

Predatory interaction between the brachyuran crab *Cancer pagurus* and decapod crustacean prey

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ABSTRACT: In laboratory experiments *Cancer pagurus* successfully subdued a wide size range of decapod crustaceans (conspecifics, *Galathea squamifera*, *Pilumnus hirtellus*, *Pisidia longicornis*, and *Porcellana platycheles*). Mishandling by *C. pagurus*, prey retaliation, and prey limb autotomy contributed to attack failure. A simple grab response dominated the pursuit phase of predatory interaction, although *C. pagurus* also pounced on, and actively stalked, decapod crustaceans. Handling times, T_h , were long (up to 1.44 h), due to an extended consumption phase. By comparison, involvement time, T_i , in unsuccessful predation attempts was much shorter (median $T_i < 180$ s for all prey species). Profitability (prey energy content (kJ)/ T_h) increased linearly with prey size for one size class of *C. pagurus* feeding on *P. platycheles*. Due to incomplete consumption, energy intake (kJ predator⁻¹ d⁻¹) from an unrestricted diet of *P. platycheles* was considerably lower than numerical predation and whole prey energy content would suggest. Nevertheless, decapod crustaceans proved to be energetically valuable, if somewhat elusive, prey for *C. pagurus*. Predation success rate of *C. pagurus* on *P. platycheles* was < 0.5 in open encounters. However, when provided with shelter, *C. pagurus* adopted ambush predation techniques to capture *P. platycheles*, thereby compensating for the relatively low predation success observed in open encounters with this decapod crustacean prey.

INTRODUCTION

Crustacean prey occur in decapod crustacean stomach contents (Hill 1976, Williams 1982, Elnor & Campbell 1987), including those of brachyuran crabs in the genus *Cancer* (Butler 1954, Gotshall 1977, Shelton et al. 1979, Stevens et al. 1982, Elnor et al. 1985). Surprisingly, there are few quantitative behavioral studies of this predation (Evans & Mann 1977, Hirtle & Mann 1978, Paul 1981, Morales & Antezana 1983, ap Rheinallt & Hughes 1985, ap Rheinallt 1986), in contrast to the extensive literature on molluscan predation by decapods (Lau 1987).

Warner (1977) considered that fast-moving prey, such as crustaceans, could generally only be captured by portunids and rapidly-moving semi-terrestrial or terrestrial crabs. However, a 'sit-and-wait' or 'ambush' predation strategy has been posited for some relatively slow-moving crabs (Hughes 1966, Hill 1979, Schembri 1981, Morales & Antezana 1983).

European edible crabs *Cancer pagurus* occupy sublittoral-fringe, and shallow sublittoral habitats on northeastern Atlantic rocky coasts (Ingle 1980). Conspicuous among the mobile epifauna of these habitats on North Wales shores, sympatric with *C. pagurus*, are several other decapod crustaceans (Lawton 1983), *Carcinus maenas* (Portunidae), *Galathea squamifera* (Galatheidae), *Pilumnus hirtellus* (Xanthidae), *Pisidia longicornis*, and *Porcellana platycheles* (Porcellanidae).

In view of the paucity of data on predatory interaction between crustaceans, the following topics were examined in this study. (1) Predation techniques used by recently captured *Cancer pagurus*. (2) Feeding performance in terms of predation success rate (sensu Holling 1966). (3) Handling times and prey profitability (defined as the ratio of prey energy content to handling time; Elnor & Hughes 1978). (4) Foraging tactics used by *C. pagurus* to exploit decapod crustacean prey.

Cancer pagurus was observed feeding on all 5 decapod crustaceans, and on conspecifics. *Porcellana platycheles* formed the principal prey species, being numerically abundant at the collection sites, and easily maintained in the laboratory.

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METHODS

Predators, *Cancer pagurus* (males only), and prey species (both sexes; Fig. 1), were collected between August 1980 and June 1981 from sublittoral-fringe habitats on 2 North Wales rocky shores; Treborth (Ordnance Survey reference SH552713), and Church Island (SH552716). Predators were placed singly in 0.4 × 0.2 m aquaria supplied with recirculating seawater (ambient temperature; salinity ca 33‰). Prey were held in single species groups in similar aquaria. Photoperiod followed natural sunrise and sunset, ranging from 16:8 to 8:16 (h light:h dark). Prey presentations commenced after 12:00 h on any given day, and frequently continued into the dark phase of the photoperiod (under low-level illumination in the near infra-red).

