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THE ECOLOGY AND BIOMECHANICS OF CRAB PREDATION ON INFAUNAL BIVALVES

by

© ELIZABETH GRACE BOULDING

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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Supervisor

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Date April 25, 1983

Abstract

Data from field and laboratory experiments suggest that the vulnerability of infaunal bivalves to crab predators is strongly influenced by shell morphology. Shell features found to influence vulnerability included: shell thickness, presence/absence of a gape, degree of inflation, and overall size. In addition, the probability of mortality to crabs for any species was strongly influenced by its population density and its handling time relative to other available prey.

The relationship between the critical size of a bivalve (maximum size of vulnerability over a fixed handling time) and crab size was determined for four different morphotypes of bivalves. This enabled assessment of the effectiveness of different shell features at reducing vulnerability to crabs. For the three types of clams where a "size refuge" was present, critical size increased with crab size. However, when offered a choice, crabs preferred clams well below the critical size and ate the clams predicted by the critical size experiment to be more vulnerable before those predicted to be less vulnerable.

To determine how these shell features decreased vulnerability, the mechanics of shell crushing by cancrid crabs was investigated. Both chelae strength and the width of chelae gape increased with crab size and were related to the maximum size of clam that could be handled efficiently. Examination of the force pulses generated by the chela of an attacking crab, revealed that thick-shelled clams resisted a greater total <u>number</u> of force pulses than did thin-shelled clams of the same body weight and thus required more time to open. This may be related to the ability of thick-shelled clams to withstand a greater load than thin-shelled clams, when loaded to failure in a tensometer. These results suggest that the mechanism responsible for this increased resistance to crabs is prolongation of the shell-breaking time. Thus even though a large, thick-shelled, tightly-closing clam could eventually be opened, it is likely to be rejected in favour of a prey with a higher profitability to the crab.

Field experiments involving the manipulation of prey density showed that the mortality rate of clams due to crab predators increased with clam density. The possible reasons for a density-dependent mortality rate include: the attraction of crabs from areas where prey density is low to where it is high because of the stronger stimulus provided to the crabs's distance chemoreceptors, the return of crabs to patches where their success rate was previously high, and/or the lack of infaunal space in areas with high clam densities, resulting in clams being forced towards the sediment surface. While both small and large crabs in the laboratory and small crabs in field enclosures preferred small clams when offered a choice, large crabs in the field readily attacked large, thick-shelled clams when the availability of alternative prey was low.

Crabs showed a marked preference for prey with a short shell-breaking time but had the ability to break into very large, well defended shells if given sufficient time. This undoubtedly contributes to crab survival during periods when the abundance of their preferred prey is low.

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This thesis would not have come about without help from many people, although I assume responsibility for any errors that may have arisen. I would like to thank my supervisor, Dr. A. R. Palmer, for encouraging me to work on shell morphology, for challenging me to think critically, and for setting high standards with his own work that inspired me to aim high. I would like to acknowledge my supervisory committee, Drs. A. R. Palmer, J. R. Spence, & A. N. Spencer, whose conscientious supervision has considerably improved this thesis. T. K. Hay deserves special mention for his encouragement, his patience, his critical evaluation of my ideas, and his technical assistance. Comments by D. A. Boag, P. Bowne, R. B. Emlet, T. K. Hay, K. P. Irons, M. LaBarbera, R. B. Lowell, R. A. Mertz, D. K. Padilla, and L. J. Richards substantially improved Chapter One; while Chapter Two was critically read by M. Antolin, D. A. Boag, P. Bowne, T. K. Hay, R. B. Lowell, and R. Ostfeld. G. J. Vermeij encouraged me to compare the vulnerability to crabs of two morphs of *Protothaca staminea*. T. Bedford, P. Bowne, R. B. Emlet, A. Forest, K. P. Irons, M. LaBarbera, C. Majewski, and S. Tveit provided considerable technical assistance and advice. I am grateful to Drs. C. J. Krebs, M. LaBarbera, W. C. Mackay, D. M. Ross, and A. N. Spencer for the loan of equipment. The members of the Department of Zoology at the University of Alberta deserve special mention for providing an intellectually stimulating environment, for being supportive, and for providing first class technical support. I would like to thank the director and staff of Bamfield Marine Station and of Friday Harbor Laboratories for use of their facilities. Also the members (both official and honorary) of the 1981 Biomechanics class at Friday Harbor for scientific and moral support. Financial support was provided by a Province of Alberta Graduate Scholarship to E. G. Boulding, and by N.S.E.R.C. operating grant A7245 to A. R. Palmer, and N.S.F. DEB-7823292 to M. LaBarbera.

This thesis is dedicated to two of my high school science teachers: V. Egan (Marine Biology) and P. J. Wilson (Physics), who can claim credit for my decision to become a scientist.

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I. INTRODUCTION

Over geological time the morphology and lifehabits of bivalve taxa have changed in response to changes in their biotic environment. An important change occurred during the Lower Cambrian, when bivalves evolved shells of calcium carbonate, probably as a defense against predators (Stanley 1976). Another major change occurred in the late Mesozoic, when infaunal forms almost completely replaced the immobile, reclining, epifaunal taxa that had previously been abundant in soft sediments (Thayer 1979). Two factors could have been responsible for this second change. 1) The increase in the number of animal taxa that disturbed the sediment through feeding or locomotion (Thayer 1979). 2) The increase in the number of predators capable of breaking mollusc shells (Vermeij 1977a). Physical models of immobile, reclining bivalves placed on the surface of modern intertidal sediments show a decreased tendency to maintain their life position with increased biotic reworking of the sediments and are vulnerable to attack by crabs (LaBarbera 1981). The poor survival of these models suggests that biotic conditions have changed since the period of the Mesozoic when these bivalves were abundant.

Predators are thus implicated as having been an important selective force on the the morphology and lifehabits of bivalves. The predator-prey relationship between shell-breaking, brachyuran crabs and shelled molluscs goes back to at least the Paleocene (Vermeij 1977a). Unlike many organisms, both crabs and bivalves have a fairly extensive fossil record, (Stanley 1977, Warner 1977). In addition the heavily calcified chela is often the best preserved part of the fossil crab (Nations 1975), and can give clues as to the crab's probable diet (Warner 1977). Thus, the geological record for the predator-prey relationship between brachyuran crabs and bivalve may contain sufficient information to elucidate the role of predators as a selective force on the morphology and lifehabits of their prey.

More is known about evolutionary changes in the shell morphology of gastropods over time, in response to predators, than is known for bivalves. The incidence of defensive gastropod shell features such as strong external sculpture, narrow elongate apertures, and apertural dentition, showed a marked increase at the end of the Mesozoic (Vermeij 1977a). Simultaneously shell features known to increase vulnerability to crabs such as open coiling, planispiral coiling, and umbilici decreased (Vermeij 1977a). Although the initial development of more resistant shell morphology may have been triggered by shell-breaking predators other than crabs (Vermeij 1977a), its appearance selected for more elaborate shell-breaking morphology in later molluscivores, including crabs. This in turn selected for even more well developed antipredator shell morphology. The same shell-breaking crabs that prey on shelled gastropods are usually able to prey on bivalves (Vermeij 1977b) and it seems reasonable that their role in bivalve evolution could have also been significant.

The evolution of antipredator shell features in bivalves could be advantageously compared with that in gastropods because of differences between the two groups in the archetypal body plan and the degree of infaunalization. However no one has attempted this, perhaps because of uncertainty over which, if any, bivalve shell features increase resistance to predators. Some of the more conspicuous antipredator shell features of gastropods, such as spines, are rare in bivalves (Stanley 1970, Vermeij 1978).

To understand the influence of crab predation as a selective force on an evolutionary time scale, it is useful to identify factors influencing its importance as a source of mortality on an ecological time scale. While crabs are known bivalve predators in many areas of the world (*e. g.* Glude 1954; Carriker, 1959; Ebling *et al.* 1964; Hill 1979), their high mobility and complex behaviour makes quantitative field data difficult to obtain. Little is known of the factors that determine whether crab predation represents a significant source of mortality for a given clam population and whether any of this mortality is differential with respect to phenotype.

In this thesis I investigate shell features of infaunal bivalves that increase their resistance to crab predators and the mechanisms by which this is achieved. I also discuss the costs and tradeoffs inherent in the possession of crab-resistant shell features. My field experiments and observations test whether relative prey density influences whether crabs are an important source of mortality for a given bivalve population. Finally I discuss how the evolution of crab chelae morphology and of crab-resistant shell features in gastropods may have interacted with the evolution of crab-resistant shell features in infaunal bivalves.

II. LAB STUDIES: CRAB-RESISTANT FEATURES OF INFAUNAL BIVALVE SHELLS

INTRODUCTION

Many gastropods have shell features which substantially increase their resistance to attack by predators such as crabs and fish (Vermeij 1976; Palmer 1979; Bertness and Cunningham 1981). Controversy exists over whether such shell features also occur in bivalves. In his monograph on shell form in bivalves, Stanley (1970) concludes that relatively little of the variation in bivalve shell morphology has evolved specifically in response to predation. In contrast, Kauffman (1969) discusses several variants from the basic bivalve shell form such as the presence of lamellae, flutes, and spines which he considers to be primarily antipredator adaptations.

Certain shell features have been postulated to directly reduce the vulnerability of clams to predators such as crabs. The proportion of clam species which permanently gape decreases in tropical areas compared to temperate areas and in shallow burrowers compared to deep burrowers (Vermeij and Veil 1978) . Vermeij and Veil (1978) argue that this reflects the pattern of predation intensity. Differences in vulnerability to crabs among different sizes of mussel have been attributed to differences in compressive shell strength, which in turn have been partially attributed to differences in shell thickness (Elner 1978). Blundon and Kennedy (1982a) compared the compressive shell strengths of several clams and suggested that thick-shelled, more inflated clams would be less vulnerable to crab predation. Griffiths and Seiderer (1980) found that the vulnerability of mussels to being crushed by rock-lobsters was related to shell shape and shell strength. Although variables such as shell thickness, degree of inflation (Cox *et al.* 1969), and the presence/absence of a gape might be expected to affect the vulnerability of clams to crab predation, these effects have not been documented experimentally.

Crabs are significant predators on infaunal bivalves and in some areas may be the largest cause of mortality for adult intertidal clams (Carriker 1959;

Walne and Dean 1972; MacKenzie 1977; Chapter III). This mortality must occur differentially with respect to different shell types if it is to be an important selective force on the morphology of clam shells.

Stanley (1975) discusses the bivalve shell as an example of morphological compromises in evolution. He argues that shell features that would be beneficial may not evolve because of adverse genetic linkage, mutual exclusion of alternatives, ontogenetic preclusion or because the archetypal body plan places constraints on future evolution. Thus, it is not sufficient to argue that the existence of antipredator shell features in many gastropods, and the high incidence of predation on bivalves, guarantees the existence of such shell features in bivalves.

Two types of experiments have been used to assess whether a certain shell feature confers increased resistance to predators. Both involve determining the "critical size" defined by Vermeij (1976) as the size above which a gastropod is no longer vulnerable to crushing by an individual predator. In the first, the critical size with the shell feature present has been compared with that after the shell feature has been removed (Palmer 1979). When this was not possible the critical size of a species possessing the shell feature in question has been compared with that of another that does not (Vermeij 1976, 1982a; Palmer 1979; Bertness and Cunningham 1981).

More knowledge of the mechanics of shell crushing by crabs may provide insight into how certain shell features decrease vulnerability. Elner (1978) used strain gauges inside an artificial mussel to study the mechanics of crushing by *Carcinus* and Elner and Campbell (1981) recorded from strain gauges attached directly to the crusher chelae of lobsters. However no studies have analyzed the force pulses generated when crabs crush clams and related them to type of shell being crushed.

In this study I investigated the contribution of a particular shell feature to a bivalve's resistance to crab predators and the mechanism by which this increased resistance is achieved. The vulnerability (susceptibility to predation) of four types of infaunal clams, differing in shell thickness and the presence/absence of a gape was ranked using two methods:

1. comparison of their critical sizes (maximum size of vulnerability for a fixed shell-breaking time)
2. their relative survival during feeding experiments

Effects of relative size, degree of inflation, and the angle at which the valves come together at the ventral margin were also investigated. The mechanics of shell-crushing by crabs was investigated using strain gauge techniques pioneered by Elner (1978) and Elner and Campbell (1981). Constraints that factors such as efficiency of burrowing and the cost of shell production may put on evolution of antipredator shell morphology in these clam species are discussed.

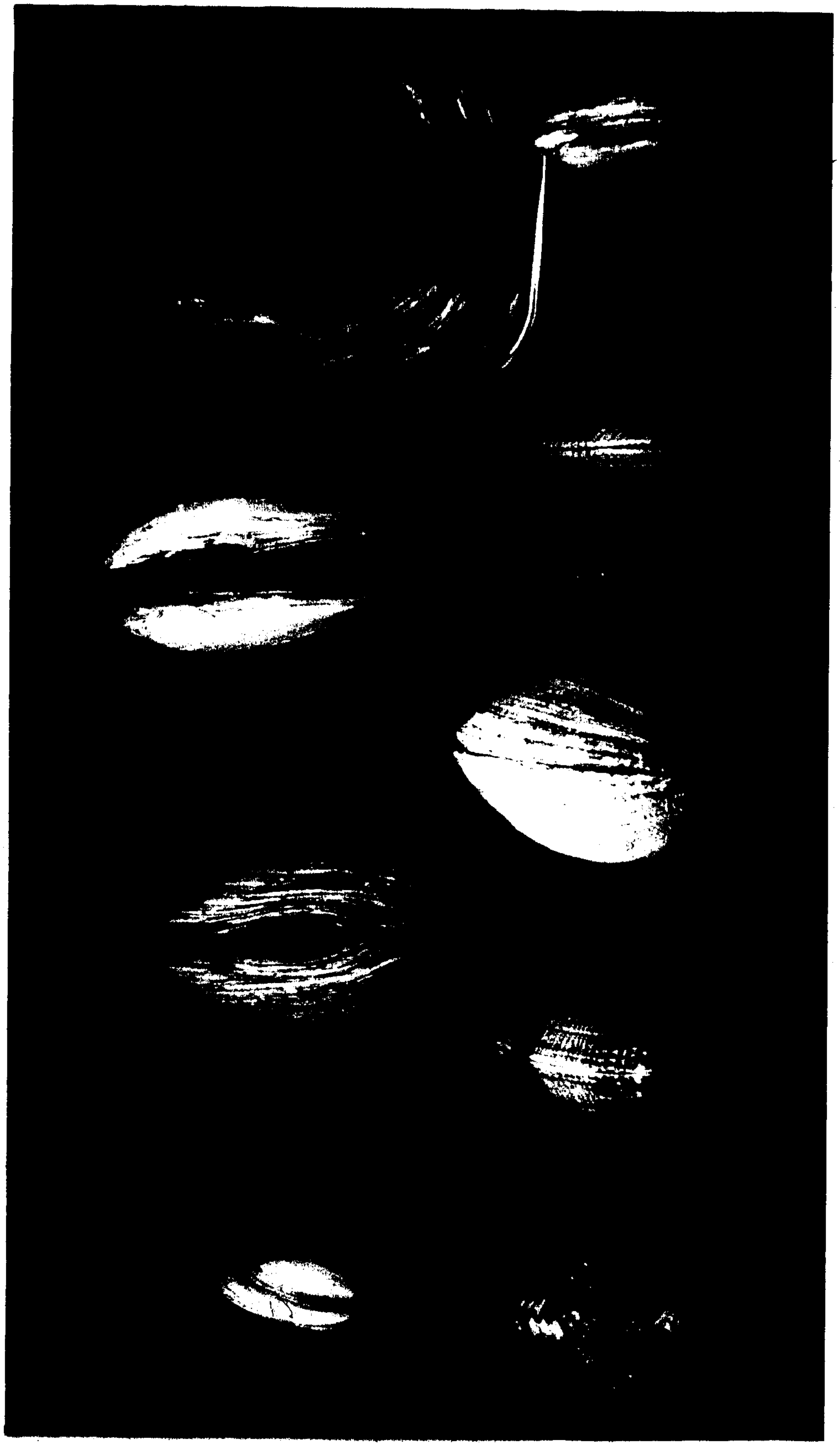
METHODS

Comparative Morphology of the Four Clams

There are conspicuous differences in shell morphology between *Protothaca staminea* (Conrad); (a thick-shelled, tightly-closing clam that I knew to suffer heavy mortality from crab predation) and other intertidal clams which occur with it (Plate 1). The three most obvious differences were size, shell thickness, and the presence or absence of a gape. With the exception of the tellinids (*Macoma inquinata* (Deshayes) and *M. nasuta* Conrad) and juveniles of all species, shallow burrowers tended to have thicker shells and to be able to close tightly.

I chose three types of clams which had shell features contrasting with those of *P. staminea* . These were a thin-shelled clam (a relatively rare morph of *P. staminea*), a thick-shelled clam with a siphonal gape (the venerid *Saxidomus giganteus* Deshayes), and a thin-shelled clam with a siphonal and commissure gape (*Mya arenaria* L.); (Plate 1). The thin-shelled morph of *Protothaca staminea* (*Protothaca*-thin) was similar morphologically to the thick-shelled morph, (*Protothaca*-thick) but could be distinguished by its more highly pigmented valves and by the smaller angle with which the valves came together at the ventral margin.

Plate 1. Eight species of clams found in Grappler Inlet, Bamfield, B.C. in approximate order from the shallowest burrowers to the deepest burrowers. From the left: front row– *Clinocardium nuttallii* (Conrad), *Tapes japonica* (Deshayes), thick–shelled morph of *Protothaca staminea* (Conrad), thin–shelled morph of *Protothaca staminea* (Conrad), *Macoma nasuta* Conrad; back row– *Macoma inquinata* (Deshayes), *Saxidomus giganteus* Deshayes, *Mya arenaria* Linnaeus, *Tresus capax* (Gould). Note the increased incidence of gaping in the deeper burrowers compared to the shallow burrowers.



All clams were collected from intertidal soft sediments in Roquefeuil Bay (48°51'N, 125°6'W) or Grappler Inlet (48°50'N, 125°6'W) near Bamfield Marine Station, British Columbia, Canada. For each clam, shell length (greatest distance from anterior to posterior), and shell width (most convex point of left valve to most convex point of right valve) were measured to the nearest millimetre. Shell thickness was measured to the nearest 0.01 mm at 3 points (1 mm apart), ~~1~~0 mm above the central ventral margin using a micrometer. To enable comparison among shells with differences in shell shape, size was expressed in terms of dry body weight. The regressions used to predict dry body weight from the external linear dimensions of live clams were obtained by collecting a wide size range of 30 individuals of each shell type. The body was removed from the shell and both were dried to constant weight at 100 °C and weighed to 0.01 gm and 0.1 gm respectively on a Mettler balance. Separate regressions were computed for each of the four types of clams (representing three species) on the $\log_{10}$ transformed data (shell length was the independent variable and dry body weight was the dependent variable).

The shell weights obtained for each of these clams were compared, to see if the means were different among the different clam types after adjusting for differences in body weight. This was done with Analysis of Covariance (ANCOVA) with dry body weight as the covariate. The means obtained were compared by orthogonal t-tests so that the relative investment in shell material by each type of clam could be ranked. This and all other statistical analysis was done using the MIDAS statistical package (Fox and Guire 1976).

Methods Used In All Crab Predation Experiments

The crab used in these experiments was the cancrid *Cancer productus* Randall, a voracious predator on molluscs, including *Protothaca*, in shallow rocky areas and adjacent soft sediment areas on the Northwest Pacific Coast (Nations 1979; Chapter III). In addition qualitative observations of the techniques used to open clams were also made for the crabs *Cancer magister* Dana, *Pugettia productus* Randall, and *Hemigrapsus oregonensis* Dana.

