Foraging behaviour of the crab *Cancer pagurus* feeding on the gastropods *Nucella lapillus* and *Littorina littorea:* comparisons with optimal foraging theory

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ABSTRACT: Juvenile *Cancer pagurus* used the left and right chelae with equal facility to immediately crush small *Nucella lapillus* and *Littorina littorea,* and to gradually chip away the shells of larger snails. Due to slippage of the chela over the apical whorls, attacks directed towards the shell aperture of larger prey were more successful than those applied to the spire. Attack success rate decreased from unity at the critical size for crushing to zero at the critical size for apertural breakage, falling more rapidly for *N. lapillus* than for *L. littorea.* Handling times rose rapidly for *N. lapillus* as prey exceeded critical size for crushing and consequently the maximum yield per unit handling time coincided with this critical size. Maximum yield for *L. littorea* was within the range of sizes that were opened by apertural breakage. Profitability curves derived from single regressions of yield and of handling time on prey size failed to predict profitability accurately. Satisfactory curves were obtained by combining separate handling time functions for prey below and above the critical size for immediate crushing. When offered a range of prey sizes, *C. pagurus* attacked all size classes, but incorporated smaller prey into the diet first as they succumbed more frequently to attack. The greater susceptibility of *L. littorea* was reflected in differential predation on this species when offered together with *N. lapillus.* Contrary to optimal foraging expectations of short persistence times when prey are of variable and relatively unpredictable profitability, *C. pagurus* persisted for up to several hours with large prey. Thus prey-size selectivity appeared to have a passive mechanical, rather than an active behavioural basis.

INTRODUCTION

Considerable attention has been directed in recent years to the analysis of predator behaviour from the perspective of optimal foraging theory (reviewed by Pyke et al. 1977, Hughes 1980, Pyke 1984). Studies on the size selection of molluscs by crabs (Decapoda: Brachyura) have contributed both to theoretical development and empirical testing of predictions based on optimal foraging premises (Elner & Hughes 1978, Hughes 1979, Hughes & Elner 1979, Hughes & Seed 1981, Blundon & Kennedy 1982, Jubb et al. 1983, Arnold 1984). The majority of such studies pertain to crabs from a single family (Decapoda: Portunidae) and,

more significantly, to 1 species within that family, *Carcinus maenas.* The aim of the present study is to test the generality of optimal foraging rules proposed for portunid crabs by using *Cancer pagurus* (Decapoda: Cancridae), a brachyuran crab with different morphological, physiological and behavioural attributes (Warner & Jones 1976, Vermeij 1977, Lawton & Elner 1985). Laboratory experiments involving *Cancer pagurus* feeding on 2 gastropod species are here described which characterize: (1) attack methods used during predation attempts and proportional attack success in terms of crab size and sex, chelal morphology, gastropod size and shell morphology; (2) the form of handling time and profitability relations taking such factors into account; (3) the extent to which prey-size selectivity of *Cancer pagurus* on gastropods reflects passive mechanical or active behavioural mechanisms of choice (*sensu* Hughes 1980).

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In North Wales, the direct-developing gastropod *Nucella lapillus* is often sympatric with *Littorina littorea,* a species having a pelagic larval stage. Hughes & Elner (1979) found that local populations of *N. lapillus,* coexisting with large populations of the portunid crab, *Carcinus maenas,* were more robust, with narrower apertures than those from sites where these crabs were absent. These features increased gastropod resistance to crab-attack, and were even more pronounced in a sublittoral fringe population of *N. lapillus* coexisting with *Cancer pagurus.* Such inter-population variation in shell morphology is much reduced or absent in *L. littorea.* Gene flow between populations during the pelagic larval stage of this species may preclude morphological adaptation to local selection factors (Currey & Hughes 1982). Collection sites for these species, around the Isle of Anglesey, North Wales, were selected so that 2 additional questions could be addressed in the study: (1) Is *C. pagurus* predation potentially responsible for the pronounced morphological attributes of sublittoral fringe *N. lapillus?* (2) What are the consequences, for susceptibility to predation, of reduced levels of morphological adaptation in *L. littorea?*

MATERIAL AND METHODS

General procedures. Juvenile *Cancer pagurus* and the gastropods *Nucella lapillus* and *Littorina littorea* were collected on ELWS tides from local shores (Table 1). Due to the low availability of small- to medium-sized *L. littorea* at the Penmon site, feeding trials with this species used snails of these sizes from Llanddwyn Island (Table 1) to supplement material from Penmon. *L. littorea* from the 2 localities have similar morphological characteristics, with the exception that some individuals from Llanddwyn Island show marked apical shell erosion (Lawton 1983).

Crabs were each placed in separate 40 × 20 × 25 cm (height) clear plastic aquaria filled to 20 cm with recirculating filtered seawater. Salinity was maintained at 33.5 to 37.0‰ and water temperatures fol-

lowed ambient air temperatures of 12.8 to 19.0 °C. Artificial lights were regulated to seasonal photoperiod. Prior to a feeding trial crabs were satiated with flesh of the prey species to be tested, then starved for 2 d to standardize hunger level (Jubb et al. 1983). *Cancer pagurus* of a wide size range (carapace width, cm) were used in preliminary trials; however, in subsequent experiments crabs from only 3 size classes were used: small (5.5 to 6.5 cm), medium (7.5 to 8.5 cm), and large (9.5 to 10.5 cm). Gastropod prey were similarly categorized into particular size classes (shell height, cm).

Enumeration data were analysed by the Log-likelihood ratio, G, using observed frequencies, and applying Yates' correction for continuity to derive an adjusted G in goodness-of-fit tests with only 2 classifications (Zar 1974). Other parametric statistical procedures were obtained from Zar (1974); non-parametric statistics were computed according to Siegel (1956).

Attack methods. Church Island *Nucella lapillus* of 0.5 to 2.1 cm shell height and *Littorina littorea* of 0.5 to 3.1 cm shell height were presented, individually, to male and female crabs of 5.5 to 12.5 cm carapace width. Behavioural responses to the prey and details of each attack sequence made by each crab were recorded, together with the success or failure of the attack.

Attack success rate. Male and female crabs from each of the 3 size classes (n = 6 to 7 per size class) were presented with Church Island *Nucella lapillus* of 0.8 to 2.5 cm shell height, subdivided into 4 size classes. The proportion of successful attacks was calculated from 10 attacks for each combination of predator-prey size class.

