

# Why do shore crabs not prefer the most profitable mussels?

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## Summary

1. We examined the link between handling time ( $T_h$ ), adopted feeding techniques, profitability curves and prey size selection to further understand the constraints that influence bivalve prey selection in shore crabs (*Carcinus maenas* L.).
2. Blue mussels (*Mytilus edulis* L.) of different sizes were used as prey. Prey size was generalized to the ratio between mussel width and major chela length (MW : MCL) and prey profitability standardized to the ratio between prey mass eaten per unit breaking time and predator mass ( $1/h T_b$ ).
3. Crabs either crushed the mussel with their claws or opened the mussel using the more time-consuming cutter technique. The latter technique was employed above a critical MW : MCL ratio (0.24). This threshold appeared to coincide with the ratio where prey profitability is maximal.
4. When a range of prey sizes were offered simultaneously, an observed MW : MCL ratio (0.14–0.16) turned out to be lower than the predicted optimal MW : MCL ratio (0.16–0.22) and lower than the MW : MCL ratio where the first crab switched feeding techniques (0.16). Crabs preferred a MW : MCL ratio of 0.16 over the optimal ratio of 0.24 when given dichotomous choices between different MW : MCL ratios.
5. Although larger and more profitable mussels can be crushed, we suggest that crabs select small crushable mussels to prevent claw wear and tear. Claw damage has a considerable effect on mating success and hence on an individual's fitness. Risk of claw damage may thus be of greater importance to a foraging shore crab than energy maximization.

**Key-words:** claw damage, energy maximization premise, feeding techniques, prey profitability, prey size selection.

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## Introduction

When selecting prey, predators are thought to weigh costs (in terms of handling time) against benefits (net energy gained) to maximize energy intake per unit handling time. This version of the energy maximization theorem (Emlen 1966; MacArthur & Pianka 1966) is often used to predict optimal prey size for molluscivorous predators (e.g. Elner & Hughes 1978; Sanchez-Salazar, Griffiths & Seed 1987; Mascaró & Seed 2000b). These predictions serve in turn as a basis for understanding how molluscivorous predators influence population characteristics of their prey species (Hughes & Seed 1995; Mascaró & Seed 2000a; Rovero, Hughes & Chelazzi 2000).

Several molluscivorous predators, however, appear to adopt criteria other than maximum energy yield to

select prey. Oystercatchers (*Haematopus ostralegus*) specialized in hammering open bivalves risk damaging their bills and avoid opening large more profitable cockles (*Cerastoderma edule*) (Norris & Johnstone 1998; Johnstone & Norris 2000). Various molluscivorous crab species are suggested to use risk of damage to their claws as the criterion for selection (Juanes & Hartwick 1990; Juanes 1992) because they, too, forage preferably on small, less profitable prey. Thus, prey size selection by molluscivorous predators is not solely determined by energy maximization, but probably also subject to constraints imposed by the risk of damaging the extremities designed to capture prey.

Predictions from the energy maximization theorem are often illustrated in ecology textbooks by data from studies on shore crabs (*Carcinus maenas*) that feed on mussels (*Mytilus edulis*) of different sizes (Krebs & Davies 1987; Begon, Harper & Townsend 1990). However, despite claims for the opposite (Elner & Hughes 1978; Seed & Hughes 1995), prey choice in shore crabs does not seem to be based on maximizing prey profitability alone, because shore crabs systematically prefer

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smaller prey than those that yield the highest prey profitability (Elner & Hughes 1978; Elner 1980). Furthermore, like most molluscivorous crabs, shore crabs forage preferably on bivalve prey well below the critical size that can be opened (Juanes 1992).

Shore crabs have dimorphic claws (chelipeds), having one claw (the major or crusher claw; Elner 1978) larger than the other (the minor or cutter claw; Elner 1978). They adopt five feeding techniques to open bivalve prey (Elner 1978), but these can be lumped into two distinctive feeding techniques (cf. Elner & Hughes 1978). When they feed on small mussels the minor chela is used to steady the prey while the major chela crushes the shell (Crothers 1968). When shore crabs are forced to feed on larger mussels the crabs adopt a second, much slower technique where the shells are cut along the valve's edges (Ameyaw-Akumfi & Hughes 1987).

In this paper we present the results of our studies on shore crab foraging behaviour in terms of breaking time, eating time, feeding techniques employed over a range of prey sizes and crab sizes and ultimate prey size selection. The objective of this study is to identify the constraints that affect bivalve prey size selection in shore crabs. In particular we intend to assess how the feeding techniques adopted are related to prey size and their profitability. We test the predicted prey choice against observations and attempt to explain deviations in terms of the risk of claw damage.

## Methods

Samples of intertidal mussels (*Mytilus edulis* L.) covering as wide a size range as possible were collected in March 2001 from a naturally occurring population on the west coast of Texel, the Netherlands. Mussels were cleaned of any attached fouling organisms after which mussel length (ML, maximum length of the shell), mussel width (MW, minimum length of the shell) and mussel height (MH, maximum height of the axis at right angles to shell length) of each individual were measured to the nearest 0.01 mm using electronic callipers. Mussels were then assigned to one of five size-classes: 3.00–8.99 mm, 9.00–14.99 mm, 15.00–20.99 mm, 21.00–26.99 mm, 27.00–32.99 mm, based on maximum shell length, referred to with the generic indicators as size-class categories 6, 12, 18, 24 and 30 mm.