The crabs were collected from Grappler Inlet and were held in separate containers without sediment in running seawater. Containers without sediment were used so that the effect of shell morphology on clam vulnerability could be separated from that of depth of burial. The containers had a floor area at least five times the area occupied by the crab; the lighting was subdued. The carapace width, propus height, and propus length (lower margin of manus and fixed finger; Nations 1979) were measured for all *C. productus*, and all molt increments were recorded. The *C. productus* were held in the lab at least a week before being used in any experiments. The crabs were maintained on a diet of *Protothaca*-thick when not being used in experiments.

Assessment of Vulnerability among Morphologies

Using Critical Size

Individual crabs were assigned randomly to one of the four clam types and offered three individuals of that clam type. When a clam had been attacked and eaten, all individuals smaller than it were removed and replaced with larger ones. This was continued until a week had passed (during which the crab continued to attempt to feed) without the crab successfully opening any of the clams. The previous (largest) clam that had been opened successfully was then considered to be the critical size of that type of clam for that given crab. Data for crabs which had molted, died, or stopped feeding before this week was up were not included.

Preliminary work had shown that rather than being fixed, the maximum size of clam that could be opened by a given crab increased with the shell-breaking time but reached an asymptote if sufficiently long times were allowed. Therefore to ensure that this asymptote had been approached, a conservatively long period of one week was chosen as the criterion for deciding that the critical size had been reached. Unfortunately the use of this criterion meant that determination of the critical size (of a given type of clam for a given crab) could take up to 2 months. This meant that the same crab could not be used to determine the critical size for all four types of clams as small crabs often molt within two months (pers. obs.).

The observed critical sizes were compared to see if the means were different among the different clam types after adjusting for any differences in crab size. This was done by ANCOVA (with crab size as the covariate), then the means obtained were compared with an orthogonal t-test so that their relative vulnerability could be ranked.

Using Preference

Individual crabs were offered simultaneously five individuals of each of the four types of clams (Table I). Each type of clam was of the same body weight. This weight was the same as that of a *Protothaca*-thick that was 80% of the predicted critical size for the respective size-class of crabs (Table I). Three replicates were established for each of three size-classes of crabs (Table I). The experiment was monitored every two days to record the order in which the clams were eaten and any shell fragments were removed. Clams that had been eaten were not replaced. The experiment was terminated for each crab when it had eaten 50% of the available clams. For each size-class of crabs, the total number of clams of each type that had been eaten was pooled. This was tested against the null hypothesis that an equal number of each type had been eaten using the G-test for goodness of fit with William's correction (Sokal and Rolhf 1981). Note that in not replacing the clams that are eaten this procedure is conservative and only substantial differences in preference will be detected.

Assessment of Vulnerability among Sizes

Crabs were offered equal numbers of each of four size-classes of *Protothaca*-thick. The size-classes of clams used were selected from those of shell length: 0.5-1.0 cm, 1.5-2.0 cm, 2.5-3.0 cm, 3.5-4.0 cm, 4.5-5.0 cm, and 5.5-6.0 cm. The small (3.5-4.1 cm) and medium (6.9-7.0 cm) size-classes of crabs were offered 3 individuals of each size-class of clams replaced daily, while the large crabs (13.8-14.4 cm) were offered 5 of each replaced

Table I. Experimental design using preference to rank vulnerability to crabs of clams with four types of shell morphology. There were initially 5 individuals of each type of clam. There were 3 crabs per size-class. To facilitate comparison of shells that differed in shape, each type of clam was of the same predicted dry body weight. This weight was that of a *Protothaca staminea* that was 80% (of the shell length) of the predicted critical size for the respective size-class of crabs.

Type of clam	Crab Carapace Width (cm)		
	Small (3.5-4.0 cm)	Medium (6.3-6.9 cm)	Large (7.7-8.3 cm)
Protothaca-thick			
shell length of critical size[1]	3.0	5.5	6.3
shell length of 80% critical size	2.4	4.4	5.1
body wt. of this size	0.13	0.86	1.3
range of shell lengths offered	(2.3-2.5)	(4.3-4.5)	(5.0-5.2)
Protothaca-thin			
shell length of equivalent size	2.3	4.3	5.0
range of shell lengths offered	(2.2-2.4)	(4.2-4.4)	(4.9-5.1)
Saxidomus			
shell length of equivalent size	2.5	4.3	4.9
range of shell lengths offered	(2.4-2.6)	(4.2-4.4)	(4.8-5.0)
Mya			
size range of equivalent size	2.9	5.5	6.4
range of shell lengths offered	(2.8-3.0)	(5.4-5.6)	(6.3-6.5)

1) Predicted from regression for *Protothaca*-thick from critical size experiments (Fig. 3; Appendix 1).

semi-weekly, because of the different rates at which they consumed clams. Although preliminary observations had shown that they were capable of opening them, the smallest two size-classes of clams were not offered to the largest crabs as concealment of the smaller clams by the larger ones might have affected the rate at which the crabs encountered them (see Hughes and Seed 1981). To prevent concealment of the smaller clams and because these size-classes were beyond the small crabs's ability, the small and medium crabs were not offered the largest two size-classes of clams. The number eaten from each size-class of clams was totaled for each size-class of crabs and tested against the null hypothesis that an equal number had been eaten from each size-class using the G-test for goodness of fit with William's correction (Sokal and Rolhf 1981).

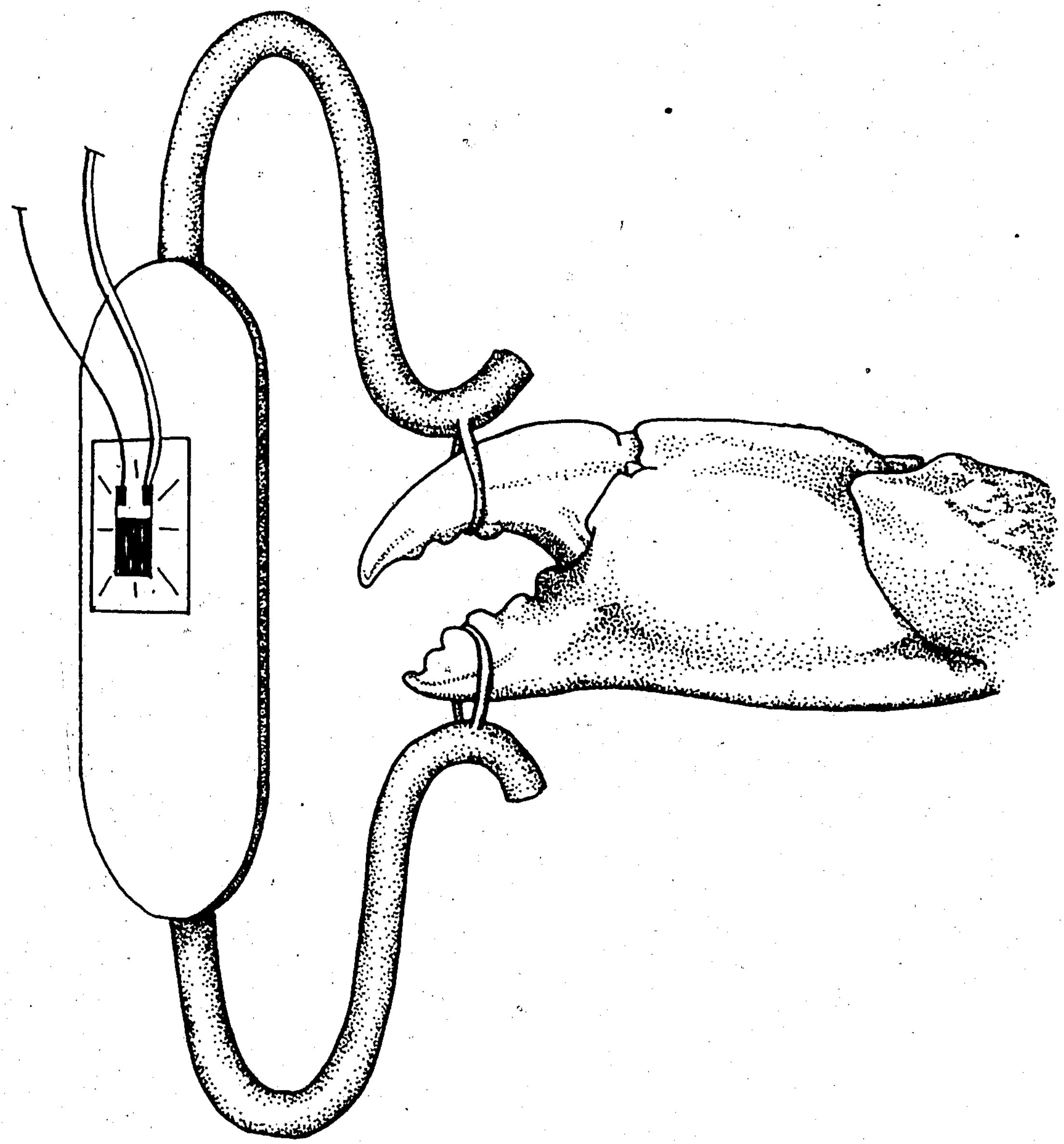
Mechanics of Crab Attack and Shell Failure

Crab Claw Mechanics

The maximum size of clam a crab could fit in its chela was estimated by measuring the maximum width of chela gape. The right chela of recent crab molts was gently opened as widely as possible and the distance, parallel to the chela's dorsal-ventral axis and in the region of the 2nd molars, was measured to the nearest millimetre.

To test whether crab strength increased with crab size (carapace width), a "calibrating device" was made. A piece of heavy wire was bent into a capital *omega* shape and a strain gauge (BEAN BAE-13-250BB-350SE) was glued to a piece of 0.03" steel shimstock and hot-melt glued to the straight edge of the wire (Fig. 1). The calibrating device was calibrated in Newtons by suspending known weights from it; a linear relationship was found between the force exerted on the calibrating device and the output of the wheatstone bridge containing the device's strain gauge. The calibrating device was then placed in the desired spot on the crab chela so that the fingers of the dactylus and the propus were in the upper and lower wire loops respectively (at the level of the third molars) and the crab was provoked into contracting its chela (Fig. 1).

Figure 1. The calibrating device used to measure the compare maximum forces that different crab chelae could exert. This device was also used to calibrate the strain gauges that were directly attached to crab chelae.



Repeated trials were made for each of 5 individuals of two different size-classes and the maximum force measured was taken to be near the maximum possible for that position on the chela. This method was used, instead of the more common procedure of measuring the force required to pull open the chela (Brown *et al.* 1979), because it resulted in more vigorous cooperation from the crabs.

Magnitude and Duration of Forces Generated

Strain gauges (BEAN BAE-13-062BB-350SE) were glued directly to the right propus of each of several crabs (Plate 2). These were calibrated in newtons by provoking the crab to squeeze the calibrating device while simultaneously recording off both strain gauges . The crabs were then allowed to feed on clams of different sizes and types and the output of the strain gauge on the chela was continuously monitored.

Observations verified that a properly soldered and waterproofed strain gauge glued onto a crab chela was relatively insensitive so that at 100X amplification a smooth baseline was attained except when the crab was exerting a force of at least 5 N with its chela. This rarely occurred unless the crab was attempting to crush a clam.

Shell Thickness and Load at Failure

Live, healthy, *Protothaca*-thick and *Protothaca*-thin were loaded using a Monsanto tensometer (Type W) to forces causing shell failure. To keep the area of shell contacted as constant as possible and of the same magnitude as that contacted by the molars of a chela of a large *C. productus*, its compression attachment was fitted with brass columns. These columns were machined until their tips had three "molars" each with an area of 4 mm^2. The clams were always loaded in the same orientation - the ventral margin was oriented down and the brass columns touched the most convex portion of the right and left valves (Fig. 2). An estimate of contact area was made by inserting carbon paper between the shell and the brass column. The clams

Plate 2. The position at which the strain gauges were attached to crab chelae.

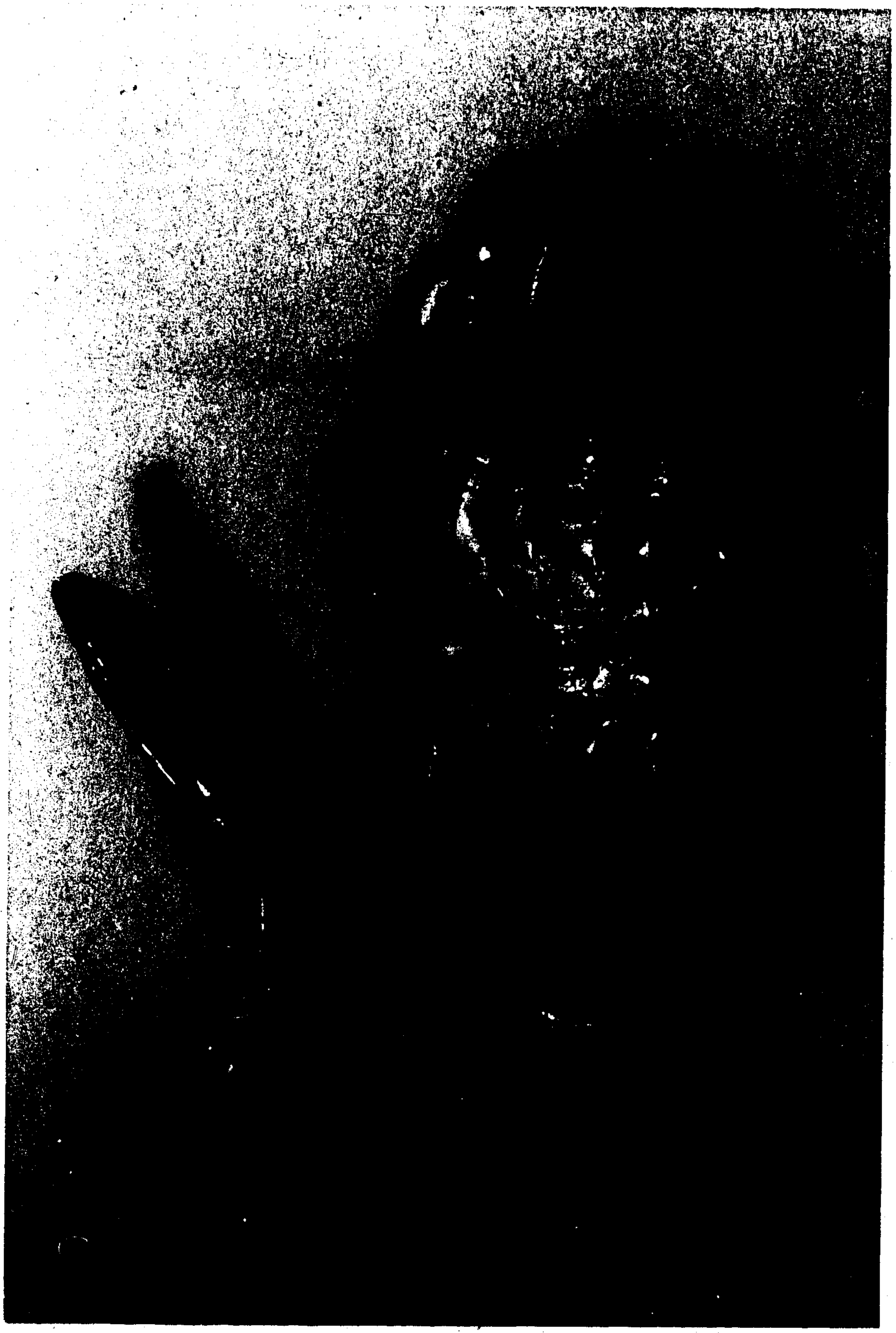
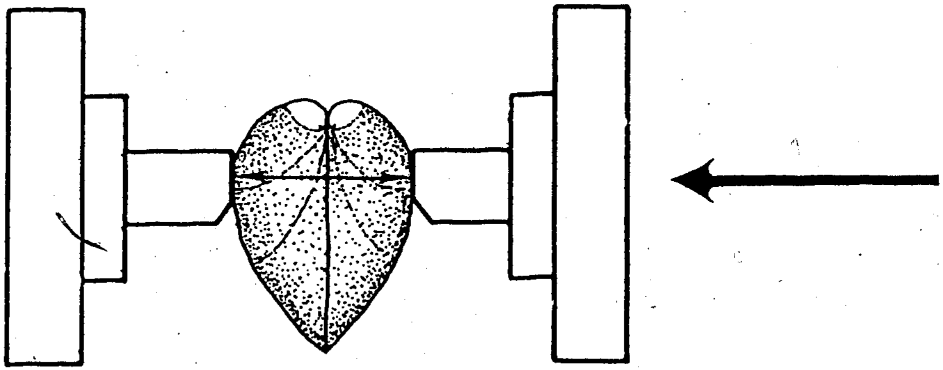


Figure 2. The orientation of the clams loaded in the tensometer (mechanical testing machine). The maximum load applied before the shell failed was considered the load at failure.



used were of the same size-class (shell length 3.3-4.1 cm).

RESULTS

Comparative Morphology of the Four Clams

Shell length was a good predictor of dry body weight, at least within a given clam population, and an r^2 of over 0.90 (N=30) was obtained for each regression (Table II).

The shell weight for *Protothaca*-thick was significantly greater than that for a *Protothaca*-thin or *Saxidomus* of the same body size and both of these were greater than that for a *Mya* of the same body size (Table II).

Shell-Breaking Behaviour of Crabs

All four species of crabs observed used two major techniques to open clams depending on the size of the clam relative to the crab. Clams small enough to fit entirely within a chela were usually crushed outright and in certain cases required only a single contraction of the chela muscles. The chela was applied at the most convex portion of the right and left valves. A load applied other than at this balance point resulted in the clam being expelled from between the two points of loading, unless it was somehow braced.

A much more time consuming technique was necessary to open larger clams. These were attacked at the ventral margin. Crabs repeatedly loaded an area of the ventral margin with one chela (often their right) while bracing the shell against their body (or even against the aquarium wall) with the other chela. This was especially important when clams such as *Protothaca* were attacked since the angle of the ventral margin is steep enough so that the crabs's chelae tended to slip off it. The clam was often reoriented between a series of force pulses but this usually involved changing the method of bracing, the angle of attack, or the chela being used, not the area that was being attacked. This repeated loading of the same general area ultimately resulted in pieces of

Table II. Comparison of the morphology of four clams and the relationships between their shell lengths and dry body weights. N=30 for each regression.

Clam species	Relative amount of shell (for clams of same body weight)[1]	Gape	Regression equation used[2,3] to predict body weight(B) from shell length(L)
1. *Protothaca staminea* (thick morph)	7.07	no	$B = 9.46 \times 10^{-3} L^{304}$ $(r^2 = 0.988)$
2. *Protothaca staminea* (thin morph)	5.00	no	$B = 11.3 \times 10^{-3} L^{297}$ $(r^2 = 0.926)$
3. *Saxidomus giganteus*	4.49	siphonal gape as adult	$B = 6.73 \times 10^{-3} L^{333}$ $(r^2 = 0.990)$
4. *Mya arenaria*	3.64	siphonal and slight com -missure gape	$B = 5.51 \times 10^{-3} L^{297}$ $(r^2 = 0.961)$

1) Adjusted means from ANCOVA on shell weight (gms) with dry body weight (gm) as covariate $p < 0.001$ (See text for details). (Orthogonal t-tests on adjusted means: (1) > (2,3) > (4) , $p < 0.001$).
2) From regressions with shell length (cm) as the independent variable and dry body weight (gm) as the dependent variable (with log base10 transformation on both variables, equations presented after being back-tranformed). r^2 = correlation coefficent. These regressions were used to predict dry body weight from shell length.
3) By expressing size in terms of body weight, shells of different shapes could be compared.

the shell flaking off, until the crab was able to insert one or both of its propusses between the valves of the clam and pry up. This usually resulted in an explosive crack which broke a large section out of one valve. The crab then gleaned the flesh from the shell by scooping it out with a chela or, for small clams, by breaking the shell into small pieces which were then held up to the mouth by the maxillipeds.

