Behavioural plasticity in prey-size selectivity of the blue crab *Callinectes sapidus* feeding on bivalve prey

FIORENZA MICHELI

Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, NC 28557, USA

Summary

1. Prey-size selectivity of predators can play an important role in determining the predators' impact on their prey. In marine systems, a pattern of preference for small-sized molluscan prey is widespread among crustacean predators, even though predators are often able to consume prey over a wider size range.

2. In laboratory tests the blue crab *Callinectes sapidus* showed preference for smaller individuals of the hard clam *Mercenaria mercenaria*. This was true for crabs starved for different durations of time, prior to experiment. Hungrier crabs tended to be less selective than the less hungry ones, although not significantly so.

3. In order to determine whether such selectivity is hard-wired (i.e. engrained) or can be modified through experience, adult blue crabs were tested for preference between two different sizes of hard clams after a phase of conditioning on different combinations of live and sham (i.e. empty valves glued together and deployed in living position) clams of the two sizes.

4. In the conditioning trial, crabs consumed more sham clams of both sizes than live clams, although sham clams did not yield any energy return. The greater consumption of sham clams by blue crabs might be explained by the lower cost of crushing dead clam shells, as dead shells seemed to be more brittle than the live ones.

5. Conditioning significantly affected size selectivity in the subsequent test trial. Crabs assigned to different conditioning treatments consumed significantly different proportions of large clams in the test trial. In particular, crabs that had consumed greater proportions of large (sham) clams during the conditioning trial also ate significantly greater proportions of large (live) clams in the test trial than those which had consumed greater proportions of small (sham) clams during conditioning.

6. These results indicate that the blue crabs' preference for small-sized clams does not result from a fixed decision rule and suggest that crabs might modify their preferences through experience. Furthermore, the relative strength of shells seemed more important than profitability ratios in determining patterns of prey-size consumption.

7. An understanding of what perceptual and cognitive constraints underlie feeding preferences of 'keystone' marine predators could help in making predictions about the impact of such predators on prey communities.

Key-words: crustacean predator, hunger level, learning, prey choice.

Journal of Animal Ecology (1995) **64**, 63–74

Introduction

Most predators do not consume prey items in proportion to their abundance, but select particular sizes and/or types of prey. Such selectivity has received much attention by ecologists. First, prey-size selectivity is a factor of fundamental importance in structuring populations and communities of prey. Prey selectivity of predators has thus been investigated in order to explain observed patterns of population and community structure (Fairweather, Underwood & Moran 1984; Sih *et al.* 1985; Hughes 1988; Hines, Haddon & Wiechert 1990; Peterson 1990; Kvitek *et al.* 1992). Second, it can be hypothesized that selectivity is widespread because the consumption of certain prey types confers a selective advantage to the forager. This 'optimality' approach has resulted in models that predict prey preferences for generalized predator–prey

combinations (Stephens & Krebs 1986). The models assume that predators have been selected to maximize their fitness, which is generally assumed to be related to the net rate of energy intake (the 'currency') (MacArthur & Pianka 1966; Pyke 1984; Stephens & Krebs 1986).

The decapod crustacean–mollusc predator–prey system has proved particularly amenable for the testing of such models (reviewed by Juanes 1992). Predatory decapods often consume relatively large quantities of molluscs, allowing rapid collection of data. Molluscs also occur in discrete sizes, so that differences in prey types can be easily quantified. Finally, the costs involved in consumption (such as search times, shell breakage and prey consumption) can be easily measured as the time needed to find, crush and consume the molluscan prey, or as the energy spent in these activities.

Early studies of prey-size selection in decapod crustaceans feeding on molluscs seemed to indicate that predators select those prey sizes which maximize their net rate of energy intake (Elner & Hughes 1978; Hughes & Seed 1981). Comparison of different currencies, however, showed that energetic efficiency (benefit/cost) was a better predictor of the preferred prey size of *Cancer magister* feeding on the hard-shelled clam *Protothaca staminea* than either the net or the gross rates of energy intake [(benefit-cost)/time and benefit/time, respectively] (Juanes & Hartwick 1990). In addition, Juanes & Hartwick (1990) proposed that claw damage (i.e. both claw breakage and claw tooth wear) induced by breaking molluscan shells is the limiting cost in prey-size selection by predatory decapod crustaceans.

In a review of 41 studies examining crab and lobster predation on gastropods and bivalves, Juanes (1992) found that most predators preferred small-sized molluscs when offered a range of sizes of hard-shelled prey. The sizes selected were generally smaller than the predicted optimum, based on rates of energy intake. Juanes (1992) concluded that decapod crustacean predators preying on hard-shelled molluscs might be constrained from maximizing net energy intake rates because of the probability of incurring claw damage as the shell strength of prey increases.

The present study focuses on the flexibility of prey-size selection by a crustacean predator, particularly on the role played by experience. Predators faced with prey of different sizes might base foraging decisions on simple rules ('rules-of-thumb'; Waage 1979; Waddington & Heinrich 1979; Janetos & Cole 1981; Stephens & Krebs 1986; Bouskila & Blumstein 1992) which approximate the optimal solution. Alternatively, crabs might learn about prey quality and base their prey preferences on past experience. Selection of small prey might thus result from two distinct behavioural mechanisms: predators may be programmed to cue on smaller molluscs (rule-of-thumb: 'choose smaller prey'), or may 'try' all prey types encountered, gain information about their characteristics, such as the benefit/cost ratio, and rank prey accordingly. Little flexibility in prey selectivity following conditioning on different prey types is expected under the first scenario compared to the second one.

Predators might also be expected to be more or less flexible in their prey choice depending on their physiological state, such as hunger level or reproductive state. In particular, animals are expected to be less selective as their hunger level increases (Lucas 1983; Hughes 1988; Croy & Hughes 1990). Actual patterns of prey-size preference could exhibit greater variability, depending on the physiological state of the predator, than observed in laboratory experiments where hunger level is standardized.

Callinectes sapidus Rathbun, the blue crab, consumes a variety of gastropod and bivalve molluscs (Laughlin 1982; Hines *et al.* 1990). Laboratory choice experiments have shown that blue crabs exhibit size selectivity when feeding on hard clams (*Mercenaria mercenaria*) (Arnold 1984; Peterson 1990), mussels (*Geukensia demissa*) (Seed 1980, 1982; Hughes & Seed 1981; Bertness & Grosholz 1985; Lin 1991), and oysters (*Crassostrea virginica*) (Bisker & Castagna 1987; Eggleston 1990). Adult blue crabs feeding on a range of sizes of hard clams preferentially consumed those smaller than 2·5 cm in length, although they were able to consume larger clams (Arnold 1984; Peterson 1990). The present study tested: (i) whether hunger level modified size selectivity of blue crabs feeding on juvenile hard clams; (ii) whether crabs changed their patterns of preference for different sizes of prey following conditioning on different combinations of prey.

Methods

EFFECT OF HUNGER LEVEL ON PREY-SIZE SELECTIVITY

In order to test whether blue crabs feeding on hard clams conform to the general pattern of preference for smaller size classes observed for many other predatory crustaceans (Juanes 1992), regardless of their hunger level, a size choice experiment was performed with crabs that had not been fed for either 1 day (non-starved treatment) or 3 days (starved treatment) prior to the beginning of the experiment. Adult male blue crabs (carapace width ranging from 124 to 158 mm) were captured with commercial crab pots near Beaufort, North Carolina, USA, and held in the laboratory for 1 week prior to the experiment, during which time they were fed with pieces of fish. Experiments were performed within four indoor flow-through wooden tanks (surface area 0·550 m^2) containing approximately 5 cm of fine sand and 20 cm of filtered sea water. Flow rate through the tanks was approximately 2·5 l min^{-1}. Each tank was divided by diagonal ply-

wood partitions into four compartments. Crabs were held separately in each compartment.