Shore crabs (*Carcinus maenas* L.) were collected at high tide from gullies in the Balgzand area in the Dutch Wadden Sea, and maintained individually in plastic aquaria (18.0 × 12.5 × 6.5 cm) with a 0.5-cm layer of sand at the bottom. Aquaria were kept submerged in a large basin with continuously running seawater. Water temperature in the basin varied between 11 and 13 °C, and photoperiod was kept constant at a 12-h light : 12-h dark cycle with experiments being carried out in the light period. Only undamaged right-handed male crabs were used in the experiments in order to

reduce variability associated with morphology and gender. Following their capture, each crab was sized according to major chela length (MCL, maximum propodus length) using electronic callipers and assigned to one of five size-classes based on MCL: 3.00–8.99 mm, 9.00–14.99 mm, 15.00–20.99 mm, 21.00–26.99 mm, 27.00–32.99 mm and referred to as generic size-class categories 6, 12, 18, 24 and 30 mm. Carapace width (CW, the maximum distance between the two prominent lateral spines) was also measured to the nearest 0.01 mm. Crabs were accustomed to circumstances in the laboratory during a period of 3 days, and trained to break and eat mussels by giving them *ad libitum* access to small mussels (sizes 6 or 12) which were eaten readily by all experimental crabs. All crabs were starved for 1 week before the start of an experiment in order to standardize hunger levels. After completion of the experiment, crabs were held for a further 10 days to make sure they were not in proecdysis, which none were.

## BREAKING TIME, EATING TIME AND FEEDING TECHNIQUES

The influence of predator size and prey size on handling times and feeding techniques was investigated by offering five individuals of each crab size-class (as based on MCL) a single mussel of each size-class and recording: (1) breaking time ( $T_b$ ), the time from the crab's first physical contact with the prey item, through the period of recognition and shell cracking, to the first bite of exposed flesh; (2) eating time ( $T_e$ ), the period from the end of the breaking time to the completion of the meal and abandonment of the empty shell (this time involves time spent by the crab manipulating and re-breaking the shell to extract all the flesh); and (3) the mechanics of the shell-breaking process, i.e. whether the shell was crushed with application of force from the chelae or whether the shell was opened by means of sawing, poking or biting, the so-called edge-cutting technique. The sum of breaking time and eating time is called the handling time ( $T_h$ ). Each combination of treatments was tested once, resulting in a total of 125 observations. The assumption of a normally distributed error term was tested by visual inspection of a probability plot of the residuals. Handling times were log-transformed. Not all crabs were able to break mussels of all sizes within a reasonable time, and these observations were truncated at the highest observed handling time (28 831 s  $\approx$  8 h).

The experimental design as well as the analysis followed a repeated-measures approach, where each of the five crab individuals (plots) per crab size-class was offered all five mussel size-classes. Analysis of handling times was performed first on all combinations of crab size and mussel size. However, this procedure led to a large number of truncated observations, which in turn may lead to an underestimation of the variances which can significantly influence the interaction term as well

as the other terms, particularly in crab size-class 6 and mussel size-class 30. Therefore, the statistical analysis was performed using only crab sizes categories 12, 18, 24 and 30 and mussel size categories 6, 12, 18 and 24, where 15 of 80 observations were truncated. This 'repeated-measures' design (Crowder & Hand 1990) was analysed statistically with the appropriate ANOVA procedures in SYSTAT 10 (Wilkinson 1990). The effect of the fixed factor crab size (3 d.f.) was tested using the random factor plots within each crab size (16 d.f.) as the error term. For the effects of the fixed factor mussel size (3 d.f.) and the interaction between crab size and mussel size (9 d.f.) the residual was used as the error term. No interaction between mussel size and plots within crab size was assumed. The temperature of the seawater varied slightly between days ( $T_{\text{average}} = 11.9 \pm 0.5$  °C), and it was unclear whether the sequence of events during a day would have an influence on the behaviour of the crabs. These latter two factors might contribute to the variability in the observed data, and therefore each individual was observed once on each day and once at each time of day, so day (4 d.f.) and time of day (4 d.f.) are blocking factors within plots, arranged in a Latin square. Thus in total five mussels were offered to each crab: one every day, but always at a different time, and each time a mussel of different size.

Predictions by Elner & Hughes (1978) on optimal prey size are based on prey profitability curves in terms of energy yield per unit breaking time. Therefore, emphasis is put upon breaking time and a further analysis by means of regression modelling was performed, to explore whether observed differences in breaking time could be related simply to the ratio between the size of the mussel (i.e. mussel width) and the size of the chela. A logit regression was applied to relate the probability of crushing to (relative) prey size (McCullagh & Nelder 1989).

#### PREY PROFITABILITY AND PREY SIZE SELECTION

A total of 19 male shore crabs were frozen and processed as described in Beukema (1976) to estimate ash-free dry mass. The relationship between crab body mass ( $M$ , g) and major chela length (MCL, mm) did not differ from an isometric relationship ( $\log(M) = -7.184 + 2.6 (\pm 0.16 \text{ SE}) \cdot \log(\text{MCL})$  ( $R^2 = 0.94$ ); slope did not differ significantly from 3), indicating a similar shape for smaller and larger crabs. Both profitability and prey size are scaled to the size of the crab to enable a single analysis for all crab size-classes combined. Prey size is given by the ratio between mussel width and major chela length (MW : MCL), profitability by the ratio between prey mass eaten per unit of breaking time and predator mass. Hence prey size is expressed by a dimensionless number, profitability has the dimension one over time.

