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Functional Ecology, Volume 7, Issue 3 (Jun., 1993), 339-345.

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Functional Ecology

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The relationship of closing force to body size for the major claw of *Uca pugnax* (Decapoda: Ocypodidae)

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Summary

1. We measured the closing force of the major claw of live fiddler crabs (*Uca pugnax*), using a flexible beam equipped with strain gauges and connected to a Wheatstone bridge and computer.
2. Crabs usually produced a series of rhythmic contractions. Maximum closing force of an individual was related approximately linearly to claw length.
3. Closing force scaled as predicted from the force expected from dimensions used to calculate muscle cross-sectional area and mechanical advantage. This suggests that the major claw, which is an extreme case of sexual selection, is fully functional as a closing device, rather than losing the closing force function, which might be expected if it was used primarily as a display to signal body size to other males or females.

Key-words: Biomechanics, Crustacea, sexual selection

Functional Ecology (1993) 7, 339–345

Introduction

Sexual dimorphism characterizes all of the species of the fiddler crab genus *Uca* (Crustacea, Ocypodidae). Females bear two small chelipeds, which are used in food gathering and for sorting sedimentary grains (Crane 1975). Males, however, have only one (minor) claw of this type. The other (major) claw is much larger, and can be as much as 50% of the male's total body weight (Crane 1975). Early in ontogeny the major claw is initially identical to the minor claw, but a poorly understood developmental event is followed by positive allometric growth through a series of moult stages (Huxley 1924).

In all species of *Uca*, the male's major claw is employed both in displays and in agonistic interactions with other males, but not in feeding (Crane 1975; Christy & Salmon 1984). Thus, the major claw should be subjected to sexual selection, where changes in size, proportions, or ornament would be related to mating success. This contrasts with the male's minor cheliped, or with the female's two small chelipeds, which should be subjected to natural selection for feeding efficiency.

A number of studies have documented significant heterogeneity among species in the male's use of the major cheliped in mating. In Asian species, males wave the cheliped, females are attracted and copulation takes place on the sediment surface. The male and female then separate. By contrast, in most American species, males wave, females approach, and both

copulation and rearing of the eggs takes place in the burrow that is guarded by the male (Christy & Salmon 1984, 1991). Males fight for burrows, and intruding males may displace a resident, especially if the intruder is larger in size (Christy & Salmon 1984). In the American *U. pugilator* claw-waving larger males are more successful than smaller males in attracting females (Hyatt 1977). In the Asian *U. vocans*, Salmon (1984) reported no relationship between claw size and mating success, although Yparreguirre (1981) reported a positive correlation. In American species, the mating success of larger males may relate to their successful defence of high-quality higher intertidal burrows.

The use of the male's major claw can deviate significantly from the norm in some species, including the use of the claw to grasp and drag females (Zucker 1986) and the relatively reduced use of the claw in waving, which is supplanted by the increased use of an acoustic display (Salmon & Atsaiades 1968). Our observations of *U. pugnax* (Smith, 1870) show it to be close to *U. pugilator*. All sexually mature males use the major claw for waving to attract females, displays to warn against encroaching males, and for grappling with other males to fight for burrows.

In other crab species chelipeds may be used to seize or to crush prey, as well as to fight other males (e.g. the stone crab *Menippe mercenaria*; Wilber 1989). In the pebble crab *Eriphia smithi* a pronounced sexual dimorphism of claw size can be related to unusually

strong agonistic interactions among males (Vannini & Gherardi 1988). In *Uca*, this trend has moved towards complete specialization of the major claw for sexual displays and combat. *Uca festae* has proportionally larger claws relative to other members of the genus and appears to have relatively more aggressive males (Crane 1975).

The dual functions of display and combat suggest the question of whether a fiddler crab claw is mechanically designed entirely to maximize closing force, and whether increased claw size is accompanied by an increasing closing force whose magnitude of increase is predictable from biomechanical principles. An alternative hypothesis might state that at large sizes the claw could not function very well and is mainly for display (Huxley 1932). The use of the claw in combat at all sizes is not in doubt (Crane 1975; J. S. Levinton & M. L. Judge, unpublished observations). The question is whether display may take precedence such that crabs are advertising falsely their ability to grab and throw an opponent. Our observations of *U. pugnax* show clearly, and consistently with others (see Crane 1975), that males retreat after encountering much larger males, with no bodily contact. In some species, the presence of larger males suppresses waving by smaller individuals (Zucker 1986).

