Handling methods used by the velvet swimming crab *Liocarcinus puber* when feeding on molluscs and shore crabs

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ABSTRACT: Velvet swimming crabs *Liocarcinus puber*, collected in Gwynedd, N. Wales, were observed feeding in the laboratory on winkles *Littorina rudis*, mussels *Mytilus edulis*, and juvenile shore crabs *Carcinus maenas*. Handling methods were recorded, and for mussels and shore crabs only, handling times were measured. Since *C. maenas* is mobile and can escape from some attacks, attack success rate was quantified for this prey. Specific methods for opening larger molluscs were apparently determined by geometry and strength of shell, which limited the positions in which the chela could exert sufficient force without slipping. No specialized opening techniques existed for small molluscs, which were crushed outright, and for shore crabs, which were torn apart without difficulty. Total handling time for both prey types was described by the equation $y = ax + b$, where $y = \log(\text{time})$; x = prey length or carapace width/log(predator carapace width). Handling time of *M. edulis* consisted of 3 components. Breaking and eating times of large mussels were positively correlated with prey size; breaking time of small mussels, which could be crushed with a single application of force, was independent of prey size. Picking-up time was short, and negatively correlated with prey size, indicating that *L. puber*, due to lack of chelal dexterity, had difficulty picking up smaller prey. Similarly, attack success rate on *C. maenas* increased with prey size. The 2 co-existing portunid crabs *L. puber* and *C. maenas* show many similarities in their prey handling behaviour. However, chelal morphologies suggest that *C. maenas* is adapted to feeding on molluscs while *L. puber* is better equipped for predation on softer, more mobile prey such as crustaceans.

INTRODUCTION

Since the initial development by Schäfer (1954) of a functional classification of crab chelae, a number of studies have described chelal morphology and mechanics in relation to the handling methods used during predation on different prey (Warner & Jones 1976, Vermeij 1977, Elner 1978, Zipser & Vermeij 1978, Brown et al. 1979, Bertness & Cunningham 1981, Blundon & Kennedy 1982, Boulding 1984). While predation on soft-bodied organisms proceeds by simple breaking up of the prey with the chelae (Caine 1974, González Gurriarán 1977, Hill 1979), many of the methods used to break open hard-shelled prey such as molluscs appear to be specialized, and may involve application of force at points where the shell is weakest (Elner 1978). However, it is uncertain to what extent observed attack methods are specific

behavioural sequences. They may instead be passive mechanical consequences of chelal and prey morphologies (Hughes & Elner 1979, Elner & Raffaelli 1980).

Not only handling methods but also characteristics of handling time curves may be explicable in terms of the interaction between chelal and prey morphologies (Hamilton 1976, Elner & Hughes 1978, Hughes & Elner 1979, Hughes & Seed 1981).

This paper presents the results of a study of handling methods and handling times of the portunid crab *Liocarcinus puber* (L.) feeding on crustaceans and molluscs. *L. puber* is an inhabitant of rocky sublittoral areas extending up to the lower shore (Christiansen 1969, Ingle 1980). Predation in the field by this species on bivalves and gastropods (Kitching et al. 1959, Ebling et al. 1964, Seed & Brown 1975) and on sea urchins (Muntz et al. 1965) has been reported. In the only extensive published study of the ecology of *L. puber*, González Gurriarán (1978) found that the main prey of a population inhabiting mussel rafts in Spain were

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Mytilus edulis and the porcelain crab *Pisidia (= Porcellana) longicornis.*

Our aims were to describe handling methods and handling time curves, and to explain them in terms of predator and prey morphologies, with comparisons where possible with *Carcinus maenas,* which coexists with *Liocarcinus puber* (pers. obs., Crothers 1970), and whose prey handling behaviour has been more extensively studied (Seed 1969, Elner 1978, 1980, Elner & Hughes 1978, Hughes & Elner 1979, Elner & Raffaelli 1980, Jubb et al. 1983, Cunningham & Hughes 1984).

