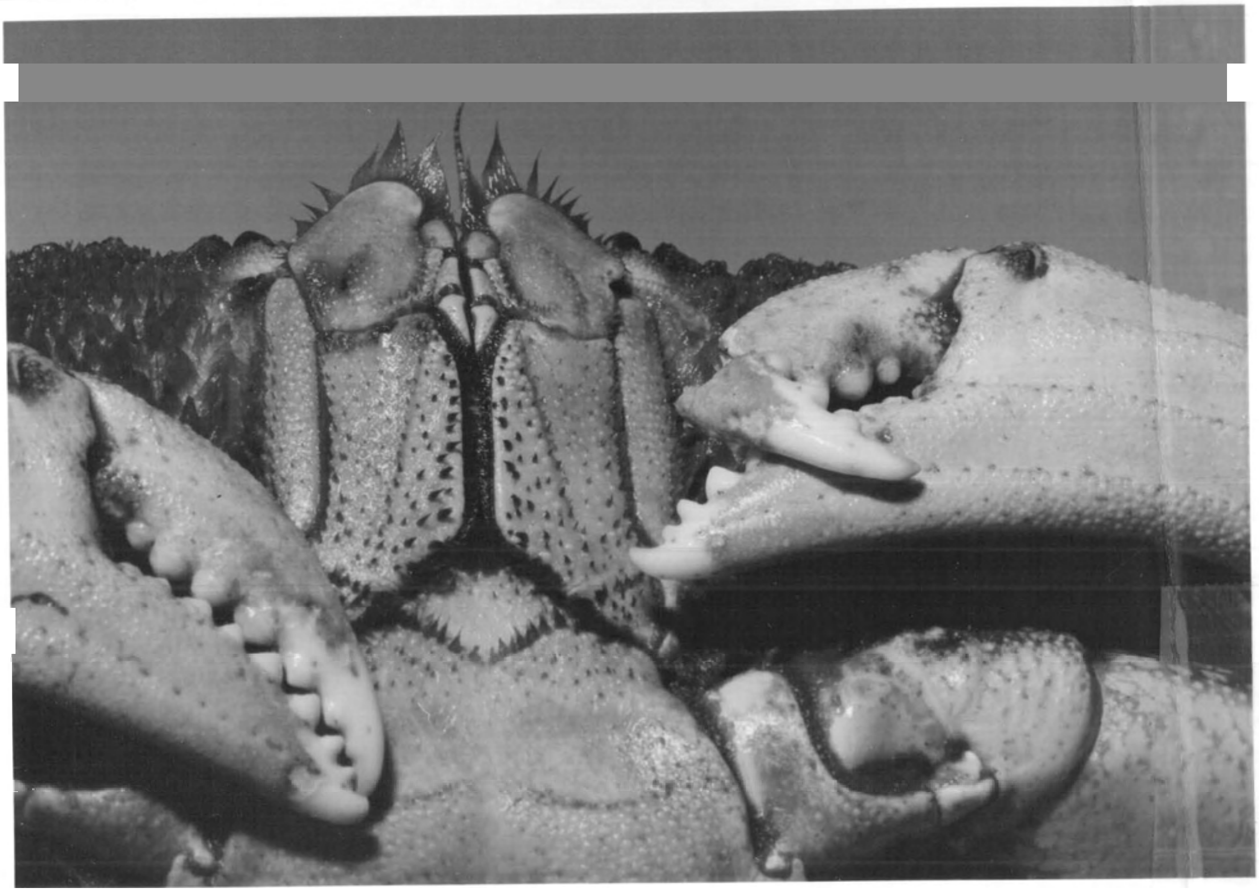

This crab broke its dactylus while attempting to crack a large clam.

THE USE OF ALTERNATIVE CURRENCIES TO PREDICT PREY PROFITABILITIES OF *CANCER MAGISTER* FEEDING ON *PROTOTHACA STAMINEA*

by

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Title of Thesis/Project/Extended Essay

The use of alternative currencies to predict prey profitabilities of *Cancer magister* feeding on *Protothaca staminea*

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Aug. 7th, 1987

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ABSTRACT

Alternative currencies were used to predict prey size selection of *Cancer magister*, a decapod crustacean, feeding on *Protothaca staminea*, a hard-shelled venerid clam. The parameters measured were: energy content of the prey, energetic cost of predation, and handling time. All of these variables were positive exponential functions of clam size. The different measures of prey value (or profitability) provided contrasting prey rankings. Both net and gross rates of energy intake ((Benefit-Cost)/Time and Benefit/Time respectively) predicted that the largest clams were the most profitable. Energetic efficiency (Benefit/Cost) predicted that the smallest clam sizes were the most profitable.

Prey-size selection experiments, offering crabs mixtures of 2 or 3 clam size classes, showed that crabs always ate more clams from the smallest clam size class offered. Thus it is the predictions from the the energetic efficiency model that provide the best fit to the results. A review of previous decapod-bivalve feeding studies indicated a consistent preference for the smallest sizes of prey available.

The use of energetic efficiency as a currency requires energetic cost to be limiting over the animal's lifetime. In this study I propose claw damage, defined as chelae breakage and claw tooth wear, as a consequence of low cycle fatigue, to be this limiting non-renewable resource. A field study of a natural population of *Cancer magister* indicated that levels of wear and breakage were significant and were related to sex and molting state.

Laboratory experiments showed that crabs with broken claws were unable to crack clams. Crabs with artificially worn claw teeth had significantly longer handling times than 'normal' crabs. Finally, the ecological effects of claw breakage in decapods are evaluated with reference to growth, molting ability, regeneration load, and reproductive success.

A FEW QUOTES

"I have an old belief that a good observer really means a good theorist."

Darwin, 1860

"We have to face the fact that while ecological work is fascinating to do, it is unbearably dull to read about..."

Elton, 1927

"... all knowledge patterns are warped, first by the collective pressure and stream of our time..., second by the thrust of our individual personalities."

Steinbeck, 1962

"The invention of alternatives to the view at the center of discussion constitutes an essential part of the empirical method..."

Feyerabend, 1975

"A Spaniard does not need to be a Surrealist. He is already irrational."

Joan Miro

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To Bill, Joanne, Fran, Thomas and the other 'assorted film-types' thanks for all the stimulation (intellectual and otherwise) and the many hours of escape that kept me somewhat sane through all this.

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friends, provided mental support and constructive criticism. I hope for their continued success.

A mis padres les quiero dedicar este trabajo y darles las gracias por su interés, cariño y paciencia durante estos dificiles años. To my sister Mary thanks for the curiosity, companionship, and encouragement (and that often-borrowed car).

Throughout my stay at SFU, Ann Hawkins has provided love, support and understanding. It is gratifying to realize how much easier the frustations of graduate life are to cope with when they can be shared.....

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I. GENERAL INTRODUCTION

Optimization is the process of minimizing costs or maximizing benefits, or obtaining the best possible compromise between the two. Evolution by natural selection is a process of optimization, in that it tends to maximize fitness (Alexander 1982; Krebs and McCleery 1984). By extension, optimality models have been used most extensively in ecology to analyse foraging behaviour. Optimal foraging theory (OFT) has been criticized (Gould and Lewontin 1979; Lewontin 1983; Myers 1983; Pierce and Ollason 1987) but remains a research topic of increasing interest (Krebs et al. 1983; Pyke 1984) and continuing review (Pyke et al. 1977; Krebs et al. 1983; Hughes 1980; Pyke 1984; Krebs and McCleery 1984; Stephens and Krebs 1986; Stearns and Schmid-Hempel 1987).

The major components of optimal foraging models can be viewed in terms of decision, currency and constraint assumptions. This study will refer to all three components but will concentrate on the choice of currency used to predict the value of different prey items to a forager.

Most classical foraging models maximize the net rate of energy gain while foraging (Krebs and McCleery 1984; Stephens and Krebs 1986). More energy is assumed to be better because a forager will be more likely to meet its metabolic requirements, and will thus be able to spend spare energy on other non-feeding activities (such as fighting, avoiding predators and reproducing). The fitness of a forager (in terms of reproductive success) is assumed to be directly proportional to the expected rate of food intake. Although most studies have used net energy intake rate as a parameter, practically it is gross energy intake rates that are measured because of the difficulty in obtaining true values for the energetic cost of predation. The distinction between gross and net rates of food gain as predictors of the optimal diet have been theoretically explored (Charnov 1973) but not empirically tested.

Energetic efficiency (the ratio of energy gained to energy lost) has recently been proposed as an alternative currency appropriate to those cases where energetic costs (or resource allocation) may be limited over the animal's lifetime (Cheverton et al. 1985; Schmid-Hempel et al. 1985). Although predictions from diet models using energetic efficiency as a currency have been shown to fit prey size selection for various animals (Sherry and McDade 1982; Stein et al. 1984), only in the case of honeybees has a theoretical basis for its use been developed (Schmid-Hempel et al. 1985; Kacelnik et al. 1986; Schmid-Hempel 1987). Schmid-Hempel and his colleagues argue that honeybee workers seem to be constrained by a limited amount of flight performance rather than by a fixed life-time available for foraging. This may be a general mechanism for foraging animals that are constrained by the allocation of a mechanical or a physiological cost from a fixed total budget.

Recent experiments involving size selection by crabs feeding mostly on bivalves and gastropods have provided quantitative tests of predictions based on OFT (Elner and Hughes 1978; Hughes 1979; Elner 1980; Hughes and Seed 1981; Blundon and Kennedy 1982a; Jubb et al. 1983; Lawton and Hughes 1985; ap Rheinallt 1986) and have pointed towards new theoretical directions (Hughes and Elner 1979; Hughes 1979; Hughes 1980). Most of these studies have used energy intake rate as the currency to measure prey value, *Carcinus maenas* as the predator, and mussels (*Mytilus edulis*) as the most common bivalve prey.

In the present study, predation by *Cancer magister* (a crab from the Northeastern Pacific) on *Protothaca staminea* (a hard-shelled venerid clam) is used to contrast and test the predictions of three different currencies: net and gross energy intake rates, and energetic efficiency.

The objectives of this study include:

1. a description of the methods of attack by crabs on the clams.
2. development of different versions of the optimal diet model to predict prey value based on different currencies from energetic content of the prey, energetic cost of predation, and handling times.
3. testing of these predictions by conducting prey-size selectivity experiments.

Boulding and LaBarbera (1986) have recently suggested that crabs are able to crush large hard-shelled clams by repeatedly loading the same region of the bivalve's shell with a chela, eventually causing fatigue of the shell material. The accumulation of low-cycle fatigue, represented by constant wear of the claw teeth and eventual breakage of parts of the chelae, will be proposed as the non-renewable and thus limiting mechanical constraint.

The final section of this thesis combines a field survey to determine the presence of claw breakage and wear, and an experiment in which the effects of claw damage on foraging behaviour is examined. The ecological effects of claw breakage are then evaluated with reference to growth and reproductive success.

II. DESCRIPTION OF PREDATOR AND PREY

Cancer magister Dana (Brachyura:Cancridae), commonly known as the Dungeness crab or the Pacific edible crab, occurs in shallow coastal waters from central California to Alaska and is fished commercially over most of its range.

Adult Dungeness crabs typically inhabit areas of sand or sandy-muddy bottoms within bays and estuaries as well as in the open ocean and may be found from mean low water to at least 90 m. Various aspects of *Cancer magister* biology have been reported by many authors (see for example Butler 1967 for a bibliography of the species). General reviews of life history and ecology have been published by Mackay (1942), Cleaver (1949), Butler (1956,1960,1961) and Selby (1980). Foraging by *Cancer magister* is opportunistic and makes almost exclusive use of the infauna (Butler 1954; Bernard 1979, 1981; Mayer 1973; Gotshall 1977; Pearson et al. 1979). Diet of the crabs changes with age and as juveniles these animals can be highly cannibalistic (Stevens et al. 1982; Stevens and Armstrong 1984). Food items are located both tactilely and chemosensorily. Hairs on the chelae and walking legs are both mechanoreceptive (Butler 1954) and chemosensitive (Barber 1960). Distance chemoreception is facilitated by aesthetascs on the outer flagellum of the antennules enabling the animal to show foraging behaviour (dactyl probing of the substratum and increased antennular flicking rates) down to concentrates of 10^{-12} g/l of *Protothaca* *staminea* extract (Pearson et al. 1979). The location of their eyes enables crabs to watch for predators while handling a prey item. As well, crabs may carry a clam before attempting to eat it using their chelipeds to brace the clam against their mouthparts. The family Cancridae is somewhat unique in that most of its members are monomorphic, i.e. both their chelae are of the same size and usually identical to each other (Nations 1975; Lawton and Elner 1985).

In this study only adult male crabs, ranging from 16.0-18.5 cm in carapace width (measured between the tips of opposite 10th anterolateral spines), were used to reduce sex and size related variation. Crabs were obtained either from local seafood dealers or from Department of Fisheries and Oceans crab samplings.

Protothaca staminea (Conrad) (Veneridae), the native littleneck clam, is a hard-shelled bivalve found in sand or gravel substrates ranging from lower California to the Aleutian Islands. They burrow to a maximum depth of 15 cm and occur from slightly above the mid-intertidal beach zone to the subtidal region. They have been recorded to a maximum water depth of 110 meters (Quayle and Bourne 1972). Field studies have shown this clam to be an important component of *Cancer magister*'s diet in British Columbia (Pearson et al. 1979, 1981; Boulding 1983). Clams used in this study were either purchased from a grower or were collected at Nanoose Bay, near Nanaimo, B.C.

III. EVALUATING THE MODELS

Introduction

The classical version of the optimal diet model attempts to rank prey types according to a measure of prey value based on a currency (usually energy intake rates). The general assumptions of the diet model are:

1. Search and handling are exclusive.
2. Encounters with prey are sequential and occur as a Poisson process.
3. Handling times, prey energy content, and encounter rates are fixed.
4. Prey are recognized immediately and without error.
5. The predator has complete information.

Not all of these assumptions always hold, but their effects can be taken into account. For example: the model components can be variable (due to random or behavioural effects (discussed later in this study); prey recognition is not always instantaneous (Elner and Hughes 1978); and since learning can occur, information is not always complete (Hughes and Dunkin 1984b).

The major predictions of the diet model are:

1. Prey types are either always taken upon encounter or never taken upon encounter.
2. Types are ranked by the currency used, usually the ratio of

energy per attack to the handling time per attack. This ratio is called the profitability (or prey value) of a prey type. Types are added to the diet in order of their ranks.