In both agonistic interactions and waving displays, males open and close the dactyl; movements are accomplished by the contraction of a pair of antagonistic muscles in the manus. These attach via apodemes to the dactyl. In claw-bearing Crustacea, closing force is a function of the cross-sectional area and character of the closer muscle, the angle of insertion of this muscle on the apodeme, and the dimensions of the claw that determine mechanical advantage (Warner & Jones 1976; Elner & Campbell 1981; Govind & Pearce 1986; Govind, Quigley & Mearow 1986). Consequently, several have tried to predict changes in mechanical advantage by an analysis of claw proportions (e.g. Vermeij 1977; Abele *et al.* 1981; Elner & Campbell 1981).

It is the purpose of this report to estimate the relationship of closing force to increasing body size and to test the hypothesis that closing force scales according to a predicted relationship to body size. The predicted changes in closing force are deduced from estimates of changing muscle mass and mechanical advantage. We tested this hypothesis by means of a method for measuring directly the closing force of the major chela of the eastern North American fiddler crab *U. pugnax*. Our scheme employs a flexible beam, which is bent by the closing claw of a live intact individual. Deformation of the beam is measured by a pair of strain gauges, whose resistance changes the voltage across a Wheatstone Bridge. Several studies have used a similar approach to study both claw closing strength and the force required by carnivorous crabs to crush molluscan prey (e.g. Elner 1978; Elner & Campbell 1981; Boulding & LaBarbara 1986).

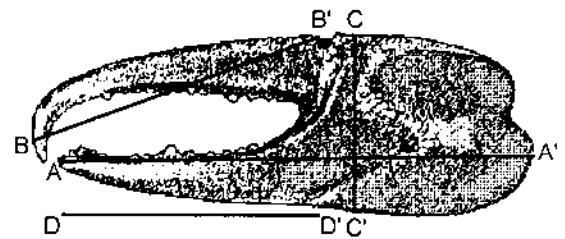


Fig. 1. The measurements taken from most specimens used in the experiments. A-A', claw length; B-B', dactyl length; C-C', claw height; D-D', pollex length. Claw depth was measured perpendicular to claw height.

Materials and methods

Adult male and female fiddler crabs (*U. pugnax*) were collected from field populations at the Flax Pond *Spartina* saltmarsh (Old Field, New York, USA) in late September 1991. Crabs were held in a laboratory recirculating sea-water system under fluorescent lights. Diurnal light and tidal cycles corresponded to those of Flax Pond, and were advanced over the holding period by means of an electronic cycling device (Chronrol, Lindberg Enterprises, San Diego, California, USA), used to operate lights and the pump system that filled and drained the tanks. During the time of low tide, most of the sand was dry, but some standing water remained. All crabs appeared to behave normally throughout the experimental period (e.g. feeding on sediments, aggressive displays). Only adult males (mean carapace length \pm SE = 11.7 ± 0.3 mm) were used for the major claw (range of claw lengths = 16.2–39.9 mm) closing force measurements and calculations. Crabs were measured for carapace, major claw, dactyl, and pollex length, as well as major claw height and width (Fig. 1).

We employed an *in vivo* technique with the whole animal rather than salt injections to a detached claw (e.g. Warner & Jones 1976) because the former method did not rely on the assumption of instantaneous transport of injected fluids to all parts of the closer muscle (Elner & Campbell 1981) and we felt it more accurately reproduced normal claw function. Crushing force of a contracting major claw was estimated from the deflection of an acrylic cantilever (Fig. 2; 63.5 mm long \times 11 mm wide \times 3 mm thick).

