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Foraging behavior of juvenile *Carcinus maenas* (L.) and *Cancer pagurus* L.

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Abstract Information concerning the way juvenile crabs choose their diet from a variety of prey types can be useful for a better understanding of community dynamics, as well as for the adequate management of natural resources. Prey size and species selection by juvenile *Carcinus maenas* (15–35 mm carapace width, CW) and *Cancer pagurus* (20–40 mm CW) feeding on four bivalves of contrasting shell morphology were investigated. When offered a wide size range of *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule* presented individually, crabs generally showed evidence of size-selective predation. *Cancer pagurus* selected larger mussels relative to the size of their chelae (relative prey size, RPS) than did *Carcinus maenas* of similar and even larger carapace width. However, the RPS of selected *O. edulis* and *Cerastoderma edule* were similar for all crabs, suggesting that certain prey features constitute effective barriers even to the powerful chelae of *Cancer pagurus*. When offered a wide size range of mussels and oysters simultaneously, all crabs consistently selected mussels. When offered *O. edulis* and *Crassostrea gigas*, crabs consumed both these oyster species in similar numbers. *Carcinus maenas* consumed similar numbers of mussels and cockles; *Cancer pagurus*, however, showed no preference for either prey in the smaller size classes but selected more mussels than cockles as prey increased in size. Although previous studies report that adult *Carcinus maenas* select prey species according to their profitability (amount of food ingested per unit of handling time, milligrams per second), consumption rates of the size classes of prey selected by juvenile shore crabs did not always parallel prey value. Although variations in crab strength can account for many of the differences between the foraging strategy of juvenile and adult *C. maenas*, our results suggest that juvenile crabs are less species selective than adults as a result of the restrictions imposed on small individuals that have limited access to larger prey.

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Introduction

There have been many previous studies concerning the feeding ecology of brachyuran crabs, for example, *Portunidae* (Haddon and Wear 1987; Seed and Hughes 1997), *Cancridae* (Boulding and Hay 1984; Juanes and Hartwick 1990), *Xanthidae* (Hughes 1989; Lin 1990), and *Calappidae* (Hughes and Elner 1989), and various aspects of foraging have been extensively documented. Most of the research has been dedicated to the study of the feeding behavior of adult crabs, and very little information has been published regarding juveniles. Not only is the spatial distribution of juveniles on the shore different from that of adults (Naylor 1958; Eriksson and Edlund 1977), but their feeding habits and food preferences also contrast with those of larger conspecifics (Ropes 1968; Scherer and Reise 1981; Rangeley and Thomas 1987).

The variability in the feeding patterns throughout a wide size range of crabs can be particularly relevant when considering the impact of crab predation on prey populations. The size-frequency distribution and abundance of crabs vary seasonally, thus affecting the overall average food intake of a crab population over a period of time (Walne and Dean 1972). On the shore, juvenile crabs are typically more abundant than adults (Crothers 1970), and the relative abundance of certain age groups, in turn, varies throughout the intertidal and shallow subtidal regions (Dare and Edwards 1981; Hunter and

Naylor 1993). Thus, differences in both the temporal and spatial distribution of a crab population will influence accessibility to prey, leading potentially to modifications of the patterns of prey mortality when crabs of different size are considered.

The aim of the present investigation was to examine the foraging behavior of juvenile *Carcinus maenas* (Linnaeus) and *Cancer pagurus* Linnaeus when presented with several bivalves of contrasting shell morphology: the blue mussel, *Mytilus edulis* Linnaeus, the edible cockle *Cerastoderma edule* (Linnaeus), the flat oyster, *Ostrea edulis* Linnaeus, and the Pacific oyster, *Crassostrea gigas* (Thunberg). Results herein are compared with those previously reported by Mascaró and Seed (2000a, b). Following a similar experimental design, these authors found that differences in size- and species-selective predation by adult *Carcinus maenas* (40–70 mm carapace width, CW) feeding on *M. edulis, O. edulis, Crassostrea gigas*, and *Cerastoderma edule* were related to the contrasting morphological features of their shells and the way these features influence prey vulnerability to predation by adult shore crabs.

Shore crabs, *Carcinus maenas*, are known to forage extensively on the mussel *M. edulis* (Dare et al. 1983) and the oyster *Crassostrea gigas* (Richardson et al. 1993). Studies have demonstrated the effect of shore crab predation on the distribution patterns of the cockle *Cerastoderma edule* (Sanchez-Salazar et al. 1987). Although cancrids have generally been associated more with predation on gastropods, various species of the genus *Cancer* have been reported to forage on commercially important bivalves (Boulding and Hay 1984).

It is uncertain to what extent laboratory observations are representative of the field situation. In natural conditions, crabs can find alternative sources of food; they are subject to inter- and intraspecific competition as well as pressures from their own predators and of abiotic environmental conditions that constrain the breadth of their foraging activities (Sponaugle and Lawton 1990; Lawton and Zimmer-Faust 1992). Bearing in mind the limits to which laboratory results can be used to assess the effect of predation on local prey populations, the present research constitutes a contribution to our understanding of the basis underlying predatory interactions between juvenile *Carcinus maenas* and *Cancer pagurus* and commercially important bivalves. Furthermore, this information can be useful for species management in polyculture, a form of aquaculture that is presently gaining interest as it can result in increased and more diverse stock productions of both freshwater and marine resources (Ardizzone et al. 1988).

Materials and methods

In June 1995, July–August 1996, and July 1997, juvenile *Carcinus maenas* (15–35 mm CW) and *Cancer pagurus* (20–40 mm CW) were collected by hand from the low shore at Treborth in the Menai Strait, North Wales. To avoid bias that may result from the crabs' previous experience with certain species of prey, only crabs collected at Treborth were used in feeding experiments, since at this site the experimental prey species are either poorly represented or absent. Crabs were maintained individually in plastic aquaria (30×20 cm) filled to a depth of 10 cm with running seawater. Water temperature in the aquaria varied between 12 and 17°C, and photoperiod was kept constant at approximately 14 h light:10 h dark, reflecting the naturally occurring water temperatures and light regime in the Menai Strait from June to October. Immediately after capture, crabs were starved for 48 h prior to experiments to standardize hunger levels. Only male crabs (as far as could be accurately determined at this size) in the late inter-moult stage were used during feeding experiments. It should be noted, however, that among *Carcinus maenas* < 30 mm CW (Hartnoll 1978) and *Cancer pagurus* < 40 mm CW, chelal size in male crabs is similar to that of females of comparable carapace width (Mascaró 1998), indicating that sexual dimorphism in chelal size is not likely to modify foraging preferences among these small crabs.