3. The inclusion of a prey type depends only on its value and on the encounter rates of types of higher rank. The inclusion of a type does not depend on its encounter rate.

This model was developed mainly for visual predators which may be expected to recognize the value of a prey item instantly. Hughes (1979,1980) has generalized the model to include finite prey recognition times. Many predators, such as crabs, use chemical or tactile cues to detect and evaluate prey value (Elner and Hughes 1978). Incorporation of prey recognition times modifies the predictions of the model such that the relative abundances of both prey items (of higher and lower prey value in the 2-type example) become important and the less valuable prey item should be included in the diet when its relative abundance is high, even when the most valuable prey type is plentiful. Elner and Hughes (1978) showed that the shore crab, *Carcinus maenas*, incorporated suboptimal mussels (calculated using energy intake rate as the currency) into its diet in proportion to their relative abundance even when optimal mussels were present in excess. They also demonstrated that crabs had a finite recognition time (1-2 seconds) in which they manipulated mussels in their chelae before accepting or rejecting them.

In this study, the general assumptions and predictions will be those of the classical diet model modified to include finite recognition times (Hughes 1979,1980). A range of clam sizes (considered prey types) will be ranked (in terms of prey value) according to three different currencies: net energy intake rate ((Benefit-Cost)/Time), gross energy intake rate (Benefit/Time), and energetic efficiency (Benefit/Cost). The first two currencies (net and gross intake rates) assume foraging (or handling) time to be the most important constraint. Energetic efficiency assumes that the energetic cost of predation is limiting and thus a constraint. The rankings obtained using each currency will then be evaluated by conducting prey-selectivity experiments.

Methods

This work was conducted at Simon Fraser University (1985-1986), the Pacific Biological Station (1983-1984), and the Bamfield Marine Station (Fall 1984). Crabs were kept individually in 50 gallon aquaria without any substrate (to eliminate search times due to digging). Salinity was maintained at 33 to 37 ppt and water temperatures followed ambient air temperatures (at SFU) and ambient seawater temperatures at 60 feet (at PBS and BMS), (ranging from 10-18° C). Artificial lights were regulated to seasonal photoperiod. Prior to a feeding trial, crabs were satiated by giving them unlimited opportunity to consume clam flesh, then starved for 3 days to standardize hunger levels. They were starved for a day between trials.

Energy content of the prey

The caloric content of clam flesh was measured in a micro-bomb calorimeter. Clams were dried to constant weight at 80° C. One gram tissue samples were collected from clams ranging from 1.48 to 5.08 cm in shell length (CL). [1]

The flesh from 23 clams (ranging from 1.48 to 5.35 cm CL) was dried to constant weight at 80° C. These data were used to calculate a dry weight/clam length regression.

Handling Time

Eleven male crabs, ranging in size from 16.0-18.5 cm in carapace width (mean=16.7 cm CW) were individually presented with randomly selected clams. Gaping clams were not used because the crabs would be able to consume the flesh without crushing the shell, thus biasing any results. A maximum of 5 clams were presented to any one crab during a feeding trial. Methods of attack were noted and the following behavioural sequences timed:

1. 'breaking time' was measured as the time from the moment the crab grasped the prey until the first consumption of flesh. This often included short periods of time (under a minute) where the clam was dropped and temporarily ignored. Times of unsuccessful attacks ('persistence times') were not included in the analysis.
2. 'eating time' was measured as the time from the first

---

[1] letters in parentheses represent abbreviations used throughout the text.

consumption of flesh to abandonment of the prey, including intermittent periods of shell breakage and inspection of shell debris towards the end of the meal.

3. 'handling time' was calculated as the sum of breaking time and eating time.

Feeding costs

The energetic cost of feeding was measured through oxygen depletion in a closed-system respirometer with a YSI model 57 meter connected to an oxygen probe with an attached stirrer. The respirometer consisted of a rectangular, clear 7.5 liter plexiglass tank (34x20x12.5 cm). A constant temperature was maintained by placing the respirometer on a water table. Any changes in temperature were compensated for automatically by the probe. The meter was connected to a chart recorder. Thus oxygen uptake could be calculated as a decreasing slope on the chart recording. Efforts were made to reduce crab motor activity by using red light, which decapods are relatively insensitive to (Goldsmith and Fernandez 1968; Fernandez 1973), covering the tank, and keeping movements of investigators in the room to an absolute minimum. Three crabs that had previously shown that they would feed in the respirometer were used in these experiments (mean length=16.6 cm, range=16.4-16.9). Crabs were picked at random and introduced into the respirometer and left there a minimum of one hour before experimentation. The box was then sealed and oxygen allowed to deplete for about 20 minutes to establish resting metabolic rates. A clam, picked at random, was then introduced. Oxygen was used up at a higher rate while feeding proceeded. The maximum rate (steepest slope) attained during a feeding trial was then subtracted from the resting rate to obtain the oxygen consumption due to feeding. Oxygen consumption was measured in parts per million and converted to ml $O_2 \cdot minute^{-1}$ (1 ml $O_2 \cdot l^{-1} = 1.4286$ ppm O_2). Calories were obtained by using the oxycalorific value of 4.63 $cal \cdot ml^{-1}$ (Elliott and Davison 1975).

Prey Value

Gross energy intake rate was calculated as the ratio of predicted energy content and observed handling time. Net energy intake is similar to the 'gross' calculation except cost is subtracted from energetic content (or benefit). Energetic efficiency was calculated as the ratio of predicted benefit and predicted cost.

Hypotheses for all statistical tests were rejected at $p<0.05$.

Results

Crab attack methods

As soon as a clam was introduced the crab oriented its antennules towards the prey and an increase in antennular flicking rate was observed. The crab then started moving towards the clam while probing the bottom of the tank with its walking legs. Following contact, the prey was swept towards the chelipeds using the pereipods. The prey was then manipulated by the crab with the third maxillipeds, the chelae and the first and second pereipods until one of the chelae could grasp the prey easily. These manipulations were frequent before the crabs attempted to break the shell. Initially outright crushing was attempted, one chelae doing the crushing and the other used to support the prey during breakage. No apparent specialization of the chelae was observed, i.e. each one was used to crush clams with an equal frequency. If direct crushing was unsuccessful, then prey was further manipulated by the crab by holding the clam between the chelipeds and slowly rotating it while the maxillipeds 'inspected' the clam (presumably to sense micro-structural cracks in the shell) until another crushing sequence was attempted. After various attempts (often dropping the clam or holding it against the body for periods of time) the clam was again re-oriented and the crab used the tip of its dactylus or propodus to chip the edges of the shell until it could insert a cheliped and break the shell from the inside. The tissue was eaten using various mouthparts to glean the meat from the shell. In most cases, no tissue was left on the shell fragments after they were abandoned. These observations are similar to those of feeding by other *Cancer* crabs (Boulding 1983; Lawton and Hughes 1985) and for juvenile Dungeness crabs feeding on a small estuarine bivalve, *Transenella tantilla* (Asson-Batres 1986).

From these observations a range of clam sizes was selected for further experiments. The upper limit of this range was 4.5 cm in clam length (CL), since clams larger than this were consistently rejected by crabs often after long periods. The lower limit of the range was 1.5 cm CL, the size of the smallest clams available in field collections.

Energy content of the prey

The mean value obtained from the eleven calorimeter bombings was 4636.87±35.07 (S.E.) cal/g dry weight of tissue. A dry weight (W, in grams) vs. clam length (CL, in cm) regression was also calculated where, $W=(CL)^{3.18} \times (10)^{-1.99}$, $r^2=0.99$, $p<0.001$. Thus, the relationship between yield or energy content (in calories) and clam length (in cm) can best be described by the equation $E=46.37 \times (CL)^{3.18}$.

Handling Time

Handling times were normalized by transformation using decimal logarithms (Kologomorov-Smirnov test, N=218, D=0.0531).

The measurement of handling times was made on two distinct groups of crabs. The first group (termed 'old', mean length=16.6 cm, range=16.0-18.5) had been kept at the Pacific Biological Station for about six months and had been fed mostly on pieces of dead herring. Freshly-caught crabs (termed 'new', mean length=16.9 cm, range=16.3-18.1) were obtained in July 1984. These crabs had cleaner carapaces (indicating a recent molt) but showed similar foraging behaviours. An analysis of covariance showed that the handling time components were significantly different for each group of crabs, with the 'old' crabs having higher mean handling, breaking and eating times over the range of clam sizes tested (Figure 1). This result is probably due to an intermolt reduction in both strength and sarcomere length in the chela-closing muscles caused by a lack of 'clam-breaking' exercise (Abby-Kalio and Warner 1984). The general trends of breaking, eating, handling times and profitabilities versus clam length were similar for both groups (Table 1). Mean handling time components were calculated for 12 size classes of prey (i.e., 1.5-1.75 , 1.75-2.00,....., 4.25-4.5 cm CL). A regression was computed to convert 'old' handling, breaking and eating times (in minutes) respectively to 'new' ones where,

$\text{New Ht}=1.052 \text{ x } (\text{Old Ht})^{0.796}$, $r^2=0.931$, $p<0.0001$

$\text{New Bt}=1.574 \text{ x } (\text{Old Bt})^{0.949}$, $r^2=0.903$, $p<0.0001$

$\text{New Et}=1.197 \text{ x } (\text{Old Et})^{0.663}$, $r^2=0.851$, $p<0.0001$

These transformed handling times along with the original 'new' handling times were used in all subsequent calculations.

When plotted against prey size, eating, breaking and handling times were best described by power functions ($\log_{10}$ transformations of both variables, Figures 2-4). When compared to eating times, breaking times seemed more variable, increasing dramatically above a prey size of 3.5 cm. This is probably due to the adoption of the 'chipping' technique when direct crushing was unsuccessful. Variance-mean regression lines of eating and breaking times were compared using an analysis of covariance (Figure 5). For analysis, the range of clam sizes was split into six groups of 0.5 cm CL (i.e. 1.5-2.0, 2.5-3.0,..., 4.0-4.5). The results indicated that the lines were significantly different from each other, with the breaking time line having significantly greater variances at corresponding mean values.

Predation Cost

An exponential relationship exists between oxygen uptake (cal/min) and clam size such that (Figure 6),

$$\text{Cost} = (10^{-2}) \times (CL^{2.86}),\ r^2=0.811,\ p<0.001$$

Prey Value

The relationship between energy intake per unit time (E/T, in cal/min) and clam length (CL, in cm) is best described by a linear regression (Figure 7) where,

$$E/T = 73.35(CL) + 82.64,\ r^2=0.16,\ p<0.01,\ N=218.$$

For the clam sizes used in this study, the values of cost ranged from 0.033 to 11.17 calories while benefit ranged from 168.35 to 5539.27 calories. Because the values of cost were so negligible when compared to benefit, the prey rankings obtained from net and gross profitabilities are almost identical.

Assimilation efficiency rates were considered to be similar for different clam sizes and thus were left out of the analyses.

This may not be true during the clam's reproductive season (for a discussion of assimilation efficiencies in Crustaceans see Grahame 1983, p. 88-96). All of the experiments in this study were performed during the winter and thus the clams used were never in a reproductive state.

The pattern in Figure 7 suggests a positive trend between the variables, i.e. prey value increases with clam size, although there is a large amount of variation above a clam size of 3.5 cm CL.

A larger part of the variation can be explained however, if an iterative technique is used to fit regression lines through the data changing the range of the independent variable included in the analysis until the highest amount of variation can be explained. The best regression found using this technique excluded clam sizes larger than 3.6 cm CL ($E/Ht=(CL)^{1.31} \times 75.54$, $r^2=0.47$, $p<0.0001$, CL=1.5-3.6 cm). Beyond this 'critical' clam size no significant regression can be computed. The large variation in profitabilities beyond a clam size of 3.6 cm is due in part to the variability in breaking times (Figure 2) and to the use of a combination of attack methods (i.e. 'crushing and 'chipping') by the crabs on large clams. If a regression is computed excluding those clams where the 'chipping' method was used (it is sometimes difficult to clearly state which method was used or whether it was a combination of the two), a larger part of the variation can also be explained ($E/Ht=(CL)^{0.92} \times 105.47$, $r^2=0.29$, $p<0.0001$, N=206).

In conclusion, it is clear that prey value increases with prey size (at least up to a clam length of 3.6 cm), although there is a large amount of scatter at the larger clam sizes due to the use of a combination of attack methods by the crabs.

When profitabilities were calculated using eating and breaking times separately, different patterns emerged. The Energy/Eating time relationship is also an accelerating function of clam size ($E/Et=CL^{1.648} \times 78.52$, $r^2=0.61$, $p<0.0001$). However, the energy intake rate per unit breaking time decreases with increasing clam sizes. Although there is a wide scatter, the regression line is significantly different from zero in a negative direction ($E/Bt=CL^{-0.542} \times 1538.15$, $r^2=0.04$, $p=0.0029$). This relationship is obviously a weak one and is probably only significant due to the large number of data points (218).

Energetic efficiency (Benefit/Cost) decreases linearly with clam size (Figure 8) and the relationship can best be described by,

$$EE=4406.24 - 942.4(CL),\ r^2=0.65,\ p<0.001$$

In summary, the alternative currencies provide contrasting qualitative predictions about how these predators should rank their prey and in what order they should be included in their diet. Both net and gross energy maximization predict that the larger clams are the most profitable (i.e profitability increases with clam size), and thus crabs should generally prefer the larger clam sizes. Energetic efficiency suggests that the smallest clams are the most profitable (i.e. profitability decreases with clam size), and thus crabs should rank clams from smaller to larger. These predictions can be tested using prey-selection experiments.

Table 1. Regressions of breaking (Bt), eating (Et), handling times (Ht) and profitabilities (E/Ht and C/E) vs clam length (CL) for 'old' (N=121) and 'new' (N=97) crabs. All regressions were significant ($p<0.05$) except those indicated by a *. Analyses of covariance showed that the handling time components were significantly different for each group, with the'old' crabs always being greater.

