J. Mar. Biol. Ass. U.K. (2000), **80**, 799–810
Printed in the United Kingdom

Foraging behaviour of *Carcinus maenas* on *Mytilus edulis*: the importance of prey presentation

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The manner in which mussels, *Mytilus edulis*, are presented to *Carcinus maenas* significantly influences crab prey-selection, resulting in different foraging behaviour. Handling techniques, breaking and handling times, percentage flesh eaten and prey value curves were compared when mussels of the following size-classes, 5–10, 10–15, 15–20, 20–25, 25–30 mm shell length, were presented singly and when they were presented as part of a group to crabs of 30–55 mm carapace width. When prey were presented singly, crabs used four size-specific opening techniques; outright crushing and directed crushing were used on smaller prey whilst boring and edge-chipping were used on larger, more resistant mussels. However, when mussels were presented as part of a group, boring and edge-chipping were never observed since larger mussels were not consumed. Handling time increased exponentially with mussel size irrespective of how mussels were presented, but, when crabs fed on mussels presented as part of a group, handling times tended to be shorter than when they fed on similar-sized mussels presented singly. The median percentage of flesh left uneaten in discarded shells ranged between 9.58 and 25.25% and was significantly greater than the median percentage of flesh left in the shells of mussels presented singly, which ranged between 4.66 and 14.70%. All resultant prey value curves were convex in shape, but the predicted optimal prey size altered with modifications in prey presentation. Similarly, when crabs of 30–65 mm carapace width were presented with groups of mussels comprised of different proportions of different sizes of mussels, size-class vulnerability was not fixed but altered significantly with the relative proportions in which these were presented. Thus, when the relative number of mussels in the smaller size groups were increased so was their vulnerability, indicating that prey size preference is flexible and not fixed.

INTRODUCTION

Prey size-selection is a common feature of the foraging behaviour of decapod crustaceans when presented with hard-shelled molluscs (see Juanes, 1992 for review). Much research has focused on the size of prey most vulnerable to the predator and the mechanisms underlying size-selective predation (e.g. Elner & Hughes, 1978; Hughes & Elner, 1979; Davidson, 1986; Ameyaw-Akumfi & Hughes, 1987). These foraging studies have used the ratio of prey flesh weight, or energy intake, to handling time (E/Th) as a measure of prey value or profitability, which is then plotted against some measure of prey size to produce prey value curves. From such prey value curves the optimal prey size, i.e. that which maximizes energy intake per unit handling time, can be predicted and subsequently tested against the size of prey preferred when the predator is presented with a choice of prey size-classes. If prey size preference coincides with the optimal prey size then the predator is considered to be foraging optimally by maximizing its net energy intake. If, however, the size of prey selected differs from that predicted then explanations other than energy maximization are sought to explain the observed pattern of predation. In foraging studies, therefore, the shape of prey value curves and the determination of prey size most vulnerable to predation have formed the central framework in which predictions of foraging behaviour are tested. Nevertheless, there are potential flaws in this framework. For example, prey value is generally determined by presenting the predator sequentially with single items of prey of different sizes, whilst prey preference is determined by presenting the prey in groups of mixed sizes, often in equal numbers in each of several size-classes (e.g. Elner & Hughes, 1978; Davidson, 1986; Seed, 1990). This assumes that the foraging behaviour of the crabs is the same under both conditions which is not necessarily true. Elner (1978) observed that when offered single mussels over a range of sizes, *Carcinus maenas* used an array of different prey size dependent opening techniques, larger mussels being opened using lengthier techniques such as boring and edge-chipping. However, on groups of mixed sizes of mussels, *C. maenas* is highly prey size selective, choosing mussels much smaller than the maximum size that can be opened (Elner & Hughes, 1978), thus the full range of opening techniques may not be utilized under this condition. This alone may lead to differences between prey value curves; indeed Lawton & Hughes (1985) showed that for *Cancer pagurus* the inclusion/exclusion of data involving lengthier opening techniques resulted in quite different prey value curves.

The prediction of prey value from flesh weight–shell length regression equations has assumed that the predator consumes all the prey flesh. However, Jubb et al. (1983) reported that when foraging on *Mytilus edulis*, *Carcinus maenas* left up to 70% of the flesh uneaten. The calculation of prey value curves using the amount of flesh eaten rather than the predicted total weight of flesh contained within a mussel may therefore alter the shape

Table 1. *Median percentages of flesh remaining in discarded* Mytilus edulis *shells attacked by* Carcinus maenas *together with the Kruskal–Wallis test for significant differences. Data presented from experiments 1 and 2.*

Crab (mm)	Single[1] (N)	Experiment 1 5:5:5:5:5[2] (N)	11:7:3:3:1[3] (N)	H	df
42.3	10.63 (16)	25.25 (15)	19.28 (48)	10.02*	2
44.5	5.76 (15)	11.26 (40)	12.86 (80)	8.97*	2
54.0[†]	14.70 (13)	25.24 (38)	–	–	–
	Single[1] (N)	Experiment 2 5:5:5:5:5[2] (N)	Single[1] (N)		
52.4	5.30 (26)	11.12 (59)	4.66 (28)	32.19*	2
54.8	5.28 (31)	9.58 (32)	7.54 (26)	13.53*	2
54.1	5.21 (29)	13.90 (45)	6.24 (29)	37.16*	2

[1], single, mussels presented singly. [2], 5:5:5:5:5, five mussels in each of the five size-classes, 5–10, 10–15, 15–20, 20–25, 25–30 mm.
[3], 11:7:3:3:1, mussels presented as 11:7:3:3:1 individuals in the five size classes. [†], crab stopped eating during trial 3, no data available.
N, number of mussels consumed; H, Kruskal–Wallis test statistic; *, $P<0.05$; df, degrees of freedom.

of the resulting prey value curve leading to different conclusions as regard to foraging behaviour.

By simply manipulating the relative number of prey in different size-classes offered to crabs, prey size vulnerability has been shown to alter (Elner & Hughes, 1978; Jubb et al., 1983; Davidson, 1986), the actual proportions of prey included in the diet reflecting the relative proportions in which these were presented. Vulnerability of prey in the field may therefore depend upon the local structure of the prey population itself. Often the pattern of size-selectivity observed in the laboratory is compared to prey size distribution patterns in the field in order to determine the influence of a particular predator over the prey population structure (Pollock, 1979; Sanchez-Salazar et al., 1987; Seed, 1990). Thus, if experimental results are to be extrapolated to the field situation then they ought to broadly reflect the manner in which the prey presents itself to the predator in the field. Such a context-sensitive approach has already been advocated (e.g. Sponaugle & Lawton, 1990; Lawton & Zimmer-Faust, 1992).