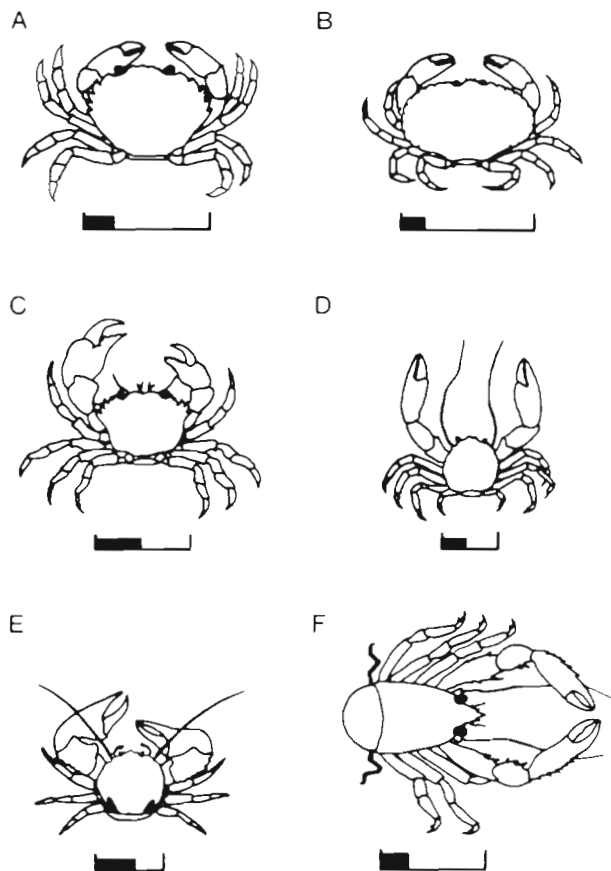


Fig. 1. Decapod crustacean prey species. Line bars indicate measured body dimension, carapace width (CW) for *Carcinus maenas* (A), *Cancer pagurus* (B), *Pilumnus hirtellus* (C), *Pisidia longicornis* (D), and *Porcellana platycheles* (E). Carapace length, CL, of *Galathea squamifera* (F) was measured from the tip of the medial spine on the rostrum to the dorsal margin of the carapace along the anterior-posterior axis. Solid bar under each illustration indicates the height of the master claw relative to the prey body dimension

Predation techniques. (1) *Porcellana platycheles* prey: Ten recently captured predators (61 to 120 mm carapace width, CW; held for < 5 d) were presented individually with 5 *P. platycheles* (6.4 to 13.9 mm CW; 1 prey d⁻¹). Each trial was observed for at least 15 min; if no attack occurred within 7 min, a 'passive' encounter was staged by gently coaxing the prey towards the predator. When an attack ensued, observations were extended until the feeding bout ended. Otherwise, predatory activity was assessed the following morning.

(2) Other decapod prey: Nine recently captured predators (70 to 91 mm CW) were presented with *Pisidia longicornis* (5.1 to 8.1 mm CW) as prey, following procedures outlined for *P. platycheles*.

Feeding performance. Feeding performance was analyzed in terms of predation success rate (Holling 1966; see also Evans & Mann 1977):

$$\text{Predation success} = \text{recognition success} \times \text{pursuit success} \times \text{attack success}$$

Where recognition success = no. of encounters leading to pursuit/no. of encounters; pursuit success = no. of captures/no. of pursuits; attack success = no. of prey or chelipeds consumed/no. of captures. Prey were encountered through direct physical contact and by olfaction, the latter being recognizable by synchronous orientation of the predators' antennules towards the prey, and an increase in antennular flicking rate (Pearson et al. 1979, Lawton & Hughes 1985).

(1) *Porcellana platycheles* prey: Six predators (75 to 85 mm CW) were presented with 4 size classes of prey (< 7.9; 8.0 to 9.9; 10.0 to 11.9; 12.0 to 13.9 mm CW), continuing until 30 observations (per size class) were obtained on pursuit and attack success. Prey (a maximum of 4 daily) were gently lowered into the aquarium 30 to 50 mm from the predator; if no pursuit occurred, a passive encounter was staged. Trials in which prey were not pursued after an encounter provided information on recognition success.

(2) Other decapod prey: Individual predators (69 to 120 mm CW) were presented with 5 prey (1 prey d⁻¹) from one of the following species: *Cancer pagurus*, *Carcinus maenas*, *Pilumnus hirtellus*, or *Galathea squamifera*. Prey were presented to 3 predators from each of 2 groups which differed in recent feeding history. The first group ($n = 12$) comprised recently captured predators (< 2 wk in captivity) which had fed on decapods in the laboratory (DEC group). The second group ($n = 12$) consisted of predators, held for > 2 wk, which had fed on molluscan prey only during captivity (MOLL group). Prey size was expressed as prey body dimension (Fig. 1)/predator CW, PROP, in this experiment which used 4 prey species, and a wide size range of predators. Predators which did not feed on a particu-

lar prey species were subsequently given 2 *Porcellana platycheles* to assess their response to alternate decapod prey.

Handling times and prey profitability. (1) *Porcellana platycheles* prey: Handling time (T_h , s) and tissue consumption (estimated visually) were recorded for 3 predators (80 to 82 mm CW). Handling times were related to prey size using prey CW (mm)/predator chela height (mm) as a measure of relative prey size, RPS. Energy content (E, kJ) of *P. platycheles*, with adjustment for incomplete prey consumption, was obtained following procedures given in the Appendix. Profitability was expressed as E/T_h , following Elner & Hughes (1978).

(2) Other decapod prey: Handling times, and involvement times (T_i , s) when predation attempts failed were recorded during the presentations described under 'Feeding performance'. Profitability relationships were not determined for other decapod prey.

Foraging tactics. For each of 4 trials, 4 to 5 *Cancer pagurus* (75 to 85 mm CW) were collected by SCUBA divers from sublittoral sites in the Menai Straits, North Wales (SH540709). *Porcellana platycheles* ($n = 12$) were given to these crabs on the day following capture. On the 3rd day in captivity, 1 predator was selected and placed into a 0.77×0.48 m observation tank. Within an oval arena of 0.2 m^2 basal area inside this tank, an opening along one side led to a shelter (inside dimensions: $135 \times 70 \times 90$ mm; W \times H \times D). On Day 4, 10 *P. platycheles* from each of 2 size classes (< 10 mm; > 11 mm CW) were placed into the arena 1 h after the onset of the dark phase. Prey were replaced twice-daily over the next 4 d to maintain prey availability. At these times, prey remains were removed, and surviving prey assessed for predator-induced injury.