		Equation	r^2
OLD	Bt=	$CL^{4.25}$ x 0.03	0.64
	Et=	$CL^{2.34}$ x 0.34	0.61
	Ht=	$CL^{3.29}$ x 0.21	0.70
	E/Ht=	$CL^{-0.11}$ x 229.09	0.002*
	C/E=	$CL^{-0.26}$ x 11220.18	0.54
NEW	Bt=	$CL^{3.55}$ x 0.04	0.70
	Et=	$CL^{1.52}$ x 0.62	0.54
	Ht=	$CL^{2.36}$ x 0.43	0.69
	E/Ht=	$CL^{0.82}$ x 109.65	0.21
	C/E=	$CL^{-1.20}$ x 7762.47	0.42

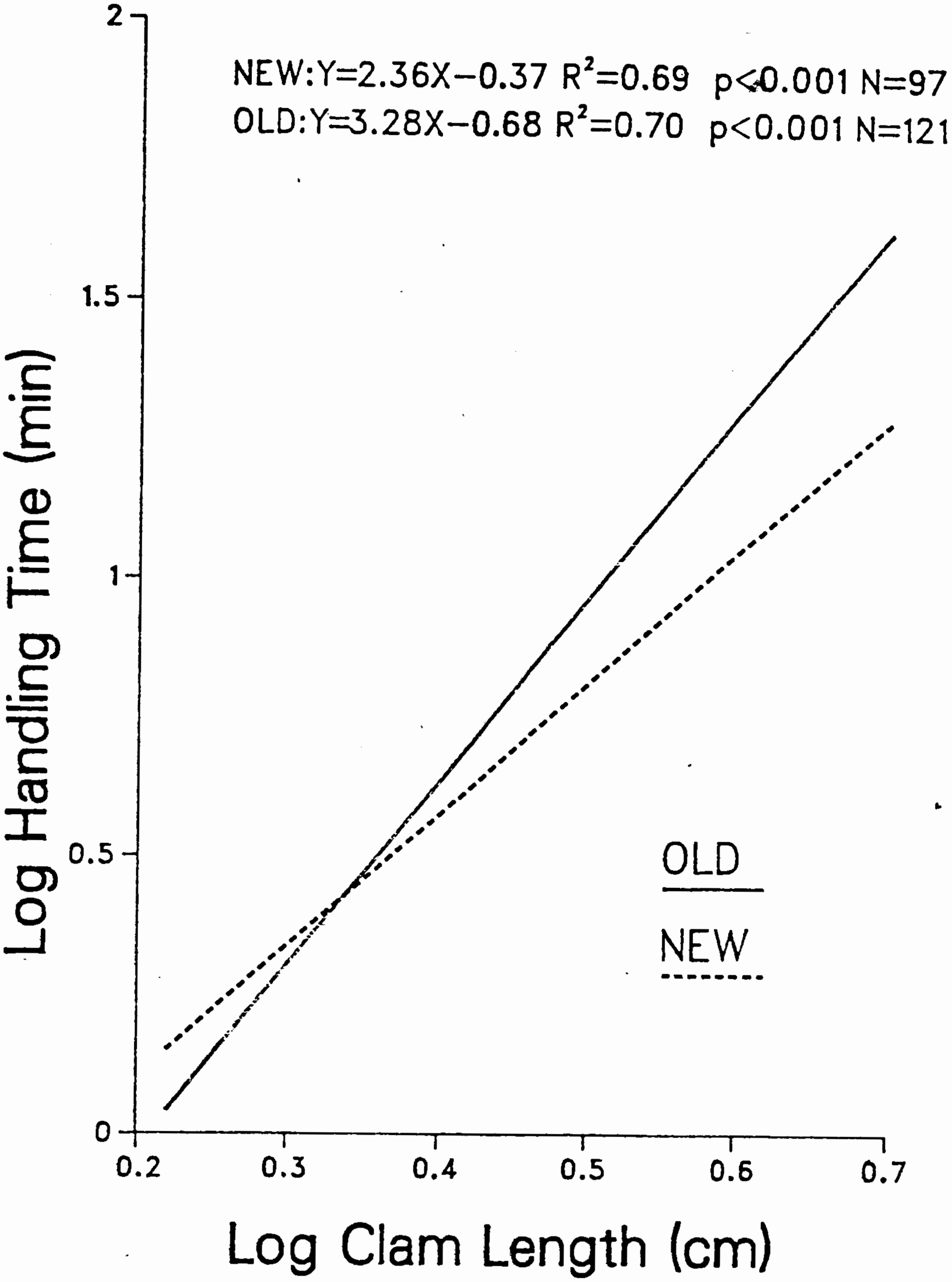

Fig. 1. Log_{10} Handling time vs. Log_{10} Clam length for 'old' and 'new' crabs. An analysis of covariance showed that the lines were significantly different from each other.

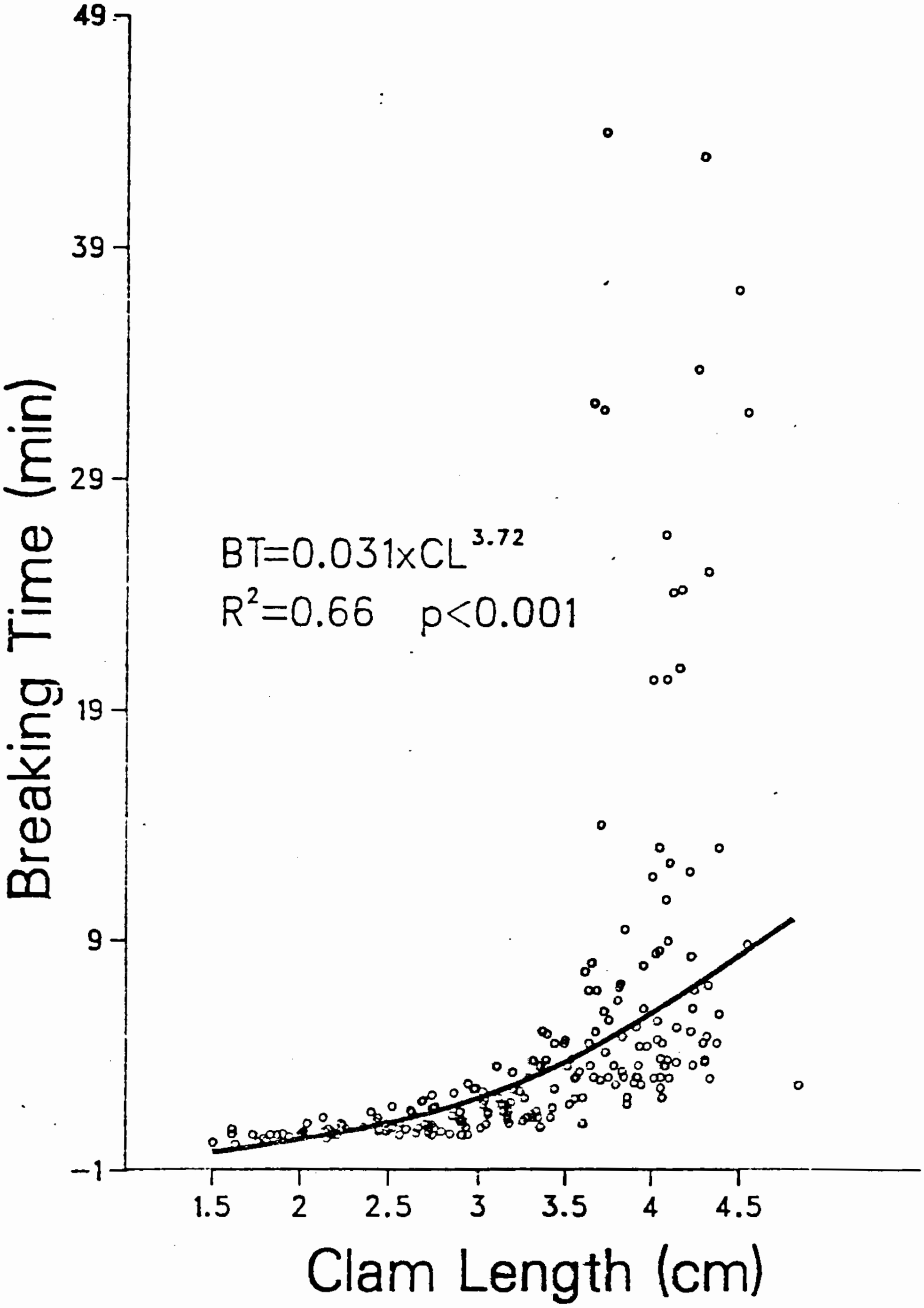

Fig. 2. The relationship between crab Breaking time (minutes) and Clam length (cm).

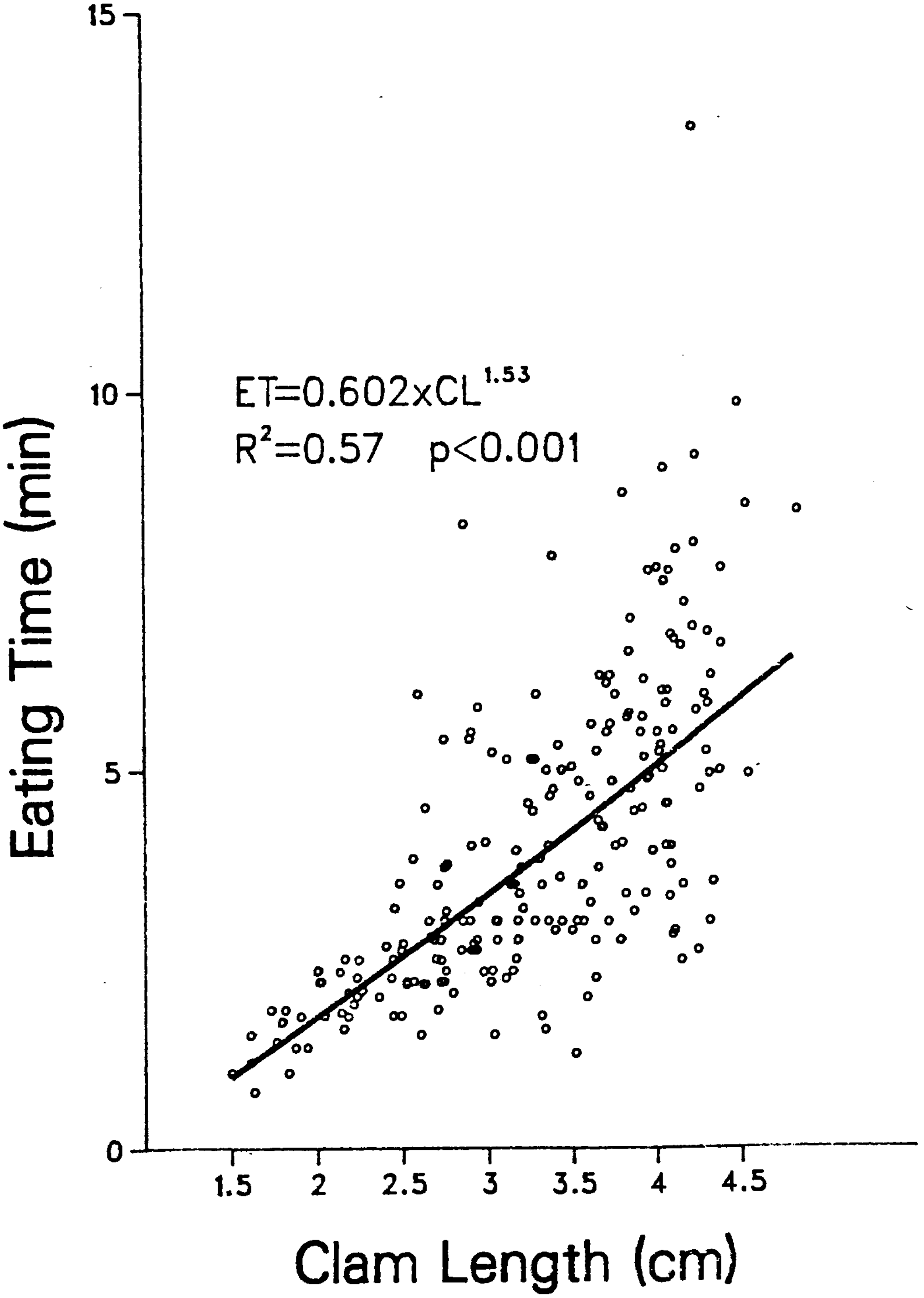

Fig. 3. Cancer magister eating times as a function of Clam length (cm).

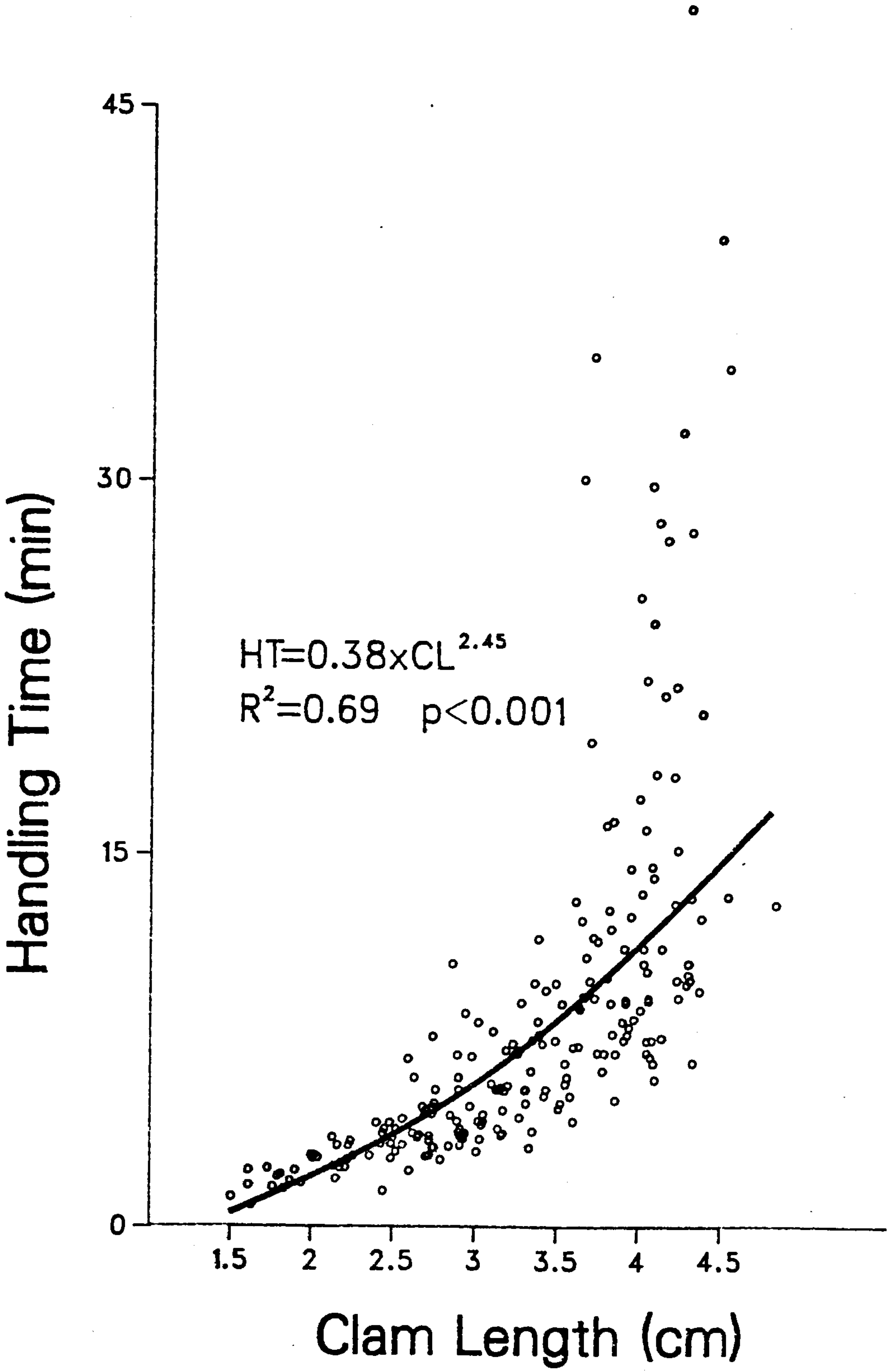

Fig. 4. The relationship between crab Handling time (minutes) and Clam length (cm).