Each crab was offered 30 clams ranging from 1·5 to 3·0 cm in length. Size structure of prey groups was standardized by dividing such size range into three size classes: 1·5–2·0 cm, 2·1–2·5 cm, and 2·6–3·0 cm length. Equal numbers (10) of clams belonging to the three size classes were offered to the crabs. Clams were buried below the sediment surface, so that they were completely covered. Crabs were introduced in the tanks and allowed to feed for 24 h. The experiment was checked every 3 h, and the clams that had been eaten were replaced in order to keep clam density and size-frequency distribution constant. Due to the non-independence of the different treatments (i.e. prey types) in multiple-choice feeding preference experiments, it is incorrect to use ANOVA for the analysis of results of this experiment (Hay, Renaud & Fenical 1988; Peterson & Renaud 1989). Roa (1992) recently pointed out that the use of multivariate analysis techniques can obviate the problem of non-independence of treatments, and suggested using the Hotelling's T^2-test for the analysis of feeding-preference experiments with more than two food categories involved. Differences in prey-size selectivity of crabs of the two different hunger levels were tested with a two-sample Hotelling's T^2-test performed on the total number of clams of each size class consumed by each crab.

EFFECT OF PREVIOUS EXPERIENCE (LEARNING) ON PREY-SIZE SELECTIVITY
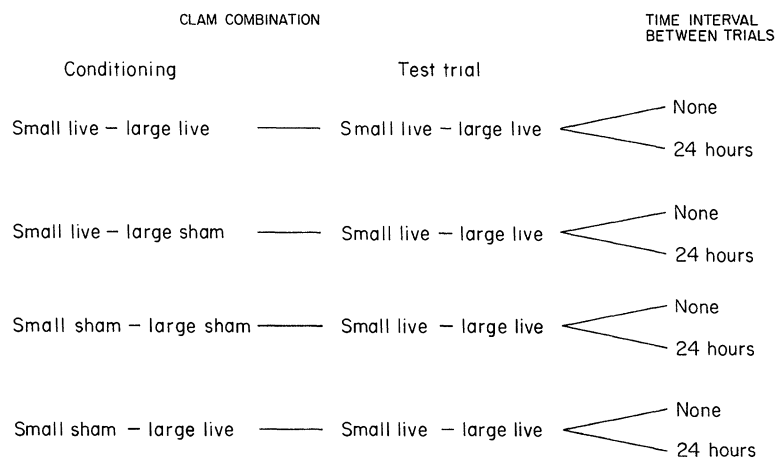
Conditioning trial

In order to determine whether experience plays a role in prey-size selectivity of blue crabs, adult blue crabs were preconditioned by exposing them to four combinations of clams of different quality (Fig. 1). Male blue crabs (carapace width ranging from 113 to 144 mm) were held in the aquaria previously described and similarly treated until the experiment was started. Crabs were then starved for 2 days and offered one of four combinations of prey types: (i) eight live small (1·5–2·0 cm length) clams and eight live large (2·5–3·0 cm length) clams; (ii) eight live small clams and eight sham large clams; (iii) eight sham small clams and eight sham large clams; and (iv) eight sham small clams and eight live large clams. Crabs had exhibited a preference for the smaller size classes in the choice experiment described above (see results) as well as in previous studies (Arnold 1984; Peterson 1990). Crabs were checked every 2 h. Each trial was terminated when at least 25% (i.e. four) of the clams had been crushed.

Sham clams were constructed by fastening together the two valves of dead clam shells with superglue. Before being glued together, the shells were filled with sand in order to mimic the weight of live clams of the same sizes. The necessary weight of sand was calculated from weight–length regressions of live (weight = 0·515 length −7·368; R^2 = 0·916; n = 50) and empty (weight = 0·198 length −2·233; R^2 = 0·768; n = 50) clam shells, and by obtaining the average weight difference between live and dead clams for clam lengths 1 mm apart.

Sham clams yielded no energetic return, thus they were unprofitable prey. If crabs did learn about prey quality, crabs that had attempted to feed on sham clams should have avoided live clams of the corresponding size in successive feeding cycles. If, on the other hand, a preference for small clams is hard-wired, conditioning on unprofitable clams should not have affected the crabs' size selectivity.

Observation of crabs feeding on the different clam types suggested that sham clams might be more easily crushed than live clams. The cost involved in preying

CLAM COMBINATION

TIME INTERVAL BETWEEN TRIALS

Conditioning   Test trial

Small live − large live ——— Small live − large live — None
                                                       — 24 hours

Small live − large sham ——— Small live − large live — None
                                                       — 24 hours

Small sham − large sham ——— Small live − large live — None
                                                       — 24 hours

Small sham − large live ——— Small live − large live — None
                                                       — 24 hours

Fig. 1. Design of the experiment testing whether experience can modify size selectivity of blue crabs preying on hard clams. Four groups of six crabs each were conditioned on four different combinations of equal numbers of small and large clams. Clams were either live, i.e. containing meat, or were sham, i.e. replicates of the live clams only containing no meat. After conditioning, all crabs were given equal numbers of small and large live clams (test trial). The test trial started right after the conditioning trial, in half of the replicates, after a 24-h interval in the other half.

66

*Flexible prey-size
selectivity of blue
crabs*

on clams of different 'types' (i.e. live or sham), therefore, might differ. In order to test whether the resistance of clam shells to breakage differed among live and sham clams, relative measurements of the strength of the clam shells were done with a Compressing Range Machine, model FT-60-D (Forney Inc., Material Testing Equipment, Wampum, PA, USA). Clams were placed between two plates of a hydraulic press, force was applied and digitally recorded at the breaking point of the shell. Shell strength was thus expressed in terms of the force (in lbs) needed to crush the clam. Shell strengths of six to nine clams of each category (small live, small sham, large live and large sham) were measured. Data were analysed with a two-way ANOVA, with clam type (live or sham) and clam size (small or large) as the fixed factors. The assumption of homogeneity of variances was tested with Cochran's test at $\alpha = 0.05$. *Post-hoc* comparison of the treatment means was carried out with the Tukey-Kramer procedure.

Test trial

In order to test the null hypothesis of a lack of an effect of experience (i.e. learning) on prey-size selectivity, all crabs were offered, after the conditioning trial, eight small live clams and eight large live clams. The second feeding trial (i.e. the test trial) started immediately after the conditioning trial in half of the replicates, and after a 24-h interval in the remaining half, yielding a total of eight treatments, each replicated three times (Fig. 1). This experimental protocol addressed two questions. (i) Is prey size selectivity of blue crabs feeding on juvenile hard clams hard-wired, or is it subjected to modification through experience? (ii) Is a possible effect of experience subjected to rapid extinction (within the first 24 h after the foraging bout)?