In this paper the foraging behaviour of the portunid crab, *Carcinus maenas*, on groups of *Mytilus edulis* is examined and compared to that observed when this crab feeds on mussels presented singly. The vulnerability of *M. edulis*

Table 2. *The effects of prey presentation on the relationships between breaking times (Tb), handling times (Th) and shell length. Slopes and intercepts from the regression equation $\log_e y = a + bx$ (where x=shell length), are compared between the three feeding trials of experiments 1 and 2 using ANCOVA (general linear model).*

Crab (mm)	Dependent Variable (mm) y	*F*-values Slopes b	 Intercepts a	N
		Experiment 1[1]		
42.3	$\log_e$ Th	1.21 ns	0.84 ns	86
	$\log_e$ Tb	0.51 ns	1.04 ns	86
44.5	$\log_e$ Th	1.16 ns	0.75 ns	139
	$\log_e$ Tb	0.48 ns	0.55 ns	137
54.0[†]	$\log_e$ Th	4.70*	–	55
	$\log_e$ Tb	7.11*	–	52
		Experiment 2[2]		
52.4	$\log_e$ Th	0.54 ns	3.50*	117
	$\log_e$ Tb	0.86 ns	0.25 ns	110
52.8	$\log_e$ Th	2.58 ns	8.72*	91
	$\log_e$ Tb	1.24 ns	0.59 ns	91
54.1	$\log_e$ Th	1.81 ns	5.08*	107
	$\log_e$ Tb	1.05 ns	0.68 ns	100

[1], trial 1, mussels presented singly; trial 2, mussels presented as five individuals in each of the following five size-classes, 5–10, 10–15, 15–20, 20–25, 25–30 mm shell length; trial 3, mussels presented in the ratio 11:7:3;3;1 in the five size-classes. [2], trial 1, mussels presented singly; trial 2, mussels presented in the ratio 11:7:3;3;1 in the five size-classes respectively; trial 3, mussels presented singly. [†], crab stopped eating during trial 3, data compared between trials 1 and 2 only. N, sample size; ns, no significant difference; *, $P<0.05$.

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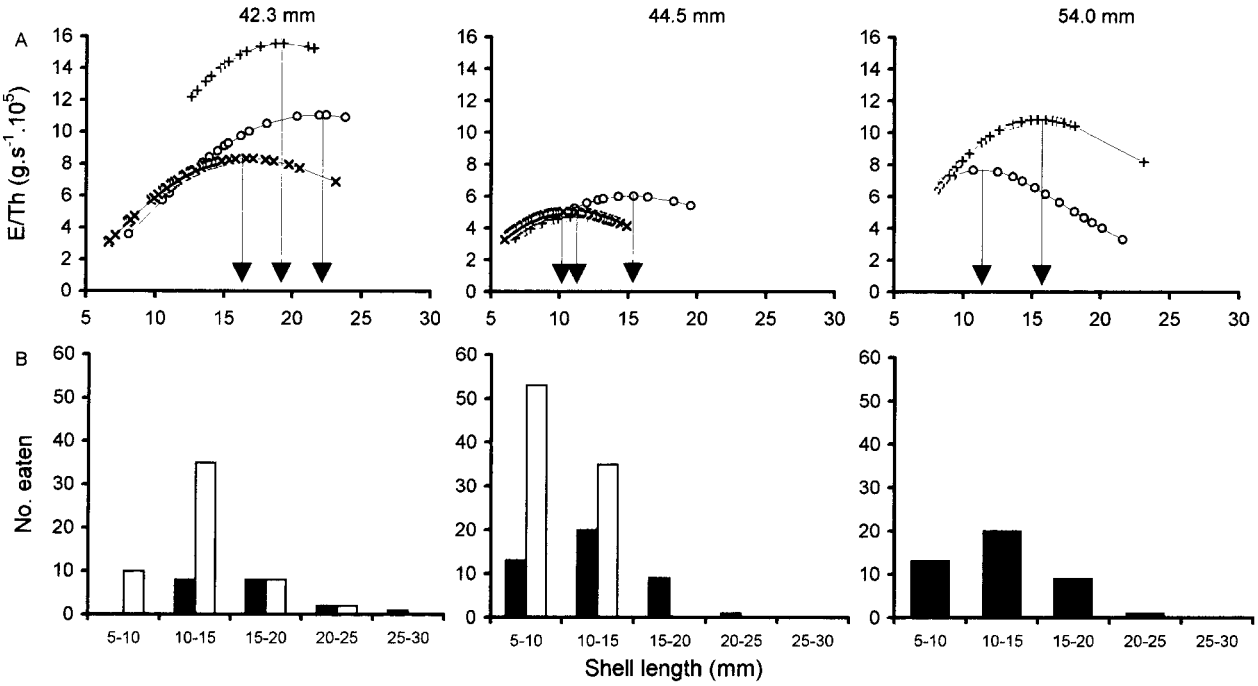

Figure 1. (A) Prey value curves determined using the regression equations relating flesh weights (E) and handling times (Th) to shell length, for three *Carcinus maenas* when foraging on *Mytilus edulis* presented singly (o, trial 1), as part of a group comprising five mussels in each of the following five size-classes; 5–10, 10–15, 15–20, 20–25, 25–30 mm shell length (+, trial 2) and as part of a group comprising 11, 7, 3, 3, 1, mussels in the five size-classes (x, trial 3). Arrows denote those sizes of mussel predicted to be the most profitable. (B) Number of mussels eaten by each crab over a five day period when mussels were presented as part of a group comprising five mussels in each of the five size-classes (closed bar, trial 2) and as part of a group comprising 11, 7, 3, 3, 1, mussels in the five size-classes (open bar, trial 3). No data from the 11:7:3:3:1 ratio are presented for the largest crab.

when presented in proportions which broadly reflect those in which they occur in a field population is also investigated.

MATERIALS AND METHODS

Collection and maintenance of Mytilus edulis *and* Carcinus maenas

Mytilus edulis were collected either from the low shore at Church Island in the Menai Strait, or the high shore at Aberffraw, on the south-west coast of Anglesey—depending on availability of the required size-classes. All mussels were gathered from a restricted area of the shore to standardize shell characteristics and flesh weights which are known to vary with tidal elevation (Seed, 1968). Only freshly collected undamaged mussels were used in experiments and these were kept in the laboratory under running seawater and conditions of ambient water temperature and light levels. *Carcinus maenas* were caught by trawling off Traeth Melynog, south Anglesey. In the laboratory, crabs were kept individually in opaque plastic aquaria (30×30×20 cm) filled to a depth of 5 cm with seawater, under conditions of ambient light levels and water temperatures. Water was changed daily and faecal debris siphoned off. To minimize potential differences in foraging behaviour arising from variations in chelal morphology, only undamaged male, crabs that were green in colour, i.e. early intermoult stage (Reid et al., 1997) were used. A high degree of variability exists between the foraging behaviour of individual crabs of the same size (e.g. Elner & Hughes, 1978), therefore, if a crab stopped eating, moulted or died during the course of an experiment it was not replaced; instead the experiment was restarted using a fresh crab. This procedure ensured that any differences arising between successive feeding trials were not attributable to variations in the foraging behaviour of different crabs.

Table 3. *Results of ANCOVA (general linear model) comparing the slopes and intercepts, from the regression equation* $\log_e y = a + bx$ *(where, y=handling time and x=shell length), between the two trials of experiment 2 in which* Mytilus edulis *were presented singly to three* Carcinus maenas.

Crab (mm)	*F*-values		N
	Slopes b	Intercepts a	
52.4	0.21 ns	0.03 ns	57
52.8	0.10 ns	0.34 ns	58
54.1	2.58 ns	0.24 ns	59

N, sample size; ns, no significant difference at $P < 0.05$.

