

**THE COSTS AND BENEFITS ASSOCIATED WITH BURIAL IN THE
SOFT-SHELLED CLAM, *MYA ARENARIA*.**

by

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B.Sc. Simon Fraser University, 1990.

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Abstract

The evolution of many morphological and behavioural traits found throughout the animal kingdom is thought to have been mediated by past predatory events. Much work in behavioural ecology indicates that animals assess the risk of predation and respond by making decisions that tend to reduce that risk. Typically, however, predation reduction is not the only factor upon which animals make survival decisions. Other important needs, such as eating and reproducing, should play a part in the decision-making process. When these demands conflict, a trade-off exists, and the benefits and costs of each of the important decision parameters must be taken into account.

My thesis investigates trade-offs between feeding and survival that the clam *Mya arenaria* experiences when choosing a burial depth in the muddy-intertidal zone. *M. arenaria* is a soft-shelled clam with both pedal and siphonal gapes. Hence, morphology does not protect against excavating predators such as the red rock crab *Cancer productus*, leaving relatively deep burial habits as the clam's only defense. I test the hypothesis that clams trade off the reduced predation risk against the increased feeding (growth) costs associated with deeper burial. My most general prediction is that burial depth increases with predation risk.

All of my research was performed at the Bamfield Marine Station, located on the west coast of Vancouver Island. I found that clams located at high beach elevations were buried less deeply than those found at low elevations. This finding was replicated and consistent over five sites. Thus, I predicted that there would be a greater predation risk for clams located at low beach elevations than at high elevations. This prediction was supported by both observations and

experiments, that showed the predation rate of clams was three times greater at low beach elevations, when burial depth was controlled. I predicted and found that clams buried more deeply were safer from excavating red rock crabs, the major predator. Morphological differences with respect to burial depth were also found. Deeper buried clams had disproportionately more soft tissue than those buried shallower. Finally, I predicted that the safety benefits of deeper burial would be offset by costs of slower feeding, hence lower growth rate. A field experiment measuring the growth of experimentally reburied clams was unsuccessful, but preliminary laboratory measurements of the filtering rate of clams supported the hypothesis.

Dedication

This thesis is dedicated to Marta Zaklan

Ovo je posveceno Mojoj Baba

Ti si prestala da ideš u školu u četvrtom razredu, ne zbog toga što si bila nesposobna, već zbog toga što nisi mogla da priuštiš cipele.

Tako, ti si poslala mene, tvoju unuku i tako omogućila moje akademsko obrazovanje koje ti nisi mogla da priuštiš.

An Ode to *Mya*

There once was a clam named Clyde
Was he big? oh man's sakes alive
He was large and (of course) deep
but he didn't make a peep
because he knew he was a clam digger's dream.

Was this clam was clever?,
oh boy was he ever,
he could work out sums in his head
there was no book he hadn't read
But one question eluded him,
What did that clam digger want to do with him?

Till suddenly one wondrous night,
All in a flash, he saw the light
He jumped up like a ballet dancer
and yelled (in clamese) "I've got the answer"

All she wants is to write a book
with my bodily parts as the main hook,
most want to eat me and put me in stew
but with me she wants to write a paper, maybe two.

Clyde pondered this horrible fate
that he might meet her instead of a mate.
And suddenly Clyde knew what to do
he was going to put her in the stew.

Now comes the rather grizzly bit
So let's not make too much of it,
Except that you must understand
That Clyde did eat that clamming mam
He ate her up from head to toe
Chewing the pieces nice and slow.

So what's the moral? what's the reason?
That I should tell you of this act of treason
The answer is simple I must say
make sure you don't study angry prey.

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Chapter 1

General Introduction

Mounting evidence indicates that animals can assess and respond to the risk of predation (Lima and Dill, 1990). Reduction of predation risk is not the only major factor upon which animals make behavioural decisions. Other important needs, such as eating and reproducing, may play a part. However, behaviours that reduce predation may be incompatible with the needs of feeding and reproduction (Werner, 1991). When such conflicting demands occur a trade-off exists, such that the benefits and costs of each of the important decision parameters must be taken into account. In this thesis I will examine the trade-off between predation risk and feeding in a marine intertidal system.

Few studies have looked at trade-offs between feeding and predation risk in marine organisms. Zwarts (1986) showed that more deeply-buried clams (*Scrobicularia plana*) were safer from predators and he claimed that they foraged less effectively. Specifically, he found that clams reduced their burial depth if they were in poor condition or if their siphons were experimentally cropped. By reducing burial depth these deposit feeders were able to increase their feeding radius, which Zwarts thought facilitated the recovery of body condition. Ambrose and Irlani (1992) found that the height of attachment of juvenile bay scallops (*Argopecten irradians*) on seagrass blades reflected a trade-off between growth rate and predation risk; high positions (15 cm above the sediment) afforded greater safety but slower growth whereas the opposite was true for scallops lower down.

Predation by crabs is thought to be a major agent of selection on behaviour and morphology of bivalves (Vermeij, 1978; 1987). Predator

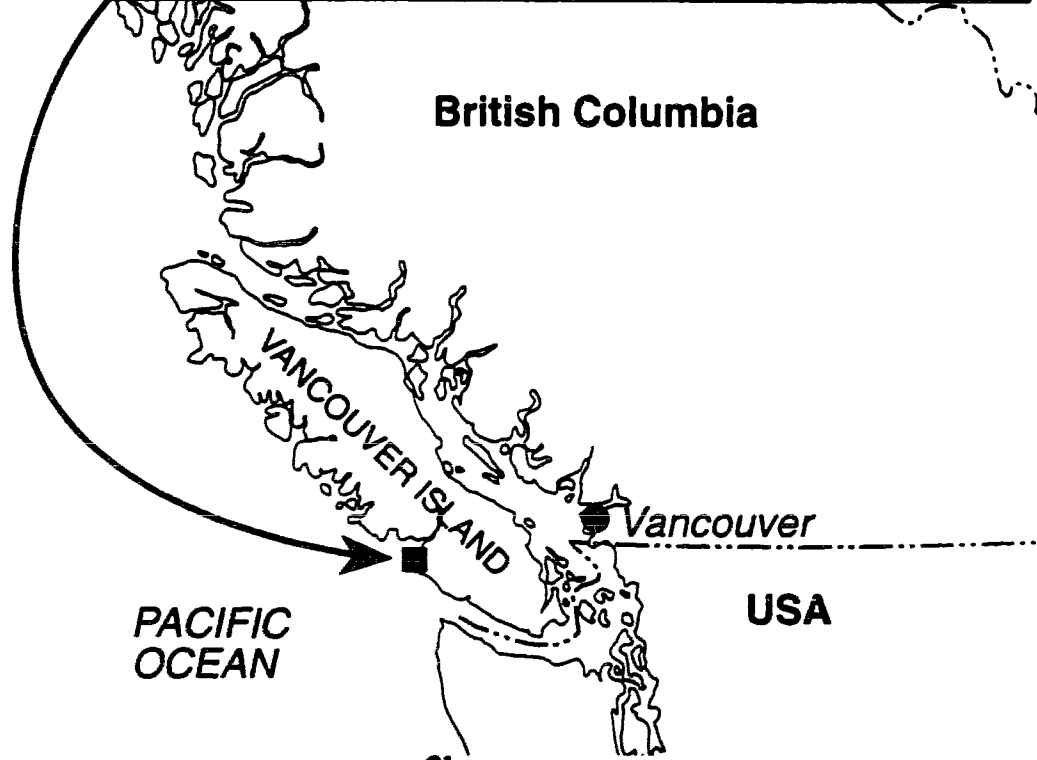
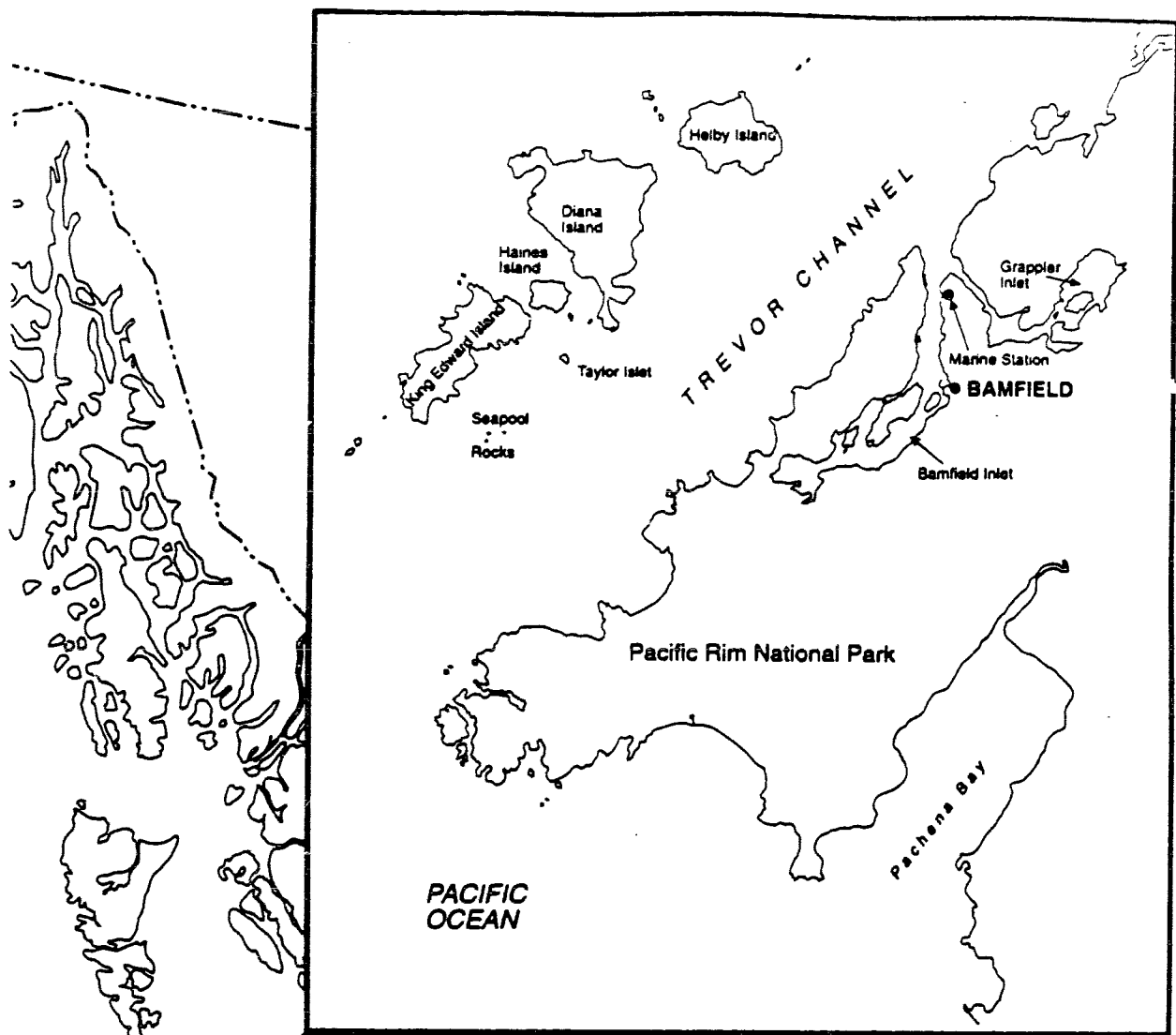
avoidance tactics may include the use of refugia, increased shell strength, or modified shell morphology. In clams with little structural protection, the use of refugia, specifically burying, would be expected. Deeper burial would increase the handling and perhaps searching time required for a crab to prey on a clam.

Improved predator avoidance with greater depth of burial has been found in a variety of burrowing species such as the clams *Mya arenaria* (Blundon and Kennedy, 1982a), *Scrobicularia plana* (Zwarts, 1986) and *Paphies ventricosa*, (Haddon et al. 1987), and the ragworm *Nereis diversicolor* (Esselink and Zwarts, 1989). For example, Blundon and Kennedy (1982b) found in a laboratory experiment that 97.5% of *M. arenaria* buried at 5 cm were consumed by crabs within a 48 h period, compared with only 15.7% of the clams buried at 20 cm. Despite the survival advantage of deep burial, not all clams bury deep (Chapter 2). This indicates that predation risk is not the only factor affecting burial depth of this clam. In this thesis I test the hypothesis that burial depth reflects a balance between two or more important behavioural considerations.

The players: *Mya arenaria* and *Cancer productus*

All research was performed at the Bamfield Marine Station, Bamfield B.C., located on the west coast of Vancouver Island (Figure 1.1). *M. arenaria*, a soft-shelled clam, (Class Bivalvia, Subclass Heterdonta, Family Myidae), has a two-four week planktonic period before settling (Witherspoon, 1982). Although some bivalve larvae prefer certain substratum types (e.g. *Crassostrea virginica*, Wood and Hargis, 1971), geographic areas (e.g. *Tellina fabula*), and beach elevations (e.g. *Spisula subtruncata*), preference has not been documented in *M. arenaria* (Emerson, 1990) nor its congeneric *M. truncata* (Muus, 1973). Instead, adult densities and horizontal distribution patterns in the intertidal zone

Figure 1.1 The Bamfield Marine Station, and Bamfield and Grappler Inlet study sites, all located in Barkley Sound, on the west coast of Vancouver Island, B.C., Canada.



are thought to be mediated mainly by water movement during the planktonic larval or postlarval periods (Emerson and Grant, 1991) and by movement of the sediment after settling (Matthiessen, 1960). After growing to 12 mm, *M. arenaria* is not known to migrate horizontally (Belding, 1930; cited in Emerson and Grant, 1991). The settling size differs geographically from 0.4 mm in Norway, (Muus, 1973) to 0.5 mm in Nova Scotia (Emerson and Grant, 1991). Other life-history traits such as size at first reproduction (20-45 mm), and age at first reproduction (2-4 years) of *M. arenaria* vary between geographic locations and studies (Virnstein, 1977; Brousseau, 1978; Commito, 1982). Growth rate is also variable. Brousseau (1978) reported that growth rate was greatest at 47.4 mm shell length and decreased thereafter, so that an 80 mm clam was about 7 years of age, and a 85 mm clam about 13 years of age. Commito (1982) reported a rapid early growth trajectory of 4.9 mm/year in the first 5 years with a size maximum of 6 cm. *M. arenaria* has been recorded to live for up to 28 years (10.96 cm; MacDonald and Thomas, 1980). Maximum recorded size is 12.2 cm (personal observation).

Soft-shelled clams are infaunal organisms living in the muddy-intertidal or in compact sand with a maximal recorded burial depth of 25 cm (Blundon and Kennedy, 1982b; personal observation). They are found on both coasts of North America (recently introduced to the west coast), and in some areas of Europe. On the east coast of the United States this bivalve is economically important as it is a favorite edible clam (Pearse et al., 1992). On the west coast, however, *M. arenaria* is not harvested commercially .

M. arenaria has a fused inhalent and exhalent siphon which it uses to feed. It is a suspension feeder using ciliary currents to move great quantities of food-laden water through its mantle cavity. The gills are thickly ciliated and act as sieves, straining food items such as microscopic plants, bacteria and organic

particles. Most bivalves are suspension feeders; however, some are deposit feeders gathering the dead cells, undigested food and organic particles that settle to the bottom (Pearse et al., 1992). As mentioned previously, *M. arenaria* has both pedal and siphonal gapes as well as two thin valves, so it is very vulnerable to crabs (Boulding, 1984). It is not an active burrower (personal observation; Chapter 3) because the ventral mantle margins are fused and the musculo-pedal region of the foot is poorly developed (Chapman & Newell, 1956; Trueman, 1966). *M. arenaria's* recorded maximum burial rate is 0.75 cm/day (Chapter 3); hence, rather than having an active escape strategy, it possesses a constant, deep burial pattern which is its only form of refuge. Clams, including *M. arenaria*, use their muscular foot for burrowing in successive cycles. Each cycle begins when the pointed foot is protruded into the substrate and is fully extended. As dilation occurs in the distal end of the foot, the valves are closed. This process forces blood into the foot, creating an anchor. The clam then expels water from the mantle cavity, loosening the mud around the shell. Finally, the clam pulls itself downward by contraction of the pedal retractor muscles (Trueman et al., 1966; Pearse et al., 1992). Since internal pressure recordings of adult *M. arenaria* rarely document digging cycles, the cycle rate is unknown (Trueman, 1966).

The red rock crab, *Cancer productus* (Phylum Arthropoda, Class Malacostraca, Order Decapoda, Family Cancridae) is a major predator of *M. arenaria* and is the other player in this system. Red rock crabs have chelae for crushing the armour of crustaceans or the shells of clams and snails. This large crab (carapace width is up to 18 cm) is harvested, although it is not as economically important as *Cancer magister*, the Dungeness crab. Estimates of crab densities in the intertidal zone range from 0.015 to 0.149 crabs/ m² (Robles et al., 1989). Crabs locate their prey by probing the sediment with their

walking legs, using the mechanoreceptors and chemoreceptors found on their claws and walking legs to determine the exact location of a clam (Case, 1964; Warner, 1977). They use their chelae to bulldoze sediment aside, and extract the clam from its burrow. Thus a distinctive, crab-shaped crater, visible after the tide recedes, marks clam predation. These pits range in size from 0.016 to 0.63 m² (Hall et al., 1993; personal observation).

There are sex and size differences in foraging strategies: older, larger and usually male *C. productus* forage both during the day and at night whereas younger, smaller generally female crabs forage primarily at night (Robles et al., 1989). Upon contacting the clam, the crab uses its pereopods to sweep the clam towards the chelipeds. It then manipulates the clam, finally grasping it with the chelae. One chela is used to crush the shell while the other is used to support the prey during breakage. Shell fragments are then torn away, exposing the soft tissue (Juanes and Hartwick, 1990). Various mouth parts are used to remove the contents from the shell. Typically, no tissue is left on the shell fragments (Boulding, 1984). The fragile shell of *M. arenaria* is easily crushed. Boulding (1984) found that even small red rock crabs were able to open large *M. arenaria*.

This thesis investigates the trade-offs *M. arenaria* faces when choosing a burial depth in a muddy-intertidal zone. I test the hypothesis that clams trade off reduced predation risk associated with deeper burial against increased feeding (=growth) rate associated with shallower burial. In Chapter 2, I will describe the finding that *M. arenaria* near the low tide mark were typically more deeply buried than were similar-sized clams closer to the high-tide mark. A growth-mortality trade-off hypothesis is proposed to explain this pattern. Chapter 3 focuses on the predator avoidance aspect of the trade-off, Chapter 4 focuses on

the feeding and growth rate aspect of the trade-off, and Chapter 5 summarizes my findings.

Chapter 2

Burial depth and tissue allocation vary with beach elevation in the soft-shelled clam, *Mya arenaria*.