Crabs were checked every 2 h during the test trial, and the experiment was terminated when at least four clams had been eaten. Crabs which had not eaten within 12 h were eliminated from the experiment. Due to space limitations, it was not possible to run all the replicates at the same time. The experiment was therefore carried out in separate trials. All eight treatments were set up in each trial, with one crab randomly assigned to each treatment. Differences among trials were minimized by treating the animals identically, prior to the experiment (see previous section), and by starting the experiments at the same time of the day (approximately 09.00 h). Water temperature, measured at the beginning of each replicate trial, dropped from $20.6\,^{\circ}$C, during the first trial, to $15\,^{\circ}$C (average $= 18.36\,^{\circ}$C, SE $= 0.51$, $n = 24$) during the last trial. There was no significant difference, however, in water temperature among the eight treatments (ANOVA: $F_{7,16} = 0.295$, $P = 0.946$).

A two-way ANOVA, with prey combination during conditioning (four levels) and time interval between conditioning and test feeding trials (two levels) as the

fixed factors, was performed on the proportion of large clams consumed by each crab. Angular transformation of proportions was applied prior analysis. Treatment means were compared, after ANOVA, with the Student-Neumann-Keul's procedure.

MECHANISM OF PREY SELECTION

A third experiment was conducted to determine whether crabs were able to distinguish between live and sham clams, before crushing their shells, by using chemical cues. Three types of clams of similar sizes (1·5–2·5 cm length) were offered to individual male blue crabs (CW 110–140 mm): live clams, sham clams (as described above), and bleached sham clams [prepared, as described above, from clam shells previously washed in diluted CLOROX® bleach (The CLOROX Co., Oakland, CA, USA) for 30 min, then thoroughly rinsed in running tap water]. The last clam type was added in order to test whether decomposing meat particles possibly associated with the sham clam shells might attract crabs to this type of prey. It is possible that immersion in CLOROX® bleach might have modified the mechanical characteristics of the clam shells. The present experiment, however, was designed to test whether crabs detected sham and live clams with similar frequencies rather than whether they crushed similar proportions of the different clam types. Characteristics of the shells other than odour, therefore, are not likely to affect results.

Trials were carried out in one of the tanks described above, after partitions had been removed, with filtered seawater flowing at approximately 0.7 1 min^{-1}. Five clams of each type were presented to each crab. Clams were buried under the sand surface at randomly assigned positions in a 50×50 cm grid of monofilament lines, so that clam types were randomly interspersed but individual clams were evenly spaced (10 cm apart from each other). The grid was removed before the crab was introduced into the aquarium. Crabs were observed by standing, as motionless as possible, approximately 1 m away from the tank. Crabs that had not started feeding within 1 h from the beginning of the experiment were excluded from the experiment. Clams had been marked with one dot of non-toxic paint (Mark-Tex Corporation, Englewood, NJ, USA) on each valve. Different paint colours had been used in order to allow identification of the different clam types. Each trial was ended after 2 h, during which time the number and type of clams found and crushed by the crab were recorded. Trials were carried out during late afternoons. Illumination was from a large window situated close to the tank. Water temperatures ranged from $24.5\,^{\circ}$C to $30\,^{\circ}$C (average $= 27.6\,^{\circ}$C, SE $= 0.53$, $n = 9$).

Data were analysed with the one-sample Hotelling's T^2-test. T^2 was calculated for the number of clams of each type found by each crab during trials, and was subsequently converted into a F-statistic, with p (num-

ber of prey types) = 3, and *n* (number of replicates) = 9, thus with $p = 3$ and $n - p = 6$ degrees of freedom (Roa 1992).

Results

EFFECT OF HUNGER LEVEL ON PREY-SIZE SELECTIVITY

There was no overall significant effect of hunger level on size selectivity by crabs ($T^2 = 5.027$, $F_{3,12} = 2.869$, $P = 0.081$). The low *P*-value, however, suggests that a possible effect of hunger level on size selectivity cannot be ruled out, and might have not been detected due to insufficient power of the test. Inspection of the data suggests that the less hungry crabs might have been more selective than the hungrier ones. The number of clams consumed in each size class by crabs starved for 1 day averaged, in fact, 65·1%, 27·9% and 7·0% of the total number consumed, for the small, medium and large clams, respectively. By contrast, for crabs starved for 3 days, 50·0%, 34·7% and 15·3% of the clams consumed were small, medium and large, respectively. Hungrier crabs had thus consumed larger proportions of clams in the least preferred (i.e. larger) size class.

A one-sample Hotelling's T^2 performed on data pooled from both treatments (starved and non-starved) indicated that clam consumption differed significantly among clam size classes ($T^2 = 38.976$, $F_{3,13} = 11.255$, $P = 0.0006$). The number of hard clams consumed by the crabs decreased with clam size (Fig. 2), in agreement with the results of previous studies (Arnold 1984; Peterson 1990). The pattern of decreasing predation mortality accompanying increasing clam size was observed in both treatments (starved or non-starved crabs) (Fig. 2). Hungrier crabs consumed overall more clams than the less hungry ones (*t*-test: $t = 3.019$, d.f. = 14, $P = 0.009$).

EFFECT OF PREVIOUS EXPERIENCE (LEARNING) ON PREY-SIZE SELECTIVITY

Conditioning trial

During the conditioning trial, crabs offered sham and live clams belonging to two different size classes consumed significantly different proportions of large clams (one-way ANOVA: $F_{3,20} = 5.241$, $P = 0.008$, $n = 6$) (Fig. 3). Crabs consumed the greatest proportion (69·1%) of large items when these were sham clams presented with small live clams. Crabs consumed similar amounts of large and small sham clams when these were presented together (44·8% large clams). Significantly lower proportions of large clams were consumed in the remaining two treatments (both large and small clams live: 27·3%; small sham and large live clams: 17·0%) compared to the treatment where small live and large sham clams were given. Crabs crushed more sham clams of either sizes than live ones, when these were presented together (i.e. in treatments 2 and 4), even though the former did not yield any energetic gain.

The force required to break the large clams was significantly greater than that required to break the small clams for the live but not for the sham clams (clam type: $F_{1,25} = 1.724$, $P = 0.201$; clam size: $F_{1,25} = 13.105$, $P = 0.001$; interaction: $F_{1,25} = 5.541$, $P = 0.027$) (Fig. 4). The prey types offered during the conditioning trial differed in the energy yielded, as only the live clams contained meat, but also in the resistance they offered to consumption by crabs. Crabs offered a choice between small live and large live clams (treatment 1), and between small sham and large live clams (treatment 4), were presented with prey of significantly different shell strength, since large live clams are stronger than both small live and small sham clams. In contrast, crabs offered a choice between small live and large sham clams (treatment 2), and between small sham and large sham clams
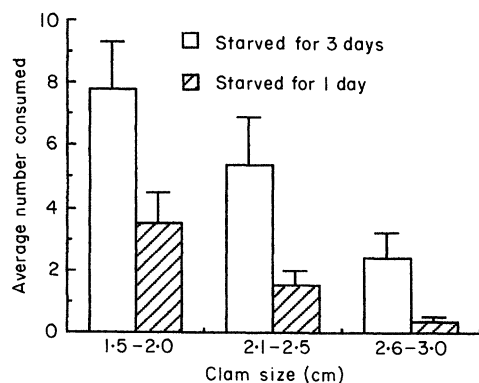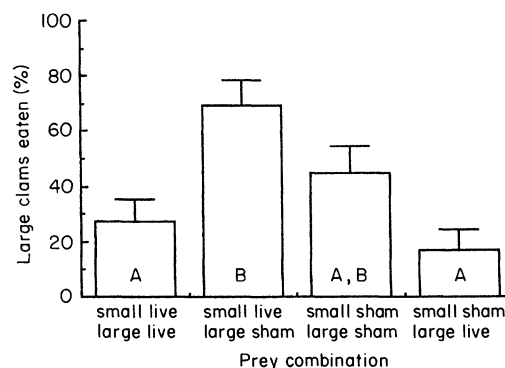
Fig. 2. Size selectivity of blue crabs of different hunger levels (starved for 1 or 3 days) feeding upon three size classes of hard clams. Here and in all other figures bars represent averages with standard errors.
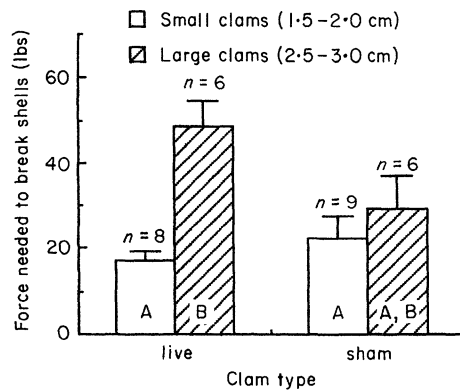
Fig. 3. Percentages of large (2·5–3·0 cm length) clams consumed by blue crabs during the conditioning trial. Four different prey combinations were offered: small live and large live clams, small live and large sham clams, small sham and large sham clams, small sham and large live clams. Bars marked with the same letter are not significantly different at $\alpha = 0.05$ (SNK).

