

Effects of experience on crab foraging in a mobile and a sedentary species

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Abstract. The effects of experience on prey and prey-patch choice were compared between two species of marine predatory crabs. The blue crab, *Callinectes sapidus* Rathbun, is highly mobile and forages in a variety of estuarine and lagoonal habitats. The Atlantic mud crab, *Panopeus herbstii* H. Milne-Edwards, is smaller and less mobile and is found mostly in oyster reefs and on shelly bottoms. In the laboratory, crabs were offered a choice between two prey types (juvenile hard clams, *Mercenaria mercenaria* Linné, and juvenile oysters, *Crassostrea virginica* Gmelin) following a preliminary phase in which crabs were trained to feed on clams only, oysters only or a mixture of the two prey types. In field enclosures, crabs were offered a choice between patches of juvenile hard clams located in an inter-tidal salt marsh and in an adjacent unvegetated inter-tidal flat after they were trained to feed in either one of the two habitat types. Both in the laboratory prey-choice and the field prey-patch choice experiments, blue crabs modified their foraging behaviour depending on previous experience. The effect of experience on their foraging behaviour did not diminish after 24 hours. Experience had no significant effects on the foraging behaviour of mud crabs. Differences in the ecological contexts (e.g. in the variability of prey quality and availability) in which the two species forage may explain the greater effect of experience on the blue crab foraging behaviour, although alternative explanations cannot be ruled out.

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Incomplete knowledge about food quality and distribution is important in determining foraging decisions (Stephens & Krebs 1986; Mangel & Clark 1988). The effects of learning (in the sense of estimating unknown environmental parameters based on past experience) on foraging decisions have been included in several foraging models (e.g. Kacelnik & Krebs 1985; McNamara & Houston 1985; Bernstein et al. 1988, 1991; Real 1991; Sih 1992). Few empirical studies, however, have attempted to quantify how much animals are able to learn and remember about the quality and distribution of food in their natural environment (Kacelnik et al. 1990; Krebs et al. 1990; Dukas & Real 1991; Real 1991).

Foragers can reduce uncertainty by sampling their environment and using this information to estimate environmental parameters or to update previous estimates (Bush & Mosteller 1955; Stephens & Krebs 1986). Some animals, however,

may not have the mobility or the cognitive capacity needed to sample their environment and update estimates of environmental parameters. External constraints on a forager's activity, for example exposure to physical stress or to predators, may also make sampling too costly. Under these scenarios, predators might base their foraging decisions on simple 'rules-of-thumb' (Janetos & Cole 1981; Bouskila & Blumstein 1992). Predators that learn about food quality and distribution in their environment are expected to modify their foraging behaviour according to their past experience, but predators that use decision rules are expected to have relatively inflexible behaviour patterns. Several authors have argued that flexible or stereotyped behaviour patterns may be favoured under different ecological conditions (Kamil & Mauldin 1987; Dukas & Real 1991, 1993; Healy 1992).

Animals with large foraging ranges are likely to encounter a wide variety of foraging situations. An ability to modify foraging behaviours following experience may be adaptive for these predators, because it allows them to modify foraging

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preferences depending on the local availability of resources and/or presence of external constraints (Hazlett 1988; Harvey & Krebs 1990; Dukas & Real 1993). In contrast, the ability to modify foraging behaviours following experience may not confer a selective advantage when animals live in a more uniform and constant environment, with abundant and temporally and spatially predictable resources. Little behavioural modification following experience may also be expected when preference for particular food or habitat types minimizes risk of predation or the intensity of competition (Strong et al. 1984; Peckarsky et al. 1994).

I compared the effects of experience on the foraging behaviour of two predatory crabs characterized by different mobility and patterns of habitat use. The two species compared were the portunid crab, *Callinectes sapidus* (the blue crab) and the xanthid crab, *Panopeus herbstii* (the mud crab). These two species are closely related (both brachyuran decapod crustaceans) and probably have nervous systems of similar complexity. Blue crabs and mud crabs consume similar types of prey and coexist in estuarine systems of the eastern United States but differ in size, morphology, mobility and habitat use. Blue crabs are large, very mobile and forage in a variety of estuarine habitats. Mud crabs are smaller, less mobile and are mainly found in sub-tidal and inter-tidal oyster reefs and shelly bottoms (Williams 1984). I predicted that the feeding behaviour of blue crabs would be more open to modification by experience than the feeding behaviour of mud crabs.

