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Variation in safety factors of claws within and among six species of *Cancer* crabs (Decapoda: Brachyura)

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To better understand how safety factors of biological structures evolve, we examined the frequency of claw failure, and the intra- and interspecific patterns of variation in maximum biting force and breaking strength in the claws of six species of *Cancer* (Linnaeus) crabs that live in sympatry along the coast of the northeastern Pacific: *C. antennarius*, *C. branneri*, *C. gracilis*, *C. magister*, *C. oregonensis* and *C. productus*. Although the breakage frequencies in natural populations were similar among species ($\approx 6\%$), they were higher than predicted based on failure probabilities calculated from laboratory measurements of biting force and breaking strength for healthy pristine claws. The incidence of claw damage was correlated with the degree of wear, suggesting that claws later in the intermolt interval were more likely to fail. Within species, safety factors increased from 3.1 to 4.6 with increasing instar number due primarily to a decline in muscle stress (force per unit area of apodeme). Surprisingly, the lower maximum muscle stress generated by later instars appeared to be due to behavioral restraint, since it was not accompanied by relatively lower muscle mass. In addition, among individuals of the same claw size, lower breaking forces were correlated with lower maximum biting force, and both were correlated with lighter cuticle and closer muscle mass, suggesting a coupling that maintains a more stable safety factor over the moult cycle. In some species, size-adjusted maximum biting forces were higher for males than females, but this paralleled differences in breaking strength, so safety factors did not differ between the sexes. Among the six *Cancer* species, one exhibited an unusually high safety factor (*C. oregonensis*, 7.4) and another an unusually low one (*C. magister*, 2.6). The remaining four species were similar to each other and exhibited an intermediate safety factor (3.6). From a phylogenetic perspective, the species with more extreme safety factors appeared to be derived from a common ancestor with an intermediate safety factor. From an ecological perspective, species more closely associated with rocky substrata, and presumably a higher incidence of hard-shelled prey, exhibited higher safety factors. But safety factors were also correlated with relative claw size, and sexual dimorphism in claw size. Although we cannot say whether habitat, diet or sexual selection are primarily responsible for the differences in safety factors observed among species, the cost of producing a relatively larger claw seems an unlikely explanation because safety factors did not differ between males and females in any of the sexually dimorphic species.

ADDITIONAL KEY WORDS:—biomechanics – crustacea – allometry – performance – chela.

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INTRODUCTION

Much effort has been invested in studying how human-made structures fail, to ensure they are constructed with suitable factors of safety (the ratio of mean strength to lifetime maximum load) (Gordon, 1968, 1978). However, we know comparatively little about how safety factors of biological structures have evolved. This is surprising given that theoretical models provide a sound basis for studying reliability (Alexander, 1981, 1997; Lowell, 1985, 1987) and that high failure rates have been documented in structures as diverse as mollusc shells (Vermeij, 1982), crab claws (Juanes & Smith, 1995), mammalian teeth (Van Valkenburgh, 1988), antlers and horns (Kitchener, 1985), and the limbs of birds and mammals (Alexander, 1981; Currey, 1984).

From studies of safety factors to date, we can make several generalizations (Alexander, 1981, 1997; Lowell, 1985, 1987; Niklas, 1989; Biewener, 1993). First, biological structures with a high contribution to fitness tend to have high safety factors. For example, the limbs of vertebrates have relatively low safety factors compared to those of vertebrae and skulls because limb-breakage does not necessarily result in death (Biewener, 1993). Second, because a massive skeleton imposes additional costs on active animals, natural selection tends to maximize strength while minimizing the weight of materials (Currey, 1977). Hence, the limbs of terrestrial mammals tend to have low and relatively constant safety factors (between 2 and 4) over a large range of body size and taxa (Biewener, 1989). Third, the safety factors of biological structures increase as environmental unpredictability increases (Alexander, 1981; Lowell, 1985) and as the number of different selection pressures operating on a single structure increases (Lowell, 1987). Safety-factor models offer a powerful tool for studying the evolution of biological structures because they help integrate the ways in which structures fail under loads, the effects of failure, and the aspects of design that affect the likelihood of failure.