A dichotomous preference test was carried out using (fresh) crabs of size 18 and 24. Starved crabs are known

to always open the first mussels encountered and to select mussels only after a short period of feeding (Jubb, Hughes & ap Rheinallt 1983). Crabs were therefore not starved but were fed excessive pollack-bait for 30 min (after which all crabs were satiated) 12 h before the start of a trial. Trials were conducted in the same aquaria in which crabs were housed. Because crabs locate individual mussels by touch, relative abundances of differently sized mussels were quantified by total surface area. The surface area ( $MW \times ML$ ,  $A$ ,  $\text{mm}^2$ ) of a mussel was related to its shell length (ML, mm) according to  $A = 0.32 \cdot ML^2$  ( $R^2 = 0.99$ ). Depending on the optimal MW : MCL ratio, mussels were assigned to four MW : MCL ratio classes. All pairwise ratio combinations were offered randomly to the crabs using four replicates, while the total surface area of all mussel sizes offered was kept equal. Three statistical models were distinguished that describe the preference process and results were analysed within the framework of the logit model (Van der Meer 1992). The most elaborate model is the full model (McCullagh & Nelder 1989), which has as many parameters as there are combinations of size-classes, so the probabilities match the observed proportions exactly for each combination of size-classes. A model of intermediate complexity is the cardinal rank model (Bradley & Terry 1952), which represents each prey type on a linear scale. The difference in scores on this scale (the so-called cardinal ranks) between two prey types is related to the preference probability by means of an s-curved logit function. The most simple model is the random choice model where probabilities equal  $1/2$ . Model selection was based on the likelihood ratio  $\chi^2$  test.

The isometric relationship between mussel length (ML, mm) and mussel width (MW, mm) for mussels that were consumed in this study was  $MW = 0.36 \cdot ML$  ( $R^2 = 0.96$ ). This relationship was used to compare the mussel size preference of crabs that have unlimited access to a range of prey sizes (Elner & Hughes 1978), with the optimal mussel size in terms of prey profitability as predicted in this study and by Elner & Hughes (1978).

#### Results

The relationship between carapace width ( $x$ ) and major chela length ( $y$ ) of crabs in this study could best be described by a two-phase linear regression model, and not by a simple isometric ( $\log(y) = \log(\alpha) + \log(x)$ ) or an allometric relationship ( $\log(y) = \log(\alpha) + \beta \cdot \log(x)$ ) (Table 1). The two-phase model is given by  $\log(y) = \log[\alpha_1(x) + \alpha_2(x > \gamma)(x - \gamma)]$ , where  $\alpha_2$  refers to an increase in the slope for carapace width greater than the breakpoint  $\gamma$ , and  $(x > \gamma)$  is a boolean function with value 1 if the condition  $x > \gamma$  is fulfilled and value 0 otherwise. Both the two-phase model as well as the allometric model differed from the isometric model (Table 1). Hitherto, the two-phase model exhibited the lowest Akaike Information Criterion (AIC) value; the

**Table 1.** Comparison of regression models to describe relationship between carapace width ( $x$ , mm) and major chela length ( $y$ , mm) for male shore crabs ( $AIC = RSS + c \cdot d \cdot \hat{\sigma}^2$ ; 'c' is set at 3 (see Atkinson (1981) for a detailed description of 'c'), 'd' is the number of estimable parameters used in the model,  $\hat{\sigma}^2$  is the mean square of the most elaborate model)

Model	Residual SS	d.f.	Model vs.	$F$	$P$	AIC, $c = 3$
1: $\log(y) = \log(\alpha) + \log(x)$	0.185	24	—	—	—	0.197
2: $\log(y) = \log(\alpha) + \beta \log(x)$	0.122	23	1	12.60	< 0.010	0.146
3: $\log(y) = \log(\alpha_1 \cdot (x - \gamma) + \alpha_2 \cdot (x > \gamma)(x - \gamma))$	0.085	22	1	12.50	< 0.001	0.121

**Table 2.** Results of the repeated measures analysis based on crab size-class categories 12, 18, 24, 30 mm MCL, and mussel size-class categories 6, 12, 18, and 24 mm ML, with log(handling time) as the dependent variable

Factor	SS	d.f.	MS	$F$ -ratio vs.	$F$	$P$
Among plots						
Crab size (C)	26.276	3	8.759	I(C)	6.738	< 0.010
Crab individual, I(C)	20.842	16	1.303			
Within plots						
Mussel size (M)	189.896	3	63.299	Residual	114.043	< 0.001
M*C	4.305	9	0.478	Residual	0.862	0.566
Day	0.610	4	0.153			
Time of day	3.572	4	0.893			
Residual	22.202	40	0.555			

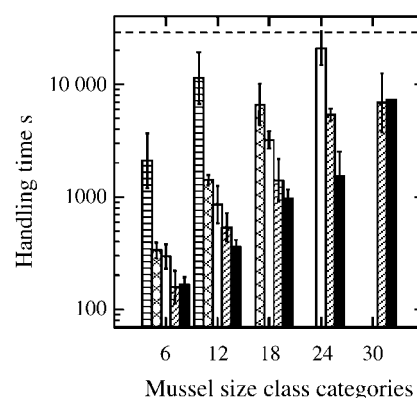
latter provides an objective criterion for selecting among statistical models that are not nested within each other (Akaike 1987) (Table 1). The 'breakpoint ( $\gamma$ )' was estimated at 30.9 (with 95% confidence limits 20.3 and 41.6) mm carapace width. We realize that carapace width and major chela length do not scale isometrically, but assume that this has a negligible effect on further analyses on MW : MCL ratios and subsequent inferences.