The manus was held fixed relative to the cantilever base while the dactyl was allowed to articulate. Thus, we measured the dynamic closing force rather than the static force (Brown, Cassuto & Loos 1979). The claw gap (distance between pollex and dactyl) was set to be a fixed percentage of the pollex, in order to maintain a constant gape angle (pilot studies suggested an optimal opening angle of $35\text{--}37^\circ$ to avoid excessive cantilever bend). The tip of the dactyl was placed through a brass loop (7.5 mm ID \times 12.5 mm OD \times 1.8 mm thick) attached to the end of the cantilever. The minimum gape distance (range of possible gapes, 2.5–14.5 mm) was controlled by a set

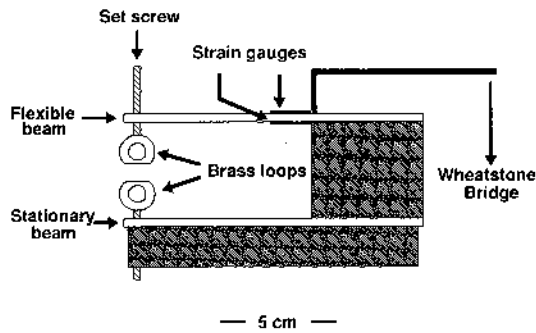


Fig. 2. The cantilever device used to measure closing force of the major claw of *Uca pugnax*. The upper beam is flexible whereas the lower beam is rigid. Strain gauges are glued to the upper and lower surfaces of the flexible beam, and voltage changes are measured by means of a Wheatstone bridge.

screw. The amount of deflection was measured by the change in resistance of two 350 ohm strain gauges (PA09-250BA-350, Micro Engineering II, Upland, California, USA) in series across a Wheatstone bridge connected to an amplifier (1K gain) (Underware Electronics).

The changes in strain gauge resistance (as the cantilever was deflected) were measured as an analogue voltage signal. The bridge/amplifier was powered by four 9-V batteries ($\pm 18\text{-V}$) (but we have since adopted the use of a regulated DC power supply of $\pm 15\text{-V}$). Prior to each use, the bridge was balanced to 0.0 V through the use of a voltmeter (Micronta 22-185A LCD Digital Multimeter). The voltage analogue signal was converted to a digital signal through an analogue to digital (A/D) board (DAS8-PGA, MetraByte Corp., Taunton, Massachusetts, USA) placed in a computer (Toshiba T3200).

Each run lasted 10 s and was sampled 400 times per second. Each run was checked for the presence of a claw closure (defined arbitrarily as twice the background noise) and for each closure the maximum voltage output was taken to correspond to force. We enticed contractions of the major claw by manipulating the crab during the experimental run. Although the crabs generally produced more than one contraction per run, we ignored peaks where the claw closed completely (i.e. the brass loops made contact) because we could not accurately estimate the total closing force. We adjusted the gape angle to minimize such occurrences. We also discarded runs with no response.

Typically, crabs exhibited a series of repeated contractions of subequal force (Fig. 3). We chose to characterize the closing force by using the maximum voltage output corresponding to the largest peak in a given 10-s experimental period; this was representative of closing force because other peaks were within 10%. It is difficult to interpret smaller forces in an experimental run; they may be due to muscle fatigue,

behavioural adjustments to our stimulation, or to natural variation especially where the crab chooses to use less than its maximum force. The data shown below, therefore, should be interpreted as a series of measurements of maximum closing force.

A total of 23 adult males was tested using the more stable DC power supply in late November and early December 1991. These results were compared with those results on 20 specimens measured in late October using the bridge/amplifier, which was then powered by batteries. Measurements were taken on 17 and 18 October, 13–27 November, and 4 December 1991. We found that the variance of measurements increased over time since collection from the field, and we therefore report mainly data from the initial October measurements.

The apparatus was calibrated by hanging a known weight on the end of the cantilever and the voltage output was measured by means of the A/D board. The calibration with the battery power source was linear and repeatable (for October data using batteries: $r^2=0.999$, $n=9$); the deflected cantilever quickly returned to zero voltage output when the force was removed. Even at the highest force used there was little drift ($<1\%$ of the measurement over 10 s). The calibration was linear throughout our range of deflections [regression for October data: Force (N) = $0.35 + 2.16 \times (V)$].

The maximum force per crab on each date was plotted as a function of claw length. Predictions for the change of expected maximum force with increasing claw length were calculated from claw dimensions necessary to estimate changes in mechanical advantage (*sensu* Warner & Jones 1976) and to estimate relative muscle cross-sectional area. The index of mechanical advantage (IMA) is equal to claw height divided by pollex length. (We used pollex length instead of dactyl length to account for the hook shape of the dactyl, which projected through the loop during our test. Pollex length was therefore a better estimate of the lever arm length.) Muscle cross-sectional area