This hypothesis was tested with laboratory and field experiments that compared the effects of experience on the foraging behaviour of blue crabs and mud crabs confronted with two foraging tasks. Both crab species frequently perform these tasks in their natural environment: choosing between different prey types (e.g. juvenile hard clams, *Mercenaria mercenaria*, or juvenile oysters, *Crassostrea virginica*) and between patches of prey in different habitat types (an inter-tidal salt marsh and an inter-tidal sand flat adjacent to a salt marsh).

Study Animals

Blue crabs and mud crabs are found in estuaries and lagoons of the eastern coast of America (the blue crab from Nova Scotia to the Caribbean, the mud crab from Massachusetts to Brazil; Williams

1984). A large proportion of the diet of both species is composed of bivalve molluscs, particularly clams, mussels and oysters. Other common prey are gastropods, fish and other crustaceans (McDermott 1960; Seed 1980; Laughlin 1982; Hines et al. 1990).

Blue crabs are large (≤ 227 mm in carapace width; Williams 1984), fast and highly mobile (Wolcott & Hines 1989; Hines & Wolcott 1990). Their last pair of pereiopods are flattened and allow swimming. Individuals can cover up to 7.5 km in approximately 2 weeks (Hines & Wolcott 1990). Blue crabs use all types of coastal habitats (Williams 1984). Their mobility and habitat use vary with sex, age, moult or reproductive stage, and external conditions such as tidal phase and season (Williams 1984; Orth & van Montfrans 1990; Wolcott & Hines 1990; Micheli, in press).

Mud crabs are smaller than blue crabs (≤ 62 mm in carapace width; Williams 1984), much slower and less mobile, and they cannot swim. They are found almost exclusively in oyster beds and shelly bottoms (Teal 1959; Williams 1984), particularly in or close to inter-tidal oyster bars bordering salt marshes, where they occupy burrows or seek shelter among live oysters and oyster shells (Teal 1959; Lin 1989; F. Micheli, personal observation).

Hard clams, *Mercenaria mercenaria* and American oysters, *Crassostrea virginica* are common prey of both blue crabs (Arnold 1984; Eggleston 1990; Peterson 1990) and mud crabs (McDermott 1960; Whetstone & Eversole 1981). Both bivalve species are found along the eastern coast of the United States, from the Gulf of St Lawrence to the Gulf of Mexico (Abbott 1974). Hard clams are infaunal bivalves found in a variety of sub-tidal and inter-tidal habitats, including sand flats, seagrass beds, oyster bars and along the edges of inter-tidal salt marshes. Average clam densities reported for the study area (Back Sound, North Carolina) are 1.6 clams/m² in unvegetated bottoms, 9.0 clams/m² within seagrass beds (Peterson et al. 1984) and 3.5 clams/m² along the edge of salt marshes (F. Micheli, unpublished data). American oysters are epifaunal bivalves that can occur both sub-tidally and inter-tidally (Haven et al. 1981). In the study area, oysters are found mostly inter-tidally, along the edge of salt marshes and in portions of inter-tidal flats bordering salt

marshes (Peterson & Peterson 1979), where they can occur at densities up to ~ 700 oysters/m² (F. Micheli, unpublished data).

EXPERIMENT 1: EFFECTS OF EXPERIENCE ON PREY CHOICE

Methods

I conducted a laboratory experiment to investigate the effects of experience on prey selectivity of blue crabs and mud crabs. This experiment had two phases. First, groups of crabs were trained to feed on different combinations of two prey types, juvenile hard clams and oysters (training phase). Second, all crabs received a mixture of equal numbers of the two prey types, and prey preferences were compared between groups of crabs that had been exposed to different prey types (test trial phase).

Experimental environment

The experiment was performed within eight indoor flow-through wooden tanks (surface area 0.55 m²) containing approximately 5 cm of fine sand covered by a 20-cm deep layer of seawater. The experiment was replicated five times between late September and late October 1994. During this time, water temperatures in the tanks ranged between 17.8 and 24.0°C. Flow rate through the tanks was constant at approximately 2.5 litres/min.

