

PREY SIZE SELECTION IN DUNGENESS CRABS: THE EFFECT OF CLAW DAMAGE¹

FRANCIS JUANES² AND E. B. HARTWICK
Department of Biological Sciences, Simon Fraser University,
Burnaby, British Columbia, Canada V5A 1S6
and
Fisheries and Oceans Canada, Pacific Biological Station,
Nanaimo, British Columbia, Canada V9R 5K6

Abstract. We investigate prey size selection by *Cancer magister*, a decapod crustacean, feeding on *Protothaca staminea*, a hard-shelled venerid clam, and test predictions of the optimal diet model using three different currencies. We also evaluate the effect of claw damage on crab feeding efficiency.

The model parameters measured were: energy content of the prey, energy 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 two or three clam size classes, showed that crabs always ate more clams from the smallest clam size class offered. Thus the predictions from the energetic efficiency model provide the best fit to the results.

The use of energetic efficiency as a currency requires energy cost to be limiting over the animal's lifetime. In this study we propose claw damage, defined as chela breakage and claw-tooth wear, as a consequence of fatigue failure (breakage of a structure due to repeated loading), to be a limiting cost. A field study of a natural population of *C. 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 undamaged crabs. Finally, the ecological effects of claw breakage in decapods are evaluated with reference to growth, molting ability, regeneration load, and reproductive success.

Key words: British Columbia; *Cancer magister*; claw breakage; claw wear; cost-benefit models; energetic efficiency; fatigue failure; foraging theory; limited cost; optimal diet; predator-prey; *Protothaca staminea*.

INTRODUCTION

Optimality models have been used most extensively in ecology to analyze foraging behavior (Alexander 1982, Krebs and McCleery 1984). 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, Hughes 1980, Krebs et al. 1983, Krebs and McCleery 1984, Pyke 1984, Stephens and Krebs 1986, Stearns and Schmid-Hempel 1987).

The currency used to predict prey value (or profitability) in the classical version of the optimal diet model is the net rate of energy intake (Krebs and McCleery 1984, Stephens and Krebs 1986). 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, it is actually gross energy intake rates that are measured because of the difficulty in obtaining true values for the energy 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.

Recent experiments involving prey-size selection by crabs feeding on bivalves and gastropods have provided quantitative tests of predictions based on OFT, all using energy intake rate as the currency to measure prey value (Elner and Hughes 1978, Hughes 1979, Elner 1980, Blundon and Kennedy 1982, Jubb et al. 1983, Lawton and Hughes 1985, ap Rheinallt 1986, Johannesson 1986, Sanchez-Salazar et al. 1987). However, in some cases predators did not always specialize on the predicted optimal prey size even when these were abundant (Hughes and Elner 1979, Hughes and Seed 1981, Jubb et al. 1983).

Energetic efficiency (the ratio of energy gained to

¹ Manuscript received 11 July 1988; revised 25 May 1989; accepted 28 May 1989.

² Present address: Marine Sciences Research Center, State University of New York at Stony Brook, Stony Brook, New York 11794 USA.

energy lost) has recently been proposed as an alternative currency appropriate to those cases where energy costs may be limited over the animal's lifetime (Cheverton et al. 1985, Schmid-Hempel et al. 1985). The incorporation of the maximization of energetic efficiency as a currency into the diet breadth model results in the same theoretical predictions as when energy intake is the currency, i.e., prey are ranked according to the currency, and inclusion of a prey type does not depend on its own encounter rate (E. L. Charnov, *personal communication*). However, the rank order of prey items may differ depending on the currency used. 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 lifetime 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.

In the present study, predation by the Dungeness crab, *Cancer magister*, on the littleneck clam, *Protothaca staminea*, was used to contrast and test the predictions of the diet model based on three different currencies: net and gross energy intake rates, and energetic efficiency. In addition, we propose "claw life" as a limiting constraint that can provide the basis for the use of energetic efficiency as a currency in the diet model.

Although much is known about the physiological effects of limb loss in crustaceans (see, for example, Skinner 1985), the effects of claw damage on foraging efficiency in decapods have not been explored in the literature. This is perhaps because levels of claw wear and/or breakage in the field have remained undocumented, and only "healthy looking" predators are chosen for feeding experiments. In this paper we attempt to determine the effects of claw-tooth wear on feeding efficiency and whether claw damage (defined as either breakage of the whole or a part of the chelae, or wear of the chelae teeth) is an important phenomenon in a natural population of decapod crustaceans. Finally we will consider the theoretical implications of claw damage with respect to growth and reproductive performance.

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 (typically on sandy/muddy bottoms) from central California to Alaska, and is fished commercially over most of its

range. Various aspects of its biology have been reported by many authors (Mackay 1942, Cleaver 1949, Butler 1956, 1960, 1961, 1967, Waldron 1958, Selby 1980). Foraging by *Cancer magister* is opportunistic and makes almost exclusive use of the infauna (Butler 1954, Mayer 1973, Gotshall 1977, Bernard 1979, 1981, Pearson et al. 1979). Food items are located both tactilely and chemosensorily (Butler 1954, Barber 1960). Crab diet changes with age, and juveniles can be highly cannibalistic (Stevens et al. 1982, Stevens and Armstrong 1984). The location of their eyes enables crabs to watch for predators while handling a prey item. Crabs may also carry a clam before attempting to eat it by using their chelipeds to brace the clam against their mouthparts (F. Juanes, *personal observation*). The family Cancridae is distinctive 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).

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 (Schmidt and Warne 1969). 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 m (Quayle and Bourne 1972). Field studies have shown that *P. staminea* is an important component of the diet of various *Cancer* crabs: *C. magister* and *C. productus* in British Columbia (Pearson et al. 1979, 1981, Boulding 1983, 1984, Boulding and Hay 1984), and *C. anthonyi* in California (Peterson 1982, 1983).