Fig. 4. Comparison of the relative shell strength (measured as the force, in lbs, needed to crush clams) of the four prey types (live small, sham small, live large and sham large clams) used in the conditioning trial. Bars marked with the same letter are not significantly different at $\alpha = 0.05$ (Tukey-Kramer).

(treatment 3), were presented with prey of similar shell strengths.

Test trial

Crabs that had fed during conditioning on different prey combinations, consumed significantly different proportions of large clams in the test trial, where all crabs were given a choice between small and large live clams (two-way ANOVA, effect of prey combination during conditioning: $F_{3,16} = 3.56$, $P = 0.038$) (Fig. 5). The effect of experience on size selectivity did not significantly diminish or change within the 24-h time interval (two-way ANOVA; effect of time interval between trials: $F_{1,16} = 1.15$, $P = 0.30$; interaction: $F_{3,16} = 0.15$, $P = 0.928$).

Differences in size selectivity of blue crabs during the test trial followed the trends observed in the conditioning trial (Figs 3 and 5). Crabs that had fed dur-
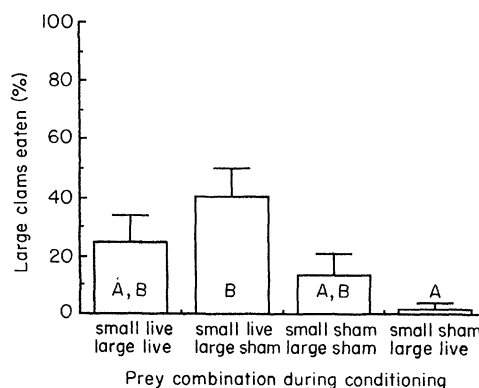

Fig. 5. Percentages of large (2·5–3·0 cm length) clams consumed by blue crabs during the test trial. Prey combinations during conditioning as in Fig. 2. Since there was no significant effect of the time interval between conditioning and test trials (i.e. 0 or 24 h) on the proportions of large clams eaten during the test trial, data for the different time intervals have been combined. Bars marked with the same letter are not significantly different at $\alpha = 0.05$ (SNK).

ing conditioning on small live clams and large sham clams (and had consumed more of the latter; treatment 2), consumed significantly more large clams in the test trial than crabs that had fed on small sham clams and large live clams during conditioning (and had consumed more of the former; treatment 4). The other two treatments, where crabs had been conditioned on either all live or all sham clams, were intermediate between treatments 2 and 4 in the test trial and not significantly different from either of them.

There were no significant differences among the total number of clams crushed by crabs assigned to different treatments either during the conditioning (one-way ANOVA, treatment effect: $F_{3,20} = 0.433$, $P = 0.732$) or the test trial (two-way ANOVA; treatment effect: $F_{3,16} = 0.954$, $P = 0.438$; time interval effect: $F_{1,16} = 0.081$, $P = 0.779$; interaction: $F_{3,16} = 0.176$, $P = 0.911$). Crabs that crushed large numbers of sham clams during conditioning did not seem to try to increase their food intake by consuming more live clams in either trial.

MECHANISM OF PREY SELECTION

There was no significant difference in the numbers of live, sham and bleached sham clams of similar sizes found by blue crabs during laboratory feeding trials (Hotelling's $T^2 = 6.156$, $F_{3,6} = 1.539$, $P = 0.30$) (Fig. 6). Nearly all of the clams found and dug out by the crabs were immediately crushed and consumed if live, or crushed and discarded if sham. Only in one case did a crab drop a live clam after unsuccessfully attempting to crush it for a few minutes.
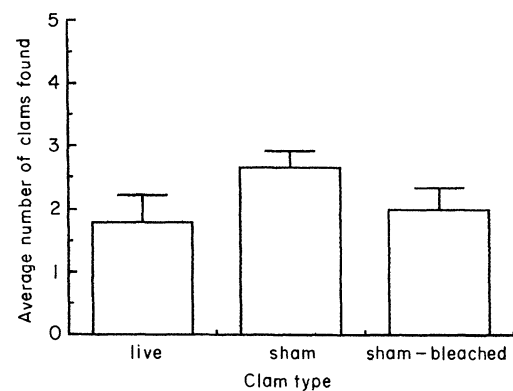
Fig. 6. Average numbers of live, sham and bleached sham clams of similar sizes (1·5–2·5 cm length) found and dug out by nine blue crabs.

Crabs probed the sediments with their pereiopods while walking. Crabs occasionally stopped, inserted their chela in the sand, extracted a clam, and immediately tried to crush it. Crabs would frequently pick up fragments of clam shells of all three types, previously crushed, and put them down again after inspecting them for few seconds with their maxillipeds.

Chemical cues associated with clams did not seem to play an important role in directing short-range

foraging movements and prey selection of blue crabs. On the contrary, these results indicate that crabs encountered the different prey types with similar frequency.

Discussion

The experiments reported here indicate that blue crabs exhibit some degree of flexibility in their prey-size selectivity. Crabs feeding on two different sizes of a bivalve prey (i.e. hard clams $<2\cdot0$ or $>2\cdot5$ cm length) in fact modified their selectivity after one feeding bout on one of four possible combinations of live or sham (i.e. containing no meat) clams of the two sizes. Further, size selectivity might also depend on the physiological state of the crabs (here manipulated as hunger levels).

Previous studies have found that prey-size selectivity changes with the predator hunger level (Werner & Hall 1974; Hughes 1988; Croy & Hughes 1990). In addition, theoretical models predict that hungrier animals should be less selective (Lucas 1983). In this case there was no significant effect of hunger level on size selectivity. The low P value, however, suggests that such an effect might have been present and that the power of the test might have been too low to detect it. The possible effect of hunger level is in the direction expected based on previous theoretical and experimental studies (citations above): selectivity tended to decrease with increasing hunger level.