Rarely, clams capable of closing tightly were opened and eaten without any visible damage to the shell but these were not considered. Clams kept too long in aquaria without any sediment sometimes lose their ability to close tightly (as the adductor muscles alone seem insufficient to resist the hinge ligament; pers. obs.). In these experiments care was taken to remove clams before this occurred. Nevertheless, clams held in aquaria seem more vulnerable than usual to this type of attack (which is probably rare under field conditions).

Preliminary experiments involving the determination of critical size showed that a single unsuccessful attack did not necessarily mean the crab was physically incapable of breaking the shell. Crabs attacking difficult to open prey sometimes would attack a clam for a time (which could result in damage to the shell) then ignore the clam for periods of up to a few days. If not provided with more easily opened prey, hungry crabs would persist in their attack (with bouts that could last for hours) and were often eventually successful. The frequency and length of these pauses between attack bouts increased as the critical size was approached (pers. obs.).

Assessment of Vulnerability among Morphologies

Using Critical Size

For *Protothaca*-thick, *Protothaca*-thin, and *Saxidomus*, critical size increased with crab size (Fig. 3, Appendix 1). The mean critical size for *Protothaca*-thick was significantly smaller than that for *Protothaca*-thin which was itself significantly smaller than that for *Saxidomus* (Table III). Recall that as critical size decreases, the vulnerability of that type of clam to crab predation is considered to decrease (see Vermeij 1976). Thus *Saxidomus* was more

Figure 3. The relationship between critical size and crab size for the three types of clams which showed a "size refuge". Critical size is given in units of body weight with a cube root transformation. The body weights were predicted from measurements of shell length using the regressions in Table II. The regression lines shown are from the ANCOVA and represent the best fit lines of a common slope through the points for each type of clam. The circled points represent the mean critical size for each type of clam after adjusting for differences in crab size. See text for methods, Table III for analysis, and Appendix 1 for raw data.

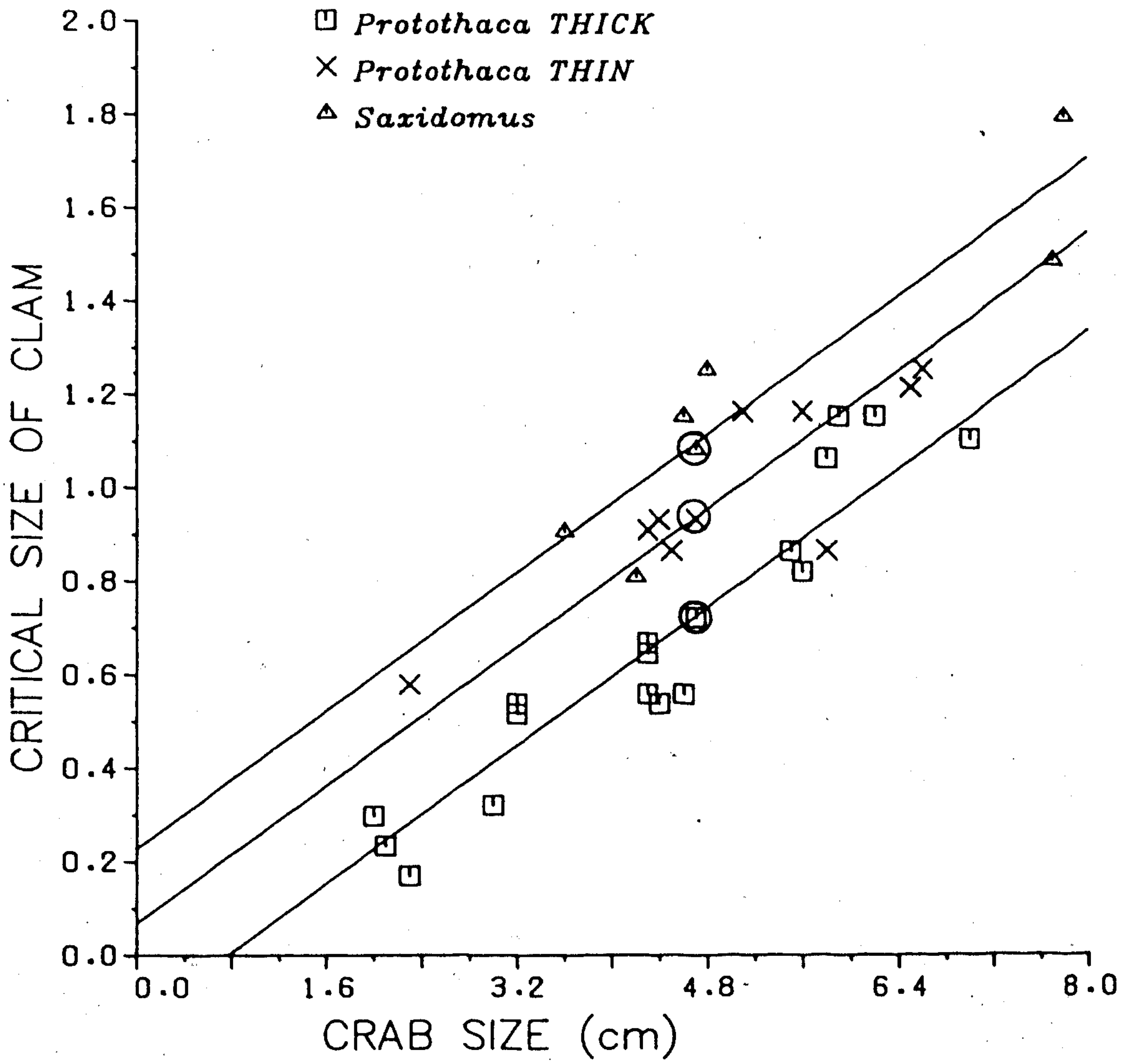

□ Protothaca THICK
× Protothaca THIN
△ Saxidomus
CRITICAL SIZE OF CLAM
CRAB SIZE (cm)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.0
1.6
3.2
4.8
6.4
8.0

Table III. ANCOVA statistics on critical size[1] for three types of clams with crab carapace width as the covariate. (From data shown in Figure 3 and Appendix 1).

Analysis of variance	d.f.	SS	MS	F	p
equality of slope	2	0.03219	0.01610	1.174	> 0.590
residual error[2]	27	0.03700	0.01370		
equality of adjusted means[3]	2	0.6305	0.3152	22.73	< 0.001
residual error[4]	29	0.4022	0.01387		

1) ANOVA was performed on the dry body weights transformed with a cube root transformation. The body weights were predicted from the shell lengths, using the regressions in Table II., In fact these three venerid clams are similar enough in shell shape so that the results of the ANCOVA are the same if shell length is used.
2) From the individual regressions for each type of clam
3) Orthogonal t-tests on adjusted means: *Protothaca*-thick < *Protothaca*-thin < *Saxidomus* ($p < 0.02$).
4) Unaccounted for by calculated common slope

vulnerable than *Protothaca*-thin which was in turn more vulnerable than *Protothaca*-thick.

I observed marked effects of a permanent gape on vulnerability to predation. *Mya* was the most vulnerable of these four types of clams and no critical size could be obtained. Even the smallest crab (carapace width=2.8 cm) that could be used in this experiment was able to open the largest *Mya* (shell length=6.3 cm, cube root of predicted dry body weight=1.09; compare with Fig. 3) available, by digging out the tissue through the siphonal gape. Crabs too large to insert a chela through the siphonal gape were easily able to crush the thin shell of this clam. The thicker-shelled *Saxidomus* was frequently attacked around the siphonal gape (Plate 3).

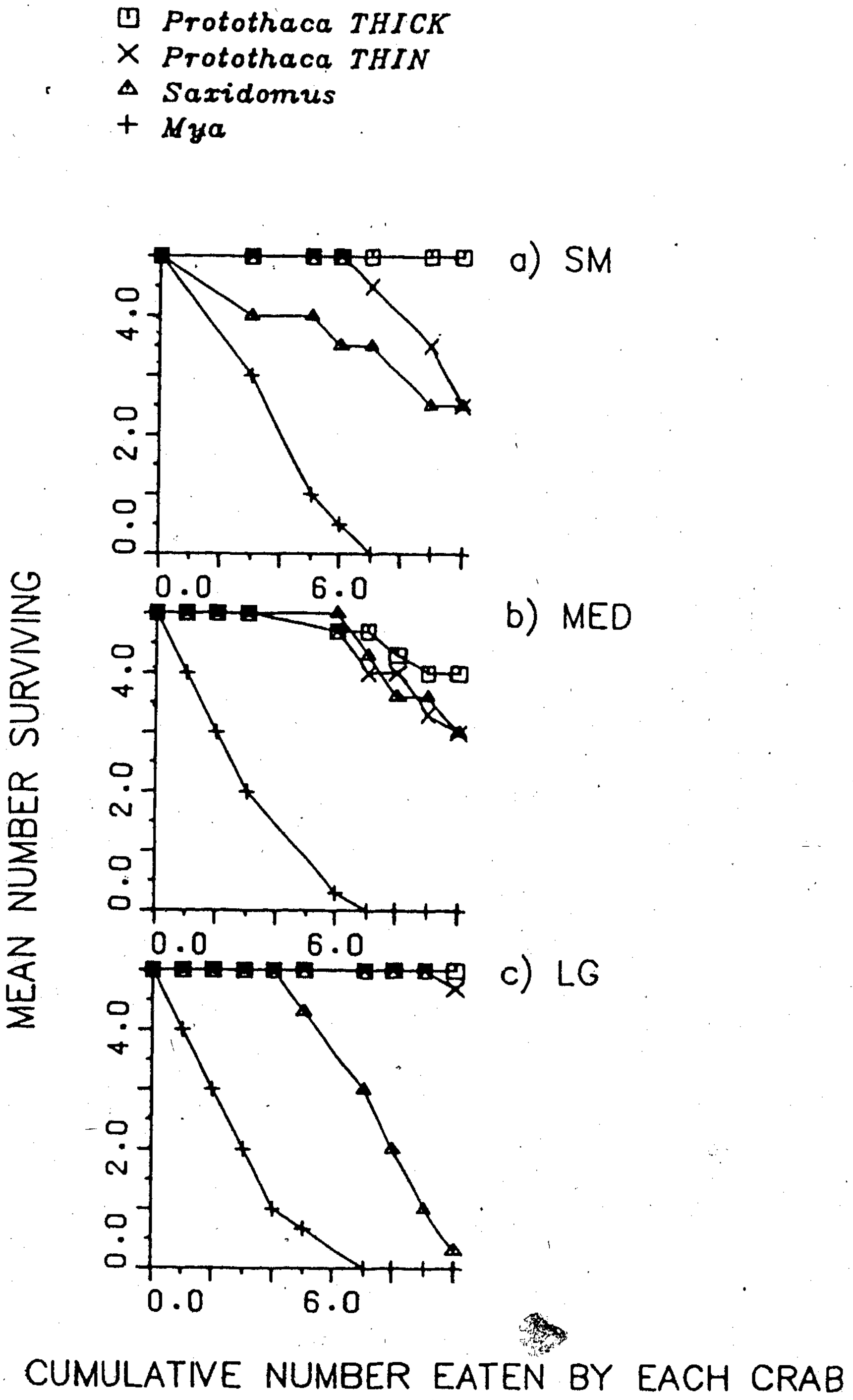
The shells of several other clam species that occurred with these four types provided little of a barrier to crabs (Plate 1). No critical size could be obtained for the small, flattened, thin-shelled tellinids: *Macoma nasuta*, or *Macoma inquinata* and crabs easily attacked *Tresus capax* through the permanent gape of its shell.

Using Preference

Even at subcritical sizes the ranking of vulnerability of these four types of clams followed that predicted from the critical size experiments. In general, the clams predicted to be more vulnerable were eaten before those predicted to be less vulnerable (Fig. 4), although the patterns are slightly different for the different size-classes of crabs. For all three size-classes of crabs *Mya* had the lowest relative survival and none were alive at the termination of the experiment (Fig. 4). *Saxidomus* and *Protothaca*-thin showed next lowest relative survival, and *Protothaca*-thick had the highest relative survival. The null hypothesis of no preference was rejected for each of the three size-classes of crabs (small: G = 16.18, $p < 0.005$; medium: G = 9.94, $p < 0.025$; large: G = 33.3, $p < 0.005$; for the smallest, medium, and largest size-class of crabs respectively). The largest crabs only showed a slight preference for *Protothaca*-thick over *Protothaca*-thin (Fig. 4c). This may be related to the

Plate 3. Left: a *Saxidomus giganteus* that has been attacked by a *Cancer productus*; note the chips around the siphonal gape. Right: a *S. giganteus* before being attacked.

Figure 4. The order in which the clam types were eaten by three different size-classes of crabs that were offered all four clam types simultaneously. The mean number of clams surviving versus the cumulative number of clams eaten by each crab is graphed separately for each type of clam. Figure 4a shows the results from the three crabs in the small (SM) size-class of crabs, 4b those from the medium (MED) crabs, and 4c those from the large (LG) crabs. (See text and Table I for details).


⊡ Protothaca THICK
× Protothaca THIN
△ Saxidomus
+ Mya
a) SM
b) MED
c) LG
MEAN NUMBER SURVIVING
CUMULATIVE NUMBER EATEN BY EACH CRAB
0.0
2.0
4.0
0.0
6.0

changes in relative shell thickness with clam age; the thin morph becomes proportionately thicker when older so the difference in thickness between the two morphs becomes less. Clams that had not been eaten, frequently had characteristic chips, at the ventral margin which indicated that they had been attacked then rejected. Even at only 80% of the critical size, the crabs were forced to use the slow method of attacking the clams at the ventral margin for all the clams except *Mya*.

Taste did not seem to affect crab preference. If body tissue from any of the four types of clams was removed from the shell and offered to a crab it was readily eaten.

Assessment of Vulnerability among Sizes

Despite their ability to open much bigger clams, all three size-classes of crabs showed a significant preference for clams well below the "critical size" (Table IV, Fig. 3). Crabs avoided breaking the thick shells of the larger clams except when necessary to obtain the body tissue. The shell-fragments from the smaller size-classes of clams were found in many small pieces while those from the larger size-classes were in large pieces (Plate 4).

Mechanics of Crab Attack and Shell Failure

The mechanics of shell crushing by crabs was investigated to elu[illegible]te the mechanism responsible for the lower vulnerability of large and of thick-shelled clams to crabs.

Crab Claw Mechanics

The relationship between crab size and chela gape and between crab size and chela strength was investigated to see if this could account for the increase of critical size with crab size.

Both chela gape and chela strength increased with crab carapace width. The maximum distance that a chela can be opened is linearly correlated with propus height (r^2=0.992, N > 5) and also with carapace width (r^2=0.995, N >

Table IV. Relationship between vulnerability and size for *Protothaca*-thick. This table shows the percentage of the total number of clams eaten, (N), that were chosen from each size-class. Because of differences in consumption rates, the small and medium crabs were offered 3 of each size-class of clams (replaced daily) while the large size-class of clams were offered 5 of each size-class (replaced semi-weekly). Dashes indicate no data for those conditions.

Crab carapace width (cm)	Clam shell length (cm)						N
	0.5-1.0 cm	1.5-2.0 cm	2.5-3.0 cm	3.5-4.0 cm	4.5-5.0 cm	5.5-6.0 cm	
Small							
3.5 cm	83 %	17 %	0 %	0 %	-	-	12
4.0 cm	86 %	14 %	0 %	0 %	-	-	14
4.1 cm	94 %	6 %	0 %	0 %	-	-	16
Medium							
6.9 cm	50 %	40 %	10 %	0 %	-	-	10
7.0 cm	37 %	50 %	1 %	1 %	-	-	16
6.9 cm	79 %	21 %	0 %	0 %	-	-	14
Large							
13.8 cm	-	-	76 %	18 %	0 %	5 %	38
14.4 cm	-	-	43 %	26 %	13 %	17 %	23
13.9 cm	-	-	60 %	30 %	10 %	0 %	20

Results of G-test goodness of fit with William's correction.
Ho: Each size-class of crabs ate equal numbers of each size-class of clams.
Small Crabs- G = 84.19, $p < 0.005$; Medium Crabs- G = 35.11, $p < 0.005$; Large Crabs- G = 62.57, $p < 0.005$.

Plate 4. Shell fragments from the size-preference experiment for the largest size-class of crabs that was used. The four piles of fragments shown were selected randomly from those from each size-class of clams. From left to right: back row- shell lehgth (2.5-3.0 cm), shell length (3.5-4.0 cm); front row- shell length (4.5-5.0 cm), shell length (5.5-6.0 cm). Note that the thicker shells of the larger clams were broken less often than those from the smaller clams.

5). When measured at the third molar a 5.1 cm male crab exerted only 43 N over an estimated contact area of 1.5 mm^2 (or an estimated stress of 29 MN/m^2), while a 13.0 cm male crab exerted a maximum force of 178 N over an estimated contact area of 3 mm^2 (or an estimated stress of 59 MN/m^2).

Magnitude and Duration of Forces Generated

Crabs took more time to open clams predicted to be more resistant than to open those predicted to be less resistant. Comparison of a recording made when a 8.6 cm female crab attacked first a 1.2 cm *Protothaca* (Plate 5A) with one made when the same crab attacked a 2.5 cm *Protothaca-thin*. (Plate 5B) reveals that it took longer to open the larger clam. Each spike represents a force pulse; note that while it took the crab more force pulses to open the larger clam than the smaller clam, there was no difference between the two clams in the average or greatest magnitude of the force pulses that were used. The same trends were seen when the same crab attacked first a *Protothaca*-thick (shell length=2.0 cm) (Plate 6A) and then a more vulnerable *Protothaca*-thin (of the same body weight; Plate 6B). Similar recordings and laboratory observations confirm that it takes more force pulses and more time to open clams predicted from the critical size experiments to be more resistant than it does to open those predicted to be less resistant. Maximum force pulses at the beginning of the attack are indistinguishable in magnitude and duration from those near the end, and perhaps represent the maximum possible for that particular crab. The duration of a single force pulse is rarely more than 10 seconds.

Shell Thickness and Load at Failure

The magnitude of the load at failure was tested for *Protothaca*-thick and *Protothaca*-thin to see if the increased shell thickness of *Protothaca*-thick provided significantly greater resistance to crushing.

Protothaca-thin failed at a significantly lower load than did the *Protothaca*-thick (Mann-Whitney U=14.0; $p < 0.0001$). There was considerable

Plate 5. Recordings from a stain gauge glued directly to the propus of an female *Cancer productus* (carapace width=8.6 cm). The output from the strain gauge was calibrated in newtons using the "calibrating device". In A the crab attacked a 1.2 cm *Protothaca* (intermediate between the two morphs) and in B (continuous record, read from left to right) a 2.5 cm *Protothaca*-thin.