Subjects

Adult male blue crabs (mean \pm SE carapace width = 122.6 \pm 2.8 mm, range = 103.0–138.0 mm; $N=15$) were captured with commercial crab pots near Beaufort, North Carolina. Adult male mud crabs (carapace width = 40.6 \pm 1.6 mm, range = 30.0–49.8 mm; $N=15$) were collected by hand in inter-tidal oyster bars in the Beaufort area. Crabs belonging to both species were held in the tanks without food for 24 h prior to experiments. All crabs were returned to their site of capture at the end of the experiments. Juvenile oysters and clams were purchased from a local hatchery (ARC Inc., Atlantic, North Carolina, U.S.A.). Oysters ranged between 19.0 and 32.0 mm in shell height (mean \pm SE = 26.0 \pm 0.1 mm; $N=300$)

and clams ranged between 12.0 and 23.8 mm in antero-posterior length (17.7 \pm 0.1 mm; $N=300$). Both crab species are able to eat oysters and clams within these size ranges (Whetstone & Eversole 1981; Arnold 1984; Eggleston 1990).

Training

During the first phase of the experiment, I fed crabs of both species with one of three combinations of prey: (1) 20 juvenile oysters, (2) 20 juvenile clams or (3) 10 juvenile oysters and 10 juvenile clams. Oysters were individually glued with cyanoacrylate glue to the inner side of valves of adult oyster shells (approximately 10 cm shell height) and were haphazardly deployed on the sediment surface, within the tanks, with juvenile oysters facing upward. Clams were pushed below the sediment surface in living position.

The presence of shell material in sediments decreases foraging success of crabs feeding on infaunal bivalves (Arnold 1984; Sponaugle & Lawton 1990). To standardize effects of oyster shells on crab foraging between all treatments, I added 20 oyster valves to tanks with clams only, and 10 oyster valves to tanks with 10 oysters and 10 clams, hence, all tanks contained 20 oyster valves of similar sizes.

Controls for bivalve mortality not due to crab predation were also set up in one or two of the remaining tanks where no crabs were added. Ten oysters and 10 clams were deployed in the control tanks. Oysters and clams in the control tanks were checked at the end of the trials and their mortality was recorded. Throughout this experiment, only 1 clam and 1 oyster died in the control tanks.

Trials lasted 1–4 days because some of the crabs ate no prey during the first 1–3 days of the experiment. I checked crabs at least twice a day until they had consumed at least one prey (but most commonly 3–20 prey) at which time I terminated the training trial. I retrieved live bivalves and crushed shells from the tanks by visually searching the sediment surface and then plowing sediments with fingers until all 20 bivalves were found. Crabs that had not consumed any prey after 4 days were excluded from the experiments.

Test trial

Immediately after termination of the training trial, all crabs received 10 juvenile oysters and 10

juvenile clams. Ten oyster valves without attached juvenile oysters were also added to all tanks to create similar conditions to those of the training trial (e.g. 20 oyster valves/tank). The test trial lasted 0.5–4 days and was monitored and sampled as described for the training trial.

Statistical analyses

The prey preferences of crabs in the test trial of the experiment were compared between the two crab species and among the three training treatments using a two-way ANOVA, with crab species and training treatment as fixed factors. The dependent variable was the difference between the number of oysters and the number of clams eaten by each crab. Using a difference provided an index of prey preference that circumvented the problem of non-independence of feeding on the two prey types in these choice experiments (Peterson & Renaud 1989).

I also performed two-way ANOVAs (1) on the total number of prey that crabs consumed during the training trial to compare feeding rates of blue crabs and mud crabs between training treatments, and (2) on the total number of prey that crabs consumed during the test trials to compare the effects of previous experience and crab species on the feeding rates of crabs on mixtures of clams and oysters.

I added date as a blocking factor in all analyses, because experiments were replicated on different dates. Because the effect of date was not significant for all analyses ($P=0.33\text{--}0.81$), I repeated analyses after pooling data from different dates (Underwood 1981). The assumption of homoscedasticity was tested with Cochran's test ($\alpha=0.05$) and was met for all analyses. Treatment means were compared, after ANOVA, with Kramer's modification of Tukey's test correcting for unequal numbers of replicates per treatment (Day & Quinn 1989).