Intertidal *M. edulis* and *Cerastoderma edule* were each collected from a naturally occurring population around Anglesey, North Wales; *O. edulis* and *Crassostrea gigas* were obtained from commercial oyster beds at the Centre for Environment, Fisheries and Aquaculture Science in the Menai Strait. All prey were maintained in plastic trays with running seawater and fed a mixture of microalgae once a day. Only undamaged prey were used and any epizoic organisms were removed from the shells.

Crabs of both species were classified into two size categories: *Carcinus maenas*: small (15–25 mm CW) and small-medium (25–35 mm CW); *Cancer pagurus*: small (20–30 mm CW) and small-medium (30–40 mm CW). Size-selection experiments were carried out by presenting three crabs of each size category with five prey items in each of several size classes of prey (Table 1), and their preferences in each case were recorded. The number and size of categories in which prey were presented varied between experiments depending on crab size. Only one species of prey was offered during any single feeding experiment. Prey items were scattered randomly over the floor of the aquaria. Any prey item consumed during 12-h feeding periods was recorded and replaced by another one of similar size to maintain constant prey availability. Experiments were run continuously until a consistent feeding pattern emerged (10 days). Results were analyzed by comparing the prey size distributions using a chi-square test to detect whether these deviated from a random choice. Since the number of size classes of prey offered to crabs was never less than five, a significant chi-square test would mean that the selected size classes would be those in which the number of prey consumed exceeded 20% of the total number of prey consumed. Comparisons of the size ranges of prey selected by different size categories and species of crabs were made using a measure of shell size relative to each size category of crab. Relative prey size (RPS) was obtained by dividing the median value of shell width (SW: minimum shell dimension) within each size class of prey offered by an estimate of the chelal height of the crabs in each size category (see Mascaró 1998).

Once the selected size ranges of each prey species had been established, paired combinations of a wide size range of prey were offered: *M. edulis*-*O. edulis*, *M. edulis*-*Crassostrea gigas*, *O. edulis*-*C. gigas*, and *M. edulis*-*Cerastoderma edule*. The size classes of prey used for these experiments were based on those selected by crabs in single-species experiments. Five prey items in each size class were scattered randomly over the floor of the aquaria, prey consumption was monitored, and consumed items were replaced as described for single-prey-species experiments. Prey-species selection experiments were run continuously until a consistent feeding pattern emerged (10 days).

To establish whether crabs selected prey species on the basis of prey value, experiments comparing the breaking time and profitability of the selected size ranges of each prey species were carried out. Three *Carcinus maenas* and *Cancer pagurus* in each size class were offered a prey item of known shell length, and the following events were recorded: (1) breaking time (T_b), the time from the first physical contact with the prey item through the period of manipulation to the point where the shell was finally opened and the flesh exposed, and (2) handling time (T_h), the time from the first physical contact through the eating period to the point at which the meal was completed and the empty shell abandoned. Dry flesh weight of prey items was calculated on the basis of the allometric equations reported by Mascaró and Seed (2000a):

$$M.edulis : \log W = -4.94 + 2.69 \log \mathrm{SL}; r^2 = 0.99; n = 35$$

$$O.edulis : \log W = -5.99 + 2.89 \log \mathrm{SL}; r^2 = 0.96; n = 35$$

$$Crassostrea\ gigas\ : logW = -6.50 + 3.30 \log \mathrm{SL}; r^2 = 0.95; n = 22$$

$$Cerastoderma\ edule : \log W = -4.86 + 2.82 \log \mathrm{SL}; r^2 = 0.99; n = 25$$

where W is dry flesh weight (in grams) and SL (in millimeters) is the maximum shell dimension (i.e., shell length). Handling time was then used to estimate prey profitability as dry flesh weight per unit of observed T_h (milligrams per second). Breaking time experiments were conducted continuously throughout a 25-day period. Analysis of variance (ANOVA) and Scheffe's method (or non-parametric test – Kruskal–Wallis and Dunn's method – on data with heterogeneity of variance) for pairwise comparisons of breaking time and profitability values between prey species were performed on the basis of the selected size ranges of prey consumed during single-prey-species experiments. In those cases where crabs exhibited no apparent size preference, the size range used was comparable to that for the selected size range of mussels. Handling time and profitability values were log transformed before ANOVA was applied.

Results

The mean number of prey items in each size class that were consumed by *Carcinus maenas* varied from one prey species to another (Fig. 1A). Small and small-medium shore crabs selected mussels of 2–8 mm and 3–12 mm SL, respectively. Small crabs selected cockles of the smallest size class offered (2–4 mm SL), whereas small-medium crabs consumed more cockles of 4–8 mm SL but also included a considerable number of the smallest cockles offered (2–4 mm SL). Very few cockles >8 mm SL were consumed by either size category of shore crabs. When *O. edulis* was offered, small crabs selected oysters of 3–9 mm SL but never consumed flat oysters >9 mm SL. Similarly, small-medium crabs selected oysters of 3–12 mm SL and never included flat oysters >15 mm SL in their diet. When *Crassostrea gigas* was offered, however, both small and small-medium crabs consumed all offered size classes of prey, although oysters from the smaller size classes (6–12 mm and 6–9 mm SL, respectively) were selected.

Results of the size-selection experiments with *Cancer pagurus* are shown in Fig. 1B. Small and small-medium edible crabs selected mussels of 4–12 mm and 5–15 mm SL, respectively. Small crabs selected cockles of 2–6 mm SL, while small-medium crabs selected cockles of 3–9 mm SL. When *O. edulis* were offered, small edible crabs selected flat oysters of 3–9 mm SL and did not consume flat oysters >15 mm SL. Small-medium crabs, however, selected flat oysters of 6–15 mm SL, although they included all offered size classes of flat oysters in their diet. When *Crassostrea gigas* were offered, small edible crabs showed no preference toward any size class of oyster offered, whereas small-medium crabs consumed more *C. gigas* of 15–18 mm and 18–21 mm SL. Both size classes of crabs, however, included all offered size classes of Pacific oysters in their diet.

Chi-square analysis on the number of consumed prey showed that the shell length of prey selected by crabs during the size-selection experiments varied among prey species (Table 2). All crabs feeding on *M. edulis*, *O. edulis*, and *Cerastoderma edule* showed a significant preference for a particular size class of prey (Table 2). When feeding on *Crassostrea gigas*, both size categories of *Carcinus maenas* and small-medium *Cancer pagurus* showed evidence of size-selective predation, whereas small *C. pagurus* consumed all offered size classes of *Crassostrea gigas* in approximately equal numbers.