Introduction

Natural variation in burial depth has been documented in many infaunal organisms such as polychaetes (Esselink and Zwarts, 1989) and bivalves (e.g. Zwarts, 1986). Bivalve burial depth varies with siphon mass (e.g. Zwarts and Wanink, 1989), length of the valve (Blundon and Kennedy, 1982b; Zwarts and Wanink, 1989), season (Reading and McGroarty, 1978; Zwarts and Wanink, 1989), body condition (Zwarts, 1986), tidal movements (Roberts et al., 1989), types of local predators (Zwarts and Wanink, 1989), and geographical location (Zwarts and Wanink, 1989). The question of why various burial depth patterns exist for bivalves has received little attention.

An infaunal organism increases its chance of survival by occupying deeper burrows, thus decreasing its risk of being washed away (e.g. Sutherland, 1982; Emerson and Grant, 1991), of being exposed to temperature extremes (e.g. Ratcliffe et al., 1981), or of being eaten (Blundon and Kennedy, 1982b). Predators of infaunal organisms search for and obtain their prey either by moving across the sediment surface or swimming above the surface sometimes digging for their prey. Organisms living at or near the surface, are at the highest risk of predation. Both predator exclusion cages and manipulative experiments show a positive correlation between burial depth and safety (see Zwarts and Wanink, 1989). However, not all clams are buried at these safer, deeper depths.

Zwarts (1986) and Zwarts and Wanink (1984, 1989) propose a trade-off that may explain why the deposit feeder, *Scrobicularia plana*, is not always buried deeply. Deposit feeders use the inhalent siphon to graze the surface around their burrows, so that a shallower burial depth for a particular individual corresponds to an enlarged feeding area (feeding radius is equal to siphon length above the sediment; Zwarts, 1986). Their work showed that more deeply buried clams are safer from predators, at the expense of a smaller feeding radius. Clams reduce their burial depth after their siphons are artificially cropped or if they are in poor condition, to recover body reserves rapidly (Zwarts, 1986). *S. plana* also digs deeper in the winter, apparently in response to an increased predation risk posed by overwintering waders (Zwarts and Wanink, 1989), but nothing is known about burying behaviour of clams in the Pacific Northwest.

Here I describe the burial depth pattern of a population of the suspension feeding clam *Mya arenaria*, in Barkley Sound, British Columbia. Zwarts and Wanink (1989) have suggested that burial depth should be less variable for suspension feeders than deposit feeders since they do not extend their siphons far above the sediment surface. Other researchers have observed that burial depth in bivalves is correlated with shell length or siphon mass (Ansell, 1962; Trueman et al. 1966), and that maximum burial depth is dependent upon siphon mass (Green, 1967; Jackson and James, 1979). However, substantial natural variation in burial depth exists for *M. arenaria*; for example, a clam with a shell length of 10 cm has a depth range of 8 to 25 cm (personal observation). Clams located at lower beach elevations are covered by water and therefore susceptible to sub-tidal predators for a greater period of the day, but also have a longer access time to food than those at higher elevations. In this chapter I will discuss the burial depth range within the context of a hypothesized trade-off between feeding and predator avoidance.

Tissue allocation

Predator-induced morphological defenses occur in many marine organisms (Havel, 1987). Changes in protective structures range from thicker shells in gastropods (*Nucella lapillus*, Palmer, 1990) to whole body morphological alternatives in carp (*Carassius carassius*; Bronmark and Miner, 1992). Production of a thicker shell decreases a snail's susceptibility to being crushed by predatory crabs. Disproportionate growth in body depth allows the carp to enter a size refuge from its gape-limited predator. Unlike the two previous examples, *M. arenaria*'s soft shell and pedal and siphonal gapes do not protect against their main predator, the red rock crab *Cancer productus* (Boulding, 1984). Even though deeper burial may increase safety (Blundon and Kennedy, 1982b; Chapter 3), the maximal burial depth is thought to be constrained by siphon length (Zwarts, 1986). Hence, deeper burial is dependent upon the generation of a long siphon, which may entail a fitness cost of reduced growth of other tissues including reproductive organs (Trevallion, 1971; Lively 1986; Harvell 1986; Havel and Dodson, 1987). Hence, *M. arenaria* in high predation risk habitats may have long siphons (improving safety) at the expense of reduced allocation to gonadal tissue (decreasing reproductive capacity). This chapter also describes differential tissue allocation by clams exposed to different predation pressures.

Materials and Methods

The study sites were intertidal mudflats located in Grappler and Bamfield Inlets, Barkley Sound (48° 53'N, 125° 20'W), on the west coast of Vancouver Island, British Columbia. The study was conducted from May to July, 1990, and from May to June, 1993.

Burial depth with respect to beach elevation

Three sites in Barnfield Inlet (b2, b3, b7) and two sites in Grappler Inlet (g5, g6) were selected. A surveyor's theodolite was used to locate positions on the beach at absolute tidal heights of 0.5 ("low") and 1.5 m ("high"). Two transects were dug, one at each tidal height, and 100 clams (50 per transect) collected at each site. The transects were approximately 0.5 m wide and from 5 to 15 m long. Transects were dug to a depth of 30 cm as *M. arenaria* has been found to burrow to a depth of 25 cm (Blundon and Kennedy, 1982b). The depth of burial, measured with a ruler to the nearest 0.5 cm, was taken as the distance from the top of the clam's shell (the siphonal end) to the bottom of a straight edge placed on the surface of the sediment. The clam was removed from the sediment, washed, and its shell length measured with vernier calipers to the nearest 0.01 cm along the longitudinal plane. Each clam was uniquely marked and collected for subsequent dissection.

Sediment analysis

To relate burial depth to features of the sediment, a simple sediment analysis was performed. Three core samples were taken from high and low beach elevations (see above) in both sites. The cores were sectioned into five depth categories: <5, 5-10, 10-15, 15-20, and 20-25 cm. A 250 g sample was taken from each core section and sieved into each the following size classes: 1 cm, 5 mm, 2 mm, 1 mm, 850 μ m, 500 μ m, 180 μ m. The sieve contents were scooped into aluminum weighing boats, dried at 80°C for 24 hours and weighed to the nearest 0.01g (\pm 0.005).

Comparison of burial ability

Three sediment cubes (4 (w) x 10 (l) x 25 (d) cm) were taken from each of the two tidal elevations and placed in separate aquaria. Thirty clams (length 4.0-6.5 cm) were randomly assigned to each of the two aquaria. Mean clam length did not differ significantly between aquaria (ANOVA, $F=0.26$, $df=1,24$; $p=0.62$). The clams were inserted into the mud with their siphonal end 1 cm above the sediment, and were allowed to bury themselves over 30 days. Burial depth was measured by carefully inserting a stick (1.5 x 12 cm) into the mud until it touched the siphonal end of the clam. The stick was marked at surface level, removed and burial depth measured. Clams were subjected to a tidal cycle, with outgoing tide at 0830h and incoming tide at 1630h.

Tissue allocation

Five hundred clams (50 from two elevations at five sites) were dissected. The siphon, the gonad, the rest of the somatic mass (hereafter referred to as other soft tissue) and the shell were separated. The digestive diverticulum and the chrystilline style were removed from the gonad and were considered as other soft tissue. The dissected clams were dried at 80°C for 24 h, and weighed to the nearest 0.01g ($\pm 0.005g$).

Data analysis

All analyses, unless stated otherwise, were performed using SYSTAT statistical software (SYSTAT, 1992). At all sites clams buried at lower beach elevations were significantly longer ($t=15.33$, $df=517$, $p<0.001$; $8.1 \text{ cm} \pm 1.8 \text{ (SD)}$) than those buried at higher elevations ($5.2 \text{ cm} \pm 2.5 \text{ (SD)}$). Clam length and burial depth were positively related for all clams irrespective of beach elevation ($r^2=0.57$, $p<0.001$; Fig. 2.1). Therefore, I used an analysis of covariance

(ANCOVA) to analyze clam burial depth with respect to beach elevation, using length as a covariate. Tissue mass also depended on clam length, so I used ANCOVAs (adjusting for length) to analyze the effect of beach elevation on siphon, gonad mass and total soft tissue. For sediment analysis, a nested ANOVA was conducted with site, beach elevation, core, depth, and sieve as classes, using SAS (SAS Institute, 1985). To examine whether burial depth differences for low versus high beach elevations could be attributed to differences in characteristics of the sediment, I performed a two-factor ANOVA with beach elevations as treatment factor and core as the nested factor.

A principal components analysis (PCA) was performed to analyze patterns of size and shape variance for the measures siphon (g), gonad (g), other (g), shell (g) and length (cm) with respect to burial depth and beach elevation (high vs. low). All mass variables were cube root transformed, and all variables log transformed to equalize the variance observed.

Results

Burial depth with respect to beach elevation

At all five study sites, clams of a given length were buried significantly deeper at lower beach elevations than at higher beach elevations (Table 2.1). This can be seen graphically by the lower intercept of the high site relationships as compared to the low site relationships (see Figures 2.1 and 2.2). At sites g6, b2, b7 and overall the slopes did not differ significantly ($p > 0.1$), but intercepts differed significantly ($p < 0.001$; Tables 2.1 and 2.2). Mean burial depth (adjusted for length) of clams found at each of the five beaches showed that there was a

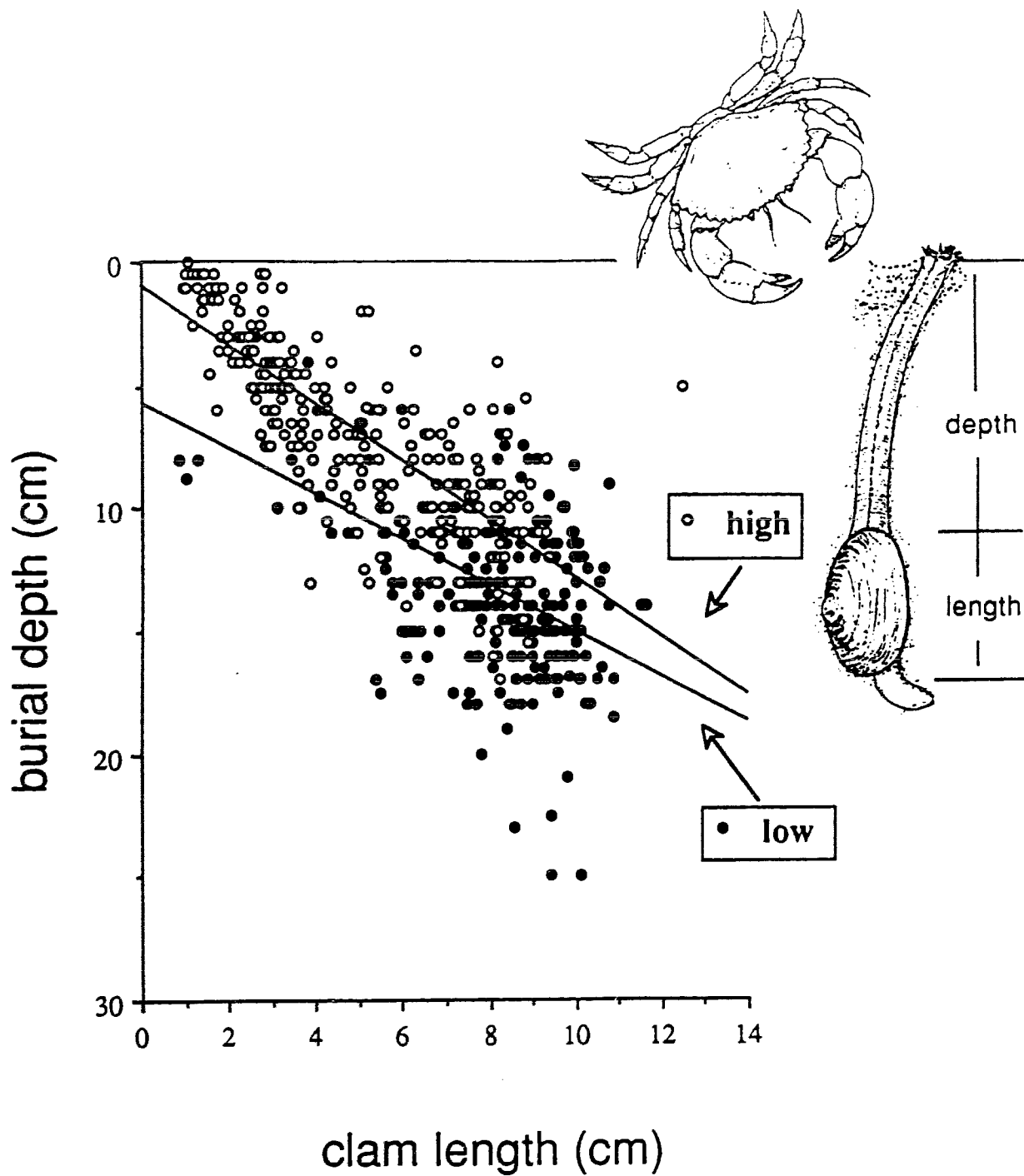


Figure 2.1 The overall relationship between clam length (cm) and burial depth (cm) for 519 clams at two beach elevations (high and low). Clams were buried significantly deeper at lower beach elevations. Summary statistics are presented in Tables 2.1 and 2.2.

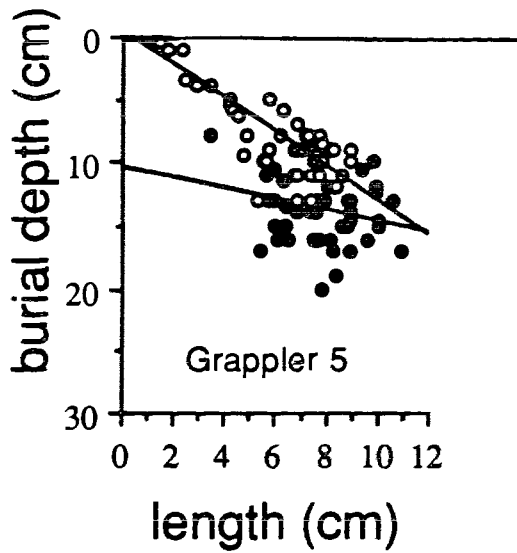


Figure 2.2 The relationship between depth of burial and clam length for each of the five sites (n=50 for each elevation at each site). Axes are the same for all graphs. Zero depth is the sediment surface. At each of the beaches the same sized clam was buried significantly deeper at lower beach elevations. (Legend 0=high beach elevation, ●=low beach elevation)

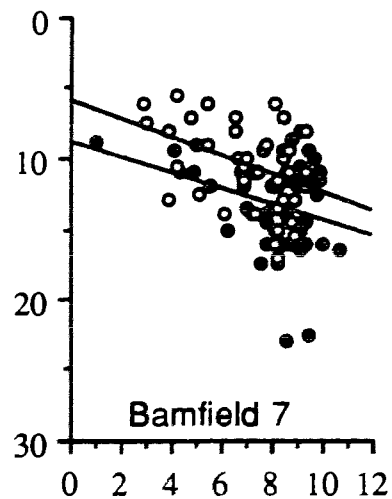
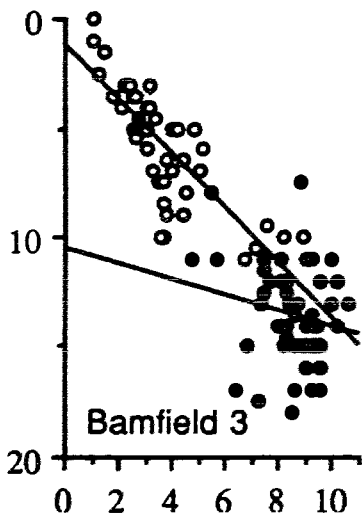
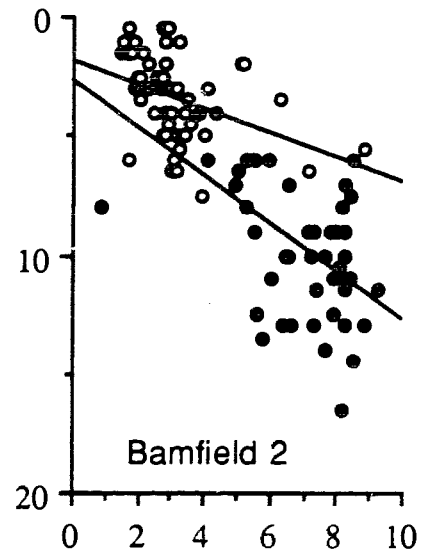
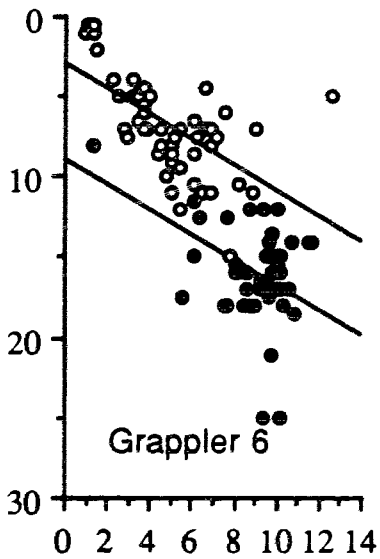


Table 2.1 Regression analysis of the clam length-burial depth relationships depicted in Figures 2.1 and 2.2. For each site the slopes and intercepts of the relationship at high and low beach elevations are reported. The regressions at each site are compared in Table 2.2.

site	elevation	intercept	slope	r ²	N
Grappler 5	high	0.38	1.34	0.75	50
	low	10.44	0.42	0.07	50
Grappler 6	high	2.99	0.79	0.36	50
	low	8.85	0.78	0.05	49
Bamfield 2	high	1.81	0.51	0.15	49
	low	2.64	1.01	0.38	50
Bamfield 3	high	1.10	1.25	0.69	51
	low	10.46	0.36	0.05	51
Bamfield 7	high	5.90	0.66	0.18	69
	low	8.80	0.56	0.10	50
Overall	high	0.97	1.19	0.62	269
	low	5.64	0.93	0.25	250

Table 2.2 ANCOVA summary tables of the clam length-burial depth relationships depicted in Figures 2.1 and 2.2. At each site the significance of the relationship ignoring tidal elevations (pooled) is tested first. All pooled relationships are significantly different from zero. The difference between slopes is tested next. If the slopes do not differ significantly, the intercepts could also be compared.