Prey value experiments

Two experiments (experiments 1 & 2) were conducted to examine foraging behaviour and resultant prey values

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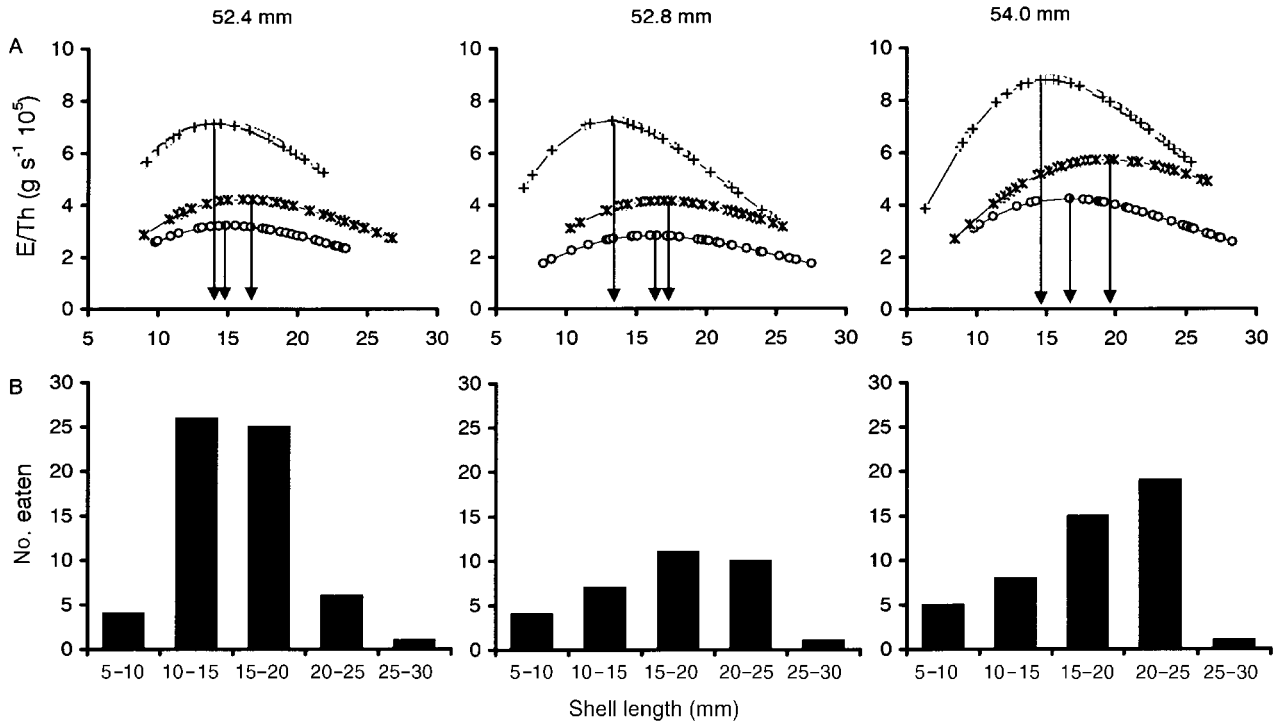

Figure 2. (A) Prey value curves determined from regression equations relating flesh weights (E) and handling times (Th) to shell length, for three *Carcinus maenas* when foraging on *Mytilus edulis* presented singly (o, trial 1 and x, trial 3) and as part of a group comprising five mussels in each of the following size-classes; 5–10, 10–15, 15–20, 20–25, 25–30 mm shell length (+, trial 2). Arrows denote those sizes of mussel predicted to be the most profitable. (B) Number of mussels eaten by each crab over a five day period when mussels were presented as part of a group comprising five mussels in each of the five size-classes (trial 2).

under different experimental protocols. Both experiments comprised three trials. Prior to the start of each trial, crabs were fed mussel flesh *ad libitum* for 48 h and left unfed for the subsequent 24 h. This procedure was designed to standardize hunger levels between trials. The length (maximum anterior–posterior dimension) of all mussels was measured to the nearest 0.1 mm using Vernier calipers and the shells coded by applying a small amount of liquid whitener upon which a number was written using a black permanent marker pen. In this way each mussel could be identified throughout a feeding period. In each trial the following events were recorded to the nearest second: breaking time (Tb), the time from when the mussel was first picked up, through any periods of prey manipulation, until the mussel was broken and the first bite of the exposed flesh taken; handling time (Th), the time from when the mussel was first picked up until the shell was finally discarded having been opened and the flesh removed and eaten. Handling and opening techniques were also recorded. Discarded shell remains were collected after each successful attack and any remaining flesh removed, placed in pre-weighed aluminium boats and dried to constant weight at 60°C over three days.

For each trial, the relationships between breaking times, handling times and shell length were determined. Both prey value (E/Th), where E is the dry flesh weight, and adjusted prey values ((E−L)/Th), where L is the amount of dry flesh left in discarded shells, were calculated using the following dry flesh weight–shell length regression equations previously determined by Burch (1998) for mussels from Church Island (1) and Aberffraw (2):

$$\log_{10} \text{ dry weight (g)} = -5.11 + 3.12 \log_{10} \text{ length (mm)}; \quad N=29,\ r^2=0.98 \qquad (1)$$

$$\log_{10} \text{ dry weight (g)} = -5.09 + 2.80 \log_{10} \text{ length (mm)}; \quad N=36,\ r^2=0.99 \qquad (2)$$

In experiment 1 the effect of presenting mussels singly as compared to part of a group was examined. The same three crabs, 42.3, 44.5, 54.0 mm carapace width (CW) were used in each trial and mussels were collected from the low shore at Church Island. In the first trial, each of the three crabs was presented with single mussels, in random sequence, ranging from 5–30 mm shell length, over a period of several days. In the second trial, the three crabs were each presented with five mussels in each of the following length-classes; 5–10, 10–15, 15–20, 20–25, 25–30 mm, spread randomly over the aquaria floor. Crabs fed on these mixed size groups of 25 unattached mussels for two consecutive hours during which time they were continuously observed. Any mussel that was picked up, regardless of whether it was subsequently eaten or not, was regarded as having been 'encountered'. The discarded shells of eaten mussels were removed and replaced with mussels of a similar size. After the two hour period, all the mussels were removed from the aquaria. This trial was repeated daily for five consecutive days. In the third trial, each crab was presented with a group of 25 unattached mussels of the following length classes; 5–10, 10–15, 15–20, 20–25, 25–30 mm in the mixed proportion of 11, 7, 3, 3, 1. This reflected the relative abundance of these size-classes within the natural