The RPSs of selected prey that were consumed by crabs in each size category are plotted in Fig. 2. Results show that crabs generally selected prey with an RPS ≤ 1, that is, smaller or equal to the height of their largest chela. When feeding on a wide size range of mussels, *Carcinus maenas* selected those with an RPS of 0.15–0.70, whereas *Cancer pagurus* selected those with an RPS of 0.28–0.97. These results indicate that edible crabs selected mussels that were slightly larger, relative to the

Table 1 Size classes (shell length in millimeters: maximum shell dimension) of *Mytilus edulis*, *Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule* that were offered to *Carcinus maenas* and *Cancer pagurus* of two size categories during feeding experiments. The number and size of categories in which prey were presented varied between experiments depending on crab size. *CW* Carapace width

	Mytilus edulis	*Ostrea edulis*	*Crassostrea gigas*	*Cerastoderma edule*
Carcinus maenas				
15–25 mm CW	2–4, 4–6, 6–8, 8–10, 10–12, 12–14 mm	3–6, 6–9, 9–12, 12–15, 15–18 mm	6–9, 9–12, 12–15, 15–18, 18–21 mm	0–4, 4–8, 8–12, 12–16, 16–20 mm
25–35 mm CW	3–6, 6–9, 9–12, 12–15, 15–18, 18–21 mm	3–6, 6–9, 9–12, 12–15, 15–18, 18–21 mm	6–9, 9–12, 12–15, 15–18, 18–21, 21–24 mm	0–4, 4–8, 8–12, 12–16, 16–20, 20–24 mm
Cancer pagurus				
20–30 mm CW	4–8, 8–12, 12–16, 16–20, 20–24 mm	3–6, 6–9, 9–12, 12–15, 15–18 mm	3–6, 6–9, 9–12, -12–15, 15–18, 18–21 mm	2–4, 4–6, 6–8, 8–10, 10–12, 12–14 mm
30–40 mm CW	5–10, 10–15, 15–20, 20–25, 25–30 mm	3–6, 6–9, 9–12, 12–15, 15–18, 18–21 mm	6–9, 9–12, 12–15, 15–18, 18–21, 21–24 mm	3–6, 6–9, 9–12, -12–15, 15–18, 18–21 mm

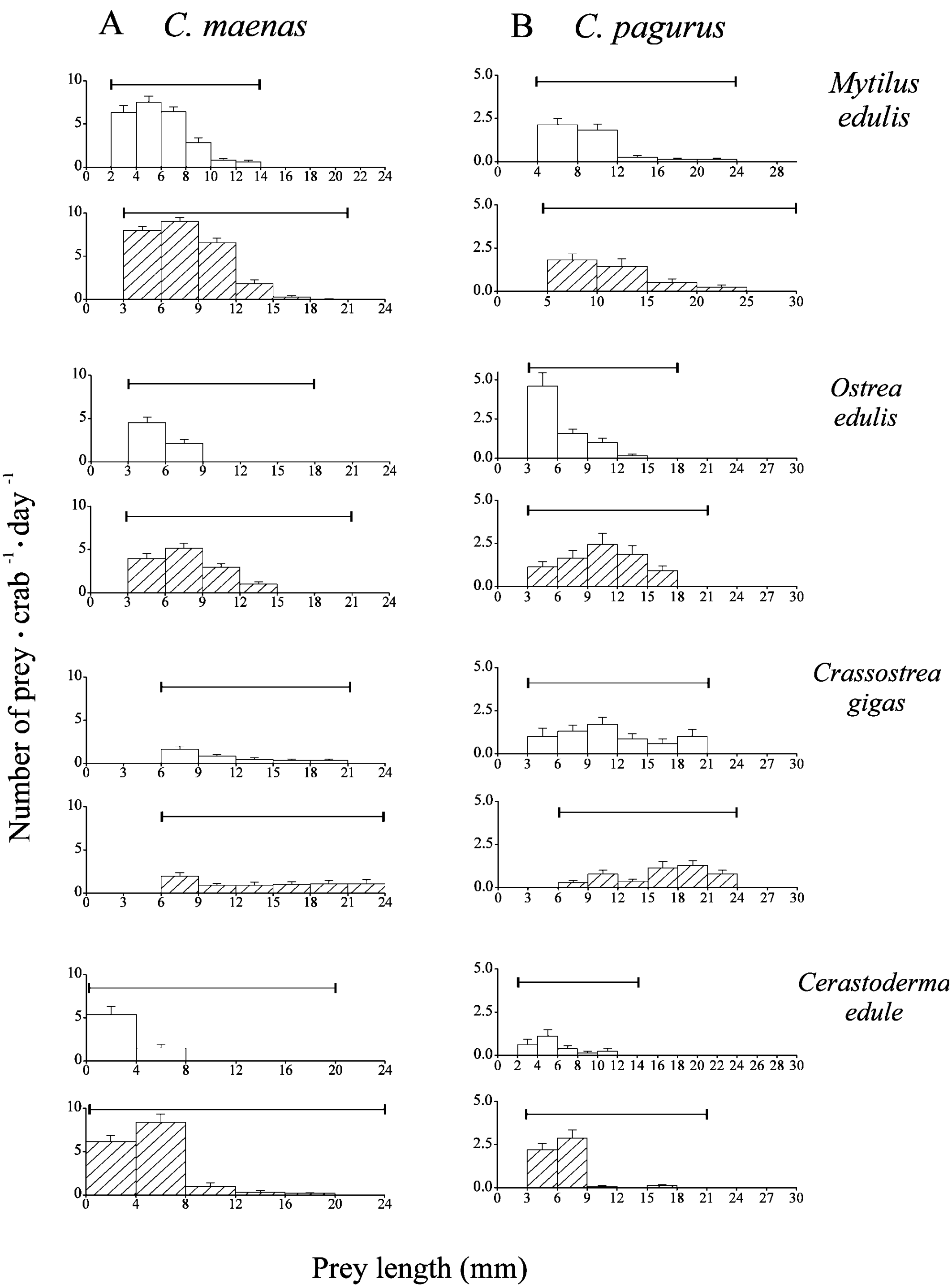


Fig. 1 Number of prey of various size classes (shell length in millimeters: maximum shell dimension) of *Mytilus edulis, Ostrea edulis*, *Crassostrea gigas*, and *Cerastoderma edule* consumed by **A** *Carcinus maenas* of 15–25 mm (*open columns*) and 25–35 mm carapace width (CW; *shaded columns*) and **B** *Cancer pagurus* of 20–30 mm (*open columns*) and 30–40 mm CW (*shaded columns*) during the single-prey-species experiments (10 days). Values are mean consumption rates · crab^{-1} · day^{-1} ± standard error (SE). *Horizontal bars* represent the range of size classes of prey that were offered to each size category and species of crab (Table 1)

size of their chelae, than those selected by shore crabs of comparable carapace width.