Predator and prey behavior was monitored each night for 2 trials (with Predators A and B). Video-recording commenced 1 h into the dark phase of the photoperiod (facilitated by low-level illumination in the near infra-red), continuing for 12 h thereafter. In the trials with Predators C and D, prey remains were collected daily to estimate energy intake ($\text{kJ predator}^{-1} \text{ d}^{-1}$) on an unrestricted diet of *Porcellana platycheles*.

RESULTS

Predation techniques

(1) *Porcellana platycheles* prey: Prey were recognized at distances of 30 to 50 mm through olfaction; however, most direct encounters were passive (65.6%; $n = 32$), following prey movement towards the predator. Three pursuit techniques were recognized. In the

grab response, the prey was swept under the predators' abdomen using one or more pereopods (median pursuit time = 30 s; $n = 18$). In the pounce response, the predator executed a rapid forward movement (from a resting position) towards the prey, which it then captured by bringing the pereopods together under the abdomen (median pursuit time = 5 s; $n = 13$). Stalking (one 47 s sequence) occurred when the predator rose from a resting position, fully extended all pereopods, and moved off slowly in pursuit of the prey. A rapid downward movement, similar to that used in the pounce response, secured the prey item.

Following capture, small prey were moved directly to the mouthparts. Attacks on larger prey were initially directed at the chelipeds, leading to autotomy in 14 attacks. Retaliation, in which a prey cheliped closed forcibly over a predator body-part, occurred in 5 attacks on large *Porcellana platycheles*, from which 4 prey escaped. Prey also escaped due to mishandling by the predator. Median subjugation time (elapsed time from taking the prey up in the claws, until immobilization) was 60 s ($n = 18$).

Consumption was the longest phase of predatory interaction (Table 1). Small prey were ingested entirely, whereas the dorsal carapace of large prey was first broken open, thus allowing the predator access to body tissues. Predators frequently removed pereopods from large prey, breaking them open to feed upon the exposed muscle tissue. Following autotomy, or as part of a feeding bout, predators also fed on one or both prey chelipeds.

(2) Other decapod prey: Predation techniques used on *Pisidia longicornis* were very similar to those used on *Porcellana platycheles*, differences being attributable to the specific morphology of each species (Fig. 1). Median pursuit time was 23 s ($n = 18$) and 7 s ($n = 3$), respectively, for the grab and pounce responses; no stalking behavior was observed. Median subjugation time for *P. longicornis* prey was 172 s ($n = 17$), while the median duration of the consumption phase approximated 10 min (Table 1).

Feeding performance

(1) *Porcellana platycheles* prey: Recognition success was higher, and less variable, for active prey encounters (0.80 ± 0.10 , mean \pm standard deviation; 67 encounters with 6 predators), than for passive ones (0.67 ± 0.21 ; 163 encounters). Pursuit success averaged 0.78 (over all methods and prey sizes). The grab response was used most frequently (67.5% of pursuits), but was less successful on large prey than the pounce response (28.3% of pursuits). Stalking behavior was observed in 5 presentations.

Table 1 *Cancer pagurus* and 2 decapod crustacean prey. Med. dur.: Median duration (s) of the consumption phase of predatory interaction

Degree of consumption	<i>Porcellana platycheles</i>		<i>Pisidia longicornis</i>	
	Med. dur.	n	Med. dur	n
Small prey, consumed entirely	196	3	671	12
Large prey, consumed in part:				
One cheliped	199	12		
Two chelipeds	305	5		
Body tissues	245	6		
Body tissues, chelipeds, and pereopods	608	10	559	12

Full attack success (in which the whole prey was subdued) was maximal at intermediate prey size (Fig. 2A). The main cause of failure with large prey was cheliped autotomy (Fig. 2B), while mishandling led to

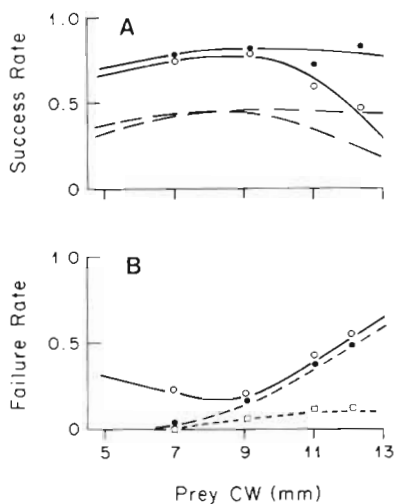


Fig. 2. *Cancer pagurus* and *Porcellana platycheles* prey. (A) Predation success. Solid lines indicate relation between attack success and prey size (CW, mm): (○) full attack success (predator subdued the whole prey); (●) total attack success (full + partial success, in which predator obtained prey cheliped only). Dashed lines indicate predation success, with and without adjustment for partial attack success. (B) Cause of failure in unsuccessful attacks. Lines indicate cumulative proportion of attacks which failed due to one of the following causes: (—) retaliation by prey; (●) autotomy of one or both prey chelipeds; (—) mishandling by predator

most failures with small prey. Retaliation occurred in only a small proportion of attacks (Fig. 2B). When the consumption of autotomized chelipeds was taken into account (partial attack success), total attack success (full + partial success) remained high for large prey (Fig. 2A). Using average values for recognition and pursuit success, data on attack success were adjusted to derive predation success rate, this being < 0.5 for all prey sizes (Fig. 2A).

(2) Other decapod prey: Predators which had recently fed on decapod prey (DEC group) were cap-

able of subduing small conspecifics (Table 2; PROP range 0.16 to 0.29); however, none of the 5 prey attacked were consumed. A distinct rejection behavior was observed when conspecifics were crushed or moved to the mouthparts for inspection. The behavior involved antero-lateral extension of the cheliped holding the prey, with release at a distance from the predator (median rejection time = 89 s; $n = 5$). At the end of the trial, by which time the predators had not eaten for 7 d, 2 *Porcellana platycheles* were consumed within 3 h.