A less detailed examination of attack success rate was undertaken for *Littorina littorea* by determining the critical shell height (*sensu* Vermeij 1976) for complete crushing of smaller prey, corresponding to the maximum size for an attack success rate of unity, and the critical shell height for apertural breakage, corresponding to the maximum size for an attack success rate greater than zero. Twelve male crabs (5.5 to 10.7 cm carapace width) were each initially presented with

Table 1. Isle of Anglesey, North Wales. Location (Ordnance Survey map reference) and exposure grade (Lewis 1964) of each collection site together with the maximum size recorded for *Cancer pagurus* (carapace width, cm), *Nucella lapillus* and *Littorina littorea* (shell height, cm) during intertidal searches. Consult Lawton (1983) for a more detailed description of the sites

Site	Location	Exposure grade	Maximum size recorded		
			Cancer pagurus	*Nucella lapillus*	*Littorina littorea*
Llanddwyn Island	SH386628	1	Not found intertidally	3.3	2.6
Penmon	SH638816	3 – 4	8.8	3.9	3.4
Church Island	SH552716	4 – 5	13.2	4.2	3.2

5 small *L. littorea*. Eaten prey were replaced daily with progressively larger individuals until 5 d elapsed without further predation.

Handling time. Male and female crabs from the 3 size classes (n = 6 to 7 per size class) were presented individually with Church Island *Nucella lapillus* of 0.5 to 2.0 cm shell height. Crabs were starved for 24 h between consecutive presentations to standardize hunger level. Methods of attack were noted and the following behavioural sequences timed: (1) if a prey was rejected, 'persistence time' was measured as the time from the moment the crab grasped the prey until rejection; (2) if a prey was not rejected, 'breaking time' was measured as the time from the moment the crab grasped the prey to the first bite of flesh exposed by breaking the shell; (3) 'eating time' was measured as the time from the first bite of flesh to abondonment of the prey, including intermittent periods of shell breakage and inspection of shell debris towards the end of the meal. 'Handling time' was calculated as the sum of breaking time and eating time.

Four medium-sized male crabs were then divided into 2 pairs. One pair of crabs was presented with a range of sizes of Penmon *Nucella lapillus* and the handling episodes timed. Handling times were recorded for the other pair as they preyed upon *Littorina littorea*.

Profitability. The yield of flesh from Church Island *Nucella lapillus* was estimated from a regression of $\log_e$ (dry flesh weight) on $\log_e$ (shell height). Data were obtained by removing the flesh from *N. lapillus* of 0.5 to 2.5 cm shell height, drying the flesh for 48 h at 60 °C, weighing the dried flesh and applying an energy conversion factor of 21.97 kJ g^{-1} (Hughes 1972). Similar data were obtained for Penmon *N. lapillus* and *Littorina littorea*. 'Profitability', the yield of flesh per unit handling time (Hughes 1980), was estimated by dividing the yield of flesh predicted by regression by each measurement of handling time. Curves relating profitability to prey size were derived by dividing the regression equation for yield of flesh by the appropriate equation for handling time, both with and without adjustment for size-specific attack success rates.

Prey-size selection. Prey-size selection was observed when crabs were presented with Church Island *Nucella lapillus*, Penmon *N. lapillus* and *Littorina littorea*, all maintained in equal numbers by replacing injured as well as eaten prey (unlimited availability), and with Church Island *N. lapillus* that were not replaced as injured or eaten (limited availability).

Unlimited *Nucella lapillus:* 4 medium-sized male crabs were presented with 5 Church Island *N. lapillus* from each of 4 size classes (indicated in Table 2), placed haphazardly over the aquarium bottom for each crab. All *N. lapillus* were inspected and debris

removed daily for 10 d, replacing injured or eaten prey with fresh ones of a similar size. The procedure was repeated for 4 medium-sized male crabs presented with Penmon *N. lapillus*.

Unlimited *Littorina littorea:* 2 male crabs from each of the 3 predator size classes were presented for 10 d with 5 *L. littorea* from each of 3 or 4 size classes (indicated in Table 2), dependent on crab size. Because *L. littorea*, unlike *Nucella lapillus*, tended to crawl up the aquarium walls and remain out of reach of the crabs, they were immobilized before experimentation by immersion in fresh water at 40 °C for 15 min, followed by immersion in sea water at ambient air temperature for 10 min. This treatment stimulated the animals to retract into the shell. Other experimental details were as described above for *N. lapillus*.

Unlimited mixture of *Nucella lapillus* and *Littorina littorea:* 4 medium-sized male crabs were each presented for 7 d with 5 Penmon *N. lapillus* and 5 *L. littorea* from each of 3 size classes (indicated in Table 3). The *N. lapillus* were heat-treated similarly to the *L. littorea*. A pair of crabs fed treated and untreated *N. lapillus* did not respond differentially to either prey (adjusted G = 2.1, d.f. = 1, P > 0.05).

Limited Church Island *Nucella lapillus:* 2 male crabs from each of the 3 predator size classes were each presented initially with 10 *N. lapillus* from 3 or 4 size classes (indicated in Fig. 6), the range in prey size being dependent on crab size. Prey were not replaced as eaten, so that exploited size classes became depleted over the 10 d experiment. Debris was removed daily but injured prey were left in the aquaria.

RESULTS

Attack methods

An olfactory response to prey was recognizable by the synchronous orientation of the antennules towards the prey together with an increase in antennular flicking rate. Following contact, prey were either swept under the abdomen and forward towards the chelipeds using the pereiopods, or swept inward by lateral extension and flexion of a cheliped. The prey was grasped most frequently with the right cheliped (adjusted G = 4.0, d.f. = 1, P < 0.05), then both chelipeds were drawn together in front of the mouth. Relatively small prey that were dropped during these actions were seldom recovered. Prey were manipulated by the 3rd maxillipeds and chelae, the 1st and 2nd pereiopods providing additional support for large prey. Such manipulations were frequent before crabs attempted to break the shell and occurred intermittently during breakage.

Nucella lapillus

Three methods of attack were recognizable:

(1) *Crushing.* Small *Nucella lapillus* were completely crushed with equal probability by either chela (adjusted G = 2.5, d. f. = 1, P > 0.05). The chela used to crush the prey was usually the one that initially had picked it up (G = 15.6, d. f. = 3, P < 0.005), the other chela being used to support the prey during breakage. Crushing involved repeated applications of force accompanied by slight reorientations of the prey within the chelal gape. Of 32 small *N. lapillus* crushed in this manner, 26 were broken by a single crushing sequence, 4 by 2 crushing sequences separated by oral manipulation, and 2 by 3 crushing sequences.