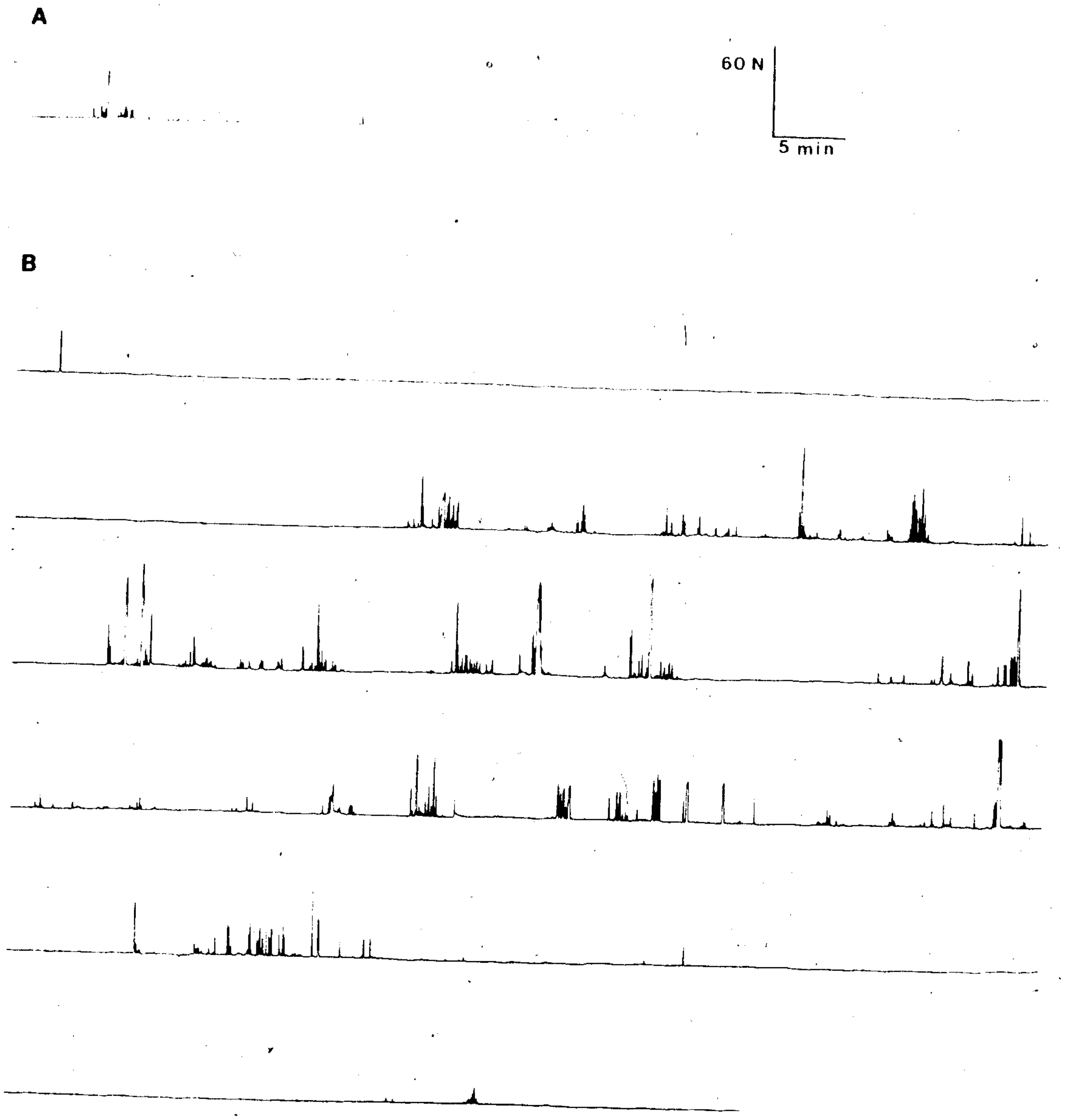
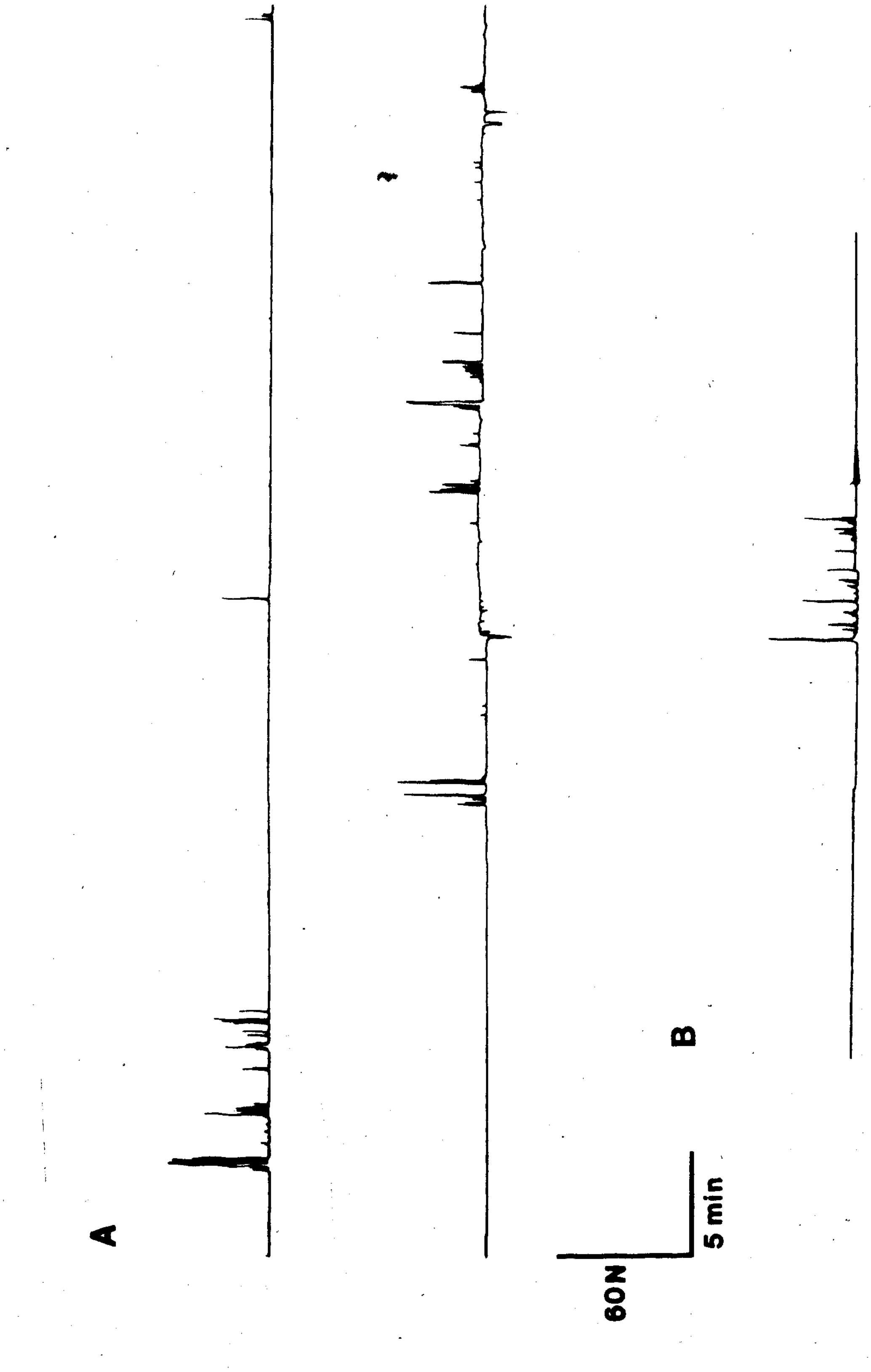

A
60 N
5 min
B

Plate 6. Recordings from the strain gauge of the same crab as in Plate 5. In A (continuous record, read from left to right) the crab was attacking a 2.0 cm *Protothaca*-thick and in B a *Protothaca*-thin of the same dry body weight.


A
B
60N
5 min

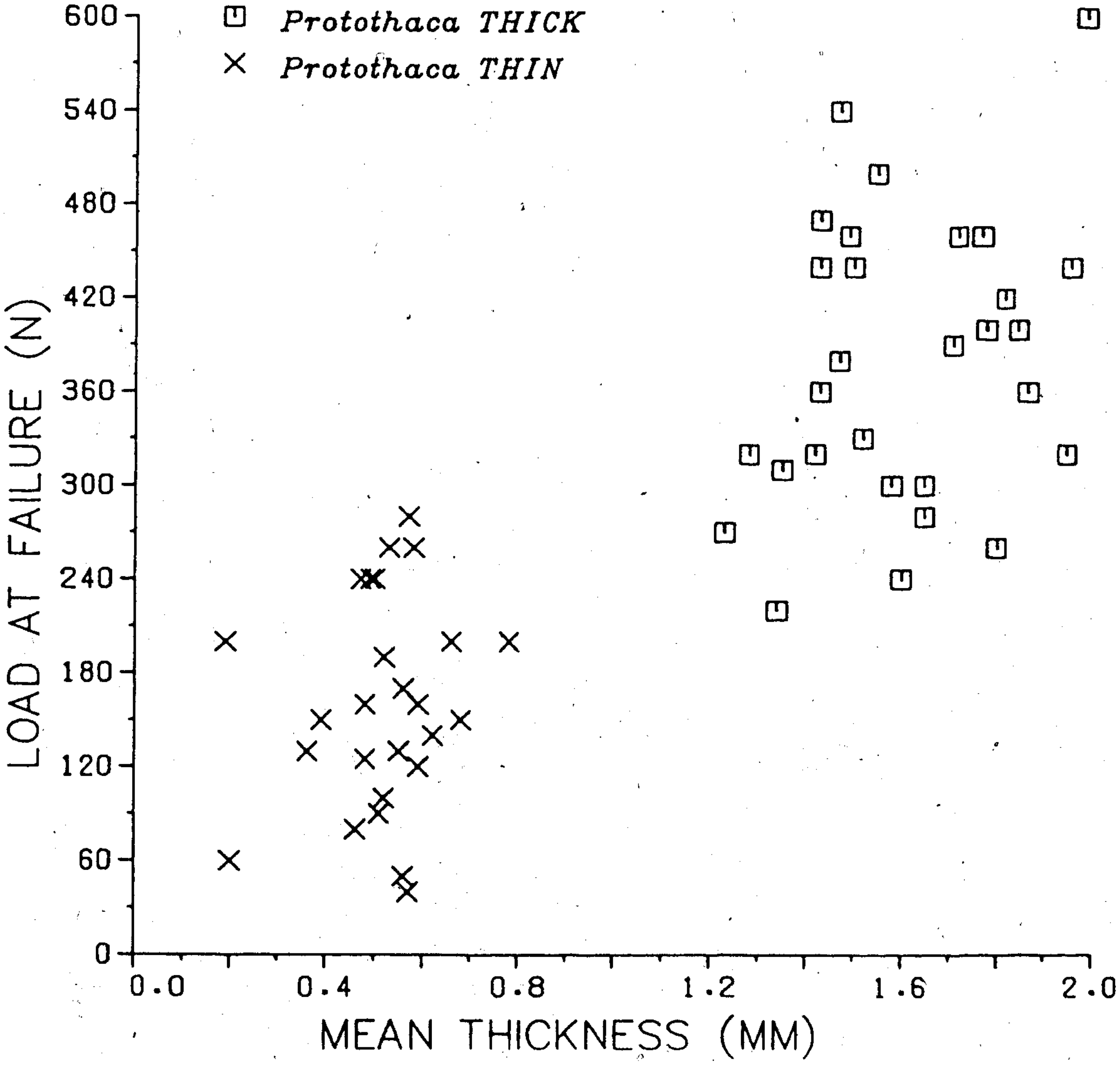
residual variance which did not correlate with any shell parameter or with contact area and which may have been related to the previous history of the shells (Fig. 5). This residual variance was higher for the thicker morph (S^2=0.8659) than the thinner morph (S^2=0.4641) The breakage patterns for shells crushed in the tensometer resembled those of shells crushed by crabs.

DISCUSSION

Shell Morphology: An Equilibrium between Opposing Selection Pressures

In these four temperate clams there were no shell features such as prominent sculpture exclusively adapted for resisting or escaping from crabs or other predators. This is not the case for some temperate gastropods (*e. g.* Palmer 1977). The reasons for this difference may be twofold. First, burrowing places a major constraint on the type of shell features that can be selected for and as a result many antipredator shell features are subtle and may actually represent exaptation (*sensu* Gould and Vrba 1982: a feature initially selected for to perform a function unrelated to its current benefit) rather than adaptation. Many of the antipredator adaptations found in epifaunal gastropod shells are high in relief, consisting of stout spines (Palmer 1979) or other strong external sculpture (Vermeij 1978; Bertness and Cunningham 1981). Shell features like these would probably hinder burrowing in clams by increasing resistance to passage through the sediment. The experiments described above show that bivalve resistance to crab predators is increased by the ability to close tightly, and by increased shell thickness. The data suggest that resistance is also increased by a more inflated shell shape, and by the valves coming together at a steep angle at the ventral margin . The subtlety of many of these antipredator shell features in bivalves may have led Stanley (1970) to conclude that predators were not a major selective force on bivalve shell morphology even though he argues that the intensity of predation on bivalves over geological time has been high (Stanley 1973, 1977).

Figure 5. The load at failure in compression for two morphs of *Protothaca staminea* loaded in a tensometer. Note that the mean load at failure was significantly greater for the thick-shelled morph than for the thin-shelled morph.



⊡ Protothaca THICK
× Protothaca THIN
LOAD AT FAILURE (N)
0
60
120
180
240
300
360
420
480
540
600
MEAN THICKNESS (MM)
0.0
0.4
0.8
1.2
1.6
2.0

In addition, although predators such as crabs are capable of digging out even deeply burrowed clams, they forage more efficiently near the surface. Many crabs, including the cancrids, forage in soft sediments by probing with their legs and chelae or by excavating pits (Warner 1977; pers. obs.). Pearson (*et al.* 1981) and Blundon and Kennedy (1982b) obtained higher mortality to crabs when clams were restricted to a shallow depth of burial than when they were allowed to burrow deeper. This would result in selection pressures from predators being lower on deep infaunal than on shallow infaunal molluscs.

The results from the critical size and preference among morphologies experiments suggest that at least three shell features can have a significant effect on bivalve vulnerability to predation by crabs: shell thickness, presence or absence of a gape, and overall shell size and shape.

Shell Thickness

The data from the critical size and clam type preference experiments show that thick-shelled clams are less vulnerable to crab predators than similar thin-shelled clams. The lower vulnerability of the thick-shelled morph of *Protothaca staminea* relative to the thin-shelled morph may simply result from its ability to withstand a larger compressive load. The thick-shelled morph was able to withstand more force pulses than the thin-shelled morph (Plate 6). The reluctance of crabs to break thick shells was further reflected in the size preference experiments where the larger (and thicker) *Protothaca-thick* were recovered in larger pieces (Plate 4).

Thicker shelled clams would be expected to also be less vulnerable to other predators. For example a thicker shell has been shown to make clams more resistant to drilling by naticids gastropods (Kitchell *et al.* 1981). In contrast Stanley (1970) argues that further shell thickening beyond about that found in *Mytilus edulis* L. serves primarily to stabilize the position of the clam in the sediment. This seems unlikely for the bivalves examined in this study, all of which are found in relatively quiet water. Further, Stanley's (1970) data show a high negative correlation between shell thickness and depth of burrowing, and between shell relief (ornamentation) and depth of burrowing. These inverse correlations provide additional support for the hypothesis that the increased shell thickness of shallow burrowing clams is in response to selection pressures from epibenthic predators.

Selection for a thicker shell in response to predation will be opposed by selective pressures related to the cost of having such a shell. The increase in overall density could be a disadvantage where rapid burrowing is desirable, because of the increase in inertial mass, or in very soft mud if sinking is a problem. Also a thicker shell could have an energetic cost or an evolutionary cost in terms of a reduced maximal rate of growth (Palmer 1981). The difference in shell thickness between the two morphs of *Protothaca* is probably a result of the faster growth rate of the thin-shelled morph. Growth rate has been shown to affect shell weight in *Mya arenaria* and slower growing clams are more inflated, rougher, and heavier than faster growing clams of the same age (Newell and Hidu 1982). Clams such as the tellinids (Plate 1) are relatively shallow burrowers and suffer a high mortality to crabs (pers. obs.) yet have thin shells. These clams might be examples of *r*-selected species which trade off increased vulnerability to predators against the ability to grow faster (by only taking the time to secrete a thin shell; Palmer 1981).

Thicker shells would have a selective advantage if they predictably increased tolerance for compressive loading. To a point this would be expected since increasing shell thickness increases its resistance to bending (Wainwright *et al.* 1976), and indeed there was a significant difference in the average load the thick and thin morphs could withstand (Fig. 5). However within each group the variance was high, especially for the thick-shelled morph. This unexplained variance suggests that other factors are involved and this might be variance in the severity of subcritical microcracks (see: Wainwright *et al.* 1976) in the outer and older layers of the shell where the clam is unable to repair them (LaBarbera pers. comm.). If it takes longer to secrete a thicker shell there may be a higher probability of small cracks forming since the material will have been exposed to more wear. Thus load at failure may only increase with shell thickness to a certain point (Boulding unpub. data).

Presence or Absence of a Gape

In terms of vulnerability to crabs a siphonal, pedal or commissure gape is analogous to the gastropod shell aperture in that it allows easy access to the body and gives the chela purchase on the shell. The results presented here, show that the shells with a gape (*Saxidomus*) were in general more vulnerable to crabs than clams of the same shell weight without a gape (*Protothaca*-thin) and were frequently attacked at or through the gape. In addition to crabs, tightly-closing bivalves are more resistant to other valve-prying predators such as the gastropod *Busycon* (Carriker 1951), starfish, and oystercatchers.

The Effect of Clam Size

The strong preference *Cancer productus* showed in the laboratory for the smallest *Protothaca*-thick they were offered was also observed in the field when juvenile crabs were offered clams in natural sediments (Chapter III); although the prey density manipulation experiment showed that crabs readily attacked large clams when the densities of alternative prey were low (Chapter III). This result contrasts with the result of no size-selection obtained by Blundon and Kennedy (1982a) for *Callinectes sapidus* preying on *Mya arenaria* but is not surprising. The data presented here show that *Mya*'s shell is an ineffective barrier to crabs and would be unlikely to strongly influence prey selection.

The increase of critical size with crab size is probably a result of the increase of both chela strength and maximum angle of chela gape with crab size. A similar pattern occurs in another decapod that uses its mandibles to crush bivalves. The maximum size of mussel that can be crushed by a Rock lobster (*Jasus lalandii*) increases with Rock lobster size (Griffiths and Seiderer 1980), presumably as does mandible strength and maximum angle of mandible gape. The rejection of larger *Protothaca* in favour of smaller ones is probably because of the thicker shell and increase in the minimum shell dimension (usually shell width) of the larger clams. The increased minimum shell dimension makes the clam too large to fit entirely within the chela, decreases the amount of force that can be applied and necessitates the use of the time consuming edge-chipping method. Thus the lower vulnerability of large clams may result from chela geometry. The blue crab *Callinectes sapidus* must use an edge chipping method for mussels too large to fit within a chela and this tactic takes an order of magnitude longer than the crushing method used for mussels that are not too large to fit (Seed 1982). This may explain why crabs that feed primarily on shelled molluscs tend to have large chelae with a relatively high height to length ratio (Warner 1977).

The geometry of structures used in feeding has also been shown to affect size preference and/or handling time in other predators. Holling (1964) obtained size-selective predation in preying mantids which corresponded to that predicted to be optimum from an analysis of the geometry of their grasping forearm. The profitability of prey eaten by Sunfish is at a maximum when the ratio of prey size to mouth size is 0.59, regardless of the size of the fish (Werner 1974). In Nunbirds the maximum width of gape of the bill limits the maximum size of prey that can be taken and determines the handling time of prey that is taken (Sherry and McDade 1982).

In addition to increasing shell-breaking time, the closer approximation of a sphere by more inflated shells minimizes the amount of shell material needed to cover a given volume of body. This might be important if there is an energetic or growth limitation cost to shell production (Palmer 1981). However Trueman (*et al.* 1966) have shown that elongate clams penetrate into the sediment more easily than more inflated ones. Thus while increasing the degree of inflation might increase shell-breaking time and decrease the amount of shell material required, it might also decrease burrowing efficiency. This is another example of the constraints that burrowing places on clam shell morphology.