Only 1 predator in the group maintained on molluscan prey (MOLL group) exhibited similar behavior (median rejection time = 109 s, $n = 3$). The other 2 MOLL group predators consumed all conspecific prey offered to them (PROP range 0.2 to 0.44). These predators actively searched for small conspecifics, attacking most of those encountered (Table 2), whereas none of the DEC group predators attempted to locate conspecifics. Pursuit and attack success rates were high, reflecting an inadequate defensive capability (Table 2). On capture, small *C. pagurus* did not readily autotomise limbs, while retaliation was ineffective due to a relatively small chela size (Fig. 1).

Predation on small *Carcinus maenas* by DEC group predators was low, with only 4 prey consumed (Table 2). Observed predation success was similarly low for the MOLL group, although these predators consumed 13 *C. maenas* overnight. Predators in both groups responded to the introduction of *C. maenas* by active searching behavior, but pursuit success on this species was low, particularly for larger predators. However, attack success on captured *C. maenas* prey was high (Table 2), again reflecting an ineffective defensive capability (Fig. 1).

Both predator groups preyed successfully on *Pilumnus hirtellus* (Table 2). Predators from the DEC group responded primarily to direct contacts, while predators in the MOLL group actively searched for *P. hirtellus*. All predators consumed the largest prey offered (maximum PROP = 0.33), although handling difficulties became evident. *P. hirtellus* reacted to predation attempts with autotomy and direct retaliation, the latter

Table 2. *Cancer pagurus* and 4 decapod crustacean prey. Predation success rate (PSR) derived as the product of recognition success (no. of encounters leading to pursuit/no. of encounters), pursuit success (no. of captures/no. of pursuits), and attack success (no. of prey or chelipeds consumed/no. of captures) for each of 2 predator groups: (A) Predators with recent (<2 wk) exposure to decapod crustacean prey (DEC group); (B) Predators held in the laboratory >2 wk, and which had fed on molluscan prey only (MOLL group). Five prey were presented to 3 predators in each species/predator grouping yielding 15 encounters, the denominator in recognition success

Prey species: Predator group:	<i>Cancer pagurus</i>		<i>Carcinus maenas</i>		<i>Pilumnus hirtellus</i>		<i>Galathea squamifera</i>	
	DEC	MOLL	DEC	MOLL	DEC	MOLL	DEC	MOLL
Recognition	0.33	0.93	0.75	0.53	0.93	1.00	0.87	0.93
Pursuit	1.00	0.79	0.55	0.36	0.64	0.88	0.28	0.43
Attack	1.00	1.00	0.60	1.00	0.78	0.73	1.00	1.00
PSR	0.33	0.73	0.25	0.19	0.46	0.64	0.24	0.40

defense being particularly effective, terminating the predation attempt in 4 cases.

Both DEC and MOLL group predators responded to the swimming movements of *Galathea squamifera* by attempting to capture these prey; however, pursuit success was low (Table 2). Due to limited size availability, some captured *G. squamifera* could not easily be consumed. Notwithstanding this size discrepancy, 22 of the 30 galatheids presented were consumed overnight. Following capture, *G. squamifera* were restrained by the pereopods while the predator attempted to immobilize the long, slender chelipeds (Fig. 1), these appendages being autotomized in most attacks, leading to escape on 3 occasions.

Handling times and prey profitability

(1) *Porcellana platycheles* prey: For predators consuming small prey entirely, or feeding on the body only (or body and pereopods) of larger prey (RPS > 0.4), handling time was linearly related to relative prey size, RPS (Fig. 3A). Handling time was also linearly related to RPS when predators fed only upon autotomized chelipeds (Fig. 3A), the slope for this latter relation being significantly higher than the former ($t = 1.967$; d.f. = 50 (1); $p < 0.05$).

Using an energy conversion factor (Appendix), and appropriate ash-free dry weight regression (Appendix; Table 3A), the energy content of prey body-parts available in each handling episode was estimated, and adjusted for incomplete ingestion (Table 3B). Realized profitability (E/T_h) increased linearly with RPS when predators consumed small prey entirely, or fed on the body only (or body and pereopods) of prey > 0.4 RPS (Fig. 3B). Profitability of large prey chelipeds alone was lower than that gained from feeding upon the body tissues of prey of equivalent RPS (Fig. 3B). Evidently, there was no energetic basis for predators concentrating on the autotomized chelipeds of large prey.