(2) *Apertural breakage.* The propodus or dactylus of 1 chela was inserted into the shell aperture and the columella grasped. The other chela then broke away the shell lip opposite the columella. Either chela was used with equal facility to hold or break the shell in such attacks. Applications of force were interspersed with periods of reorientation that became more frequent with larger prey. The technique was successful in 98 cases out of 164 observed attacks on large *Nucella lapillus.* Shell lip material was readily removed up to the point of maximum retraction of the snail. The operculum then obstructed further insertion of the dactyli and 64 attacks were observed to fail at this stage.

(3) *Apex removal.* Crabs frequently grasped the columella with 1 chela while attempting to crush the apex of the shell with the other. This technique was only rarely successful (in 2 cases), the process being hindered by slippage of the chela over the apical shell whorls.

Littorina littorea

Prey opening techniques were comparable to those used on *Nucella lapillus* with some qualifications due to the larger shell aperture and thinner shell of *Littorina littorea.* At prey sizes just above the maximum crushed outright, the shell was completely broken by indiscriminate attacks to the apertural margin. At larger sizes attacks were directed to the centre of the shell lip, leaving a spiral gash along the whorls and the columella intact. Towards the critical prey size, the apices of some shells could not be opened completely, resulting in only partial prey consumption. At these large prey sizes the operculum of *L. littorea* was effective in protecting against crab attack. Crabs were frequently observed attempting to remove the apices of *L. littorea,* but this technique was never successful, even with Llanddwyn Island snails showing marked apical shell erosion.

Attack success rate

Nucella lapillus

The proportion of successful attacks, based on data for all methods of attack, was not significantly different between male and female crabs within any predator-prey size class (Log-likelihood ratio, all P > 0.05). Attack success rates declined steeply from unity at the critical size for crushing to zero at the critical size for apertural breakage (Fig. 1A). These critical sizes increased with increasing crab size but for crabs of a given size they spanned no more than a 0.8 cm increment in shell height of the prey (Fig. 1A).

Littorina littorea

Critical size for crushing and apertural breakage were separated by an increment in shell height of about 1.0 to 1.5 cm (Fig. 1B). These critical sizes increased almost in parallel as crab size increased, the
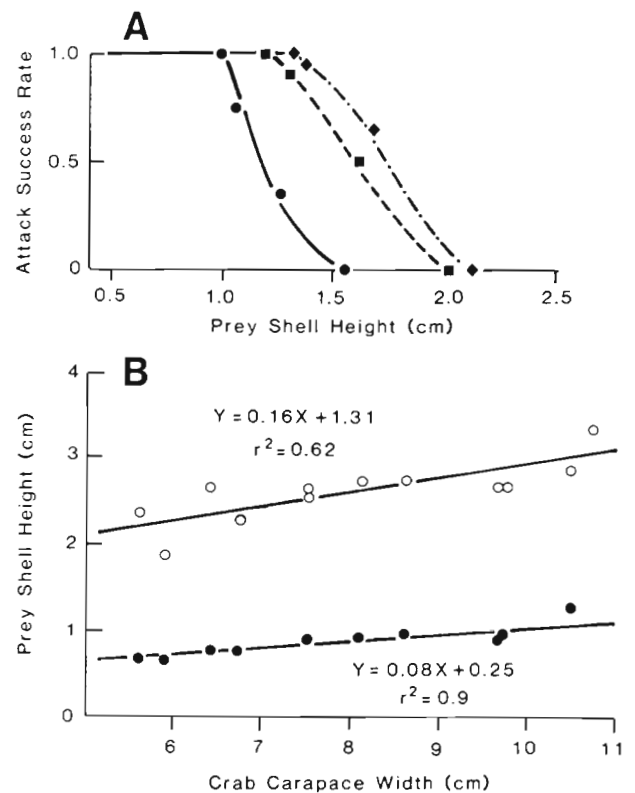

Fig. 1 *Cancer pagurus.* (A) Attack success rate on Church Island *Nucella lapillus.* Curves fitted by eye. Crab size classes: small (●); medium (■); large (◆). (B) Critical sizes of *Littorina littorea* susceptible to crushing (●) and apertural breakage (○). Critical sizes defined as mean size of largest shell broken by an attack method, and smallest size resistant to breakage by that method

critical size for crushing being less variable than that for apertural breakage (Fig. 1B).

Handling time

Persistence time, in unsuccessful attacks on Church Island *Nucella lapillus,* increased with increasing prey size, but there was much variation about the trend (Fig. 2).
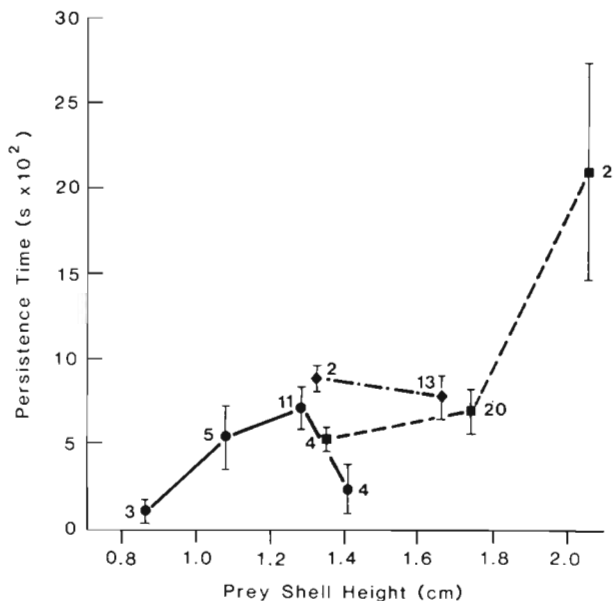

Fig. 2. *Cancer pagurus.* Mean persistence time (with SE and number of observations) in unsuccessful attacks on Church Island *Nucella lapillus.* Symbols for crab size class as in Fig. 1A

Handling time components of successful attacks (breaking time, handling time) appeared to be accelerating functions of prey size, and for a given sized prey were longer for smaller crabs, although there was considerable variation at large prey sizes (Fig. 3 & 4). Initial regression analysis involved determining the fit of linear, exponential and power functions to data from each size class (irrespective of attack method). Whereas exponential and power functions gave significant improvements in fit to breaking time data over linear functions, differences between the correlation coefficients of these functions were not significant (Fisher's transformation, all $P > 0.05$) in any size class (Fig. 3). A similar result was obtained for handling time data, and only parameters for exponential functions are displayed (Fig. 4).