Assessment of Vulnerability to Crab Predators

A similar ranking of comparative vulnerability was obtained using species preference as was obtained using critical size. The assessment using species preference took less time since shell-breaking time was fixed and was less sensitive to differences among crabs since all types of clams were fed to each crab.

I did not attempt to predict whether a given type of clam could be opened by a given crab (by comparing the maximum force a crab could generate with its chela with the load required to crush a clam of that type in the tensometer) even though this method has been used by other investigators (*e. g.* Blundon and Kennedy 1982a) and takes the least amount of time. There were two major reasons for this decision: first the molars on crab chelae act as stress concentrators (Brown *et al.* 1979) so the point stresses where the molars contact the shell are much higher than those where the tensometer contacts it (the calcium carbonate that makes up the shells is a brittle material and would be expected to be very sensitive to stress concentrations) and second, even if it were possible to mimic exactly the contact area and angle of force application by a crab chela (and because the plates of a typical compression attachment are not jointed, the angle of force application can not be mimicked), crabs open large clams by repeatedly loading them with their chela, not by loading them only once (Plates 5 and 6). Also many crab-resistant shell features such as the ability to close tightly and a steep angle at the ventral margin are not likely to be detected by loading clams in a tensometer. However I do consider loading clams in a tensometer useful to determine whether the observed differences in vulnerability result from differences in shell strength.

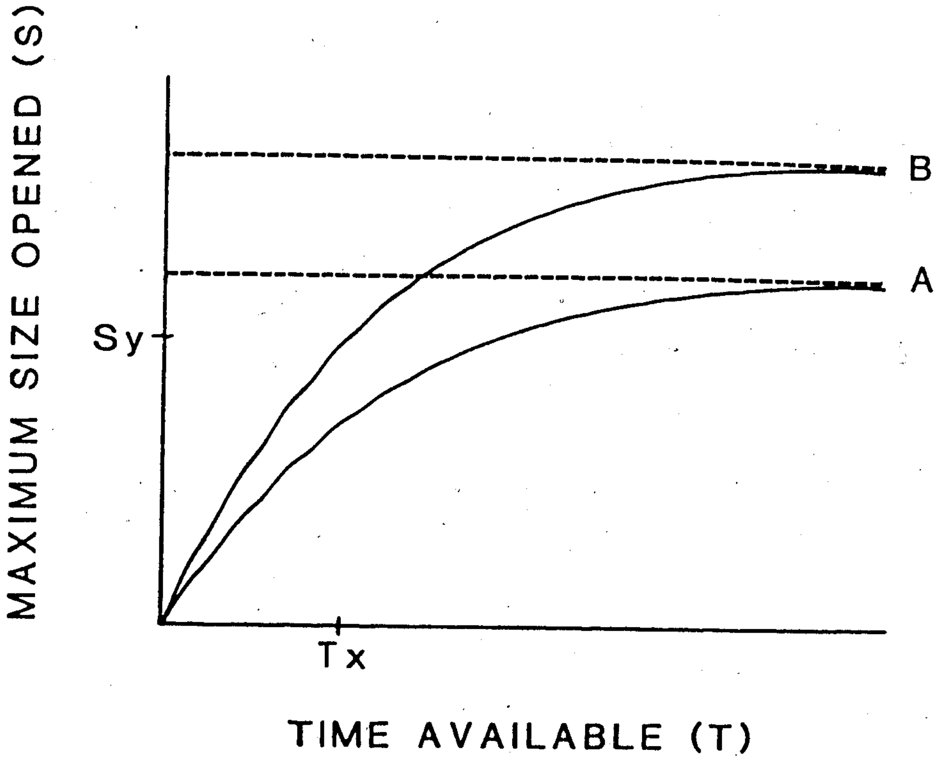
Assessment of the comparative vulnerability of shelled prey to *Cancer productus* and for crabs with similar behaviour is difficult because of the complex technique used to open large prey. The pulsed nature of force application by the chela observed here has also been noted for other decapods that prey on shelled molluscs (Zipser and Vermeij 1978; Elner 1978; Elner and

Campbell 1981). This repeated loading of the shell material could cause fatigue damage to occur, which would weaken the shell. This would result in the probability of failure being a function of shell-breaking time as well as absolute chela strength (Boulding and LaBarbera, in prep). Elner and Hughes (1978, p. 106) found that shell-breaking time increased asymptotically with shell length for *Carcinus* preying on mussels. If less time is allowed it will be erroneously concluded that the crab is unable to open the shell. This makes critical size difficult to determine.

Figure 6 shows the theoretical relationship between the maximum size of clam that can be opened by a given crab and the shell-breaking time allowed. If a decision is made to save time by using an allowed shell-breaking time where the curve is still a fair distance from the asymptote (as I did in the clam type preference experiment), the amount of shell-breaking time allowed per prey item and the availability and type of alternative prey must be held constant. This increases the probability that differences observed are real differences in vulnerability. Care should be taken to insure that the observed rank of preference is due to differences in shell features and not in response to other factors such as chemical or behavioural differences. In addition, although working at a distance from the asymptote is a more efficient way of ranking comparative vulnerability, the magnitude of "critical size" obtained this way can not be compared to values obtained by other workers who may have allowed a different shell-breaking time.

Some confusion seems to exist in the literature with equating "critical size" with an absolute size-refuge from crab predation when it has not been shown that that critical size no longer increases with shell-breaking time (*e. g.* Bertness and Cunningham 1981). Effective size-refuges from predation, at least on an ecological time scale, are functions of many variables, and can probably only be determined accurately in the field (*e. g.* Paine 1976) and can be at sizes below the absolute limitations of the predator (R. T. Paine, pers. comm.).

Figure 6. The hypothetical relationship between the maximum size of shelled prey that can be opened by a given predator (critical size) versus the time that prey is available to the predator. Curve A is for a more resistant mollusc species, (species A) and curve B is for a less resistant species (species B). A is the asymptote representing maximum size of vulnerability for species A while B is the asymptote for species B. Note that critical size becomes more dependent on time if only short times are allowed. The vulnerability of different clams can also be efficiently ranked using preference, if the time allowed for attack is kept constant. For example a crab offered molluscs of size Sy from both species for a period Tx , would have time to break open the more vulnerable species B, but would not have time to open A.


MAXIMUM SIZE OPENED (S)
B
A
Sy
Tx
TIME AVAILABLE (T)

Shell-Breaking Time and Probability of Mortality to Crab Predation

Even when less than the critical size, clams that were thick-shelled and/or tightly-closing survived longer because they were not persistently attacked until the densities of the thin-shelled, gaping clams were low (Fig. 4). The size preference experiments showed that the crabs preferred the smaller clams, further supporting the hypothesis that the crabs were selecting the more easily opened clams (Table IV). The recordings from the strain gauge showed that crabs took many more force pulses to open thick-shelled *Protothaca* than to open thin-shelled *Protothaca* (Plate 6). Similar trends were found when the recordings from a crab attacking large *Protothaca* were compared with those from the same crab attacking smaller ones (Plate 5). These results suggest that total shell-breaking time has a strong influence on prey selection by *Cancer productus*. When provided with abundant prey, another crab, *Carcinus*, selects mussels for which the ratio of energetic value over shell-breaking time is at a maximum (Elner and Hughes 1978).

Predators such as crabs would be expected to prefer prey with short shell-breaking times because it simultaneously increases prey profitability (energy intake per unit time) and decreases the total amount of time the predator has to spend foraging. Total time should be important to these and other predators which are heavily preyed upon by conspecifics and their own predators (pers. obs.) and whose foraging time in the intertidal is constrained by the time available during a high tide. Hughes and Seed (1981) have suggested that time minimization (*sensu* Schoener 1971) and not just energy maximization is important for the portunid *Callinectes sapidus* preying on the mussel, *Geukensia demissa*. Risk to predation can influence prey selection, as has been documented experimentally for the backswimmer *Notonecta hoffmanni* (Sih 1980). Thus the possession of shell features that increase shell-breaking time (such as a thick shell) might substantially reduce the probability that a crab would persist in attacking long enough to open the clam. That this tactic may be commonly used by prey to decrease their profitability and therefore attractiveness to predators is suggested by the long handling times required by many predators.

to exploit their prey. For example the oyster drill, *Urosalpinx* spp., may require over 3 1/2 days to penetrate an oyster (Carriker and Van Zandt 1972). The intertidal gastropod, *Acanthina*, changes from selecting prey with a high profitability to selecting prey with a short handling time as the time remaining for foraging becomes less (Menge 1974). Resistance by bivalves to crushing predators such as crabs is best explained as the sum of a number of shell features that greatly increase shell-breaking time rather than the attainment of a size refuge from all predation. Characteristics of bivalves that would increase shell-breaking time and might therefore decrease vulnerability include large size, ability to close tightly, degree of inflation, steepness of ventral margin, and depth of burial in the sediment.

III. FIELD STUDIES: CRAB RESPONSE TO PREY DENSITY

INTRODUCTION

The experimental study of predation by snails and starfish in the rocky intertidal has contributed much to our understanding of marine ecosystems (Connell 1961, 1972; Paine 1966, 1969, 1976; Dayton 1971). More recently, attempts have been made to experimentally study the impact of predation on invertebrates living intertidally in soft sediments using techniques developed in the rocky intertidal (Woodin 1974; Young *et al.* 1976; Virnstein 1977; Reise 1978). In contrast to the slow-moving predators, such as snails and starfish that are important in wave-exposed rocky intertidal areas, highly mobile predators, such as crabs, fish, and birds, are thought to be important in intertidal soft sediments (Young *et al.* 1976; O'Connor and Brown 1977; Virnstein 1977; Reise 1978).

Unfortunately the high mobility and complex behaviour of these important soft sediment predators makes experimental manipulation of their densities very difficult. Further, techniques such as predator exclusions which have been used extensively in the rocky intertidal can cause serious experimental artifacts used in soft-sediments (Virnstein 1978; Hurberg and Oliver 1980). Thus the study of highly mobile predators in soft sediments may require the development of new experimental techniques.

Crabs are implicated as important predators on bivalve populations and in some areas are believed to be responsible for the observed low densities of wild clams and the poor survival of planted hatchery-reared clams (Glude 1954; Carriker 1959; Whetstone and Eversole 1978). Most quantitative investigations of the impact of crab predation on the distribution and abundance of clams have relied on techniques such as crab stomach analysis, estimates of crab population density, and/or laboratory experiments (*e. g.* Walne and Dean 1972; Whetstone and Eversole 1978). The factors which influence crab behaviour in the field and determine whether or not crab predation represents a significant source of mortality for a given clam population, have rarely been investigated.

While crabs can be very selective about what they eat in the laboratory (Walne and Dean 1972; Elner and Hughes 1978), stomach analysis typically shows them to be opportunistic predators in the field (*e. g.* Bernard 1977; Hill, 1979). This discrepancy could perhaps be reconciled if more was known about factors that influence the patterns of mortality due to crabs in field populations of their prey.

This study examines crab predation of Native littleneck clams (*Protothaca staminea*). The methods used include: crab–exclusion/inclusion with cages, manipulation of clam density, following crab daily movements using acoustic telemetry and crab net movements using mark and recapture. The results suggest that cancrid crabs are attracted to local high densities of their prey and consequently the mortality rate of the clams from crab predation increases with increasing clam density.

METHODS

Clam Size and Mortality Due to Small Crabs

The Predator Exclusion/Inclusion Experiment

A study area was selected in a small bay within Roquefeuil Bay (48°51'N, 125°6'W) near Bamfield Marine Station, B.C., Canada. The site was protected from large waves by an offshore reef. Juvenile crabs (mostly *Cancer productus*) were common intertidally in the sand in this bay while adults were common subtidally in the eelgrass (*Zostera*) beds. The density of clams at a tidal height of 0.6 meters (above lowest low water datum, Canadian Hydrographic Services) was less than 21 clams/m² (Table V) and most of these were tellinids and less than 20 mm in shell length.

On a transect parallel to the water's edge at a tidal height of 0.6 meters, 13 points were chosen randomly and each assigned randomly to one of 4 treatments. The four treatments were 1) "predator exclusion" 2) "single crab inclusion" 3) "three crabs inclusion" 4) "unprotected" (with a buried fence around the perimeter). There were four replicates of the "three crabs inclusion" treatment and three replicates of the other three treatments.

Table V. Estimated natural clam densities at the sites of the field experiments.[1]

Site	Experiment	Tidal height(m)	Clam species (in rank order)	Clam Density /0.25 m^2 (S.E.)[2]
Roquefeuil Bay	Predator Exclusion/Inclusion	0.6	*Macoma inquinata*	18.6 (2.87)
			Protothaca staminea	3.1 (0.780)
			Saxidomus giganteus	0.38 (0.140)
Grappler Inlet (winter-spring run)	Prey Density Manipulation	1.0	*Macoma inquinata*	8.4 (1.26)
			Saxidomus giganteus	5.7 (1.39)
			Protothaca staminea	3.3 (0.790)
Grappler Inlet (summer run)[3]	Prey Density Manipulation	< 1.0	*Macoma inquinata*	2.5 (0.670)
			Saxidomus giganteus	0.9 (0.276)
			Protothaca staminea	0.21 (0.133)

1) The number of unmarked clams recovered upon sampling these field experiments.
2) Of clams > 10 mm in shell length.
3) The summer run was conducted 2.0 m towards the water's edge from the winter-spring run.

Cages were constructed of 12 mm galvanized steel mesh, overlayed with 4 mm VEXAR mesh attached to an aluminum frame (0.5 m X 0.5 m X 0.25 m (high)) with a trap door in the roof to allow access (Plate 7). The buried fence of the "unprotected" treatment was designed to prevent horizontal movement of the clams and was constructed of 4 mm VEXAR (0.5 m X 0.5 m X 0.15 m (high)). The fences and the sides of the cages were buried to a depth of 0.15 m.

Care was taken to disturb the sediment and natural infauna being enclosed little as possible. This was done to maximize the advantages of working in natural sediments as opposed to a laboratory simulation of them. However this approach does have the disadvantage that the initial density of natural clams is not known and must be estimated from the density of unmarked clams upon sampling. This adds to the variance among replicate enclosures but reduces the probability of experimental artifacts from disturbing the sediment.

Native littleneck clams (*Protothaca staminea* Conrad, Veneridae) of three size-classes (9 - 15 mm, 17 - 24 mm, and 26 - 32 mm) were collected from the Bamfield area. Note that all experiments described in this Chapter used exclusively the thick-shelled morph of *P. staminea*. Each clam was marked on the hinge with a dot of Martex tech-pen ink using a different colour ink for each size-class. Fifteen clams of each size-class, or a total of forty-five clams, were placed in each treatment. Temporary lids of 4 mm VEXAR were sewn onto the fences of the "unprotected" treatment to allow any disturbed sediment to resettle and the clams that had been planted to burrow. This was done because observations during high tide suggested that crabs were attracted to recently disturbed areas. A week later (July 1, 1981) these lids were removed and an appropriate number of marked *Cancer productus* (carapace width 45 - 55 mm) were placed in the enclosed treatments with crabs.

The experiment was sampled 3 weeks later The cages or fences were removed and the surface was combed first with fingers, then with a clam fork and any live clams [illegible] fragments were set aside. All the sediment that had

Plate 7. The cages used in the predator exclusion/inclusion experiment. Note that the sediment and natural infauna being enclosed was disturbed as little as possible and that this cage still has eelgrass (*Zostera*) growing inside it.

been enclosed was dug up to a depth of 0.3 m then sieved through a floating sieve (0.5 m X 0.5 m) of 5 mm mesh. The marked clams that had been placed in each enclosure were separated into 4 categories: alive, crab-crushed, dead with no shell damage, and missing. The number of clams in each of these categories was determined by counting hinges. The shell fragments of clams suspected of being crushed by crabs were compared with others known to have been crushed by crabs in the laboratory. The numbers and condition of the marked crabs in the "crab" treatments were recorded. In addition, the number of the natural bivalves (of shell length > 10 mm), crabs, and predaceous gastropods present in each enclosure was noted.

While all live clams were retained by the sieve this was not true of the fragments of shells that had been crushed by crabs, particularly those in the smallest size-class. This meant that some treatments had a very high proportion of missing clams. For this reason the crab-crushed and missing categories were lumped together since the majority of the missing clams had probably been crushed by crabs. This lumping introduced no bias as an equal amount of effort was expended processing and sorting each sample and all processing was done without knowledge of which treatment the sample represented. A simulation of the "single crab inclusion" treatment was set up in an aquarium containing 10 cm of sand. This was sampled, three weeks later by picking out the shell fragments by hand. There were only two missing clams and a higher proportion of crushed shells than in the field samples (Appendix 2); this provides additional evidence that lumping was justified.

Clam Density and Mortality Due to Large Crabs

The Prey Density Manipulation Experiment

A study area was selected in Barge Bay in Grappler Inlet (48°50'N, 125°6'W) near Bamfield Marine Station. The site was protected from wave exposure and there was little current. The sediment was pebbles mixed with fine sand with a mean particle size of 6.6 mm ($M_\phi = 2.7$) and poorly sorted ($\sigma_\phi = 1.8$; Inman 1952). The natural bivalve density (at a tidal height of 1.0

m) consisted mostly of tellinids of a shell length less than 20 mm.

On a 24 m transect, parallel to the water's edge at a tidal height of 1.0 m, ten points were selected randomly and each assigned randomly to one of two treatments: "sparse" and "dense". Ten fences of 4 mm VEXAR mesh (0.5 m X 0.5 m X 0.15 m (high)) were carefully buried so they enclosed the sediment at these points such that 10 mm remained protruding above the sediment surface. Native littleneck clams (*Protothaca staminea*) were air dried then sprayed with fluorescent orange paint and divided into three size-classes (30 - 35 mm; 40 - 45 mm; 50 - 55 mm). Five individuals of each size-class were placed in the sparse treatments and twenty of each were placed in the dense treatments. Thus the sparse treatments contained 15 *Protothaca* plus whatever clams were present naturally (Table V) while the dense treatment contained 60 *Protothaca* plus the natural clams. Temporary lids of 4 mm VEXAR were sewn on the fences for the first week. These were removed Dec. 9, 1981.

The experiment was visited at least semimonthly intervals and any orange shell fragments visible inside the fenced areas were collected. In addition any shell fragments found outside the fences were collected and their position was recorded. In February the area within one of the fences was dug up to check the progress of the experiment. The fence was reburied at a new location, randomly chosen on the transect, and the marked clams were replaced inside it and again protected with a VEXAR lid for a week.

Diving observations of the experimental area were made at high tide during the day and at night. In addition, qualitative observations of the types of crabs and other predators present were made from boats and 4 side entry crab traps set in Barge Bay to qualitatively sample the predators present. After 6 months (May 26, 1982) the enclosures were sampled using the same procedure as was used in the previous field experiment. The growth increment was measured where more than 1 mm of growth had occurred by measuring the increase in shell height due to (unpainted) new shell material.

This experiment was repeated but run for only 3 months (June 5, 1982 - Sept. 1, 1982) instead of 6. Three changes were made to reduce problems discovered in the first run of the experiment: 1) Only the smaller two size-classes of clams were used because the largest size-class seemed unable to rebury itself successfully (Plate 8). 2) Each of two size-classes used were spray painted with a different colour of spray paint: pink for the 30 mm size-class and yellow for the 40 mm size -class. 3) Finally, to allow identification of stray clams each clam had its enclosure number marked on it with permanent felt pen.

Laboratory Experiments

To determine approximate maximal feeding rate of large *Cancer productus*, 4 male crabs (carapace widths 111 - 170 mm) were starved for a week. They then were offered four clams of each of three size-classes (shell length 31-35 mm; 45-48 mm; 58-60 mm). The number of clams eaten of each size-class was recorded after 24 hours.