METHODS

Velvet swimming crabs *Liocarcinus puber,* collected by hand or from baited pots at various sites on the Llŷn Peninsula, Gwynedd, N. Wales, were held in a recirculating seawater system at ambient temperature and under fluorescent lights on manual control. For experimentation, crabs were placed individually in 23 × 43 cm clear plastic aquaria in which behavioural sequences could be observed directly and timed with a stopwatch. Prey used were mussels *Mytilus edulis* L., collected from Bangor Pier (Ordnance Survey map reference SH584733), winkles *Littorina rudis* Maton, collected from Gorad, Bangor (SH574726), and juvenile shore crabs *Carcinus maenas* (L.), also collected from Gorad.

Two main series of experiments were performed. The first series, involving all 3 prey species, was designed to elucidate the handling methods used by *Liocarcinus puber.* The second series, designed to measure handling times, involved only *Mytilus edulis* and *Carcinus maenas.* Since *C. maenas* is a mobile prey able to escape from a proportion of attacks, an additional experiment was carried out to quantify the attack success rate associated with this prey.

Handling methods. Liocarcinus puber of both sexes, ranging from 2.8 to 8.5 cm carapace width, were observed continuously as they fed on individually presented prey. About 20 *L. puber,* not necessarily the same individuals, were used for each species of prey. A hundred presentations of *Mytilus edulis* and of *Carcinus maenas,* and 50 of *Littorina rudis,* were made, and the sizes of predator and prey were recorded in each case. For purposes of comparison, 3 male *C. maenas* of 7 to 7.5 cm carapace width were observed as they fed on *Mytilus edulis.*

Handling times. (i) *Mytilus edulis* prey. Sixteen male and 4 female *Liocarcinus puber,* ranging from 2.8 to 8.5 cm carapace width, were fed whole mussels for 7 d, starved for 72 h to standardize hunger level, and then fed with 5 *M. edulis* (range of shell lengths 0.6 to 3.1 cm) presented at intervals of about 24 h to elimi-

nate satiation effects. Three phases of handling were timed: (a) picking-up time, the time between first response to prey and its transfer to the mouthparts with the chelae; (b) breaking time, the time elapsing between picking up the prey and taking the first bite of exposed flesh; (c) eating time, the time from the first bite of flesh to the abandonment of the remains, including time taken to re-break the shell and extract all the flesh. Predator carapace width, heights of both chelae, and prey shell length, width, and height were recorded for each presentation. Water temperature varied between 12.8 and 18.0°C and was recorded for each presentation.

Handling times. (ii) *Carcinus maenas* prey. Seventeen male and 6 female *Liocarcinus puber,* of 3.1 to 8.6 cm carapace width, were fed juvenile *Carcinus maenas* for 7 d, starved for 72 h to standardize hunger level, and then fed with 5 *C. maenas* (range of carapace widths 0.4 to 2.1 cm) at 24 h intervals, obviating satiation effects. Handling time was recorded as the time elapsing between initial grasping of the prey and the termination of feeding, recognizable by cleaning movements of the mouthparts. Predator carapace width, heights of both chelae, and prey carapace width were recorded for each presentation. Water temperature varied between 13.4 and 16.8°C and was recorded for each presentation.

Attack success rate. Experimental procedure was as for the handling time experiments with *Carcinus maenas* prey, and the same individual predators were used, but each predator was presented 10 prey at 24 h intervals, dropped individually in front of it. Each presentation was observed until the prey was eaten or, after 60 s, had escaped into a corner of the aquarium.

RESULTS

Handling methods

Mytilus edulis prey

Mussels dropped into the tank were usually grasped immediately by the chelae and pereiopods of *Liocarcinus puber,* then manipulated by the chelae and maxillipeds. Small mussels were sometimes located by sweeping movements of the chelae. Following initial manipulation, mussels were usually supported at 1 end by the smaller, cutter chela (Fig. 1) and at the other by the maxillipeds while the larger, crusher chela (Fig. 1) applied pressure. After a series of applications of force, each prey was reoriented, using the chelae and maxillipeds, breaking attempts continuing until the shell cracked and the first bite of flesh was taken.