#### BREAKING TIME, EATING TIME AND FEEDING TECHNIQUES

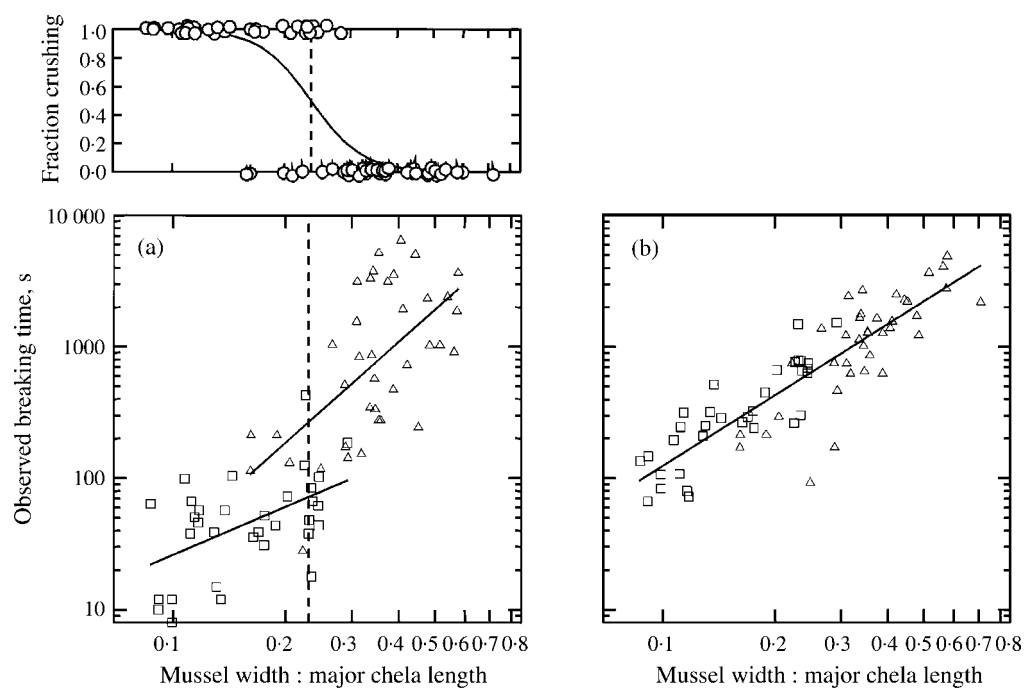
Most of the variation in handling time could be attributed to the main factors 'mussel size' and 'crab size' (Table 2). The interaction term was not significant. All crabs needed more time to open and eat larger mussels than smaller ones, but larger crabs needed less time than smaller crabs (Fig. 1).

Shore crabs adopted two feeding techniques when offered mussels; they either crushed the mussel or they cut the valves' edges, depending on mussel size. A logit regression showed a significant breakpoint at mussel width : major chela length = 0.24 ( $\pm 0.014$  SE) (Fig. 2a). Hence, if the width of the mussel was approximately more than a quarter of the major chela length, shore crabs tended to open the mussel by the slower method of cutting, sawing or biting, instead of crushing the mussel.

In exploring whether these differences in breaking time could be attributed to a simple relation between the size of the mussel relative to the size of the chela, several models are proposed (Table 3), where a distinction is made between crabs that adopt the crusher technique ( $i = 0$ ) and cutter technique ( $i = 1$ ). Basically,

**Fig. 1.** Average handling times (s) of mussel size-class categories 6, 12, 18, 24 and 30 mm ML given for crab size categories 6 (horizontally hatched bars), 12 (cross-hatched bars), 18 (open bars), 24 (obliquely hatched bars) and 30 mm MCL (solid bars), with standard error bars indicated. Note that observations are truncated at dotted line denoting highest observed handling time ( $T_h = 28\,831$  s).

these models differ in two aspects. First, breaking time can be described either by a simple allometric relation with the ratio mussel width ( $x_1$ ) to major chela length ( $x_2$ ) (models 1 and 2), or by a more complicated allometric relation with mussel width and major chela length as two separate independent variables (models 3 and 4). Secondly, similar relations ( $\beta, \gamma, \delta$ ) or dissimilar relations ( $\beta_i, \gamma_i, \delta_i$ ) are distinguished between crabs that adopt the crusher and cutter technique. In all proposed models, different intercepts are assumed for the crusher and cutter technique. Model 1 is nested within models 2 and 3, and model 2 is nested within model 4. Model 2 differed from model 1 (Table 3). Model 3 did not differ from model 1, and model 4 did not differ from model 2 (Table 3). Model 2 also showed

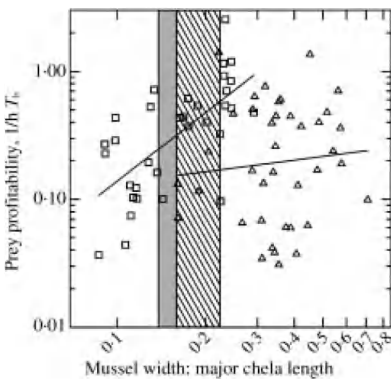


**Fig. 2.** (a) The relationship between observed breaking time (s) and ratio mussel width : major chela length and relationship between probability of crushing and ratio mussel width : major chela length; both graphs show the threshold (0.24) at which crabs switched feeding techniques. (b) The relationship between observed eating time (s) and the ratio mussel width : major chela length. Calculated regression lines are shown (see text);  $\square$  denotes crusher technique ( $n = 33$ ) and  $\triangle$  denotes cutter technique ( $n = 39$ ).

the lowest AIC-value and thus best described the joint effect of mussel size and chela size on breaking time with a simple ratio of mussel width and chela length. The cutter technique showed a greater increase in breaking time with increasing ratio of mussel width to chela length than the crusher technique (Fig. 2a). Model 2 is parameterized for the crusher technique as  $\log(y) = 6.061 + 1.2 \log(x_1/x_2)$ , and for the cutter technique as  $\log(y) = 9.514 + 2.7 \log(x_1/x_2)$ . A similar analysis revealed that eating time ( $z$ ) did not differ between feeding techniques (Fig. 2b) and is parameterized as  $\log(z) = 9.069 + 1.9 \log(x_1/x_2)$ .