Using data from all 3 size classes, multiple linear regression, with a dependent variable of $\log_e$ (breaking time) on prey shell height with dummy independent variables of crab size, sex and attack method,
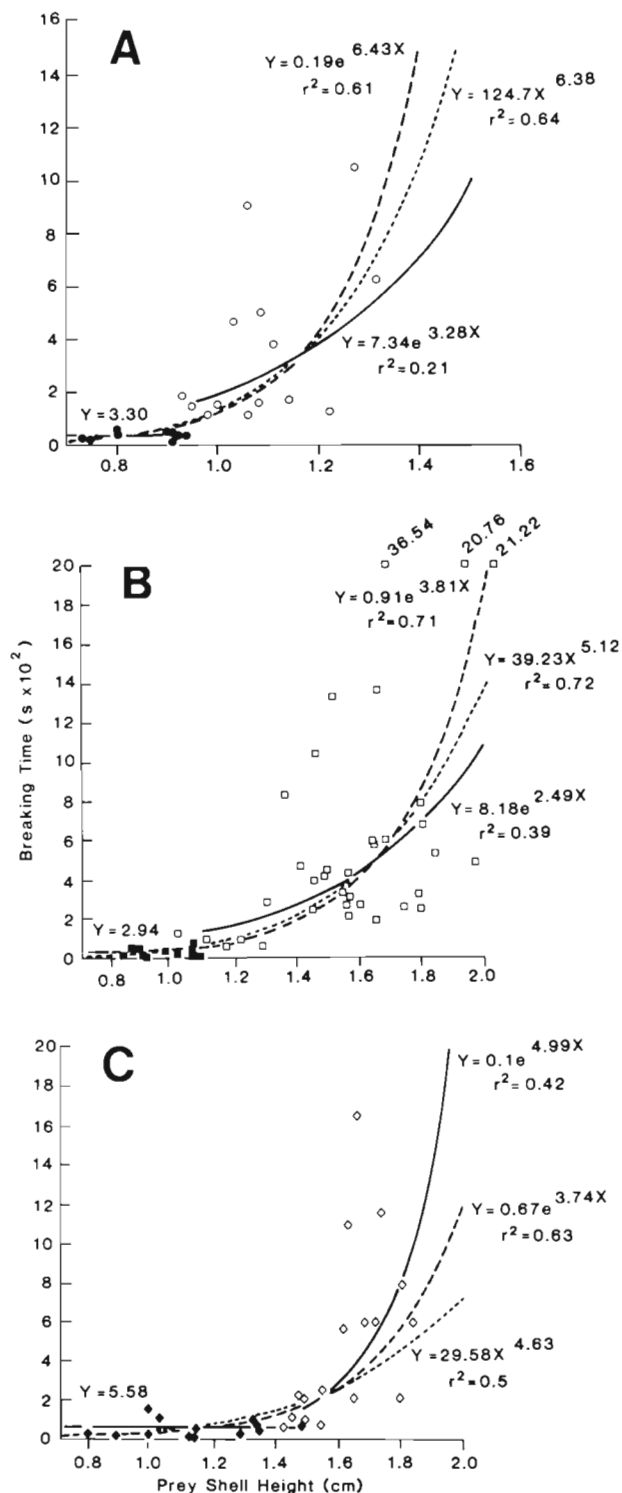

Fig. 3. *Cancer pagurus.* Breaking time in successful attacks on Church Island *Nucella lapillus.* Crab size classes: (A) small; (B) medium; (C) large. Solid symbols indicate that crushing was used, open symbols that apertural breakage was used as the attack method. Values for exceptionally long breaking times offset diagonally above data points. Regression functions: dual function (———); exponential (– – –); power (- - - -). Vertical and horizontal scales in A differ from those in B and C
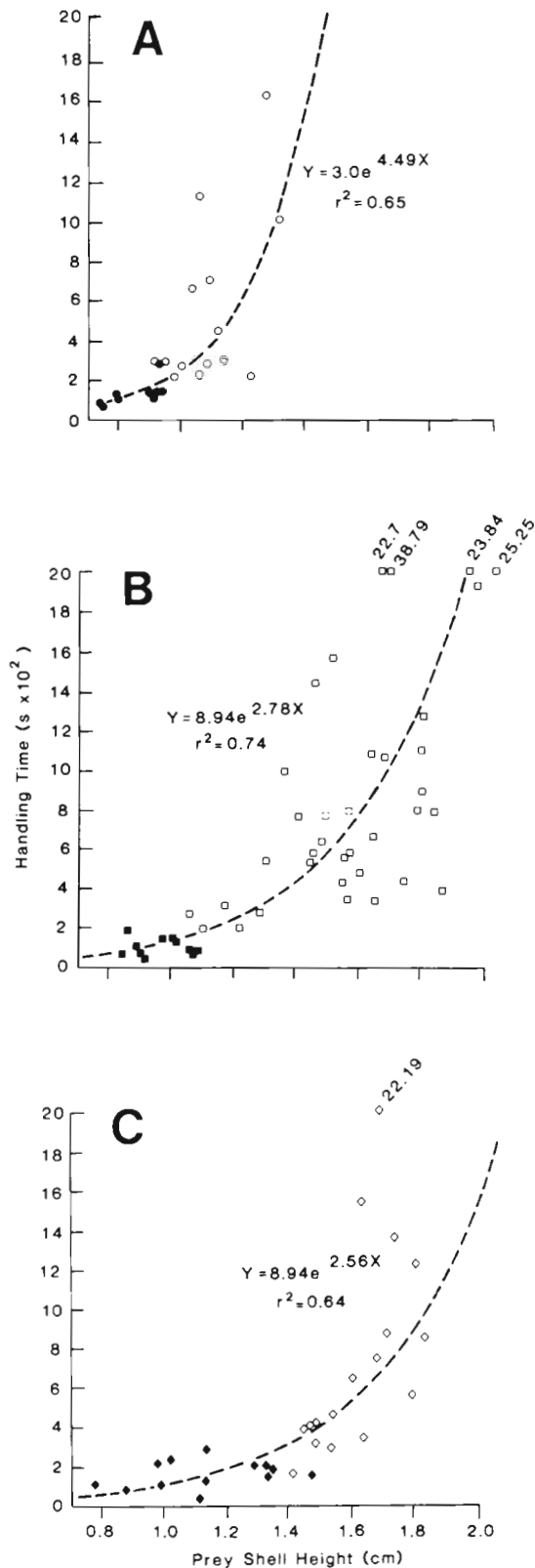
showed sex not to be a significant determinant of breaking time (P > 0.10), whereas crab size, prey size and attack method were all significant (all P < 0.001). Interactions between the independent variables were not significant (all P > 0.05). In view of this result, a dual function analysis of the breaking time relation was performed. Breaking time for prey that were crushed was not significantly dependent on prey size (P > 0.05) or on crab size (P > 0.25), the mean value for the pooled data being 42.5 ± 29.3 s (SE). For prey opened by the apertural breakage method both prey size (P < 0.0001) and crab size (P < 0.001) were significant determinants of breaking time. Exponential and power functions gave equally good fits to the apertural breakage data for crabs in each size class (difference between correlation coefficients, Fisher's transformation, all P > 0.05) and only parameters of the exponential functions are given (Fig. 3).