Both starved and fed blue crabs offered different sizes of juvenile hard clams consumed greater proportions of the smaller clams, thus conforming to the general pattern of preference for smaller size classes of bivalve prey observed in this species (Hughes & Seed 1981; Arnold 1984; Bisker & Castagna 1987; Peterson 1990) and in many other decapod crustacean species (Juanes 1992). Prey profitability is usually a function of prey size (Davies 1977; Schoener 1971). In the case of hard-shelled molluscan prey, profitability generally declines with size (Elner & Hughes 1978; Hughes 1979; Elner 1980; Jubb, Hughes & ap Rheinallt 1983; Lawton & Hughes 1985; ap Rheinalt 1986; Davidson 1986), as the cost of breaking shells increases faster than the meat reward. Prey size could thus be used by predators as an estimator of prey profitability. Species that have limited ability to learn and remember may rely heavily on inflexible decision rules (Dukas & Real 1991), such as 'choose smaller prey' in the case of crabs preying on size-structured bivalve populations. Compelling evidence that some animals exhibit fixed, stereotyped behaviours in acquiring resources has been provided for bumble bees (Waddington & Heinrich 1979) and for ocypodid crabs (Zimmer-Faust 1990).

This experiment provides evidence in support of the alternative hypothesis, that blue crabs exhibit a flexible behaviour when feeding on hard clams of different sizes. Blue crabs, in fact, consumed sig-

nificantly different proportions of small and large clams following conditioning on combinations of small and large clams of different profitabilities. Behavioural plasticity in food preferences, and in other characteristics of a species repertoire, might represent an adaptation to life in unpredictably variable environments (Hazlett 1988). Capability to gain information about environmental variability would guarantee a rapid response to changes in resource quality and distribution. As a result of behavioural flexibility, crabs (Wicksten 1977; Blackstone & Joslyn 1984), and possibly other generalist predators, can rapidly take advantage of new resource types.

The biogeographic range of *C. sapidus* covers a vast portion of the North and central Atlantic coast of America, from Nova Scotia to the Caribbean (Williams 1984). Blue crabs also exhibit a wide tolerance for salinity variations, being found along estuaries, from nearly fresh to oceanic waters. These predators are thus faced, during their lifetime, with a vast array of potential prey and possible combinations of prey. The range of sensory stimuli in an animal's environment could select for increased cognitive abilities, so that one might expect generalist predators, such as blue crabs, to show a greater ability to learn about prey quality than predators specialized on one or few prey types (Papaj & Prokopy 1989; Dukas & Real 1991, 1993).

During the conditioning trial, crabs offered live and sham clams of two distinct size classes in all four possible combinations, consumed significantly different proportions of large clams, with crabs assigned to one of the treatments (treatment 2) consuming even more large (sham) than small (live) clams. In this treatment, crabs consumed more large than small clams despite the fact that the former were sham clams, yielding no energetic return. Similarly, sham small clams were preferred to large live, more profitable clams. Live clams are more profitable than sham clams regardless of what currency is used to quantify profitability, since sham clams yield no energetic gain, hence they have zero gross rates of energy intake (benefit/handling time) and energetic efficiencies (benefit/cost), and negative net rates of energy intake [(benefit/cost)/handling time].

Crabs are not likely to encounter 'sham' prey (i.e. shell valves containing sediments) often in their natural environment, and thus to have been selected to solve this foraging problem. The present experiment, however, simulates the situation of a forager encountering novel prey of different qualities, and tests the hypothesis that invertebrate predators faced with a vast array of potential prey are equipped with simple decision rules determining their prey choice.

The incapability of blue crabs to distinguish between sham and live prey may have important consequences in regulating predator–prey interactions of crabs and bivalves. Shell substrate, for example, is known to protect infaunal bivalves from their pred-

ators (Arnold 1984; Gibbons & Castagna 1985; Sponaugle & Lawton 1990). Experimental addition of sham clams to field plots containing live bivalves also protected the live clams from predation (Peterson & Black 1993). Both natural shell debris and sham clams are thought to disrupt foraging of predators by providing a physical obstacle. Results of this study suggest an alternative mechanism by which the presence of dead shell might reduce predation intensity on live prey. Dead shell may be a counter target for predators' activity, acting as alternative 'prey' rather than as physical structure. Laboratory observations seem to support this hypothesis: two species of portunid crabs (*C. sapidus* and *Ovalipes ocellatus*) feeding on juvenile hard clams on a substrate of sand and shell debris frequently picked up and attempted to crush dead shells and even gravel (Sponaugle & Lawton 1990).

Preference for sham clams could not be attributed to their greater detectability by blue crabs. Encounter rates, in this experimental setting, did not differ for live, sham and bleached clams. Preference seems best explained by a lesser resistance of dead clam shells to breakage, possibly due to the decomposition of the organic matrix of shells causing shells to become more brittle.

Measurements of the shell strength of live and sham clam shells indicated that the shells of large sham clams had similar resistance to breakage than small clams of both types. Large live clams, on the contrary, were more resistant than both live and sham small clams (Fig. 4). Crabs consumed larger proportions of the weaker prey (i.e. the small clams) when presented with prey of significantly different shell strengths (treatments 1 and 4). When offered prey of similar shell strengths, crabs consumed similar proportions of the two prey sizes (treatment 3), or even more large clams (treatment 2), indicating that clam large size *per se* does not deter crab predation.

The results of this experiment suggest that crabs may use shell strength as the only cue of prey quality, possibly learning which prey have more easily crushed shells. Easily crushed sham clams were preferred over live ones even though they contained no flesh. Crabs, therefore, did not seem to be able to measure the amount of energy they obtained from their prey and to select their prey based on profitability ratios. As Juanes & Hartwick (1990) and Juanes (1992) suggested, crabs might be constrained in their diet choice by the cost associated with claw wear rather than by a limited time available for foraging, as assumed in traditional optimal foraging models (Stephens & Krebs 1986). These authors proposed claw damage and wear as a long-term limiting cost to be introduced in more realistic dynamic foraging models (Houston *et al.* 1988; Mangel & Clark 1988).

Another constraint possibly limiting the range of prey sizes consumed by crustacean predators might be the relative ease with which prey are handled. Prey

that are too small might slip from the crab claws, thus increasing handling times. These two constraints (the probability of incurring claw damage and the ease with which prey can be handled), might explain the preference for intermediate-sized prey observed in the crabs *Carcinus maenas* (Elner & Hughes 1978; Jubb *et al.* 1983), *Liocarcinus puber* (ap Rheinallt 1986) and *Ovalipes catharus* (Davidson 1986) feeding on *Mytilus edulis*.

Crabs that succeed in maximizing their 'claw life', even at the expense of net energetic intake, might be expected to have greater fitness than crabs that maximize rates of energetic intake. Under this scenario, it should be possible to predict prey preferences of crabs, and possibly of other predators that rely on degradable parts such as claws, teeth and beaks to consume their prey, by ranking prey solely according to their resistance to breakage. In the case that these predators measure prey resistance to consumption rather than their profitability in terms of energy, such predictions might be accurate even if not based on profitability ratios.

Evidence that animals can track rewards associated with food items has been provided for amphibians (Jaeger & Rubin 1982), birds (Krebs *et al.* 1977; Krebs, Healy & Shettleworth 1990; Schuler 1990) and bumble bees (Real 1990, 1991; Dukas & Real 1991). The fact that the capability of measuring energetic gain is common to such taxonomically distant animal groups might indicate that this capability is not necessarily related to the complexity of an animal's nervous system. Crabs might cue on shell strengths, rather than on energy content of prey, not because their nervous system is too simple to measure prey profitability, but because of the overwhelming importance of the mechanical properties of prey on the life-long fitness of predators.