Two types of strength distribution and two types of load distribution should be considered. First, strength can refer either to the load just sufficient to initiate yielding or to the load required to cause fracture (Alexander, 1981); our references to safety factors refer only to the latter. Second, the load used to compute a safety factor can refer to loads generated by the organism itself (intrinsic) or to loads imposed by the environment (extrinsic). For example, the load borne by the lower leg bone of a running deer includes internal forces due to movement (i.e. ground reaction force) and muscular contraction, both of which the deer controls. Alternatively, extrinsic loads, such as those generated by attacking predators or accidental falls, often produce the highest stresses (Biewener, 1989). Both intrinsic and extrinsic loads may influence the evolution of a structure's strength. Where a single selection pressure predominates then the load determining the strength can be inferred with relative certainty. However, when multiple selection pressures act on a structure, calculations of intrinsic safety factors can be used as a baseline against which to compare other selection pressures (Lowell, 1987).

Unfortunately, loads and strengths may be quite variable within species, so probabilities of failure must be modelled statistically. Furthermore, if load and strength variation are correlated among individuals, probabilities of failure may be substantially overestimated. Ironically, few studies have investigated how safety factors vary among individuals in natural populations, even though average ratios have been calculated for numerous taxa (Alexander, 1981). We would expect safety factors to be dynamic in space and time for living structures, because costs and benefits of traits change with size (Gilliam, 1982; Werner & Gilliam, 1984; Werner, 1986) time (Ludwig & Rowe, 1990; Rowe & Ludwig, 1991) and with changes in the environment. Strength and load may vary in many different ways relative to one another, and these associations may help provide clues about how safety factors have evolved (details in Appendix). Without knowledge about the relation between strength and load among individuals and populations within species, observations on the evolution of safety factors will remain speculative.

Unfortunately, reliable data on the mean maximum lifetime load are nearly impossible to obtain for the structures of most organisms so estimates of safety factors are often approximate (Biewener, 1993). However, crab claws offer a unique system with which to study the evolution of safety factors for three reasons. First, crabs like all arthropods must moult to grow, so ecdysis represents the 'death' of an old claw and a 'birth' of a new one. Even muscle is degraded during ecdysis (Mykles, 1992). Thus, the intermolt interval can be considered the 'lifetime' for an individual claw, which may be as short as 18 to 25 days (Read *et al.*, 1991). A short 'claw life' also means data may be realistically obtained on actual mean maximum lifetime load and mean strength. Second, self-loading forces (intrinsic loads) of claws can be measured easily in the laboratory for individuals that differ in sex, age, and size, so specific hypotheses about safety factor variation may be tested; these have been reported for several decapod species [for a review of species bite-force values see Blundon (1988) and Preston *et al.* (1996)]. Third, field breakage frequencies for natural populations are easy to ascertain for members of many decapod taxa and reflect all natural causes of failure (for review, see Juanes & Smith, 1995). These true breakage frequencies are important to know because they drive the evolution of safety factors (Lowell, 1985). Clearly, decapod claws offer considerable potential for studying the evolution of safety factors.

Crabs of the genus *Cancer* offer several advantages for a study of claw safety-factor variation. First, detailed life history data exist for four of the six species we studied (Orensanz & Gallucci, 1988). This allowed us to make comparisons among species for known instars. Second, we were able to assess phylogenetic effects (Harvey & Purvis, 1991) on patterns of safety-factor variation via the historical data of Nations (1975), and the molecular phylogeny of Harrison (1997). Finally, the six species we examined use their claws in a variety of ways, from catching fast, 'soft' crangon shrimp (Stevens, Armstrong & Cusimano, 1982) to crushing slow, hard-shelled snails (Zipser & Vermeij, 1978), so we were able to test for associations between safety factors and a variety of ecological attributes. Differences in overall claw morphology among *Cancer* crabs, which presumably reflect differences in diet, can be found in Nations (1975) and in Lawton & Elner (1985).