All but the smallest mussels had to be broken several
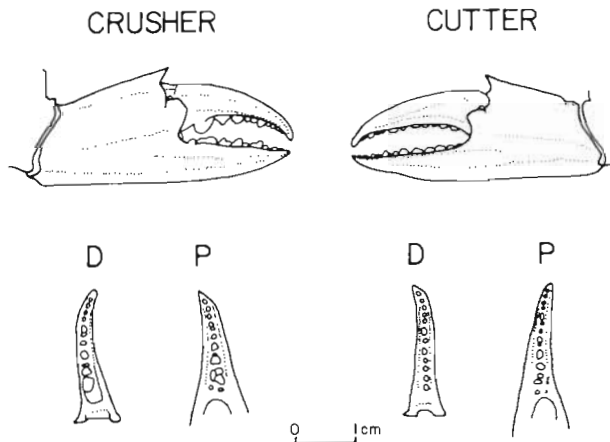
CRUSHER   CUTTER

Fig. 1. *Liocarcinus puber*. Crusher and cutter chelae of a male crab, carapace width 7.5 cm, with diagrams of the rows of teeth on the dactyli (D) and propi (P)

times for extraction of all the flesh. Pieces of shell were usually passed to the mouth by the cutter chela. The mandibles gripped the flesh while the cutter chela or third maxillipeds pulled outwards and downwards to separate shell and flesh. The maxillae and first and second pairs of maxillipeds manipulated small pieces of shell and flesh.

A mussel was only discarded after most shell fragments had been passed through the mouthparts several times and all flesh gleaned thoroughly. Following this the chelae swept the floor of the aquarium, searching for any shell fragments that had been missed.

The posterior end of the mussel shell was broken in 35 presentations, the umbonal end in 55 and the middle region in 7. Umbonal breakage was significantly more frequent than posterior breakage ($G = 4.49$, $df = 1$, $P < 0.05$). The crusher chela was used to break open the prey in 89 presentations, the cutter chela in 7 and the mouthparts in 3. The difference in frequency between crusher and cutter was highly significant ($G = 82.95$, $df = 1$, $P < 0.001$). Force was applied laterally to break the mussel shell in 60 presentations and dorsoventrally in 37 ($G = 5.51$, $df = 1$, $P < 0.05$). The end of the mussel held uppermost, whether umbonal or posterior, was more frequently broken ($G = 88.33$, $df = 1$, $P < 0.001$).

The 2 smallest mussels were crushed immediately by the crusher chela, but the precise orientation of the prey relative to that of the chela was not discernible. A large mussel was prised open by insertion of the dactyli of both chelae between the valves.

Littorina rudis prey

Littorina rudis dropped into the aquarium were usually grasped immediately and passed to the mouth-

parts as described for mussels. Again, small prey were sometimes located by sweeping movements of the chelae. Breaking attempts ensued a few seconds after manipulation by the maxillipeds. Small *L. rudis* were crushed to tiny fragments, often by a single application of force, but larger *L. rudis* were often left with the topmost whorl and part, or all, of the columella intact. Other large *L. rudis* were broken into small fragments.

The following successful breaking methods were recorded: (a) breaking the shell across the base with the crusher chela, while the cutter chela and mouthparts supported the prey; (b) breaking the lip and lower body whorl with the dactylus of the crusher chela inserted into the shell aperture, the cutter chela holding the columella; (c) breaking the shell apex with the crusher chela; (d) indiscriminate crushing by the mouthparts; (e) indiscriminate crushing by the crusher chela.

For medium and large prey, Method (a) was most commonly and Method (b) rather less frequently used. Both methods initially produced a semicircular hole centered on the lip of the shell, except for smaller prey where initial damage was more extensive. Method (c) was attempted frequently but was rarely successful. Methods (d) and (e) were used for small prey, Method (d) especially for the smallest prey.

Chelae and mouthparts were often used to reorient the prey during breaking. Attempts to break shells using the cutter chela were frequent but never successful. The cutter chela was used to pass shell fragments to the mouth for gleaning. The large proximal peg on the dactylus of the crusher chela (Fig. 1) was used frequently, but often unsuccessfully, in attempts to crush the shell after initial breaking had reduced the latter to a shape fitting into the back of the chela. The distal teeth of the crusher chela were sometimes used to break the shell, as for example in Method (b) where the closed chela exerted a force perpendicular to the shell surface, pressure being transmitted via the distal teeth. Usually, however, initial breaking involved teeth halfway along the chela.

After flesh had been extracted from the shell, the chelae swept the floor of the aquarium, picking up any shell fragments that had been dropped and passing them to the mouth. Shell fragments from which all flesh had been gleaned were ejected in the exhalant respiratory current.