Profitability

Yield of flesh was related to the size of Church Island *Nucella lapillus* by the regression equation: $y = 3.30x - 2.29$, $n = 70$, $r^2 = 0.96$, where $y = \log_e$ (flesh content, kJ) and $x = \log_e$ (shell height, cm).

When calculated with breaking time, the observed profitability of Church Island *Nucella lapillus* peaked at the critical size for crushing (Fig. 5). Profitability curves derived from exponential and power functions fitted to breaking time data (irrespective of attack method) failed to predict these high profitabilities. Closer correspondence to observed profitability was obtained when the constancy of breaking time for small prey was taken into account, as in the dual function analysis (Fig. 5). Inclusion of eating time tended to smooth the transition between the 2 breaking methods (compare Fig. 3 with Fig. 4), yielding profitability relations with less marked optima.

Using the limited data on handling time of Penmon *Nucella lapillus* and of *Littorina littorea*, together with regressions of predicted yield for these morphs (Lawton 1983), comparisons were made of the profitabilities of the 3 prey types to medium-sized *Cancer pagurus* (Fig. 6). Profitability curves for Penmon *N. lapillus* were comparable with those for Church Island *N. lapillus* indicating an optimal size close to the critical size for crushing. *L. littorea* were considerably more profitable than both *N. lapillus* morphs, reaching an optimum within the range of sizes opened by apertural breakage. Adjustments for declining attack success rates at larger prey sizes steepened the descent, past the optima, but did not improve the fit to the data (Fig. 6).
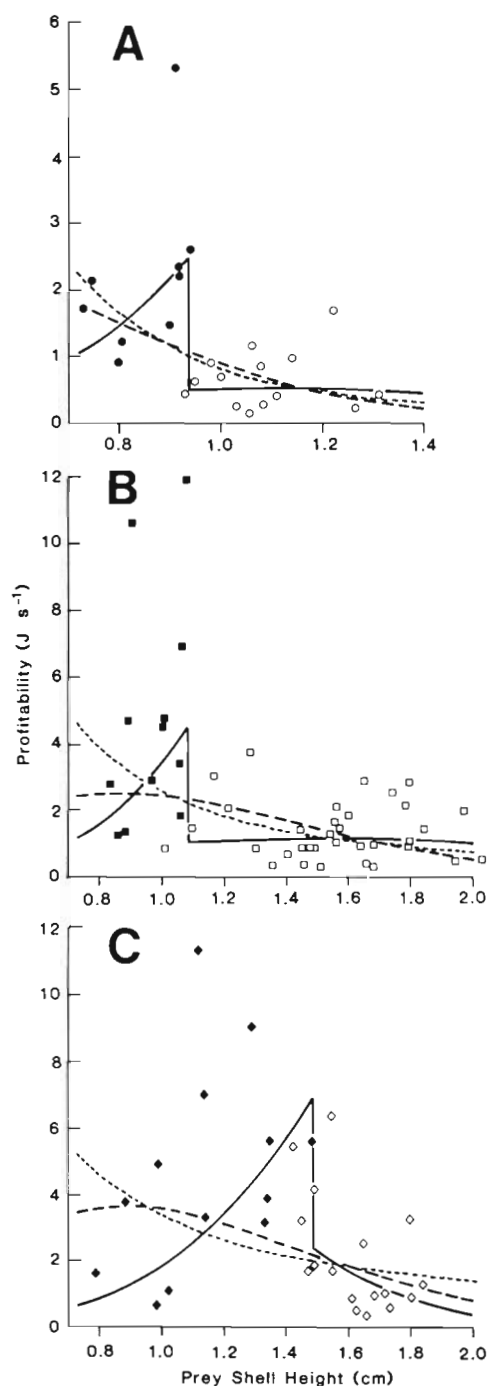
Fig. 4. *Cancer pagurus*. Handling time in successful attacks on Church Island *Nucella lapillus*. Plotting details as in Fig. 3, except that scales in A are consistent with those in B and C
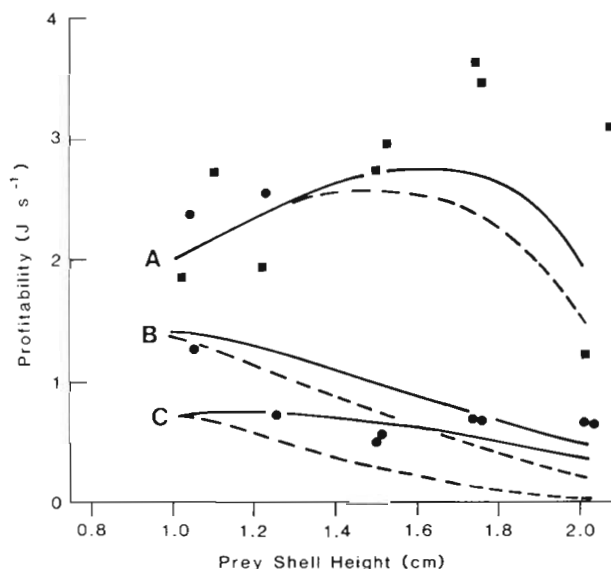
Fig. 6. *Cancer pagurus*. Profitability of 3 gastropod morphs to medium-sized crabs. Ratios of predicted yield to observed handling time are given for *Littorina littorea* (■) and Penmon *Nucella lapillus* (●). Profitability curves, derived from regressions of yield on prey size for each morph and exponential regressions fitted to observed handling times, are shown with (—-) and without (——-) adjustment for size-specific attack success rates for (A) *L. littorea*; (B) Penmon *N. lapillus*; (C) Church Island *N. lapillus*

Fig. 5. *Cancer pagurus*. Profitability of Church Island *Nucella lapillus* expressed as the ratio of predicted yield to observed breaking time with profitability curves derived from single regression of yield on prey size (see text) and regression functions for breaking time (Fig. 3). Other plotting details as in Fig. 3

Prey-size selection

Unlimited *Nucella lapillus*

Attack frequencies and ingestion frequencies on Church Island *Nucella lapillus* over different prey

sizes were not significantly different among crabs (Table 2, both G < 1.8, d. f. = 3, P > 0.5). The number of prey attacked decreased from the smallest to the largest size class (Table 2, Friedman 2-way ANOVA by ranks, χ_r^2 = 6.5, d. f. = 2, P < 0.05). Larger prey yielded less frequently to attack, the survivors sustaining injuries ranging from chipping of the apertural margin to opening of the whorl up to the point of maximum opercular retraction. Unsuccessful attacks continued unabated throughout the trials. The number of prey successfully opened and eaten decreased from the smallest to the largest prey (Table 2, Friedman test, χ_r^2 = 8.0, d. f. = 2, P < 0.005).