In experiments with *O. edulis*, shore crabs and edible crabs of both size categories selected prey of a similar RPS (0.17–0.58 and 0.25–0.54, respectively), whereas *O. edulis* of an RPS >0.6 were very rarely opened by any crab (Fig. 2). When *Crassostrea gigas* were offered, however, small-medium *Carcinus maenas* selected

Table 2 Chi-square tests on the total number of prey consumed by two size categories of *Carcinus maenas* and *Cancer pagurus* during the single-prey-species experiments (10 days). The selected[a] size ranges of prey (shell length in millimeters: maximum shell dimension) are shown in parenthesis when tests proved statistical significance; *NS* no significant departure from an expected uniform distribution

	M. edulis	*O. edulis*	*Crassostrea gigas*	*Cerastoderma edule*
Carcinus maenas				
15–25 mm CW	*** (2–8)	*** (3–9)	*** (6–12)	*** (2–4)
25–35 mm CW	*** (3–12)	*** (3–12)	* (6–9)	*** (2–8)
Cancer pagurus				
20–30 mm CW	*** (3–12)	*** (3–9)	NS	** (2–6)
30–40 mm CW	*** (5–15)	* (6–15)	* (15–21)	*** (3–9)

*$P<0.05$; **$P<0.01$; ***$P<0.001$

[a] Since the number of size classes in which prey were offered was never less than five, when chi-square tests on prey size distributions were significant, the selected size classes were those in which the number of prey consumed exceeded 20% of the total number of prey consumed

Crassostrea gigas of an RPS of 0.29–0.43, whereas small shore crabs selected relatively larger Pacific oysters (RPS: 0.48–0.93). Small and small-medium *Cancer pagurus* selected *Crassostrea gigas* of an RPS of 0.23–0.65 and 0.76–1.04, respectively. When feeding on *Cerastoderma edule*, shore crabs selected cockles of a slightly lower RPS (0.13–0.64) than did edible crabs of comparable carapace width (RPS: 0.19–0.73).

The total numbers of each prey species that were consumed daily by each size category and species of crab and the corresponding biomass (in milligrams) are shown in Table 3. Both size categories of *Carcinus maenas* and *Cancer pagurus* consumed more mussel flesh than any of the other bivalves offered, although differences were generally greater between mussels and oysters than between mussels and cockles. Whereas both size categories of *Carcinus maenas* also consumed more *M. edulis* than any other bivalve, both size categories of *Cancer pagurus* consumed relatively similar numbers of all prey species. *C. pagurus* generally consumed less biomass and fewer numbers of all prey species than did *Carcinus maenas* of comparable carapace width. There was a general trend toward greater number and biomass consumption as crabs increased in size.

When *M. edulis* were offered in combination with either *O. edulis* or *Crassostrea gigas*, shore crabs and edible crabs of both size categories markedly selected mussels (Fig. 3). When crabs were offered a choice between *O. edulis* and *C. gigas*, neither *Carcinus maenas* nor *Cancer pagurus* selected either oyster species. All shore crabs consumed both *M. edulis* and *Cerastoderma edule* in similar numbers. Although edible crabs of both size categories showed no preference for either mussels or cockles in the smaller size classes, they both selected more mussels than cockles as prey increased in size.

Figure 4 illustrates the mean profitability of the selected size ranges of prey consumed by crabs expressed as RPS. Results indicate that the ranking order of prey profitability did not always parallel the order in which prey were consumed by crabs. Analysis of variance

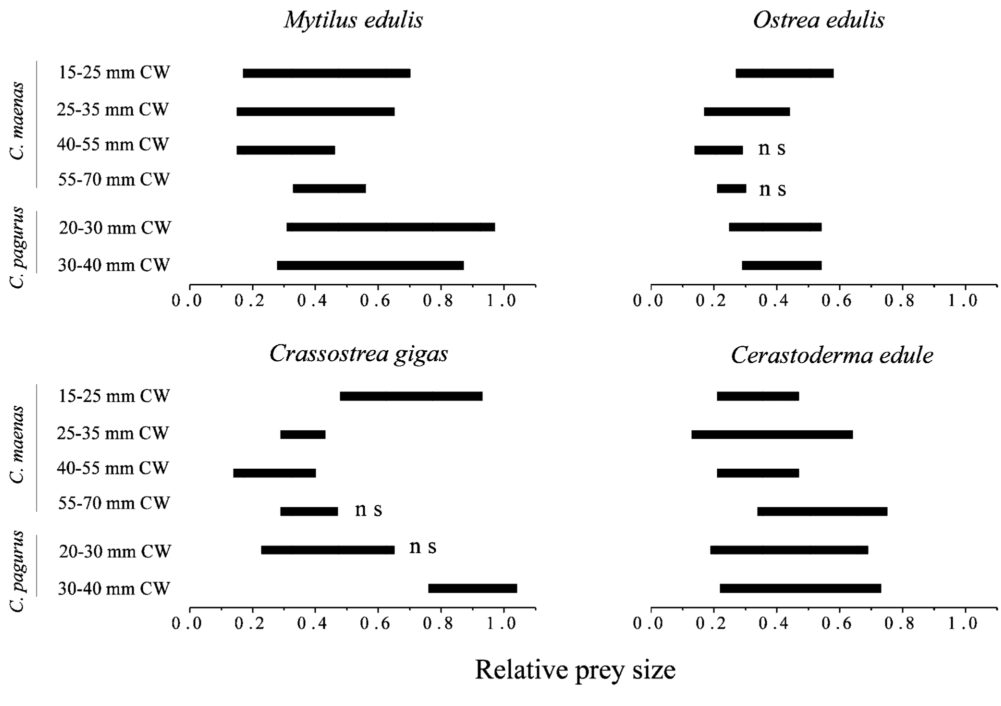


Fig. 2 Relative prey size (RPS) of prey selected (i.e., those consumed in numbers that exceeded 20% of the total number of prey) by *Carcinus maenas* and *Cancer pagurus* of two size categories during single-prey-species experiments; *ns* denotes those size categories of crabs where significant size-selective feeding could not be detected. Data concerning *Carcinus maenas* 40–70 mm CW were taken from Mascaró and Seed (2000a)