MATERIAL AND METHODS

Claw breakage and wear in natural populations

Frequencies of natural claw breakage were tallied for six *Cancer* species collected from various shallow water sites in the vicinity of the Bamfield Marine Station, Bamfield, British Columbia, Canada. We collected crabs in May, June, and July of 1996. Intertidal species (*C. antennarius*, *C. oregonensis* and *C. productus*) were captured by hand during low tides. Two of the subtidal species (*C. magister* and *C. gracilis*) were obtained using commercial traps, which were retrieved within 24 hours of baiting. The third subtidal species (*C. branneri*) was caught by hand using SCUBA. Each species was collected from a single site: *C. antennarius*, Kirby Point South Bay (48°50′54″N, 125°12′00″W); *C. branneri*, Ross Islets (48°52′12″N, 125°09′54″W); *C. gracilis*, Burlo Inlet (48°49′06″N, 125°08′54″W); *C. magister*, Bamfield Inlet (48°49′06″N, 125°08′30W); *C. oregonensis*, Execution Rock (48°48′54″N, 125°06′12″W); and *C. productus*, Grappler Inlet (48°49′54″N, 125°06′54″W). Gender was determined from relative abdominal width (females>males); carapace width was measured to the nearest 0.1 mm with vernier calipers between the 8th and the 9th anterolateral carapace teeth (tooth numbering system according to Nations, 1975). The degree of tooth wear on the claws was rated as: 1 - no visible wear; 2 - intermediate wear (i.e. visible tooth wear, but greater than half the volume of the teeth present); 3 - extreme wear (i.e. approximately half or more of the volume of the teeth was absent). For a similar numerical index, see Juanes & Hartwick (1990).

In the laboratory, individual claws were assessed as 'broken' or 'not broken'. A claw was 'broken' if part or all of either the dactyl or pollex was missing. A claw that had broken in the previous intermolt was recognized as a partially regenerated appendage and was not considered broken. Damage to a claw can occur in other ways, such as a puncture wound or a detached dactyl apodeme. Although these other forms of claw failure were noted, they were excluded from statistical analyses because of their rarity. Differences in the frequency of breakage among the six *Cancer* species and between sexes were analysed using the χ^2-test (Sokal & Rohlf, 1995).

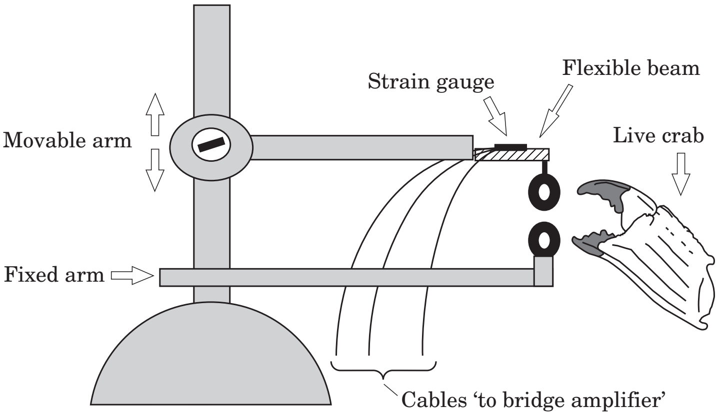

Figure 1. Apparatus used to measure bite-forces in live crabs. The flexible beam, with mounted strain gauge, was attached to a swing-arm microscope stand. The strain gauge was connected to a bridge-amplifier which was in turn connected to a chart recorder.

Experimental animals

To analyse claw performance, several mid-intermolt crabs of each species were selected based our estimation of claw wear (claw index 2, as described above). Unfortunately, no other diagnostic traits for time of intermolt exist in *Cancer*. Crabs with damaged or regenerating claws, or those unable to move their dactyl, were rejected.

All experimental crabs were tagged and housed individually in plastic mesh containers (20 cm × 14 cm × 9 cm), which were fully submerged in running sea water (salinity ≈ 32%, 10–12°C) in a large fibreglass aquarium (150 cm × 90 cm × 10 cm). Biting forces were measured within 7 days of collection, because maximum force and consistency tended to decline with time in the laboratory, perhaps due to reduced aggression in response to being handled (G.M.T., unpublished). Artificial lighting was regulated to seasonal photoperiod. Crabs were fed shucked mussels (*Mytilus* spp.) every evening after the biting force trials were finished.