Results and Discussion

Training

During training, there was a significant interaction between crab species and training treatment on prey consumption rates ($F_{2,19}=4.65$, $P=0.02$; Fig. 1a). Blue crabs ate significantly more prey in the treatment where only clams were given

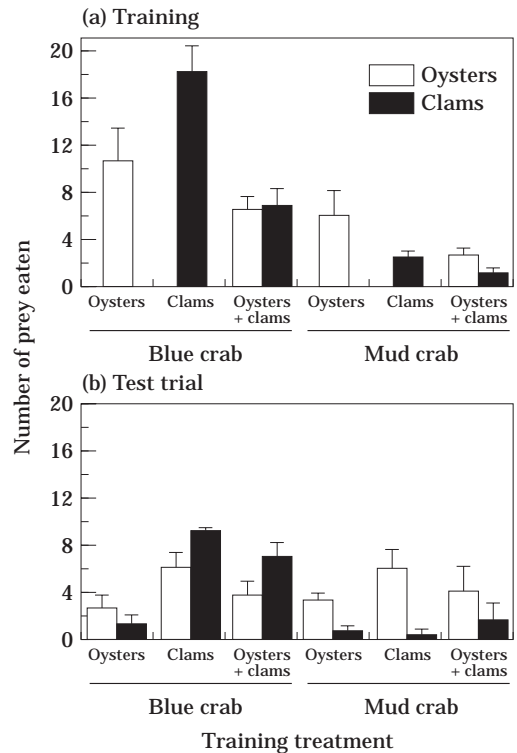


Figure 1. (a) Number of bivalve prey consumed by blue crabs and mud crabs during the training trial of the laboratory prey-choice experiment; (b) number of juvenile oysters and juvenile clams consumed by blue crabs and mud crabs in the test trial of the laboratory prey-choice experiment. During training, crabs received either 20 juvenile oysters, 20 juvenile clams or 10 oysters and 10 clams. In the test trial, all crabs received equal numbers of oysters and clams. Bars (+1 SE) represent averages of 3–5 trials.

than in the treatment where only oysters were given (Tukey–Kramer post hoc test). In the treatment where equal numbers of clams and oysters were given, blue crabs had prey consumption rates that were intermediate and not significantly different from the other two treatments (Tukey–Kramer post hoc test). Mud crabs ate similar numbers of prey between the three training treatments (Tukey–Kramer post hoc test), although there was a trend for a greater consumption of oysters than clams (Fig. 1a).

Test trial

Pre-exposure to juvenile oysters, juvenile clams, or a mixture of oysters and clams had different

effects on prey preferences (training treatment \times crab species interaction: $F_{2,20}=3.68$, $P=0.04$) and overall feeding rates (training treatment \times crab species interaction: $F_{2,20}=3.63$, $P=0.04$) of blue crabs and mud crabs in the test trial (Fig. 1b). Mud crabs ate more oysters than clams regardless of training treatment. Blue crabs were less selective and more flexible in their prey choice, showing a non-significant trend towards greater consumption of oysters than clams when trained on oysters, and greater consumption of clams than oysters when trained on clams or on a mixture of clams and oysters ($P>0.05$; Tukey–Kramer post hoc test; Fig. 1b).

Experience with different prey types did not affect feeding rates of mud crabs in the test trial, but it had a significant effect on feeding rates of blue crabs (Fig. 1b). During the test trial, blue crabs trained to feed on clams or mixtures of clams and oysters had significantly greater feeding rates than blue crabs trained to feed on oysters (Tukey–Kramer post hoc test). Mud crabs had similar feeding rates between all training treatments (Tukey–Kramer post hoc test).

One explanation for the significant effect of experience with oysters or clams on subsequent feeding rates of blue crabs is that crushing oysters may impose strain and wear of the crabs' claws (Juanes & Hartwick 1990), thereby affecting their ability to crush hard-shelled prey during subsequent feeding bouts. Alternatively, clams in the size ranges used in this experiment may be a higher quality prey than oysters for blue crabs, and thus blue crabs may be more active and spend more time searching for prey after encountering clams than oysters. The hypothesis that blue crabs prefer clams to oysters was not supported by results of the training trial, however, where blue crabs consumed similar numbers of the two prey types in the mixed-prey treatment (Fig. 1a).