METHODS

Crabs were kept individually in 190-L (50-gallon) aquaria without any substrate (to eliminate search times due to digging). Salinity was maintained at 33 to 37 g/L and water temperatures followed ambient air temperatures or ambient seawater temperatures at 18 m (ranging from 10° to 18°C). Artificial lights were regulated to seasonal photoperiod. Prior to a feeding trial, crabs were satiated by providing them with unlimited opportunity to consume clam flesh, then starved for 3 d to standardize hunger levels. They were starved for a day between trials. Only adult male crabs, ranging from 16.0 to 18.5 cm in carapace width (CW, measured between the tips of opposite 10th anterolateral spines), were used in order to reduce sex- and size-related variation. Crabs were obtained either from local seafood dealers or from Department of Fisheries and Oceans crab samplings. Clams used in this study either were purchased from a grower or were collected at Nanoose Bay, near Nanaimo, British Columbia, and were always obtained during non-reproductive periods (August to March in British Columbia; Quayle 1943, Quayle and Bourne 1972).

Energy content of the prey

Clams were dried to constant mass at 80°C. One-gram tissue samples were collected from clams ranging from 1.48 to 5.08 cm in clam shell length (CL), and then energy content was measured in a microbomb calorimeter.

The flesh from 23 clams (ranging from 1.48 to 5.35 cm CL) was dried to constant mass at 80°, and a dry mass/clam length regression was determined.

Handling time

Eleven male crabs, ranging in size from 16.0 to 18.5 cm in carapace width (mean = 16.7 cm) were presented with randomly selected individual 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 five clams was presented to any one crab during a feeding trial. Methods of attack were noted and the following behavioral 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 (<1 min) where the clam was dropped and temporarily ignored. Times of unsuccessful attacks ("persistence times") were not included in the analysis, since they were rare and only occurred with very large clams (CL > 4.3 cm).

2) "Eating time" was measured as the time from the first consumption of flesh to the completion of the meal when the shell was finally abandoned. This measure included 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.

Handling time measurements were made on two distinct groups of crabs. The first group (termed "old," mean carapace width = 16.6 cm, range: 16.0–18.5 cm) had been kept at the Pacific Biological Station for ≈6 mo and had been fed mostly on pieces of dead herring. When the 1984 crab season opened, freshly caught crabs (termed "new," mean length = 16.9 cm, range: 16.3–18.1 cm) were obtained. These crabs had cleaner carapaces (indicating a recent molt) but were observed to use similar feeding methods. The statistical difference between "old" and "new" handling-time components was determined by comparing slopes and adjusted means of the appropriate regressions using analysis of covariance.

Feeding costs

The energy 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-L plexiglass tank (34 × 20 × 12.5 cm). A constant temperature was maintained by

placing the respirometer on a water table. Any changes in temperature were automatically compensated for by the probe. Oxygen uptake rates were then calculated from slopes displayed on a 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 demonstrated successful feeding in the respirometer were used in these experiments (mean carapace width = 16.6 cm, range: 16.4–16.9 cm). Crabs were selected at random and introduced into the respirometer and left there for at least 1 h before experimentation. The box was then sealed and oxygen allowed to deplete for ≈20 min to establish resting metabolic rates. A clam, picked at random, was then introduced. Oxygen intake rate increased while feeding proceeded. The maximum rate (steepest slope) attained during the feeding trial was then subtracted from the resting rate for that trial to obtain the oxygen consumption due to feeding. Clam respiration was not a factor since clams always closed their valves (and thus did not respire) when handled or in the presence of a predator. Oxygen consumption rates were measured in microliters per litre per minute and converted to millilitres of oxygen per litre of seawater per minute (1.4286 $\mu\text{L/L} = 1 \text{ mL O}_2$). Energy cost was obtained by using the oxyenergetic conversion value of 19.4J/mL (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 energy intake calculation except cost is subtracted from energy content (or benefit). Energetic efficiency was calculated as the ratio of predicted benefit and predicted cost.

Prey-size selection

A total of fourteen crabs (mean length = 17.4 cm, range: 16.5–18.2 cm) was used in size-selection experiments. Crabs were starved for 3 d 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 cm, 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 h, after which the remaining clams were removed and noted. The crabs were starved for 24 h between feedings, after which the same combination of clams was again offered. This pattern continued for up to ten feeding periods.

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

Hypotheses for all statistical tests were rejected at $P < .05$.

Claw damage

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 ≈ 800 crabs was sampled from nine different sites over a 4-d period. Animals were caught by standard baited crab traps (retrieved after 24 h in the water) and by a beam trawl. Both of these techniques selected for crabs with CW > 10.0 cm. The animals were sexed (using the width of their abdomen), measured (carapace width), the state of each cheliped noted, and molting condition visually assessed (pre-molt, intermolt, or post-molt; see Butler 1961, Hartnoll 1982, Skinner 1985). 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 and were thus scored a 3.

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, Snow and Nielsen 1966). These mating marks can serve as an indicator of breeding activity and molting state, and thus of relative exoskeleton age in male crabs in the following way. Our sampling was conducted in May before the peak in mating was expected to occur (Mackay 1942, Cleaver 1949, Butler 1960). At this time, males are molting while females have not commenced. Although some females have been reported to delay molting for a year occasionally (Hankin et al. 1985), adults are thought to molt annually. Thus, three distinct groups can be identified in our data: (1) females carrying an exoskeleton at least 1 yr old; (2) males with mating marks probably obtained during the previous summer's mating period (and therefore also inhabiting 1-yr-old exoskeletons, since no soft or newly molted females were found); and finally, (3) males without mating marks, representing the newly molted individuals. This last group contained both 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 ≈ 11.0 cm CW (or ≈ 3 yr of age), although sexual activity is not appreciable until the males have CW ≈ 14.0 cm (Butler 1960, Selby 1980).