Biting force measurements

During normal use of the claw, in feeding, defence and sexual combat, crabs may bite on objects varying in shape, size and the degree of hardness, and they may position the object at any point along the occlusive surface (Brown, Cassuto & Loos, 1979; Seed & Hughes, 1995). Furthermore, occlusive regions along the dactyl and pollex are complex and vary among decapod families and therefore any choice of experimental force parameter is arbitrary (Brown *et al.*, 1979). We chose to measure both bite-and break-forces just inside the tip of the dactyl and pollex, because this position can be replicated among species.

Individual crabs were removed from the water and encouraged to grasp a strain gauge (Fig. 1) and bite as firmly as possible. Crabs were grasped firmly by both claws so that movement of the body or other limbs would not affect the biting force measurements (e.g. by unwanted twisting or pushing by the chelipeds), and bites suspected of being influenced by other forces other than the dactyl lever system were discarded. This method is preferred here because it produces greater bite forces than two other known methods, [see Blundon (1988) for details]. Another technique, where the strain gauge is attached directly to the cuticle of the claw-dactyl (Boulding & LaBarbera, 1986), may be superior at assessing more realistic bite force because the investigator does not handle the crabs directly. However, this was not practical for the large number of crabs we studied, and furthermore, the direction of the bending force was more consistent among individuals than other methods would tend to be. In addition, we found that lightly rubbing the inside of the propus-dactyl joint along the occlusive surface helped considerably to elicit a maximal bite.

To obtain a biting force mesurement, the pollex tip was inserted into a lower, immobile steel ring, while the movable finger was inserted into an upper ring mounted on a flexible steel beam (2 mm thick) (Fig. 1). The contact position of the rings with the dactyl and pollex, during biting force measurements, was between the tip and the first tooth along the occlusive surface. The deflection of the steel beam was measure by two strain gauges (Bean BAE-13–250BB–350TE; 350Ω), which were embedded on the steel beam with epoxy resin. These strain gauges were connected to a Wheatstone bridge and a chart recorder. To ensure comparable biting forces among claws of different size, the distance between the inner margins of the rings was adjusted to approximately 60% of the maximum claw gape by repositioning the entire upper movable arm on which the flexible-beam/strain gauge was fixed (Fig. 1). Deflections of the upper ring were calibrated with five known weights that spanned the range of known possible biting forces (4.6–112 Newtons). The apparatus was calibrated both before and after each session. The average of these two curves was used to calibrate biting forces from the chart records for that session.

Each session included bite measurements from both the right and left claws, in succession, of approximately 7–10 crabs. To avoid possible biases, we alternated between the right claw first and left claw first in successive trials. A maximum of two measurements were obtained per claw per day, and were always separated by at least four hours to avoid effects of stress or fatigue. To minimize possible 'day effects', bite forces were measured for all crabs held in the lab and for as many species as possible during each session. The mean number of bites per claw varied from 6.9 to 8.2 among the crab species. Claws for which fewer than 4 bites out of 8 or 10 trials were excluded from the analysis, since this may have indicated a stressed individual, such as a tear in the apodeme along the dactyl, which was noted for one crab.

Estimated biting force calculations

To determine whether biting forces differed among species and sizes of crabs due to differences in muscle stress (force per unit area of apodeme) or to other factors during maximal contraction, we computed the maximum potential biting force for each claw. Maximum potential biting forces were calculated using measures of closer apodeme area (i.e. a measure of the cross-sectional area of the closer muscle), mechanical advantages (*MA*), and angle of pinnation. Methods were similar to those used by Wainwright (1988) to calculate potential pharyngeal musculature biting forces of individual fish and by Alexander (1983) to compare the maximum potential biting forces of the dimorphic claws of the American lobster *Homarus americanus*. The average stress (S) per unit of cross-sectional area was determined as