(2) Other decapod prey: Handling times ranged up to

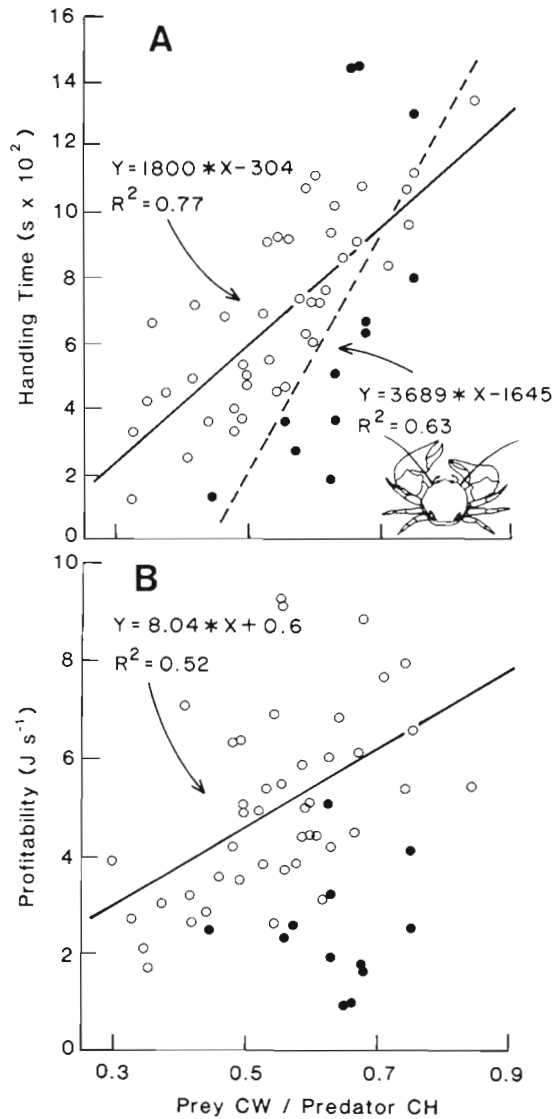


Fig. 3. *Cancer pagurus* and *Porcellana platycheles* prey. (A) Handling time, T_h , (○) T_h when feeding on whole prey; (●) T_h when feeding on autotomized chelipeds. Equations are in the form $Y = BX + A$, where $Y = T_h$ (s) and $X = \text{prey CW (mm) / predator chela height (mm), RPS}$. (B) Profitability. Symbols as for (A). Equation is for profitability of whole prey, where $Y = \text{profitability (J s}^{-1}\text{)}$, and $X = \text{RPS}$ as in (A)

Table 3. *Cancer pagurus* and *Porcellana platycheles* prey. Regression equations used in estimation of prey profitability. (A) Ash-free carbonate corrected dry weight, AFCC, of prey body-parts related to prey size, CW: equations in the form $\log_e Y = \log_e A + B \log_e X$, where $Y = \text{AFCC (g) of body-part (body and pereopods, bp; cheliped, ch; whole prey, w)}$, and $X = \text{CW (mm)}$. (B) Proportion of prey left as remains, P_r , related to relative prey size, RPS: equations in the form $Y = A + BX$, where $Y = \text{mean } P_r \text{ (AFCC of remains, g/AFCC available for consumption, g; } n = 4)$, and $X = \text{RPS (prey CW, mm/predator chela height, mm)}$

Y	A	B	n	r ²
(A)				
AFCC _{bp}	-8.679	2.789	28	0.96
AFCC _{ch}	-10.318	3.415	28	0.97
AFCC _w	-8.714	3.069	28	0.95
(B)				
P _r (whole prey)	-0.207	0.574	5	0.98
P _r (cheliped)	0.126	0.371	5	0.88

1.44 h for other decapod prey, with considerable overlap between proportional prey size categories (Table 4). As was the case with *Porcellana platycheles*, these extreme handling times were due principally to an extended consumption phase. By comparison, involvement time in unsuccessful predation attempts was much shorter. Median T_i, regardless of the cause of attack failure (autotomy, retaliation, mishandling, or rejection of conspecific prey), was <180 s for each species.

Foraging tactics

Both of the video-monitored predators occupied shelter during inactive periods (Predator A for ca 8 h each night). Out of shelter activity for Predator A was most pronounced from the time of high tide to that of the subsequent low tide (Fig. 4). During activity periods outside shelter Predator A showed limited response to prey encounters (2 pursuits out of 119 encounters during night 1; 0.02 as a proportion). Conversely, a higher proportion of prey encounters at the shelter elicited

pursuit (8 out of 15 encounters during night 1; 0.53). Differential response was also evident in the amount of time engaged in feeding activity outside shelter for Predator A (38 min over 4 nights) compared to time engaged in feeding within shelter (Fig. 4). Predator B only left the shelter on 1 occasion (for 10 min on the second night), but was observed at the entrance, and to be active within shelter on other nights.

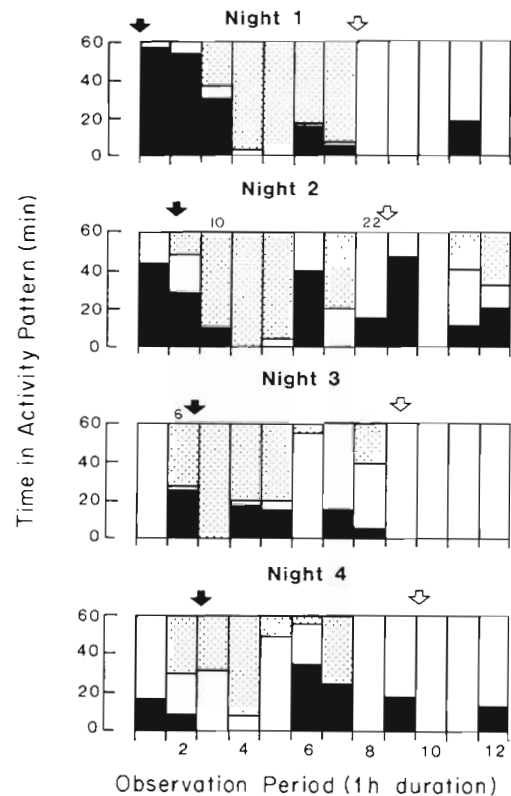


Fig. 4. *Cancer pagurus* and *Porcellana platycheles* prey. Activity pattern of Predator A, monitored for 12 h each night over 4 d. Open portion of each bar: time in shelter (with no feeding observable) during each 1 h observation period; stippled portion: time spent in general activity outside shelter; solid portion: time engaged in foraging activity within or directly from shelter. Numbers above individual bars on Nights 2 and 3 indicate amount of time engaged in foraging activity outside shelter. Solid arrow: time of high tide; open arrow: time of low tide, for each night