Several crab species have been reported to attack any prey encountered, regardless of size or species, and consume only those which yielded after a certain time (Vermeij 1976; Lawton & Hughes 1985; Brown & Haight 1992). On the other hand, an active choice of more vulnerable prey seems to play an important role in other crab species (for example in *Carcinus maenas*; Elner & Hughes 1978; Johannesson 1986; and *Ovalipes catharus*; Davidson 1986). Hughes (1989) proposed the hypothesis that tropical crabs might exhibit a greater capability to assess the vulnerability of molluscan prey than temperate crabs because of the longer co-evolution with their prey. As an alternative hypothesis, it is suggested here that tropical predatory crabs might exhibit higher cognitive abilities because they are exposed to a greater diversity of potential prey compared to what is found at higher latitudes. Higher cognitive abilities might be expected in consumers which encounter and handle a wider variety of prey types (Dukas & Real 1993).

Furthermore, there is strong morphological evidence of co-evolution between gastropod shell thick-

ness and other morphological prey defences (for example operculum shape and shell ornamentation) and specializations of claws of mollusc-eating crabs. Such an arms-race may have progressed further in the Indo-West Pacific than in other tropical or temperate regions, presumably because of the greater age of the former ocean basin (Vermeij 1976, 1978, 1987). The relative ease with which crabs crush shells of their molluscan prey seems to play a most important role in shaping interactions within this predator–prey system on both ecological and evolutionary scales.

Crabs exposed to different prey combinations during the conditioning trial exhibited significant differences in size selectivity in the test trial, where all crabs were offered identical prey combinations. This result indicates that size selectivity of blue crabs is not hardwired but, on the contrary, is subjected to modification through experience. Learning has already been observed among crustaceans. Grapsid crabs can learn the location of their burrows (Abele, Campanella & Salmon 1986). Stomatopods learn and remember characteristics of home cavities (Reaka 1980), and to open snail prey more efficiently (Caldwell & Childress 1990). Hermit crabs can learn and remember characteristics of gastropod shells (Hazlett 1992).

A theoretical model (McNamara & Houston 1987) predicts that the weight that animals give to past experience, when making foraging decisions, should decline with increasing variability of environmental conditions. Based on such a prediction, it would be reasonable to expect that generalistic and highly mobile predators, such as blue crabs (Hines *et al.* 1990; Hines & Wolcott 1990), would base their prey choice only on most recent foraging experience. This prediction seems to be supported by the fact that crabs modified their size selectivity in the test trial after sampling only a few clams (during the conditioning trial), so that modification of size selectivity occurred after only a few encounters with new prey types. Modification of size selectivity, however, seemed subject to slow extinction. An effect of conditioning was in fact still significant 24 h after the conditioning trial.

During the time interval between the conditioning and test trials, crabs were not allowed to feed on other prey items. Foraging on different prey types has been shown to interfere with the capability of retaining information gained during previous foraging in other invertebrates (Menzel 1979; Stanton 1983; Lewis 1986). Blue crabs' selectivity may not be affected by previous experience for over 24 h in the field, where animals can come in contact with a variety of different prey types. This hypothesis remains to be tested.

Modification of prey size selectivity following conditioning on different prey combinations might have occurred because of at least three distinct mechanisms: (i) crabs might become more efficient at handling a particular clam size with experience; (ii) they might develop a 'search image' (Timbergen 1960) for that clam size and become more successful at finding it; or (iii) they might learn to recognize the preferred prey upon encounter, thus being more persistent on one size of clams than on the other.

Crabs that consumed a greater proportion of large clams during the conditioning trial could have learned to handle large clams more efficiently and, therefore, could prey more effectively on this size class in successive feeding trials. Crabs that consumed the greatest proportion of large clams during conditioning (treatment 2), also consumed significantly more large clams during the test trial compared to crabs that ate the fewest large clams during conditioning (treatment 4). Since crabs frequently use different techniques to crush bivalves of increasing sizes (Juanes 1992, and references therein), they may perfect their handling skills through practice. Butterflies, for instance, have been shown to learn nectar extraction techniques on particular flower species and to prefer that species on successive foraging bouts (Lewis 1986). A limited capability for learning and recalling the different extraction techniques needed with different flower species was proposed by Darwin (1876) as a possible explanation for flower constancy in insects. Similarly, other invertebrates, such as predatory gastropods (West 1988) and stomatopod crustaceans (Caldwell & Childress 1990), can increase their predatory efficiency through experience.

Alternatively, the effect of conditioning on size selectivity during the test trial might be explained by the development of a search image in the crabs that consumed greater proportions of large clams during conditioning. The development of search images, traditionally attributed to vertebrates, has also been shown for invertebrates (Gould 1985). Under this scenario, crabs that recognize large clams as the preferred prey might concentrate on searching for large clams in successive feeding bouts. The foraging technique of blue crabs feeding on infaunal clams (i.e. probing the sediments with their walking legs until contact with a clam), however, does not seem to support this hypothesis. From the observations conducted in the last experiment reported here (see 'Mechanism of prey selection') and from casual observations of foraging crabs, crabs seemed to dig out and attempt to crush any clam encountered.

As a third hypothesis, the mechanism of selection might be that of adjusting giving-up times depending on prey quality. Crabs may detect different prey types with similar frequencies, but subsequently persist in attempting to crush prey recognized as the preferred ones, while having shorter giving-up times when handling less preferred prey. Direct measurements of handling times, search rates, and sequences of encounter with prey and of acceptance and rejection of prey encountered, are needed in order to discriminate among these alternative mechanisms.

In conclusion, this work indicates that the pattern of preference for small-sized molluscs widely observed

72

*Flexible prey-size
selectivity of blue
crabs*

among predatory crustaceans (Juanes 1992) does not result from a fixed decision rule by which prey are ranked based on their relative sizes (Stephens & Krebs 1986), but rather that crabs might learn through experience with different prey sizes and possibly species to recognize preferred prey. Furthermore, preference rankings seemed to be established based on relative strength of shells rather than on profitability ratios.

Perceptual, learning and memory constraints play a fundamental role in shaping the foraging behavior of predators, thus in determining their impact on prey communities (McNamara & Houston 1985; Abrahams 1986; Mangel & Clark 1988; Bernstein, Kalcenik & Krebs 1988, 1991; Kalcenik, Brunner & Gibbon 1990; Krebs *et al.* 1990). In terrestrial systems, for example, the study of learning and memory abilities of butterflies and bumble bees has improved our understanding of plant–insect interactions (Real, Ott & Silverfine 1982; Stanton 1983; Lewis 1986; Papaj & Prokopy 1989; Real 1990, 1991). Similarly, an understanding of what perceptual and cognitive constraints underlie feeding preferences of marine predators could help in making predictions about the role of predation in structuring marine communities.

Acknowledgements

References

Abele, L.G., Campanella, P.J. & Salmon, M. (1986) Natural history and social organization of the semiterrestrial grapsid crab *Pachygrapsus transversus*. *Journal of Experimental Marine Biology and Ecology*, **104**, 153–170.

Abrahams, M.V. (1986) Patch choice under perceptual constraints: a cause for departures from an ideal free distribution. *Behavioural Ecology and Sociobiology*, **19**, 409–415.

Arnold, W.S. (1984) The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* Rathbun, on the hard clam, *Mercenaria mercenaria* (Linne'). *Journal of Experimental Marine Biology and Ecology*, **80**, 207–219.

Bernstein, C., Kalcenik, A. & Krebs, J.R. (1988) Individual decisions and the distribution of predators in a patchy environment. *Journal of Animal Ecology*, **57**, 1007–1026.