<i>Grappler site 5</i>			
Source of variation	df	F	p
pooled	1, 96	34.52	<0.001
slopes	1, 96	15.77	<0.001
intercepts	1, 96	NA	

<i>Grappler site 6</i>			
Source of variation	df	F	p
pooled	1, 95	5.67	<0.05
slopes	1, 95	1.98	NS
intercepts	1, 95	6.10	0.015

<i>Bamfield site 2</i>			
Source of variation	df	F	p
pooled	1, 95	39.12	<0.001
slopes	1, 95	0.13	NS
intercepts	1, 95	0.61	NS

<i>Bamfield site 3</i>			
Source of variation	df	F	p
pooled	1, 98	81.19	<0.001
slopes	1, 98	15.54	<0.002
intercepts	1, 98	NA	

<i>Bamfield site 7</i>			
Source of variation	df	F	p
pooled	1, 115	4.67	0.033
slopes	1, 115	1.58	NS
intercepts	1, 115	6.1	0.015

<i>Overall</i>			
Source of variation	df	F	p
pooled	1, 515	860.64	<0.001
slopes	1, 515	2.63	NS
intercepts	1, 515	115.98	<0.001

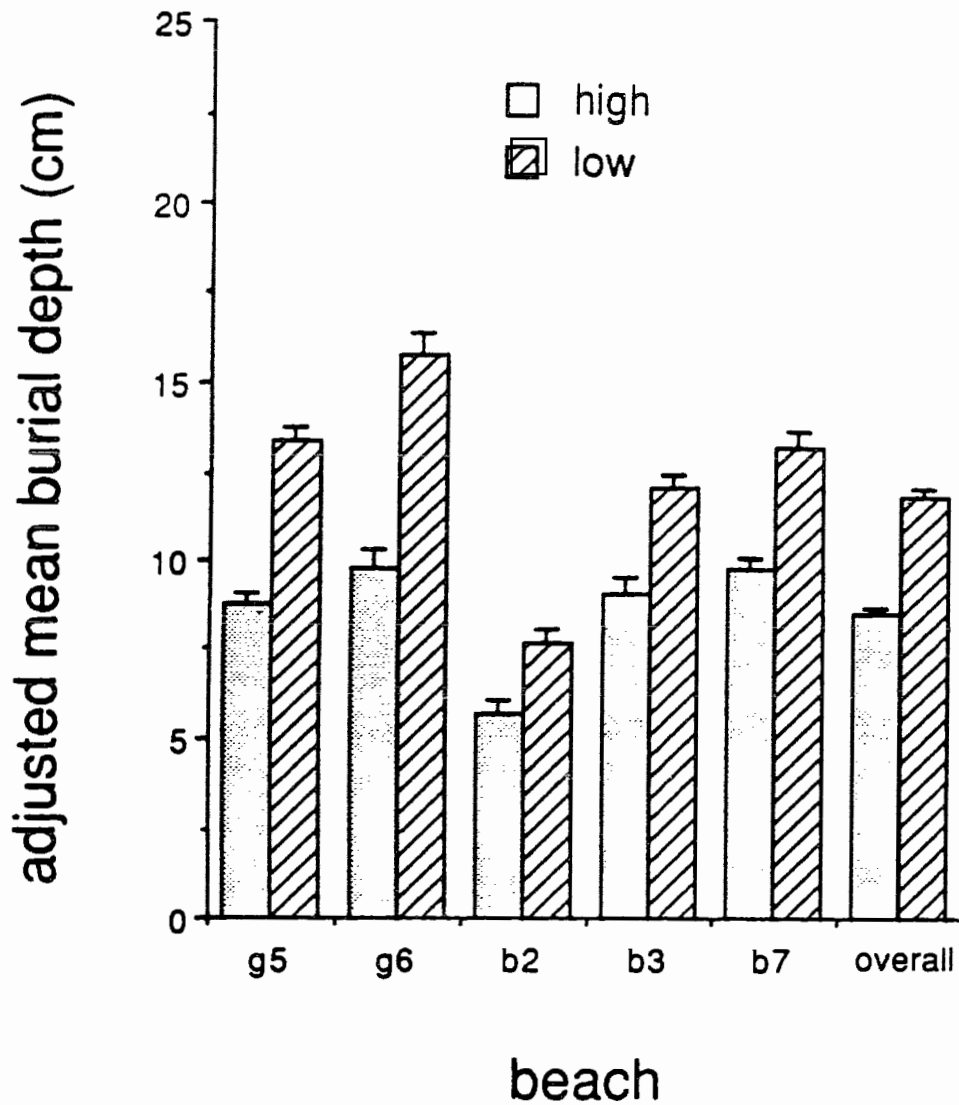


Figure 2.3 Mean (adjusted for length; SD is shown; N=50 for each bar) burial depth of clams found at each of the five beaches comparing high and low beach elevations. At each of the sites there is a significant difference in burial depth between high and low beach elevations, clams found lower being on average deeper.

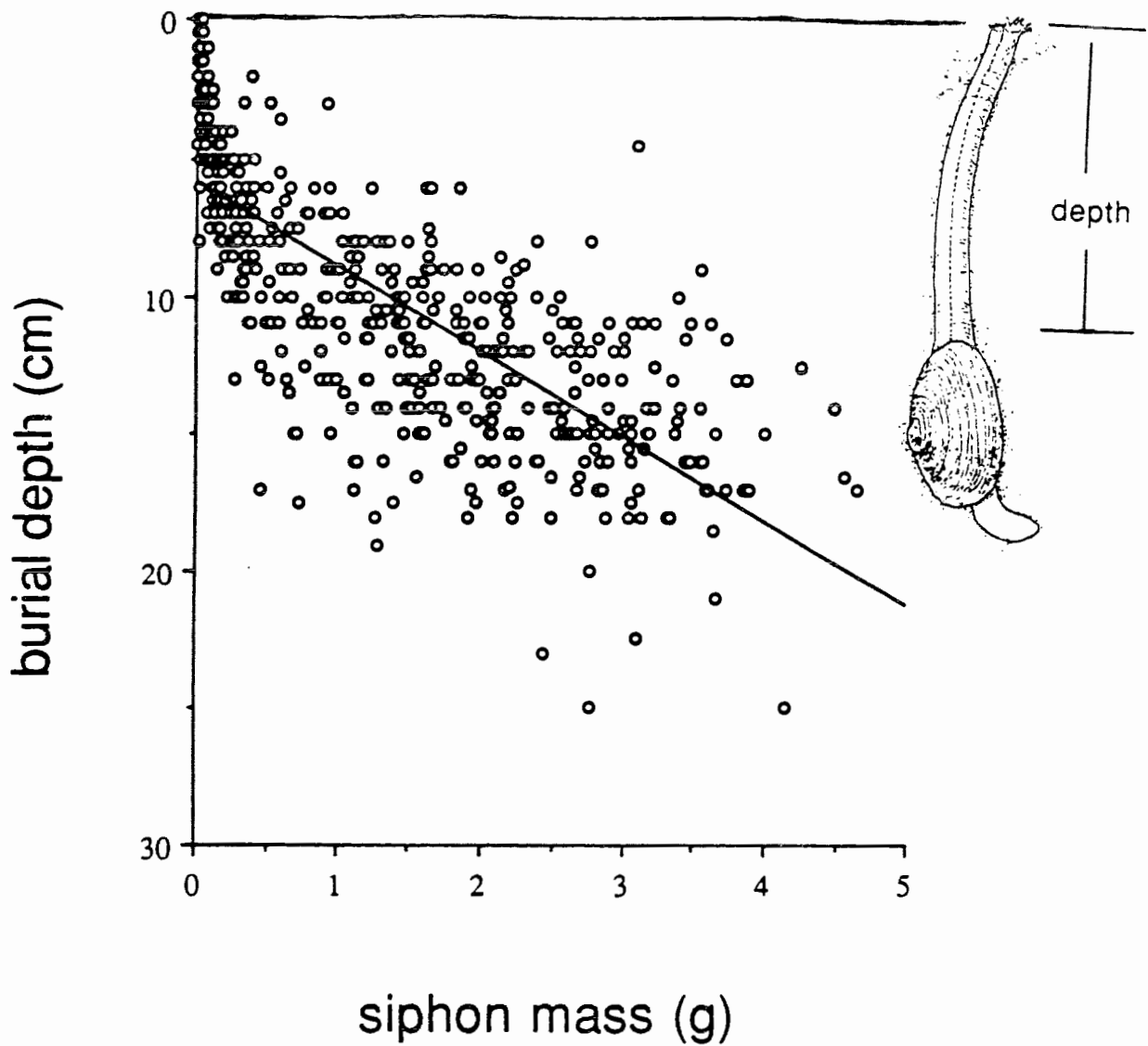


Figure 2.4 The relationship between siphon mass (g) and burial depth (cm) for all sites (g 5, g6 and b2, b3 and b7) and both (high and low) beach elevations (N=497). Zero depth is the sediment surface.

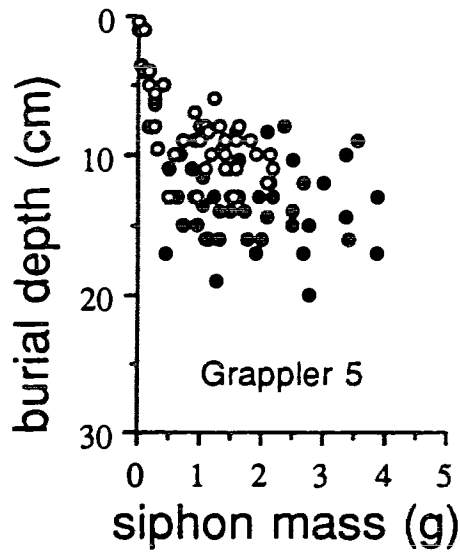
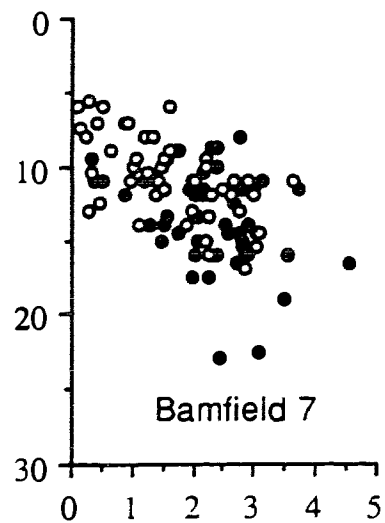
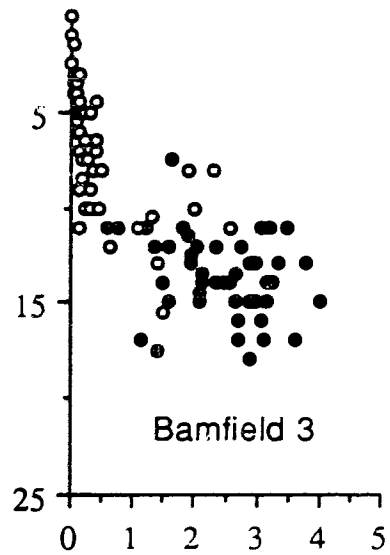
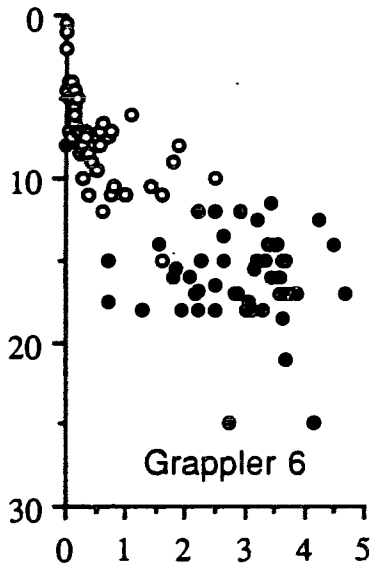


Figure 2.5 The relationship between burial depth (cm) and siphon mass (g), with respect to beach elevation (high, N=248 and low, N=249). Axes are the same for all graphs. Sites are shown separately. Zero depth is the sediment surface.
Legend ○=high; ●=low



significant difference ($p < 0.001$) in burial depth between high and low beach elevations; clams found lower were on average buried deeper (Figure 2.3). At all five study sites, log siphon mass (g) was positively correlated with log burial depth (intercept=-2.28; slope=0.36; $r^2=0.72$, $p < 0.001$; Figure 2.4). Figure 2.4 is displayed without log transformation to emphasize the great variation in burial depth (cm) with respect to siphon mass (g). In Figure 2.5 regression lines are not shown because the slopes of high and low siphon mass were not homogeneous, so the assumptions of an ANCOVA were violated.

Sediment Analysis

A nested ANOVA revealed a statistically significant difference in sediment composition within and between sites. There was no effect of site ($F = 1.1$, $df = 1, 227$, $p = 0.72$) however all 2-, 3- and 4-way interactions with site were significant (p 's < 0.05 in all cases). There was a significant beach elevation effect ($F = 14.2$, $df = 1, 227$, $p < 0.001$) and there were significant 2-, 3- and 4-way interactions with beach elevation. There was a significant effect of depth ($F = 18.6$, $df = 4, 192$, $p < 0.001$) and there were significant 2-, 3- and 4-way interactions with depth. There was a significant effect of sieve size ($F = 5626.11$, $df = 6, 192$, $p < 0.001$) and there were significant 2-, 3- and 4-way interactions with sieve size. Overall then, there was a significant sediment mass difference for each of the different sieve sizes and at each of the nested levels (site, elevation, core, and depth). There was also a significant difference in the overall sediment distribution between the two beach elevations.

Comparison of burial ability

A nested ANOVA (with core nested within beach elevation) revealed no significant difference in burial depth after 30 days for clams placed in sediment

from the low ($2.2 \text{ cm} \pm 1.69 \text{ (SD)}$) and high beach elevations ($2.1 \text{ cm} \pm 1.36 \text{ (SD)}$); $F=0.11$, $df=1,2$, $p=0.73$).

Tissue allocation

At four of the five sites, clams buried at lower beach elevations had significantly heavier siphons (adjusted for length) than those at higher beach elevations (Figure 2.6). Moreover, at three of the five sites clams buried at lower beach elevations had significantly heavier gonads for their length than those found higher (Figure 2.6). However, the opposite trend was present at site b2, where clams higher on the intertidal had significantly heavier siphons for their length ($p=0.03$) and gonads for their length ($p < 0.001$). At site b7 there was no significant difference in gonad mass ($p=0.35$). I also found that at four of the five sites, clams at lower beach elevations had significantly more soft tissue for their length than those found at higher elevations (see Figure 2.7). Once again, an opposite trend was present at site b2, where clams found at higher elevations had significantly more soft-tissue than those found at lower elevations.

Principal Components Analysis of tissue allocation

A principal components analysis (PCA) was performed to analyze patterns of tissue allocation in *M. arenaria*. The specific question addressed was whether there was disproportionate growth of one measured dimension (length (cm) shell (g), gonad (g), siphon (g) or other soft tissue (g)) with respect to another. The first component (PC I) accounted for 91.7% and 87.9% of the variance found in the clams high and low in the intertidal, respectively (Table 2.3). All the coefficients are large and positive for PC I, which can be interpreted as a factor for general size.

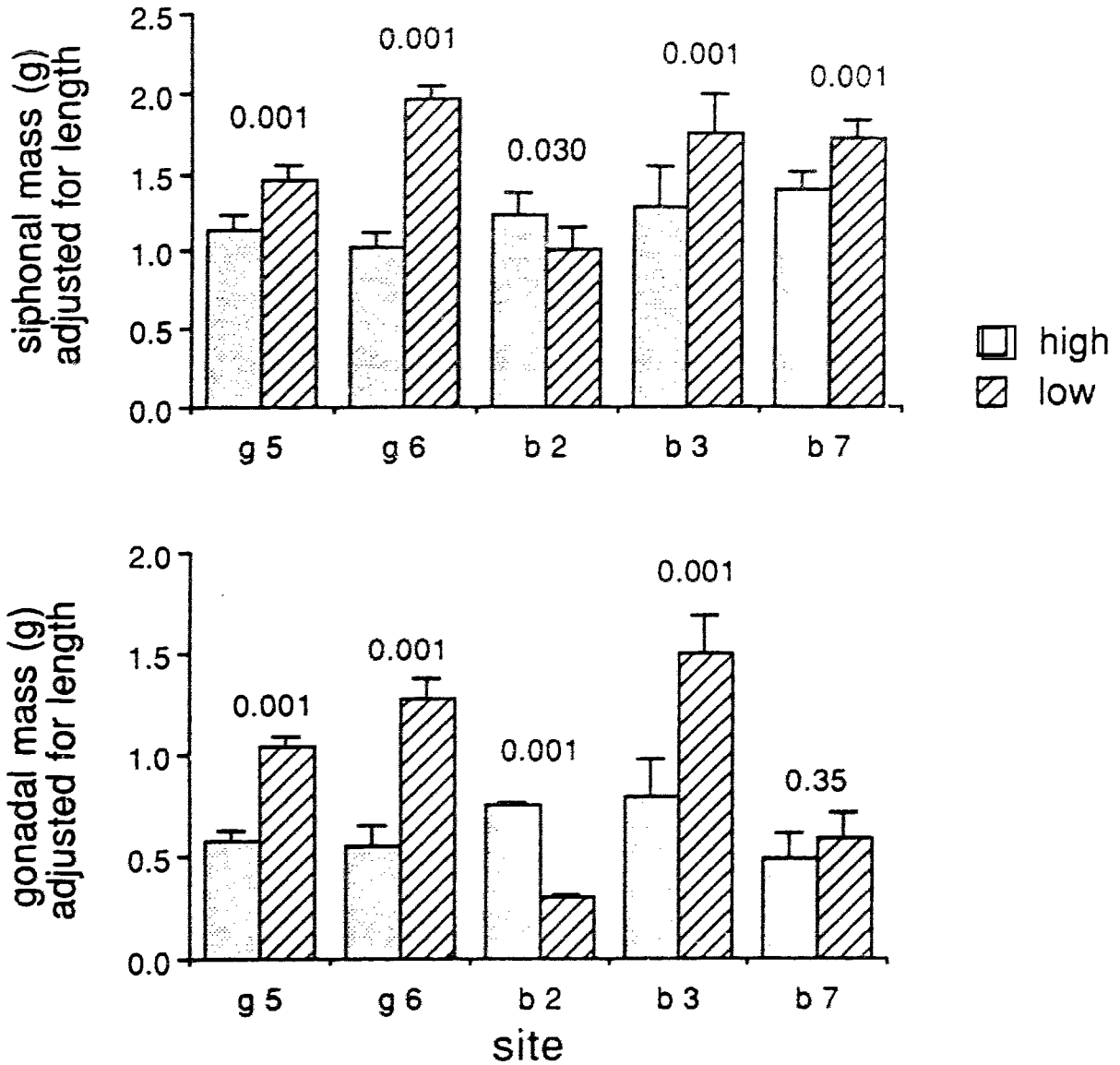


Figure 2.6 Adjusted mean mass of siphon and gonad in ciams found at high (N=248) and low (N= 249) beach elevations (based on ANCOVA with length as covariate). p values for the t-test comparing means are shown above the bars.