$$S = F_1 (A \sin 2\alpha)^{-1}$$

where F_1 is the force where the closer apodeme inserts on the dactyl, ($F_1 = F_2/MA$ where F_2 is the force measured at the dactyl tip and $MA = L_1/L_2$, where L_1 is the proximal and $L2$ the distal lever arm of the dactyl), A is the area of one side of the closer apodeme measured, and α is the angle of pinnation (Govind & Blundon, 1985). F_2 and MA were obtaind for all crabs, but angles of pinnation were measured on claws from three males of similar sizes to those used to obtain the true biting force measurements for each species, following the method of Warner *et al.* (1982). We then computed a mean muscle stress, S^*, for all claws in the study. Unlike the muscles of vertebrates, which have a relatively constant stress ($\sigma = 20\,\mathrm{N \cdot cm^{-2}}$) (Prosser, 1973), the muscle stress of decapods varies. For example, the stress of claw-closer muscles can range from a high of 220 $\mathrm{N \cdot cm^{-2}}$ in stone crabs, *Menippe mercenaria* (Blundon, 1988), to a low of 43.0 $\mathrm{N \cdot cm^{-2}}$ in American lobsters, *H. americanus* (Elner & Campbell, 1981). The average stress calculated by Warner & Jones (1976), for the claw-closer muscle of the Atlantic *C. pagurus* (72.1 $\mathrm{N \cdot cm^{-2}}$, at 15°C) is slightly lower than the one we obtained for all six *Cancer* species pooled ($S^* = 81.4\,\mathrm{N \cdot cm^{-2}}$, ± 2.00 S.E., N = 135, at 10–12°C).

We then calculated the maximum potential biting force at the dactyl tip (P'_{MA}) for each individual claw using the apodeme area (A) and mechanical advantage (MA) of that claw, and average of the maximal muscle stress computed for each claw (S^*):

$$P'_{MA} = A \cdot S^* \cdot MA.$$

This calculation assumes that the dactyl pivot is frictionless.

Estimated bite-forces were only used to compare against break forces and actual bite forces and were not used to calculate safety factors.

Estimation of instar

The instar category of crabs was estimated using published size-at-instar regressions. Data for *C. gracilis*, *C. magister*, *C. oregonensis*, and *C. productus* were from Orensanz & Gallucci (1988), while data for *C. antennarius* were from Carroll (1982). No data were available for *C. branneri* so size-at-instar was estimated to be intermediate between the next largest and the next smallest species (*C. gracilis* and *C. oregonensis* respectively). For all species, males and female sizes-at-instar were pooled. Size-at-instar is influenced by many environmental factors, such as temperature (Kondzela & Shirley, 1993), salinity (Loehr & Collias, 1981; Tasto, 1983), and size at settlement (Ebert *et al.*, 1983), so our estimates of instar were necessarily approximate.

Morphometry and breaking force

After the last biting force measurement, chelipeds were autotomized to allow more accurate measurement of size and shape, and to measure breaking strengths.

Chelipeds were autotomized usually within 2–3 days and always within a maximum of 14 days of the last biting force measurement. After autotomy, claw wet weight was taken, and an outline of the claw was drawn in a plane parallel to the closer apodeme using a camera lucida attached to a Wild M5A dissecting microscope. When necessary, a 0.3 × reducing lens was used. Claw dimensions (see Palmer *et al.*, submitted) were digitized from the calibrated drawing with a Summagraphics drawing tablet (20 dots/mm resolution). Claw linear dimensions (i.e. claw height and/or claw length) were used as our measure of claw size for the intraspecific analyses. However, claw wet weight as a measure of claw size was preferred for all interspecific comparisons, because linear dimensions can produce spurious conclusions when claw-shape differences exits among species.

Breaking forces were obtained within 1 h of autotomy by clamping claws (see Palmer *et al.*, submitted), and suspending a container from the tip of the pollex using a loop of 4 mm diameter steel wire. Lead weights of up to approximately 80% of the estimated breaking force were gently added; sand was then poured into the container at a constant rate (approx. 5 g/s) until the claw broke. The weight of the container and its contents were converted to force (Newtons). The position of the load wire and the outline of the fracture margin were recorded on each claw drawing. Claws broke at various locations, but location had only a weak effect on breaking force (Palmer *et al.*, submitted) and only 4% shattered along the lower margin of the pollex (these were excluded from the analyses, for details see Palmer *et al.*, submitted), which would indicate failure due to local buckling (Wainwright *et al.*, 1976). The claws were held in sea water or kept wet continuously until broken, as drying alters the mechanical properties of crustacean cuticle (Hahn & LaBarbera, 1993).