To determine whether fluorescent paint affected the palatability of clams to crabs, 5 *Cancer productus* (carapace width 89 - 111 mm) and 1 *Cancer magister* (154 mm) were offered 5 painted and 5 unpainted clams (shell length 30 - 35 mm). Clams were replaced as they were eaten. All 6 crabs ate at least 5 clams. All crabs were held in individual containers in free running seawater.

Crab Movement

Acoustic telemetry

Three *C. productus* were trapped in Grappler Inlet using side entry crab traps. A transmitter (Smith-Root Electronics model SR69A) was fastened to a harness attached with underwater epoxy (Sea Goin' 'Poxy Putty; Permalite Plastics) to the crab's carapace. The crabs were released at the point of capture within a day after capture. Crabs were located from a rowboat using a directional hydrophone (Smith-Root Inc., Model SR-70H) decoded aurally. The position of the crab and the depth of the water were recorded on a map prepared from aerial photographs. To test for behavioural artifacts caused by the transmitter, another crab was fitted with a harness of the same type to which an object of the same shape and weight as the transmitter was attached. It was held in the lab and its behaviour was observed.

Tagging

Fifty-five adult *C. productus* and ten adult *C. magister* were trapped in Grappler Inlet, measured, tagged, then released at the point of capture. The tags used were numbered plastic spaghetti tags (Floyd Tags Inc., Seattle, Wash.) which were sewn through at the epimeral line with a curved needle then knotted with a figure 8 knot (after Butler 1957; Snow and Wagner 1965). Eight *C. productus* were tagged in this manner then held in the laboratory for over 3 months. Posters offering rewards for the return of tagged crabs were placed in conspicuous places around the town of Bamfield.

RESULTS

Clam Size and Mortality Due to Small Crabs

The purpose of this experiment was to determine whether small *Cancer productus* showed size-selection when preying on *Protothaca staminea* in natural sediments and to compare the predation intensity on these clams from 3 small *Cancer productus* per 0.25 m^2 with that from the natural crab predators present in Roquefeuil Bay.

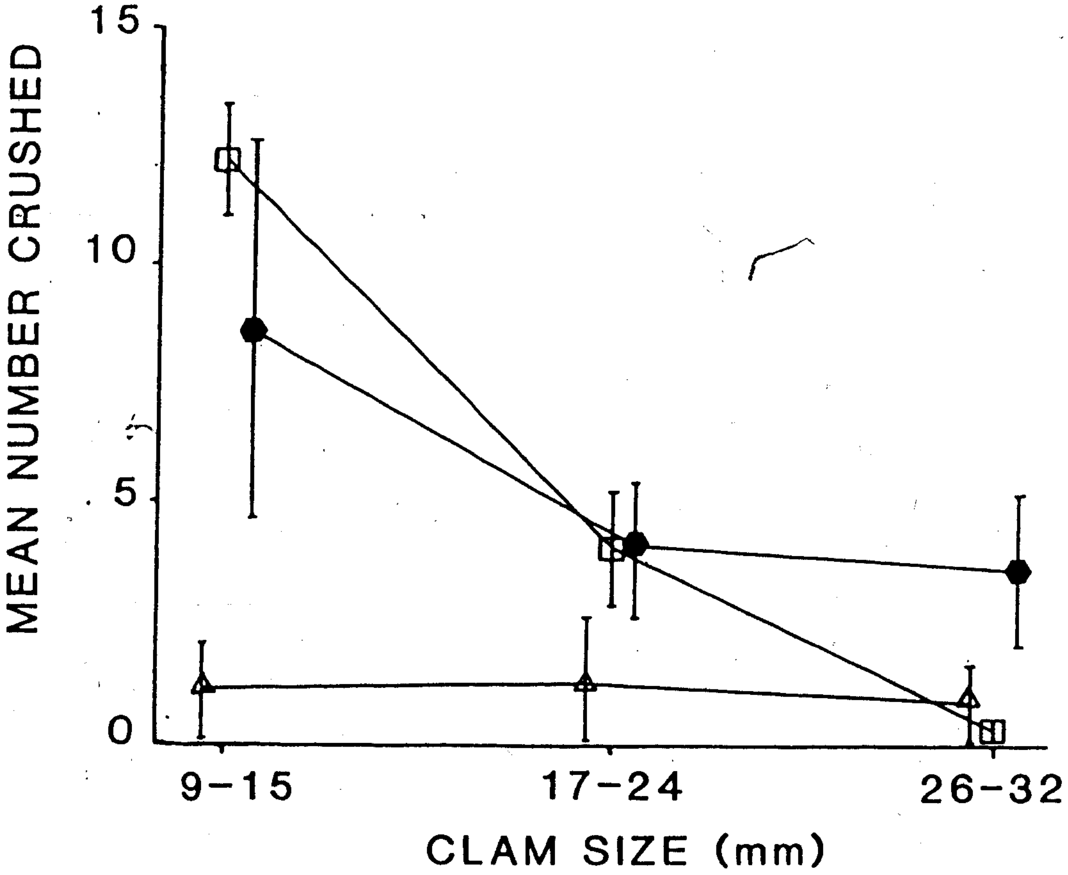
There was no evidence of any serious cage artifacts in this experiment: neither increased sedimentation nor immigration of small predators into the cages was evident. The crabs in the cages seemed to eat well and none escaped. However maintaining a constant predation pressure was difficult. In one replicate (A5) of the three crabs inclusion, a crab molted and was not replaced and in another replicate of this treatment (B8) two extra *Cancer productus* juveniles (3.8 cm and 4.5 cm) were found in the cage when it was sampled (Appendix 2). In a replicate (B7) of the "single crab inclusion" the crab died without being noticed which resulted in the replicate behaving like those in the "predator-exclusion" treatment (Appendix 2). The "three crabs inclusion" treatment was more successful, probably because there were 3 crabs present; thus it was highly probable that at least one crab remained alive and in an intermolt stage and continued feeding.

The crabs in the "three crabs inclusion" treatment showed size selection by eating significantly more of the clams in the smallest size-class than in the larger two size-classes (Fig. 7; Kruskal Wallis, p = 0.008). There were significantly more of the small clams eaten in the "three crabs inclusion" treatment than in the "predator exclusion" treatment (Fig. 7; Mann Whitney U, p = .02).

The "unprotected" treatment had about the same mean mortality attributed to crabs as did the "three crabs inclusion" treatment (Fig. 7). This was higher than expected from the ambient crab density. The highest recorded density of juvenile *Cancer productus* found naturally near the transect was less than one juvenile per 0.25 m^2 which is lower than the three juveniles per 0.25 m^2 of the "three crabs inclusion" treatment. The higher mortality shown by the largest size-class of clams in the "unprotected" treatment relative to the "three crabs inclusion" treatment (Fig. 7), and larger chips on the margins of the recovered shell fragments, suggested that crabs larger than those used in the "crab-inclusion" treatments had been responsible for the mortality in the "unprotected" treatment. The intensity of crab predation on the "unprotected" treatment was not uniform for all replicates. Two of the three replicates showed a high mortality due to crabs while the other replicate was untouched (Appendix 1). This observed patchiness and the higher than expected predation intensity suggested another field experiment to test whether crab predation on clams was dependent on clam density.

Figure 7. The mean number (with standard errors) of clams either recovered crushed by crabs or missing for each of several treatments of the predator exclusion/inclusion experiment (for explanation see text, for raw data see Appendix 2).

The white triangles represent the means for the "predator-exclusion" treatment, the white squares the "three crabs-inclusion" treatment, and the dark hexagons the "unprotected" treatment. To estimate number of clams crushed by crabs as opposed to those missed upon resampling, subtract the means for the predator-exclusion treatment from those treatments in which the clams were exposed to crabs.


MEAN NUMBER CRUSHED
15
10
5
0
9-15
17-24
26-32
CLAM SIZE (mm)

Clam Density and Mortality Due to Large Crabs

The clams used in this experiment were larger and conspicuously marked with fluorescent paint. This resulted in fewer missing clams which allowed direct estimation of the percent mortality due to crabs by counting the number of hinges in the chipped shell fragments recovered.

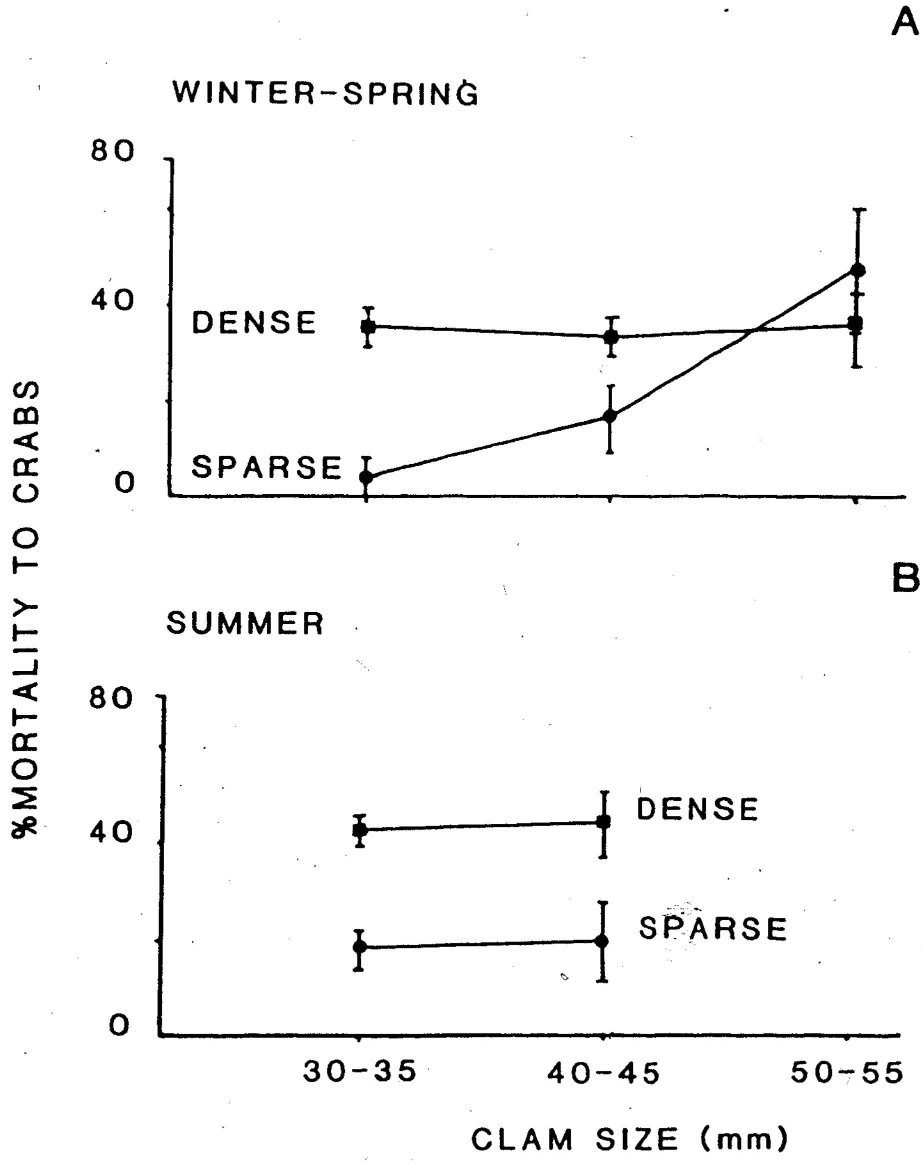
There were more missing clams in the winter-spring run of this experiment (N=40) than in the summer run (N=11). In the winter-spring run, fifteen of these missing clams were found (with chip marks characteristic of crabs) in the eelgrass below the fences. Clams were also found in the eelgrass in the summer run but as they were marked with their replicate number they could be assigned to a treatment.

Nearly all of the clams in the smallest two size-classes (30-35 mm; 40 - 45 mm) reburied themselves within a day. This was not true of the clams in the largest size-class (50-55 mm) which seemed unable to rebury themselves and remained on the surface of the sediment (Plate 8).

The smallest size-class of clams showed a measurable amount of growth in 25% of the individuals recovered alive in the winter-spring run (after 6 months) and in 47% of those recovered in the summer run (after 3 months). Some of the intermediate size-class of clams showed some growth though not enough to measure accurately. None of the largest size-class of clams showed any growth. The smallest size-class of clams grew about 3 times as fast during the summer months (0.55 mm/month; S.E.=0.06; N=36) as during the winter-spring months (0.15 mm/month; S.E.=0.02; N=19). There was no significant difference between the sparse and the dense treatments in clam growth rates (Mann Whitney U, $p > 0.72$).

The largest size-class of clams (50 - 55 mm) showed no difference in percent mortality attributable to crabs between the sparse and the dense treatments during the winter-spring run (Fig. 8a). The smaller two size-classes showed a significantly higher percent mortality in the dense treatments than in the sparse treatments in the winter-spring run (Fig. 8a, Two-way Friedman rank sums test on cell medians, $p < 0.05$) and in the summer run (Fig. 8b, $p <$

Figure 8. The mean number (with standard errors) of clams in each size-class recovered crushed by crabs in the prey density manipulation experiment. 2a) The winter-spring run: the means for the dense treatment (squares) and the sparse treatment (circles). For raw data see Appendix 3. 2b) The summer run: the means for the dense treatment (squares) and the sparse treatment (circles). For raw data see Appendix 3.


A
WINTER-SPRING
80
40
0
DENSE
SPARSE
B
SUMMER
80
40
0
DENSE
SPARSE
%MORTALITY TO CRABS
30-35
40-45
50-55
CLAM SIZE (mm)

0.05), but there was no significant difference in percent mortality due to crabs between the smallest (30 – 35 mm) and medium (40 – 45 mm) size-classes for either run of the experiment.

The four male crabs that had been starved in the laboratory ate a mean number of 3.3 clams each (S.E.=0.48) in 24 hours and showed no preference for any of the three size-classes (Table VI). In the laboratory the crabs showed no preference for painted clams over unpainted clam (N=51 clams; G-test with correction for continuity; Sokal and Rohlf 1981). Crabs were observed to carry clams around the aquarium by using their chelae to brace the shell against their mouthparts frequently enough to suggest that they may also do this in the field.

Four species of crabs were caught in side entry crab traps that had been placed subtidally in the bay where the enclosures were. These were *Cancer productus*, *Cancer gracilis*, *Cancer magister*, and *Pugettia producta*. I have observed adults of all four of these crab species eat *Protothaca staminea* up to at least 45 mm under laboratory conditions.

Casual observations from boats suggest that these crabs are primarily nocturnal foragers and cancrid crabs were observed twice in the vicinity of the enclosures. Scuba divers counted 7 *C. gracilis* (carapace width 40 – 103 mm) and 7 *C. productus* (carapace width 50 – 135 mm) in the vicinity of the enclosures during a night high tide (3.4 m). On a similar dive during a daytime high tide (3.3 m) divers found only one *C. productus* and this one was not in the vicinity of the enclosures.

Crab Movement

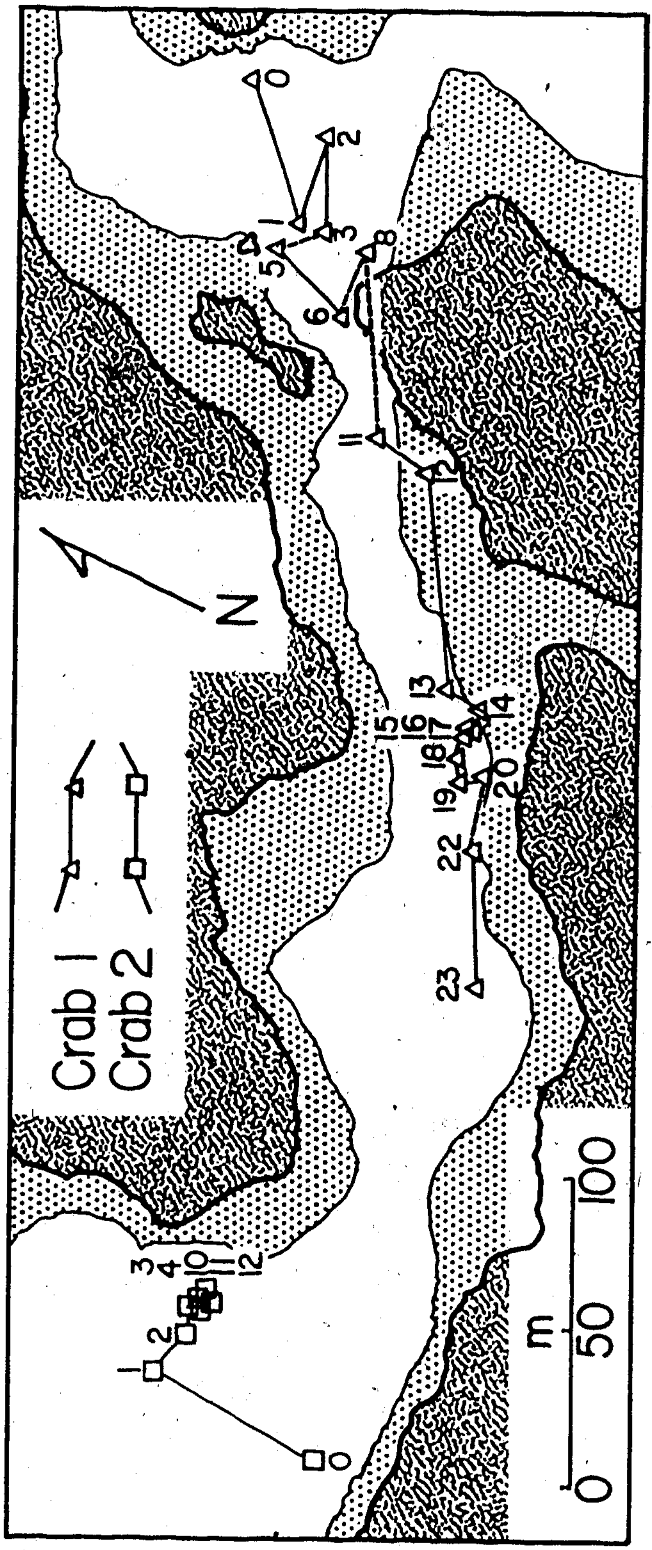
Acoustic Telemetry

One of the transmitters failed soon after the crab was released, but the other two crabs were tracked for 23 days and 13 days respectively (Fig. 9). Crabs tended to stay in water at least 1.0 m deep, sometimes spending several days in one spot and sometimes travelling > 50 m per day. Both crabs remained in Grappler Inlet. The crab with the simulated transmitter ate well

Table VI. The percentage eaten from each size-class of clams during 24 hours by male *Cancer productus* starved for the previous week. (N is the total number of clams eaten by each crab). They were initially offered four clams of each size-class.

Crab carapace width (cm)	Clam shell length (cm)			N
	3.1-3.5 cm	4.5-4.8 cm	5.9-6.0 cm	
11.1 cm	67 %	0 %	33 %	3
13.8 cm	50 %	0 %	50 %	2
14.8 cm	25 %	50 %	25 %	4
17.0 cm	50 %	25 %	25 %	4

Figure 9. The net daily movements of the two crabs tracked using acoustic transmitters. The numbers on the points represent the days that have elapsed since the crab was released. The clear areas are subtidal, the stippled areas are intertidal, and the mottled areas are land above highwater.


Crab 1
Crab 2
N
m
0
50
100
0
1
2
3
4
5
6
8
11
12
13
14
15
16
17
18
19
20
22
23
0
1
2
3
4
10
11
12

under laboratory conditions.

Tagging

While 3/10 (30 %) of the *Cancer magister* were recaptured, only 1/55 (2 %) of the *C. productus* were recaptured (Fig. 10). This *C. productus* was not recaptured in a side entry crab trap but was found newly dead on the beach. The bait in the side-entry crab traps frequently showed signs of being eaten, even when suspended from the top of the trap which suggested that the smaller crabs were easily able to escape from the trap. One *C. magister* showed a net movement of 150 m in 2 weeks but the other 3 were recaptured close to where they had been tagged (Fig. 10).