For the laboratory experiments, five undamaged crabs (mean CW = 17.4 cm, range: 16.8–18.3 cm) were selected and anesthetized. Their claw teeth were filed down to approximate extreme levels of wear observed in the field (an index value of 2). In addition, three

crabs that had naturally damaged chelipeds (missing part of one dactylus and/or propodus) when collected were also used. After a 2-wk acclimation period, during which crabs were fed crushed clams daily, they were again starved for 3 d before experimentation began. Handling time components were measured for a range of clam lengths (1.5–4.0 cm) using the same methods as before. The results were compared to the previously obtained "new" handling-time components.

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 (see Pearson et al. 1979). 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 pereopods. The prey was then manipulated by the crab with the third maxillipeds, the chelae, and the first and second pereopods, until one of the chelae could grasp the prey. These manipulations were frequent before the crab attempted to break the shell. Initially outright crushing was attempted, one chela doing the crushing and the other being used to support the prey during breakage. No apparent specialization of the chelae was observed. If direct crushing was unsuccessful, then the prey was further manipulated by the crab by holding the clam between the chelipeds and slowly rotating it until another crushing sequence was attempted. If still unsuccessful, the clam was again reoriented, 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. Shell fragments were then torn away until clam flesh was exposed. 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, 1984, 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 the feeding experiments. The upper limit of this range was 4.5 cm in clam shell length (CL), since clams larger than this were consistently rejected by crabs, often after long periods of attempted crushing. 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 (\pm SE) energy value obtained from the eleven bombings of clam tissue was 19405.30 ± 146.77 J/g dry mass of tissue. A tissue dry mass (M, in grams) vs. clam length (CL, in centimetres) regression was also calculated, in which $M = CL^{3.18} \times 10^{-1.99}$; $r^2 = 0.99$,

TABLE 1. Regressions of breaking (BT), eating (ET), and handling (HT) times (seconds) vs. clam length (CL) (centimetres) for "old" ($N = 121$), "new" ($N = 97$) and "worn" ($N = 32$) crabs.*

	Equation	r^2	Equality of slopes		Equality of adj. means	
			F	P	F	P
Old	BT = $CL^{4.25} \times 1.57$	0.64	0.068	0.797	11.35	0.0029
	ET = $CL^{2.34} \times 20.42$	0.61	14.67	0.001
	HT = $CL^{3.29} \times 12.30$	0.70	4.74	0.041
Worn	BT = $CL^{3.10} \times 5.75$	0.32	0.399	0.528	7.83	0.006
	ET = $CL^{1.72} \times 42.66$	0.52	0.272	0.602	24.03	0.0001
	HT = $CL^{2.41} \times 35.48$	0.51	0.012	0.914	17.96	0.0001
New	BT = $CL^{3.55} \times 2.40$	0.70				
	ET = $CL^{1.52} \times 37.15$	0.54				
	HT = $CL^{2.36} \times 25.70$	0.69				

* All regressions were significant ($P < .05$). Equality of slope tests were performed to compare both "old" and "worn" to "new" crabs. If the slopes were homogeneous ($P > .05$), an analysis of covariance was used to compare adjusted means. This test showed that for all adjusted means compared, "old" and "worn" handling time components were significantly greater than corresponding "new" handling time components.

$P < .001$. Thus, the relationship between yield or energy content (E, in joules) and clam length (in centimetres) can best be described by the equation

$$E = 194.06 \times CL^{3.18}.$$

This relationship would only hold for clams in a non-reproductive state, as used in this study. Peterson (1982) showed that the energy content of *P. staminea* varies substantially with reproductive condition.

Handling-time components

Handling times were transformed, using decimal logarithms, to meet the assumptions of parametric analysis (Kolmogorov-Smirnov test comparing data with a normal distribution, $N = 218$, $D = 0.0531$, $P > .05$).

An equality-of-slopes test (Table 1) showed that the slopes of the eating and handling time regressions for "old" and "new" crabs were significantly different from each other but were homogeneous for the breaking time regressions. A comparison of adjusted means for breaking times showed them to be significantly different from each other (Table 1), with the "old" crabs having higher mean breaking times over the range of clams tested. 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 (HT, BT, and ET, in seconds), respectively, to "new" ones, where

$$\text{New HT} = 2.452 \times (\text{Old HT})^{0.794};$$

$$r^2 = 0.933, P < .0001$$

$$\text{New BT} = 0.792 \times (\text{Old BT})^{0.949};$$

$$r^2 = 0.903, P < .0001$$

$$\text{New ET} = 4.761 \times (\text{Old ET})^{0.663};$$

$$r^2 = 0.851, P < .0001.$$

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

When plotted against prey size, eating and breaking times as well as total handling times were best described (as compared to linear functions; Fisher's transformation) by power functions (\log_{10} transformations of both variables; Figs. 1–3). Variance–mean regression lines of eating and breaking times were computed (Fig. 4) by splitting the range of clam sizes into six groups of 0.5 cm CL (i.e., 1.5–2.0, 2.0–2.5, . . . , 4.0–4.5). The slopes of these lines were homogeneous ($F = 0.019$, P

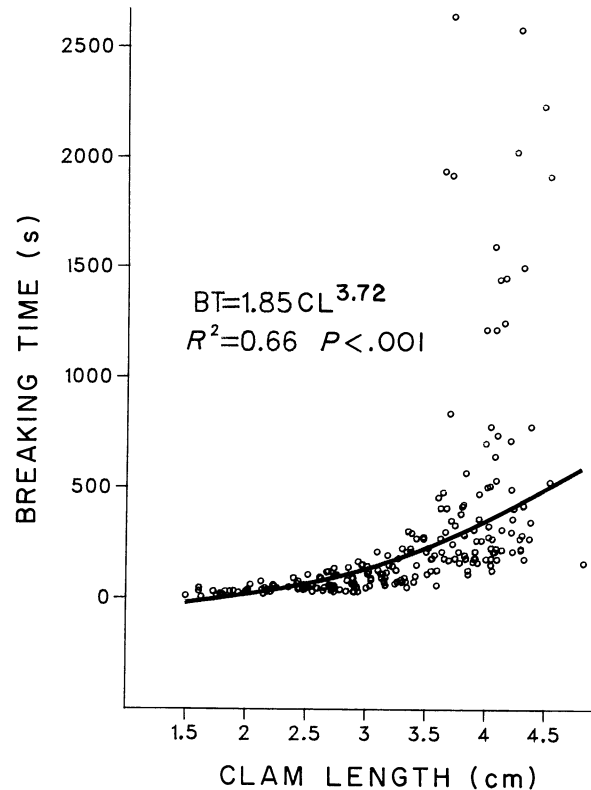


FIG. 1. The relationship between crab breaking time (BT) and clam length (CL).