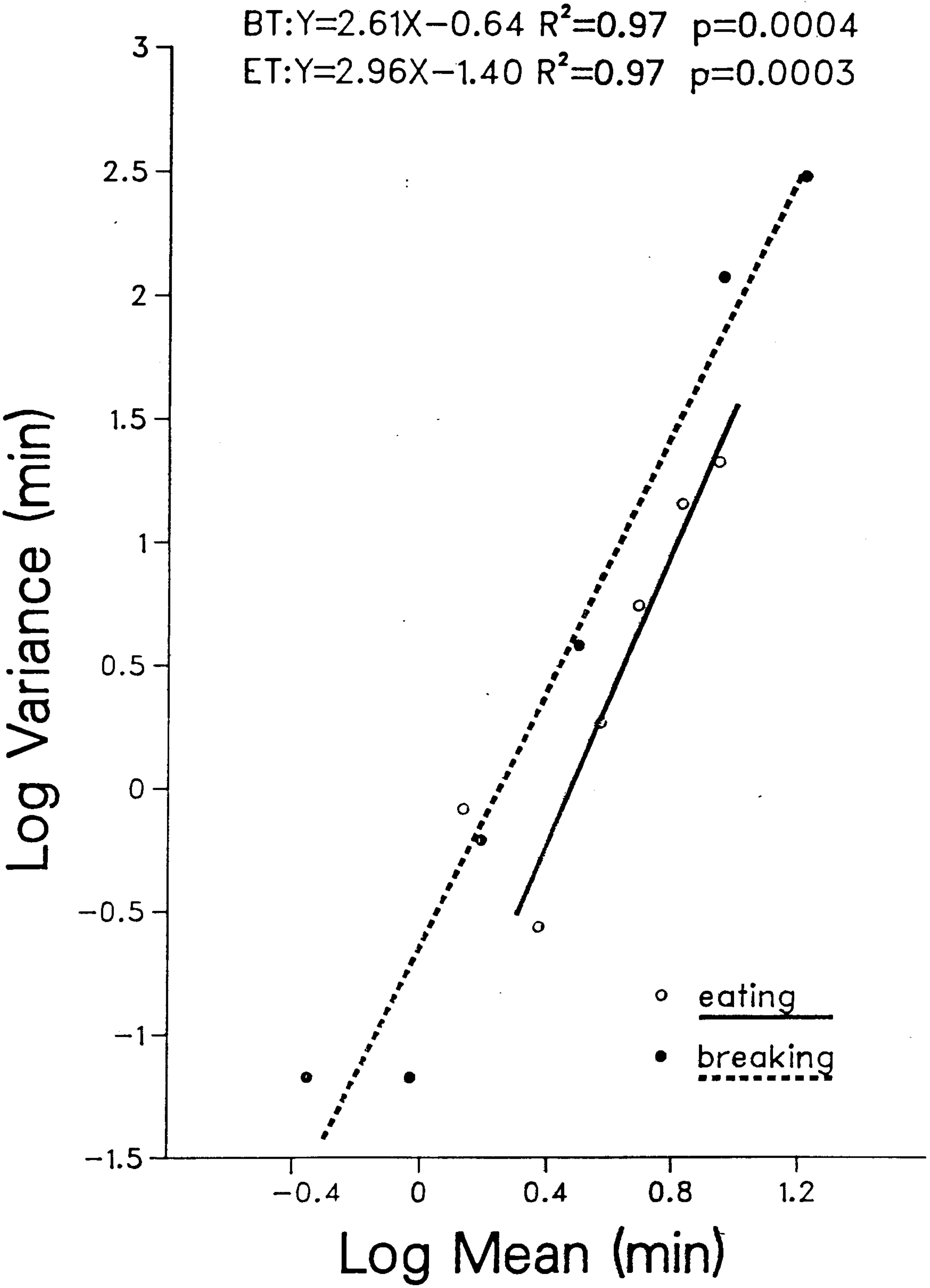

Fig. 5. Log_{10} Variance vs. Log_{10} Mean for 'eating' and 'breaking' times. An analysis of covariance showed that these lines were significantly different from each other.

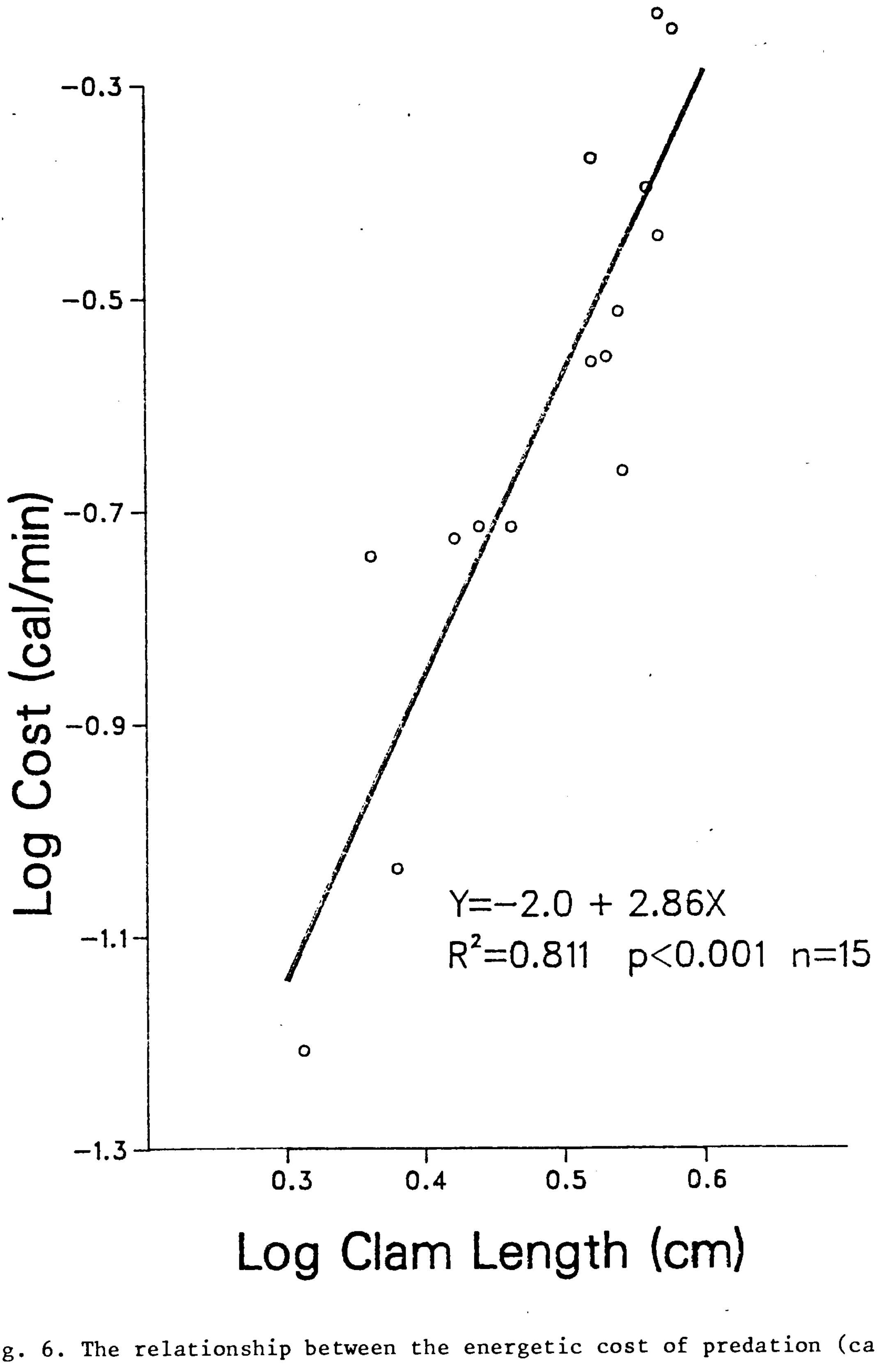

Fig. 6. The relationship between the energetic cost of predation (cal/min) and Clam length (cm).

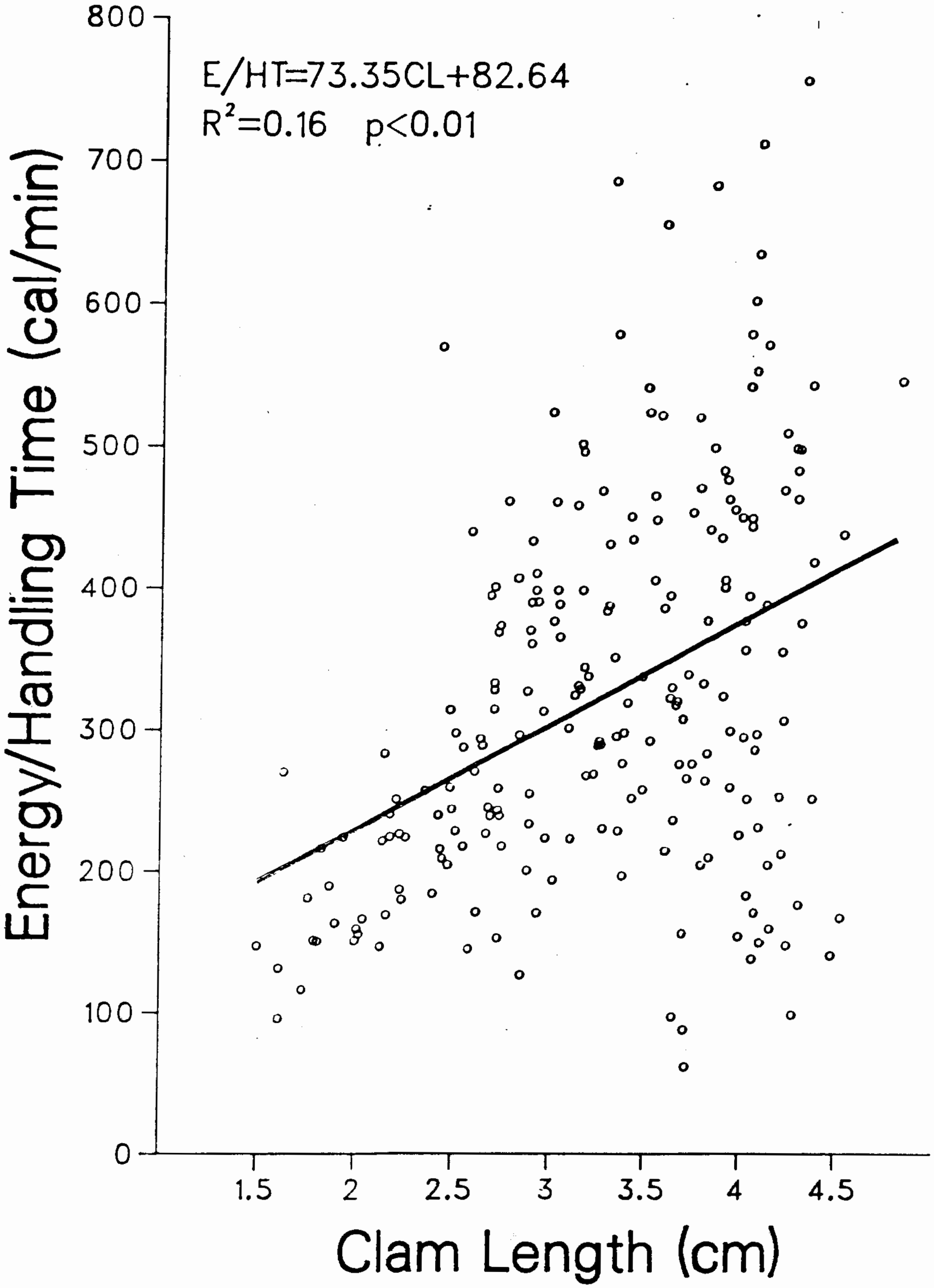

Fig. 7. Profitability (measured as the rate of energy intake per unit handling time in cal/min) vs. Clam length (cm).