EXPERIMENT 2: EFFECTS OF EXPERIENCE ON PREY-PATCH CHOICE

Methods

I conducted a field experiment to investigate the effects of experience on the prey-patch choice of blue crabs and mud crabs. This experiment also comprised two phases. First, crabs were exposed

to prey (juvenile hard clams) either in an inter-tidal salt marsh or in an adjacent inter-tidal sand flat (training phase). Second, all crabs were tested for preference between patches of clams set up in both habitat types (test trial phase). This experiment was conducted separately with blue crabs and with mud crabs.

Experimental environment

Experiments were conducted within six rectangular enclosures ($8.5 \times 3.0 \times 1.3$ m) built in Back Sound, North Carolina, U.S.A., with 8-mm Vexar mesh (Internet Inc., Minneapolis, Minnesota, U.S.A.) supported by wooden posts. The longest sides of enclosures were perpendicular to the edge of a *Spartina alterniflora* Loisel salt marsh and placed so that enclosures encircled equal areas of salt marsh and adjacent inter-tidal sand flat. Enclosure walls were buried 15 cm into the sediments. At high tide, the water within the enclosures was approximately 1.1 m deep, and at low tide both vegetated and unvegetated portions of all enclosures were exposed to air. Because of the slope of the shore, the centres of the salt-marsh portions of the enclosures were slightly higher than the centres of the sand-flat portions (mean \pm SE = 0.9 ± 0.35 cm; $N=6$). Plant densities were determined by counting *Spartina* shoots within two 0.5-m^2 quadrats haphazardly placed within the vegetated portion of each enclosure (29.5 ± 4.25 shoots/ 0.5 m^2 ; $N=12$). Plants were 1.0–1.5 m tall. A sediment core (5×5 cm) was taken from the centre of both the vegetated and unvegetated portion of all enclosures for sediment grain-size analysis (Folk 1980). Sediments contained $7.0 \pm 1.0\%$ silts and clays in the sand flat habitat and $10.1 \pm 0.9\%$ in the salt marsh habitat ($N=6$). Very fine sands ($3.0\text{--}4.0\ \phi$ units; Folk 1980) were the dominant size fraction of sediments from both habitats (sand flat: $86.6 \pm 1.3\%$; salt marsh: $81.9 \pm 1.6\%$; $N=6$). Before the start of the experiments, I visually checked enclosures for several consecutive days and removed all animals found to minimize alternative prey available to the crabs.

Experiments testing the effects of experience on prey-patch choice by crabs were conducted in June and July 1994 with blue crabs and in August and September 1994 with mud crabs. I replicated experiments eight times with blue crabs and nine times with mud crabs.

Subjects

Adult male blue crabs (mean \pm SE carapace width = 122.1 ± 2.2 mm, range = 110.0–140.0 mm; $N=16$) were captured with commercial crab pots near Beaufort, North Carolina. Adult male mud crabs (carapace width = 34.9 mm \pm 0.8 mm, range = 30.3–41.0 mm; $N=15$) were collected by hand in inter-tidal oyster bars in the Beaufort area. Handling of crabs was the same as for experiment 1. Juvenile clams were purchased from a local hatchery (ARC Inc., Atlantic, NC, U.S.A.). Clams ranged between 12.2–20.0 mm in length (16.1 ± 0.2 mm; $N=60$).

Training

During the first phase of the experiment, crabs were trained to feed on juvenile hard clams in only one of the two habitat types available, either the salt marsh or the sand flat. At the beginning of each training trial, I deployed 50 clams within a 1-m² patch marked at the corners with steel stakes either in the salt marsh or in the sand flat portion of each enclosure, approximately 1 m away from the vegetation edge. Throughout the experiments, two enclosures containing no crabs served as controls for clam losses not due to predation; the other four enclosures received one crab each. Treatments were assigned to specific enclosures at random. After 2 days, I terminated the training trial and retrieved live clams and crushed shells from the patches. To facilitate clam recovery, clams were deployed at the intersections of a monofilament-line grid supported by a PVC frame. Thus, clams were regularly spaced within patches and could be easily found, at the end of each trial, by superimposing the grid on the patches and finger-plowing sediments at the grid intersections.