**PREY PROFITABILITY AND PREY SIZE SELECTION**

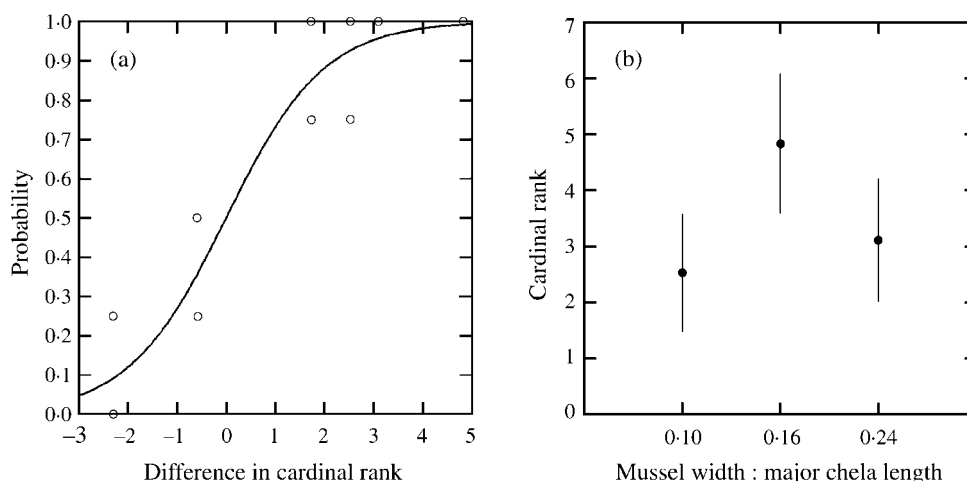
Correcting prey profitability ( $1/h T_b$ ) for crab body mass showed that for each feeding technique prey profitability always increased with increasing mussel width in relation to major chela length (Fig. 3). The optimal size in terms of prey profitability coincided with the ratio of 0.24 MW : MCL where crabs switched feeding



**Fig. 3.** Relationship between prey profitability based on observed breaking time ( $1/h T_b$ ) and the ratio mussel width : major chela length, where  $\square$  denotes crusher technique ( $n = 33$ ) and  $\triangle$  denotes cutter technique ( $n = 39$ ). Grey box denotes observed preferred prey size with unlimited availability to a range of prey sizes in relation to major chela length for crabs of carapace width 50–55 mm (–crab size 30), as observed by Elner & Hughes (1978). Dashed box denotes expected preferred prey size in relation to major chela length for crabs of carapace width 50–55 mm, as observed by Elner & Hughes (1978) (see also Table 4).

**Table 3.** Comparison of regression models to describe the allometric relationship between mussel width  $x_1$  (mm), major chela length  $x_2$  (mm) and breaking time  $y$  (s) for male shore crabs with  $i = 0$  for crusher technique or  $i = 1$  for cutter technique

Model	Residual SS	d.f.	Model vs.	<i>F</i>	<i>P</i>	AIC, <i>c</i> = 3
1: $\log(y) = \alpha_i + \beta \log(x_1/x_2)$	65.985	69	–	–	–	73.68
2: $\log(y) = \alpha_i + \beta_i \log(x_1/x_2)$	61.182	68	1	5.338	< 0.01	71.44
3: $\log(y) = \alpha_i + \gamma \log(x_1) + \delta \log(x_2)$	65.977	68	1	0.649	NS	76.25
4: $\log(y) = \alpha_i + \gamma_i \log(x_1) + \delta_i \log(x_2)$	56.397	66	2	2.800	NS	71.78



**Fig. 4.** Results of the cardinal rank model visualized by two plots that show the estimated relationship between the probability of taking the smallest mussel and the difference in cardinal rank (a), and the relationship between the cardinal rank, including standard errors, and the ratio mussel width : major chela length (b).

**Table 4.** Observed and expected preferred mussel sizes in a diet with unrestricted prey availability (after Elner & Hughes 1978) with accompanying MW : MCL ratios. Major chela length is derived from  $\log(\text{MCL}) = \log(0.512(\text{CW} - 30.9) + 0.178(\text{CW} > 30.9)(\text{CW} - 30.9) + 0.512 \cdot 30.9)$ ;  $\text{MW} = 0.36 \text{ ML}$

Carapace width (mm)	Major chela length (mm)	Observed preferred size (mm)		MW : MCL observed preferred mussel size	Expected preferred size (mm) based on $E/T_b$		MW : MCL expected preferred mussel size
		Mussel length	Mussel width		Mussel length	Mussel width	
50–55 (~crab size 30)	29–32	12.5	4.5	0.14–0.16	15.0–17.5	5.4–6.3	0.16–0.22
60–65	36–39	17.5	6.3	0.16–0.18	20.0–22.5	7.2–8.1	0.18–0.23
70–75	43–46	22.5	8.1	0.18–0.19	22.5–27.5	8.1–9.9	0.18–0.23

techniques. This optimal ratio corresponded with the expected preferred optimal mussel size in relation to major chela length as observed by Elner & Hughes (1978) (Table 4). However, the actual observed preferred mussel sizes by crabs feeding on a range of mussel sizes as observed by Elner & Hughes (1978) were lower than the expected preferred size range (Table 4), and for crabs of size 50–55 mm carapace width (~crab size 30) lower than MW : MCL ratio (0.16), where in this study the first crab switched feeding techniques (Fig. 3).

In the dichotomous preference test the four MW : MCL ratio classes were set at 0.10; 0.16 (where the first crab switched feeding techniques); 0.24 (optimal ratio); and 0.36. The total surface area of all mussels within each ratio class equalled  $4026 \text{ mm}^2$  ( $\pm 191 \text{ mm}^2 \text{ SD}$ ). The deviance of the full model is by definition equal to zero. The full model (deviance = 0, d.f. = 0) did not differ from the cardinal rank model (deviance = 6.4, d.f. = 9). The cardinal rank model differed from the random choice model (deviance 43.0, d.f. = 12) (Fig. 4a). A cardinal rank model with different prey size preference of crabs of size 18 and size 24 did not show a significantly better fit (deviance 4.9, d.f. = 6). The MW : MCL = 0.16 class got the largest cardinal rank, followed by the optimal MW : MCL

ratio = 0.24. The largest ratio (0.36) was least attractive (Fig. 4b).