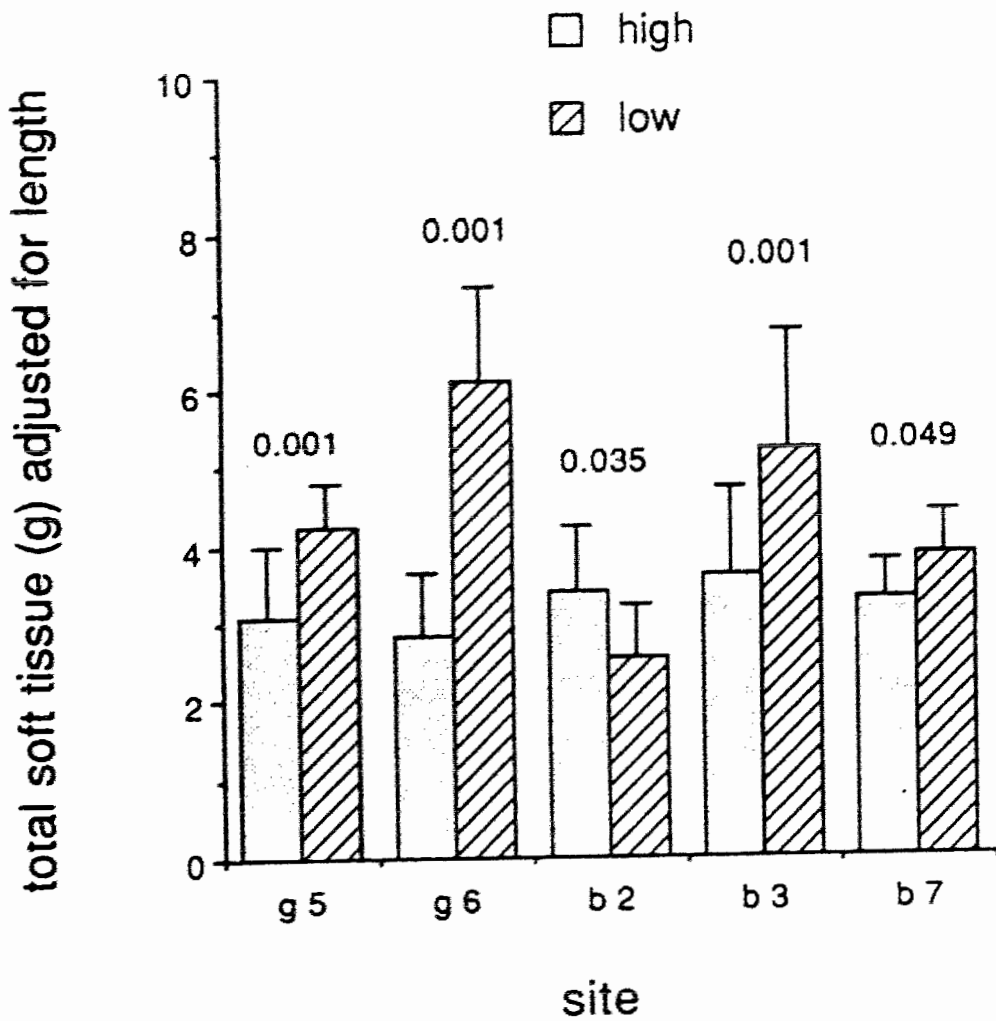


Figure 2.7 Adjusted mean mass of total soft tissue in clams found at high (N=248) and low (N=249) beach elevations (based on ANCOVA with length as covariate). p values for the t-test comparing means are given above the bars.

Table 2.3 Principal components of the *M. arenaria* covariance matrix for clams found at high and low beach elevations. "Other" refers to soft tissue other than siphon and gonad.

		Beach Elevation			
		high		low	
Principal Component		i	ii	i	ii
soft tissue	siphon mass(g)	0.97	0.08	0.97	0.03
	gonad mass (g)	0.95	0.23	0.91	0.34
	other mass (g)	0.98	0.11	0.96	0.16
hard tissue	shell mass (g)	0.92	- 0.38	0.88	-0.43
	shell length (cm)	0.98	- 0.27	0.96	-0.18
% variance explained		91.66	4.41	87.92	6.74

The second component (PC II) accounted for 4.4% and 6.7% of the variance found in the clams found high and low in the intertidal (Table 2.3). Both PC II results were bipolar, with some of the coefficients positive and some negative. As PC II increased, soft tissue increased at a higher rate than hard tissue (Bookstein et al., 1985; Tables 2.3, 2.4 and 2.5).

Multiple regression analyses were performed using a factor called general size as well as each of the components of size and shape (siphon, gonad, other tissue, shell and length) as the independent variables (predictors) and depth as the dependent variable. I performed a multiple regression in order to describe the direction and strength of the relationship between several independent variables (clam dimensions) and a continuous dependent variable (depth). I created a general size factor for clams at low beach elevations using the equation: $\text{size} = (0.97)(\text{siphon}) + (0.91)(\text{gonad}) + (0.96)(\text{other tissue}) + (0.88)(\text{shell}) + (0.96)(\text{length})$. The coefficients in the equation corresponded to the loading coefficients of PCI for each variable (Crespi and Bookstein, 1989). A parallel analysis was done to examine tissue allocation amongst clams found at high beach elevations. The 'size' factor was produced using the equation: $\text{'size'} = (0.97)(\text{siphon}) + (0.95)(\text{gonad}) + (0.98)(\text{other tissue}) + (0.92)(\text{shell}) + (0.98)(\text{length})$. The coefficients in the equation were the corresponding coefficients of PCI, for each variable. Numerical results are summarized in Table 2.6.

The multiple regressions revealed that as depth increases, siphon mass increases disproportionately with respect to 'size' for clams located at both low and high beach elevations. This is shown mathematically by a significant and positive coefficient of the variable (β_i ; Table 2.6). A significant positive result is also seen for gonad mass at both beach elevations. The regression revealed that

Table 2.4 Descriptive statistics and a correlation matrix for five measures of *M. arenaria* at high beach elevations. "Other" refers to soft tissue other than gonad or siphon.

measure	mean	S.D.	Correlations				
			siphon	gonad	other	shell	length
siphon (g)	0.73	0.82		0.92	0.96	0.87	0.96
gonad (g)	0.32	0.45			0.93	0.80	0.88
other (g)	0.78	0.88				0.85	0.95
shell (g)	13.23	16.42					0.90
length (cm)	5.20	2.54					

Table 2.5 Descriptive statistics and a correlation matrix for five measures of *M. arenaria* at low beach elevations. "Other" refers to soft tissue other than siphon and gonad.

measure	mean	S.D.	Correlations				
			siphon	gonad	other	shell	length
siphon (g)	2.09	1.03		0.88	0.92	0.88	0.93
gonad (g)	1.29	1.00			0.88	0.77	0.81
other (g)	2.41	3.28				0.84	0.90
shell (g)	36.68	21.82					0.90
length (cm)	8.11	1.79					

Table 2.6 Multiple regression analysis equations obtained by using the PCA component 'size' and each of the components of size (siphon mass, gonad mass, other tissue mass, shell mass and shell length; see Table 2.3) to predict depth in the equation:
 Depth = β_1 (PC size) + β_2 (component) + error. Equations are shown for both high and low beach elevations for all sites.

Beach elevation	Tissue component	β_1	SE	β_2	SE
Low	siphon mass	-1.20*	0.64	14.75*	3.63
High		0.32	0.22	4.07*	1.43
Low	gonad mass	-0.029	0.44	5.04*	1.52
High		0.56*	0.18	1.67*	0.80
Low	other mass	0.94	0.57	2.11*	2.93
High		0.55*	0.23	2.55	1.58
Low	shell mass	3.47*	0.41	-9.99*	1.79
High		1.44*	0.20	-1.45*	0.51
Low	shell length	2.39*	0.54	-6.42*	3.1
High		0.99*	0.26	-0.58	1.84

* significantly different from zero ($p < 0.05$)

as depth increases there is a disproportionate increase of other soft tissue mass with respect to 'size', but only for clams located at low elevations. For all clams, as depth increases, there is a disproportionate and significant decrease in shell mass. Finally, there is a significant decrease in length with respect to 'size' for clams located at lower elevations only (see Table 2.6).

Discussion

Burial depth with respect to beach elevation

Individual *M. arenaria* of the same length were buried deeper at lower beach elevations than at higher elevations (Figures 2.1, 2.2 and 2.3; Tables 2.1 and 2.2). This microgeographic pattern was consistent among five separate beaches located in two different inlets. Clams located at lower beach elevations are submerged, and therefore susceptible to sub-tidal predators, for a greater period of the day than those at higher elevations. Hence, the exposure to predators such as *C. productus* increases with decreasing beach elevation. One explanation for this burial depth pattern is that it results from a behavioural adaptation of clams to differential crab predation. This hypothesis would predict that clams susceptible to predation for longer periods of time, (those at lower beach elevations) would bury deeper. A second explanation is that the pattern does not reflect a behavioural adaptation, but results instead from selective prey removal. *M. arenaria* may bury at random depths, but shallowly-buried clams are preferentially removed by crabs. Those that escape predation longer are larger and hence deeper, and the average deeper burial of low-elevation clams is due to the higher rate of predation. Both these hypotheses, predict that there would be a small number of shallowly-buried clams located at lower beach

elevations. In order to discriminate between these two hypotheses further experimentation is needed (see Chapter 3).

Mean length was always greater for clams located at lower beach elevations (Figure 2.3). Control of *M. arenaria's* intertidal zonation is through sediment transport and water movements (a random process; Emerson and Grant, 1991) and after 12 mm *M. arenaria* can not move horizontally (Belding, 1930; cited in Emerson and Grant, 1991). Since settling is thought to be a random process clams found at the high and low beach elevations may be the same age. If this is true, then the significant difference in size may be an indication of poorer feeding, and hence slower growth at higher elevations. I could not quantify age, as estimates are difficult and generally not accurate after clams are seven years old (MacDonald and Thomas, 1980).

There is a positive correlation between siphon mass and burial depth, so that longer shelled clams and clams with larger siphonal masses (g) tend to occupy deeper burrows (e.g. Blundon and Kennedy, 1982b; Zwarts and Wanink, 1989; this study). Zwarts and Wanink (1989) only reported mean burial depths with respect to siphon weight size classes, therefore burial depth variation was not emphasized. I found large variation in the siphon mass and burial depth distribution in *M. arenaria* (Figure 2.4) at all five study sites and for all size classes of clams (Figure 2.5). For example, a clam with a 1.5 g siphon has a burial depth range of 4-18 cm. Likewise, clams buried at 10 cm have siphon masses of 0.32 to 3.5 g. This variation suggests that burial depth is not always constrained by length or siphonal mass, but may instead be a condition dependent behavioural choice. Only five out of 500 clams were found buried deeper than 20 cm (see Grappler 6 and Bamfield 7 in Figures 2.2 and 2.5), in spite of the fact that clams have been found as deep as 25 cm. Perhaps this abrupt decrease in the number of *M. arenaria* found below 20 cm is an indication

of a disproportionate decrease in benefits of deeper burial with respect to increased costs associated with that depth.

Sediment Analysis and Comparison of Burial Ability

Clams at lower beach elevations occupied deeper burrows than those at higher elevations. This pattern appears not to be attributable to variation in characteristics of the sediment. My analysis of sediment mass with respect to size, elevation, beach and depth, revealed significant differences between cores collected from low and high elevations. However, these physical differences were not manifested biologically, as there were no significant differences in final burial depth when comparing clams that buried in sediment obtained from each of the two different beach elevations.

Tissue Allocation

I found that at four of the five sites, clams located at lower beach elevations had significantly more soft-tissue (siphon, gonad and other) than individual clams at higher elevations (Figure 2.7). These differences in soft tissue masses suggest there are differential feeding opportunities. Clams at lower beach elevations were covered by water for a greater period of the day, and therefore may have a longer time to feed.

The overall greater soft-tissue mass at lower beach elevations conflicts with the original hypothesis, which states that if burial depth represents a trade-off between feeding and safety, clams make a corresponding trade-off in terms of tissue allocation. As burial depth increases (clams located at lower beach elevations) siphon mass increases at the expense of gonadal tissue. However, my results revealed no evidence of such a trade-off (Figure 2.6). Comparing clams from different feeding areas (high and low beach elevations), may not be

the best method to discover somatic/reproductive trade-offs. A better method of comparison would be between similarly sized clams buried at the same beach elevation differing only in their burial depth. A second explanation for the lack of observed reproductive/somatic trade-off may be differential energy requirements for producing gonadal versus siphonal tissue. If minimal energy is required for producing gametes, there may not be a direct trade-off between these two parameters. Instead gonad production may be state dependent, so that body condition and surrounding environmental factors influence gonad production.

Clams located at lower beach elevations generally had larger siphonal masses than clams located at higher beach elevations. However, at beach b2, the opposite trend was observed. This difference may be due to the relatively steeper slope of site b2 than the other four sites, creating a correspondingly shorter horizontal distance for the predator *C. productus*. Therefore, *M. arenaria* high on site b2 may be exposed to more intense predation (Chapter 3) than at other sites. I suggest that the clams respond to the situation by producing a proportionately larger siphon to be able to increase their burying depth. Although the differences in gradient may explain why b2 have proportionately larger siphons than other high elevation clams, it does not explain why high elevation clams at this beach have larger siphons than low elevation clams.

Principal Components Analysis of tissue allocation

The first component (PC I; size and shape) described the majority of *M arenaria's* measurement variance found for both beach elevations. This was a measure of variation in general size (Table 2.3). The second component, PCII, accounts for a smaller amount of variance, and shows that as depth increases, both soft and hard tissue increase but that hard tissue increases at a lower rate. Although only a small amount of variation is explained by the second component, this same

bipolar trend is observed at both beaches, which suggests this represents a true pattern in nature.

The multiple regression analysis revealed several tissue allocation patterns with respect to burial depth. Deeply-buried clams, irrespective of beach elevation, have relatively larger siphonal masses (Table 2.6). As burial depth increases the clams may be growing disproportionately wider (larger radius) as well as longer siphons. The amount of water that can be moved by a given force (generated by the clam) through a tube of a given length (the siphon) varies inversely with the the siphon length and proportionately with its radius to the fourth power (Poiseuille's equation; Vogel, 1981; see Chapter 4). Hence, assuming an equal force generated by the clams, longer siphons filter proportionately less water (food), but widening the siphon allows the clam to increase its filtering rate exponentially.

Commuto (1982) suggested that reproduction in *M. arenaria* is delayed in order to divert resources into rapid early growth. Clams have indeterminate growth so that larger clams, which are generally more deeply buried, tend to be older than smaller less deeply buried clams. The multiple regression also revealed that as depth increases (and hence age) there is a disproportionate increase in gonad mass (Table 2.6). This result was found at both tidal heights and corroborates Commuto's (1982) suggestion. The regression analysis also showed that as depth increases, shell mass and length decrease disproportionately (at both beach elevations) relative to other measures. Perhaps more deeply buried (therefore larger) clams are growing thicker instead of longer shells. My preliminary analysis of growth data (personal observation, unpublished) supports this idea. Other soft tissue (excluding siphon and gonad) was found to increase significantly in clams found buried deeper when located at low beach elevations. However, there was no significant trend for clams at high

elevations. Overall then, hard and soft tissue growth rates follow different trajectories. A similar trend was discovered in the mussel *Geukensia demissa* (Borrero and Hilbish, 1988). Hard tissue (shell length) is generally used as an indicator of soft tissue mass, thus it is important to note that they are not as closely associated in *M. arenaria* as previously thought.

The difference in shell and soft tissue growth rates with respect to depth may be due to differences in organic content of the tissues. Shells (hard tissue) have a lower organic content than soft tissue (Jorgensen, 1976; Price et al., 1976). Hard tissue growth occurs via deposition of material from the water (Tanaka et al., 1986) and thus may have only partial dependence on metabolic carbon (Wilbur and Saleuddin, 1983). Therefore, seasonal variation in food availability and levels of inorganic elements in the water may have different effects upon the rates of growth in shell and soft tissue (Borrero and Hilbish, 1988).

In conclusion, I found that there was variation in burial depth, so that clams were buried more deeply at lower beach elevations than at higher beach elevations. I also found that more deeply buried clams and clams at lower beach elevations had proportionately larger siphon, gonad and overall soft tissue masses than did their higher elevation and shallower conspecifics. Therefore, deeper burial is not associated with a trade-off between reproductive potential (as measured by gonad size) and siphon length. Clams located at lower beach elevations had significantly more soft tissue mass than did those located at high elevations, which does suggest that there are increased feeding opportunities at lower elevations, but perhaps at an increased survival cost (Chapter 3).

Chapter 3

Predation by crabs as a selective force on burial depth in the soft-shelled clam, *Mya arenaria*.

Introduction

Crab predation is thought to be a major selective agent in the evolution of bivalve shell morphology. Species of clams that occupy shallow positions in the sediment and are easily accessible to crabs (e.g., the little-neck clam *Protothaca staminea*) are characterized by thick, robust shells and a lack of both pedal and siphonal gapes (Vermeij, 1978; 1987). In contrast, clams with thin shells and gapes typically occupy deeper, safer, positions in the sediment (e.g. up to a depth of 25 cm in *Mya arenaria*; Blundon and Kennedy, 1982b; Chapter 2). Behavioural differences between infaunal prey items are also thought to be influenced by predation pressures. Protective behaviour for an infaunal organism might include either rapid burial in the presence of a predator, or a constant deep burial depth.

The hypothesis that clams adjust their position in the sediment in response to risk of predation has not been thoroughly investigated. Bivalve predation risk has been shown to decrease significantly with increasing depth of burial (Blundon and Kennedy, 1982b; Virnstein, 1977; Holland et al., 1980; Haddon et al., 1987). These results, however, were not obtained under natural conditions and may be laboratory artefacts. In this chapter I investigate the risk of predation on *M. arenaria* by its main predator, the red rock crab *Cancer productus* (Boulding, 1984). I show, in three separate experiments, that

predation by the red rock crab is a selective force on burying behaviour of *M. arenaria*.

For *M. arenaria* the probability of predation varies as a function of duration of exposure to predators, which is in turn dependent on beach elevation. *M. arenaria* are only vulnerable to predation by red rock crabs during high tide, as these crabs are rarely observed in the intertidal zone during low tide (Robles et al., 1989). As a consequence, clams inhabiting lower elevations on the beach are susceptible to predation by aquatic predators for longer periods and are found to be buried deeper than clams living at higher beach elevations (Chapter 2).

I assessed predation risk by crabs in two ways. First, I estimated predation pressure by counting pits dug by crabs (see below). Second, I used clam reburial experiments to estimate predation pressure by crabs. I will consider each of these methods in turn.

Red rock crabs use their chelae to dig the clams from their protective burrows, leaving a characteristic 'crab pit' which is often accompanied by a broken clam shell (personal observation). I assumed that each crab pit indicated a successful predation event by a red rock crab, but it is possible that these pits also indicate failed attempts, inflating my assessment of predation risk. Other potential predators of *M. arenaria*, such as crows (*Corvus caurinus*), glaucous-winged gulls (*Larus glaucescens*) and the sunflower star (*Pycnopodia helianthoides*) were present in my study area. *P. helianthoides* is known to produce pits when excavating prey (Allen, 1983). However, sunflower seastars were either absent or found at low densities at each of my study sites (personal observations). Furthermore, when consuming clams, *P. helianthoides* leave the valves whole, whereas shells known to have been attacked by crabs were chipped or cracked. Pits are not produced by birds during foraging events.