Table 4. *Cancer pagurus* and 4 decapod crustacean prey. Median handling times, T_h (in h), with range and number of observations (in parentheses). Prey/predator size ratio, PROP = prey CL or CW (mm)/predator CW (mm)

PROP	<i>Cancer pagurus</i>	<i>Carcinus maenas</i>	<i>Pilumnus hirtellus</i>	<i>Galathea squamifera</i>
0.1–0.19		0.11 (1)	0.93 (5)	0.54 (3)
0.2–0.29	0.50 (4)	0.69 (7)	(0.30–1.27)	(0.51–0.58)
0.3–0.39	(0.48–0.61)	(0.23–0.99)	0.86 (12)	0.56 (4)
>0.4	0.78 (3)		(0.30–1.44)	(0.21–1.18)
	(0.44–1.34)		0.44 (1)	
	1.12 (1)			

Porcellana platycheles detected and avoided predators at distances of 30 to 50 mm, increasing locomotory rate, and/or changing direction of movement. A total of 178 avoidance responses were noted during Night 1 of the trial with Predator A. Prey did not move extensively when the predators were in shelter, but aggregated (in groups of 2 to 5) along the arena sides. Prey activity increased following predator emergence from shelter.

Shelter-related foraging behavior, directly observed for predators A and B, included attacking prey which moved across the shelter entrance, returning to the shelter with a prey item captured during general activity, and specific attack movements from within shelter. In the latter case, the predator exited from shelter, captured a prey and immediately returned.

Using numerical predation data, consumption was confirmed to be greatest within the shelter for all 4

Table 5. *Cancer pagurus* and *Porcellana platycheles* prey. Numerical predation over a 4 d period. Data are separated by the time (Night/Day) and location (Shelter/Arena) of prey consumption, inferred from the location of prey remains, collected twice-daily

Predator identity	Time and location of prey consumption				Total
	Night		Day		
	Shelter	Arena	Shelter	Arena	
A	37	11	3	0	51
B	10	0	4	2	16
C	15	1	7	2	25
D	6	3	10	2	21

predators (G test, all $p < 0.05$; Table 5). As interactions were not significant (G test, $G_{(int)} = 2.8$; d.f. = 3; $p > 0.25$), these data were pooled (G test, $G = 48.14$; d.f. = 1; $p < 0.001$). Predation was heaviest overnight in the trial with Predator A (G test; $G = 47.88$; d.f. = 1; $p < 0.001$); however, there was no significant diurnal variation in predation for the other 3 predators (G test; all $p > 0.1$).

After adjustment for incomplete prey ingestion, daily energy intake ($\text{kJ predator}^{-1} \text{d}^{-1}$) of Predators C and D was shown to have decreased progressively over the course of each trial (Table 6). Total energy intake over 4 d was 67.6% less (mean percentage reduction) than numerical predation and whole prey energy content would suggest (Table 6).

DISCUSSION

Predation techniques and feeding performance

In these laboratory experiments, *Cancer pagurus* did not pursue all decapod prey which were encountered (either by direct physical contact or olfaction), leading

Table 6. *Cancer pagurus* and *Porcellana platycheles* prey. Energy intake (based on numbers of prey consumed) over a 4 d period, without and with adjustment for incomplete prey ingestion. Data are presented in the form of energy intake ($\text{kJ predator}^{-1} \text{d}^{-1}$, derived following procedures described in text and Appendix

Predator identity	Day of trial	Energy intake ($\text{kJ predator}^{-1} \text{d}^{-1}$)		
		Unadjusted	Adjusted	Percentage reduction
C	1	38.69	15.09	61.0
	2	19.08	8.34	56.3
	3	7.42	0.14	98.1
	4	12.74	0.91	92.9
	Total	77.93	24.48	68.6
D	1	14.33	5.41	62.3
	2	35.69	14.05	60.6
	3	17.97	6.43	64.2
	4	20.60	3.74	81.9
	Total	88.59	29.63	66.6

to recognition success rates less than unity. This result may have been an artifact, reflecting differences in individual predator feeding state at the time of presentation. While noting that juvenile shore crabs *Carcinus maenas* provide a strong attack stimulus to the portunid crab *Liocarcinus puber*, ap Rheinallt (1986) documented instances of contacts with specific prey sizes being ignored when mixtures of different-sized *C. maenas* were presented. Therefore, prey abundance may also influence recognition success. For crabs actively foraging in the wild, encounters would most likely occur with single decapod crustacean prey, and recognition success may be expected to approach unity (see also Evans & Mann 1977).

Pursuit success on decapod crustaceans was high (Fig. 2; Table 2), except for particularly fast moving species (*Carcinus maenas*, *Galathea squamifera*). Three pursuit techniques were recognized, more complex behavior than that used to capture epifaunal molluscs, where pursuit is simply the act of picking the prey up in the claws. The grab response was less efficient than pouncing at large relative prey size, most likely due to difficulties in capturing such prey using the pereopods only. Conversely, pouncing was less successful on small prey which were difficult to locate under the abdomen, and consequently escaped (Fig. 2B). The location of prey, relative to the predator, in these 2 pursuit techniques appeared to be determined principally by mechanoreception. Ap Rheinallt (1986) described similar pursuit behaviors for *Liocarcinus puber* preying on *C. maenas*.