## Discussion

Optimal intake rates are no longer defined by energy maximization alone. It has already been suggested to use Charnov's model on diet choice (where predators encounter one prey item at a time) (Charnov 1976) as a means of describing a constraint on intake rate rather than as the explicit optimality model (Norris & Johnstone 1998). Extensions of the diet choice model (Gilliam 1990) include predation risk minimization and predict that foragers should minimize predation risk per unit energy gain. This behaviour, however, is very plastic and in the absence of predators a number of animals have been shown to no longer minimize predation risk but to follow the energy maximization premise (Werner *et al.* 1983). In the classical example of prey size selection based on the energy maximization premise (where predators encounter multiple prey items) (Emlen 1966; MacArthur & Pianka 1966), shore crabs preferably selected mussels smaller than the predicted most profitable size (Elner & Hughes 1978). Therefore, we revisited the latter study and combined handling time, adopted feeding techniques, profitability

curves and preferred prey sizes as observed in this study and by Elner & Hughes (1978) to investigate multiple constraints in bivalve prey size selection by shore crabs.

We studied crabs of different sizes that fed on a range of mussel sizes and found that shore crabs shifted from the method of directly crushing the entire mussel to the time-consuming cutter technique when the width of the mussel offered was 0.24 times the length of the major chela. The highest prey profitability was also reached at that point and was in agreement with the optimal mussel width to major chela length ratio (MW : MCL), as predicted by Elner & Hughes (1978). However, crabs selectively preferred suboptimal prey sizes (Elner & Hughes 1978); for instance, crabs of carapace width 50–55 mm (~crab size 30) preferred mussels within the range 0.14–0.16 MW : MCL, which was lower than the expected preferred size range (0.16–0.22 MW : MCL) (Elner & Hughes 1978) and lower than the ratio (0.16 MW : MCL), where in this study the first crab switched to the cutter technique. Although the ratio MW : MCL of the actual preferred mussel sizes as observed by Elner & Hughes (1978) increased with increasing crab size, this ratio was always lower than the optimal ratio of 0.24 (Table 4). The preferred MW : MCL ratio for crabs of 35–47 mm carapace width in our prey size selection experiment was also not the optimal ratio of 0.24 but 0.16, confirming that shore crabs select suboptimally in terms of prey profitability.

In our and Elner & Hughes's (1978) prey size selection experiments it was observed that crabs preferably adopted the crusher technique to open mussels. This preference for smaller size-classes of molluscan prey well below the critical size that can be opened by crushing is characteristic of many crabs (Juanes 1992). It would seem that crabs prefer to crush in the safe zone, i.e. although larger mussels can be crushed, crabs select small mussels to prevent chela wear and damage. Juanes & Hartwick (1990) demonstrated that Dungeness crabs (*Cancer magister*) with damaged (broken dactylus or propodus) or worn chelae were unable to feed successfully on a hard-shelled bivalve (*Protothaca staminea*). Elner (1980) showed that shore crabs with smaller-than-average chelae (i.e. presumably regenerating) selected smaller-sized mussels than 'normal' crabs. Furthermore, the probability of incurring damage to the chelae is likely to increase with increasing breaking time (Juanes 1992), pressing crabs to reduce breaking time and select for easily crushable small mussels.

Although not predicted, the observed preferred MW : MCL ratio increased with increasing crab size (Elner & Hughes 1978). Older and thus larger crabs spend more time between successive moults and eventually lose the ability to moult (Crothers 1967). Crabs that prolong intermoult or enter terminal moult develop stronger and thicker carapaces and chelae (Reid *et al.* 1997), and the crusher chelae of these crabs are capable of exerting greater forces (Kaiser, Hughes

& Reid 1990). These crabs can also apply crushing forces in slower pulses, which is known to be more effective in propagating stress fractures in the shells of molluscan prey (Boulding & Labarbera 1986). Crabs in prolonged intermoult or terminal moult would thus be able to crush larger mussels and increase their prey profitability without increasing the risk of chela wear or damage.

Previous studies have reported that mussel width is indeed an important characteristic determining prey size selection in shore crabs (Kaiser, Hughes & Gibson 1993) and in other crab species (Boulding 1984) and decapods (Griffiths & Seiderer 1980). Breaking force required to crush mussels scales linearly with shell mass (Currey 1979; Vermeij & Currey 1980; Piersma, Koolhaas & Dekinga 1993). For crabs of 8–55 mm carapace width a simple ratio of mussel width and major chela length best described their joint effect on breaking time, indicating that the relatively greater forces needed to break a shell are compensated by a relatively larger increase in chela crushing force. The latter can be explained when the mechanical properties of the chela muscle are considered. Crushing force of the major chela is exerted by a large pennate flexor in the chela (Kaiser *et al.* 1990), which has fibres of length  $\lambda$  that exert a stress (force per unit cross-sectional area)  $\sigma$  (Alexander 1983). The total cross-sectional area of the fibres in the flexor muscle with volume  $V$  is  $V/\lambda$ , resulting in a total exerted force of approximately  $V \cdot \sigma / L$  (Alexander 1983). As the parameters  $\lambda$  and  $\sigma$  are probably constant among individuals of the same species (Lee 1993), differences in exerted force due to differences in chela size are mainly determined by differences in muscle volume  $V$  that scale with muscle mass. This indicates that the relatively greater forces needed to break a shell are indeed compensated by a relatively larger increase in chela crushing force. One study confirms a linear increase of major chela crushing force with crab body mass (Preston *et al.* 1996), but others report that maximum closing force of the chelae is a linear measure of chela length (Lee 1993; Levinton & Judge 1993; Block & Rebach 1998).

Considering the feeding techniques in terms of energy maximization per unit breaking time, shore crabs gain relatively higher profitabilities when handling small crushable prey (relative to their chela length) than when handling prey that are large relative to their chela length. In accordance with Elner & Hughes (1978) we used  $E/T_b$  as a measure of prey profitability. Breaking time increased linearly with mussel size for the crusher technique and cubically for the cutter technique, while eating time increased quadratically with mussel size for both feeding techniques. This implies that the predicted prey size preference of crabs would even shift to larger prey if prey profitability is expressed as  $E/T_h$  instead of  $E/T_b$ , which is a more obvious choice.