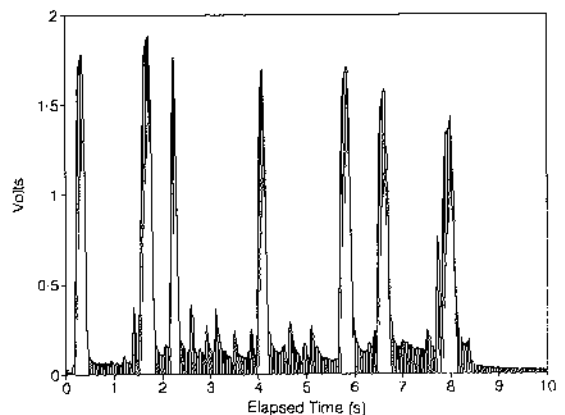


Fig. 3. An example of a trace of voltage output from the apparatus, as a male *Uca pugnax* grabbed onto the brass rings and closed its major claw.

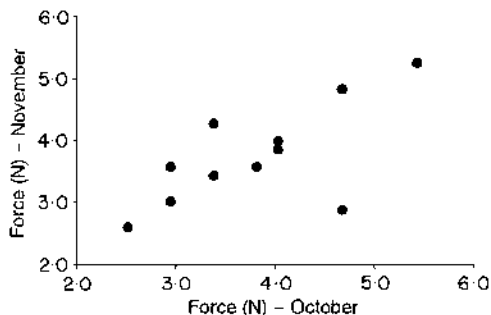


Fig. 4. Relationship between maximum closing force of individual crabs that were measured both in October 1992 and November 1992.

is modelled by taking the muscle mass within the manus to be in the form of an ellipsoid with (manus) length M , (manus) width W , and (manus) height H . We assume that the angle of insertion of muscle fibres into the apodeme is invariant with claw size. The index of muscle cross-section area IXA is:

$$\left[\frac{4}{3} \pi \left(\frac{M}{2} \right) \left(\frac{H}{2} \right) \left(\frac{W}{2} \right) \right]^{2/3}$$

Thus, the index of force $IF = IMA \times IXA$. IF was compared with the measured individual maximum force MF .

Results

Figure 3 shows an example of a trace where a male contracted the claw several times during our 10-s test run in November. In most cases where a crab contracted more than once, variation in peak voltage was modest, usually less than 10–20%. We also found considerable relative repeatability for the same crabs between runs spaced several weeks apart. Figure 4 illustrates this with a plot of maximum closing force of a group of crabs, measured between two periods in October and November that were 3–5 weeks apart.

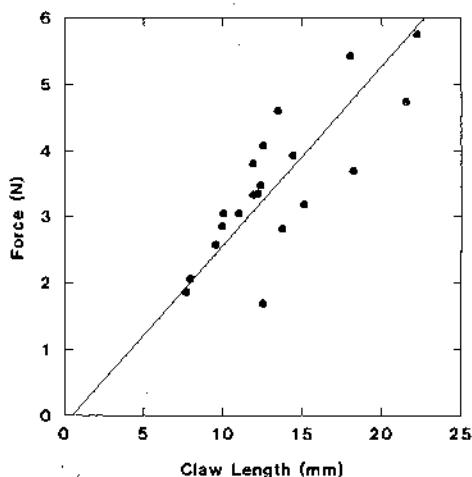


Fig. 5. The relationship between claw length and maximum closing force for *Uca pugnax*. Linear fit was obtained using a major axis regression (ANOVA on regression, $P < 0.001$).

We measured a total of 29 different crabs in October, November, and December.

The relationship between maximum closing force MF and claw length is illustrated in Fig. 5. MF has an approximately linear relationship to claw length (ANOVA on linear regression: $F_{1,18} = 31.00$, $P < 0.001$). The relationship is strengthened somewhat (but not significantly) when maximum force is regressed against IF , our measure of predicted force, which was derived from an estimate of mechanical advantage and muscle cross-sectional area (for MF – claw length relationship: $r^2 = 0.795$, for MF – IF relationship: $r^2 = 0.949$). Figure 6 illustrates the relationship of muscle mass to manus exoskeleton weight. The slope is approximately linear, which suggests that the manus is filled with muscle to the same extent, irrespective of body size.