Bernstein, C., Kalcenik, A. & Krebs, J.R. (1991) Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. *Journal of Animal Ecology*, **60**, 205–225.

Bertness, M.D. & Grosholz, E. (1985) Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distribution. *Oecologia*, **67**, 192–204.

Bisker, R. & Castagna, M. (1987) Predation on single spat oysters *Crassostrea virginica* (Gmelin) by blue crabs *Callinectes sapidus* Rathbun and mud crabs *Panopeus herbstii* Milne-Edwards. *Journal of Shellfish Research*, **6**, 37–40.

Blackstone, N.W. & Joslyn, A.R. (1984) Utilization and preference for the introduced gastropod *Littorina littorea* (L.) by the hermit crab *Pagurus longicarpus* (Say) at Guilford, Connecticut. *Journal of Experimental Marine Biology and Ecology*, **80**, 1–9.

Bouskila, A. & Blumstein, D.T. (1992) Rules of thumb for predation hazard assessment: predictions from a dynamic model. *American Naturalist*, **139**, 161–176.

Brown, K.M. & Haight, E.S. (1992) The foraging ecology of the Gulf of Mexico stone crab *Menippe adina* (Williams et Felder). *Journal of Experimental Marine Biology and Ecology*, **160**, 67–80.

Caldwell, R.L. & Childress, M.J. (1990) Prey selection and processing in a stomatopod crustacean. *Behavioural Mechanisms of Food Selection* (ed. R.N. Hughes), Vol. G 20, NATO ASI Series, pp. 143–164. Springer-Verlag, Berlin-Heidelberg, Germany.

Croy, M.I. & Hughes, R.N. (1990) The combined effects of learning and hunger in the feeding behaviour of the fifteen-spined stickleback (*Spinachia spinachia*). *Behavioural Mechanisms of Food Selection* (ed. R.N. Hughes), Vol. G 20, NATO ASI Series, pp. 215–234. Springer-Verlag, Berlin-Heidelberg, Germany.

Darwin, C. (1876) *The Effects of Cross- and Self-Fertilization in the Animal Kingdom.* Murray, London.

Davidson, R.J. (1986) Mussel selection by the paddle crab *Ovalipes catharus* (White): evidence of flexible foraging behavior. *Journal of Experimental Marine Biology and Ecology*, **102**, 281–299.

Davies, N.B. (1977) Prey selection and the search strategy of the spotted flycatcher (*Muscicapa striata*): a field study on optimal foraging. *Animal Behaviour*, **25**, 1016–1033.

Dukas, R. & Real, L.A. (1991) Learning foraging tasks by bees: a comparison between social and solitary species. *Animal Behaviour*, **42**, 269–276.

Dukas, R. & Real, L.A. (1993) Cognition in bees: from stimulus reception to behavioral change. *Insect Learning: Ecological and Evolutionary Perspectives* (eds D.R. Papaj & A.C. Lewis), pp. 343–373. Chapman & Hall, London.

Eggleston, D.B. (1990) Foraging behavior of the blue crab, *Callinectes sapidus*, on juvenile oysters, *Crassostrea virginica*: the effects of prey density and prey size. *Bulletin of Marine Sciences*, **46**, 62–82.

Elner, R.W. (1980) The influence of temperature, sex, and chela size in the foraging strategy of the shore crab, *Carcinus maenas* (L.). *Marine Behaviour and Physiology*, **7**, 15–24.

Elner, R.W. & Hughes, R.N. (1978) Energy maximization in the diet of the shore crab, *Carcinus maenas*. *Journal of Animal Ecology*, **47**, 103–116.

Fairweather, P.G., Underwood, A.J. & Moran, M.J. (1984) Preliminary investigations of predation by the whelk *Morula marginalba*. *Marine Ecology Progress Series*, **17**, 143–156.

Gibbons, M.C. & Castagna, M. (1985) Biological control of predation by crabs in bottom cultures of hard clams using a combination of crushed stone aggregate, toadfish and cages. *Aquaculture*, **47**, 101–104.

Gould, J.L. (1985) How bees remember flower shapes. *Science*, **227**, 1492–1494.

Hay, M.E., Renaud, P.E. & Fenical, W. (1988) Large herbivore versus small sedentary herbivores and their resistance to seaweed chemical defenses. *Oecologia*, **75**, 246–252.

Hazlett, B.A. (1988) Behavioural plasticity as an adaptation to a variable environment. *Behavioural Adapatations to the Intertidal Life* (eds G. Chelazzi & M. Vannini), Vol. 151, NATO ASI Series A, pp. 317–332. Plenum Press, New York.

Hazlett, B.A. (1992) The effect of past experience on the size of shells selected by hermit crabs. *Animal Behaviour*, **44**, 203–205.

Hines, A.H., Haddon, A.M. & Wiechert, L.A. (1990) Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake bay. *Marine Ecology Progress Series*, **67**, 105–206.

Hines, A.H. & Wolcott, T.G. (1990) Blue crab movement and feeding measured by ultrasonic telemetry. *Bulletin of Marine Science*, **46**, 246.

Houston, A., Clark, C., McNamara, J. & Mangel, M. (1988) Dynamic models in behavioural and evolutionary ecology. *Nature (London)*, **332**, 29–34.

Hughes, R.N. (1979) Optimal diets under the energy maximization premise: the effects of recognition time and learning. *American Naturalist*, **113**, 209–221.

Hughes, R.N. (1988) Optimal foraging in the intertidal environment: evidence and constraints. *Behavioural Adaptations to the Intertidal Life* (eds G. Chelazzi & M. Vannini), Vol. 151, NATO ASI Series A, pp. 265–282. Plenum Press, New York.

Hughes, R.N. (1989) Foraging behaviour of a tropical crab: *Ozius verreauxii. Proceedings of the Royal Society London B*, **237**, 201–212.

Hughes, R.N. & Seed, R. (1981) Size selection of mussels by the blue crab *Callinectes sapidus*: energy maximizer or time minimizer? *Marine Ecology Progress Series*, **6**, 83–89.

Jaeger, R.G. & Rubin, A.M. (1982) Foraging tactics of a terrestrial salamander: judging prey profitability. *Journal of Animal Ecology*, **51**, 167–176.

Janetos, A.C. & Cole, B.J. (1981) Imperfectly optimal animals. *Behavioural Ecology and Sociobiology*, **9**, 203–209.

Johannesson, B. (1986) Shell morphology of *Littorina saxatilis* Olivi: the relative importance of physical factors and predation. *Journal of Experimental Marine Biology and Ecology*, **102**, 183–195.

Juanes, F. (1992) Why do decapod crustaceans prefer small-sized molluscan prey? *Marine Ecology Progress Series*, **87**, 239–249.

Juanes, F. & Hartwick, E.B. (1990) Prey size selection in Dungeness crabs: the effect of claw damage. *Ecology*, **71**, 744–758.

Jubb, C.A., Hughes, R.N. & ap Rheinallt, T. (1983) Behavioral mechanisms of size-selection by crabs, *Carcinus maenas* (L.) feeding on mussels, *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology*, **66**, 81–87.

Kalcenik, A., Brunner, D. & Gibbon, J. (1990) Timing mechanisms in optimal foraging: some applications of scalar expectancy theory. *Behavioural Mechanisms of Food Selection* (ed. R.N. Hughes), Vol. G 20, NATO ASI Series, pp. 61–82. Springer-Verlag, Berlin, Germany.