Carcinus maenas prey

Liocarcinus puber readily preyed on *Carcinus maenas*, 'pouncing' on prey which were introduced into the tank. Larger prey were grasped in one or both chelae, whilst smaller prey were enclosed by the

chelae and pereiopods, but often escaped between the latter. Larger *C. maenas* that had escaped the initial attack were pursued, *L. puber* apparently using vision. The smallest *C. maenas*, after being passed to the mouth by the cutter chela, were held by the third maxillipeds while the other mouthparts tore off and manipulated pieces before ingesting. Larger *C. maenas* were held by the chelae, while the mouthparts tore pieces off; the chelae were also used to break up the largest prey. After a prey had been eaten, pieces that had been dropped accidentally were swept up by the chelae, passed to the mouth and processed for ingestion.

Handling time

Least squares regression equations were fitted to the data, and several different forms of the relation between handling time and relative prey size were tested. The best fit was that which maximized the coefficient of correlation (r). Only those terms contributing significantly to multiple and polynomial regressions were retained.

Mytilus edulis prey

Picking-up time was negatively correlated with prey size within the range presented, the curve of best fit being a polynomial

$$y = -39.7x + 42.5x^2 + 20.6 \qquad (1)$$

where y = picking-up time s; x = $\log_e$ (prey length, cm/crusher chela height, cm); $n = 100$, $r = 0.44$, $P < 0.001$.

Breaking time was independent of mussel size for prey length to crusher chela height ratios below 0.9, but was positively correlated with mussel size above this threshold (Fig. 2):

$$y = 11.0x - 9.6z - 1.5 \qquad (2)$$

where y = $\log_e$ (breaking time, s); x = mussel length, cm/crusher chela height, cm; z = mussel width, cm/ crusher chela height, cm; $n = 50$, $r = 0.68$, $P < 0.001$.

Eating time increased with prey size (Fig. 3), the line of best fit being

$$y = 2.25x + 4.28 \qquad (3)$$

where y = $\log_e$(eating time, s); x = mussel length, cm/ $\log_e$(carapace width, cm); $n = 100$, $r = 0.85$, $P < 0.001$.

Total handling time was best represented by a curve of the same form,

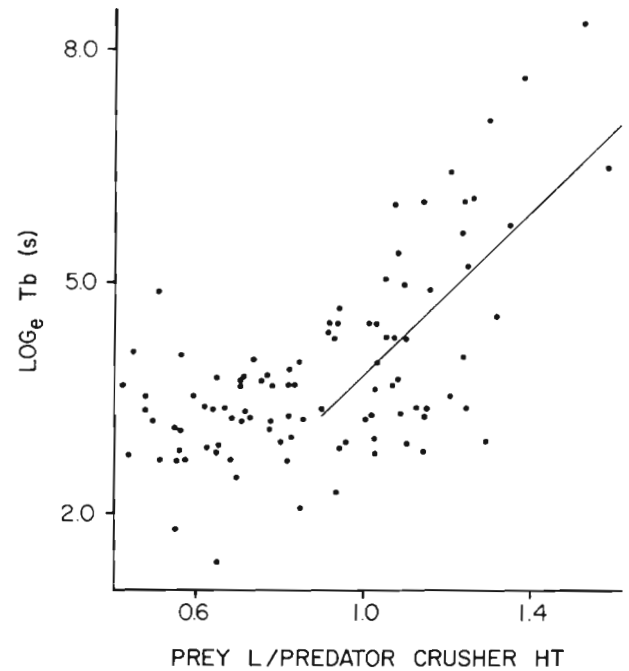$$y = 2.27x + 4.30 \qquad (4)$$

$n = 100$, $r = 0.83$, $P < 0.001$.