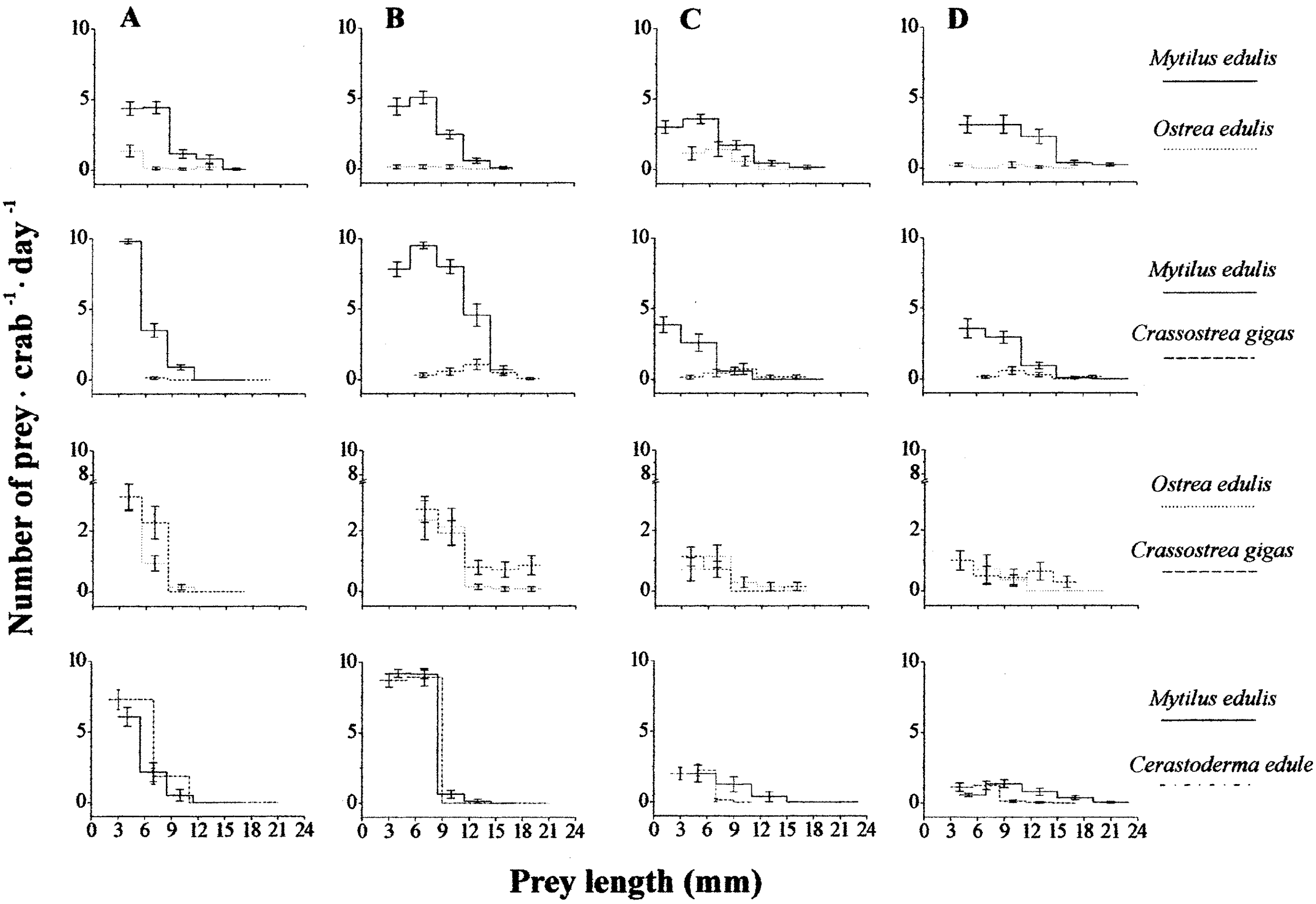
Table 3 Ingested biomass (in milligrams) corresponding to the total number of prey items (in parenthesis) in all offered size classes of *M. edulis*, *O. edulis*, *C. gigas*, and *C. edule* consumed daily by *C. maenas* and *C. pagurus* of two size categories during single-prey-species experiments. Biomass was estimated on the basis of the dry flesh weight of an individual prey item of a shell length equivalent to the median value of its size class. Values are mean consumption rates · $crab^{-1}$ · day^{-1}

	M. edulis		*O. edulis*		*Crassostrea gigas*		*Cerastoderma edule*	
Carcinus maenas								
15–25 mm	46.8	(24.5)	1.1	(6.6)	4.7	(3.6)	3.8	(6.9)
25–35 mm	102.7	(25.8)	6.7	(13.1)	21.2	(6.8)	44.6	(16.1)
Cancer pagurus								
20–30 mm	26.3	(4.4)	2.1	(7.3)	10.5	(6.4)	6.8	(2.5)
30–40 mm	45.1	(4.0)	9.6	(8.0)	19.2	(4.6)	19.2	(5.3)

showed that for all size categories and species of crabs, profitability of the selected size range of *M. edulis* was significantly greater than that of both *O. edulis* and *Crassostrea gigas* (Table 3). No significant differences were detected between profitabilities of the selected size ranges of *O. edulis* and *Crassostrea gigas*. Profitabilities of *M. edulis* and *C. edule* were similar for both small-medium *Carcinus maenas* and *Cancer pagurus*. However, for small *Carcinus maenas* and *Cancer pagurus*, mean profitability values of mussels were significantly higher than those of cockles (Table 4).

Analysis of variance of the breaking times of the selected size ranges of prey revealed that small-medium *Carcinus maenas* took significantly longer to break mussels than cockles (Table 5). Small-medium *Cancer pagurus* took significantly longer to break *Crassostrea gigas* than *M. edulis* of the selected size range (Table 5). Among small crabs, however, significant differences were only detected between prey species with the highest and the lowest breaking times (*C. gigas* > *Cerastoderma edule*). No significant differences were ever detected between the breaking times of the two oyster species.

