743	2	2.858	NSD
4-1	3.62	0.288	12.569	4	3.791	SD
4-2	3.171	0.281	11.285	3	3.442	SD
4-3	2.271	0.281	8.082	2	2.858	SD
3-1	1.349	0.288	4.684	3	3.442	SD
3-2	0.9	0.281	3.202	2	2.858	SD
2-1	0.449	0.288	1.559	2	2.858	NSD

APPENDIX VII

Multiple range test for gut residence times (minutes)

Error df = 54

treatment:	CM	CGM	SS	CA	CGS
rank:	1	2	3	4	5
value:	263.462	301.250	310.455	329.615	368.929

Comparison	Difference	SE	q_{calc}	Range	q_{table}	Decision
5-1	105.467	13.786	7.650	5	3.977	SD
5-2	67.679	15.865	4.265	4	3.737	SD
5-3	58.474	14.422	4.055	3	3.399	SD
5-4	39.314	13.786	2.852	2	2.829	SD
4-1	66.153	14.040	4.712	4	3.737	SD
4-2	28.365	16.086	1.763	3	3.399	NSD
4-3	19.160	14.665	1.307	2	2.829	NSD
3-1	46.993	14.665	3.204	3	3.399	NSD
3-2	9.205	16.634	0.553	2	2.829	NSD
2-1	37.788	16.086	2.349	2	2.829	NSD

APPENDIX VIII

Multiple range test for egestion rates (mg snail^{-1} hour^{-1})

Error df = 90

treatment:	CA	CGS	SS	CGM	CM
rank:	1	2	3	4	5
value:	0.650	2.285	2.577	4.490	4.850

Comparison	Difference	SE	q_{calc}	Range	q_{table}	Decision
5-1	4.2	0.276	15.217	5	3.977	SD
5-2	2.565	0.276	9.293	4	3.737	SD
5-3	2.273	0.287	7.920	3	3.399	SD
5-4	0.36	0.276	1.304	2	2.829	NSD
4-1	3.84	0.268	14.328	4	3.737	SD
4-2	2.205	0.268	8.228	3	3.399	SD
4-3	1.913	0.280	6.832	2	2.829	SD
3-1	1.927	0.280	6.882	3	3.399	SD
3-2	0.292	0.280	1.043	2	2.829	NSD
2-1	1.635	0.268	6.101	2	2.829	SD

VITA

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