DISCUSSION

Crab Response to Patch Density

The clams in the patches where the clam density was high showed a greater percent mortality due to crabs than did those in the patches where the density was low (Fig. 8). Two mechanisms could give rise to this pattern. First, if clams in the high density patch had an inadequate amount of room for burial, some clams would be forced towards the surface of the sediment. Native littleneck clams (*Protothaca staminea*) forced to live nearer to the surface of the sediment have been shown to have a higher percent mortality to *Cancer magister* than those allowed to burrow to normal depths (Pearson *et al.* 1981). If a higher density resulted in more clams being forced to the surface a pattern of density dependent predation might result. While this mechanism may be partially in operation, I did not observe large numbers of the small (30–35 mm) and medium (40–45 mm) clams at the sediment surface. However the artificial proximity to the surface of the largest size-class of clams is probably the explanation for their high mortality in both treatments (Plate 8). Also although the "dense" treatment of the winter–spring run had a higher clam

Figure 10. The net movement between tagging and recapture for the four crabs that were recaptured. The clear areas are subtidal, the stippled areas are intertidal, and the mottled areas are land above highwater. "T" represents the location where a given numbered crab was captured, tagged, then released and "R" represents the location where it was recaptured. Crab 1 was a 18.0 cm *Cancer magister*, recaptured after 6.5 months, Crab 2 was a 16.3 cm *C. magister*, recaptured after 6.5 months, Crab 3 was a 16.8 cm *C. productus*, recaptured after 4.5 months, and Crab 4 was a 16.5 cm *C. magister*, recaptured after 0.5 months.

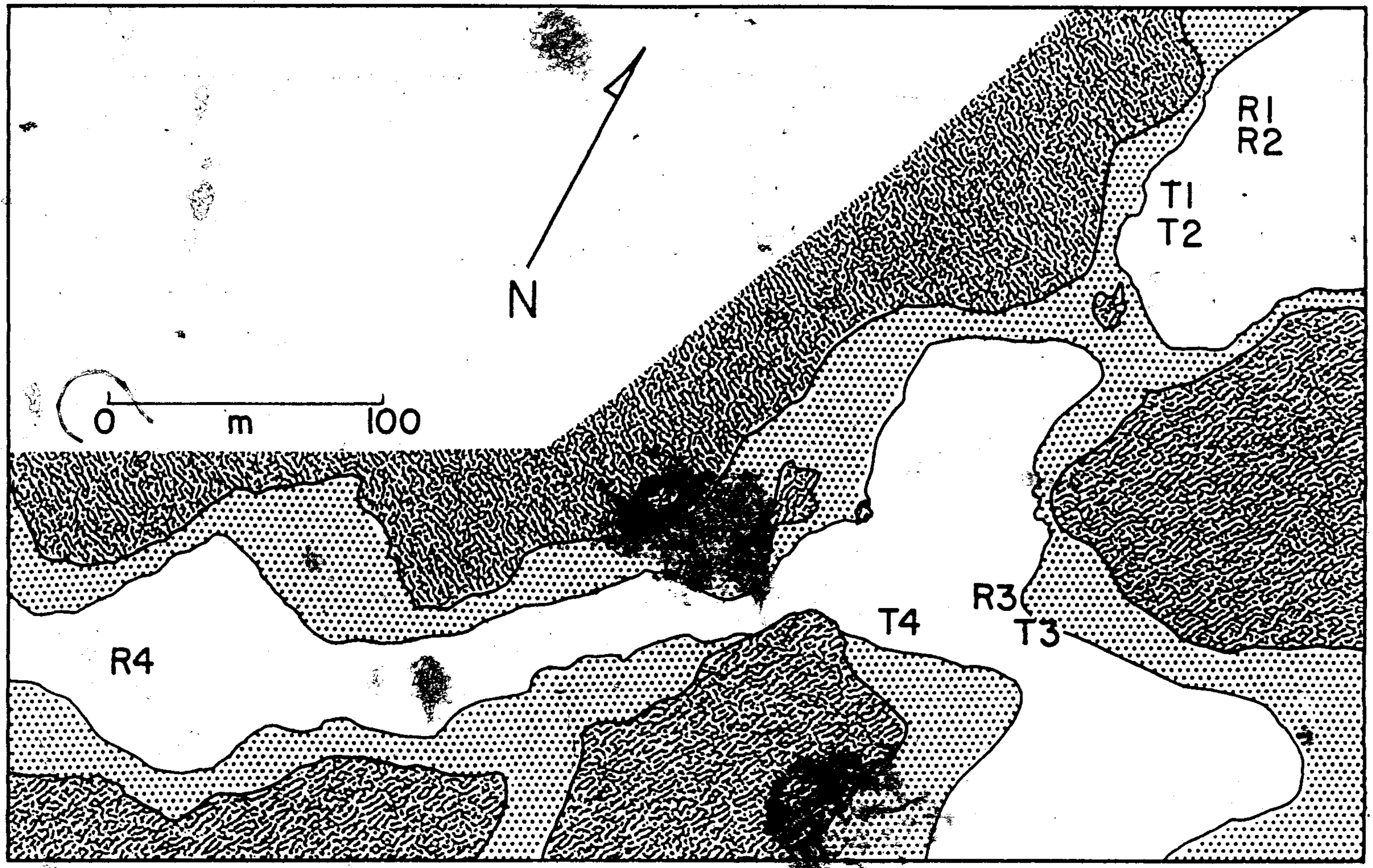

N
0
m
100
R1
R2
T1
T2
R3
T3
T4
R4

Plate 8. The enclosures used for the prey density manipulation experiment. Note that the large clams on the surface are the 50-55 mm *Protothaca staminea*. This size-class was incapable of reburying once dug up by crabs and was used only in the first run of this experiment. This same type of enclosure was used for the "unprotected" treatment of the predator exclusion/inclusion experiment.

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density (> 60 clams per enclosure) than [illegible] "dense" treatment of the summer run (> 40 clams per enclosure), it showed a lower percent mortality due to crabs over 6 months (approximately 35%) than the summer run did after only 3 months (approximately 45%; Fig. 8) although there may be seasonal differences. In addition natural densities of clams in a nearby lagoon in Roquefeuil Bay regularly exceed three times the highest density used in this experiment. This suggests some other mechanism is involved than clams being forced towards the surface.

Crabs might be more strongly attracted to patches of high prey density than patches of low prey density. *Cancer magister* uses its antennules as distance chemoreceptors and has the ability to detect extracts of the Native littleneck clam (*Protothaca staminea*) at a concentration of 10^{-10} grams per liter (Pearson *et al.* 1979). Higher concentrations of clam extract were shown to initiate probing with the claws and walking legs and other feeding behaviours. If crabs are able to estimate prey density by chemoreception this might result in more crabs being initially attracted to the high density patches and/or in the same crabs returning to the same high density patch on successive high tides. Either of these would result in a higher percent mortality to crab predation in the dense patches than in those less dense. If an increase in local crab density is responsible for the higher percent mortality of the dense treatment, the percent mortality to crabs would not necessarily continue to increase with clam density. Cancrid crabs are extremely aggressive towards each other (pers. obs.) and would be unlikely to tolerate high densities of other crabs when foraging.

Crabs might concentrate their search effort on the high density patches because less time is required to obtain each clam. While they may obtain the approximate location of the clam using distant chemoreception, the exact location is probably obtained using mechanoreceptors and/or contact chemoreceptors on their claws and on their walking legs (Case 1964; Warner 1977). The probability of contacting a clam would be expected to be higher per probe in dense patches than in less dense patches. The time required per clam would be further reduced if the higher density resulted in more than one clam being obtained from each hole dug by the crab.

Other mobile predators have been shown to forage preferentially in patches of high prey density though there are few marine examples. Deermice (*Peromyscus leucopus*) tended to concentrate on the highest densities of sawfly cocoon prey (Holling 1959). Great tits were found to concentrate their searching time on the patches with the highest food density and to persist in searching patches that previously had contained a high food density (Smith and Dawkins 1971). Oystercatchers feeding on cockles have been found to aggregate in the patches of highest prey density (O'Connor and Brown 1977). And the foraging intensity by fiddler crabs on a given patch was found to be directly correlated to its food density even when this involved the crabs moving a considerable distance from the safety of their burrows (Robertson *et al.* 1980).

Some models of optimal foraging in patches have assumed the predator is unable to assess the prey density and therefore the profitability of a given patch until it has sampled it (*e. g.* Oaten 1977). The well developed distance chemoreception of these crabs might allow them an approximate estimate of food availability before sampling occurs. These models also assume that a predator's decision on when to leave a patch is based on the time interval since the last prey was captured (Oaten 1977). If these crabs are able to assess prey density using distance chemoreception they might have more accurate information on which to base their decision.

Crab Movement

The acoustic telemetry and recapture of tagged crabs showed that these crabs have the ability to move long distances (> 50 m/day) but at least a portion of the population remains in the same local area. Snow and Wagner (1965) tagged 966 Dungeness crabs (*Cancer magister*) and (over 3 years) recovered 95 tagged crabs; 76% from within the same bay and 24% 3.5–34 miles from where they were tagged. There is no commercial fishery for crabs near Grappler Inlet so it is difficult to estimate the number of tagged crabs that left the Inlet. However no tagged crabs were caught by the sports fishery in nearby Bamfield Inlet (distance= 1 km). The acoustic telemetry data show (Fig. 9) that there was considerable variation in the distance moved in a given day even for individual crabs.

The acoustic telemetry data and field observations suggest that as adults these crabs prefer to remain in at least 1 m of water (except during copulation or molting; Boulding unpub. data). This may be to avoid terrestrial predators such as gulls and raccoons both of which I have observed to be voracious predators on crabs. The green shore crab (*Carcinus maenas*) tends to remain in at least 0.5 m of water when foraging, presumably to avoid predaceous birds (Dare and Edwards 1981).

Two other observed behaviours may also be explained as avoidance of predators. Crabs were most active at night, perhaps to avoid predation by visual predators such as birds and fish. Large clams (known from my laboratory experiments to have handling times in order of hours) were often carried down to the eelgrass (*Zostera*) beds below the cages before being opened and eaten. This might be to avoid predators or to avoid being [illegible] or robbed by larger crabs.

Prey Selection

Laboratory and field experiments have shown that crabs prefer smaller clams when given a choice (Table IV, Fig. 7). Yet all the clams used in the prey density manipulation experiment were large yet showed a very high mortality due to crabs. This may be because of the lack of alternative prey in Grappler Inlet which is, in turn, probably attributable to the high density of predators such as crabs. All three of these species of cancrid crabs have broad diets (Bernard 1977). But the low density of bivalves and polychaetes that occur naturally in the soft sediment areas and the small balanoid barnacles and large thick-shelled snails (*Thais lamellosa*) that occur in the rocky areas of Grappler Inlet might represent a lower profitability than does a high density of large bivalves. Hill (1979) showed that the mangrove crab (*Scylla serata*) spent more time in the areas of the estuary that had the highest number of prey organisms.

Potential Experimental Artifacts

The act of transplanting clams could cause increased mortality by attracting predators or if the transplanted clams failed to reestablish themselves. The VEXAR tops sewn onto the top of the enclosures protected the clams for a week which seemed sufficient time for the clams to reburrow and the sediment to resettle (with the exception of the 50–55 mm size-class present in the first run). At least some of the smaller two size-classes of clams used in the prey density manipulation experiment reestablished themselves sufficiently well enough to show a significant amount of growth after only 3 months. There was no difference between the two treatments in the ability of the clams to reestablish themselves. The proportion showing growth, the amount of growth, and the proportion of dead undamaged shells recovered, was not different for the two treatments.

Some of the most common artifacts in caging experiments in soft sediments are caused by disruption in water flow or unplanned modifications of predator behaviour (Virnstein 1978). While disruption of water flow can be a serious problem in certain caging experiments if high flow conditions causes sedimentation (Hurberg and Oliver 1980), these field experiments were done in quiet water and no sedimentation was observed. When adult *Cancer productus* are put in cages they refuse to eat and excavate large pits in their attempt to escape (Boulding 1980). Juvenile *C. productus* burrowed into the sediment and showed normal feeding behaviour although I can not exclude the possibility that the juvenile crabs in the "crab inclusion" treatments did not eat as voraciously as they would have if they had been free. The different response of adult and juvenile crabs to caging probably reflects differences in their mobility. Juvenile crabs are primarily intertidal, living under boulders and in soft sediments and move relatively little compared to the adults (pers. obs.). Thus different techniques must be used to study predation by adult *C. productus* than are used for studying the juveniles.

The undersediment fences protruded only 10 mm above the sediment surface and would be expected to have fewer potential artifacts than a cage. There is potential for the attraction of small predators, because of the increased three dimensional structure, and for the exclusion of predatory gastropods that are too large to crawl through the mesh and too small to crawl over it. Aggregation of small predators inside the enclosures was not observed. It is possible that crabs were attracted to the fences but this would not affect differences between the two treatments (since both treatments were fenced), only the actual number of clams that were eaten. Any small predatory gastropods should have been present in roughly equal numbers inside and outside the enclosures since the enclosed sediment had been disturbed as little as possible during installation. Large naticid gastropods were not present intertidally in Roquefeuil Bay or Grappler Inlet and naticid drilled shells were very rare. Even if the gastropods were present the fences should have not been sufficient to exclude them. Peterson (1982a, 1982b) used similar undersediment fences yet observed a high incidence of predation by gastropods. Thus the enclosures probably did not affect the mortality patterns that were observed for these clams.

Estimation of Mortality Agent from Shell Fragments

To estimate the source of mortality from shell fragments unambiguous identification is necessary. The known predators of *Protothaca staminea* in Grappler Inlet are starfish, small mammals such as raccoons, birds such as gulls and diving ducks, predatory gastropods, octopus and crabs. Only the shell fragments from clams dropped by birds could be confused with those crushed by crabs, but these can be told apart by location and by breakage patterns. The site of the prey density manipulation experiment was bordered with rocky outcroppings. Although no marked and only two unmarked *Protothaca staminea* were ever found near these there were shell fragments of the Japanese littleneck clam (*Tapes japonica*). *Tapes* is generally found higher in the intertidal and buried shallower in the sediment than *Protothaca* (pers. obs.), attributes that could increase its vulnerability to bird predators (Glude 1963). The method by which these crabs attack clams too big to fit entirely within their claw often results in characteristic chips on the ventral margin and a U-shaped channel with ragged edges where the crab has broken the valve further (Chapter II). This contrasts with the relatively straight edges found on the shell fragments of shells dropped by birds (pers. obs).

The prey density manipulation experiment differs from most mark and recapture experiments using venerid clams in that many of the "missing category" clams were found (because of the bright fluorescent paint on their valves) and the predator responsible for their death was identified. Peterson (1982a) lost up to 54% of the hard clams (*Mercenaria mercenaria*) he originally planted. These clams were removed by an unidentified agent and were not missed upon resampling as his resampling efficiency was 99%. In his experiment there were significantly more of the clams in the smaller size-classes missing than of those in the larger ones. This suggests to me that by not knowing the fate of these "missing clams" he is underestimating the importance of clam mortality due to crabs. In another of his experiments the percent mortality attributed to crabs was never density dependent if only the broken shell fragments found inside the enclosures were considered but the percentage of missing clams was significantly density dependent 3/12 times (Peterson 1982b). Peterson partially attributes these missing clams to predation by *Cancer antennarius*. The problem with having a large number of animals whose fate can not be accounted for is that the relative importance of different mortality agents could be ranked incorrectly. Although conspicuously marking clams with fluorescent paint could affect their susceptibility to some predators such as birds, the laboratory results suggest that it does not affect their susceptibility to crabs and is one of the few methods of accurately estimating bivalve mortality due to crabs in the field.

The Impact of Crabs on their Prey Populations

Estimation of the potential impact these crabs have on their prey populations is difficult because of their broad diet, their high mobility, and their response to prey density. The predator exclusion/inclusion experiment showed that the predation intensity on a given patch of clams (as observed in the "unprotected" treatments) could not be predicted by knowing the density of juvenile crabs at low tide and the rate at which they ate clams (in the crab inclusion treatments). Indeed, even if the relationship between percent mortality due to crabs and crab density could be determined, there would still be the problem of deciding how, where, and when to measure crab density in the field. The assumptions of conventional techniques for estimating population density such as mark and recapture would be violated by adult crabs. The best method of determining percent mortality to these crabs is probably to mark the prey population (if it is possible to uniquely identify prey attacked by crabs) and/or to use SCUBA to survey that area of the bottom during night high tides.

The impact of a highly mobile predator such as a crab on a prey population would be expected to be quite different from that of a slow-moving predator such as a snail because of the difference in the speed with which the predator can respond to changes in the local density of their prey. Although the whelk (*Busycon*) also uses chemoreception to detect clams and must also dig them out of the sediment (Carriker 1951), whelk predation on hard clams was never found to be density dependent (Peterson 1982a).

The positive, density-dependent feeding response shown by these crabs would probably result in a more uniform distribution of their prey so long as the crabs are reasonably abundant. This would tend to prevent a patch of prey from undergoing wide fluctuations in density relative to other patches. If a similar response to prey density occurs in other decapods it might explain why East Coast lobsters and cancrid crabs prevent outbreaks of sea urchins (Mann and Breen 1972; Wharton and Mann 1981) even though urchins are not a preferred prey when urchin densities low (Breen 1974; Drummond-Davis *et* *al.* 1982). It may also explain why mariculture projects that artificially increase the local density of a prey species may be economic failures because of extremely high mortality due to crabs (*e. g.* Mottet 1980).

IV. CONCLUDING DISCUSSION

Two major conclusions arise from this work. First, certain shell features decrease the vulnerability of infaunal bivalves to crab predators, probably by increasing the time required to break open the shell. These features include large size, increased shell thickness, and a more inflated shape with a steep ventral margin. Second, crabs respond to prey density. In the field the mortality rate due to crabs was higher in the patches where the clam density was high than in those where it was low.

I will discuss how vulnerability of bivalves to crabs could interact with crab response to prey density but first would like to clarify several points. The first is whether the preference of crabs for clams with a short shell-breaking times can result in significant differential mortality at subcritical sizes. Initially, differential mortality resulting from the achievement of critical size would seem much more important than differential mortality resulting from crab preference. This is because critical size would seem to represent an absolute mechanical limit above which the clam is invulnerable, no matter how long it is exposed to the crab. Alternatively preference, would seem to be a function of so many variables, such as hunger, the quantity and composition of the alternative prey available, and the risk of predation, that it would seem relatively unimportant in evolutionary time. However the data presented here shows that even at subcritical sizes, crab preference can result in substantial and predictable differential mortality (Fig. 4), and suggests that critical size may result from the interaction of crab behaviour with the mechanics of shell breaking and not just represent an ultimate mechanical limit.

Ultimate mechanically limiting cases do exist, for example a recently settled juvenile crab would be unable to get its claw around the ventral margin of a large *Protothaca staminea*, however in most cases the critical size probably occurs before such limits are reached. Critical size is probably results from the handling time becoming so long that it is more profitable for the crab to sit still and conserve energy (in the lab) or to search for alternative prey (in the field) rather than continue to try to open the shell. In other words, the crab probably "gives up for good" and does not attempt another attack bout. This is supported by the considerable variation observed among the critical sizes obtained for crabs of the same size (Fig. 3) and by the increase in the frequency and the duration of pauses between attack bouts, as the critical size is approached. Crabs of the same size have very similar chelae and if the mechanics of shell breaking were the only consideration, then the critical sizes obtained for crabs of the same size should be similar. The fact that the values obtained are quite different may be partially due to variation in shell strength among clams of the same size or in crab skill but suggests that variation in giving up times (depending on hunger and previous experience), may also be important.