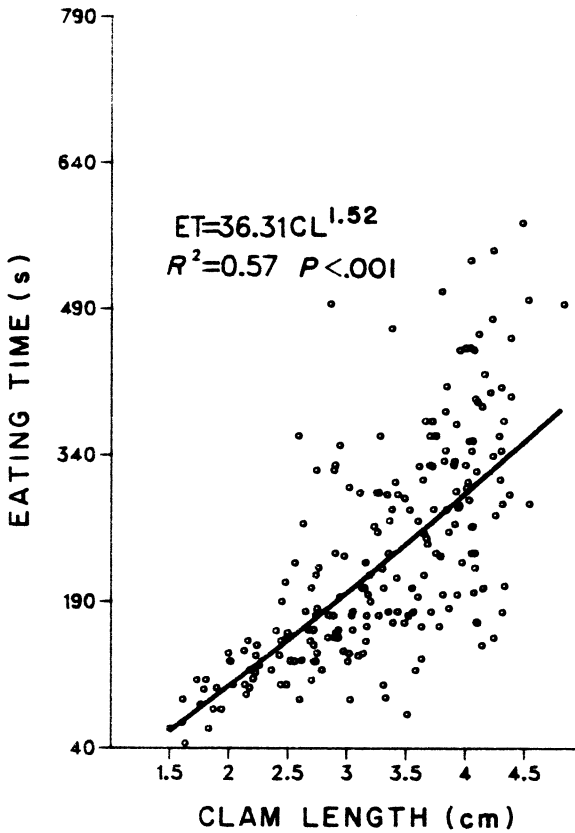


FIG. 2. *Cancer magister* eating times (ET) as a function of clam length (CL).

= .9196), allowing a comparison of adjusted means using an analysis of covariance. The results showed that the breaking time regression line had significantly greater variances at corresponding mean values ($F = 34.88, P = .0002$).

Predation cost

An exponential relationship exists between oxygen uptake (as an indicator of energy cost, in joules per second) and clam size (in centimetres) such that (Fig. 5)

$$\text{Cost} = 10^{3.16} \times \text{CL}^{2.86}; r^2 = 0.811, P < .001.$$

Prey value

The relationship between gross energy intake per unit handling time (E/HT , in joules per second) and clam length (CL, in centimetres) is best described by a linear regression (Fig. 6), where

$$E/HT = 5.776 + 5.069CL;$$

$$r^2 = 0.16, P < .01, N = 218.$$

For the clam sizes used in this study, the values of cost ranged from 0.138 to 46.75 J while benefit ranged from 704.54 to 23×10^3 J. 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: 88-96). The assumption would hold in this study since only clams in a non-reproductive state were used for all experiments.

The pattern in Fig. 6 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. At each iteration, larger clams were systematically eliminated from the analysis (by decreasing the maximum clam size in 0.1-cm intervals) until the greatest amount of variation could be explained. The best regression found using this technique excluded clam lengths >3.6 cm:

$$E/HT = \text{CL}^{1.31} \times 5.2689;$$

$$r^2 = 0.47, P < .0001, \text{CL: } 1.5\text{--}3.6 \text{ cm.}$$

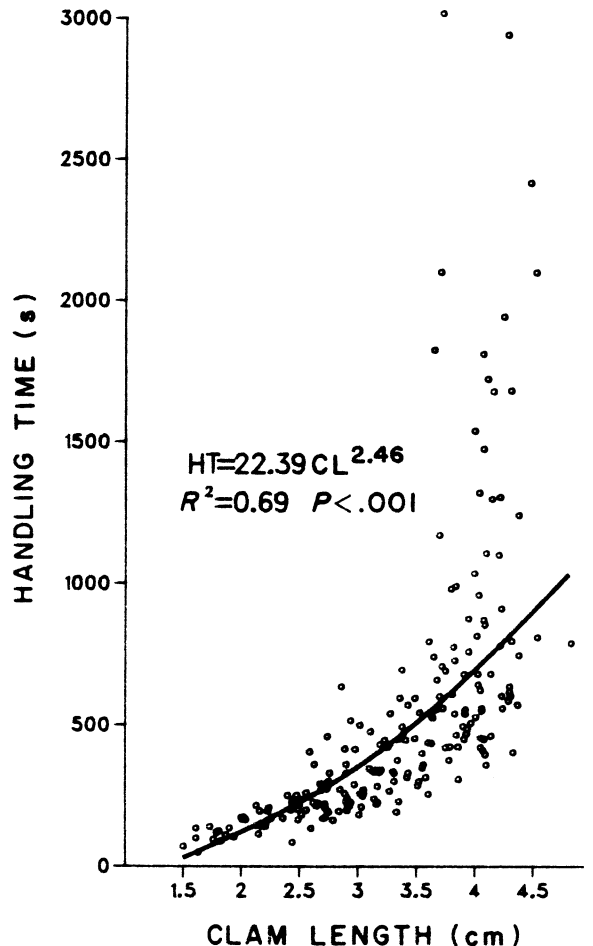


FIG. 3. The relationship between crab handling time (HT) and clam length (CL).