Fig. 3 Number of prey of various size classes consumed by **A** small and **B** small-medium *Carcinus maenas*, and **C** small and **D** small-medium *Cancer pagurus* during experiments in which prey were offered simultaneously (10 days). Values are mean consumption rates · $crab^{-1}$ · day^{-1} ± SE. The size classes of prey used for these experiments were based on those selected by crabs in single-species experiments and are represented by the total length of each plotted line



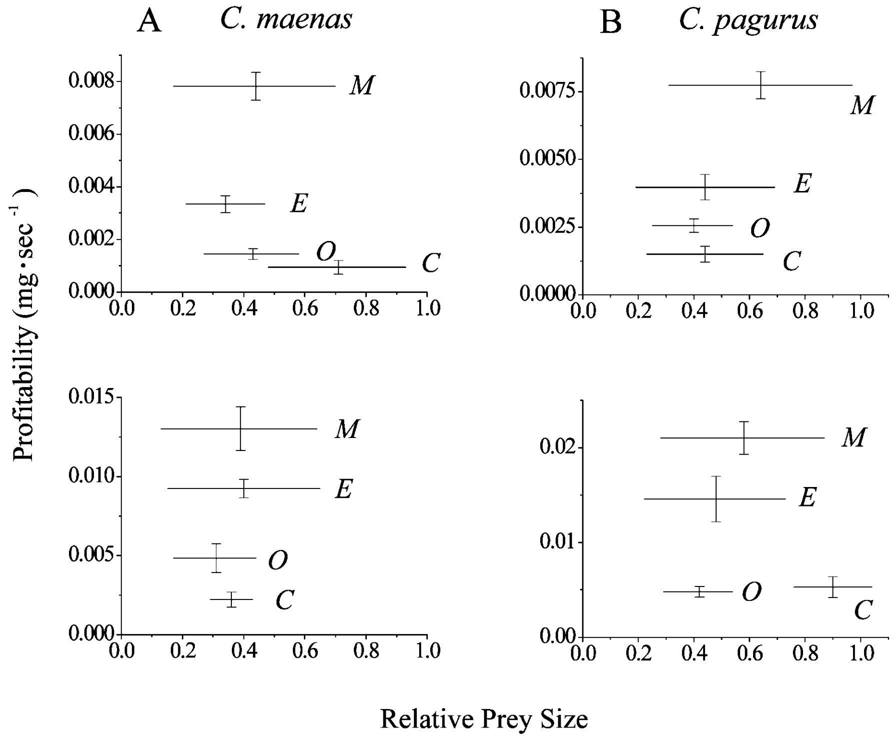


Fig. 4 Mean profitability (±SE) for the selected size range (RPS) of *M. edulis* (*M*), *O. edulis* (*O*), *Crassostrea gigas* (*C*), and *Cerastoderma edule* (*E*) consumed by small (*upper* **A**) and small-medium (*lower* **A**) *Carcinus maenas* and small (*upper* **B**) and small-medium (*lower* **B**) *Cancer pagurus* during handling-time experiments. Significant differences were found between profitability of prey species for all four size categories of crabs (Table 4)

Because crabs generally took similar amounts of time to open all four bivalves, these results suggest that differences in profitability between the selected size ranges of prey were mainly due to differences in their biomass.

Discussion and conclusions

Prey size selection has been frequently reported in a diversity of brachyuran crabs feeding on various species of hard-shelled prey (e.g., Juanes 1992; Hughes and Seed 1995). In the present study juvenile *Carcinus maenas* and *Cancer pagurus* consumed the smallest size classes of *M. edulis* and *Cerastoderma edule* in numbers higher than expected purely by chance (Table 2), suggesting that size-selective predation occurs among these crab–bivalve interactions. However, when feeding on *O. edulis* and *Crassostrea gigas*, both the degree of crab selectivity and the size ranges of selected prey varied with crab size and species (Table 2; Fig. 1). These results indicate that differences in the patterns of size selection among prey species were mainly due to the contrasting morphological features of their shells, and the way these features influence the vulnerability of these prey to crab predation.

The difficulty in comparing the size ranges of the four bivalve species that were selected by *Carcinus maenas* and *Cancer pagurus* emphasizes the need to establish a measure of prey size that takes into account morphological differences between the crab chelae and prey shells that are relevant to crab foraging behavior. Since mechanical advantage of the crusher chela in *Carcinus maenas* and both chelae in *Cancer pagurus* does not vary markedly within crab species (Mascaró 1998), a measure of prey size relative to mechanical advantage is of limited use when prey selection among crabs of different size but of the same species is compared. Relative prey size, calculated as the minimum linear dimension of the shell/chelal height, not only takes into account intra- and interspecific differences in chelal size and strength but reflects the importance of shell shape, volume, and position of prey when handled by crabs in diverse attack strategies (see also Lawton 1989). Figure 3 shows that crabs generally selected prey smaller than or equal to the height of their largest chela (RPS ≤ 1). This is not surprising, since size-selective feeding is strongly related to chelal height (Rheinallt 1986) and testifies to the importance of considering the geometry and crushing resistance of the molluscan shells when studies of crab foraging behavior studies are carried out.

Comparisons between the selective feeding behavior of *Carcinus maenas* and *Cancer pagurus* of similar carapace width based on RPS showed that the relative size of *M. edulis* selected by small and small-medium *C. pagurus* (0.31–0.97 and 0.28–0.87, respectively) was higher than the RPS of those selected by *Carcinus maenas* of comparable carapace width (small: 0.17–0.70; small-medium: 0.15–0.65). Furthermore, the RPS of *M. edulis* selected by *Cancer pagurus* in the present study is higher than that reported by Mascaró and Seed (2000a) for *Carcinus maenas* of 50–70 mm CW feeding on the same mussel species (RPS: 0.15–0.56). These results suggest that *Cancer pagurus* can readily crush larger mussels, relative to the size of their chelae, than *Carcinus maenas* of similar and even greater chelal height. Previous studies have related differences in prey size selection

Table 4 Results of analyses of variance (ANOVA) and pairwise comparisons using Scheffe's method on profitability of *M. edulis* (*M*), *O. edulis* (*O*), *Crassostrea gigas* (*C*), and *Cerastoderma edule* (*E*) selected by *Carcinus maenas* and *Cancer pagurus* of two size categories; *Diff. mn* difference between means; *SEM* standard error of the mean; *LCI* low limit of confidence interval; *HCI* high limit of confidence interval; *NS* no significant difference between pairs of variables

	F	Pairwise comparison	Diff. mn	SEM	LCI	HCI	*P*
Carcinus maenas							
15–25 mm	48.19**	M-O	0.76	0.088	0.50	1.02	*
		M-C	1.03	0.098	0.74	1.31	*
		O-C	0.26	0.113	–0.07	0.59	NS
		M-E	0.37	0.085	0.12	0.62	*
25–30 mm	34.17**	M-O	0.31	0.081	0.072	0.54	*
		M-C	0.67	0.081	0.44	0.91	*
		O-C	0.36	0.100	0.07	0.65	*
		M-E	–0.12	0.061	–0.30	0.05	NS
Cancer pagurus							
20–30 mm	33.75**	M-O	0.48	0.071	0.27	0.68	*
		M-C	0.74	0.086	0.49	0.99	*
		O-C	0.26	0.101	–0.03	0.56	NS
		M-E	0.29	0.068	0.10	0.49	*
30–40 mm	29.47**	M-O	0.63	0.079	0.40	0.86	*
		M-C	0.62	0.094	0.35	0.89	*
		O-C	–0.01	0.109	–0.33	0.30	*
		M-E	0.18	0.089	–0.08	0.44	NS