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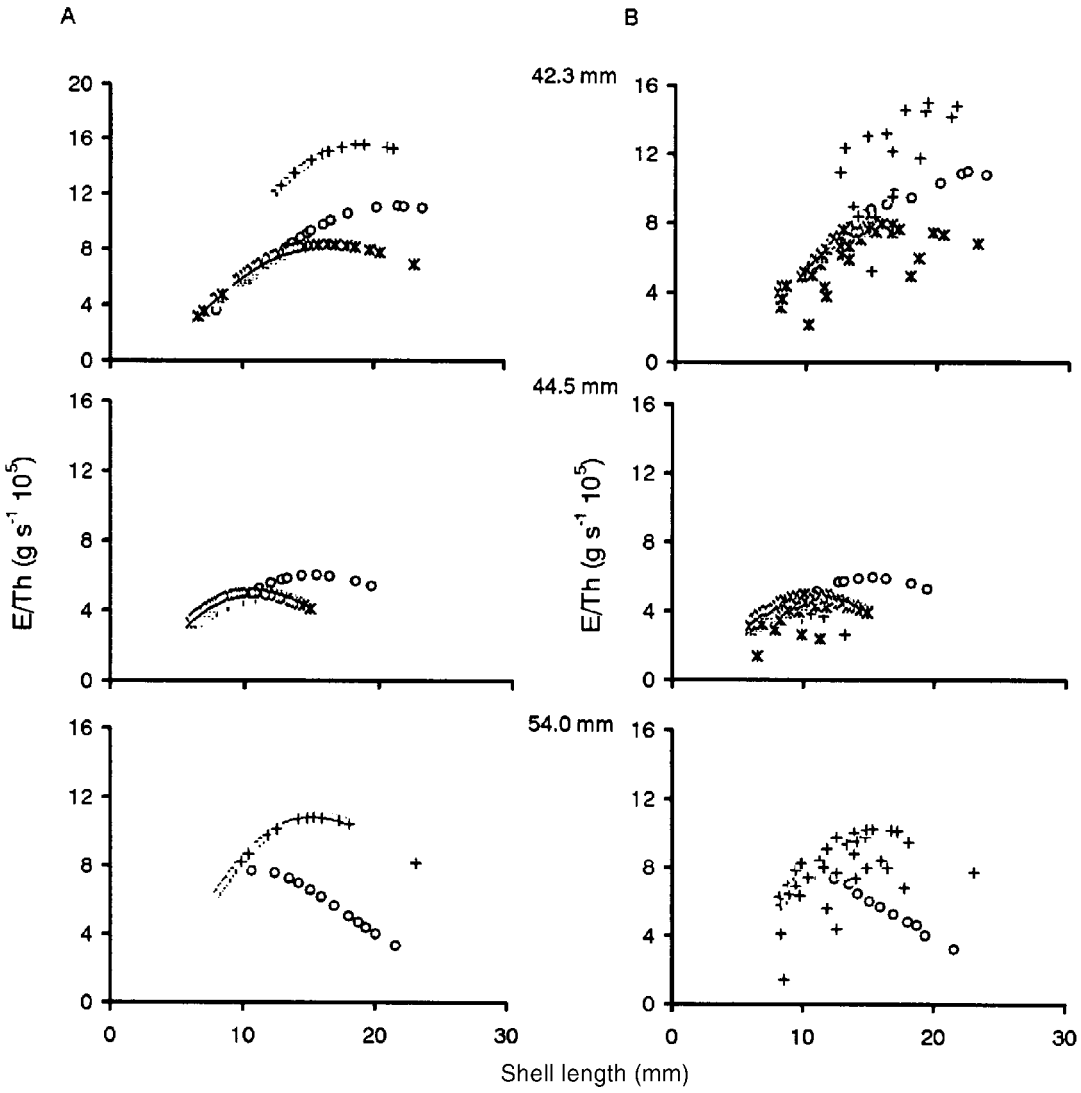

Figure 3. Comparison of (A) prey value curves obtained from the regression equations of flesh weight (E) and handling time (Th) on shell length, with (B) adjusted prey value ((E−L)/Th) curves, where L is the amount of flesh left in a discarded mussel shell, for three *Carcinus maenas* foraging on *Mytilus edulis* presented singly (o, trial 1), as part of a group comprising five mussels in each of the following size-classes; 5–10, 10–15, 15–20, 20–25, 25–30 mm shell length (+, trial 2) and as part of a group comprising 11, 7, 3, 3, 1, mussels in the five size-classes (x, trial 3).

low shore mussel population at Church Island during October 1995 (Burch, 1998). Each crab was allowed to feed for two consecutive hours each day for five consecutive days. Again, crabs were continuously observed throughout the two hour period, mussels were replaced as eaten, a record made of all mussels encountered and all mussels removed after the two hour feeding period.

Experiment 2 was designed to examine whether handling efficiency improved between successive feeding trials. Three crabs, 52.4, 52.8, 54.1 mm CW were used in each trial and mussels were collected from the high shore, Aberffraw. In the first trial crabs were presented with single mussels, in random sequence, from the size range 5–30 mm, over several consecutive days. In the second trial, each crab was presented with a group of 25 mussels in the ratio 11:7:3:3:1 in the length size-classes, 5–10, 10–15, 15–20, 20–25, 25–30 mm respectively. The mussels were scattered randomly over the aquaria floor. Crabs were allowed to feed for two consecutive hours each day for five days, during which time the shells of any mussels which had been eaten were removed and replaced with mussels of similar size. The number of encounters with mussels in each size-class were recorded. After the two hour feeding period all the mussels were removed from the aquaria. The third trial was the same as the first trial with crabs being presented with single mussels from the size range 5–30 mm shell length in random sequence.

Prey vulnerability

Two experiments (experiments 3 & 4) were conducted to examine prey size vulnerability. Both experiments comprised two trials. A three day period, in which crabs were fed mussel flesh *ad libitum* for the first 48 h and left unfed for the subsequent 24 h, was allowed to elapse prior to every trial to standardize hunger levels. During each

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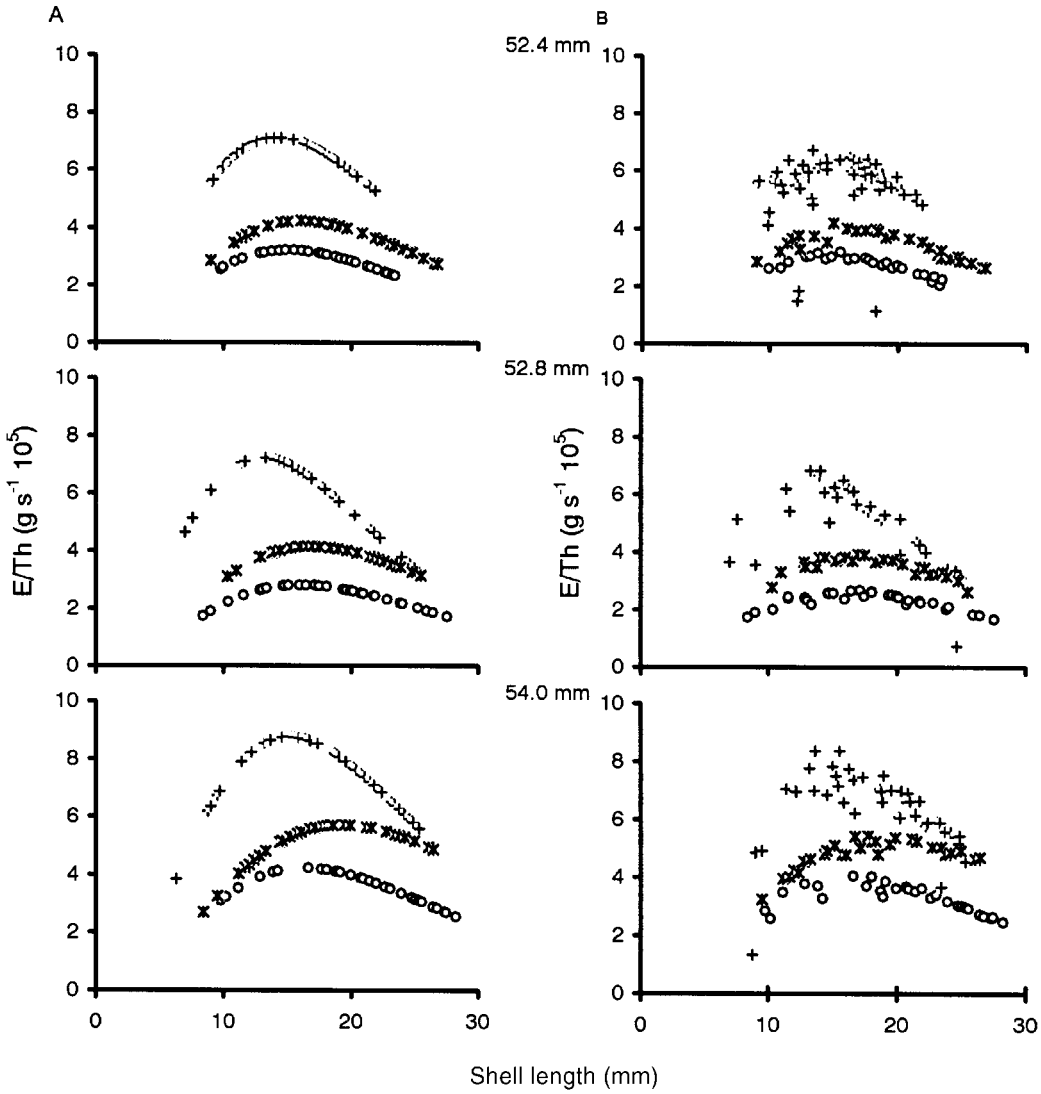