Fig. 2. *Liocarcinus puber*. Breaking times (Tb) of *Mytilus edulis* prey plotted against prey length (L) relative to predator crusher chela height (HT). Regression line is the line of best fit for a simple regression of breaking time against 1 prey dimension only, $y = 5.33x - 1.58$. At relative prey sizes below 0.9, breaking time is independent of prey size
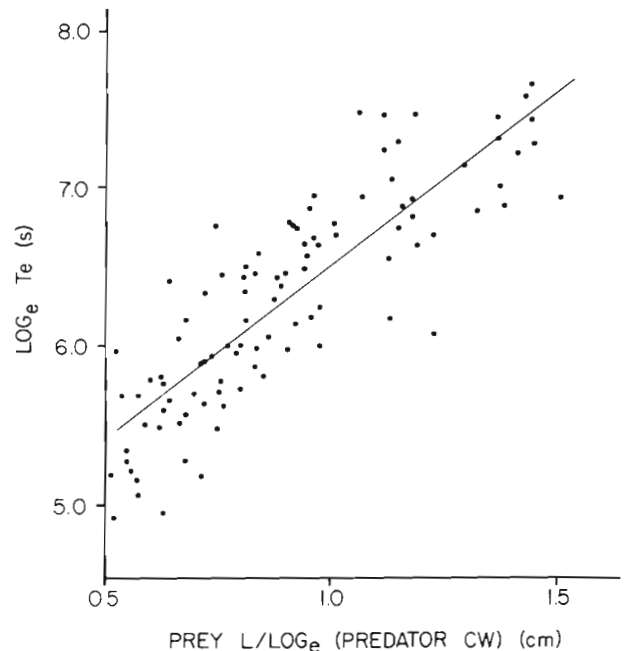

Fig. 3. *Liocarcinus puber*. Eating times (Te) of *Mytilus edulis* prey plotted against prey length (L) relative to predator carapace width (CW). Regression line drawn from Equation (3)

There were no significant differences between male and female *Liocarcinus puber* in the components of handling time (analyses of covariance, P > 0.05 in all cases). Inclusion of temperature did not significantly improve any of the relations.

Carcinus maenas prey

Handling time increased with relative prey size (Fig. 4), the curve of best fit being

$$y = 4.73x + 2.67 \qquad (5)$$

where y = $\log_e$ (handling time s); x = prey carapace width, cm/$\log_e$(predator carapace width, cm); n = 115, r = 0.92, P < 0.001.
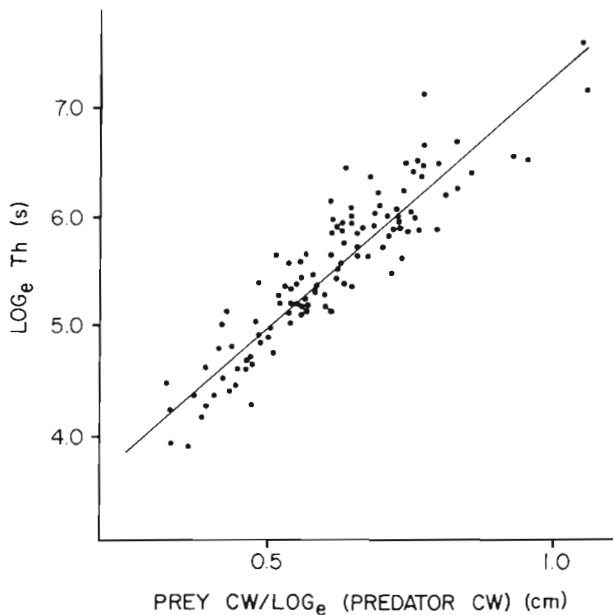

Fig. 4. *Liocarcinus puber.* Handling times (Th) of *Carcinus maenas* prey plotted against prey carapace width (CW) relative to predator carapace width (CW). Regression line drawn from Equation (5)

Handling times were not significantly different between male and female *Liocarcinus puber* (analysis of covariance, F = 0.003, df = 1,112, P > 0.9) but when crusher chela height was substituted for predator carapace width in the above relation, the slopes of the regressions differed significantly (F = 9.23, df = 1,111, P < 0.01).

Inclusion of temperature in a multiple regression significantly improved the correlation (F = 11.09, df = 1,112, P < 0.001). Handling times were shorter at higher temperatures:

$$y = 4.77x - 1.31t + 6.20 \qquad (6)$$

where t = $\log_e$ (temperature °C).