Test trial

Following training, all crabs were offered a choice between clam patches of equal densities (20 clams/m²) located in both habitat types, approximately 1 m away from the vegetation edge. To determine whether any effect of experience on the crabs' patch preferences diminished through time, the test trial began right after terminating the training trial in half of the replicates, and after a 24-h interval in the other half.

The test trial lasted 1 day, after which I recovered live clams and crushed shell from each patch. Enclosures that had served as controls during the training trial and that did not contain a crab were treated identically to predator enclosures containing one crab throughout each experimental trial. Therefore, clam patches were set up and retrieved following identical protocols in the predator and control enclosures. Predation on clams was determined by adding the number of clams crushed and missing from each patch. Missing clams could have been carried off by crabs, lost due to sampling error or migrated from patches. I assumed that all the possible mechanisms causing missing clams, except crab predation, were identical between enclosures with crabs and control enclosures without crabs. Therefore, missing clams due to predation could be teased apart from missing clams due to sampling error and clam migration by comparing clam losses between predator and control enclosures with ANOVA (see Statistical analyses). At low tide, I visually searched each enclosure and captured and released crabs. Replicate trials were excluded from analyses if I found other potential clam predators (whelks or crabs) in enclosures at the end of trials.

Statistical analyses

Field enclosure experiments were analysed using three-way ANOVAs with predator treatment (enclosures with one crab added or control enclosures with no crabs added), training treatment (clams in the salt marsh habitat or in the sand flat habitat during training) and time-interval treatment (zero or 24-h interval between training and the test trial) as fixed factors. The dependent variable in the ANOVAs was the difference between the number of clams crushed or missing in the vegetated and unvegetated prey patches at the end of the test trial. Because experiments with blue crabs and mud crabs had not been conducted contemporaneously, separate ANOVAs were performed on experiments investigating the effects of experience on prey-patch choice of blue crabs and mud crabs. Three-way ANOVAs were also performed on the total number of clams crushed or missing from enclosures to compare total clam losses in the enclosures among the experimental treatments.

As in experiment 1, I added date as a blocking factor in all analyses, because experiments were replicated on different dates. The effect of date was not significant for all analyses ($P=0.12-0.91$). When the probability level for the effect of date was greater than 0.25, the analyses were repeated after pooling data from different dates (Underwood 1981). The assumption of homoscedasticity was tested with Cochran's test ($\alpha=0.05$) and was met for all analyses. Treatment means were compared, after ANOVA, with Kramer's modification of Tukey's test correcting for unequal numbers of replicates per treatment (Day & Quinn 1989).

Results and Discussion

Training

During training, blue crabs consumed similar numbers of clams in the salt marsh (mean \pm SE = 27.4 ± 2.9 ; $N=8$) and in the sand flat habitats (23.3 ± 6.6 ; $N=8$; $t_7=0.63$, $P=0.55$). In contrast, mud crabs ate significantly more clams in the salt marsh (29.5 ± 3.2 ; $N=8$) than in the sand flat habitat (16.0 ± 3.7 ; $N=8$; $t_7=3.01$, $P=0.02$).

Test trial

Training to feed on clam patches located in different habitat types had a significant effect on prey-patch choice of blue crabs in the test trial (predator treatment \times training treatment interaction: $F_{1,22}=8.09$; $P=0.009$). Blue crabs trained to feed on clams in the salt marsh habitat consumed more prey in this habitat than in the sand flat during the test trial, where crabs were offered a choice between clam patches of equal densities located in both habitat types (Fig. 2a). Blue crabs trained to feed on clams in the sand flat habitat consumed similar numbers of prey in the two habitat types during the test trial (Fig. 2a). This significant effect of training treatment on prey-patch choice of blue crabs was not diminished after a 24-h interval between training and test trials (time interval effect: $F_{1,22}=0.36$, $P=0.56$), indicating that blue crabs could also remember what they had learned for at least several hours. No other main effects and interaction terms in the ANOVA were significant ($P=0.17-0.49$).