Although crabs may minimize predation risk by minimizing handling times (Gilliam 1990), this behaviour

is very plastic and when resources are exceptionally rich or when predators are absent (as in this study) foraging animals follow the energy maximization premise (Werner *et al.* 1983; Gilliam & Fraser 1987). Hence, to explain the mismatch between optimal and observed prey preferences in shore crabs, risk of claw damage due to chelae fatigue or dactylus breakage cannot be discarded. Both claw damage and claw autotomy in males of different crab species have a considerable effect on sexual behaviour and eventual mating success (Weis 1976; Sekkelsten 1988; Smith 1992; Juanes & Smith 1995). For instance, shore crabs in the mating season congregate in hot spots where male crabs fight vigorously over access to females, which are only receptive for a limited period of time in summer (Van der Meeren 1994). Because only undamaged (large) males are more likely to get access to receptive females than others are (Lee & Seed 1992; Abelló *et al.* 1994; Reid *et al.* 1994), fitness is greatly reduced with claw damage and possible subsequent claw autotomy. Risk of claw damage is not unlikely and may to molluscivorous crabs even be of greater importance in terms of fitness than short-term energy maximization. In studies on patch choice (Clark *et al.* 1999) and prey size selection (Jubb *et al.* 1983; Ameyaw-Akumfi & Hughes 1987; Hughes & Seed 1995; Mascaró & Seed 2000a; Rovero *et al.* 2000), a predator is assumed to maximize its fitness by maximizing its rate of energy intake. This assumption is met only partially if other constraints outweigh energy maximization and may alter conclusions on optimal prey size selection and a predator's potential to influence its prey population structure.

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### References

- Abelló, P., Warman, C.G., Reid, D.G. & Naylor, E. (1994) Chela loss in the shore crab *Carcinus maenas* (Crustacea: Brachyura) and its effect on mating success. *Marine Biology*, **121**, 247–252.
- Akaike, H. (1987) Factor analysis and AIC. *Psychometrika*, **52**, 317–332.
- Alexander, R. & McN. (1983) *Animal Mechanics*, pp. 10–11. Blackwell Scientific Publications, Oxford.
- Ameyaw-Akumfi, C. & Hughes, R.N. (1987) Behaviour of *Carcinus maenas* feeding on large *Mytilus edulis*. How do they assess the optimal diet? *Marine Ecology Progress Series*, **38**, 213–216.
- Atkinson, A.C. (1981) Likelihood ratios, posterior odds and information criteria. *Journal of Econometrics*, **16**, 15–20.
- Begon, M., Harper, J.L. & Townsend, C.R. (1990) *Ecology: Individuals, Populations, and Communities*, pp. 299–302. Blackwell Scientific Publications, Oxford.
- Beukema, J.J. (1976) Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. *Netherlands Journal of Sea Research*, **10**, 236–261.
- Block, J.D. & Rebach, S. (1998) Correlates of claw strength in the rock crab, *Cancer irroratus* (Decapoda, Brachyura). *Crustaceana*, **71**, 468–473.
- Boulding, G.E. (1984) Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. *Journal of Experimental Biology and Ecology*, **76**, 201–233.
- Boulding, G.E. & Labarbera, M. (1986) Fatigue damage: repeated loading enables crabs to open larger bivalves. *Biology Bulletin*, **171**, 538–547.
- Bradley, R.A. & Terry, M.E. (1952) The rank analysis of incomplete block designs. I. The method of paired comparisons. *Biometrika*, **39**, 324–345.
- Charnov, E.L. (1976) Optimal foraging: attack strategy of a mantid. *American Naturalist*, **110**, 141–151.
- Clark, M.E., Wolcott, T.G., Wolcott, D.L. & Hines, A.H. (1999) Intraspecific interference among foraging blue crabs *Callinectes sapidus*: interactive effects of predator density and prey patch distribution. *Marine Ecology Progress Series*, **178**, 69–78.
- Crothers, J.H. (1967) The biology of the shore crab *Carcinus maenas* (L.) 1. The background-anatomy, growth and life history. *Field Studies*, **2**, 407–434.
- Crothers, J.H. (1968) The biology of the shore crab *Carcinus maenas* (L.) 2. The life of the adult crab. *Field Studies*, **2**, 579–614.
- Crowder, M.J. & Hand, D.J. (1990) *Analysis of Repeated Measures*. Chapman and Hall, New York.
- Currey, J.D. (1979) The effect of drying on the strength of mollusc shells. *Journal of Zoology*, **188**, 301–308.
- Elner, R.W. (1978) The mechanics of predation by the shore crab, *Carcinus maenas* (L.), on the edible mussel, *Mytilus edulis* L. *Oecologia*, **36**, 333–344.
- Elner, R.W. (1980) The influence of temperature, sex and chela-size in the foraging strategy of the shore crab *Carcinus maenas* (L.). *Marine and Freshwater 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.
- Emlen, L.M. (1966) The role of time and energy in food preference. *American Naturalist*, **100**, 611–617.
- Gilliam, J.F. (1990) Hunting by the hunted: optimal prey selection by forager under predation hazard. In: *Behavioural Mechanisms of Food Selection* (ed. R.N. Hughes), pp. 797–818. NATO ASI Series G: Ecological Sciences (20). Springer Verlag, Berlin.
- Gilliam, J.F. & Fraser, D.F. (1987) Habitat selection under predator hazard: test of a model with foraging minnows. *Ecology*, **68**, 1856–1862.
- Griffiths, C.L. & Seiderer, J.L. (1980) Rock-lobsters and mussels-limitations and preferences in a predator-prey system. *Journal of Experimental Biology and Ecology*, **44**, 95–109.
- Hughes, R.N. & Seed, R. (1995) Behavioural mechanisms of prey selection in crabs. *Journal of Experimental Biology and Ecology*, **193**, 225–238.
- Johnstone, I. & Norris, K. (2000) Not all oystercatchers *Haematopus ostralegus* select the most profitable common cockles *Cerastoderma edule*: a difference between feeding methods. *Ardea*, **88**, 137–153.
- 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 effects of claw damage. *Ecology*, **71**, 744–758.
- Juanes, F. & Smith, L.D. (1995) The ecological consequences of limb damage and loss in decapod crustaceans: a review and prospectus. *Journal of Experimental Biology and Ecology*, **193**, 197–223.