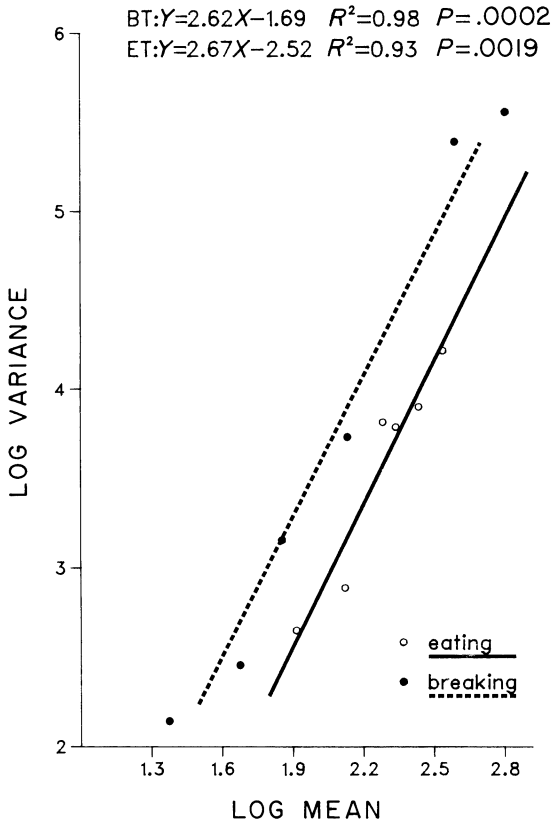


FIG. 4. Log_{10} variance vs. Log_{10} Mean for eating (ET) and breaking (BT) times (measured in seconds). The slopes of these lines were homogeneous ($F = 0.019$, $P = .920$). An analysis of covariance indicated that these lines had significantly different adjusted means ($F = 34.88$, $P = .0002$).

Beyond this "critical" clam size no significant regression can be computed. 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:

$$E/HT = CL^{0.92} \times 7.356;$$

$$r^2 = 0.29, P < .0001, N = 206.$$

In any case, 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 energy intake rates were calculated using eating and breaking times separately, different patterns emerged. The energy/eating time relationship is also an accelerating function of clam size ($E/ET = CL^{1.656} \times 5.51$; $r^2 = 0.61$, $P < .0001$). 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 ($E/BT = CL^{0.542} \times 107.23$; r^2

= 0.04, $P = .0029$). 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 (Fig. 7), and the relationship can best be described by

$$B/C = 4406.24 - 942.4CL; r^2 = 0.65, P < .001.$$

In summary, the alternative currencies provide contrasting qualitative predictions about how crabs 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 prey 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 prey size), and thus crabs should rank clams from smaller to larger.

Prey-size selection

The results show that crabs, irrespective of which clam combination they were offered, generally ate more smaller clams than expected by chance (Tables 2 and

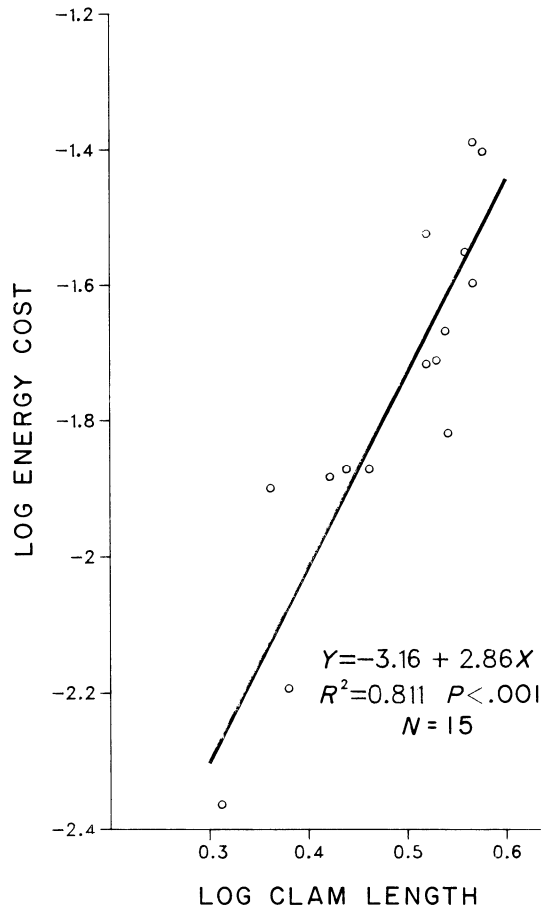


FIG. 5. The relationship between the energy cost of predation (in joules per second) and clam length (in centimetres).

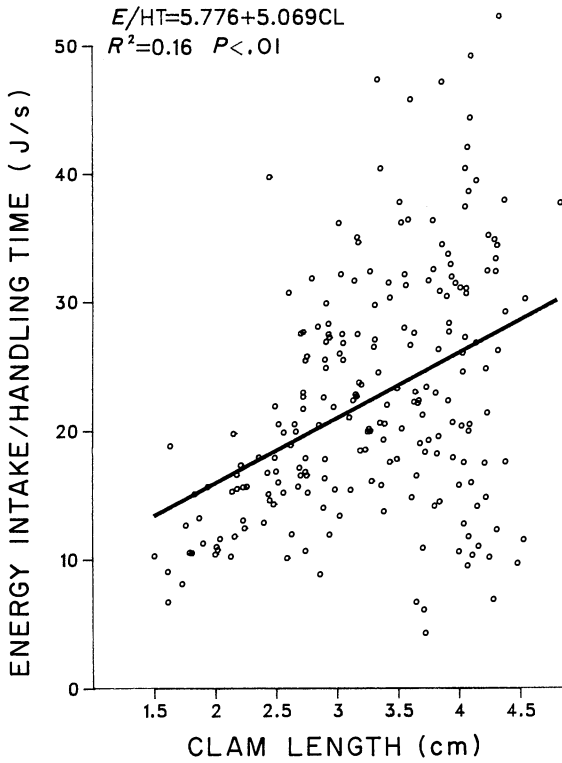


FIG. 6. Profitability (measured as the rate of gross energy intake per unit handling time, E/HT) vs. clam length (CL).