When more easily opened prey are available, the probability of mortality to crabs for a clam with a long shell-breaking time may be extremely low. The order in which the clams were eaten in the preference-among-morphologies experiment (Fig. 4), was remarkably consistent with the rank of the adjusted mean critical sizes obtained by ANCOVA (Table III, Fig. 3), even though the crabs were quite capable of opening the most resistant clam offered. The clams used in the preference experiment were large enough so that the most resistant species was approximately 80% of its critical size and this probably resulted in shell morphology outweighing all the other variables that might have conceivably affected preference. Thus a more productive approach might be to consider critical size a limiting case of preference rather than an entirely different entity.

A second important point concerns the correlation of load at failure with the number of cycles of loading that can be withstood (Fig. 4, Plates 5 and 6). Three mechanisms could account for this, none of which are mutually exclusive.

1. The crab could require longer to chip through the thicker shell.
2. Thicker shells would be stiffer and bend less than thinner shells when loaded with the same load. If the shell behaves approximately like a beam, this results in the tensile strain being less on the inside of the shell for a given load (Wainwright *et al.* 1976), and might allow thick shells to

withstand a greater load without failing.

3. I have data which suggests that the repeated loading of the shell by the crab chela results in fatigue damage (see Wainwright *et al.* 1976, p. 184) which results in the shell failure at a lower load than if it had been loaded only once (Boulding and LaBarbera in prep.). The fatigue life of metals at a low number of loading cycles may be related to the total amount of inelastic strain energy it contains (Lefebvre and Ellyin, submitted). Each time a structure is loaded, a certain amount of inelastic strain energy is absorbed and the amount absorbed increases with the load applied (Wainright *et al.* 1976, p. 14). Unlike the elastic strain energy absorbed by a structure, the inelastic strain energy is not recovered if the load is removed and in a brittle material such as a bivalve shell probably goes into the propagation of microcracks. Failure may occur when this inelastic strain energy, summed over all cycles, totals the amount of inelastic strain energy that could be absorbed by the structure during a single cycle of loading (Lefebvre and Ellyin, submitted). Thus the ability of the thicker shells to withstand more loading cycles than the thin shells could be related to their ability to withstand a greater load when loaded only once.

Another unresolved point is the contrast between 1) the strong preference shown by crabs in the laboratory (Table IV) and in the field enclosures (Fig. 7) for the smallest clams offered and 2) the high mortality rate of all size-classes of *Protothaca*-thick (crab-resistant) clams in the manipulation of prey density experiment (Fig. 8). In the laboratory, starved crabs showed no detectable size selection when allowed *ad libitúm* amounts of three size classes of *Protothaca*-thick (Table VI) and this agrees with results obtained for starved *Carcinus* fed different size-classes of mussels provided *ad libitum* (Jubb *et al.* 1983). In addition, the data from the critical size experiments show that even very small crabs can be forced to eat very large clams if alternative prey is not available (Fig. 3). This is evidence that the degree of prey selection exhibited by a crab is a function of its hunger state and the availability of alternative prey. Since the crabs responded to the prey density differences between the two treatments of the density manipulation experiment, a reasonable extrapolation would be that they would also respond to the density of other species they prey on. Thus the mortality rate to crabs of the clams in a given patch may not only be a function of clam density within that patch relative to other patches, but may also be a function of the density and handling time of the alternative prey available.

Changes in an organism's biotic environment influence the evolution of that organism which, in turn can result in changes in its biotic environment. If the mortality rate of a prey population to these crabs is affected by the density and handling time of the alternative prey, it is plausible that the evolution of defensive shell morphology in gastropods has interacted with the evolution of defensive shell morphology and of infaunalization in bivalves . Predators capable of breaking a mollusc shell often are capable of preying on a variety of molluscs (Vermeij 1977b). Such predators probably concentrate their efforts on prey with a high profitability. Characteristics of bivalves that would increase their profitability to crabs include: a short shell-breaking time, a shallow depth of burial, and a high density. If a predator is preying on a prey with a high profitability, such as a thin-shelled, epifaunal gastropod, there would be strong selection for prey features, such as more elaborate defensive shell morphology, that decreased its profitability to the predator. This could increase the predation pressure on the other prey species since they now have a higher profitability relative to the previously highest ranking prey. This would select for features that decreased their profitability as prey; for example bivalves might retreat deeper into the sediment which increases the time required to find them and to dig them up, or develop a thicker, more inflated shell which will increase their shell-breaking time.

An increase in the incidence of crab-resistant shell features would result in a decrease in the profitability of the prey available to crabs and could result in strong selection for shell-breaking morphology that reduced the amount of time required to exploit shelled prey and increased the size-range of potential prey. Prolonged periods of low prey abundance can result in very high selection coefficients for a morphological feature that improves the size-range of or the efficiency with which prey can be exploited. Very high selection intensities for large beaks have been documented for Darwin's finches during a drought where the abundance of seeds was markedly reduced and the size and hardness of those that were present was markedly increased (Boag and Grant 1981). Thus, I do not agree with Vermeij's argument (1982b) that coevolution between predators and prey is only likely when the prey can cause the death of the predator.

The potential for evolution of both crab chelae and shelled prey could lead to an "arms race" (*sensu* Vermeij 1976) in which selection for more elaborate crab-resistant shell morphology interacts with selection for more elaborate shell-breaking morphology. This "race" would not continue indefinitely, at some point the evolutionary or energetic cost of the antipredator shell morphology (Palmer 1981), or of the increasing infaunalization that prey require to decrease their profitability to the predator, or the cost of the morphology that the predator requires to efficiently exploit the prey, would probably outweigh the benefits. For example, while large, specialized, chela would increase the efficiency with which shelled prey could be exploited, specialization may entail certain costs. For these crabs an increase in the chela height to length ratio would allow a greater degree of gape for a chela of the same weight and would allow larger shelled prey to fit entirely within the chela, markedly increasing the efficiency with which such prey can be crushed. Chelae that are highly specialized for crushing shelled prey are severely limited in the other functions they can perform (Warner 1977) and could, for example, be too blunt to efficiently probe the sediment and have fixed fingers which are too thick to peel open gastropod shells with small apertures. Also the energetic cost to maintain large, heavily calcified chela with a lot of muscle fibers may be very high, especially in juvenile crabs where molting is frequent. The chela morphology of crabs that prey on a wide variety of shelled invertebrates, such as these cancrids, probably represents a compromise between the type of chela morphology needed to crush large shells efficiently, and other chelae functions such as probing in soft sediments, defense from predators, and aggressive interactions among crabs. Thus, as has previously been discussed for bivalve shell morphology, chela morphology represents an equilibrium between opposing selection pressures. It is conceivable that if the cost to benefit ratio of more elaborate crab-resistant shell morphology increased faster than the cost to benefit ratio of more elaborate shell-breaking morphology that the prey species might go extinct.

The tendency for this "arms race" to escalate, and the increasing cost of participation, may explain the feasibility of strategies other than the development of morphological defenses. A possible example of this is the tellinid bivalves that may counter the disadvantage of the minimal protection afforded by their thin shells with the advantage of the fast growth rate and opportunistic life history strategy that is then possible. Another strategy that may be employed is the reduction of profitability by reducing body size so that the number of calories per unit time the predator obtains is low relative to alternative prey (Palmer 1983). While selection for chela morphology that allowed more efficient crushing of large shells might be more pronounced when prey density is low, selection for crab-resistant shell morphology in bivalves might be more pronounced when bivalve densities are moderately high. Crabs are more selective when prey is adequate to satiate them than when it is not (Elner and Hughes 1978; Jubb *et al.* 1983; Table IV; Table VI) and this results in greater differential survival of the more resistant prey when overall prey density is high (Elner and Hughes 1978; Fig. 4; Table IV). Thus it is important to examine selection intensities at various densities of predators and prey before evaluating the relative importance of crab predators as a selective force on bivalve shell morphology.

There are several logical extensions of this work that I plan to follow up for my Ph. D. research. These experiments suggest that the degree of prey selection shown by these crabs is influenced by prey density. A key aspect of my study will be the manipulation of prey density in areas with high densities of natural infauna and in areas with low densities of natural infauna.

This will allow me to examine how the degree of selection shown by the crabs and the mortality rate attributable to crabs varies with the density and the different components of the handling time of the alternative prey available. While the crab movement data presented here show that crabs are capable of moving relatively long distances (> 50 m/day) and forage in the intertidal during night high tides, more precise data are needed if the factors influencing their local movements, such as predator avoidance, are to be identified. To some extent this can be accomplished by more dives during night high tides and more observations from boats and from shore. But these methods of obtaining this data are slow and are likely to disturb the crabs. Methods of telemetry exist that allow resolution of the position of the animal to one or two meters, by comparing the time of signal arrival among several fixed receivers (Hawkins *et al.* 1979), and these methods could be used to correlate crab movement with factors such as the position of their predators.

More detailed knowledge of the time crabs require to exploit different types of shelled prey would test whether prey vulnerability is a simple function of shell-breaking time. The technique of recording from a strain gauge glued to crab chelae is the most accurate method of obtaining the amount of time a crab takes to break open a mollusc shell; the time actually spent applying force to the shell can be distinguished from the time for which the shell is only being held. This technique also allows measurement of the magnitude and duration of the force pulses that must be exerted to cause shell failure. I have recordings for clams of different sizes and shell thicknesses but would like to expand this to include mollusc species with different types of shells and crabs with different types of chela morphology. After considerable work, I have overcome many of the technical difficulties with this technique. A test movie taken with a strobe flash suggests that these crabs are unable to detect rapid pulses of light. This will enable the use of a video camera with a strobe flash to automate correlation of the crab's behaviour with the force pulses it generates with its chela, and will not require the amount of light needed to do this manually. One of the most serious remaining problems with this technique is the time required to acclimate the crabs to the restraining effect of the wires that connect the strain gauge to the wheatstone bridge and the chart recorder. Acoustic transmitters with built in wheatstone bridges had been built in packages of dimensions 47 mm X 13 mm (Pincock and Luke 1975). If the strain gauge on the chela could be connected directly to the wheatstone bridge on a transmitter glued to its back, the wire tethering it to the chart recorder would be unnecessary. The frequency of the sonar pulses emitted by the transmitter could be made to be proportional to the amount of force was being exerted and could be recorded onto a tape recorder and later passed through a frequency to voltage converter, and into a chart recorder. This would allow this technique to be used in more natural habitats such as in large tanks or in the field.

Finally, I have obtained data that suggest these crabs repeatedly load large shells resulting in the fatigue of the shell material so that the shell fails at a lower load than it would have, had it not been previously loaded (Boulding and LaBarbera, in prep). I am interesting in pursuing this to determine in which situations fatigue failure is important in shell-breaking predation. I also have data (Boulding and LaBarbera, in prep) which show that a cancrid crab chela manages to keep its outside surface in compression under almost any loading conditions. This is probably advantageous because the outside layer (the epicuticle) is the layer that is calcified. Since crab cuticle, like most brittle materials is stronger in compression than in tension, this design maximizes the strength of the chela. But how this is accomplished and how the crab avoids fatiguing its chela along with the clam's shell warrants further investigation.

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APPENDIX ONE. LABORATORY DATA: RANKING VULNERABILITY AMONG MORPHOLOGIES USING CRITICAL SIZE

The Critical (maximum size) of clam that a given crab could open under the conditions of this experiment[1]. (This is the raw data shown in Figure 3 and analysed in Table III).

Crab carapace width (cm)	Crab sex	Clam Species	shell length (cm) largest opened	next largest offered	largest offered	cuberoot predicted[2] dry body weight (gms $^{1/3}$)
2.0	M	*Protothaca*-thick	1.4	1.4	1.4	0.30
2.1	M	*Protothaca*-thick	1.1	1.6	1.6	0.23
2.1	M	*Protothaca*-thick	1.1	1.4	1.6	0.23
2.3	M	*Protothaca*-thick	0.8	1.0	1.6	0.17
3.0	M	*Protothaca*-thick	1.5	1.6	3.7	0.32
3.2	F	*Protothaca*-thick	2.4	3.1	4.0	0.51
3.2	M	*Protothaca*-thick	2.5	2.8	3.6	0.54
4.3	F	*Protothaca*-thick	2.6	3.0	5.7	0.56
4.3	F	*Protothaca*-thick	3.1	4.0	5.0	0.67
4.3	F	*Protothaca*-thick	3.0	3.4	3.6	0.64
4.4	F	*Protothaca*-thick	2.5	2.9	2.9	0.54
4.6	M	*Protothaca*-thick	2.6	3.0	4.5	0.56
5.5	M	*Protothaca*-thick	4.0	4.5	5.5	0.86
5.6	M	*Protothaca*-thick	3.8	4.0	6.1	0.82
5.8	F	*Protothaca*-thick	4.9	5.6	5.6	1.1
5.9	M	*Protothaca*-thick	5.3	5.3	5.3	1.2
6.2	F	*Protothaca*-thick	5.3	5.5	5.5	1.2
7.0	F	*Protothaca*-thick	5.1	5.1	5.1	1.1
2.3	M	*Protothaca*-thin	2.6	2.9	2.9	0.58
4.3	M	*Protothaca*-thin	4.1	4.5	5.5	0.91
4.4	M	*Protothaca*-thin	4.2	4.7	4.9	0.93
4.5	M	*Protothaca*-thin	3.9	4.2	4.5	0.86
5.1	M	*Protothaca*-thin	5.3	5.6	5.9	1.2
5.6	F	*Protothaca*-thin	5.3	5.4	5.4	1.2
5.8	F	*Protothaca*-thin	3.9	4.5	5.1	0.86
6.5	M	*Protothaca*-thin	5.5	5.7	5.7	1.2
6.6	M	*Protothaca*-thin	5.7	6.2	6.2	1.3
3.6	M	*Saxidomus*	4.1	4.9	5.5	0.90
4.2	M	*Saxidomus*	3.7	4.1	6.3	0.81
4.6	M	*Saxidomus*	5.1	5.6	6.9	1.2
4.8	M	*Saxidomus*	5.5	5.9	5.9	1.3
7.7	M	*Saxidomus*	6.4	7.4	8.0	1.5
7.8	M	*Saxidomus*	7.6	8.1	8.1	1.8

1) Crabs were initially offered three individuals of their assigned clam type. These were replaced by successively larger clams until at least a week had passed without the crab opening a clam. The previous clam opened was considered the critical size.

2) Of the largest clam opened (see methods and Table II for explanation of cuberoot body weight).

APPENDIX TWO. FIELD DATA: PREDATOR EXCLUSION/INCLUSION EXPERIMENT

Number of clams recovered in each of four categories: Alive (AL), Crab crushed (CC), Dead Undamaged (DU), and Missing (MI), for each of three size-classes. Total number of clams initially planted was 15 of each size class. (See Figure 7 for means and standard errors, text for analysis).

No.	Treatment	Small clams				Medium clams				Large clams			
		AL	CC	DU	M	AL	CC	DU	M	AL	CC	DU	M
A 3	Predator-Exclusion	14.	0.	1.	0.	14.	0.	1.	0.	14.	0.	1.	0.
B 6	Predator-Exclusion	11.	0.	1.	3.	11.	0.	0.	4.	15.	0.	0.	0.
C 9	Predator-Exclusion	15.	0.	0.	0.	14.	0.	1.	0.	12.	0.	1.	2.
A 1	Inclusion-One Crab	11.	1.	0.	3.	15.	0.	0.	0.	15.	0.	0.	0.
B 7	Inclusion-One Crab	14.	0.	0.	1.	13.	0.	1.	1.	15.	0.	0.	0.
C11	Inclusion-One Crab	11.	1.	0.	3.	16.	0.	0.	0.	15.	0.	0.	0.
A 4	Inclusion-Three Crabs	5.	0.	0.	10.	13.	1.	1.	0.	15.	0.	0.	0.
M 5	Inclusion-Three Crabs	5.	4.	0.	6.	13.	0.	0.	2.	15.	0.	0.	0.
C12	Inclusion-Three Crabs	0.	4.	0.	11.	9.	6.	0.	0.	15.	0.	0.	0.
B 8	Inclusion-Three Crabs	1.	9.	0.	5.	8.	5.	0.	2.	13.	1.	1.	0.
A 2	Unprotected	4.	3.	0.	8.	8.	6.	1.	0.	10.	2.	0.	3.
B10	Unprotected	13.	0.	1.	1.	14.	1.	0.	0.	13.	0.	1.	1.
C13	Unprotected	1.	5.	0.	9.	9.	3.	0.	3.	10.	4.	0.	1.
Lab:	Inclusion-One Crab	6.	8.	0.	1.	12.	2.	0.	1.	15.	0.	0.	0.

APPENDIX THREE. FIELD DATA: PREY DENSITY MANIPULATION EXPERIMENT

Number of clams recovered in each of four categories: Alive (AL), Crab crushed (CC), Dead Undamaged (DU), Missing (M). Total number of clams initially planted was 5 of each size class for the sparse treatments and 20 of each size class for the dense . (See Figure 7 for means and standard errors, text for analysis).

Winter-Spring Run

No.	Treatment	Size-class	AL	CC	DU	M
a 4	sparse	small	5.	0.	0.	0.
a 4	sparse	medium	4.	1.	0.	0.
a 4	sparse	large	1.	3.	0.	0.
b 2	sparse	small	3.	1.	1.	0.
b 2	sparse	medium	3.	2.	0.	0.
b 2	sparse	large	1.	4.	0.	0.
c 7	sparse	small	4.	0.	0.	1.
c 7	sparse	medium	4.	1.	0.	0.
c 7	sparse	large	4.	1.	0.	0.
d 9	sparse	small	4.	0.	0.	1.
d 9	sparse	medium	4.	0.	1.	0.
d 9	sparse	large	3.	2.	0.	0.
e 6	sparse	small	6.	0.	0.	0.
e 6	sparse	medium	3.	0.	0.	2.
e 6	sparse	large	4.	1.	0.	0.
f 1	dense	small	14.	5.	1.	0.
f 1	dense	medium	12.	4.	0.	4.
f 1	dense	large	14.	3.	0.	3.
g 3	dense	small	12.	7.	0.	1.
g 3	dense	medium	13.	7.	0.	0.
g 3	dense	large	9.	9.	0.	2.
h10	dense	small	11.	5.	0.	4.
h10	dense	medium	14.	4.	0.	2.
h10	dense	large	8.	4.	1.	7.
i 8	dense	small	9.	5.	0.	6.
i 8	dense	medium	11.	9.	0.	0.
i 8	dense	large	7.	11.	1.	1.
j 5	dense	small	9.	10.	1.	0.
j 5	dense	medium	10.	6.	0.	4.
j 5	dense	large	10.	3.	1.	6.

Summer Run

No.	Treatment	Size-class	AL	CC	DU	M
e 3	sparse	small	3.	1.	0.	1.
e 3	sparse	medium	3.	1.	0.	1.
c 7	sparse	small	4.	1.	0.	0.
c 7	sparse	medium	5.	0.	0.	0.
b 8	sparse	small	3.	1.	0.	1.
b 8	sparse	medium	3.	2.	0.	0.
a 9	sparse	small	4.	1.	0.	0.
a 9	sparse	medium	2.	1.	0.	2.
d 4	sparse	small	5.	0.	0.	0.
d 4	sparse	medium	5.	0.	0.	0.
g 1	dense	small	10.	9.	1.	0.
g 1	dense	medium	14.	6.	0.	0.
i 2	dense	small	8.	10.	0.	2.
i 2	dense	medium	12.	8.	0.	0.
j 6	dense	small	13.	7.	0.	0.
j 6	dense	medium	5.	12.	0.	3.
f 10	dense	small	12.	8.	0.	0.
f 10	dense	medium	9.	9.	0.	1.
h 5	dense	small	11.	8.	1.	0.
h 5	dense	medium	14.	6.	0.	0.