Stalking behavior, a distinctive pursuit technique, has not previously been reported for a cancrivore crab. Hughes (1966) observed similar behavior for *Ocypode ceratophthalmus* feeding in the field on sentinel crabs

Macrophthalmus grandiderii. Prey were perceived by *O. ceratophthalmus* either visually, or by response to movements of prey pereopods in shallow puddles. Due to the low occurrence of stalking behavior in the present study, the specific cues used by *Cancer pagurus* could not be firmly established. Schembri (1981) described stalking behavior by the leucosid *Ebalia tuberosa* which adopted a characteristic position in which the claws were stretched forward in front of the body and held parallel to the substrate. Schembri (1981) speculated that because the chelae carry a variety of chemo- and mechano-receptors, *E. tuberosa* may be comparing sensory inputs from both claws to orientate to a stimulus source. *C. pagurus* similarly held the claws forward in front of the body during stalking behavior observed in the present study.

Cancer pagurus successfully subdued a wide size range of decapod crustacean prey, although retaliation and autotomy contributed to attack failure with some relatively large prey individuals. Proportional prey size (PROP), expressed as prey carapace length, CL/predator CW was not truly representative of galatheid prey size. At PROP = 0.3, the total estimated length (from the tips of the outstretched chelipeds to the posterior end of the flexed abdomen) of a 22 mm CL *Galathea squamifera* presented to an 87 mm CW *C. pagurus* was 71 mm.

All decapod prey species reacted to the presence of *Cancer pagurus* by avoidance behavior and increased locomotory rate. Following capture, differences in defensive capability were apparent. Adult stages of small decapod species (*Pilumnus hirtellus*, *Porcellana platycheles*), particularly males, possessed relatively larger chelipeds than juvenile *Carcinus maenas* and *C. pagurus* of equivalent CW (Fig. 1), and were more capable of resisting attack. Differences were also apparent in the frequency of use of autotomy as a defensive measure. Other more subtle behavioral differences may be involved in susceptibility. Weiss (1970) stated that lobsters *Homarus americanus* preyed less effectively on *Cancer borealis* than on *Cancer irroratus* due to the adoption of a closed defensive chela position in the former species and an open lateral merus display in the latter.

Rejection of conspecific prey by *Cancer pagurus*, observed in this study, provides behavioral verification for the presence of intraspecific avoidance responses in crustaceans, as postulated by Hancock (1974), and Chapman & Smith (1978) from the results of trapping experiments (see also Richards & Cobb 1987). These preliminary results, which indicate an influence of feeding history on propensity for intraspecific predation, were further explored in a subsequent series of experiments in which predator diet was more closely controlled (Lawton 1983).

Handling times and prey profitability

In crustacean:bivalve predatory interaction, breaking time and eating time (sensu Elner & Hughes 1978) may be readily distinguished. Equivalent handling components in crustacean:crustacean interactions (subjugation and consumption) could not be partitioned accurately. Overall handling time (T_h) was thus the only time component used to examine profitability (see also ap Rheinallt & Hughes 1985, ap Rheinallt 1986).

For one size-class of *Cancer pagurus* feeding on *Porcellana platycheles* prey, profitability increased with RPS (Fig. 2B). Additional handling episodes, observed during preliminary experiments with *P. platycheles*, suggested that this relationship may not hold for all crab sizes (unpubl.). With the additional consideration that a proportion of attacks on large decapod prey may result in the consumption of prey chelipeds only, profitability to be realized from a given-sized crustacean prey would clearly be difficult for the predator to assess during the predatory interaction.

Estimation of profitability was further complicated by the fact that prey of large RPS were only partially ingested, perhaps reflecting a limitation in predator foregut capacity and food clearance rate. On examination, the foregut stomachs of *Cancer pagurus* feeding on large *Porcellana platycheles* were found to be packed with flesh and exoskeletal material (pers. obs.). For *Carcinus maenas* (8 to 16 mm CW) presented to *Liocarcinus puber* (70 to 80 mm CW), ap Rheinallt (1986) determined mean profitabilities of 3 to 5 J s⁻¹ for individual predators at the onset of prey size-selection experiments. These values fall within the range of profitabilities recorded for *P. platycheles* prey offered singly to *C. pagurus* in the present study (Fig. 3b). However, as *C. maenas* prey were consumed by *L. puber*, handling times lengthened, and so profitabilities fell to 1 to 2 J s⁻¹ (ap Rheinallt 1986). While *L. puber* could easily break open *C. maenas* prey, it also did not separate flesh and exoskeleton prior to ingestion, and ap Rheinallt (1986) noted incomplete consumption of large *C. maenas* prey by *L. puber*.

Hill (1976) suggested that loss of hard prey structures, such as exoskeletal material, was through regurgitation of stomach content on a periodic basis. In the present study, *Cancer pagurus* was observed to regurgitate finely macerated exoskeletal material up to 30 h after consuming *Porcellana platycheles* prey (pers. obs.). Haddon & Wear (1987), as part of a larger study on feeding biology, monitored regurgitation of shell fragments by the portunid crab *Ovalipes catharus* after feeding these crabs to satiation on small (< 10 mm shell length) bivalves *Paphies subtriangulata*. At 9.5°C, the average time taken for crabs 49 to 110 mm CW to

regurgitate shell fragments was 16.7 h (range 14.5 to 21 h). Much shorter times were recorded for a second group of crabs (all 93 mm CW, $n = 14$) feeding on *P. subtriangulata* at 19.5°C (average time to regurgitation = 3.75 h; range = 3.17 to 5.33 h). Haddon & Wear (1987) contrasted their findings with the reference by Hill (1976) to finding small amounts of shell debris in *Scylla serrata* foreguts after 8.5 d. In other feeding experiments, Haddon & Wear (1987) observed no regurgitation of exoskeleton fragments when the thalassinid shrimp *Callinassa filholi* was used as prey, speculating that *O. catharus* was able to break down shrimp exoskeleton in the foregut. The relatively long time to regurgitation observed in the present study may reflect partial breakdown of ingested exoskeletal material. As regurgitation of indigestible material renders the foregut ready for another meal (Haddon & Wear 1987), this long retention time may be implicated in the progressive reduction in prey consumption on an unrestricted diet of *P. platycheles* (Table 6).