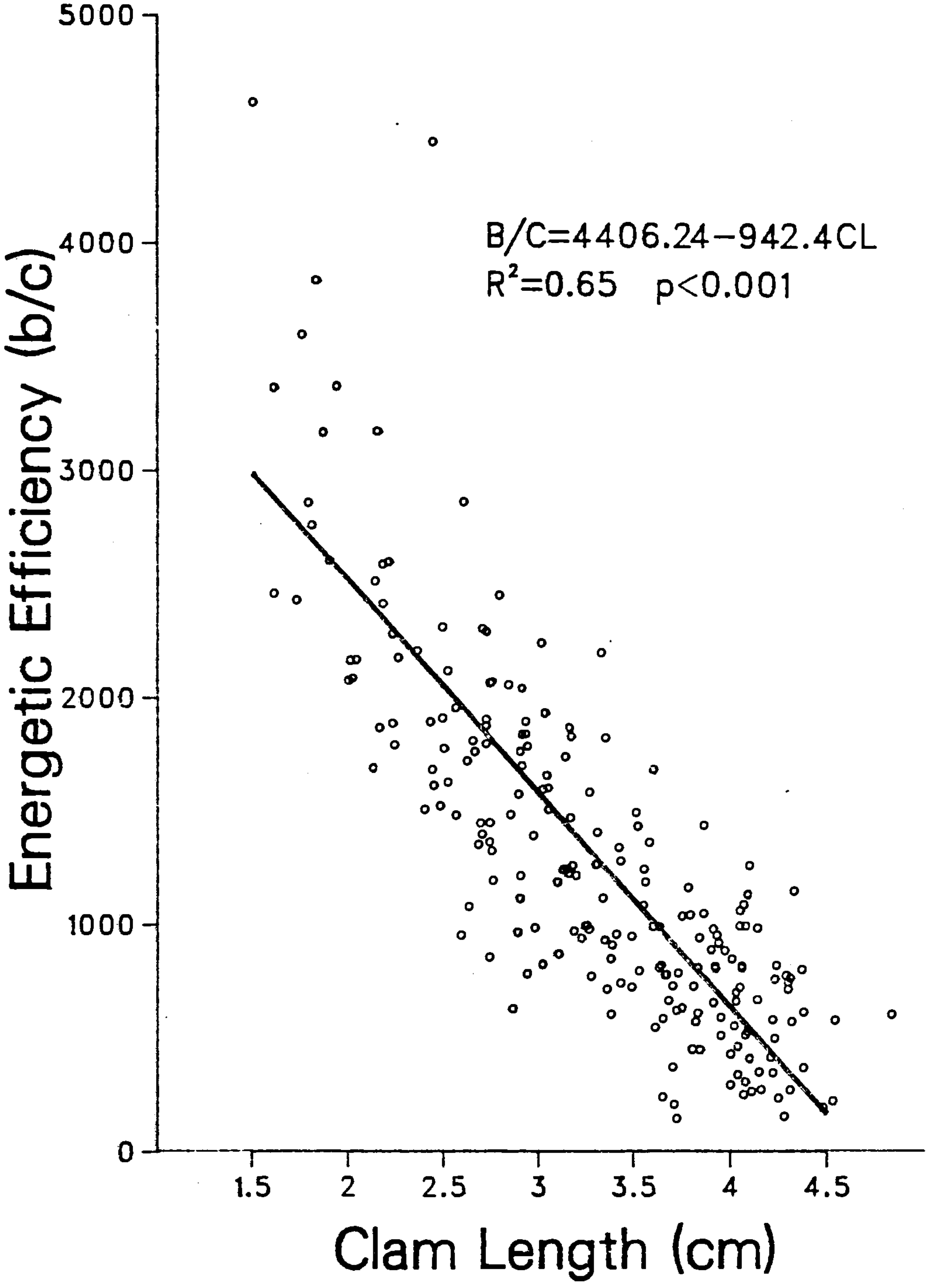

Fig. 8. Profitability (measured as the ratio of Benefit to Cost) vs. Clam length (cm).

IV. TESTING THE PREDICTIONS

Methods

A total of fourteen crabs (mean length=17.4 cm, range=16.5-18.2) were used in these experiments. Crabs were starved for two days before experimentation to standardize hunger levels. The range of clam sizes was split into six size classes of 0.5 cm length (1.5-2.0, 2.0-2.5, 2.5-3.0, 3.0-3.5, 3.5-4.0 and 4.0-4.5, termed size class 0 to 5 respectively). Equal numbers of clams randomly chosen from two (termed 'two-choice' experiment) or three (termed 'three-choice' experiment) size classes were offered to each crab by spreading them on the bottom of each tank. They were left for 24 hours, after which the remaining clams were removed and noted. The crabs were starved for 24 hours between feedings after which the same combination of clams was again offered. This pattern continued for up to ten feeding periods.

A further set of experiments were conducted to verify whether crabs could select between starved and unstarved clams of similar sizes. The purpose of this experiment was to determine what mechanism crabs use to select clams (i.e. whole clam weight, clam size or meat weight). Crabs were offered equal numbers of similarly sized clams from each group using the same procedure as above. Unstarved clams had been freshly received; starved clams had remained unfed in the laboratory for four months. A random sample of ten clams from each group showed no differences in clam length but significant differences in both wet and dry weights of clam tissue ($t=5.5341$, $p=0.001$ for dry weights and $t=3.5878$, $p=.01$ for wet weights).

The clam selection data were analyzed using a Chi square test to detect differences from a random choice.

Results

The results show that crabs, irrespective of which clam combination they were offered, ate more smaller clams than expected by chance (Tables 3-5). This trend is emphasized when the total numbers of clams eaten are pooled for the two-choice and the three-choice experiments respectively. The 3-size class combination can be further tested using a nonparametric Tukey-type multiple comparison (Table 4). This analysis indicates that the trend is stepwise (i.e. small>medium, small>large and medium>large). Therefore *Cancer magister*'s preference decreases with increasing prey size. Furthermore, crabs selected randomly between starved and unstarved clams of similar size ($X^2=0.593$, $p>0.05$).

Table 2. Crabs eat more small than large clams when given a choice of two size classes. * represent significant values of the Chi square statistic.

Clam size classes offered	Crab#	#Days	# eaten Small	Large	X^2
0 vs 2	3	5	47	27	5.4*
	6	5	66	48	2.84
	14	4	39	20	6.1*
	Total	14	152	95	13.1*
0 vs 3	12	5	79	32	19.9*
1 vs 2	2	6	67	69	0.03
	1	7	83	58	4.43*
	7	5	82	8	60.8*
	6	3	37	16	8.32*
	Total	21	269	151	33.2*
2 vs 3	2	5	47	7	29.6*
	3	4	35	10	13.9*
	5	5	42	40	0.05
	12	3	47	18	12.94*
	Total	17	171	75	9.3*
2 vs 4	4	6	33	25	1.1
	8	7	63	18	25.0*
	13	3	19	1	8.6*
	Total	16	115	44	31.7*
2 vs 5	11	6	48	4	37.23*
3 vs 4	5	10	46	42	0.18
	9	4	29	9	10.6*
	12	4	36	12	12.0*
	Total	18	111	63	13.2*
4 vs 5	11	5	36	0	36.0*
Overall Total		102	981	464	184.96*

Length composition of size classes are indicated in the text.

Table 3. Crabs consume more clams in the smallest size classes when given a choice among three size classes.

Clam sizes classes offered	Crab#	#Days	numbers eaten Small	Medium	Large	X^2
1 vs 3 vs 5	10	5	22	6	2	22.4*
	11	5	21	23	7	8.9*
	12	2	10	10	5	2.0
	Total	12	53	39	14	22.12*
0 vs 3 vs 5	12	3	20	15	3	12.02*
2 vs 3 vs 4	12	4	47	24	3	39.22*
2 vs 3 vs 5	11	2	18	10	2	12.8*
Overall Total		21	138	88	22	81.89*

Length composition of size classes are indicated in the text.

Table 4. Results of Tukey-type multiple comparison. S, M, L are the small (0,1,2), medium (3) and large (4,5) size classes respectively. D is the difference in rank sums, SE is the standard error, q is the test statistic and is calculated as D/SE. The null hypothesis is rejected if $q>3.314$ (the critical value of q for $p<0.05$).

Comparison	D	SE	q
S vs M	289.5	78.1	3.706
S vs L	640.5	"	8.201
M vs L	351.0	"	4.494

Discussion

The results indicate that there is a strong size selective behaviour in *Cancer magister* feeding on *Protothaca staminea*. When given a choice of prey sizes, these crabs will eat significantly more small clams than expected by chance. When clams of three size classes are available, the preference is stepwise. These results are in direct opposition to the predictions of the diet model using energy maximization as a currency. Thus, profitabilities calculated using net energy intake per unit handling time fail to predict *Cancer magister*'s size-selective preferences when feeding on *Protothaca staminea*. The maximization of energetic efficiency (Figure 8) provides a much better fit to the observed feeding preferences. This suggests that for this predator-prey combination the maximization of the ratio of energy gained to energy lost, where spent energy is non-renewable and thus limited, may be the appropriate currency to predict prey rankings. In this case, it would therefore be improper to subtract cost from benefit to calculate prey value using net energy intake rate maximization since one does not compensate for the other (and in fact it has a negligible effect in the present model). Thus the animal may not be constrained by a fixed time available for foraging but instead by a limited amount of expendable cost.

Stein et al. (1984) showed that the maximization of energetic efficiency was the best predictor (when compared to a net and gross energetic intake model) of the selective predation by redear sunfish among genera and sizes of three freshwater snails. Sherry and McDade (1982) used this measure of profitability to predict prey selection and handling in two neotropical hover-gleaning birds (these birds snatch insects and small vertebrates while hovering). Both studies showed a correlation existed between energetic efficiency and prey preference but provided no theoretical basis for its use.

Schmid-Hempel et al. (1985) and Cheverton et al. (1985) showed that the maximization of energetic efficiency could accurately predict crop-filling behaviour in honey bees. They suggested that in honey bees individual workers seemed to be constrained by a limited flight budget (Neukirch 1982). Once this budget is used up due to a breakdown of the flight mechanism, the worker can no longer forage. Thus they would maximize the delivery of nectar per unit of expenditure. Kacelnik et al. (1986) indicated that although both energetic efficiency and net rate of gain could explain Nunez' (1982) observation that honey bees filled their crops more fully for higher flows and longer travel times, only energetic efficiency provided a good quantitative fit for acceptable assumptions of load weights.

Bernatchez and Dodson (1987) showed that energetic efficiency (defined as the minimization of cost per unit distance) correctly predicts the migration behaviour of semelparous fishes whose energy reserves are exhausted during migration (thus where the cost is limiting). The relationship does not hold for iteroparous species (repeat spawners).

Claw breakage due to fatigue damage

During feeding, crabs were sometimes observed to break part of their dactylus, and in two instances lose their entire chelipeds, when attempting to crush large clams. This led me to investigate the possibility of the proposed limited cost representing a fixed amount of lifetime claw 'operation'. Thus claw breakage in crabs might be a similar process to the breakdown of the flight mechanism and the subsequent inability to forage in honey bees, and would provide a theoretical explanation for the use of energetic efficiency as a currency to predict prey size selection in crabs.

Brown et al. (1979), in describing the biomechanics of crab claws, demonstrated that the tips were the areas where most force was applied. Thus any loss of these tips would significantly decrease claw efficiency.

Boulding and LaBarbera (1986) have shown that repeated loading by crabs (*Cancer productus*) enables them to open larger clams (*Protothaca staminea*) than they would be able to directly crush. Their experiments demonstrated that *Cancer productus*, a congeneric which is also found sympatrically with *Cancer magister*, could directly crush only the smallest sizes of *Protothaca staminea*. Repeated loading eventually causes low cycle fatigue of the shell material. The few data available suggest that more force pulses ('squeezes') were required to open larger clams; that the thick-shelled morph required more force pulses than the thin-shelled morph of the same size; that initial force pulses were indistinguishable in magnitude and duration from those near the end of the attack; and that the relationship between number of pulses required and clam length was exponential (Boulding 1984).

Types of failure are usually classified in a twofold way: by the duration of time taken for failure to occur, and by the amount of deformation that occurs before failure. The time taken may be very short, if failure takes place as a result of impact loading or may be longer if it is the result of static loading. Fatigue failure occurs when the loads are applied intermittently over a matter of hours, days or weeks. The deformation may (e.g. local buckling of the locust femur) or may not (e.g. the breaking of most bones and the smashing of bivalve shells) contribute to the failure (Wainwright et al. 1976).

Low cycle (<50,000 cycles) fatigue has been reported in some detail for human leg bones (Wainwright et al. 1976), for strips of oyster nacre (Currey and Brear 1984), and has been shown to be an exponential process (Sandor 1972). There are two force components generated every time a brittle structure is loaded: an elastic component that is recoverable upon unloading and, a plastic component that is not recoverable and that takes the form of microcracks. Thus fatigue damage is caused by the cyclic accumulation of plastic strain (Sandor 1972). Lefebvre and

Ellyin (1984) have suggested that the amount of plastic strain energy that a given structure can absorb is fixed, and that failure will occur when this limit is reached whether the limit occurs during a single loading with a large load or after many loading cycles with smaller loads.

If a crab, by repeatedly loading a clam is building up plastic strain on the clam it must also be accumulating similar forces in the cuticle of its own chelae. However, the crab claw, because of its higher organic content (see below) would be less susceptible to fatigue than the more brittle bivalve shell. Gosline (pers. comm.), a noted worker on the biomechanics of biological materials, suggests that this process is likely and probably similar to the effects of compression on bone. The crustacean cuticle and bone are similar structurally in that they are both considered fibrous composite materials found in an amorphous matrix (Wainwright et al., 1976). Bone's main constituents are collagen, other proteins, protein-polysaccharides and glycoproteins and some form of calcium phosphate; compared to chitin, lipoproteins and calcium salts in crab cuticles (Welinder 1975).

Fatigue failure in bone is well described as compared to crustacean cuticle (Wainwright et al. 1976) and is a similar process to that hypothesized for clams under cyclic stress (Boulding and LaBarbera 1986).