Krebs, J.R., Erichson, J.T., Webber, M.I. & Charnov, E.L. (1977) Optimal prey selection in the great tit (*Parus major*). *Animal Behaviour*, **25**, 30–38.

Krebs, J.R., Healy, S.D. & Shettleworth, S.J. (1990) Spatial memory of Paridae: a comparison of a storing and a non-storing species, the coal tit, *Parus ater*, and the great tit, *P. major. Animal Behaviour*, **39**, 1127–1137.

Kvitek, R.G., Oliver, J.S., DeGange, A.R. & Anderson, B.S. (1992) Changes in Alaskan soft-bottom prey communities along a gradient in sea otter predation. *Ecology*, **73**, 413–428.

Laughlin, R.A. (1982) Feeding habits of the blue crab, *Callinectes sapidus* Rathbun, in the Appalachicola Estuary, Florida. *Bulletin of Marine Science*, **32**, 807–822.

Lawton, P. & Hughes, R.N. (1985) Foraging behavior of the crab *Cancer pagurus* feeding on the gastropods *Nucella lapillus* and *Littorina littorea*: comparisons with optimal foraging theory. *Marine Ecology Progress Series*, **27**, 143–154.

Lewis, A.C. (1986) Memory constraints and flower choice in *Pieris rapae. Science*, **232**, 863–865.

Lin, J. (1991) Predator–prey interactions between blue crabs and ribbed mussels living in clumps. *Estuarine and Coastal Shelf Science*, **32**, 61–69.

Lucas, J.R. (1983) The role of time constraints and variable prey encounter in optimal diet choice. *American Naturalist*, **122**, 191–209.

MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *American Naturalist*, **100**, 603–609.

McNamara, J.M. & Houston, A.I. (1985) Optimal foraging and learning. *Journal of Theoretical Biology*, **117**, 231–249.

McNamara, J.M. & Houston, A.I. (1987) Memory and the efficient use of information. *Journal of Theoretical Biology*, **125**, 385–395.

Mangel, M. & Clark, C. (1988) *Dynamic Modelling in Behavioural Ecology*. Princeton University Press, Princeton, New Jersey.

Menzel, R. (1979) Behavioural access to short-term memory in bees. *Nature (London)*, **281**, 368–369.

Papaj, D.J. & Prokopy, R.J. (1989) Ecological and evolutionary aspects of learning in phytophagous insects. *Annual Review of Entomology*, **34**, 315–350.

Peterson, C.H. (1990) On the role of ecological experimentation in resource management: managing fisheries through mechanistic understanding of predator feeding behavior. *Behavioural Mechanisms of Food Selection* (ed. R.N. Hughes), Vol. G 20, NATO ASI Series, pp. 821–846. Springer-Verlag, Berlin-Heidelberg, Germany.

Peterson, C.H. & Black, R. (1993) Experimental tests of the advantages and disadvantages of high density for two coexisting cockles in a Southern Ocean lagoon. *Journal of Animal Ecology*, **62**, 614–633.

Peterson, C.H. & Renaud, P.E. (1989) Analysis of feeding preference experiments. *Oecologia*, **80**, 82–86.

Pyke, G.H. (1984) Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics*, **15**, 523–575.

Reaka, M.L. (1980) On learning and living in holes by mantis shrimp. *Animal Behaviour*, **28**, 111–115.

Real, L.A. (1990) Short-term energy maximization and risk-aversion in bumble bees: a reply to Possingham *et al. Ecology*, **71**, 1625–1628.

Real, L.A. (1991) Animal choice behavior and the evolution of cognitive architecture. *Science*, **253**, 980–986.

Real, L.A., Ott, J.R. & Silverfine, E. (1982) On the trade-off between the mean and the variance in foraging: effect of spatial distribution and color preference. *Ecology*, **63**, 1617–1623.

ap Rheinallt, T. (1986) Size selection by the crab *Liocarcinus puber* feeding on mussels *Mytilus edulis* and on shore crabs *Carcinus maenas*: the importance of mechanical factors. *Marine Ecology Progress Series*, **29**, 45–53.

Roa, R. (1992) Design and analysis of multiple-choice feeding-preference experiments. *Oecologia*, **89**, 509–515.

Schoener, T.W. (1971) Theory of feeding strategies. *Annual Review of Ecology and Systematics*, **11**, 369–404.

Schuler, W. (1990) Are rules of thumb sufficient for the starling's choice of food according to gain in energy? *Behavioural Mechanisms of Food Selection* (ed. R.N.

Hughes), Vol. G 20, NATO ASI Series, pp. 127–142. Springer-Verlag, Berlin, Germany.

Seed, R. (1980) Predator–prey relationships between the mud crab, *Panopeus herbstii*, the blue crab, *Callinectes sapidus* and the Atlantic ribbed mussel *Geukensia* (= *Modiolus*) *demissa*. *Estuarine and Coastal Marine Sciences*, **11**, 445–458.

Seed, R. (1982) Predation of the ribbed mussel *Geukensia demissa* by the blue crab *Callinectes sapidus*. *Netherland Journal of Sea Research*, **16**, 163–172.

Sih, A., Crowley, P., McPeek, M., Petranka, J. & Strohmeier, K. (1985) Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics*, **16**, 269–311.

Sponaugle, S. & Lawton, P. (1990) Portunid crab predation on juvenile hard clams: effects of substrate type and prey density. *Marine Ecology Progress Series*, **67**, 43–53.

Stanton, L.S. (1983) Short-term learning and the searching accuracy of egg-laying butterflies. *Animal Behaviour*, **31**, 33–40.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton, New Jersey.

Tinbergen, L. (1960) The natural control of insects in pine woods. I. Factors influencing the intensity of predation by songbirds. *Archives Neerlandaises de Zoologie*, **13**, 265–343.

Vermeij, G.J. (1976) Interoceanic differences in vulnerability of shelled prey to crab predation. *Nature (London)*, **260**, 135–136.

Vermeij, G.J. (1978) *Biogeography and Adaptation: Patterns of Marine Life*. Harvard University Press, Harvard, Massachussetts.

Vermeij, G.J. (1987) *Evolution and Escalation*. Princeton University Press, Princeton, New Jersey.

Waage, J.K. (1979) Foraging for patchily-distributed hosts by the parasitoid, *Nemeritis canescens*. *Journal of Animal Ecology*, **48**, 353–371.

Waddington, K.D. & Heinrich, B. (1979) The foraging movements of bumblebees on 'vertical inflorescences': an experimental analysis. *Journal of Comparative Physiology*, **134**, 113–117.

Werner, E.E. & Hall, D.J. (1974) Optimal foraging and size selection of prey by the bluegill sunfish (*Lepomis machrochirus*). *Ecology*, **55**, 1042–1052.

West, L. (1988) Prey selection by the tropical snail *Thais melones*. A study of interindividual variation. *Ecology*, **69**, 1839–1854.

Wicksten, M.K. (1977) Shells inhabited by *Pagurus hirsutiusculus* (Dana) at Coyote Point Park, San Francisco Bay, California. *Veliger*, **19**, 445–446.

Williams, A.B. (1984) *Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida*. Smithsonian Institution Press, Washington, DC.

Zimmer-Faust, R.K. (1990) Foraging strategy of a deposit feeding crab. *Behavioural Mechanisms of Food Selection* (ed. R.N. Hughes), Vol. G 20, NATO ASI Series, pp. 557–568. Springer-Verlag, Berlin, Germany.