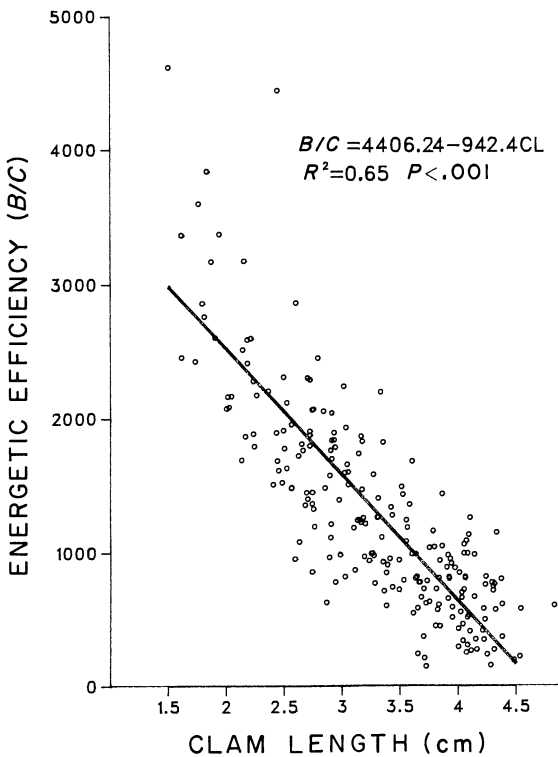


FIG. 7. Prey value (measured as the ratio of benefit to cost, B/C) vs. clam length (CL).

TABLE 2. Numbers of clams eaten by the listed individual crabs when given a choice of two size classes.

Clam size classes† offered	Crab number	No. days	No. eaten		χ^2
			Smaller	Larger	
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
4 vs. 5	11	5	36	0	36.0*
Overall total		102	981	464	184.96*

* $P < .05$.

† Clams were divided into six size classes in increments of 0.5 cm shell length. Thus, size classes 0 to 5 represent clam lengths of: 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 cm, respectively.

3). This trend is emphasized when the total numbers of clams eaten are pooled for the two-choice and the three-choice experiments respectively. The three-size-class combination can be further tested using a non-parametric Tukey-type multiple comparison (see Zar 1984) which uses rank sums instead of means (Table 4). This analysis indicates that the trend is stepwise (i.e., small > medium, small > large, and medium >

TABLE 3. Numbers of clams eaten by the listed individual crabs when given a choice among three size classes. Length compositions of clam size classes are indicated in Table 2 footnote.

Clam size classes offered	Crab number	No. days	Number eaten			χ^2
			Small	Medium	Large	
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
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*

* $P < .05$.

TABLE 4. Results of Tukey-type multiple comparison (Zar 1984:199). S, M, L are the small (0,1,2), medium (3), and large (4,5), clam size classes respectively. (Length compositions of size classes are indicated in Table 2 footnote.) D is the difference in rank sums, SE is the standard error, and q ($= D/SE$) is the test statistic.*

Comparison	D	SE	q^*
S vs. M	289.5	78.1	3.706
S vs. L	640.5	78.1	8.201
M vs. L	351.0	78.1	4.494

* The null hypothesis is rejected if $q > 3.314$ (the critical value of q for $P < .05$).

large). Therefore *Cancer magister*'s preference decreases monotonically with increasing prey size.

Claw damage in field-collected specimens

Among females, more than half the claws showed some wear, and $\approx 12\%$ of the claws were broken (Fig. 8). 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 because most mature males would have molted recently. However, some breakage could have been caused by fighting in the crab trap or in the net before retrieval.

Among "mated" males (those with mating marks, and thus expected to have exoskeletons that were at least 1 yr old), 60% of the claws were worn and 22%

were broken (Fig. 8). Only 3% (4/123) of these individuals had both chelipeds broken.

Laboratory experiments—claw damage

Handling-time regressions of "new" animals were compared to those with artificially worn teeth using an analysis of covariance after testing for homogeneity of slopes (Table 1). A comparison of adjusted means showed that crabs with worn claws had significantly greater mean handling times for that range of clams tested (Table 1).

Those crabs with parts of the chelipeds broken were never observed to consume even the smallest clams available (20 feeding trials with clam sizes ranging from 1.5 to 4.0 cm CL). Attempts to crack the shells were observed but none of these was successful. When offered previously opened clams all damaged crabs readily consumed the clam tissue.

DISCUSSION

The results indicate that there is a strong size-selective behavior 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 *C. magister*'s size-selective preferences when feeding on *P. staminea*. The maximization of energetic efficiency (Fig. 7) provides a much better fit to the observed feeding preferences, in that

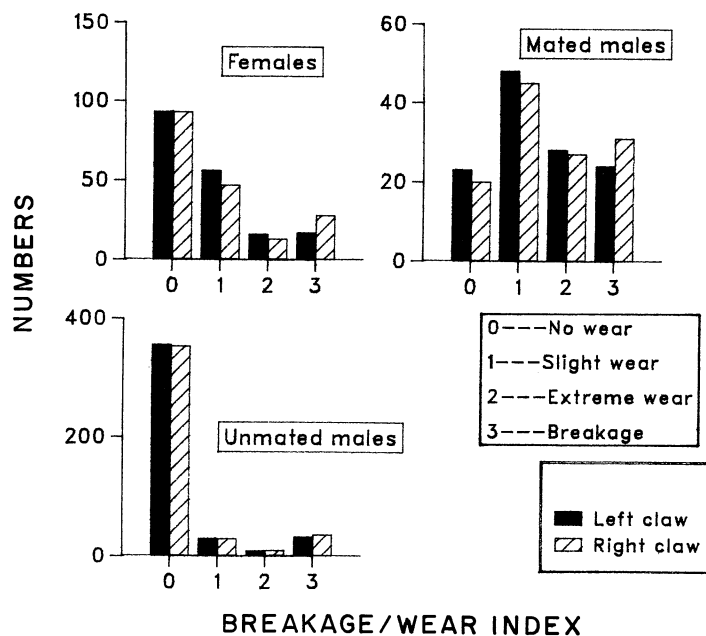


FIG. 8. Numbers of broken chelipeds and level of claw-tooth wear in a natural population of *C. magister* near Tofino, British Columbia, in May 1986. Mated and unmated males were distinguished by the presence or absence of mating marks.