Figure 4. Comparison of (A) prey value curves obtained from the regression equations of flesh weight (E) and handling time (Th) on shell length with (B) adjusted prey value ((E−L)/Th) curves, where L is the amount of flesh left in a discarded mussel shell, for three *Carcinus maenas* foraging on *Mytilus edulis* presented singly (o, trial 1 and x, trial 3), as part of a group comprising five mussels in each of the following size-classes; 5–10, 10–15, 15–20, 20–25, 25–30 mm shell length (+, trial 2).

trial, crabs were allowed to feed on groups of mussels for six consecutive hours during which time the number of mussels eaten from each size-class was recorded every two hours and their shell remains removed to prevent unopened mussels becoming obscured by shell debris. Shell remains were examined to determine the opening methods used and eaten mussels were replaced with ones of similar size to maintain constant prey availability. No direct observations were made of crab behaviour during either experiment.

In experiment 3, prey size vulnerability when mussels were presented as equal numbers in each of several size-classes and when they were presented in a modified proportion comparable to that found in a natural mussel population, was examined. The same 12 crabs (30–65 mm CW) were used in both trials and mussels were collected from Church Island. In the first trial each crab was presented with five mussels in each of the following five size-classes; 5–10, 10–15, 15–20, 20–25, 25–30 mm shell length. In the second trial, the same crabs were then presented with 25 unattached mussels, 5–10, 10–15, 15–20, 20–25, 25–30 mm shell length in the modified proportion of 11, 7, 3, 3, 1. Both trials lasted seven days. Results were analysed using the *G*-test.

Experiment 4 was designed to investigate prey vulnerability when mussels were presented in two different proportions reflecting those of populations occurring on the same shore but at different tidal elevations, i.e. whether the prey size-selection of a tidally migrating crab could change during a single foraging excursion. Mussels were collected from the high shore at Aberffraw only, to ensure that any differences between the trials were not attributable to differences in variables such as shell strength and shape which are known to alter with tidal level (Seed, 1968). The same six crabs (40–65 mm CW) were used in both trials. In the first trial, crabs were presented with groups of mussels in the ratio 11:7:2:2:3, in the size-classes, 5–10, 10–15, 15–20, 20–25, 25–30 mm. This proportion was derived from a high shore sample taken from the mussel population at Aberffraw in June 1997 (Burch 1998). In the second trial the same crabs were then presented with groups of mussels in the ratio

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Table 4. *Prey size selection when* Carcinus maenas *is presented with groups of mixed sizes of* Mytilus edulis *in experiments 1 and 2. The total number of mussels eaten, the number encountered and the percentage eaten:encountered in each size-class is presented. The optimal size-classes of mussels, determined from the predicted prey value curves, are highlighted.*

		Experiment 1			
		5:5:5:5:5[1]		11:7:3:3:1[2]	
Crab (mm)	Mussel size (mm)	No. eaten (no. encountered)	% eaten:encountered	No. eaten (no. encountered)	% eaten:encountered
42.3	5–10	0 (1)	–	11 (13)	84.6
	10–15	8 (8)	100	13 (44)	75.1
	15–20	**8 (16)**	**50.0**	**8 (26)**	**30.8**
	20–25	1 (49)	20.4	2 (38)	5.3
	25–30	1(129)	0.7	0 (33)	0
44.5	5–10	12 (16)	75.0	57 (65)	87.7
	10–15	**30 (36)**	**83.3**	**37 (81)**	**45.7**
	15–20	2 (66)	3.0	0 (30)	0
	20–25	0 (58)	0	0 (25)	0
	25–30	0 (80)	0	0 (18)	0
54.0†	5–10	13 (14)	92.9	– –	–
	10–15	21 (29)	72.4	– –	–
	15–20	**9 (44)**	**20.5**	– –	–
	20–25	1 (42)	2.3	– –	–
	25–30	0 (85)	0	– –	–
		Experiment 2			
		11:7:3:3:1[2]			
52.4	5–10	4 (6)	66.7	– –	–
	10–15	**27 (28)**	**96.4**	– –	–
	15–20	24 (38)	63.2	– –	–
	20–25	5 (37)	13.5	– –	–
	25–30	1 (22)	4.6	– –	–
52.8	5–10	3 (5)	60.0	– –	–
	10–15	**7 (11)**	**63.6**	– –	–
	15–20	9 (14)	64.3	– –	–
	20–25	10 (33)	30.3	– –	–
	25–30	1 (11)	9.1	– –	–
54.1	5–10	5 (6)	83.3	– –	–
	10–15	**9 (14)**	**64.3**	– –	–
	15–20	**14 (22)**	**63.6**	– –	–
	20–25	19 (33)	57.6	– –	–
	25–30	1 (11)	9.1	– –	–

[1], 5:5:5:5:5, five mussels in each of the following five size-classes, 5–10, 10–15, 15–20, 20–25, 25–30 mm shell length. [2], 11:7:3:3:1, mussels presented as 11:7:3:3:1 individuals in the five size-classes. †, crab stopped eating during trial 3, no data available.

10:3:3:2:5:2 in the size-classes, 5–10, 10–15, 15–20, 20–25, 25–30, 30–35 mm shell length; this proportion was derived from a sample taken from the mid-shore at Aberffraw in June 1997 (Burch, 1998). Both trials lasted five days and the results were analysed using the *G*-test.

RESULTS

Prey handling

When feeding on mussels presented singly, *Carcinus maenas* employed a range of techniques to open *Mytilus edulis*. These techniques were prey size dependent; smaller mussels were crushed outright, medium-sized mussels were opened after several crushing attempts directed on either the anterior or posterior regions of the valves, whilst the more time-consuming opening techniques of boring and edge-chipping were used only to open larger mussels. However, when feeding on groups of mussels, crabs used only the shell-crushing techniques and neither boring nor edge-chipping were observed. The feeding behaviour of *C. maenas* on single and groups of mussels differed in other respects. A crab rarely rejected a mussel that had been presented singly and once the mussel was opened would spend prolonged periods severing the posterior adductor muscle, garnering mantle edge flesh and gleaning shell fragments that had been dropped accidentally. Only after the shell had been thoroughly gleaned and discarded did the crab initiate further search behaviour. When foraging on groups of mussels, crabs would gather several mussels simultaneously, using their pereiopods and two mussels would be held, one in each

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Table 5. G-*tests on the total number of* Mytilus edulis *consumed by different size categories of* Carcinus maenas *in experiments 3 and 4.*

Crab (mm)	N	*G*	df
Experiment 3			
30–35	3	30.6**	4
40–45	3	39.9**	4
50–55	3	96.0**	4
60–65	3	71.7**	4
Experiment 4			
40–45	2	14.3*	5
50–55	2	12.6*	5
60–65	2	28.7**	5

G, test statistic; N, number of crabs in each size-class; *, $P<0.05$; **, $P<0.01$; df, degrees of freedom.

chela, before one was rejected. Whilst a mussel was being manipulated by the chelae the pereiopods remained outstretched, exploring the immediate vicinity for other prey items. This behaviour, which frequently resulted in the rejection of a held mussel in favour of another touched by the pereiopods, usually stopped once the mussel held in the chela was opened, but would resume before the mussel had been thoroughly gleaned. A greater percentage of flesh tended to be left in the discarded shells of mussels presented in groups, compared with that left in mussels when presented singly (Table 1), i.e. single mussels were gleaned more extensively.