Crabs differed significantly in their attack and ingestion frequencies on Penmon *Nucella lapillus* over different sized prey (Table 2, both G > 16.5, d. f. = 3, P < 0.001). The number of prey attacked did not decrease significantly from the smallest to the largest size classes (Table 2, Friedman test, χ_r^2 = 3.5, d. f. = 2, P > 0.25), but the numbers successfully opened and eaten did (Table 2, Friedman test, χ_r^2 = 6.5, d. f. = 2, P < 0.05). There was a significant interaction between crab identity and prey size in the number of prey attacked (G = 15.9, d. f. = 6, P < 0.025).

Unlimited *Littorina littorea*

Crabs differed significantly in their attack and ingestion frequencies over different sized prey (Table

Table 2. *Cancer pagurus*. Prey-size selection on 3 gastropod shell morphs presented with replacement. Values of mean daily attack frequency (± SE, n = 10) over 10 d for individual crabs. Proportional success (based on total attack frequency) on each prey size class is given in parentheses

Gastropod shell morph	Crab carapace width (cm)	Prey size class (shell height, cm)			
		1.0 – 1.5	1.5 – 2.0	2.0 – 2.5	2.5 – 3.0[a]
Church Island *Nucella lapillus*	8.2	2.1 ± 0.38 (0.95)	0.7 ± 0.33 (0.43)	0.6 ± 0.31 (0.33)	
	8.3	2.1 ± 0.38 (0.95)	0.4 ± 0.16 (0.50)	0.6 ± 0.22 (0.16)	
	8.5	2.6 ± 0.40 (0.84)	0.5 ± 0.22 (0.20)	0.1 ± 0.10 (0)	
	8.6	1.7 ± 0.42 (0.94)	0.5 ± 0.17 (0.20)	0.3 ± 0.21 (0)	
Penmon *Nucella lapillus*	7.6	1.8 ± 0.53 (0.89)	1.1 ± 0.31 (0.27)	2.0 ± 0.47 (0.20)	
	7.7	1.6 ± 0.34 (0.81)	0.5 ± 0.22 (0.8)	0.5 ± 0.22 (0.20)	
	7.8	2.6 ± 0.31 (0.92)	1.8 ± 0.47 (0.67)	0.8 ± 0.39 (0.50)	
	8.6	2.0 ± 0.36 (0.95)	2.5 ± 0.48 (0.68)	1.8 ± 0.33 (0.56)	
Littorina littorea	6.4	1.8 ± 0.36 (0.89)	2.0 ± 0.37 (0.60)	0.8 ± 0.36 (0.50)	
	6.7	1.4 ± 0.34 (1.00)	0.8 ± 0.36 (0.75)	0.3 ± 0.30 (0)	
	7.5	4.6 ± 0.22 (0.98)	4.1 ± 0.31 (0.93)	2.2 ± 0.42 (0.50)	
	7.9	2.3 ± 0.42 (0.91)	2.5 ± 0.48 (0.88)	2.1 ± 0.35 (0.81)	
	9.7	4.1 ± 0.41 (0.98)	3.9 ± 0.38 (0.90)	2.6 ± 0.43 (0.70)	0.4 ± 0.22 (0.25)
	9.8[b]	2.6 ± 0.68 (1.00)	3.6 ± 0.57 (1.00)	2.4 ± 0.80 (0.84)	1.4 ± 0.57 (0.27)

[a] This size class presented only to the largest crabs in the *L. littorea* treatment
[b] This trial continued for 8 d

2, both G > 82.4, d. f. = 5, P < 0.001). Neither the number of prey attacked nor the number eaten differed significantly among prey size classes (Table 2, Friedman test, all P > 0.167). There was a significant interaction between crab identity and prey size in the number of prey eaten (G = 22.4, d. f. = 10 P < 0.025).

Unlimited mixture of *Nucella lapillus* and *Littorina littorea*

Crabs differed significantly in their attack and ingestion frequencies among prey categories (species, size, Table 3, both G > 14.4, d. f. = 3, P < 0.005). Interactions between crab identity and prey category were significant (attacks, G = 30.3, d. f. = 15, P < 0.025; ingestions, G = 34.9, d. f. = 15, P < 0.01). The frequency of attack was significantly different among prey categories (Table 3, Friedman test, χ_r^2 = 21.6, d. f. = 5, P < 0.001) as was the frequency of those eaten (Friedman test, χ_r^2 = 18.7, d. f. = 5, P < 0.01).

Littorina littorea were more heavily preyed upon than *Nucella lapillus*, the largest *L. littorea* being eaten more frequently than the smallest *N. lapillus* (Table 3).

Limited Church Island *Nucella lapillus*

Crabs consistently opened and ate the smallest snails first, taking larger ones as the smallest snails became depleted (Fig. 7). All sizes of snail, however, were attacked throughout the trials and shells of larger surviving prey were frequently damaged.

DISCUSSION

Attack methods

Crushing of smaller gastropods, changing to apertural breakage of larger ones, described herein for *Cancer pagurus*, are attack methods also used by

Table 3. *Cancer pagurus*. Prey-size selection on 2 gastropod shell morphs presented at equal density and with replacement. Values of mean daily attack frequency (± SE, n = 7) for individual crabs. Proportional success (based on total attack frequency) on each prey size class is given in parentheses