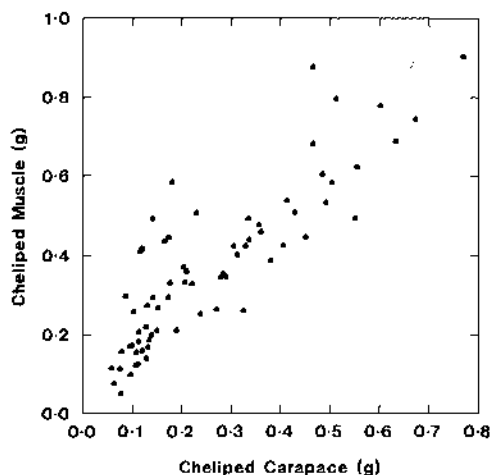


Fig. 6. The relationship between muscle mass and cheliped carapace mass in *Uca pugnax* (data courtesy of M. Weissburg).

Does the change in measured claw closing force MF as a function of body size scale with the expectation from the model of changing IF as a function of body size. The specimen with the largest values respectively of MF and IF was arbitrarily set to $MF = 1$, $IF = 1$, and values for all other specimens were calculated as proportions of the maximum (we had complete data for only 13 animals). This gives relative values as a proportion of the maximum of 1. Relative MF and IF are plotted in Fig. 7. The actual data fit well to the predicted relative forces. A major axis (model II regression) analysis (of all points but the one corresponding to the one used to set the normalized maximum force) shows the estimated slope to be 0.97, where 1.00 would be expected as a perfect fit to the model. The 95% confidence limit to the slope is 0.72–1.30.

Discussion

The dual-strain gauge method produced stable traces,

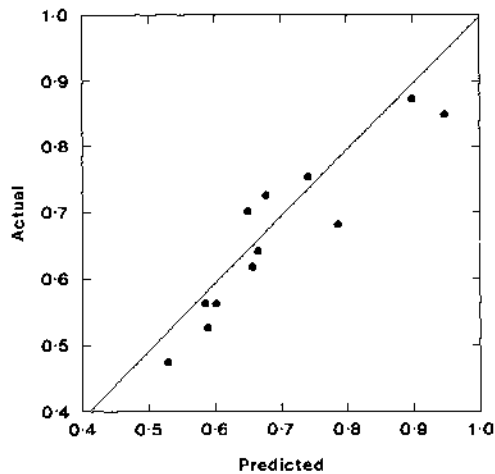


Fig. 7. The relationship between relative index of force ('Predicted') and the relative actual force ('Actual') for *Uca pugnax*. Linear fit was obtained using a major axis regression (ANOVA on regression, $P < 0.001$)

with relatively little relative variation in maximum closing force between successive dates. The repeatability is important, since the crabs are not pinching combatants but are grabbing brass rings. There is no 'natural' stimulus, as in the study of closing force in molluscivorous crabs (Boulding & LaBarbara 1986). Although our measurements are probably accurate and our results are at least precise, one must interpret the absolute values with some caution.

Over the size range of crabs we employed, the data suggest an approximately linear relationship between maximum closing force and carapace length. The ratio of muscle weight to excised claw weight was constant as a function of claw size. We could predict, furthermore, the relative change in closing force with increasing claw size, by using changes in biomechanically relevant claw dimensions. These results suggest that the male's major claw functions as a pinching device at all claw sizes studied, and that there is no relative loss of function with increasing claw size.

Our results comparing changes in force to those predicted from claw dimensions are the first to test an important assumption, made in the comparative studies of claw dimensions, that morphometric data alone can be used to estimate differences in closing force (e.g. Vermeij 1977; Abele *et al.* 1981). At the intraspecific level, claw dimensions alone are a useful predictor of relative force. Unfortunately, as taxonomic distance increases, such morphometric data may be inadequate because:

1. The character of the muscle fibres themselves may differ substantially among taxa (Govind 1984; Govind *et al.* 1986).
2. The angle of insertion or total muscle cross-sectional area per unit volume of manus may differ substantially among taxa.
3. Other factors such as innervation may differ.