*$P < 0.05$; **$P < 0.001$

by different species of crabs to their contrasting chelal morphology and general feeding behavior (Rheinallt and Hughes 1985). Bisker and Castagna (1987) showed that mud crabs, *Panopeus herbstii*, had higher predation rates on *Crassostrea virginica* spat than did blue crabs, *Callinectes sapidus*, of similar carapace width. The authors explained their results in terms of the presence of a large molariform tooth in the claw of *P. herbstii* that gives it a distinct mechanical advantage when crushing bivalve shells. Although such a structure is absent from the chelae of *Cancer pagurus*, edible crabs possess powerful monomorphic claws that operate at a signifi-

Table 5 Results of ANOVA and pairwise comparisons using Scheffe's method on breaking time of *M. edulis* (*M*), *O. edulis* (*O*), *Crassostrea gigas* (*C*), and *Cerastoderma edule* (*E*) selected by *Carcinus maenas* and *Cancer pagurus* of two size categories. Kruskal–Wallis and Dunn's method were used for data with heterogeneity of variance; *Diff. mn* difference between means; *SEM* standard error of the mean; *LCI* low limit of confidence interval; *HCI* high limit of confidence interval; *Diff. md* difference between medians; *SD* standard deviation; *NS* no significant difference between pairs of variables

	Test	Pairwise comparison	Diff. mn	SE	LCI	HCI	*P*	Diff. md	SD	Diff. md/SD
Carcinus maenas										
15–25 mm	ANOVA ($F=6.08$**) and Scheffe	M-O	–0.41	0.168	–0.91	0.08	NS			
		M-C	–0.46	0.187	–0.101	0.08	NS			
		O-C	–0.05	0.214	–0.68	0.58	NS			
		M-E	0.25	0.162	–0.22	0.72	NS			
25–30 mm[a]	Kruskal–Wallis ($H=14.67$**) and Dunn	M-O					NS	5.8	6.67	0.87
		M-C					NS	4.4	6.67	0.66
		O-C					NS	1.4	8.26	0.17
		M-E					*	19.0	5.03	3.78
Cancer pagurus										
20–30 mm	Kruskal–Wallis ($H=2.44$, $P=0.49$)	M-O	–	–	–	–	–			
		M-C	–	–	–	–	–			
		O-C	–	–	–	–	–			
		M-E	–	–	–	–	–			
30–40 mm	ANOVA ($F=8.84$ ***) and Scheffe	M-O	–0.20	0.092	–0.46	0.07	NS			
		M-C	–0.55	0.109	–0.86	–0.23	*			
		O-C	–0.35	0.126	–0.71	0.02	NS			
		M-E	–0.06	0.103	–0.36	0.23	NS			

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

[a] Standard error difference = 2.64

cantly higher mechanical advantage than the master chelae of shore crabs (Warner and Jones 1976; Mascaró 1998), allowing edible crabs to exert greater compressive forces than shore crabs of comparable body size.

Differences in the foraging strategies between crab species are partly determined by specific morphological features of the mouth parts and chelipeds but can also be related to differences in behavioral adaptations (e.g., adaptations to swimming or burrowing) that influence crab preference for certain foraging areas (Sponaugle and Lawton 1990). Juvenile crabs from the genus *Cancer* use their monomorphic claws to crush prey, usually molluscs and crustaceans, whereas larger individuals can use their claws to dig prey out of the sediment or for burrowing (Hall et al. 1993). These crabs are restricted to the lower shore beneath stones (adults live mainly offshore on sandy/muddy bottoms), have a generally retiring, relatively quiescent habit, and have been reported to persist with prey for up to several hours, even when alternative items were available (Lawton and Hughes 1985). *Carcinus maenas*, like other portunids, is a tidally migrating species that actively explores and forages in the intertidal zone (Hunter and Naylor 1993). Shore crabs have a varied diet of worms and molluscs, scavenge on dead animal material, and readily reject prey that do not quickly yield (Ropes 1968). An active exploring behavior might increase the probability of *C. maenas* encountering and attempting to open a wider diversity of prey types, whereas the more sedentary and tenacious nature of *Cancer pagurus* might cause crabs to persevere in attacking prey in their immediate surroundings. That both *Carcinus maenas* and *Cancer pagurus* were maintained under the same experimental conditions (i.e., bare-floor aquaria, no tidal variations), despite the differences in foraging strategies and behavioral adaptations between them might have influenced the foraging behavior of crabs observed in this study compared to crabs in their natural habitats. However, natural conditions such as refuges or the influence of tidal variations would probably accentuate the interspecific differences in crab foraging behavior observed throughout this study.

Differences in the order in which several size classes of *M. edulis* were taken by *Carcinus maenas* and *Cancer pagurus* testify to the importance of specific crab characteristics, such as chelal strength and morphology, and crab behavior, in prey size selection. Nevertheless, these differences varied with the prey species that was offered, indicating that interspecific differences in crab foraging behavior are also influenced by the degree of vulnerability among bivalve prey. When crabs were offered *Cerastoderma edule* individually, neither the shell length nor the RPS of selected cockles differed markedly between crab species (Table 2; Fig. 2). When crabs were offered *O. edulis*, the shell length and RPS selected by small *Carcinus maenas* and *Cancer pagurus* were also similar. Although the relatively inflated shell of *Cerastoderma edule* might constitute a highly effective barrier to even the most powerful chelae of *Cancer pagurus*, the reluctance of small crabs of both species to feed on large size classes of *O. edulis* probably reflects the equal difficulty that these crabs experience when manipulating the relatively wider shell of the flat oyster. When feeding on *Crassostrea gigas*, however, the patterns of size selection of *Carcinus maenas* and *Cancer pagurus* of comparable body size differed considerably (Fig. 1). The RPS of Pacific oysters selected by both size categories of *C. pagurus* was substantially larger than that selected by small-medium *Carcinus maenas*, suggesting that large *Crassostrea gigas* are more vulnerable to crushing by *Cancer pagurus* than by *Carcinus maenas*. If variations in prey vulnerability can influence the degree to which crabs predict prey value (Hughes and Elner 1979; Elner and Raffaelli 1980), then it is reasonable to suggest that they can determine, at least in part, the foraging tactic that is most appropriate for each prey species. In this context, results from the present work constitute further evidence of the complex relationship between crab chelae and prey shell, and the importance of this relationship in determining feeding habits and prey preferences of different species of crabs.