- Jubb, C.A., Hughes, R.N. & Rheinallt, A.T. (1983) Behavioural mechanisms of size-selection by crabs, *Carcinus maenas* (L.) feeding on mussels, *Mytilus edulis* L. *Journal of Experimental Biology and Ecology*, **66**, 81–87.
- Kaiser, M.J., Hughes, R.N. & Gibson, R.N. (1993) The effect of prey shape on the predatory behaviour of the common shore crab *Carcinus maenas* (L.). *Marine and Freshwater Behaviour and Physiology*, **22**, 107–117.
- Kaiser, M.J., Hughes, R.N. & Reid, D.G. (1990) Chelal morphometry, prey-size selection and aggressive competition in green and red forms of *Carcinus maenas* (L.). *Journal of Experimental Biology and Ecology*, **140**, 121–134.
- Krebs, J.R. & Davies, N.B. (1987) *An Introduction to Behavioural Ecology*. Blackwell Scientific Publications, Oxford.
- Lee, S.Y. (1993) Chela height is an acceptable indicator of chela strength in *Carcinus maenas* (Linnaeus, 1758) (Decapoda, Brachyura). *Crustaceana*, **65**, 115–117.
- Lee, S.Y. & Seed, R. (1992) Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Liocarcinus holsatus*. *Marine Ecology Progress Series*, **84**, 151–160.
- Levinton, J.S. & Judge, M.L. (1993) The relationship of closing force to body size for the major claw of *Uca pugnax* (Decapoda: Ocypodidae). *Functional Ecology*, **7**, 339–345.
- MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *American Naturalist*, **100**, 603–609.
- Mascaró, M. & Seed, R. (2000a) Foraging behavior of *Carcinus maenas* (L.): comparisons of size-selective predation on four species of bivalve prey. *Journal of Shellfish Research*, **19**, 283–291.
- Mascaró, M. & Seed, R. (2000b) Foraging behavior of *Carcinus maenas* (L.): species-selective predation among four bivalve species. *Journal of Shellfish Research*, **19**, 293–300.
- McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*. Chapman & Hall, London.
- Norris, K. & Johnstone, I. (1998) The functional response of oystercatchers (*Haematopus ostralegus*) searching for cockles (*Cerastoderma edule*) by touch. *Journal of Animal Ecology*, **67**, 329–346.
- Piersma, T., Koolhaas, A. & Dekinga, A. (1993) Interactions between stomach structure and diet choice in shorebirds. *Auk*, **110**, 552–564.
- Preston, S.J., Revie, I.C., Orr, J.F. & Roberts, D. (1996) A comparison of the strength of gastropod shells with forces generated by potential crab predators. *Journal of Zoology*, **238**, 181–193.
- Reid, D.G., Abelló, P., Kaiser, M.J. & Warman, C.G. (1997) Carapace colour, inter-moult duration and the behavioural and physiological ecology of the shore crab *Carcinus maenas*. *Estuarine, Coastal and Shelf Science*, **44**, 203–211.
- Reid, D.G., Abelló, P., Warman, C.G. & Naylor, E. (1994) Size related mating success in the shore crab *Carcinus maenas*. *Journal of Zoology*, **232**, 397–407.
- Rovero, F., Hughes, R.N. & Chelazzi, G. (2000) When time is of the essence: choosing a currency for prey-handling costs. *Journal of Animal Ecology*, **69**, 683–689.
- Sanchez-Salazar, M.E., Griffiths, C.L. & Seed, R. (1987) The effect of size and temperature on the predation of cockles *Cerastoderma edule* (L.) by the shore crab *Carcinus maenas* (L.). *Journal of Experimental Biology and Ecology*, **111**, 181–193.
- Seed, R. & Hughes, R.N. (1995) Criteria for prey size-selection in molluscivorous crabs with contrasting claw morphologies. *Journal of Experimental Biology and Ecology*, **193**, 177–195.
- Sekkelsten, G.I. (1988) Effect of handicap on mating success in male shore crabs *Carcinus maenas*. *Oikos*, **51**, 131–134.
- Smith, L.D. (1992) The effect of limb autotomy on mate competition in blue crabs *Callinectes sapidus* Rathbun. *Oecologia*, **89**, 494–501.
- Van der Meer, J. (1992) Statistical analysis of the dichotomous preference test. *Animal Behaviour*, **44**, 1101–1106.
- Van der Meeren, G.I. (1994) Sex- and size-dependent mating tactics in a natural population of shore crabs *Carcinus maenas*. *Journal of Animal Ecology*, **63**, 307–314.
- Vermeij, J. & Currey, J.D. (1980) Geographical variation in the strength of thaidid snail shells. *Biology Bulletin*, **158**, 383–389.
- Weis, J.S. (1976) Effects of environmental factors on regeneration and moulting in fiddlers crab. *Biology Bulletin*, **150**, 151–162.
- Werner, E.E., Gilliam, J.F., Hall, D.J. & Mittelbach, G.G. (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, **64**, 1540–1548.
- Wilkinson, C.M. (1990) *SYSTAT: the System for Statistics*. Systat Inc., Evanston, IL.

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