The major claw of *Uca* is used both as a display

device and in combat between males (e.g. Crane 1975). As the crab grows, the major claw grows with positive allometry until it attains nearly half of the body weight. There are two apparent costs generated by this extravagant sexually selected limb. First, the major claw is not used in feeding, and males may compensate for this cost by feeding more rapidly with the minor claw (Caravello & Cameron 1987) or by feeding for a longer period of time (Valiela *et al.* 1974). The other cost relates to the large amount of striated muscle in the manus of the male's major claw, which consumes oxygen and therefore increases metabolic requirements (Weissburg 1990). Because the striated muscle is a considerable proportion of the striated muscle of the entire body (c. 25% in *U. pugnax*) and the major claw is used in male contests for burrows, the metabolic cost may be considerable. The closer muscle of *U. pugnax* is of the slow type and functionally compatible with the function of gripping (Govind *et al.* 1986), which is in turn consistent with the functioning required in male-male combat. Even while foraging, the proportional change in energetic costs of *U. pugnax* as a function of body size is far greater for males than for females.

The dual functions of display and combat are also found in antelopes and in deer. There is a very slight positive allometry in basal area of antelope horns relative to body weight (Packer 1983) and a strong intraspecific and interspecific positive allometry for the size of deer antlers, relative to various measures of body size (e.g. Huxley 1931; Gould 1974).

In deer, the trend of increasing antler size reached a bizarre crescendo in the now extinct Irish elk, *Megaloceros giganteus*, with lateral antler spreads of up to 12 feet. Gould (1974) demonstrated that the Irish elk's antler size was to be expected from the overall among-species antler to body size regression. He argued, however, that various details of antler morphology suggested that the larger antlers could not be used as effective fighting weapons. Instead, larger antlers merely marked larger bodies, which would serve as a warning signal to competing males. Huxley (1932) also questioned whether the Irish elk's antlers could be functional as combat weapons. Kitchener (1987) more recently provided convincing functional morphological and crystallographic evidence of combat, but this does not necessarily prove that Gould was wrong in surmising an increased role for display over combat as the antlers increase in size (see also Barnosky 1985).

The difference of interpretation among proponents of display vs fighting is important, since increasing antler size might have been just a correlated property of increasing body size, with no necessary use in combat. In other words, the increased antler size might derive from a developmental constraint where antler size is tied to body size, even if the deer took advantage of the size to display to other males. Overall, however, it is the base of the horn that matters in

fighting. The basal area of the horns of bovids and cervids scales with increasing body size as would be expected from the demands of collisions during fighting (Kitchener 1985). Deer, therefore, maintain the potential for combative function over the entire range of body sizes.

In the case of fiddler crabs, our results suggest that closing force does not diminish with increasing adult body size and, presumably, increasing age. While signalling is an important part of the function of the major chela in *U. pugnax* and in other species of the genus, it is clear that the closing function is maintained fully.

Despite the apparent metabolic cost, function is maintained. It is therefore plausible to assert that the increased claw size in larger crabs still serves the crab functionally as a pinching device, whose force can be smoothly extrapolated from smaller animals. Indeed, our closing force range of c. 2–6 N is comparable to closing forces measured for the similarly sized predatory shore crab *Carcinus maenas* (Elner 1978), although claws of these species have differing sizes and dimensions. The claw is not merely a hollow threat to its opponent. Our results suggest that it is every bit the weapon at all ages and sizes.

The apparent rhythm of claw closure that we often observed is of interest, especially when we compare it to crabs specialized for crushing prey (Elner 1978; Zipser & Vermeij 1978; Boulding & LaBarbara 1986). Molluscivorous crabs break shells by rhythmically loading on the same point, eventually causing fatigue damage (Boulding & LaBarbara 1986). The repeated loading has been interpreted as an adaptation to apply force pulses persistently to the same point, but our results suggest that such rhythmicity can exist even when crushing is not the objective. Unfortunately there is little evidence to assess the damage that male fiddler crabs do to each other, but crushing or even tearing of the carapace is clearly uncommon. This suggests that rhythmic contractions of the chela may not have evolved specifically for loading force on a point, even if the rhythm may have been co-opted in evolution for this purpose.

Acknowledgements

This study benefited greatly from discussions with G. Vermeij, R. Elner and J. Orensanz. We are especially grateful to T. Daniel, who lent us a Wheatstone bridge, strain gauges and provided invaluable advice and help with the construction and design of the apparatus. M. Weissburg also contributed important advice and provided the data on striated muscle mass for *U. pugnax*. We thank C. K. Govind, who kindly reviewed a draft and are also grateful to two anonymous reviewers who made useful suggestions for revision. Partially supported by a grant from the US National Science Foundation.

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Received 24 July 1992; revised 17 November 1992;
accepted 17 November 1992