When crabs were offered a wide size range of oysters and mussels simultaneously, small-medium *C. maenas* and *Cancer pagurus* consistently selected *M. edulis* (Fig. 4). Contrasting results were obtained when crabs were offered a choice between a wide size range of *O. edulis* and *Crassostrea gigas*, since neither small-medium *Carcinus maenas* nor *Cancer pagurus* exhibited any marked preference for either oyster species (Fig. 4). Comparisons between mean profitability of the selected size ranges of each prey species showed that small-medium crabs obtained a greater energy return when consuming mussels than oysters, whereas *O. edulis* and *Crassostrea gigas* were equally profitable. When given a choice between *M. edulis* and *Cerastoderma edule*, small-medium *Carcinus maenas* and *Cancer pagurus* consumed both prey species in similar numbers (Fig. 4). Small-medium *Carcinus maenas* and *Cancer pagurus* also obtained a similar energy return when consuming mussels and cockles (Table 4). The rank order of prey profitability, therefore, clearly paralleled the order in which prey species were ranked according to consumption rates during feeding experiments (Fig. 3). Previous reports (Mascaró 1998) have shown that opening methods used by juvenile *Carcinus maenas* and *Cancer pagurus* to open *M. edulis, O. edulis, Crassostrea gigas*, and *Cerastoderma edule* of the preferred size range did not vary markedly either within or between prey species. In the present study, crabs used similar crushing methods to open the selected size ranges of each prey species, and small differences in prey opening techniques probably did not have a strong effect on prey profitability. These results provide an indication that prey value can influence prey species selection by crabs >25 mm CW.

Results similar to those reported here have been previously reported by Mascaró and Seed (2000a, b) for adult *Carcinus maenas*, where crabs also consumed the selected size ranges of *M. edulis*, *O. edulis*, *Crassostrea* *gigas*, and *Cerastoderma edule* as predicted by the rank order of their profitability. Their results indicated that differences in profitability among prey species were due mainly to differences in biomass, although breaking times also influenced the position of prey as ranked by their value to crabs. The authors concluded that adult *Carcinus maenas* feeding on prey near the optimal size selected prey species based on shell characteristics that correlated well with prey value.

When the feeding behavior of small crabs was examined, however, prey value did not always parallel the consumption rates of the selected size classes of prey. Although small *C. maenas* and *Cancer pagurus* selected mussels and oysters as predicted by their ranked profitability (Figs. 3, 4), small crabs obtained a significantly higher energy return when feeding on the selected size classes of *M. edulis* than on *Cerastoderma edule* (Table 4) but consumed mussels and cockles at similar rates (Fig. 3). Since both small *Carcinus maenas* and *Cancer pagurus* selected similar size classes of *M. edulis* and *Cerastoderma edule* (Table 2), and since mussel and cockle breaking times were not statistically different for small crabs of either species (Table 5), a strategy of prey species selection based solely on prey value fails to explain entirely results obtained for crabs <25 mm CW.

Variation in crab strength relative to size results in the size range of prey that is accessible to larger, and hence stronger, crabs being greater than for smaller and weaker ones (Lee and Seed 1992). *Carcinus maenas* >25 mm CW actively forage across the shore during high tide (Naylor 1958). Most shore crabs <25 mm, however, tend to be rather more sedentary and do not make these tidal migrations (Dare et al. 1983). Food restrictions and the risk of predation are probably most severe for smaller crabs, whose already limited food resources are depleted by larger individuals (Ropes 1968; Klein-Breteler 1975; Lawton 1989). That small crabs in the present study consumed mussels and cockles in similar numbers despite the lower profitability of the latter might be explained by the need to gain sufficient energy in the shortest time possible to satisfy their metabolic requirements and escape predation by larger crabs of the same or other species.

Rangeley and Thomas (1987) related differences in the proportions of gastropods and barnacles in the diets of juvenile and adult *Carcinus maenas* to variations in the size range of prey that crabs of different size could successfully attack. Juvenile *C. maenas* feed on a narrow size range of prey, reduced by their lack of chelal strength, dexterity, and time required to open prey over a certain size limit. A feeding strategy that includes a wider variety of prey species of a smaller size range might allow these crabs to ingest sufficient biomass to meet the energy requirements for their rapid growth. Large crabs, on the other hand, were always able to open barnacles of any size but had many unsuccessful attacks on gastropods. From the present study, it appears that juvenile shore crabs are limited in their choice in terms of prey size and are thus forced to be less selective regarding prey species. Adult *C. maenas* do not have such a restriction in prey size selection and can thus afford to be more species selective.

Our results suggest that the degree of crab selectivity when presented with mussels and cockles is more restricted among smaller than among larger crabs, presumably as a result of the limitations imposed on small individuals that have restricted access to larger prey items. The reasons why small crabs excluded oysters from their diets, however, remain unexplained. Differences in shell shape, associated with the difficulty in handling the relatively flatter oyster species, and the ability to learn to identify more rewarding prey might explain the reluctance of even the smallest crabs to consume *O. edulis* and *Crassostrea gigas* reported throughout these and other (Dare et al. 1983; Richardson et al. 1993) experiments.

When adult *Carcinus maenas* (40–70 mm CW) were offered a wide range of mussels and cockles simultaneously, crabs showed no preference for either species among the smaller sizes of prey but selected more mussels as prey size increased (Mascaró and Seed 2000a). *Cancer pagurus* in the present study selectively fed on mussels and cockles in a pattern that was more reminiscent of that exhibited by larger, adult *Carcinus maenas* than that of juvenile shore crabs of comparable size. If differences in chelal size and strength make smaller *C. maenas* less species selective in their feeding behavior than larger crabs, then interspecific differences in chelal morphology and occlusive geometry among *C. maenas* and *Cancer pagurus* of similar body size would be expected to have an effect on the degree of prey selectivity in these crabs. Previous studies comparing the crushing abilities of different brachyuran crabs have suggested that those possessing stronger and larger chelae are able to exploit a wider size range of hard-bodied prey (Lee and Seed 1992). These findings, together with variations in the general behavior of different crab species (e.g., aggression, use of refuges, local distribution on the shore), might help to explain some of the differences between the feeding behavior exhibited by *Carcinus maenas* and *Cancer pagurus* reported throughout the present experiments.

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