Crows were not seen to excavate in my study area, and, lacking a long probing bill, they can only obtain clams located at or near the surface (Richardson, 1985). Glaucous-winged gulls were only observed on my study sites between October and March, at which time recorded predation occurrences for *M. arenaria* were low compared to the summer months.

Risk of predation on clams was also assessed using a field reburial experiment. Blundon and Kennedy (1982b) reported that, under laboratory conditions, clams that were buried more deeply in the substrate were preyed on by crabs significantly less often than those buried at shallower depths. In my second experiment I manipulated clam burial depth at both high and low elevation study plots within the intertidal zone. This experiment was designed to assess directly how burial depth and position in the intertidal zone (i.e., duration of exposure to predation risk) affect predation risk of *M. arenaria* in its natural environment.

If predators are a significant source of mortality, then prey would be expected to evolve characteristics that reduce their vulnerability (Vermeij, 1982). Such predator-induced adaptations may include cryptic or aposematic coloration, protective armor, chemical defenses, and responses to alarm substances (Lima and Dill, 1990). Prey alarm responses, such as fleeing, are often elicited by chemical substances that are passively released from wounded conspecifics. Alarm response behaviours have been described for a variety of aquatic taxa including fish (Hugie et al., 1991), amphibian tadpoles (Kulzer, 1954; cited in Atema and Stenzler, 1977), marine gastropods (Atema and Stenzler, 1977; Marko and Palmer, 1991), sea urchins (Snyder and Snyder, 1970), sea anemones (Lawn and Ross, 1982), barnacles (Palmer et al., 1982), and crinoids (Shaw and Fontaine, 1990). Responses to alarm substances may differ from responses to predator odour. For example, von Frisch (1941; cited in

Atema and Stenzler, 1977) showed that the fresh water minnow *Phoxinus laevis*, when faced with the odour of its natural predator, froze, and sank slowly to the bottom. This response contrasts markedly with its fleeing response, elicited by the odour of a wounded conspecific. Similarly, the snail *Nassarius vibex* buries itself when exposed to extract from a conspecific, but emerges from the sand and flees when a predator is nearby (Snyder, 1967) and engages in a third behaviour, "flipping", when contacted by a predator (Gore, 1966). However, alarm responses to perceived predation risk have not yet been demonstrated in bivalves. In Chapter 2, I showed that *M. arenaria* located at lower beach elevations were buried deeper than those at higher beach elevations. Perhaps differences in burial depth are a reflection of differential removal of smaller, more shallowly-buried clams located at lower beach elevations, and not the result of an avoidance behaviour. To test if burial depth differences could be explained by predator avoidance I performed a third set of experiments. I exposed individuals to a variety of sensory cues such as predator odour, wounded conspecific extract and tactile stimuli, and recorded their behavioural responses.

Materials and Methods

The field component of this study was conducted during July of 1990 and from May 1992 to August 1993 on intertidal mud flats located in Grappler and Bamfield Inlets, Barkley Sound, located on the west coast of Vancouver Island, British Columbia (48° 53'N, 125° 20'W). Laboratory work was conducted at the Bamfield Marine Station (May-August, 1993).

Field crab pit observations

I chose two study sites in Bamfield Inlet (b2, b3). I estimated absolute tidal heights at each site using tables and predictions prepared by the Marine Environmental Data Service for 1990 and 1992. These standardized tables enabled me to determine sea level (0.0 m), and I used a surveyor's theodolite to locate positions on the beach corresponding to tidal heights of 0.2, 0.6, 1.0 and 1.4 m above sea level. I defined the 'low' elevation plot as the area between 0.2 m and 0.6 m, the 'middle' plot as the area between 0.6 and 1.0 m and the 'high' plot as the area between 1.0 and 1.4 m. The sides of each plot were parallel to the shore and were a consistent length of 50 m. At site b2 the areas for high, medium and low plots were 262, 263 and 250 m², respectively, while at site b3 the corresponding areas were 235 and 224 and 261 m², respectively.

Crab pits were counted on a daily basis. I thoroughly raked each study site approximately 24 h before the initial observations, and every day thereafter, to avoid re-counting crab pits. I repeated this process over nine successive days of a sequence of particularly low tides. During each of these sampling days all study plots within the intertidal were covered by water at least once during the day (i.e., it was also a HH (high high) tidal cycle). I performed this procedure at both study sites (b2 and b3), twice in 1990 and twice in 1992.

Clam density estimates were obtained by digging five 0.5 x 0.5m quadrats to a depth of 30 cm in each of the three study plots (high, medium and low) at each site (b2 and b3). Only clams exceeding 0.5 cm in length (anterioposteriorly) were counted.

The probability that a clam was eaten by a crab was calculated as the total number of crab pits observed over the nine day sequence, divided by the estimated number of clams in each study plot. The daily probability of

consumption, $P(c)$, was this quantity, divided by nine. I estimated the probability of clam surviving predation for a full year as

$$P(\text{survival}) = 1 - P(c)^{365}$$

Field reburial experiment

Three hundred-thirty clams (5-7 cm long) were collected from several beaches in Grappler Inlet (May and June 1992) and painted with unique markings to facilitate identification. Each clam was buried in the intertidal zone on one of two beaches, one in Grappler Inlet and one in Bamfield Inlet. I used a surveyor's theodolite to demarcate five elevations in the intertidal zone: 0.2, 0.4, 0.6, 0.8 and 1.0 m above sea level. At the Grappler Inlet site, a total of 225 clams were buried, 45 at each of the five beach elevations. At each elevation 15 clams were buried at each of three depths: 5, 15 or 25 cm below the sediment surface, measured from the siphonal end of the clam. At the Bamfield Inlet site, a total of 105 clams were buried, 21 at each intertidal elevation. At each elevation seven clams were buried at each of the three experimental depths: either 5, 15 or 25 cm below the sediment surface. At both study sites, clams were spaced approximately one metre apart on a transect along each elevational plot. Clams were randomly assigned to experimentally-controlled burial depths along the transect. To ensure minimal movement from the experimental depth of burial, I placed a screen made of 1 mm² plastic mesh around the pedal end of each clam, inhibiting the intrusion of the foot into the sediment. A monofilament line was sewn through the top end of the screen and was then glued to each clam's side, such that the line extended 25 cm above the sediment surface (i.e., a clam buried at 5 cm had 30 cm of line attached). A label was attached to the end of each line. I checked lines periodically to

ensure that clams did not migrate vertically in the sediment (i.e., the length of line above the sediment remained at 25 cm).

M. arenaria cannot extend its siphon rapidly through the sediment (Blundon and Kennedy, 1982b). Therefore, to minimize mortality due to suffocation at reburial, clams were covered with a maximum of 5 cm of sediment per day until all were completely covered. To eliminate predation during reburial all clams were protected with a roll of 2.5 cm² mesh chicken wire prior to initiation of the burial experiment. Predation events were recorded at weekly intervals between 15 July 1992 and 10 August 1992, and at bi-monthly intervals between September 1992 and May 1993. Clams were considered to have been eaten if either the screen mesh or at least one valve of a shell was found. All shells recovered were chipped at either the pedal or the siphonal end, characteristic of crab predation.

Laboratory measurements of burial behaviour

In this experiment I measured the change in burial depth of clams in response to a series of treatments intended to simulate predation risk. All work was performed from June to August 1993. One hundred-eighty clams (3.5-6.5 cm long) were collected at Bamfield Inlet. Clams were individually labeled with plastic tags, attached with monofilament fishing line by sewing the line through a small piece of 1 mm² plastic mesh glued to the right valve. Five aquaria (each 60 x 30 x 30 cm) were placed in each of three large holding tanks (120 x 120 cm) housed in a covered area on the foreshore of the Bamfield Marine Station. I filled each aquarium with intertidal mud to a depth of 15 cm. To minimize variation in sediment particle size among aquaria, I collected sediment from a single source in Bamfield Inlet and sieved it through a 1 cm² mesh screen. Each aquarium had an independent supply of sea-water and

was surrounded on four sides by black plastic, to isolate it from other aquaria. I randomly assigned twelve clams to each aquarium, placed with their siphonal end 1 cm above the sediment. Every morning at 0830h I drained water from the aquaria and refilled them every evening at 1630h. Mesh cages were placed directly under the sea water flow to minimize sediment disturbances. I used a within-subjects experimental design, meaning that the group of 12 clams in an aquarium was tested in four (or five; see below) consecutive 2-week treatments, with the restriction that no group was tested more than once in any particular treatment.

There were five treatment types: (1) control, (2) odour of crushed conspecific, (3) presence of a crab predator, (4) odour of crushed conspecific and a crab predator, and (5) tactile stimulus. In the control treatment only fresh sea water flowed over the clams. In the 'crushed conspecific' treatment, a *M. arenaria* was crushed between two rocks and a puree of its soft-tissue was placed (for 2 minutes) in a fine sieve through which sea water flowed during each incoming tide. In the 'crab' treatment, a male red rock crab was placed in a mesh cage (30 X 10 cm) in the aquarium each evening at high tide and removed during low tide the following morning. Incoming water flowed through the crab cage first, and then onto the sediment. For the 'crushed conspecific and crab treatment', I simultaneously subjected clams to crushed conspecific juice and a caged predator (as described for treatments (2) and (3)). The final treatment was a tactile stimulus. I used a 20-cm glass rod to prod the sediment after the incoming and preceding the outgoing tides. This treatment was intended to mimic the mechanical disturbance of the sediment produced by a crab's walking legs.

At the start of each 2-week experimental period the sediment in each aquarium was sifted eliminating differential packing of the substrate, and clams

were placed back at the surface. Responses to experimental treatments were recorded as burial depth (measured from sediment surface to siphonal end of clam) at the end of each 2-week period.

Data Analysis

All analyses were performed using SYSTAT (SYSTAT, 1992) statistical software. I used a two-way ANOVA to test if there were year or site effects on the abundance of crab pits on my study plots. Since there were no significant interaction terms, I pooled the data. The abundance of crab pits at high, medium and low beach elevations was then compared using a one-way ANOVA, with the measured abundance in each of the four nine-day sequences as the variable. I compared the density of clams between sites and beach elevations using a two-way ANOVA.

A log-linear model was used to determine if there were interactions between depth and beach elevation in the survival of clams. I used 2 by 3 contingency table analyses to evaluate whether predation risk varied with burial depth independent of beach elevation; and a 2 by 5 contingency table to evaluate if predation risk varied with beach elevation independent of burial depth.

In the laboratory experiments on clam burial behaviour, the effects of trial period on clam burial response, and the effect of preceding treatment type on burial response, were analyzed using a MANOVA (depth was the dependent variable, sources were individual clams, trial period, preceding treatment type, and treatment type). An ANOVA was also used to compare clam burial depth variability between treatments.

Results

Field crab pit observations

I found no significant interaction terms between study site, beach elevation or sampling year in the abundance of crab pits ($p > 0.1$ for all). Therefore, I pooled the data from both years (1990 and 1992) and both sites (b2 and b3). There were no significant differences in clam densities with respect to beach elevation ($F=18.12$, $df=2,2$, $p=0.094$; Table 3.1). However, sample sizes were small, greatly reducing the power of the test. I found that mean daily crab pit densities (which I took to be crab predation rates) were significantly higher for low elevation plots compared to higher beach elevations ($F=105.28$, $df=2,126$, $p < 0.0001$; Table 3.1). Pairwise comparisons revealed significant differences ($p \leq 0.01$ for all) in crab pit densities between each tidal elevation at both sites. The average crab pit densities per day were 0.087 ± 0.0004 (SE) for low beach elevation plots, 0.057 ± 0.0002 (SE) for medium plots and 0.030 ± 0.0003 (SE) for high plots (Table 3.1). The mean density of pits differed significantly between sites ($F=50.86$, $df=1,126$, $p < 0.001$; 0.18 ± 0.007 (SE) for b3 and 0.11 ± 0.007 (SE) for b2). At each site, clam density was the same at each beach elevation but predation risk was approximately three times greater at lower elevations.

Annual survival estimates using crab pit and clam densities revealed that clams buried at lower beach elevations suffered greater crab predation than those clams buried higher ($F=92.48$, $df=2, 126$, $p < 0.01$; Fig. 3.1).

Table 3.1 Mean number and density of crab pits, and estimated clam density in relation to beach elevation (high, medium and low plots) and year (1990 and 1992) at Bamfield Inlet sites b2 and b3. Crab pit data are averaged daily counts over two separate low tide sequences of nine successive days. The lower plots are exposed to predation (i.e. covered by water) for greater amounts of time. Average water coverage times over a 9 day cycle were 1164 min/day for the low plot, 1098 min/day for the medium plot, and 963 min/day for the high plot.

beach elevation (plot)	year	site	mean no. crab-pits per day (SD)	mean crab pit density (m^{-2}) per day (SD)	clam density (m^{-2}) (SD)
low	1990	b2	19.5 (4.2)	0.078 (0.005)	26.1 (3.9)
		b3	24.0 (3.9)	0.092 (0.005)	19.9 (5.9)
	1992	b2	19.9 (2.9)	0.080 (0.002)	25.0 (4.8)
		b3	20.7 (4.3)	0.096 (0.002)	25.0 (3.2)
medium	1990	b2	16.1 (2.2)	0.061 (0.003)	24.2 (2.9)
		b3	15.2 (3.9)	0.068 (0.001)	21.3 (3.2)
	1992	b2	11.0 (4.8)	0.046 (0.002)	22.0 (6.4)
		b3	12.1 (2.8)	0.054 (0.001)	21.9 (4.8)
high	1990	b2	8.5 (2.8)	0.030 (0.003)	31.3 (8.3)
		b3	10.9 (2.0)	0.046 (0.002)	22.1 (6.9)
	1992	b2	4.6 (3.2)	0.018 (0.001)	24.0 (5.9)
		b3	6.4 (2.6)	0.027(0.002)	20.8 (6.0)

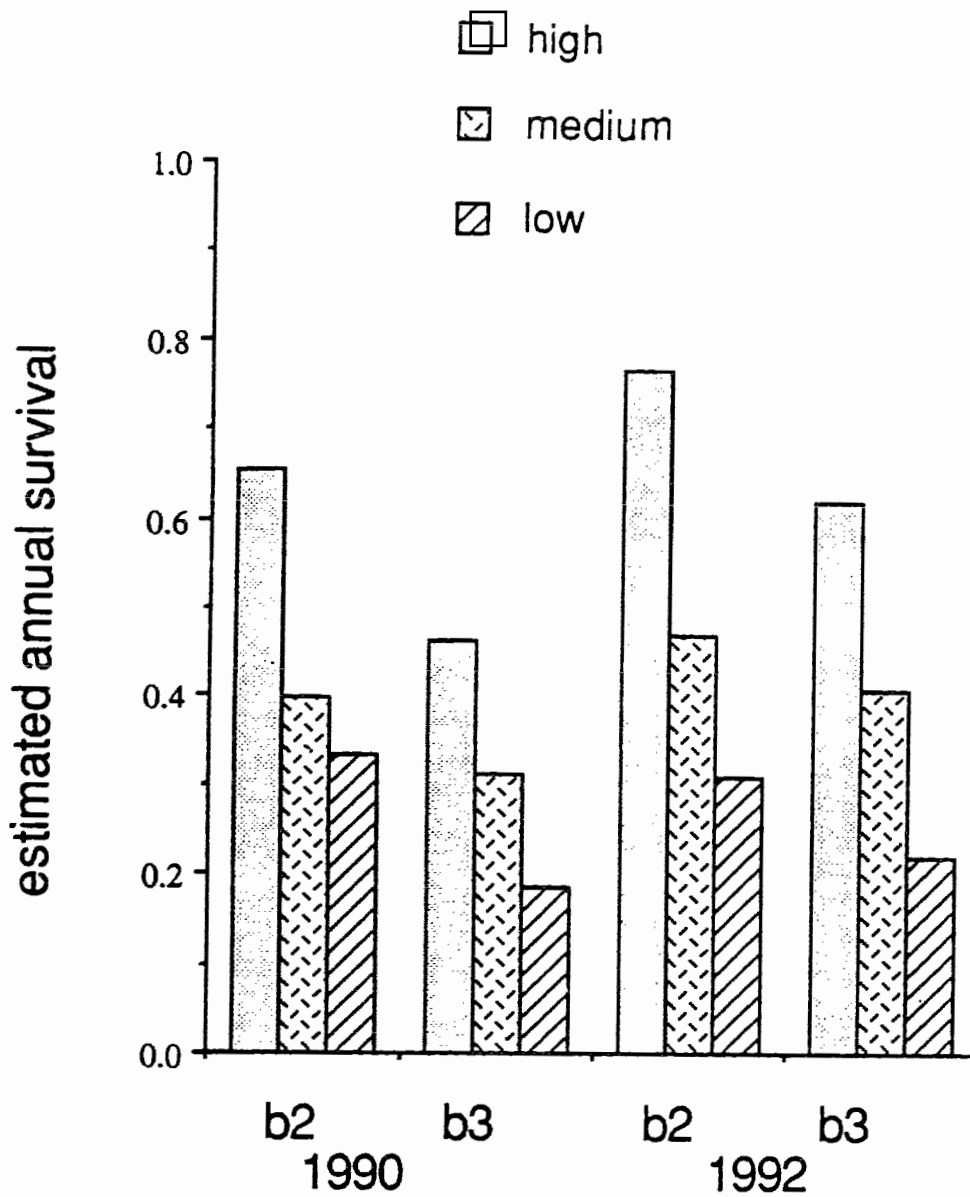


Figure 3.1 The relationship between a clam's position on the intertidal (low, medium or high) and its estimated annual survival probability, at sites b2 and b3, during 1990 and 1992.

Field reburial experiment

I recovered 49 marked clams that I judged to have been eaten by crabs, 17% of the total (38 of 225) at the Grappler site and 10.5% of the total (11 of 105) at the Bamfield site. There were significantly more clams consumed (77.6%) between May and September 1992-3, than between October 1992 and April 1993 (22.4%; chi-square = 66.67, df=1; $p < 0.001$).

A log-linear model revealed no interaction between depth and beach elevation ($p = 0.58$) for either of the beaches. Therefore, the number of clams eaten at each depth was analyzed independently of beach elevation. Burial depth had a significant effect on predation rate for both beaches (chi-square=31.25, df=2, $p < 0.001$). Red rock crabs ate significantly more clams buried at 5 cm than buried at 15 cm (chi-square=13.8, df=1, $p < 0.001$), or buried at 25 cm (chi-square=24.9, df=1, $p < 0.001$). However there was no significant difference between the number of clams eaten when comparing clams buried at 15 and 25 cm (chi-square=2.4, df=1, $p = 0.12$; Table 3.2 and Figure 3.2).