they both rank prey in the same order. 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 energy 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 that 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 behavior 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, resulting in a breakdown of the flight mechanism, the worker can no longer forage. Thus bees maximize the delivery of nectar per unit of energy 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 masses.

Bernatchez and Dodson (1987) showed that energetic efficiency (defined as the minimization of cost per unit distance) correctly predicts the migration behavior of semelparous fishes whose energy reserves are exhausted during migration (i.e., 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 us to investigate the possibility of the proposed limited cost representing a fixed amount of lifetime claw use. Claw breakage in crabs might be a process similar to the breakdown of the flight mechanism and the subsequent inability to forage in honey bees, and could provide a theoretical explanation for the use of energetic efficiency as a currency to predict prey-size selection in crabs.

Boulding and LaBarbera (1986) have shown that *Cancer productus*, a congeneric that is also found sympatrically with *Cancer magister*, could directly crush only the smallest sizes of *Protothaca staminea*. Their experiments demonstrated that repeated loading, eventually causing low-cycle fatigue damage of the shell material, enabled crabs to open larger clams than they would be able to crush directly.

If a crab, by repeatedly loading a clam, is building up plastic strain on the clam shell, it must also be accumulating similar stress forces in the cuticle of its own chelae. However, the crab claw, because of its higher organic content (Wainwright et al. 1976) and its sclerotization (a process that increases mechanical strength of appendages by bonding together chitin molecules; Welinder 1974, Brown 1975), will withstand more force cycles before reaching fatigue damage (and thus have a longer "fatigue life"; see Broek 1982) than the more brittle bivalve shell. J. M. Gosline (*personal communication*), suggests that fatigue failure in crab cuticles under cyclic stress is likely to be a similar process to that described for bone (Wainwright et al. 1976). The crustacean cuticle and bone are similar structurally in that they are both considered fibrous composite materials found in an amorphous matrix (Welinder 1975, Wainwright et al. 1976).

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). 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.

If chelae fatigue failure is an important process, damaged claws should be visible in a natural population of *C. magister*. The results of our field survey indicate that two forms of damage, claw wear and breakage, occur in a natural population. The extent of wear and presence of breakage varied with sex and was dependent on the individual's molting state (Fig. 8). Tooth wear is likely to be a continuous process (easily documented by an observer), which has the effect of increasing handling times and energy costs by reducing the efficiency with which a crab can crush a clam (Table 1). 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). Claw breakage due to fatigue damage occurs once a critical load is reached. Fatigue failure can result from either impact loading (e.g., fighting) or from the intermittent accumulation of plastic strain generated every time a brittle structure (such as a clam) is loaded (Sandor 1972, Lefebvre and Ellyin 1984). There is no way to distinguish between these or to estimate the extent of fighting in a natural population.

Our laboratory observations indicate that claw dam-

age may arise as a consequence of clam-feeding behavior. In addition, the 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 behavior.

There may be a direct relationship between a cheliped's extent of wear and its proximity to fatigue failure (and thus breakage). The exact nature of this relationship could be obtained empirically by measuring wear levels frequently while controlling diet. 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.

Ecological effects of claw wear and breakage

The physiological effects of limb loss in crustaceans have been investigated in some detail (Skinner 1985). Little information exists on the ecological and physiological effects of claw-tooth wear and partial claw breakage. It is likely that the extent of claw damage (or breakage) in *Cancer magister* males has a considerable effect on sexual behavior and eventual mating success (Juanes 1987). Breakage and wear will reduce feeding efficiency and therefore energy accumulation before the mating period. A deterioration of food quality and quantity has been shown to reduce the growth increment (increase in size at a molt) and lengthen the intermolt period (time between molts) in various crustaceans (Hartnoll 1982). Breakage may also reduce fighting ability, visual attractiveness to females (Atema and Cobb 1980, Salmon 1983, Huber 1985, Atema 1986), and ability to hold onto a female during the pre- and post-molting embrace (Hazlett 1986). Sekkelsten (1988) has shown that a handicap, such as missing chelae, has a negative effect on male shore crab (*Carcinus maenas*) mating success. Medium-sized males with broken chelae, although abundant in the population, were never found mating.

Skinner (1985) recently reviewed the effects of the loss of chelipeds and/or other limbs on the molting and regenerative process in crustaceans. 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. Thus loss of limbs may initiate precocious mating, shorten the molt interval by up to 40%, and/or reduce the growth increment by up to 50%. Field studies have shown that intensive regeneration can affect the size of the regenerates themselves and the overall dimensions of the animal (Churchill 1918, Niwa and Kurata 1964, Edwards 1972). 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 the limb 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 effect 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. This could result in a decrease in the growth increment and a deformation of regenerating claws (in fact, we observed many crabs with malformed claw tips, presumably due to earlier breakage).

A reduced growth rate is likely to have important effects on reproductive success of crabs. For males a smaller size would create a disadvantage in fighting ability and subsequent access to females. Mayer (1973) demonstrated an allometric relationship between female body size and brood size in *Cancer magister*; therefore smaller females will produce fewer eggs. Premature molting, caused by extensive limb loss, could also have severe consequences if there is an optimum time at which to molt.