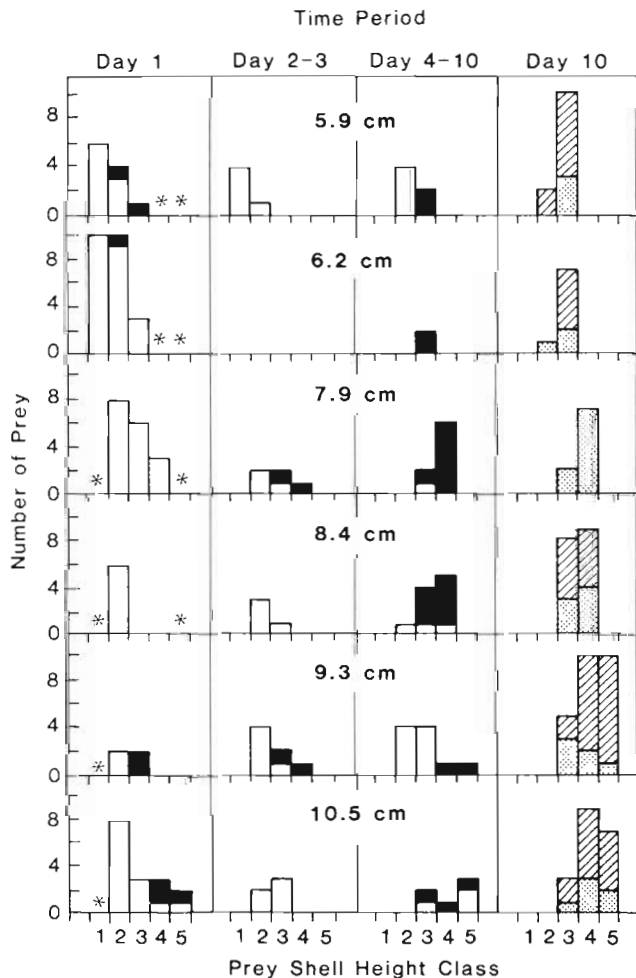| Crab carapace width (cm) | Prey species and size class (shell height, cm) | | | | | |
| | Penmon *Nucella lapillus* | | | *Littorina littorea* | | |
	1.0 – 1.5	1.5 – 2.0	2.0 – 2.5	1.0 – 1.5	1.5 – 2.0	2.0 – 2.5
7.5	0.14 ± 0.14 (1.00)	0.14 ± 0.14 (0)	0 –	2.28 ± 0.42 (0.87)	2.43 ± 0.48 (0.59)	1.86 ± 0.26 (0.38)
7.8	0.80 ± 0.26 (1.00)	1.10 ± 0.46 (1.00)	0.71 ± 0.29 (0.60)	3.70 ± 0.29 (0.96)	2.86 ± 0.14 (0.95)	3.29 ± 0.42 (0.74)
8.1	0.71 ± 0.29 (1.00)	0.43 ± 0.20 (0)	0.72 ± 0.36 (0.40)	2.70 ± 0.64 (1.00)	2.60 ± 0.37 (1.00)	1.86 ± 0.55 (0.70)
8.2	1.71 ± 0.47 (0.83)	1.57 ± 0.43 (0.91)	1.43 ± 0.53 (0.90)	2.42 ± 0.72 (1.00)	2.28 ± 0.68 (0.94)	2.14 ± 0.46 (0.87)

Fig. 7. *Cancer pagurus*. Prey-size selection on Church Island *Nucella lapillus* presented without replacement. Number of prey eaten (open bar) and number sustaining new injury (solid bar) in each of 3 time periods. Number of prey remaining intact after 10 d (hatched bar) and those alive, but bearing shell injury (stippled bar), also given. Prey shell height classes (cm): 1 (0.5 to 1.0); 2 (1.0 to 1.5); 3 (1.5 to 2.0); 4 (2.0 to 2.5); 5 (2.5 to 3.0); ✱ size class not presented in a trial. Carapace width (cm) of crab is indicated for each trial

C. productus (Kitching 1976, Bertness 1977, Zipser & Vermeij 1978), *C. irroratus* (Beattie & Elner 1982), *C. borealis* (Dudley 1980, Beattie & Elner 1982) and *C. gracilis* (Vance 1972).

The equal facility with which *Cancer pagurus* held or broke prey with either chela contrasts with the specific roles associated with the cutter and crusher chelae of *Carcinus maenas* (Elner 1980) and other portunid crabs (Hughes & Seed 1981, Du Preez 1984). Furthermore, no sexual differences in prey handling capability were detected for the juvenile *C. pagurus* used in the present study.

The critical sizes for crushing *Nucella lapillus* and *Littorina littorea*, beyond which *Cancer pagurus* uses apertural breakage, depend more on the shape than on the strength of the shell, probably reflecting a loss of grip and of mechanical advantage when holding larger shells. Thus the shell widths of these critical sizes are more closely matched than are shell height or resistance to compression (Table 4). Shell shape is also implicated in the susceptibility of medium-sized prey as crabs experienced difficulty in breaking open prey which had shell apertures approximating the cross-sectional area of the dactyli. Shell thickness assumes greater importance in determining attack success as the critical size for apertural breakage is reached.

Profitability

Profitability curves derived from single regressions of yield and of breaking time on size of Church Island *Nucella lapillus* failed to account for the high profitabilities coinciding with the critical size for crushing (Fig. 5). A better fit was obtained using dual breaking time functions, based on the attack method used. A similar approach was used by Hughes & Elner (1979) for *Carcinus maenas* feeding on *N. lapillus* and by

Table 4. *Cancer pagurus*. Morphological attributes of critical size for crushing of *Nucella lapillus* and *Littorina littorea*. Values of prey shell height (H), shell width (W) and force (F) required to crush shells of the indicated height

Crab carapace width (cm)	Prey species					
	Church Island *Nucella lapillus*			*Littorina littorea*		
	H (cm)[a]	W (cm)[a]	F (kN)[b]	H (cm)[c]	W (cm)[c]	F (kN)[d]
6.5	0.94	0.60	0.119	0.75	0.66	0.193
7.7	1.08	0.69	0.189	0.84	0.73	0.215
9.6	1.48	0.94	0.391	1.00	0.85	0.254
12.1	1.64	1.04	0.468	1.20	1.01	0.303

[a] Measurement of individual prey prior to consumption
[b] Lawton (1983)
[c] Predicted from equations relating critical H and W to crab carapace width
[d] Currey & Hughes (1982); from their Fig. 5

Mittelbach (1981) for the bluegill sunfish feeding on zooplankton. In both cases, however, the size threshold was judged by eye from graphed data without explicit reference to attack method.

The low precision of the handling time relations for *Cancer pagurus* feeding on Church Island *Nucella lapillus* is due in part to the grouping of data from a number of crabs in each size class, and also reflects variability in robustness between similarly sized shells of this morph (Hughes & Elner 1979, Lawton 1983). Of greater concern, the form of the profitability curve was shown to be sensitive to the type of regression used to predict handling time. Single exponential functions and power functions yielded domed and monotonically decreasing curves respectively (seen most clearly in Fig. 5C), and thus different predicted optima, when fitted to the same data on handling time. This problem has not been appreciated in previous papers on optimal foraging in brachyuran crabs which have relied on such predictions for *a posteriori* interpretations of diet selection.