Although much work has been done on the biology of the arthropod cuticle (see for example Neville 1975, Hadley 1986), little is known about its mechanical properties (Wainwright et al. 1976). Crustacean cuticle is a composite material with a multi-layered structure. The outer epicuticle contains a layer of highly oriented lipid and a tanned lipoprotein layer. Beneath is the procuticle. It has an outer 'pigmented layer' which is always tanned and nearly always calcified (calcite), a 'calcified layer' which is calcified but not tanned, and finally an inner uncalcified, untanned layer. The layers vary in their relative thicknesses (Dennell 1947, 1960). Tanning is the process of adding a substance that establishes more than one linkage, either electrovalent or particularly covalent, between itself and the chain molecules (chitin), so increasing the number of linkages present in the system. Those skeletal proteins that owe their stability to tanning by orthoquinones are called sclerotins and are present in crustacean appendages (Brown 1975). Thus cuticle hardness will also be dependent on the amount of tanning present. Preliminary investigations indicate that areas that are sclerotized tend to be stiffer and stronger than untanned areas (A.C. Neville, pers. comm. in Wainwright et al. 1976). Welinder (1975) showed that the most intensive growth after molting in *Astacus fluviatilis* (a freshwater crayfish) was found in the propodite (a part of the arthropod appendage) cuticle, which increased its weight ninefold in 14 days. The dominating substance to be deposited in this period was calcium salts. Additionally, it is those structures that need great mechanical strength (walking legs and claws) that have a greater content of calcium salts than the carapace, whereas the relative protein content is the same (Welinder 1974). These analyses are further complicated by the unknown effects of mineral grain sizes and the mechanical consequences of the pore canals which pass through the procuticle from the underlying epidermis.

A thorough knowledge of the mechanical properties of the material under study (levels of elastic and plastic strain, force amplitudes applied, etc.) is necessary for the prediction of final failure (Sandor 1972).

Feeding and prey-size selection in Decapods

The effect of decapod (mostly lobsters and crabs) predation on bivalve populations has been documented many times. Some of these studies observed size selection behaviour in the predators often in a qualitative manner. Table 5 presents a summary of these studies. Although for the most part prey sizes tend to increase with predator sizes, the overwhelming trend is for decapods to selectively consume bivalves of the smallest size when given a choice (Table 5). The exceptions occurred when decapods were offered mussels, mostly *Mytilus edulis*, a thin-shelled bivalve. A lack of size selection was observed when crabs were offered soft-shelled clams (*Mya* spp.). In one case (Hughes and Seed 1981), the highest energy intake rates coincided with the smallest mussel sizes and it is thus possible that in all the other studies where prey selection models were not used small bivalves would always offer the highest profitabilities (in terms of energy per unit time). Various authors (Lawton and Hughes 1985; Elner and Jamieson 1979; Hughes and Seed 1981) when interpreting seemingly 'non-optimal' behaviour suggest that prey size selectivity appeared to have a passive rather than an active behavioural basis. Another possibility is that a different currency may have been maximized and thus in all these instances decapods were minimizing the risk of claw breakage and the rate of claw wear by consistently selecting the smallest prey available. This pattern is also apparent in studies of crabs feeding on various snails (Table 5). Hughes and Dunkin (1984a) found that the dogwhelk, *Nucella lapillus*, preferred mussels smaller than those predicted to be the most profitable. They explained this as a trade-off to minimize predation risk or dislodgement or desiccation associated with longer handling times for larger mussels. An alternative explanation could be a trade-off to minimize radula wear although radulae have relatively fast regeneration rates (Barnes 1982). Those studies that showed energy maximization behaviour or no size selection would indicate that for those bivalves, because of their thin shells, there is no significant increase in predation cost with increased bivalve size or that very few squeezes will open a bivalve of any size.

Studies of *Carcinus maenas* and *Liocarcinus puber* feeding on *Mytilus edulis* (Elner and Hughes 1978; Jubb et al. 1983; ap

Rheinallt 1986) suggested that one of the reasons why the smallest clams were 'non-preferred' and were often dropped was that their chelae had difficulty grasping smaller prey and were very inefficient at gleaning their flesh. This behaviour was not observed in this study. *C. magister* was equally adept at feeding on even the smallest clams offered. Hughes and Seed (1981) noted that *Callinectes sapidus* had finer and more dextrous chelae than those of *C. maenas*, enabling efficient gleaning of flesh from small prey. This is the same study that showed the smallest prey having the largest profitabilities.

The different technique used to open large clams, chipping the shell, may also be a factor in making these clams non-preferred. The chipping technique tends to depend more on edge-chipping by the claw tips (or dactylus tips) which are then probably more susceptible to breakage. During edge-chipping, the crab's chela slips ventrally on the shell as the crab squeezes its chela around the ventral margin of the shell. The net force at a given chela molar can be resolved into two vectors: a large compressive vector normal to the shell surface and a smaller shearing vector parallel to the shell surface (Boulding and LaBarbera 1986). This combination of forces will lead to a type of fatigue failure named pitting (Boresi et al. 1978) and is also likely to increase stress on the chelae teeth and the claw tips.

Table 5. A summary of decapod-bivalve studies indicates that the smallest prey are usually preferred. SL is shell length, CW is carapace width, SH is shell height and CL is carapace length.

Predator	Prey	Comments	Source
Neopanope sayi *Cancer irroratus*	*Mercenaria mercenaria*	Crabs consumed 87% of clams in smallest groups (4.5-25 mm SL).	Mackenzie 1977
Callinectes sapidus	*M. mercenaria*	Crabs <75 mm CW preyed equally on 5 and 10 mm SL clams. Crabs 75-125 mm CW concentrated on 10 mm SL clams. Crabs >>125 mm preyed equally on 10 and 25 mm SL clams.	Arnold 1984
Carcinus maenas	*Mytilus edulis* *Nucella lapillus*	All crabs (27-57 mm CW) preferentially preyed on smallest mussels (15-21 mm SL). Small and medium crabs (34-41mm CW) ate mostly small snails (10-17 mm SH). Large crabs (45-47 mm CW) ate equally from medium (20 mm) and small snails.	Ebling et al. 1964
Callinectes sapidus *Panopeus herbstii*	*Geukensia demissa*	"Most crabs selected the smaller size classes of mussels (<20 mm SL) and only when these had been completely depleted did they proceed to attack larger prey."	Seed 1980
C. sapidus	*G. demissa*	"small mussels (<20 mm SL) were always eaten whenever encountered even when grossly outnumbered by larger prey."	Seed 1982
Cancer pagurus *Carcinus maenas* *Portunus sp.* *Eupagurus sp.*	*Modiolus modiolus*	Both *Carcinus* (50-55 mm CW) and *Cancer* (78-150 mm CW) showed no preference among small and medium mussels (15-50 mm SL). *Portunus* (52-72 mm CW) and *Eupagurus* (47-90 mm CW) took more of the smallest mussels (7-34 mm SL).	Seed and Brown 1975
C. maenas	*M. mercenaria*	"size selection was biased towards the smaller prey offered."	Walne and Dean 1972

C. sapidus	*M. mercenaria*	Mortality decreased as prey size increased. "Crabs may be selecting the smaller clams in the trays."	Whetstone and Eversole 1978
C. sapidus	Various soft clams	"blue crabs generally showed no size-selective or species-selective feeding behaviour."	Blundon and Kennedy 1982a
Cancer productus	*Protothaca staminea* and other bivalves	For all 3 size classes of crabs *Mya* had had the lowest relative survival. *Saxidomus* and *Protothaca*-thin showed next lowest, while *Protothaca*-thick had the highest. All crabs showed a significant preference for the smallest size of *Protothaca*-thick offered.	Boulding 1984
Ovalipes punctatus	*Donax serra* *Bullia rhodostoma*	Crabs 40-45 mm CW preferred smallest sizes of whelks. Larger crabs (45-65 mm CW) had the highest preference for whelks in the 25-30 mm size class. The diet of crabs <50 mm CW consisted mainly (82-92%) of *Donax* <40 mm CL, while for crabs >50 mm CW only 52-58% of the diet consisted of these sizes. For all crabs, the percentage of clams >55 mm CL included in the diet was <5%.	Du Preez 1984
Cancer magister	Various clams	Crabs tended to consume more bivalves in the smallest size classes.	Jamieson unpubl.
Cancer irroratus *H. americanus*	*Placopecten magellanicus*	Crabs and lobsters preferred smaller scallops (40-55 mm SH).	Jamieson et al. 1982
C. irroratus *H. americanus*	*P. magellanicus*	Small lobsters (70-80 mm CL) and small rock crabs (90-100 mm CW) preferred smallest sizes of scallops offered (20-30 mm SH). Large predators (lobsters 130-140 mm,crabs 120-130 mm) preferred medium size classes of prey.	Elner and Jamieson 1979
H. americanus *C. irroratus* *N. sayi*	*Crassostrea virginica*	"when provided with a range of oysters from 10-35 mm SL, lobsters (55-98 mm CL) and rock crabs (32-107 mm CW) could all open oysters of 25-30 mm SL, but they usually selected smaller oysters."	Elner and Lavoie 1983

C. sapidus	*G. demissa*	"*C. sapidus* preferred smaller to larger mussels."	Hughes and Seed 1981
Jasus lalandii	*Aulacomya ater* *Choromytilus meridionalis*	"Rock lobsters prefer small mussels (<20 mm SL)".	Griffiths and Seiderer 1980
Various crabs	*Pecten maximus*	All crabs preferred smaller scallop sizes.	Lake et al. 1987
C. maenas	*M. edulis*	Medium-sized mussels (2.25 cm SL) were consistently preferred over small (1.25 cm SL) or large (2.75 mm SL) ones.	Jubb et al. 1983
C. maenas	*M. edulis*	Crabs of all sizes preferred mussels slightly smaller than those predicted from an energy maximization model.	Elner and Hughes 1978
Liocarcinus puber	*M. edulis*	"Intermediate-sized mussels predominated in the diet. Due to limited chelal dexterity, small mussels were difficult to grasp and easily dropped."	ap Rheinallt 1986
C. maenas	*N. lapillus*	Predation was heaviest on the smallest size class (15-20 mm SH), less on the middle size class (20-25 mm SH) and least on the largest size class (25-30 mm SH). The smallest size classes (6-7 mm) were occasionally rejected when dropped accidentally.	Hughes and Elner 1979
C. maenas	*Littorina saxatilis*	"When given a range of size classes the crabs always selected the smallest snails.	Johannesson 1986
C. pagurus	*N. lapillus*	With unlimited prey, "the number of prey successfully opened and eaten decreased from the smallest to the largest prey." With limited prey, "crabs consistently opened and ate the smallest snails first."	Lawton and Hughes 1985
Nucella lapillus	*M. edulis*	"Dogwhelks preferred mussels smaller than those predicted to be the most profitable."	Hughes and Dunkin 1984a

Handling time variation

The large variability in the handling time components suggests that crabs would not be able to accurately predict the handling times of their prey from any measure of body size. Boulding and LaBarbera (1986) showed that body size accounted for only 65% of the variation in static strength of *Protothaca staminea* (20-60 mm in shell length). In scallop shells, shell thickness and corrugation amplitude explained 64% of the shell's tensile compliance (Pennington and Currey 1984). The remaining variation in static strength and thus part of the large variation in breaking times may be due to the accumulation of microcracks on the outside surfaces of clam shells. These microcracks result from wear or previous loading history (i.e. unsuccessful predator attacks). These areas of the shell would then be more vulnerable to tensile stress (Boulding and LaBarbera 1986) and if detected by the predator would be an ideal place for it to attempt an attack. This would explain the careful inspection performed by crabs on the shells of larger clams, the large persistence times (up to 6 hours in my observations) spent by crabs on large clams and the fact that a given crab could rapidly crack a clam that it had persistently tried to open in the previous feeding trial.

The results of this study suggest several factors which should be considered by researchers working on decapod-bivalve feeding studies since they may explain a large part of the variability in the observed handling time components. These factors include: physical state of the chelipeds; 'clam-eating' experience; individual ability of the crab; and past 'mechanical history' of the clams (researchers should thus be careful not to repeatedly use clams once they have been attacked by crabs).

Partial Preferences

The existence of partial preferences remains a much discussed topic (see Krebs and McCleery 1984; Stephens 1985; and Stephens and Krebs 1986). The general view is that they occur because some of the assumptions of optimal diet theory do not always hold.

In this study, various assumptions of the classical diet model do not hold. Handling times are shown to be variable for similar clam sizes perhaps due to the accumulation of microcracks and to the extent of 'clam-eating experience' (i.e. 'old' vs. 'new' crabs). Prey value is also variable, especially at large clam sizes, because of the variation in handling times and the combination of behavioural methods used to attack these large clams. Since crabs use tactile and chemical cues to evaluate prey, recognition times are finite. Finally, encounter rates during any one feeding trial are not fixed since they change as clams are eaten. Thus it is not surprising that partial preferences occur in this study (see Hughes 1979, 1980 for a theoretical discussion of partial preferences applied to crab foraging).

Predation Costs

The metabolic cost of foraging has not been frequently measured. One of the assumptions of the classical optimal diet model is that energetic costs per second of handling time are similar for different prey (or different sizes of the same prey) (Krebs and McCleery 1984). The present results show an exponential relationship between costs and prey size, although these costs become negligible when compared to the benefits gained.

Pough and Andrews (1985) measured the cost to a lizard of pursuing, subduing and swallowing its prey. These costs were only 0.2 to 0.4% of the utilizable energy of the crickets eaten. The authors thus suggest that costs can be ignored for most ecological purposes. Meyer and Guillot (1986) measured the energetic costs of ten behaviour patterns in mice placed in a respiratory chamber. They concluded that the low energetic cost of each behavioural bout (ranging from 1.51 ml CO_2/g/hr (rest) to 4.9 ml CO_2/g/hr (locomotion)) as compared to the daily energetic intake of the mouse, suggested that the behaviour transitions were not to be ascribed to energetical reasons. These conclusions would be somewhat different if the costs measured corresponded to a non-renewable resource. In that case, the comparison of energy gained and energy lost would be meaningless.

The costs measured in the present study are more representative of the breaking costs than the eating costs since it was the highest rate of oxygen uptake (represented by the maximum slope obtained from the chart recording during each feeding bout) that was measured. This maximum occurred mostly early in the feeding period before eating commenced. The data suggest that the cost of predation in this case is the cost of creating force pulses. The use of a closed-system respirometer prevented me from obtaining results from clam sizes larger than 3.78 cm CL (clams larger than this have long handling times associated with them and the foraging crab would thus deplete all the oxygen in the tank). More exact measurements of the costs expended during the different parts of a foraging bout could be obtained with the use of a flow-through respirometer.