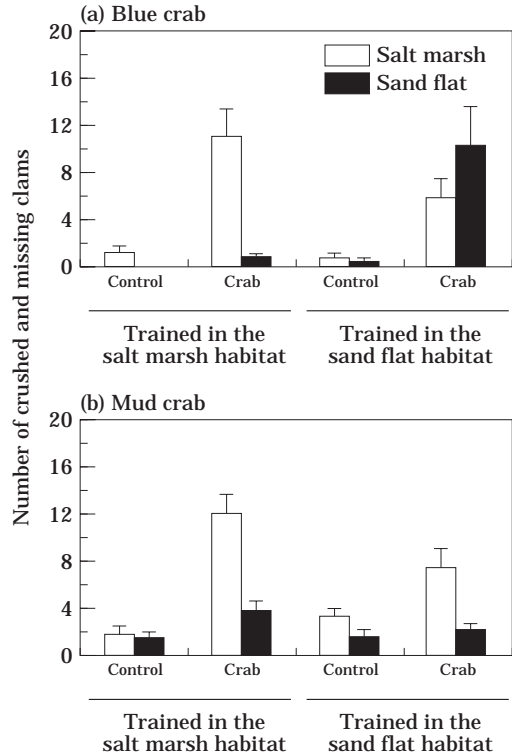


Figure 2. Number of juvenile clams missing or crushed by (a) blue crabs and (b) mud crabs at prey patches of equal density (20 clams/m^2) in vegetated (salt marsh) and unvegetated (sand flat) inter-tidal habitats during the test trial of the prey-patch choice experiment. Crabs had been trained to feed on clams located either in the salt marsh or in the sand flat habitat. Bars ($+1 \text{ SE}$) represent averages of 6–9 trials.

In the test trial, the total number of clams crushed or missing from field enclosures containing one blue crab was significantly greater than in the control enclosures containing no crabs (predator treatment effect: $F_{1,19}=37.28$, $P=0.0001$), indicating that addition of blue crabs to enclosures significantly increased clam losses. The effects of training treatment, time interval between training and test trials and all interaction terms on the total number of crushed or missing clams in the test trial were not significant ($P=0.22-0.43$).

Experience did not significantly affect prey-patch choice of mud crabs. There were no significant effects of training treatment and time-interval treatment on prey-patch choice of mud crabs and

no significant interactions between factors in the ANOVA ($P=0.09-0.68$). In the test trial, mud crabs had greater feeding rates in the salt marsh than in the sand flat, regardless of which habitat they had been trained to feed in during the training phase of the experiment, but clam losses were similar between the two habitats in the control enclosures with no crabs added (predator treatment effect: $F_{1,24}=24.38$, $P=0.0001$; Fig. 2b).

There was a significant interaction between the effects of training and predator treatment on the total number of clams crushed or missing from enclosures in the mud crab experiment ($F_{1,20}=6.79$, $P=0.02$). In both training treatments, the total number of clams crushed or missing was significantly greater in enclosures where one mud crab was added than in controls (Tukey-Kramer post hoc test). Total clam losses were also greater in enclosures with crabs pre-exposed to clams in the salt marsh habitat than in enclosures with crabs pre-exposed to clams in the sand flat habitat (Tukey-Kramer post hoc test). All other main effects and interaction terms in the ANOVA comparing total clam losses between treatments were not significant ($P=0.12-0.98$).

GENERAL DISCUSSION

Experience significantly affected the predation rates of blue crabs at prey patches located in different habitat types (Fig. 2a). There was also a non-significant trend for experience to affect prey choice of blue crabs (Fig. 1). In a previous study, experience also modified prey-size selectivity of blue crabs feeding on hard clams of different sizes (Micheli 1995). In both studies, the effect of experience did not diminish after 24 hours. These results indicate that blue crabs learn about prey type and prey location, retain this information for at least 24 hours and modify their foraging behaviour accordingly. In contrast, experience had no significant effects on prey (Fig. 1) and prey-patch (Fig. 2b) choice of mud crabs. There was a non-significant trend for mud crabs trained to feed on clams in a salt marsh to have greater predation rates in this habitat than mud crabs trained in a sand flat (Fig. 2b).