Attack success rate

Attack success rate increased with prey size when observations were divided into 6 prey-size categories, each containing approximately equal numbers of observations (Fig. 5). The interaction between attack success rate and relative prey size was significant
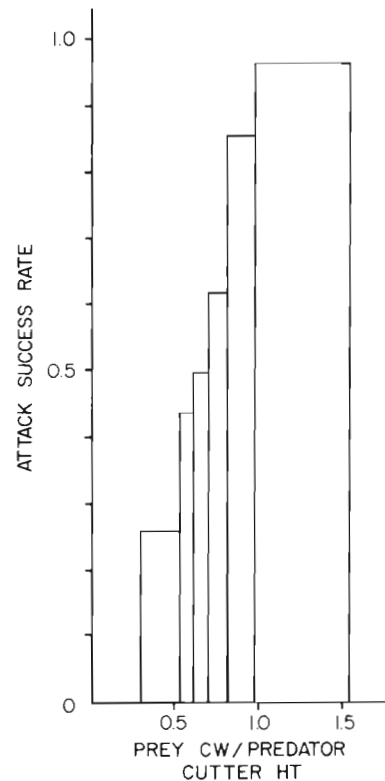

Fig. 5. *Liocarcinus puber.* Attack success rate on *Carcinus maenas* prey plotted against prey carapace width (CW) relative to predator cutter chela height (HT)

(G = 66.2, df = 5, P < 0.001). The best fit to the data was obtained when relative prey size was defined as the ratio of prey carapace width to predator cutter chela height.

DISCUSSION

Handling methods

Handling methods used by *Liocarcinus puber* on molluscan prey were determined by the geometry and strength of the shell, which limited the positions available for *L. puber* to exert sufficient force without the chela slipping. Small prey could be crushed indiscriminately either by the mouthparts or by the crusher chela, whereas larger, stronger shells increasingly limited the number of successful opening methods.

Observations suggested that after a random initial attack on the umbonal or posterior end of *Mytilus edulis*, *Liocarcinus puber* attacked both ends of *M. edulis* alternately, reorientation following each series of breaking attempts. Mussels larger than those used in the present experiments could not be crushed in any position and were attacked by the much slower process of chipping the edges of the valves (pers. obs.).

Littorina rudis shells were evidently difficult to grip without the chelae slipping. In the early stages of an attack, the shell tended repeatedly to slide over the proximal peg of the crusher chela, but in so doing, small flakes of shell were sheared off. When the shell was sufficiently reduced, it was pushed to the back of the chela where the proximal peg could exert force at a high mechanical advantage. Large *L. rudis* could only be accommodated by a wide chelal gape and so were particularly prone to slipping. Many prey were broken incompletely and still contained flesh after predation.

Carcinus maenas were easily torn apart by the chelae and mouthparts of *Liocarcinus puber* and did not mechanically restrict attack-behaviour to recognizable patterns. Attack success rate depended on the ability of *C. maenas* to escape between the pereiopods or to struggle free of the chelae of *L. puber*. The efficiency of prey enclosure by the pereipods and the firmness of chelal grip are both likely to increase with increasing relative prey size, thus explaining the associated increase in attack success rate.

Handling time

For all but the largest *Mytilus edulis* and for *Carcinus maenas*, ingestion was the longest handling process and, since ingestion rate may be determined by mouthpart and stomach size, handling time was more closely related to carapace width than to chela height. This explains the significant difference in handling time between male and female *Liocarcinus puber* feeding on *C. maenas* when predator size was expressed in terms of chela size, male crabs having much larger chelae relative to carapace width than females. A similar difference in predation on *M. edulis* may have been masked by the low number of females used and the more variable handling time.

The relation between handling time and relative prey size was increasing and non-linear, outstripping the increase in prey weight or volume as prey size increased (ap Rheinallt 1982). With *Carcinus maenas*, handling times of large individuals were very long, and although the increased thickness of the carapace may have retarded breaking slightly, more important were the deceleration of ingestion and the frequent pauses, possibly caused by accumulating fragments of

exoskeleton in the cardiac stomach of *Liocarcinus puber*. It is known that clearance rates of hard material (bone and shell) from crab foreguts are very slow (Hill 1976).

With *Mytilus edulis*, breaking time was a significant component of handling time, although usually much shorter than eating time. Small mussels were difficult for crabs to pick up, but the weak negative correlation between picking-up time and mussel size did not affect handling time noticeably since picking-up time was relatively short (never longer than 120 s). Small mussels could be broken by a single application of force and breaking time did not increase with prey size over the smaller range. At larger mussel sizes, more than 1 attempt was necessary to break the shell and breaking time rose steeply. As described for *Carcinus maenas* feeding on mussels (Elner 1978), *Liocarcinus puber* applied a series of pulsed forces to the prey and probably broke larger *M. edulis* by gradually extending small fractures in the shell microstructure. Because of the direct mechanical relation, breaking time was more closely correlated with chela height of *L. puber* than with carapace width.