Handling-time variation

The variation in profitabilities beyond a clam size of 3.6 cm is due in part to the variability in breaking times (Figs. 1 and 4) and in part to the use of a combination of attack methods (i.e., "crushing" and "chipping") by the crabs on large clams. This large variability suggests that crabs would not be able to accurately predict the handling times of their prey from any measure of body size, especially for the larger clams. 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) and can affect the length of fatigue life (number and strength of force pulses required to reach fatigue failure; Broek 1982). 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 could explain the careful inspection performed by crabs on the shells of larger clams. Vermeij (1982) has suggested that unsuccessful predation is a necessary condition for the evolution of antipredatory characteristics, and has shown that sublethal damage was common in most predator-prey interactions.

The importance of past feeding history can be in-

ferred from the statistical difference in handling-time components between "old" and "new" crabs (Table 1). Abby-Kalio and Warner (1984) showed that this result can be due to an intermolt reduction in both strength and sarcomere length in the chela-closing muscles caused by a lack of "clam-breaking" exercise.

Excavation costs

Vermeij (1978, 1987) has suggested that crab predation has been a major selective agent in the evolution of bivalve and gastropod shells and behavior patterns. Prey defenses, such as increases in shell strength and morphology, the use of refugia, and/or camouflage, may have evolved in response to that selection.

Boulding (1984) showed that the vulnerability of burrowing bivalves to shell-breaking predation by crabs was strongly influenced by shell features such as size, shell thickness, degree of inflation, and the presence or absence of a gape. Thus crabs (*C. productus* and *C. magister*), when given a choice among four species of clams, preferentially ingested clams in order of their morphological vulnerability.

Depth of burial may also be an important prey defense by increasing the handling and/or search times of foraging predators. There is some evidence to suggest that depth of burial may only be an important constraint for larger clams. Haddon et al. (1987) showed depth of burial in similarly-sized toheroa (*Paphies ventricosa*) to be a significant deterrent of predation only for those clams buried at 26 cm. No significant differences were found in numbers of toheroa eaten by paddle crabs (*Ovalipes catharus*) among the 0, 5, and 10 cm depth treatments. This difference could potentially be due to probing behavior by the crab, which would equalize the costs of detecting clams buried to the depth of probing. In addition to vertical dactyl probing and prey removal, crabs (*Cancer borealis*, *Carcinus maenas*, and *Pagurus longicarpus*) have been observed to initially excavate a vertical pit (of up to 30 cm in depth) and then continue foraging by laterally searching for prey (Auster and Crockett 1984). This lateral excavation would allow predators equal access to different prey sizes at variable depths. In addition, Richardson (1985) showed that even though clam burying depth increased with clam size (for the Japanese littleneck clam, *Venerupis japonica*), relative prey availability to crows (*Corvus caurinus*) was a function of predator searching technique. Thus, when probing, prey availability was an increasing function of clam size, while, when digging, the smaller (and shallower) clams were more available.

Clam burial depth, and thus potential susceptibility to predators, has also been shown to vary with season (Zwarts and Wanink 1989) and substrate type (Peterson 1982, Gibbons 1984, Fouke 1988). Peterson (1983), in an extensive field study, found that although *Protothaca staminea* was found buried deeper than the thicker-shelled *Chione undatella*, predation rates by

Cancer anthonyi on *P. staminea* were higher. Large numbers of dead crushed shells were also found for three epifaunal thin-shelled species (*Crepidula onyx*, *Bulla gouldiana*, and *Mytilus edulis*) and two infaunal thin-shelled bivalves (*Macoma nasuta* and *Apolymetis biangulata*) that live at sediment depths below those occupied by *Protothaca* and *Chione*. In contrast, crushed shells of a thick-shelled epifaunal species (*Cerithidea californica*) were rare. These results suggest that shell morphology may be a more important constraint to shell-crushing predators than prey burial depth.

In an extensive literature survey, Juanes (1987) found that the overwhelming trend (for over 30 decapod-mollusc predation studies) was for crabs and lobsters to preferentially consume the smallest size of bivalve or snail available when given a choice. In about half of these studies, the prey used were not burrowing species (e.g., mussels, snails, oysters, whelks, scallops), which implies that prey burial depth is not always an important component of the predation process in decapod-bivalve (and snail) predatory interactions.

In this study we considered prey selection for different size classes of prey by removing the confounding effect of prey burial depths. The effect of variable search costs will only be significant however, if the correlation between clam size and burying depth is very strong (for all prey sizes) and if the excavation times are large enough to reverse the prey rankings calculated from the energy intake rate model.

Predation costs

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

The costs measured here were more representative of the breaking costs than the eating costs, since the highest rate of oxygen uptake usually occurred early in the feeding period before eating commenced. These data suggest that the cost of predation in this case is the cost of creating force pulses.

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 of breaking time. Elnor and Hughes (1978) also found that, when their studied prey (*Mytilus 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 of total time.

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 is instead the cost of breaking a shell. Energetic efficiency, the ratio of energy gained to energy lost (and this cost is mostly due to each squeeze), provides the better predictions of size selection in *Cancer magister*. Thus, both the currency and the constraint (the cost of crushing shells rather than handling time) differ from the classical optimal diet model.

ACKNOWLEDGMENTS

We thank B. Roitberg, G. Jamieson, L. Dill, R. Ydenberg, E. Charnov, D. Conover, S. Fouke, P. Lawton, M. Stanhope, J. Brown, D. Dyfe, and A. Hawkins for stimulating discussions and comments on the paper. A. Phillips, B. Smith, C. Usselman, J. and W. McClorie, and M. Connelly provided valuable assistance in the field and laboratory. We are grateful to the staffs of the Pacific Biological Station and the Bamfield Marine Station for their logistical and technical assistance. Dr. C. H. Peterson and an anonymous reviewer significantly improved the quality of the manuscript.

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