Differences between the ecological contexts in which these two species feed may explain the different effects of experience on the predatory behaviour of blue crabs and mud crabs. Blue

crabs feed in a variety of habitat types, characterized by different prey populations. Different types of prey often require predators to use different searching and handling techniques. For example, consumption of epifaunal and sessile prey species, such as oysters, requires crabs to use different sensory and motor skills compared with those needed to find and consume infaunal and unattached prey, such as clams. The effect of experience on prey selection of blue crabs may be viewed as adaptive, because it allows them to opportunistically exploit the prey species and sizes that are most common in each of the habitat types that they visit. In contrast, mud crabs generally feed within a single habitat type (oyster reefs) where oysters are their most abundant prey. Preference for oysters ensures that mud crabs feed on the most abundant prey species in their habitat.

Different adaptive pressures operating on species may select for different cognitive capacities (Domjan & Galef 1983; Kamil & Maudlin 1987; Sherry & Schacter 1987). Correlative studies of encephalization among mammals with different feeding habits and foraging ranges showed that among bats, rodents and primates, species with larger foraging ranges have larger brains relative to their body sizes than more sedentary species (Eisenberg & Wilson 1978; Harvey & Krebs 1990). Foragers with larger ranges encounter a wider variety of sensory stimuli than more sedentary or specialized ones. Harvey & Krebs (1990) hypothesized that a wider range of sensory stimuli may select for increased cognitive abilities. Results of the present study appear to support this prediction, because the species with larger foraging ranges, the blue crab, was able to learn and remember the quality and distribution of prey in its environment, but the more sedentary species, the mud crab, did not modify its foraging behaviour, however, need to be corroborated by additional tests involving more than two predator species.

An alternative explanation for the difference in the effects of experience on foraging behaviour observed between blue crabs and mud crabs is that the cost of obtaining information about prey quality and distribution may be higher for mud crabs than for blue crabs. Blue crabs are larger and more mobile than mud crabs and can move between prey patches more rapidly. Because of their smaller body size and lower mobility, mud

crabs may perceive changes in external conditions on a smaller scale than blue crabs. In the field experiment, mud crabs might have been able to perceive changes in prey availability within each prey patch, rather than between the two prey patches. Finally, mud crabs and blue crabs are also likely to have different susceptibility to predation. Blue crabs are preyed upon by larger conspecifics, fish and birds (Hines et al. 1990; Prescott 1990; Moody 1994; Smith 1995). As blue crabs grow larger, however, few predators can attack them. In contrast, even the largest mud crabs can be consumed by large fish and crabs. Sampling different habitat types, particularly unvegetated ones where crabs may be more susceptible to predators, may entail higher costs for mud crabs than for blue crabs and may explain the result of a lower flexibility of habitat use by mud crabs. For mud crabs, elevated risk of predation in the unvegetated habitat may outweigh the benefit of finding food in this habitat type.

In addition to mobility and size, other characteristics of the two crab species differ, such as their morphology and possibly their sensory abilities. These differences may affect their foraging efficiency between prey and habitat types. For example, morphological or sensory constraints may prevent mud crabs from feeding efficiently on clams or in inter-tidal sand flats. Other potential differences between the two species were minimized by choosing species that live in the same system and feed on the same prey and by comparing their behaviour during foraging tasks that both species commonly perform in their natural environment.

Different effects of experience on foraging behaviour of predators may have important consequences for the patterns of mortality of their prey, and thus for their role in structuring prey communities. Based on the results of this study, predation by mud crabs is expected to cause predictable patterns of mortality among juvenile bivalves, with greater mortality of epifaunal than infaunal bivalves and in salt marshes than in adjacent unvegetated intertidal flats. In contrast, predation by blue crabs is expected to cause more variable patterns of bivalve mortality, changing with the relative abundance of different prey species and sizes, the relative prey abundance between different habitats and with the intensity of competition and risk of predation

by higher-order predators (this study; Micheli, in press). Patterns of predation by blue crabs on bivalves are expected to vary seasonally and spatially depending on the external conditions encountered by the crabs and even on the individual history of each crab.

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