The number of clams eaten at each elevation was analyzed independently of burial depth. Beach elevation was divided into five categories, high (1.0 m), medium-high (0.8 m), medium (0.6), medium-low (0.4) and low (0.2). No significant difference in numbers of clams consumed was found when comparing high, medium-high and medium beach elevations (chi-square=0.14, df=2, $p = 0.93$), and so these three positions on the intertidal were collapsed into a new group called "High." There was also no significant difference between the two groups called medium-low and low (chi-square=1.01, df=1, $p = 0.32$), and so these positions were collapsed into a new group called "Low." As this was a post-hoc test, I used Bonferoni's approach to obtain a conservative acceptance level of $p = 0.005$. As predicted, clams at low beach elevations

Table 3.2 Numbers of *M. arenaria* eaten by *C. productus* at different beach elevations and burial depths in Grappler (N= 225; Table 3.2A) and Bamfield (N=105; Table 3.2B) Inlets. Numbers in parentheses represent percentage of total clams eaten. High, medium high, medium, medium low and low are 0.2, 0.4, 0.6, 0.8 and 1.0 m above sea level respectively.

Table 3.2A		Beach Elevation					
clam depth	high	medium	medium	medium	low	total no.	
	high			low		clams eaten	
5 cm	4	3	4	7	8	26 (34.6%)	
15 cm	0	1	1	2	4	8 (10.7%)	
25 cm	0	0	0	2	2	4 (5.3%)	
total no.	4	4	5	11	14	38	
clams eaten	(8.9%)	(8.9%)	(11.1%)	(24.4%)	(31.1%)	(16.9%)	

Table 3.2B							
clam depth							
5 cm	1	1	0	2	3	7 (20.0%)	
15 cm	0	0	1	1	1	3 (8.7%)	
25 cm	0	0	0	0	1	1 (2.9%)	
total no.	1	1	1	3	5	11 (10.5%)	
clams eaten	(4.8%)	(4.8%)	(4.8%)	(14.3%)	(23.9%)		

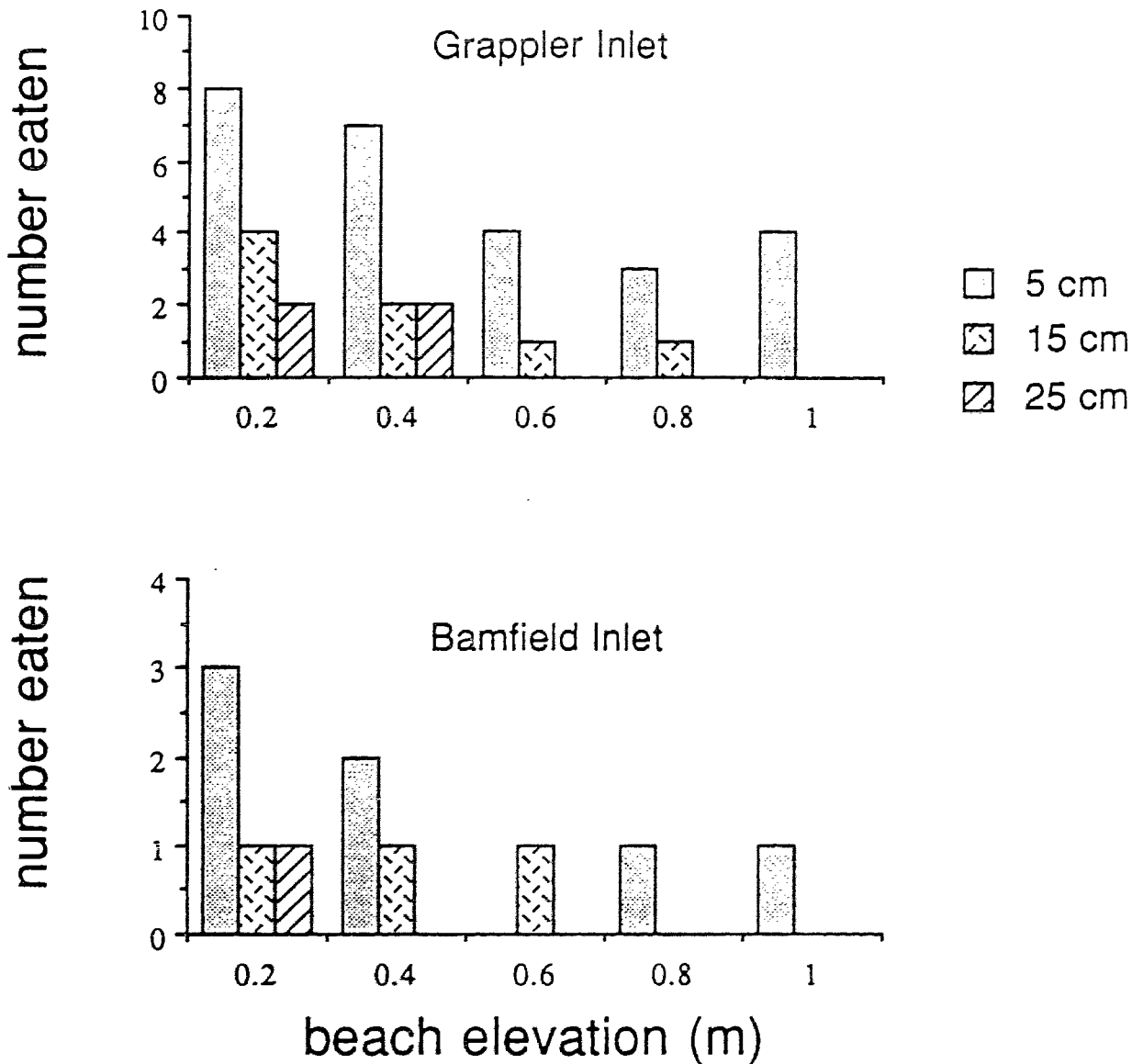


Figure 3.2 Numbers of *M. arenaria* eaten by *C. productus* at different beach elevations and burial depths in Grappler (total number buried = 225) and Bamfield Inlets (N=105). Numbers consumed are divided into burial depth categories of 5, 15 or 25 cm. 0.2, 0.4, 0.6, 0.8 and 1 m refer to elevation above sea level.

experience greater mortality than clams at high elevations (chi-square=17.93, df=1, $p < 0.001$).

All recovered marked shells had chipped valves, or only remnants of the umbo (hinge region) were found. Both are clear indicators of crab predation. However, in two cases only the screen mesh and tag were found, and therefore it is not certain that these two clams were eaten by red rock crabs.

Laboratory measurements of burial behaviour

In each of the five treatments, burial depth did not vary significantly with clam size ($p \leq 0.25$ for all treatment types). A MANOVA revealed a significant treatment effect ($F=27.36$, $df=4,340$, $p < 0.001$) on individual burying rate. Clams buried significantly deeper in the tactile ($3.89 \text{ cm} \pm 0.28$ (SE); $p < 0.001$) and crab treatments ($2.72 \text{ cm} \pm 0.27$ (SE); $p=0.033$) than in the control. However, there was no significant difference between the other treatment types and the control (crush conspecific & crab: $p=0.36$; crush: $p=0.24$; Tables 3.3 and 3.4 and Figure 3.3). There were significant trial period effects ($F=3.65$, $df=3,340$, $p=0.013$) and previous treatment type effects ($F=2.90$, $df=4,340$, $p=0.022$; Tables 3.5 to 3.8).

Discussion

Field crab pit observations

Previously, *C. productus* was not thought to be an abundant predator throughout Bamfield Inlet (Robles et al., 1989). However, my data suggest that red rock crabs have a significant impact on *M. arenaria* populations. Rates of predation, as indicated by crab pit density, were inversely related to position on

Table 3.3 *M. arenaria's* burial depth response (cm) to 5 different treatment types [(1) control, (2) odour of a crushed conspecific, (3) odour of a crushed conspecific and crab, (4) presence of a crab predator (5) a tactile stimulus]. All burial depths are significantly different from zero ($p < 0.001$)

treatment type	mean burial depth (cm)	SE
control	1.80	0.25
crush	2.31	0.29
c&c	1.62	0.29
crab	2.72	0.27
tactile	3.89	0.23

Table 3.4 Results of a Tukey post-hoc comparison of mean burial depth responses of clams that were subjected to different experimental treatments (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$)

	control	crush	c&c	crab	tactile
control		NS	NS	*	***
crush			*	NS	***
c&c				***	***
crab					***
tactile					

Table 3.5 The effect of previous treatment type [(1) control, (2) odour of a crushed conspecific, (3) odour of a crushed conspecific and crab, (4) presence of a crab predator, (5) a tactile stimulus], on the response (measured in burial depth (cm)) of *M. arenaria* to the succeeding treatment type. All burial depths are significantly different from zero ($p < 0.001$)

previous treatment type	mean burial depth (cm) in the next treatment	SE
control	2.85	0.19
crush	3.14	0.30
c&c	1.62	0.29
crab	1.95	0.38
tactile	2.52	0.44

Table 3.6 Results of a Tukey post-hoc comparison of mean burial depth responses of clams subjected to different preceding treatments. (* $p \leq 0.05$; ** $p \leq 0.01$)

	control	crush	c&c	crab	tactile
control		NS	**	*	NS
crush			**	*	NS
c&c				NS	NS
crab					NS
tactile					

Table 3.7 The effect of trial period (weeks 1-2, 3-4, 5-6 or 7-8) on *M. arenaria's* mean burial depth (cm) response. All burial depths are significantly different from zero ($p < 0.001$).

trial period	mean burial depth (cm)	SE
1 (weeks 1-2)	2.14	0.29
2 (weeks 3-4)	2.26	0.14
3 (weeks 5-6)	2.83	0.14
4 (weeks 7-8)	2.43	0.14

Table 3.8 Results of a Tukey post-hoc comparison of mean burial depth responses of clams in each trial period. (* $p \leq 0.05$; ** $p \leq 0.01$).

	1	2	3	4
1 (weeks 1-2)		NS	*	NS
2 (weeks 3-4)			**	NS
3 (weeks 5-6)				*
4 (weeks 7-8)				

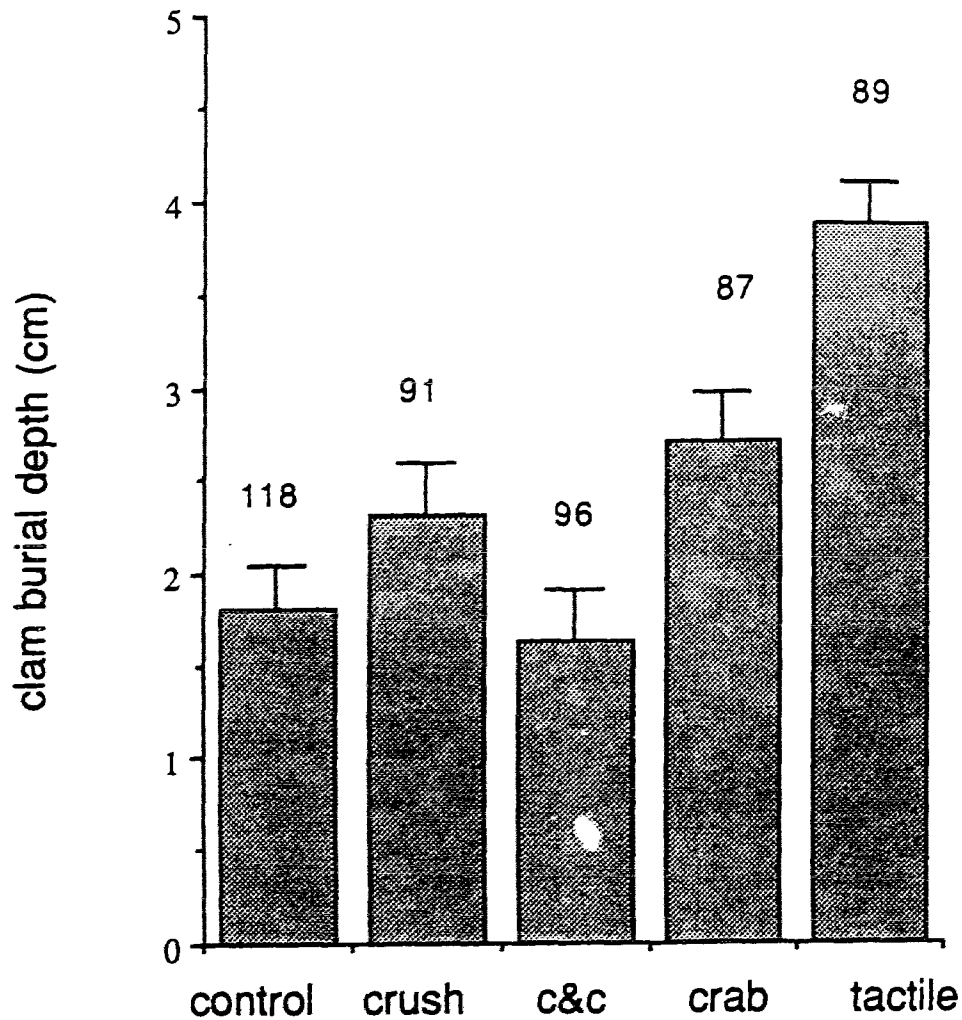


Figure 3.3 *M. arenaria's* average burial depth (cm) response (with standard errors) to five different treatments. The treatments were, (1) control, (2) the odour of a crushed conspecific, (3) the presence of a crab, (4) the odour of a crushed conspecific and the presence of a crab (c&c), and (5) a tactile stimulus intended to mimic the mechanical disturbance of the sediment produced by a crab's walking legs. Sample sizes are listed above each treatment type.

the beach (height above sea level; Table 3.1). The result that predation rates were highest in low elevation study plots is consistent with the idea that the subtidal predators have greater access to infaunal prey lower on the beach. Since clam densities were homogeneous for all positions on the beach, I conclude that the extent of crab predation on clams was primarily a function of the amount of time different parts of the intertidal zone were submerged.

The rate of predation by crabs was estimated using the crab pit and clam density data. Clams found at the lowest beach elevation were subject to the greatest mortality; mean estimated annual survival rates for such clams ranged from 20 to 35%. From these estimates, most clams living in the lowest portion of the intertidal zone should be two to three years of age. Growth and age relationships are not known for *M. arenaria* on the west coast, and this prediction cannot be checked directly against clam size. However, *M. arenaria* on the east coast (Maine, USA) have an average annual growth rate of 0.5 cm per year (Commito, 1982). Using a growth rate of 0.5 cm/year and the mean lengths of clams at low study plots gives an estimate of 2-6 years of age, which is similar to the age class distribution predicted by my mortality estimates. Mortality estimates of *M. arenaria* made here were based on several assumptions. First, I assumed that clam predation is a random event and that each clam has an equal chance of being consumed during any given day; this assumption clearly is not satisfied. As clams grow they are able to bury deeper into the sediment, where they are safer (Blundon & Kennedy, 1982b; this study). Second, I assumed that the probability an individual clam will be consumed was inversely related to clam density. This assumption is consistent with findings by Haddon et al. (1987; prey *Paphies ventricosa* and the crab *Ovalipes catharus*), but not with those of Boulding and Hay (1984), who found a positive direct relationship between density and the probability of the clam *Protothaca*

staminea being consumed by the crab *C. productus*. Third, my mortality estimates assume that each crab pit represents one successful predatory event, or a multiple capture. However, it is also possible that a given pit represents an unsuccessful foraging event. Finally, I assume equal rates throughout the year, which is incorrect as clam predation rate was significantly higher in the summer than in the winter.

I found that crab pit densities at site b2 were significantly greater than at site b3. This difference may be due to the steeper slope of site b2. A steeper gradient would correspond to a shorter horizontal (walking) distance between elevations. Thus, if a crab were to exploit the high-elevation portion of site b3, it would need to invest more time into traveling than if it were to forage at the same elevation at site b2. With increased travel time there may be increased chance of being caught at the higher elevation during a receding tide at site b3, as at a steeper beach the tide recedes at a slower rate than at a less steep beach. At site b3, I observed a crab in its pit stranded during a receding tide.

Field reburial experiment

Clams buried shallower in the sediment suffered greater predation than did those buried deeper in the sediment, corroborating previous findings that deeper positions are safer (Blundon and Kennedy, 1982b; Roberts et al. 1989). The experiment also showed that clams lower on the beach suffered greater predation than did clams higher on the beach (see Table 3.2 and Figure 3.2), when burial depth was equal.

Laboratory measurements of burial behaviour

Clams buried deeper when exposed to crabs (either in the physical or chemical form) than when subjected to crushed conspecifics or the control (Tables 3.3

and 3.4, Figure 3.3). This result indicates that clams can and do respond to perceived predation risk by burying deeper, and supports the hypothesis that the microgeographic pattern observed in Chapter 2 is a result of a behavioural adaptation by clams.

Crabs may often be in the vicinity of their prey in the submerged intertidal zone, hence clams may be routinely exposed to physical and chemical cues of the presence of these crabs. However, the odour of a crushed conspecific may have limited persistence during a brief duration of a predatory event. It is possible that clam odour diffusion may also be constrained by the depth and shape of a crab-pit itself. Therefore clams may not be able to effectively evaluate risk using clam odour as a cue. Since *M. arenaria* bury very slowly (maximum recorded burying depth attained in a two week period was 8.2 cm, and the average was 2.9 cm) and depth of burial is their only refuge, they respond to the most reliable and constant indicator of predation risk; the tactile and sensory cues of *C. productus*.

In addition to significant treatment effects, there was also a significant preceding treatment effect. Because there was a balance of treatment types among replicates these results are not confounding. When clams did not perceive predation risk in the preceding treatment (crush or the control treatment) they buried significantly deeper in the next experimental period. When clams did perceive predation risk in the preceding treatment (tactile or crab) they did not bury as deeply in the next trial period (Tables 3.5 and 3.6).

When clams were subjected to crab odour only, they buried significantly deeper than when in the control group. This result, however, was not seen when clams were subjected to both a crushed conspecific and crab odour (c&c) simultaneously. This puzzling outcome may be a consequence of the preceding

treatment effect, period effect, or perhaps sampling error. Further investigation is needed.

A significant period effect also emerged so that clams in period 3 buried significantly deeper than they did in trial periods 1, 2 and 4 (Tables 3.7 and 3.8). Clams buried successively deeper in each trial period (period 1 < 2 < 4 < 3), except period 4, when they buried significantly shallower than in trial period 3. This pattern may be attributable to starvation throughout the experimental period. It is possible that in each period of the experiment the clams were balancing the foraging/risk trade-off differently. Perhaps during the first three periods the clams were reacting to the perceived predation risk so that they were maximizing their burial depth in order to minimize their risk of predation. However, by trial period 4 they had not fed for two months and perhaps buried less deep so as to forage more efficiently (Chapter 4). Such behavioural changes with respect to satiation levels have been documented in another sensory experiment; alarm responses decreased as starvation levels increased in the marine mud snail, *Nassarius obsoletus* (Stenzler and Atema, 1977).

In summary, clams at lower beach elevations and buried shallower in the sediment, were under greater risk of predation. Moreover, clams typically chose greater burial depths in response to experimentally presented predator stimuli that were presumably more threatening.

Chapter 4

The costs of deep burial in the soft-shelled clam, *Mya arenaria*.