Prey value: experiments 1 and 2

Since different prey value curves have been associated with different opening techniques (see Lawton & Hughes, 1985; Burch, 1998) and given that *C. maenas* utilized the lengthier handling methods only when presented with single mussels (see above), our analysis of breaking and handling times included only those data for mussels which had been crushed. This enabled direct comparison of Tb and Th to be made between the trials when mussels were presented singly or as part of a group. In both prey value experiments, the relationships between breaking/handling times and shell length were linearized by $\log_e$ transformation of the dependent (y) variable (Tb/Th) prior to regression. The handling time-shell length regression equations were subsequently used in the calculation of prey value. In experiment 1, no significant differences in Tb and Th could be detected between trials for either of the two smaller crabs although the slopes of both Tb and Th were significantly different for the largest crab (Table 2). Plots of prey value against mussel length determined in each of the three trials of experiment 1 are presented in Figure 1A, from which it is clear that differences in the prey value curves arose between the three trials. When mussels were presented as a group rather than singly the size of prey predicted to be most profitable shifted to a smaller size-class for the two

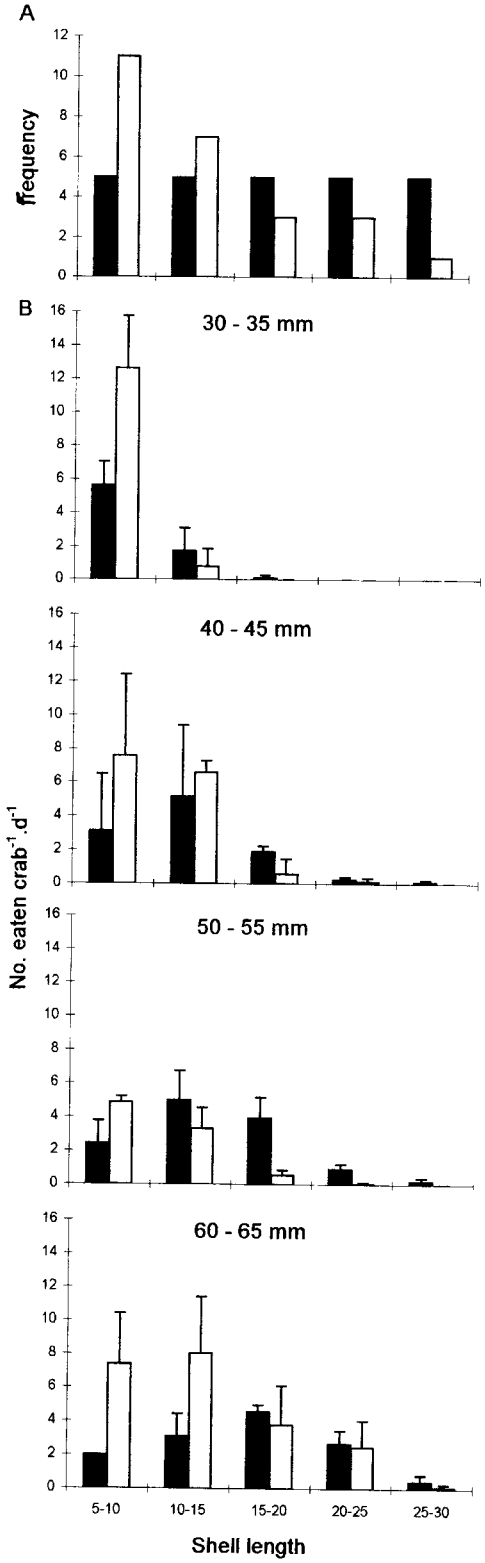

Figure 5. (A) Length–frequency diagram showing the relative proportions of mussels presented to crabs. Mussels were presented as five individuals in each of the following five size-classes 5–10, 10–15, 15–20, 20–25, 25–30 mm shell length (closed bars) and as 11, 7, 3, 3, 1, individuals in each of the five size-classes; representative of the population at the low shore Church Island (open bars). (B) Mean number of *Mytilus edulis* (±SD) consumed each day by three *Carcinus maenas* in each of four different size-classes, when mussels were presented as five mussels in each of the five size-classes, (closed bar) and when mussels were presented as 11, 7, 3, 3, 1, individuals in the five size-classes (open bars).

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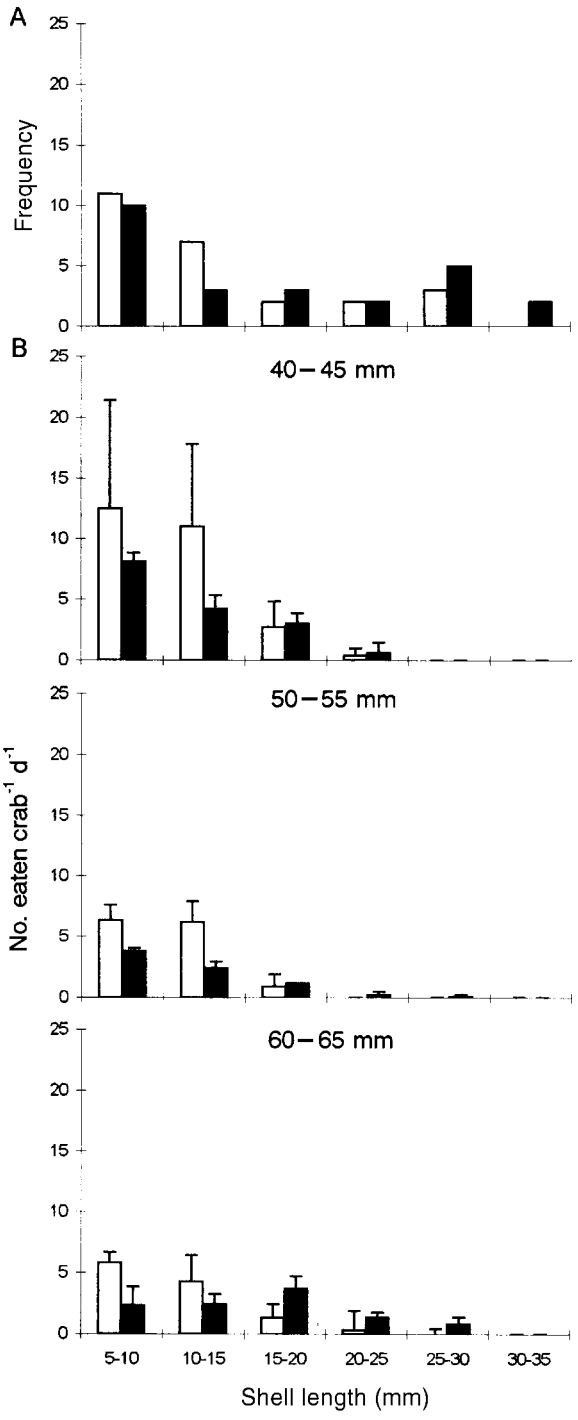