Foraging behaviour

Although optimal prey sizes were predicted from relations between yield, handling time, attack success rate and prey size (Fig. 6), there was little evidence that *Cancer pagurus* actively selected these optima (Table 2 & 3). Even in the presence of alternative prey, crabs exerted high attack frequencies on large, unprofitable gastropods, inflicting considerable damage on shells without gaining access to the flesh.

When presented with *Nucella lapillus* without replacement of eaten prey, *Cancer pagurus* consumed smaller items first, gradually broadening the diet to include larger items as prey were depleted (Fig. 7). This, however, did not represent the adjustment of diet selection to the availability of prey Throughout the

trials crabs attacked all sizes of *N. lapillus* indiscriminately, but because of their weaker shells and associated shorter handling times, smaller snails were eaten faster and depleted sooner than larger ones.

Such a mechanism of differential size-specific predation may cause diets to correspond approximately with those predicted by optimal diet theory (Hughes & Elner 1979). Indiscriminate attacks on all potential food items, which are subsequently rejected if they do not yield to initial attack, would be an optimal mechanism for a predator foraging among prey of unpredictably varying profitability. Thus *Carcinus maenas* adopted a short persistence time of 0.25 to 2.75 min when preying upon *Nucella lapillus* (Hughes & Elner 1979), and the littorinids *Littorina nigrolineata* and *L. rudis* (Elner & Raffaelli 1980). *Cancer pagurus*, in contrast, persisted with prey for varying times up to several h, even when other prey were available.

The foraging behaviour exhibited by *Cancer pagurus* on shelled gastropods seems to be based primarily on passive mechanical selection and is markedly different to that of portunid crabs. The foraging behaviour of *C. pagurus* among *Mytilus edulis* also contrasts with that observed for portunid crabs (Elner & Hughes 1978, Hughes & Seed 1981, Jubb et al. 1983) and again appears to have a passive mechanical basis (Lawton 1983). Clearly, evidence from a wider spectrum of genera will be required before we may generalize on the mechanisms governing prey choice by brachyuran crabs.

Impact on local gastropod populations

Hylleberg & Christensen (1978) and Hadlock (1980) reported a size refuge from *Carcinus maenas* predation for *Littorina littorea*, and Elner & Raffaelli (1980) observed that *L. rudis* and *L. nigrolineata* could also

gain a refuge in size from this species. Hughes & Elner (1979) found a maximum size of 2.7 cm for sheltered shore *Nucella lapillus* successfully attacked by adult *C. maenas* and noted that Church Island *N. lapillus* above 1.0 cm were immune to *C. maenas* predation. The present study reveals a much more limited potential for the attainment of a size refuge from *Cancer pagurus* predation, particularly for *L. littorea*. Even on reaching a size of 2.0 cm *L. littorea* could be opened by *C. pagurus* as small as 5.6 cm (Fig. 1B).

Predatory impact in the field will depend on the size-frequency distribution and relative abundances of crabs on different shores; it may be expected that an equilibrium between adaptation and pressure has been reached for most gastropod populations (Hughes & Elner 1979). The 2 sheltered shores examined in this study, Penmon and Church Island, have similar densities of *Cancer pagurus*, but differ in population size-frequency distribution (Table 1; Lawton 1983). Adult Penmon *Littorina littorea* may be vulnerable to large *C. pagurus* (Fig. 1B), but it is unlikely that they are exposed to predation from this source. Nonetheless, medium-sized *C. pagurus*, which are found at Penmon, maintained high predation rates on Penmon *L. littorea* when offered singly (Table 2) and when offered together with *Nucella lapillus* (Table 3).

Hughes & Elner (1979) record predation rates for adult *Carcinus maenas* (6 to 6.95 cm) on *Nucella lapillus* from Trwyn-y-Penrhyn (Map ref. SH 629797), a sheltered shore approximately 1 km from Penmon. These data may be compared with those obtained in the present study for medium-sized *Cancer pagurus* (7.5 to 8.5 cm) feeding upon Penmon *N. lapillus*. The mean numbers of gastropods eaten (gastropods d^{-1} ± SE) from the size classes common to both studies are shown in Table 5. A larger size class of *N. lapillus* (2.5 to 2.99 cm) was presented to *C. maenas*, but few prey were taken (0.03 ± 0.02 gastropods d^{-1}). Medium-sized *C. pagurus* exerted the above predation rates in addition to the consumption of small *N. lapillus* (1.0 to 1.49 cm) at a rate of 1.8 ± 0.23 gastropods d^{-1}.

Carcinus maenas may exert selection against weaker shells in gastropod populations by adopting a foraging strategy of attacking all encountered prey but quickly rejecting those that do not yield (Hughes & Elner 1979). The present finding that *Cancer pagurus* persists for long periods in attacks on gastropods, frequently inflicting damage on relatively large, strong shells, provides a mechanism for greater selection pressure and corroborates the hypothesis stated by Hughes & Elner (1979), that the massive shells of sublittoral fringe *Nucella lapillus* at Church Island have resulted from *C. pagurus* predation. The less extreme morphological adaptation in the Penmon morph parallels the variation in *C. pagurus* size-frequency distribution between these 2 shores.

Reduced levels of morphological adaptation in *Littorina littorea* lead to increased susceptibility to crab predation and differential predation on this species when offered together with *Nucella lapillus*. In the present experiments *L. littorea* were immobilized by heat coma and so were unable to exploit their escape reaction of climbing upwards out of reach of predators (Hadlock 1980). Relatively lower predation rates have been recorded for other crabs, *Cancer borealis* and *C. irroratus*, preying on naturally mobile *L. littorea* (Beattie & Elner 1982). Behavioural escape responses have been reported for other gastropods having pelagic dispersal phases (Schmitt 1981, Watanabe 1983), which suggests that behavioural responses to predation pressure may not be constrained to the same extent as morphological adaptations are (Currey & Hughes 1982) by gene flow between populations (Lawton 1983).

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Table 5. *Carcinus maenas* and *Cancer pagurus*. Rates of predation on 2 size classes of gastropod

Prey shell height (cm)	Predation rate (gastropods d^{-1} ± SE)	
	Carcinus maenas	*Cancer pagurus*
1.5 – 1.99	0.4 ± 0.20	0.9 ± 0.33
2.0 – 2.49	0.02 ± 0.01	0.5 ± 0.18

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