Introduction

Studies of burrowing organisms have found that greater burial depth provides improved safety from predators (Virnstein, 1979; Holland et al. 1980; Blundon and Kennedy, 1982b; Zwarts 1986; Zwarts and Wanink, 1989; Chapter 3). *Mya arenaria* living at lower beach elevations, where risk of predation is highest, tend to occupy deeper burrows (Chapter 2). However, there is great variation in burial depth, which suggests that there may be an energetic or reproductive cost to deeper burial; otherwise, a clam of a given size might be expected to occupy the deepest (safest) burrow possible. This chapter investigates the costs to *M. arenaria* buried at various depths. Foraging costs of increased burial depth for clams are suggested by hydrodynamic theory. As a suspension feeder, *M. arenaria* obtains its food particles by filtering water, and therefore its rate of food intake should be proportional to the rate of flow through the siphon. Poiseuille's equation for flow through a tube can be used to investigate how depth of burial might affect the feeding of a clam. For a clam buried at depth L (=tube (siphon) length) generating a pressure differential Δp (likely proportional to body size) the flow rate Q is:

$$Q = \frac{\Delta p \pi a^4}{8\mu L}$$

where a is the radius of the tube (the siphon) and μ is the viscosity of sea water (Vogel, 1981). Thus, deeper burial should reduce the flow, which reduces the feeding rate, and ultimately the rate of growth.

In this chapter I will attempt to determine if there are differential growth patterns in *M. arenaria*, and if these patterns are associated with burial depth or beach elevation. I hypothesize that clams found buried at shallower depths, and at lower beach elevations, will grow more than those found buried deeper and higher in the intertidal. I also attempt to measure directly the feeding rate as a function of burial depth.

Materials and Methods

Growth comparisons

This study was conducted from May 1992 to June 1993 in Bamfield and Grappler Inlets, Barkley Sound (48° 53'N, 125° 20'W), Vancouver Island, British Columbia. I chose a total of three muddy intertidal sites, one in Grappler and two in Bamfield Inlet. Using a surveyor's theodolite, sampling locations were selected at two heights: low (0.5 m above sea level) and high (1.5 m). I excavated, measured and labeled 300 clams (50 clams x 2 heights x 3 beaches) from one location in Bamfield Inlet. Length was measured (anterioposteriorly) with vernier calipers (to the nearest 0.01 cm) and both valves were labeled with paint (Tech brand). Fifty clams were reburied, at each of the high and low sampling locations. Clams of similar size were randomly assigned to one of three burial depths (5, 15 or 25 cm).

Each clam was buried in a plastic tube (BigO drainage pipe; radius, 12.7 cm; length, 30 cm). To prevent the clams from adjusting their depth of burial vertical movement was restricted by placing four (12 (L) x 1.5 (w) x 0.05 cm (d) cm) wooden sticks above and four below each clam. BigO pipes were used for several reasons. First, this method ensured live burial at a certain depth. *M. arenaria* takes between 6 hours and 1 day to push its siphon through 5 cm of

sediment. Therefore it was important to limit the amount of sediment placed over them (Blundon and Kennedy, 1982b; personal observation). By using these pipes as a protective casing, I could control the reburial process. Second, the tubes facilitated relocating and removing the clams. Finally, the tubes protected the clams from predation.

In September 1992, I removed the clams from the tubes, measured, and then reburied them in the same tube and at the same depth. Clams were left in that state until June 1993, when they were measured again.

Filtration rate experiment

I tested the assumption that deeper-buried clams feed at slower rates by measuring the particle ingestion rate of clams in experimental filtering units made of PVC tubing. A 20-cm long, 3.8-cm radius cylinder was glued into a 5.1-cm (radius) modifier and then glued to a 5.2-cm (radius) x 6.35-cm (depth) cup. I placed three evenly spaced aerators within each cylinder to keep the solution mixed. A clam buried at a depth of 0, 5 or 10 cm in sediment was placed in each of the long cylinders (Figure 4.1). A control cylinder with sediment but no clam was also used. Clams were acclimated in their cylinders for two weeks before experiments were initiated. I ensured that clams were filtering by suspending a vivid red food dye above their siphons before experiments began: If the clam was filtering the dye entered the siphon. A Carmine solution (1.00 g of Carmine in a 1000 ml sea water; Fisher Scientific Co.) was filtered with sea water through a millipore filter into an Erlenmyer flask, and 300ml was placed into each of the four experimental units. The optical density at 520nm was measured with a spectrophotometer (LKB Biochrom Novaspec) in small samples withdrawn from the suspension. I recorded two spectrophotometer readings (% absorbance) at the beginning of the experiment, and at every hour thereafter for 10 hours.

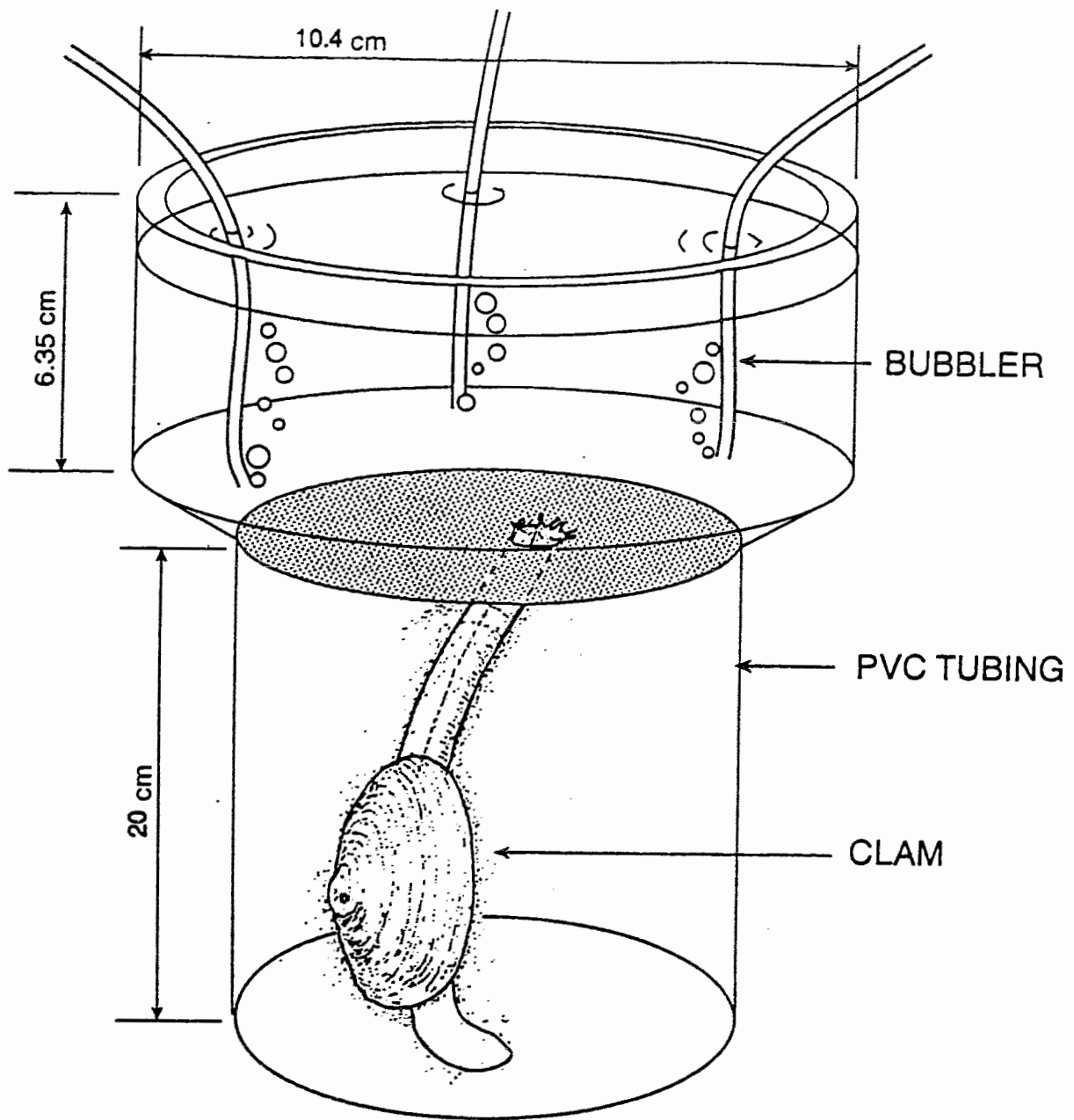


Figure 4.1 A sketch of the filtration rate experimental apparatus. The model depicts a 20 cm long, 3.8 cm radius cylinder glued to a 5.2 cm (radius) x 6.35 cm (depth) cup. Located in the cup are three aerators. *M. arenaria* is shown buried in the sediment within the long cylinder.

The Carmine solution was removed and replaced and the entire procedure was repeated 11 times.

Data analysis

I performed all analyses using SYSTAT (SYSTAT, 1992) statistical software.

I was able to test only three individual clams in the filtration rate experiment, one in each of the three burial depth treatments. Thus, no inferential statistics were used to analyze the data.

Results

Growth comparisons

Clam growth was found to be dependent on burial depth (ANOVA $F=7.28$, $df=2$, 169 , $p=0.003$). A Tukey post-hoc test showed that clams buried at 15 cm grew significantly more ($0.20 \text{ cm} \pm 0.120$ (SD)) than did clams at 5 cm ($-0.05 \text{ cm} \pm 0.13$ (SD); $p<0.001$), but not significantly more than those at 25 cm ($0.023 \text{ cm} \pm 0.20$ (SD); $p=0.11$) in one year. On average, clams at 5 cm experienced no measurable growth (Figures 4.2 and 4.3).

Clams at high beach elevations grew significantly more ($0.298 \text{ cm} \pm 0.109$ (SE)) than did those at lower elevations ($-0.0596 \text{ cm} \pm 0.201$ (SE); T-test; $df=1,163$, $F=5.92$, $p < 0.001$; Figures 4.2 and 4.3). Tukey's multiple comparisons showed that smaller clams grew significantly more than larger clams did (see Table 4.1; Figures 4.4 and 4.5). Although these differences are statistically significant it is important to note that in general growth was very limited compared to growth rates measured by Commito (1982) and Brousseau (1978).

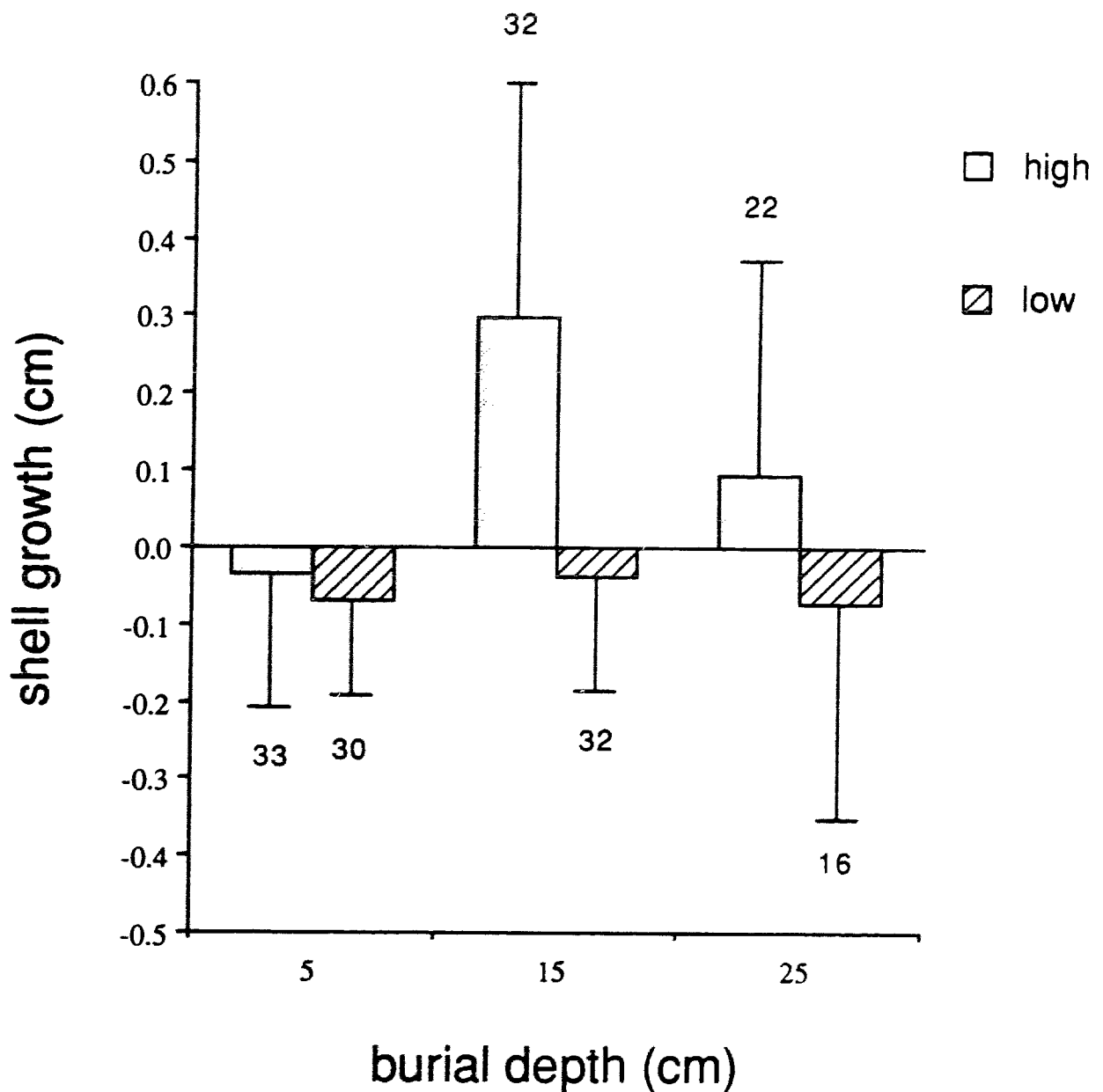


Figure 4.2 Average growth in length of *M. arenaria* in one year (May 1992-June 1993) amongst three beaches (g3, b1 and b2) and all size classes (size range of 5-10 cm), for two different beach elevations (high and low). Error bars represent standard deviations and numbers represent sample sizes.

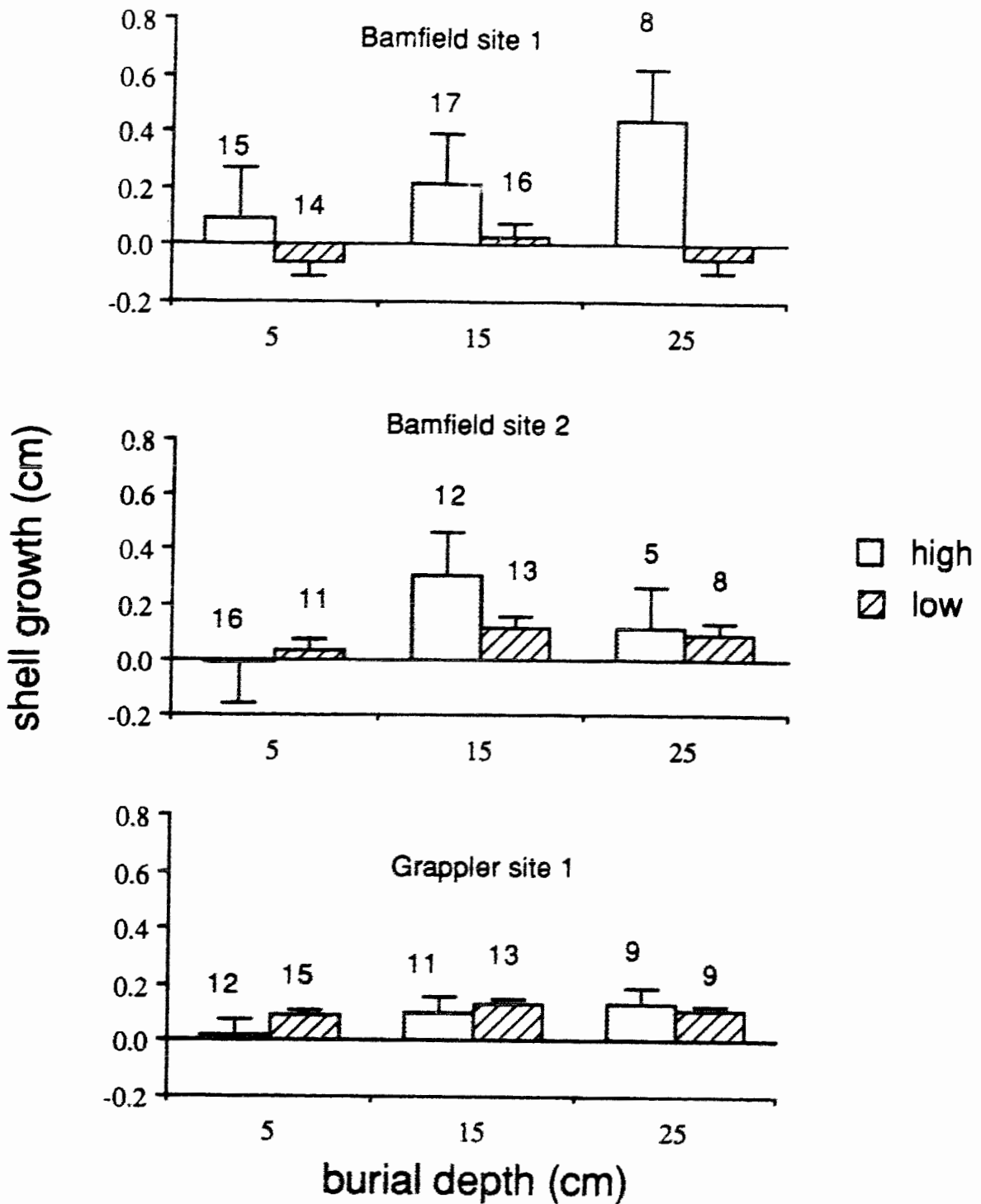


Figure 4.3 Average growth in one year for *M. arenaria* (May 1992- June 1993) comparing three different sites: Bamfield site 1, Bamfield site 2 (b2 and b3) and Grappler site 3 (g3), and two beach elevations (high and low). Error bars represent standard deviations and numbers represent sample sizes.

Filtration rate experiment

As predicted, clams buried deeper filtered at a slower rate than did the clam buried close to the surface (Figure 4.6), showing that depth of burial was inversely proportional to filtration rate. The change in filtration resistance was more apparent when comparing clams buried at 0 and 5 cm than when comparing clams buried at 5 and 10 cm (Figure 4.6).

Discussion

Growth comparisons

Clams buried at higher elevations on the beach grew significantly more than those at lower elevations. In fact, clams buried lower in the intertidal zone, on average, did not grow (Figures 4.2 and 4.3). This finding contradicts observations on natural populations (see Chapter 2) and my prediction that growth should be proportional to water coverage (i.e., those at lower beach elevations should grow quicker). However, overall growth rate was small, and the clams may have been unduly negatively influenced by the BlgO tubes in which they were buried.