Comparison with *Carcinus maenas*

Compared to other portunids, both *Liocarcinus puber* (Fig. 1) and *Carcinus maenas* (Fig. 6) have relatively strong chelae (Vermeij 1977). When feeding on molluscs, *L. puber* shares many similarities in handling behaviour with *C. maenas*. We observed *L. puber* using 3 of the 4 opening methods described by Elner & Raffaelli (1980) for *C. maenas* feeding on *Littorina rudis* and *L. nigrolineata*. *C. maenas* observed feeding on mussels by Cunningham & Hughes (1984) broke them open more frequently at the umbonal end than at
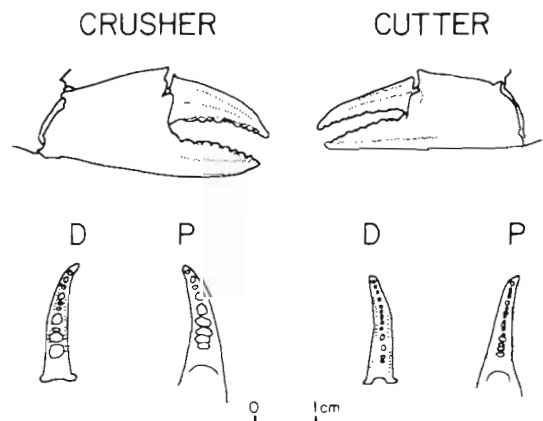

Fig. 6. *Carcinus maenas*. Crusher and cutter chelae of a male crab, carapace width 7.5 cm, with diagrams of the rows of teeth on the dactyli (D) and propi (P)

the posterior end, and tended to break open the end which was held uppermost, as did *L. puber* observed in the present study.

Present observations revealed that male *Liocarcinus puber* of 7 to 7.5 cm carapace width break small mussels (1 to 2 cm shell length) faster than male *Carcinus maenas* of similar size (Elner & Hughes 1978). For larger prey, however, breaking time increases more steeply for *L. puber,* eventually overtaking that for *C. maenas.* In addition, eating time per unit dry weight is longer for *L. puber* feeding on all sizes of mussels (ap Rheinallt 1982).

While the mussel population used by Elner & Hughes (1978) was different to that used in the present study, it seems that the observed differences are explicable in terms of chelal morphology (Fig. 1 & 6). Small mussels are picked up and manipulated more deftly by the chelae of *Liocarcinus puber* than by those of *Carcinus maenas.* Our observations suggested that the crusher chela of *C. maenas* is particularly unsuited to manipulating small prey. Larger mussels, however, are less likely to slip out of the crusher chela of *C. maenas* because the chelal teeth are broader, whilst the dactylus and propus are more nearly parallel when applying force (Fig. 6). Moreover, because of the wider gape between the proximal surfaces of the dactylus and propus (Fig. 6), mussels can be pushed further back in the crusher of *C. maenas* and broken by more proximal teeth operating at a higher mechanical advantage. Therefore *C. maenas* breaks open large mussels more rapidly than does *L. puber.* Since re-breaking of the shell following the first bite of exposed flesh contributes significantly to eating time at large prey sizes, large mussels are eaten more slowly by *L. puber,* but the longer eating time for small prey is explained by the observation that *L. puber* gleans flesh from mussels much more thoroughly than does *C. maenas.* The reason for this is unknown.

The crusher chela of *Carcinus maenas* appears to be better equipped for exerting purely compressive forces on large smooth objects, whilst that of *Liocarcinus puber* appears to be better equipped for holding irregularly shaped or mobile prey. *L. puber* is probably able to exert greater shear forces, whilst the low mechanical advantage at the tips of the chelae permits faster movement and greater dexterity. Chelal morphologies suggest, therefore, that *C. maenas* is more suited to feeding on slow-moving, hard-shelled prey such as molluscs. *L. puber,* while possessing a proximal peg on the crusher which can be considered an adaptation to feeding on molluscs (Vermeij 1977), is better able to deal with faster-moving, softer-bodied prey. This is confirmed by the general behaviour of both species, *L. puber* being much more active and fast-moving than *C. maenas* (pers. obs.).

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