It is interesting that both costs (this study) and number of squeezes (Boulding 1984) seem to vary exponentially with clam size. Since the number of force pulses is probably also directly related to breaking times, the strategy of minimizing the number of squeezes would in a sense mean that breaking times are also limited. This is emphasized by the observed negative correlation between clam length and energy intake per unit breaking time. Elner and Hughes (1978) also found that, when their prey (*M. edulis*) were in unlimited supply, the peaks of the diet curves were closer to the predicted optimal mussel sizes based on breaking time than those predicted using total handling time. Lawton and Hughes (1985) obtained a better fit to their results using dual breaking time functions, based on the attack method used by *C. pagurus* feeding on *Nucella lapillus*. However, from a theoretical perspective if time was the limiting factor (or constraint), these animals should maximize energy per unit total time. This study has shown that this currency does not predict the direction of size-selective feeding behaviour on hard-shelled clams in *Cancer magister*.

A basic assumption of the classical optimal diet model (Krebs and McCleery 1984; Stephens and Krebs 1986) is that handling and searching for prey are mutually exclusive activities. Thus they constitute different decisions: eat or search. This study did not take into account burial depths of clams and thus ignored travel times (or search times). The inclusion of travel time, or in this case digging time, might alter some of the model predictions. Field studies have shown that larger clams are less abundant generally and can bury themselves deeper in the substrate than smaller individuals (Schmidt and Warme 1969; Richardson 1985). Various studies have demonstrated that depth of burial in infaunal bivalves can act as a refuge from crab predation (Blundon and Kennedy 1982b; Haddon et al. 1987). *Protothaca staminea* forced to live near the surface are more vulnerable to predation by *Cancer magister* than those allowed to burrow to normal depths (Pearson et al. 1981). Thus the smaller size classes would be more accessible to foraging crabs and would be encountered more often than the larger sizes. Underwater observations have shown that crabs, living in similar habitats in the Western Atlantic, may forage in groups by excavating 'communal' pits once a prey population of some critical density is located by the vertical dactyl probing method (Auster and Crockett 1984). Boulding (1983,1984) and Boulding and Hay (1984) in an extensive field study, showed that both *Cancer productus* and *Cancer magister* were attracted to high clam densities from a distance.

The results of this study suggest that it is not overall foraging (or handling) time that is critical for this crab species (feeding on a hard-shelled clam), but instead the cost of breaking a shell. Thus it is energetic efficiency, the ratio of energy gained to energy lost (and this cost is mostly due to each squeeze), that provides the better predictions of size selection in *Cancer magister*. Thus, it is both the currency and the constraint (the cost of crushing shells rather than handling time) that differ from the classical optimal diet model. The relative importance of these different currencies and constraints could be ascertained in future studies by comparing them directly. This test would involve offering clams of equal profitability (in an energy maximization sense) but different energetic efficiencies by manipulating cost, benefit or handling time components. These manipulations would require either chipping the shell or interchanging clam tissue from smaller and larger clams. Presentation of chipped clams would bias any results since the crabs are primarily attracted to their prey by chemoreception and leaking clam extract would direct the crabs towards these damaged prey (personal observation). Results of the choice experiments offering starved and unstarved clams showed that the crabs did not discriminate among them although there were significant differences in wet/dry weight of the tissue. However, the specific gravity of bivalve meat is close to one, the specific gravity of seawater (Andrews 1961). Thus any space within the shell not occupied by a starved clam would be taken up by water. This will create no perceptible differences in whole clam weight.

Summary

1. Energy content, predation cost and the handling time components were all positive functions of clam size.
2. Profitability calculated as energy per unit handling time also provided a positive relationship with clam length.
3. Predictions from net and gross energy intake rate models were identical.
4. Energetic efficiency (Benefits/Costs) was a negative function of clam size.
5. Crabs preferred the smallest clam sizes offered. This preference for small sizes is a general pattern in most decapod-bivalve studies.
6. These results coincide with the predictions of the energetic efficiency model.
7. The limiting cost could be represented by 'claw life'.

V. ECOLOGICAL EFFECTS OF CLAW WEAR AND BREAKAGE

Introduction

In the previous sections of this thesis arguments have been oulined suggesting that claw damage in decapod crustaceans may act as a constraint in maximizing rates of energy intake when feeding on hard-shelled bivalves.

Claw damage is defined as either breakage of the whole or a part of the chelae, or wear of the chelae teeth. The physiological effects of limb loss in crustaceans have been investigated in some detail (see for example Skinner 1985). Little information exists on the ecological and physiological effects of claw tooth wear and partial claw breakage. Observations during the present study indicate that this damage may arise as a consequence of clam feeding behaviour (for example: two crabs lost whole chelipeds and three others broke their claw tips while feeding on large clams; and wear of the chelae teeth was noted in crabs that had not recently molted). Instances of claw damage due to foraging behaviour in the field remain undocumented. Butler (1960) and Snow and Neilsen (1966) showed that another type of claw wear, occurring on the inside of the propodus and termed 'mating marks', was created by the pre- and post-mating behaviour of *Cancer magister*.

In this section the ecological effects of claw damage are investigated by,

1. examining adult crabs to estimate levels of claw wear and breakage in a natural population of *Cancer magister*, and relating these results to sex and season.
2. manipulating levels of claw tooth wear in the laboratory to ascertain the effect on feeding behaviour.
3. observing the feeding behaviour of various crabs with broken chelipeds.

In addition, the potential effects of claw damage on regeneration, molting ability, growth and reproductive performance of decapods are considered.

Methods

A field survey was conducted near Tofino (an important crab fishing area in British Columbia) off the west coast of Vancouver Island in May 1986. A total of about 800 crabs were sampled from nine different sites over a four day period. Animals were caught by standard baited crab traps (soaking time of 24 hrs.) and by a beam trawl. Both of these techniques selected for crabs larger than 10.0 cm in carapace width. The animals were sexed (using the width of their abdomen), measured (carapace width), the state of each cheliped was noted, and molting condition assessed (pre-molt, intermolt, or post-molt). A numerical index was created to evaluate the extent of claw wear and breakage. '0' represented no tooth wear, '1' indicated slight wear, '2' represented extreme wear where half or more of the volume of the teeth had disappeared, and '3' indicated breakage of any portion of the cheliped. Most of the breakage occurred on claw tips. Deformed chelipeds were considered to have been broken during a previous intermolt period. The males were further checked for the presence of 'mating marks', which are abrasions found on the inner surfaces of the chelipeds and caused by close contact during the pre-mating embrace (Butler 1960).

For the laboratory experiments, five crabs (mean length=17.4 cm, range=16.8-18.3) were randomly selected from a freshly collected group of fifteen animals and were aenesthesized. Their claw teeth were filed down to approximate extreme levels of wear observed in the field (an index value of '2'). After a two week acclimation period, the crabs were placed in the experimental tanks and were individually presented with randomly selected clams. Handling times were collected for a range of clam sizes using the same methods as before. The results were compared to the previously obtained 'old' and 'new' handling time components using an analysis of covariance. The original 'new' handling times served as a good control since they were obtained from crabs collected at the same time of year as the animals in this experiment. Finally, three crabs that were found to have damaged chelipeds (missing part of one dactylus and/or propodus) were kept in the lab and their feeding behaviour observed.

Results and Discussion

Interpretation of claw damage in field-collected specimens

Butler (1960) and Snow and Nielsen (1966) have shown that some abrasions on crab claws may arise during mating. These 'mating marks' serve as an indicator of breeding activity, molting state, and thus relative exoskeleton age in male crabs. Mating in *Cancer magister* occurs from June until September in British Columbia waters (MacKay 1942; Cleaver 1949; Butler 1960). Adult males (>10.0 cm) tend to molt early in the year (January until May) while the female molting occurs immediately before copulation. *Cancer magister* has an elaborate mating behaviour. It is thought that males are attracted to females mostly through pheromones. The male holds the female in premating embrace (sternum to sternum) for up to a week until ecdysis occurs, at which time the female reverses her position (female carapace to male sternum). Copulation follows within two hours. The male then carries the female in a post-mating embrace for about two days until her carapace hardens. Laboratory observations have shown that what Butler (1960) termed 'mating marks' are due to extreme wear of the chelipeds created by the frequent stroking of the female carapace in the premating period (Snow and Neilsen 1966).

In the present study, sampling occurred in May before the peak in mating was expected to occur. At this time, the males are molting while the females would have not yet commenced.

Since these animals are thought to molt annually as adults, although some females have been reported to occasionally delay molting for a year (Hankin et al. 1985), three distinct groups can be identified: females carrying (or inhabiting) an exoskeleton which was at least one year old, males with mating marks which were probably obtained during the previous summer's mating period and therefore also had one year old exoskeletons (since no soft or newly molted females were found, that year's mating probably had not began) and finally, males without mating marks which represented the newly molted individuals. This last group contained the animals with the cleanest carapaces (i.e. no fouling) which usually indicates recent molting, and any immature males present. Males are thought to mature at a carapace width of about 11.0 cm, or approximately 3 years of age. However, sexual activity is not appreciable until the males are about 14.0 cm in size (Butler 1960).

The results (Figure 9) indicate that claw wear and breakage occurs in a natural population. The rate of wear and presence of breakage varies with sex and is dependent on the individual's molting state. Overall, the extent of wear and breakage were similar for each claw confirming the observation that both chelipeds are used with equal frequency when cracking clams. Among females, more than half the claws showed some wear and approximately 12% of the claws were broken. Only 4% of the females (7/181) had two broken claws. Since there is no method to differentiate among old and new exoskeletons in this group, rates of wear or time of breakage cannot be estimated. The 'unmated' males had a smaller proportion of wear (9%) and breakage (8%) in their claws. Any wear and breakage detected in this group would probably correspond to immature pre-molt males. However, some breakage could have been caused by fighting in the crab trap or in the net before retrieval.

The highest proportions of worn (60%) and broken claws (22%) were found among the 'mated' males. Only 3% (4/123) of these individuals had both chelipeds broken. As explained previously, the animals in this group would be expected to have exoskeletons which were at least a year old. The tooth wear can be wholly attributed to feeding behaviour. Breakage can be due to fatigue damage but can also be a consequence of fighting. There is no way to distinguish between these or to estimate the extent of fighting in the natural population. Additionally, higher levels of wear and breakage were observed in animals inhabiting an area which also had high densities of a small very hard clam (*Transennella spp.*).

Laboratory experiments

In the laboratory, those crabs with parts of the chelipeds broken were never observed to consume even the smallest clams available. Attempts to crack the shells were observed but none of these were successful. When offered previously opened clams the crabs readily consumed the clam tissue.

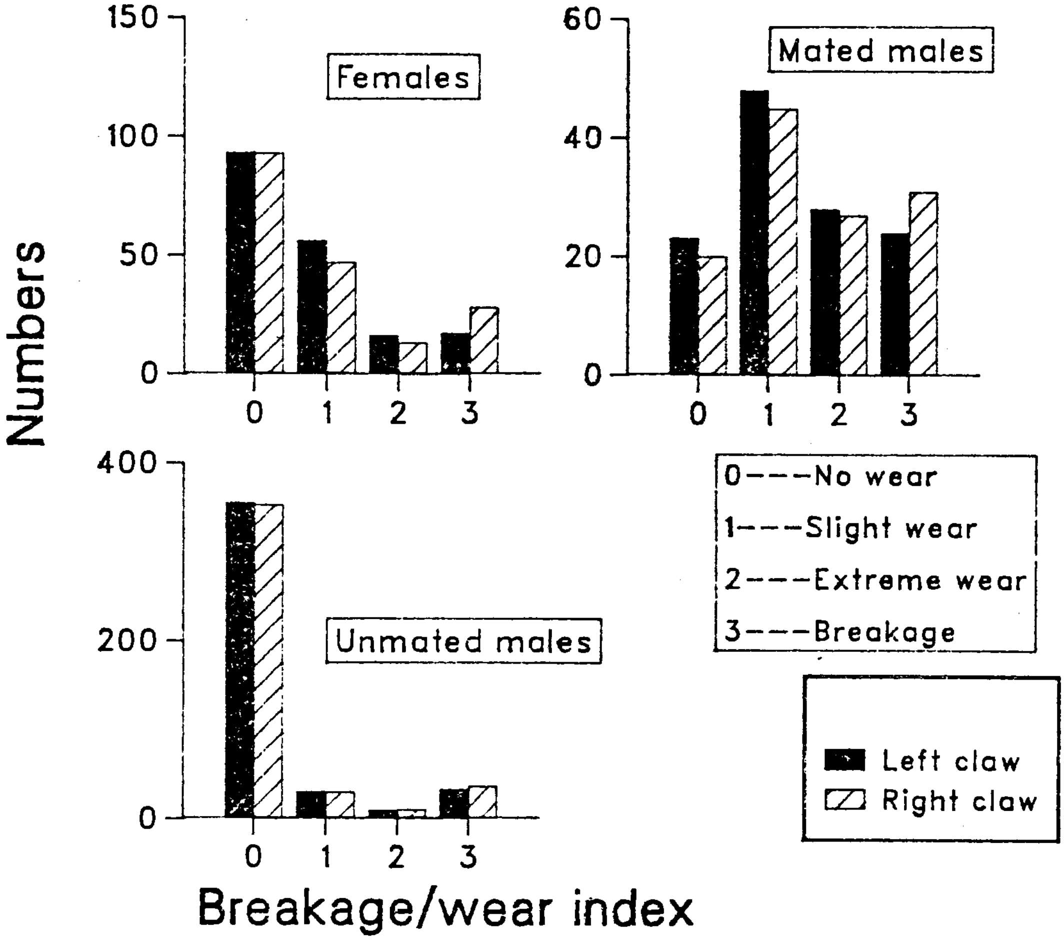

Fig. 9. Numbers of broken chelipeds and level of claw tooth wear in a natural population of C. magister off Tofino in May 1986. 'Mated' and 'unmated' males were distinguished by the presence or absence of mating marks.

When compared to 'new' animals, those with artificially worn teeth had significantly longer breaking, eating and handling times for that range of clams tested (Figure 10). A crab with blunt teeth will exert the same level of force per squeeze, but this force will not be as effective in causing fatigue in the clam shell because of the worn contact points. More force pulses will be required per clam, increasing the cost of predation. Thus any size of clam will be less profitable to the animal since it will obtain less benefit per unit of cost expended. Increased handling times may also increase predation risk.

The increased handling, breaking and eating times were statistically indistinguishable from those obtained from the 'old' crabs (Figure 10). Thus, losing experience by not eating clams (which are a major component of the diet) is potentially similar to the effects of wear. However, loss of experience and the subsequent reduction in strength and in sarcomere length in the chela closer muscles, will act to decrease the level of force the animal is able to apply during each squeeze thereby increasing the cost of predation.