Incomplete prey ingestion has not been taken into account in some estimates of the dietary contribution of crustacean prey. Wolcott (1978) noted that 87% of the diet of *Ocypode quadrata* was comprised of the mole crab, *Emerita talpoidea* (46%), and the bivalve *Donax variabilis* (41%). Based on whole prey energy content, *E. talpoidea* was estimated to contribute 62% of the energy intake whilst *D. variabilis* represented only 22%. Hill (1979) carried out a similar analysis for the portunid crab *Scylla serrata*, showing that the crab *Ceratophthalmus algoense* contributed a disproportionate amount to the energy budget than would be expected from its frequency of occurrence in stomach contents. A similar conclusion was reached by Evans & Mann (1977) in their analysis of laboratory experiments on predation by the lobster *Homarus americanus* on *Carcinus maenas* and the sea urchin *Strongylocentrotus droebachiensis*. In each of these studies, comparisons were based on the relative calorific content, and body masses of intact prey available to the predators. While the present results substantiate that crustaceans are energetically valuable prey, they cast doubt upon the validity of ranking prey species according to whole prey energy content, and frequency of occurrence in stomach contents.

Foraging tactics

When presented with an unrestricted diet of *Porcellana platycheles*, *Cancer pagurus* recently collected from the field conducted most of their feeding activities from within shelter, exhibiting low predatory responses to prey encountered during activity periods outside shelter. These observations confirm that *C. pagurus*

can successfully ambush mobile epifaunal prey. Consideration of feeding behavior and activity pattern provide an indication of situations in which *C. pagurus* may use ambushing from its repertoire of foraging techniques. Prey were ambushed both before and after apparently tidally-synchronized activity periods. Such rhythmic activity may correspond to foraging periods in the wild when *C. pagurus* acts as a 'searcher' (sensu Hughes 1980), moving over a range of subtidal habitats, feeding on sedentary (mussels) or slow-moving prey (gastropods). Before such periods, and upon reoccupation of shelter at the end of a tidal cycle, *C. pagurus* may capture prey which are within its shelter, or which pass close enough to be ambushed. Using similar reasoning, Morales & Antezana (1983) concluded that porcellanid crabs were a more accessible prey item than gastropods or mussels to the relatively sedentary Chilean stone crab *Homalaspis plana*. Documentation of ambush predation in natural habitats is obviously required to confirm these laboratory observations: such evidence could be obtained by filming a particular shelter system, known to be frequented by *C. pagurus*, over a number of tidal cycles.

In a subsequent laboratory study (Lawton 1987), diel activity and foraging behavior of juvenile lobsters *Homarus americanus* was investigated using time-lapse video recording and behavioral time-budget analysis. Mussels *Mytilus edulis*, provided as prey, were picked up, apparently nonselectively, when lobsters ventured out from shelter, and were immediately taken back to shelter for consumption. Lawton (1987) suggested that this shelter-related foraging behavior may minimize risk to juvenile lobsters from fish predation. This consideration may apply to *Cancer pagurus* which is a common prey of local predatory fish, such as the bass *Dicentrarchus labrax* (Sant 1978).

Inclusion of shelter availability as a feature of laboratory predation experiments using *Cancer pagurus* (present study), and *Homarus americanus* (Lawton 1987), yielded novel insight into decapod crustacean foraging behavior. While it remains crucial to obtain field verification of these behavior patterns, there is considerable scope for further laboratory work in settings which recreate structural elements found in natural habitats.

APPENDIX

Profitability of *Porcellana platycheles* prey

Twenty-eight prey (5.8 to 13.4 mm CW), collected from the Treborth site, were killed by immersion in freshwater near boiling point, a procedure which induced autotomy. Weight determinations were made separately for the 2 chelipeds (ch2), and for the body and pereopods (bp) of each prey. Samples were dried at

60°C for 48 h to give dry weight (DW), and at 600°C for 2 h to obtain ash-free dry weight (AFDW). This was a biased estimate of AFDW due to endothermic reactions during ashing (Klein-Breteler 1975), thus AFDW values were weighted to derive ash-free carbonate corrected dry weight (AFCC) of various prey body parts. (1) Whole animal ($AFCC_w = AFCC_{ch2} + AFCC_{bp}$). (2) Body with pereopods ($AFCC_{bp}$). (3) One cheliped ($AFCC_{ch1} = AFCC_{ch2}/2$). AFCC values were related to prey CW to determine tissue weight available for consumption (Table 3A).

To adjust for incomplete consumption of large prey (RPS > 0.4), 5 predators (77 to 87 mm CW) were presented with whole prey, and with single chelipeds from prey of known CW. Four records of the AFCC of remains ($AFCC_r$) were obtained at the following RPS values (± 0.02): 0.4, 0.5, 0.6, 0.7, 0.8 (whole prey); 0.4, 0.5, 0.6, 0.7 (chelipeds). Mean values of the proportion of remains, P_{rem} , ($AFCC_r/AFCC_w$ or $AFCC_r/AFCC_{ch1}$) were then related to RPS to yield appropriate correction factors (Table 3B).

Energy content, E, of ingested prey body tissue was derived using a conversion factor, applicable to decapod crustaceans, of 22.195 kJ g^{-1} (AFCC basis; Cummins & Wuycheck 1971).

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