Figure 6. (A) Length–frequency diagram showing the relative proportions of mussels presented to crabs. Mussels were presented as 11, 7, 2, 2, 3, individuals in the following five size-classes, 5–10, 10–15, 15–20, 20–25, 25–30 mm shell length; representative of the population from the high shore Aberffraw (closed bars), and with 10, 3, 3, 2, 5, 2, mussels respectively in the six size-classes 5–10, 10–15, 15–20, 20–25, 25–30, 30–35 mm shell length; representative of the mid shore population at Aberffraw (open bars). (B) Mean number of *Mytilus edulis* (±SD) consumed each day by two *Carcinus maenas* in each of three size-classes when presented with a group of mussels representative of the high shore population (closed bars) and the mid shore population (open bars) at Aberffraw.

smaller crabs and to a larger size-class for the largest crab. Moreover, for the two smaller crabs, the relative number of mussels in each size-class also influenced prey value, the predicted optimal size shifting to the smaller size-classes through the sequence—single, equal and modified proportions. This shift in profitability accompanied alterations in the vulnerability of mussels; when the number of mussels in the smallest size-class was increased (the modified proportion) then the vulnerability of this size-class also increased (Figure 1B).

No significant differences in Tb could be determined between the three trials of experiment 2 (Table 2). However, significant differences in Th existed between the three trials (Table 2) but not between the two trials in which mussels were presented singly (trials 1 & 3) (Table 3). It is concluded that when prey were presented in groups handling times were significantly reduced compared to those recorded when similar sized prey were presented singly. The resultant effect is to elevate the prey value of mussels presented in a group, such that all sizes of mussel are more profitable than those of a similar size presented singly (Figure 2A). As in experiment 1, the size of prey predicted to be most profitable altered (Figure 2A); shifting to smaller sizes when mussels were presented in a group. Neither the prey value curves derived from single nor from grouped prey consistently predicted the preferred prey size-class accurately (Figure 2A,B).

Comparisons of the median percentage flesh left in discarded shells, using the non-parametric Kruskal–Wallis test, found significant differences between the three trials (Table 1) with more flesh left unconsumed when mussels were presented as a group. This was also true for the largest crab in experiment 1 (CW=54.0 mm); significantly more flesh remained in discarded shells when mussels were presented in a group (trial 2) than when they were presented singly (trial 1), ($U=137$, $P<0.05$, Mann–Whitney U-test). Comparisons of prey value curves (E/Th) with adjusted prey value curves ((E-L)/Th) (Figures 3 & 4) demonstrate that such decreased consumption of flesh does not influence the basic shape of these curves, nor does it affect their position relative to the prey value curves derived from trials where mussels are presented singly.

Both prey value experiments demonstrate that the optimal prey size-class, predicted from the prey value curves in Figures 1A & 2A, was not always that with the highest ratio of prey eaten to prey encountered (highlighted in Table 4); indeed up to 80% of encountered prey in these size-classes were rejected. Furthermore, the preferred size-class (that from which most mussels were eaten) was not consistently that with the highest ratio of prey eaten to those encountered (Table 4). However, despite the low number of encounters with mussels within the smallest size group, the percentage of mussels eaten relative to those encountered was always high (60–83%). From experiment 1 it is also clear that when prey were presented in equal numbers in each of the size-classes, encounter rate increased with prey size-class but the number eaten tended to decrease (Table 4). When these crabs were presented with the modified group, with its increased proportion of mussels in the smallest size-class, the encounter rate with these smaller mussels also increased.

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Prey vulnerability: experiments 3 and 4

Prey size vulnerability was significantly affected by the relative proportions in which mussels of different sizes were presented (Table 5). It is clear from experiment 3 that when mussels are presented in equal numbers in each of several size-classes, the size of preferred prey increases with increased crab size; this trend is less obvious when mussels are presented in the modified proportion and preferred prey size was shifted to smaller-classes mirroring the bias towards these size-classes in this mussel group (Figure 5). Similarly, significant alterations in prey preference with relative proportions of mussels in different size-classes were observed in experiment 4 (Table 5). When crabs fed on the simulated high shore population, which contained proportionately more mussels in the smaller size-classes, more of these smaller sizes were included in the diet than when the same crabs fed on the simulated mid-shore population (Figure 6). The shifts in prey size preference observed in both experiments could not be attributed to the eating out of all the mussels in the previously preferred size-class since no crab ever ate all the mussels within a single size-class.

DISCUSSION

The prey size selection and foraging behaviour of *Carcinus maenas* on *Mytilus edulis* altered with the manner in which mussels were presented. When mussels were presented in a group of mixed sizes *C. maenas* did not use the more time-consuming opening techniques of boring and edge-chipping. This behaviour conforms to that predicted by the energy maximization premise of the optimal foraging theory. Mussels opened by boring or edge-chipping techniques tend to be larger and have relatively longer handling times which thus reduces their prey value; consequently these should not be eaten if prey of higher value are also present (Elner & Hughes, 1978; Hughes, 1980). However, other theories would also explain this particular behaviour. Decapod crustaceans consistently select prey smaller than the maximum size that can be opened (Juanes, 1992) and this may also be explained by a need to minimize chelal damage (Juanes & Hartwick, 1990) or minimize foraging time (Hughes & Seed, 1981). Regardless of the underlying mechanism, the observed difference in foraging behaviour on single and grouped prey indicates that optimal and preferred prey sizes should be determined under the same conditions.

Importantly, this study revealed that the manner in which mussels are presented to crabs alters the size of prey predicted to be most profitable: different sizes of prey were predicted to be the most profitable when prey were presented singly and when they were part of a group. Given that predictions from prey value curves (normally derived when prey are presented singly) are compared with the observed preferred prey size (derived by presenting prey in groups) to determine the mechanisms underlying foraging behaviour, then both should be determined in the same way if these mechanisms are to be assessed accurately. Variations between prey value curves resulted from differences between handling times which, for all but the two smallest crabs (CW=42.3 and 44.5 mm), were significantly shorter when prey were presented within a group than when presented singly. Differences in handling times could not be attributed to the use of different opening techniques since only those handling times for prey which had been crushed were used in our comparisons between prey presented singly and prey presented as part of a group: nor could the differences in prey value curves be entirely attributed to increased handling efficiency over consecutive trials. Cunningham & Hughes, (1984) found that when *C. maenas* fed on *M. edulis*, breaking times were reduced to 30% of the original value after crabs had fed on 5–6 mussels and whilst this information was gained rapidly it was lost slowly over several days. Although breaking times differed significantly between trials for the largest crab (CW=54.0 mm) in experiment 1, in experiment 2, in which the effect of learning was investigated, no differences between breaking times could be detected between the three trials. This strongly suggests that there was no improvement in handling efficiency between trials. Furthermore, in experiment 2 there were no detectable differences in handling times between the two trials in which prey items were presented singly (trials 1 & 3), again implying that there was no significant improvement in handling efficiency over time. Instead, the authors conclude that the reduced handling times with grouped mussels are due to some attribute of the group itself.