In conclusion, crabs show two forms of mechanical constraints in their chelipeds. Tooth wear which is likely to be a continuous process, (which can be documented by an observer), and which has the effect of increasing handling times and energetic costs by reducing the efficiency with which a crab can crush a clam. Wear is also likely to have drastic effects on the efficiency of foraging on the large clams since the chipping mechanism is even more dependent on the forces created by the chelae teeth (Boulding and LaBarbera 1986). Secondly, claw breakage which is probably a more discontinuous process building up to a threshold and whose progress cannot be detected by an observer. When the critical load is reached, a portion of the claw will break. Laboratory observations indicate that various forms of breakage made the animals unable to forage successfully on clams. A more detailed study is necessary to quantify the exact effect of various levels of breakage on feeding behaviour.

There may be a direct relationship between the extent of wear and the proximity to fatigue damage. The exact nature of this relationship could be obtained empirically by measuring wear levels frequently while controlling diet. The slope of this hypothetical line will vary depending on the proportions and sizes of hard-shelled molluscs in the diet. Different forms of this curve could therefore represent different crab habitats. The relative proportions of dental microwear have been used to distinguish groups of animals (mostly mammals) with different diets (Walker et al. 1978; Teaford and Walker 1984). Males and females may also show different strategies depending on habitat and relative importance of chelipeds in their ecology and reproductive success. The laboratory observations showed, however, that these animals were still able to forage on cracked clams. Thus in the field, after breakage occurs, crabs may have to switch to a less preferred prey. This study also did not ascertain the effects of claw damage on other aspects of

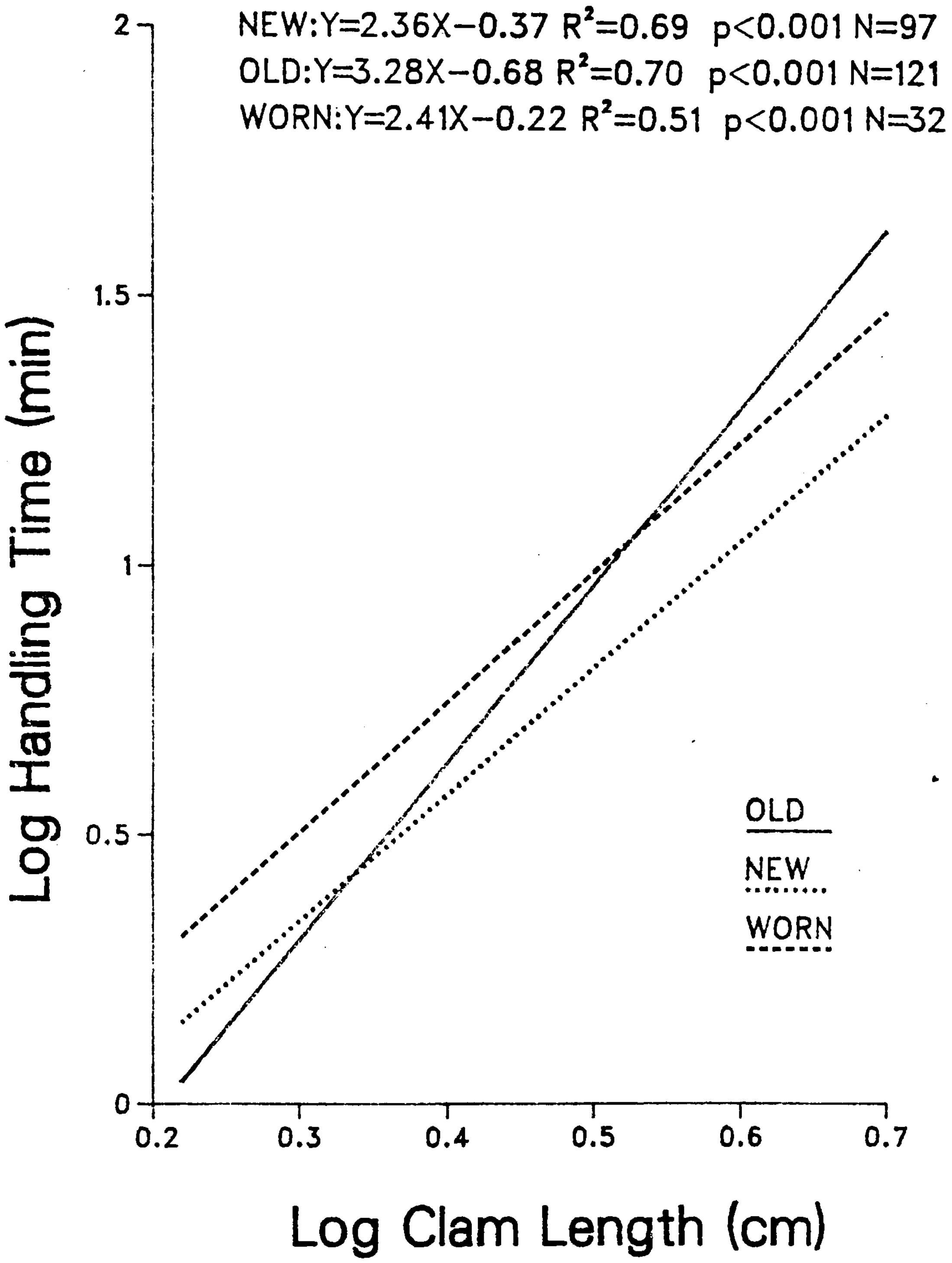

Fig. 10. Log_{10} Handling time vs. Log_{10} Clam length for 'old', 'new' and 'worn' crabs. Covariance analysis showed that 'old' and 'worn' were both different from 'new', but not different from each other.

foraging behaviour such as digging ability, chemoreception and mechanoreception.

Claw damage and sexual behaviour

There are many other potential effects of claw breakage on the ecology and subsequent reproductive success of decapods. Most of the ecological effects are undocumented and probably remain to be examined.

Little is known about male-male competition or mate choice in this genus. Among the Brachyura the only extensive work is in the genus *Uca*, a semi-terrestrial species, where males fight over burrows with which to attract females, who tend to select larger males as mates (Salmon 1983). In this genus claws are an important part of the courtship display. Salmon (1983) argues that among aquatic brachyurans, chemical signals for mate attraction are more important than visual or acoustic ones although there is no evidence to support this view. The fact that the claw size/body size ratio, in most brachyurans, is larger in males than in females after maturity suggests that larger chelipeds are important. Atema (1986) has shown that female lobsters, *Homarus americanus*, are the active searching partner in courtship, choosing locally dominant males. The attractive features of the male are suspected to be intrasexual aggressive behaviour and chemical cues. Dominance in lobsters is almost entirely size dependent. In laboratory studies, a small difference in lobster claw size is highly predictive of the outcome of a staged fight (Atema and Cobb 1980). Thus the post-maturity male investment in large claws may be primarily an adaptation to establish dominance and eventual mating success. Atema (1986) speculates that large claws in lobsters could serve as a mate selection signal for females, indicating bigger, better males, but it remains to be shown whether females can ascertain claw size during courtship. Hartnoll (1974) suggested that the sexual dimorphism of the chelae in crabs is a consequence of their widespread use by the male in combat, display and courtship. Huber (1985) showed common occurrences of intra-sexual injury when competing for mates in *Trapezia* spp. (Brachyura, Xanthidae). Although it was not clear which sex does 'the choosing', both males and females paired with the larger of two prospective mates significantly more often than expected on the basis of random pairing. The effect of a missing or partially broken cheliped on sexual behaviour has not been thoroughly investigated. Hazlett (1986), as an anecdotal note, observed that an individual of *Pagurus traversi* (a hermit crab) that lacked the minor cheliped attempted to mate with a female but was rejected after grasping her ambulatory legs (part of the hermit crab pre-copulatory habits involves cheliped vibratory movements and mutual appendage stroking) with his remaining (major) cheliped. This sequence was repeated six times before the male gave up.

It is likely that the extent of claw damage (or breakage) in *Cancer magister* males has a considerable effect on sexual behaviour and eventual mating success. Breakage will reduce feeding efficiency and therefore energy accumulation before the mating period. Breakage may also reduce fighting ability, visual attractiveness to females and ability to hold onto a female during the pre- and post-molting embrace.

Molting and Regeneration

Molting and regeneration has been studied in some detail in the Crustacea (see review by Skinner 1985). Decapod growth occurs as a discontinuous process. Periodic shedding of the calcareous exoskeleton (molting or ecdysis) results in incremental growth. Growth during the intermolt period is considered negligible in the brachyurans. At each molt the old integument is shed and rapid and extensive growth occurs during the short period before the new integument hardens. During ecdysis the body swells from the uptake of water and the soft crab emerges from the old exoskeleton. Following ecdysis the new exoskeleton calcifies and hardens. Immediately upon emergence *Cancer magister* individuals 85-160 mm in carapace length have attained approximately 55-70% of the final postmolt size; the remaining increase occurring within approximately three hours via further water uptake. The absorbed water is subsequently replaced with new tissue over a period of approximately two months (Cleaver 1949; Waldron 1958; Barnes 1982).

A consequence of the discontinuous nature of crustacean growth is that it can be broken down into two components. One is the molt increment or growth factor, the increase in size at a molt. The second is the intermolt period or molt interval, the duration between two successive molts and thus the length of an instar. Growth increments of instars of both sexes of *Cancer magister* have been found to be comparable up to the onset of sexual maturity (slope=1.22-1.23). Growth slows down following the molt in which sexual maturity is attained (slope=1.04-1.07 for males, 0.864-0.892 for females). After sexual maturity, male crabs in British Columbia waters molt once a year and the growth increase is relatively constant (Butler 1961).

A deterioration of food quality and quantity has been shown to reduce the molt increment and lengthen the intermolt period in various crustaceans (Hartnoll 1982). The loss of appendages will also reduce the growth increment while it can either shorten or lengthen intermolt period depending on such factors as the number of appendages lost and whether the loss occurs early or late in the intermolt.

Skinner (1985) recently reviewed the effects of the loss of chelipeds and/or other limbs on the molting and regenerative process. Loss of limbs may initiate precocious mating and shorten the intermolt period by up to 40%. Her studies on intensive regeneration led her to the concept of a 'regenerative load', where biotic and abiotic factors limit the extent of potential regeneration during the proecdysial period. Intensive regeneration can affect the size of the regenerates themselves and the overrall dimensions of the animal. In Alaska king crab

(*Paralithodes camtschatica*) caught in the wild, the size of a regenerated limb has been calculated to reach that of its unregenerated contralateral partner after four (Edwards 1972) to seven (Niwa and Kurata 1964) molts. In the blue crab, *Callinectes sapidus*, chelae that were lost at one or two ecdyses before the crab attained puberty never reached normal size (Churchill 1918). Thus, the growth increment can be reduced by up to 50% if intensive regeneration is required. Cleaver (1949) showed that if limb loss in *Cancer magister* occurred late in the cycle of ecdysis, three molts were generally required for complete replacement. If the loss occurred earlier in the cycle development could begin shortly after loss, when it remains shrunken and curled within the sac until it is withdrawn from the sac at the time of shedding. In summary, a crustacean's capacity to meet its regenerative load depends in part on its metabolic reserves and in part on the time available during proecdyses to prepare for regeneration.

The effects of breakage of part of a limb on regeneration and molting may be similar to the effects of whole limb loss since it will act as an increase in regenerative load. Some of the crabs collected during the survey were observed to have malformed claw tips, presumably due to an earlier breakage. Crabs that suffer breakage of a whole or a part of a claw will firstly not be able to build up the same level of metabolic reserves as a healthy crab. Additionally, breakage will increase regenerative load which can potentially decrease the growth increment at molting. For males this would create a disadvantage in fighting ability because of a smaller size and damaged claws. Mayer (1973) demonstrated an allometric relationship between female body size and brood size; therefore smaller females will produce fewer eggs. Premature molting, caused by extensive limb loss, could also have important effects if there is an 'optimum' time at which to molt.

Summary

1. The field survey indicated claw breakage and wear occur in a natural population.
2. The rates of wear/breakage varied with sex and molting state.
3. Laboratory experiments showed that wear resulted in increased handling times.
4. Claw breakage prevented animals from cracking clams.
5. Claw breakage may have drastic effects on growth and reproductive success of *Cancer magister*.

VI. CONCLUSIONS

My work has provided a theoretical framework for the integration of physiological and behavioural ecology by outlining claw wear and breakage as a constraint in maximizing net rate of energy intake. Net rates could be calculated because a cost of feeding parameter was empirically deduced. However predictions obtained using gross vs. net energy intake rates as currencies did not differ. Versions of the diet model employing these currencies also failed to predict prey-size selection in *Cancer magister*. If, conversely, cost is thought of as having a limited budget whereby intake cannot replace spent cost, then a new measure of profitability, energetic efficiency, can be used to predict foraging behaviour. A correlation was observed between prey choice and the predictions of the model using this new currency. It is hypothesized that the limited cost (or resource) in this system is claw life. Thus the currency has a biological basis and is not just a simple correlation. Claw damage (wear and/or breakage) may be widespread in decapods that use low cycle fatigue to crack their bivalve prey. Previous studies have found that crab predators maximize the rate of energy intake when feeding on bivalve prey. In the present study, the use of hard-shelled clams as prey revealed claw damage as a potential mechanical and physiological constraint. The results of this thesis suggest areas for future research such as,

1. A more in-depth study concerning the biomechanical

properties of arthropod cuticles. Much is known about their chemical properties but almost nothing about their biomechanics. This kind of work would answer questions such as, how and when does fatigue occur in decapod chelipeds? What is the budget of squeezes per claw-lifetime? What is the relationship between number of squeezes and prey size? What is the effect of breakage on molting and regeneration?

2. More field studies should be conducted on this animal. Aspects of sexual behaviour such as mate choice and intra-sexual competition need to be examined. How does claw damage affect sexual behaviour and competitive ability? Are there seasonal variations in the diet composition?
3. The patterns of wear and breakage over a year should be investigated. Do animals feed more intensively during the periods of rapid growth after molting?
4. What are the rates of wear/breakage between habitats, and how are they related to the variety of food types found in each habitat? Do these rates vary between sexes and between animals of different ages which may molt more often?
5. With the kind of information outlined above the ultimate goal of building a dynamic foraging model is possible. This model would attempt to predict potential foraging decisions over a molting cycle.

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