A second explanation for the smaller growth rate of clams buried at lower beach elevations is finer sediment size. When burying the clams in their cages I placed finer grained sediment in the lower elevation cages. This is because there is more fine grained sand closer to the sediment surface at low beach elevations and due to the pace of the incoming tide I had to use sediment found at the surface level. Sediment size is known to effect growth rate so that clams buried in finer grained sediment grow at slower rates than those in coarse grained material (Emerson, 1990), a fact that may have influenced the measurements I made here.

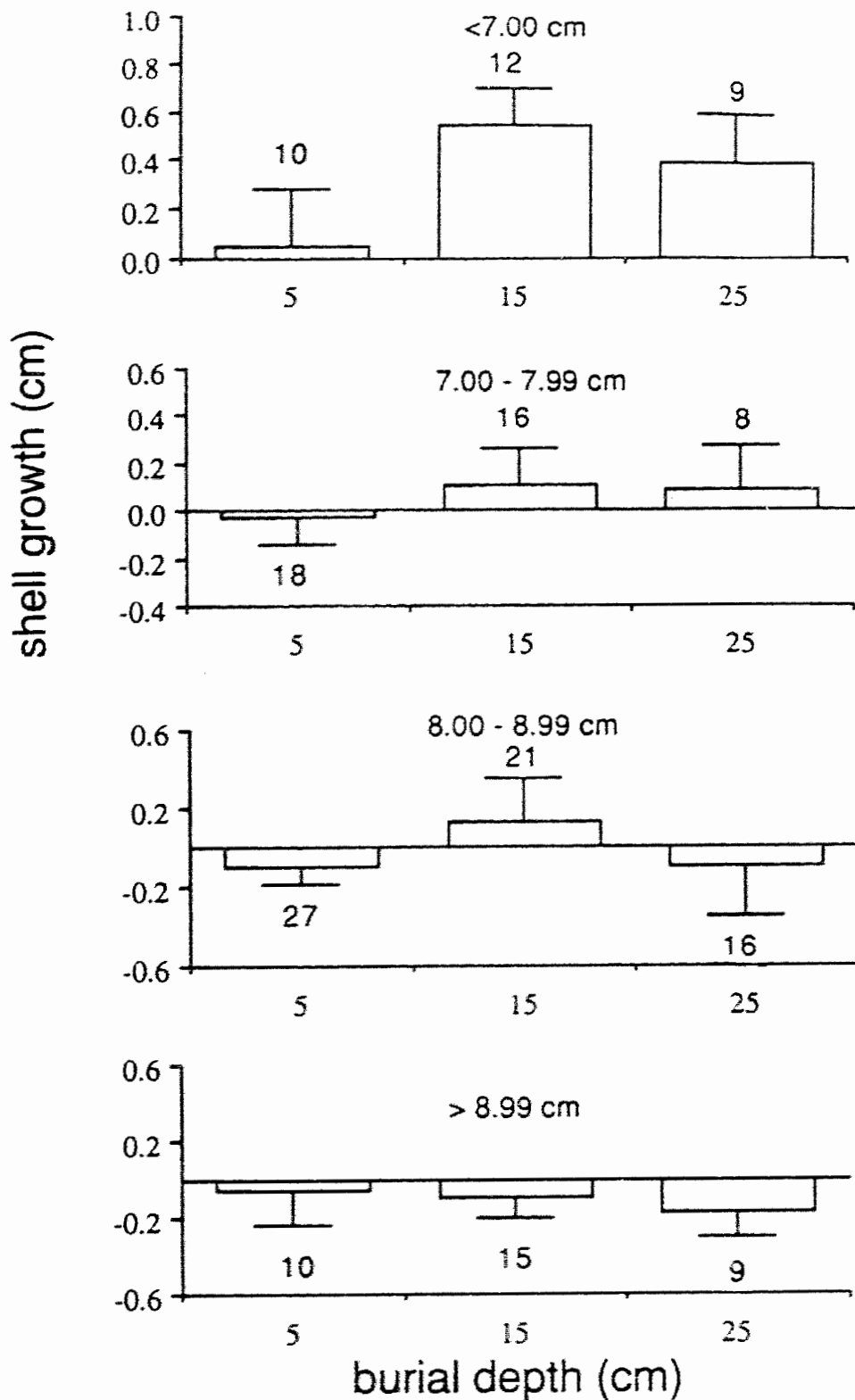


Figure 4.4 Average growth of *M. arenaria* for all three sites in one year (May 1992- June 1993). Graphs compare 4 size classes: < 7.00; 7.00-7.99; 8.00-8.99 and > 8.99 cm. Error bars represent standard deviations and numbers represent sample sizes.

Table 4.1 Tukey multiple comparisons of shell growth patterns shown in Figure 4.4: Matrix of pairwise comparison probabilities of growth rates of clams differing in their initial sizes (cm). (** $p \leq 0.01$; *** $p \leq 0.001$)

		Initial clam size (cm)			
Initial clam size (cm)		< 7.00	7.00-7.99	8.00-8.99	> 8.99
< 7.00			**	***	***
7.00-7.99				**	**
8.00-8.99					NS
> 8.99					

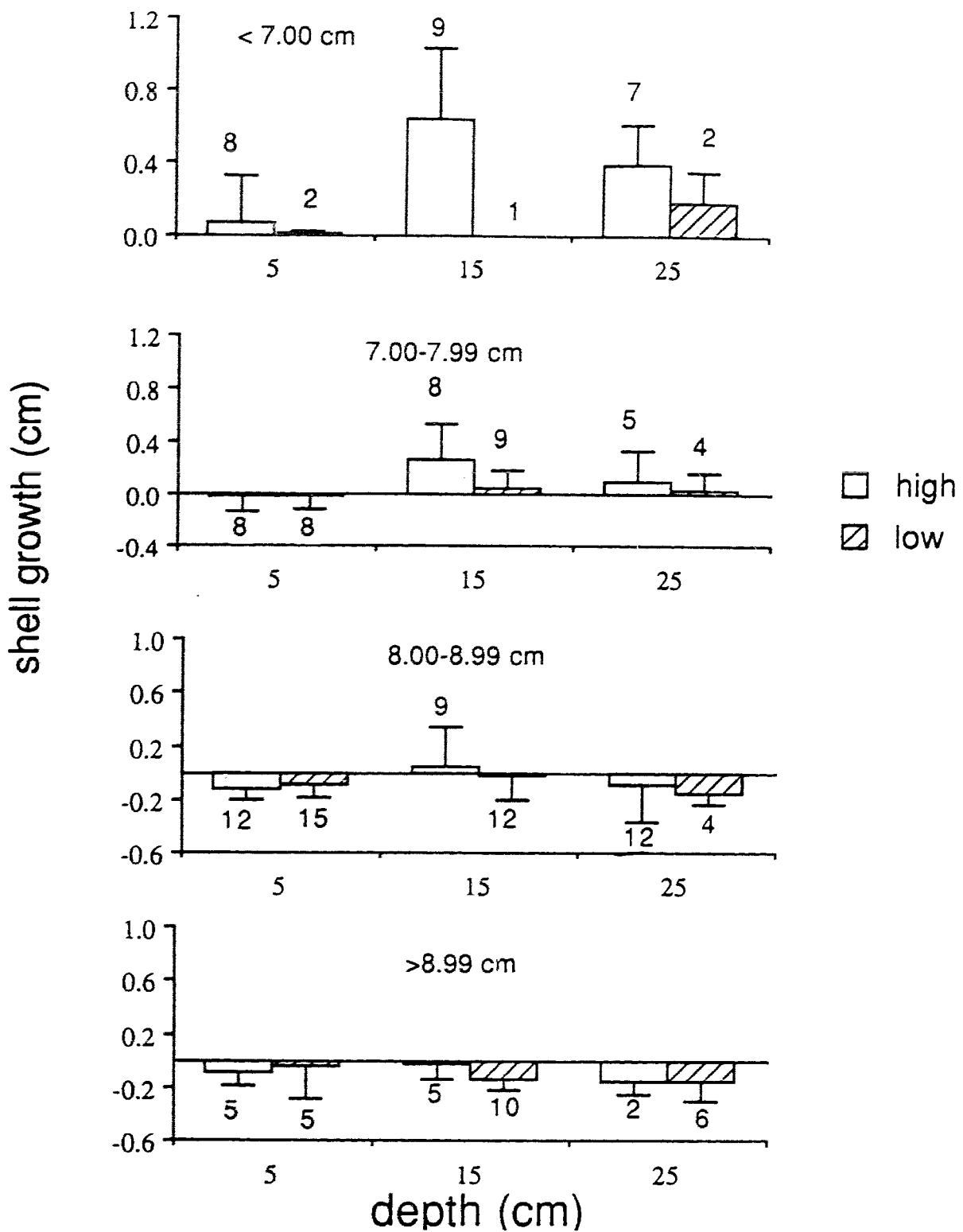


Figure 4.5 Average growth of *M. arenaria* across all three sites in one year (May 1992- June 1993). Graphs compare four different size classes: < 7.00 cm; 7.00-7.99; 8.00-8.99; > 8.99 cm as well as two beach elevations (high and low). Error bars represent standard deviations and numbers represent sample sizes.

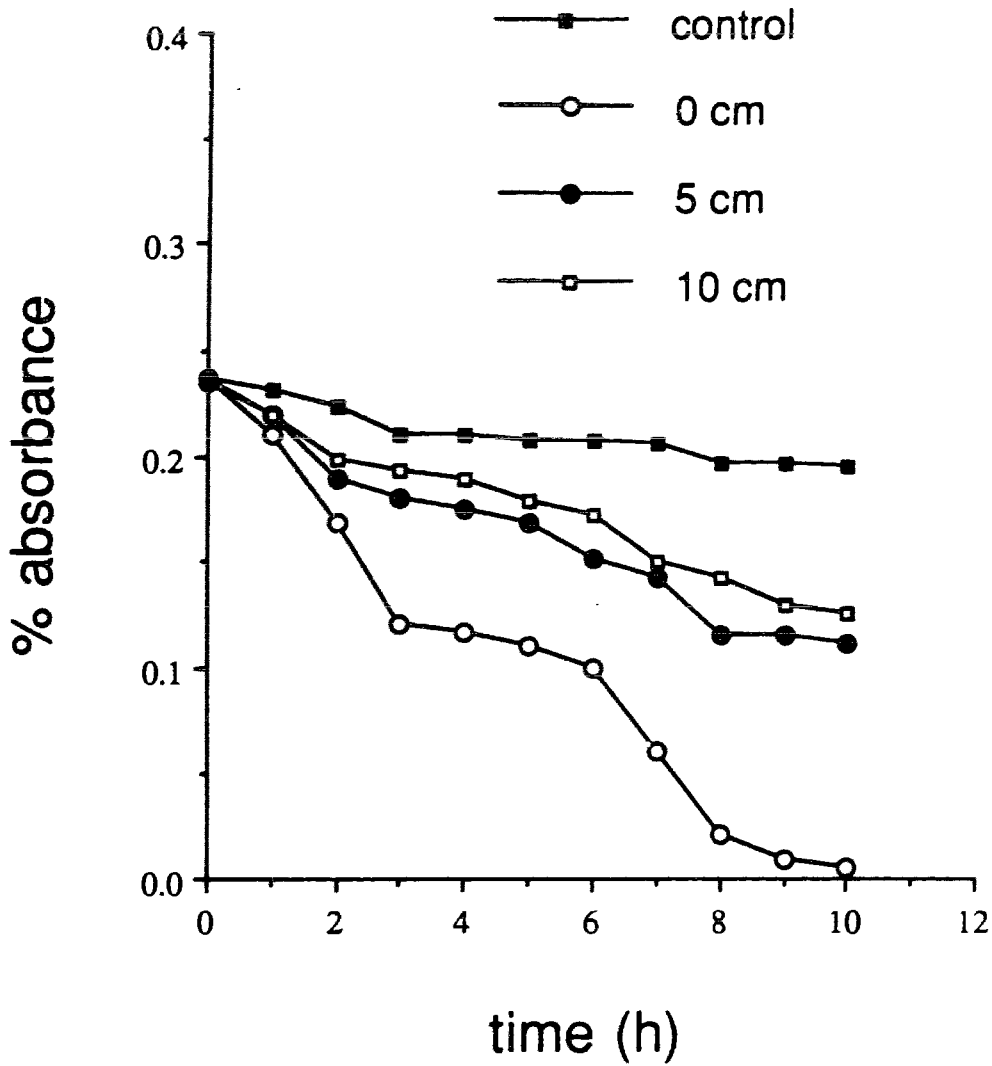


Figure 4.6 Successive absorbancy readings (% absorbance) of carmine suspension above *M. arenaria* buried at three different depths: shallow (0 cm), medium (5 cm) and deep (10 cm). Readings are averaged from 11 different trials on the same clams and show concentration changes over time.

Another finding contrary to my hypothesis was that clams buried at 15 cm grew significantly faster than those buried at 5 cm. Although clams buried at 15 cm grew more than those at 25 cm, this difference was not statistically significant, nor was there a difference between the growth of clams buried at 25 and 5 cm. Clams buried at 5 cm, on average, did not grow (Table 4.1 and Figures 4.2 and 4.3). The unusual pattern of negative growth might also be attributed to stress caused by the BigO tubes (Bayne, 1973). It is possible that these clams were buried too close to the surface. This interpretation is supported by the finding that clams buried at 5 cm consistently (88.2%) broke the restraining wooden sticks below them, indicating attempts at deeper burial. Likewise, clams buried at 25 cm (53%) often broke the popsicle sticks located above them. Clams buried at the 15 cm mark never broke these restraining devices. These observations provide strong evidence for a preferred burial depth.

A third growth pattern observed related to the clam's initial length. Generally, growth rate decreased with size. This suggests that I should have used smaller clams to obtain significant growth rate differences between clams buried at different depths.

Filtration rate experiment

My results indicate, as predicted, that clams buried at the shallow depth (0 cm) filtered at a higher rate than those found buried deeper (5 and 10 cm). Since *M. arenaria* is a suspension feeder and obtains its food particles by filtering water, I assume that the amount of food obtained is proportional to flow rate. Deeper clams seem to be filtering less and therefore should grow at a slower rate. These data are consistent with the hypothetical trade-off between safety and growth. However, further work with a larger sample size is needed before any substantive conclusions can be drawn.

Chapter 5

General Conclusions

This thesis has focused upon the trade-offs between foraging and the risk of predation that the marine bivalve, *Mya arenaria*, should balance to survive and reproduce.

Studies of burrowing organisms have shown that burial depth increases safety from predators (Virnstein, 1979; Holland et al. 1980; Blundon and Kennedy, 1982b; Zwarts 1986; Zwarts and Wanink, 1989; this study). If predation is the only selective force on burial depth, then all clams should be buried deep. However, I observed large variations in burial depth (Chapter 2) at all my study sites. For example 5 cm long clams had a range of burial depth of 3-15 cm (Figure 2.1). Also I observed much burial depth variation with respect to siphon mass, so that a clam possessing a 1.5 g siphon has a burial depth range of 4-18 cm.

M. arenaria in different regions face different predators. In Bamfield Inlet the main predator is the red rock crab, *Cancer productus*. In the Netherlands the main predators are the curlew, *Numenius arquata* (Zwarts and Wanink, 1984) and the oystercatcher, *Haematopus ostralegus* (Zwarts and Wanink, 1989), whereas on the east coast of the United States the main predators are the blue crab, *Callinectes sapidus* (Blundon and Kennedy, 1982a) and the moon snail, *Lunaticus heros* (Commito, 1982). Burial depths of *M. arenaria* differ between these latter two localities, which may be attributed to the predator's foraging abilities. Curlews and oystercatchers can dig further into the sediment layer than the blue crab, hence the *M. arenaria* found in The Netherlands bury deeper than their Chesapeake Bay conspecifics (Zwarts and Wanink, 1989).

Thus, responses to predator species can be important in understanding clam burying behavior.

Many causes of variance in burial depth have been observed. Bivalve burial depth has been reported to vary with siphon mass (e.g. Zwarts and Wanink, 1989), length of the valve (Blundon and Kennedy 1982b, Zwarts and Wanink 1989), season (Reading and McGroarty, 1978; Zwarts and Wanink 1989), body condition (Zwarts, 1986), tidal movements (Roberts et al., 1989), types of local predators (Zwarts and Wanink, 1989), and geographical location (Zwarts and Wanink, 1989). I showed (Chapter 2) that the relation between burial depth and clam size varies with beach elevation, such that individual *M. arenaria* are buried more deeply at lower beach elevations.

I also showed that there were morphological differences with respect to beach elevation and burial depth. In terms of morphological changes, siphon, gonad and shell mass increased with increasing depth. However, clam length decreased with increasing depth. Deep burial is dependent upon the generation of a long siphon, which may entail a fitness cost of reduced reproductive potential (Trevallion, 1971; Lively, 1986; Harvell, 1986; Havel and Dodson, 1987). I hypothesized that *M. arenaria* in high predation risk areas may have long siphons (improving safety) but at the expense of reduced gonads (decreasing their reproductive capacity). My results revealed no evidence of such a trade-off (Figure 2.7). Instead, I found that clams at lower beach elevations had significantly more soft-tissue (siphon, gonad and other) than individual clams at higher elevations (Figure 2.8). There could only have been more tissue if there was increased feeding opportunity for clams located at lower beach elevations.

In Chapter 3, I found that risk of predation was a function of both beach elevation and depth of burial; clams found at lower beach elevations and

shallower depths were preyed upon significantly more often than those at higher elevations and deeper depths (Table 3.2). A laboratory experiment showed that clams buried more deeply when they were subjected to their predator (either in the physical or chemical form), than when subjected to crushed conspecifics or the control (Figure 3.2). Therefore, clams appear to evaluate predation risk and react accordingly.

In Chapter 4, I investigated the potential energetic costs to deeply buried *M. arenaria*. As *M. arenaria* is a suspension feeder, the amount of food obtained will be proportional to the flow rate through the siphon. Foraging costs of increased burial depth for clams are suggested by hydrodynamic theory. Specifically, Poiseuille's equation states that the amount of water that can be moved by a given force (generated by the clam) through a tube of a given length (the siphon) varies inversely with the siphon length and proportionately with its radius to the fourth power (Vogel, 1981). Preliminary results showed that deeper buried clams have a lower filtration rate than those buried at shallower depths. Feeding rate is likely proportional to flow rate, hence these results suggest that initial burial (0-5 cm) is energetically costly as body weight should increase at a slower rate. However, the results also suggest that beyond 10 cm there is no extra growth cost with increased burial depth.

Thus, clams may be faced with a trade-off. By burying deep, a clam decreases its risk of predation but may also decrease its rate of food intake. My finding that clams at lower beach elevations are buried significantly deeper than those at higher beach elevations is consistent with this hypothesized trade-off. Clams at higher beach elevations, and those buried more deeply, were at a lower risk of predation. My field results, however, did not support the idea, that these clams grew more slowly as a result.

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