Significantly more flesh remained in discarded shells when mussels were presented in groups, indicating that reduced handling times were probably due to the shorter periods of time spent gleaning an opened mussel. When a crab fed on a group of mussels its pereiopods were generally in contact with several mussels simultaneously and a mussel held in the chelae would often be rejected for one touched by a pereiopod. Jubb et al. (1983) proposed that such behaviour arose in response to the relative strengths of stimuli received simultaneously from the chelae and pereiopods—The Relative Stimulus Hypothesis. Pereiopod stimulus increases with increases in the size and number of mussels touched, whilst chelal stimulus increases with increases in the size of mussel held in the claw; with chelal stimulus overriding pereiopod stimulus once a held mussel starts to break. The acceptance or rejection of a held mussel is, therefore, a balance between conflicting stimuli and the rejection of a mussel before its flesh has been fully gleaned may have a similar explanation. Chemoreceptors are present on the mouthparts and chelae of *C. maenas* (Crothers, 1967) and the strength of the stimulus received from the mussel presumably will decrease as the mussel flesh is progressively gleaned. If, at the same time, the crab is in contact with other mussels, it is reasonable to suppose that a point will be reached when the chelal stimulus will be weaker than that received from the pereiopods and that this point will be reached before the mussel is fully gleaned. In contrast, when crabs are feeding on mussels presented singly there is little to interfere with this chelal stimulus and consequently the mussel is gleaned more extensively. The rejection of an incompletely gleaned mussel appears to be energetically advantageous. Initially flesh is readily extracted from an opened mussel but this becomes increasingly more difficult when only the more adherent adductor muscle and mantle tissue remains.

When adjusted prey value ((E−L)/Th) curves are plotted it is clear that although less flesh is consumed when mussels are presented in groups, adjusted prey value is still higher for these mussels compared with those of similar size that were presented singly. It is concluded that the extensive gleaning of mussels presented singly is inefficient, the increases in energy gain failing to offset the increased handling times required to garner this flesh.

Previous studies have shown a correlation between the size range of *M. edulis* most vulnerable to predation by *C. maenas* and the size of mussel predicted to be the most profitable, suggesting that *C. maenas* 'selects' prey which maximizes its net energy intake (see Elner & Hughes, 1978; Cunningham, 1983; Ameyaw-Akumfi & Hughes, 1987). However, in the present study, when the proportion of mussels eaten to those encountered was analysed, up to 80% of the mussels in the size-classes predicted to be most profitable were rejected. Under the energy maximization premise the most profitable sizes of prey should always be eaten when encountered (Hughes, 1980). The rejection of a high proportion of 'optimal' prey therefore makes it unlikely that *C. maenas* selects its prey solely on the basis of energy return. The rejection of a high proportion of optimally sized mussels recorded in this study was also observed by Jubb et al. (1983). Under their Relative Stimulus Hypothesis, the balance of chelal and pereiopod stimuli should lead to the rejection of small mussels held in the chelae because the stimuli received from mussels in contact with the pereiopods will override the chelal stimulus whilst larger mussels are rejected because they cannot be easily opened. Such behaviour would inevitably result in the preferred predation of medium-sized mussels. Whilst these different effects of stimuli were observed, and certain aspects of our data conform to the Relative Stimulus Hypothesis, this hypothesis predicts that a high proportion of small mussels should be rejected immediately; this, however, did not happen since the smallest mussels tended to be eaten as encountered.

An alternative hypothesis of prey size-selection is therefore proposed in which the observed patterns of selection arise from the passive response of the crab to encounter rate, which increases with prey size, and attack success rate, which decreases with prey size. When prey is presented in equal numbers in each of several size-classes, medium-sized prey should predominate in the diet. This appears to be the mechanism underlying prey selection in many planktivorous fish (see Juanes & Conover, 1994 and references therein) and appears to be the mechanism underlying size-selection by *C. maenas* in this study. When mussels were presented as five individuals in each of five size-classes, encounter rate increased but attack success rate decreased with increasing mussel size. If prey size preference was the result of active selection by the predator then the preferred prey size class and prey size class with the highest eaten to encounter ratio should always correspond. This, however was not consistently true in this study, occurring only in three out of seven occasions when crabs exhibited a clear preference for a particular size-class. It is concluded, therefore, that the observed patterns of prey selection in *C. maenas* occur passively as a result of encounter and attack success rate, with larger mussels being excluded from the diet because they are difficult to break, and smaller mussels being excluded because they are less frequently encountered. This conclusion supports the findings of Davidson (1986) who showed that when *Mytilus edulis aoteanus* was presented in equal numbers in each of several size-classes to the portunid, *Ovalipes catharus*, medium-sized mussels predominated in the diet. However, small mussels were nearly always eaten when encountered and the proportion of small mussels in the diet could be increased simply by increasing their proportion in the sample.

The vulnerability of hard-shelled molluscs to crab predation has previously been shown to alter when structural elements of the environment are included in the experiments (e.g. Arnold, 1984; West & Williams, 1986; Sponaugle & Lawton, 1990; Lin, 1991; Lee & Kneib, 1994). Under these more natural conditions the intensity of predation effort can be reduced (Arnold, 1984; Sponaugle & Lawton, 1990; Lin 1991) and the size of prey most vulnerable to predation altered, as the environment provides an affective refuge for certain size-classes (West & Williams, 1986; Lee & Kneib, 1994). Our results indicate a further possibility, that prey vulnerability may also vary with characteristics of the prey population. By increasing the relative abundance of mussels in the smaller size-classes, the size range most vulnerable to crab predation shifted to smaller prey size. However, since none of the experimental crabs ate all of the mussels in the previously preferred size-class, this shift could not be attributed to the 'eating out' of these mussels. Instead the shift in vulnerability appears to be a real response of the crabs to changes in the proportions of mussels presented in each size-class. Vulnerability also shifted when prey was presented in two different proportions that reflected the relative availability of mussels in local high and mid shore populations. Since mussels from the same tidal level were used in both of the trials, alterations in vulnerability are not attributable to those physical differences that occur between mussels at different tidal levels (Seed, 1968). Smaller size-classes of prey were relatively more abundant in the simulated high shore population. When crabs fed on this population, smaller mussels were more vulnerable to predation than when crabs fed on the simulated mid shore population which contained proportionately more mussels in the larger size-classes; indeed in this mid shore population larger mussels actually became more vulnerable. This suggests that *C. maenas* has a flexible foraging behaviour and given that *M. edulis* population structure can vary not only between shores (Burch, 1998) but also with tidal elevation (Robles et al., 1990; Lintas & Seed, 1994; Burch, 1998), such flexibility will enable crabs to deal effectively with more heterogeneous environments. Our results also have important implications for foraging studies. Patterns of prey distribution in the field are sometimes compared with the patterns of prey vulnerability observed in the laboratory (Pollock, 1979; Griffiths & Seiderer, 1980; Seed, 1990) in order to determine the influence of the predator in the field. Given the flexibility in the preferred prey sizes observed in these experiments it is clear that steps toward greater context sensitivity need to be taken if laboratory results and field observations are to be integrated.

This research was conducted under a Natural Environment Research Council (NERC) funded PhD studentship awarded to A.B. We are grateful to Berwyn Roberts and Gwyn Jones who helped with the collection of the animals. We would also like to thank the four anonymous referees, whose comments greatly improved this paper.

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Submitted 27 January 2000. Accepted 13 June 2000.