RESULTS

Claw breakage and wear in natural populations

The frequency of claw breakage did not differ significantly among the six species (χ^2 test, $\chi^2 = 10.07$, $P = 0.073$), nor did it differ between males and females for all species pooled ($\chi^2 = 0.008$, $P = 0.978$). All six species exhibited varying degrees of claw wear. Neither wear levels nor frequency of breakage differed between right and left sides for all six species combined ($\chi^2 = 2.27$, $P = 0.132$). However, individuals with ‘extreme wear’ had a higher breakage frequency than those with ‘no wear’ or ‘intermediate wear’ ($\chi^2 = 15.32$, $P < 0.001$), suggesting that crabs later in the intermolt interval were more likely to break their claws (Fig. 2). All species exhibited a similar pattern, except *C. branneri* for which only two claws of ‘extreme wear’ were sampled and both were not broken. Separate analyses for each species were not possible because of small sample sizes.

The relation between claw wear and claw breakage may be confounded because the frequency of injured crabs further along in the intermolt interval will be inflated by inclusion of crabs that broke their claw earlier. Since no method exists to differentiate between old and new exoskeletons in *Cancer*, rates of wear or time of breakage cannot be precisely determined (Juanes & Hartwick, 1990). However, when the possible effects of time on claw-breakage frequencies were removed, by

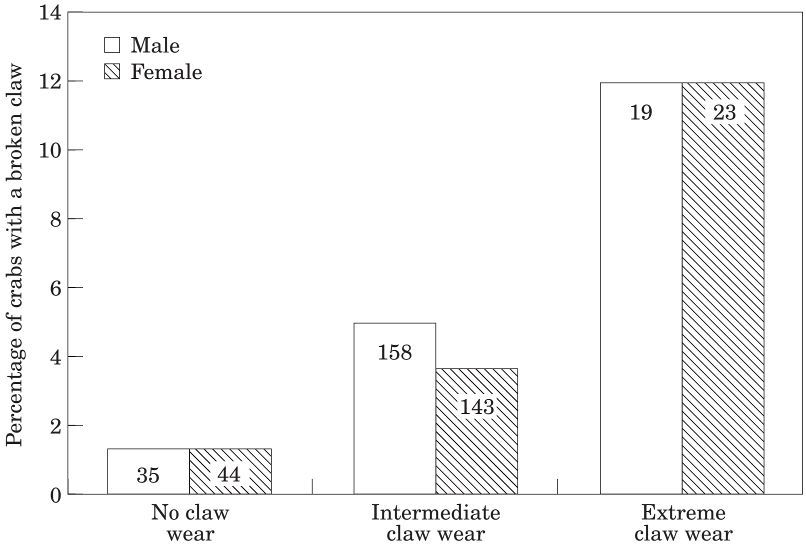

Figure 2. Pooled claw breakage frequencies for field-collected crabs from six *Cancer* species (*C. antennarius*, *C. branneri*, *C. gracilis*, *C. magister*, *C. oregonensis* and *C. productus*), grouped according to claw-wear categories and sex. The percentage of crabs with a broken claw was computed from the total in each category (the number inside each bar). See results for statistical analyses.

discounting the number of broken claws in a higher wear category by the proportion broken in the next lower wear category, this pattern still held: crabs with 'extreme' claw wear exhibited a higher proportion of broken claws than individuals with 'no wear' or 'intermediate wear' (χ^2 test, $\chi^2=6.61$, $P=0.037$). Note that this makes no assumption about duration of time in a given wear category, only about cumulative probabilities.

Intraspecific variation in claw performance

Pollex breaking force, median biting force, and estimated maximum biting force all increased with increasing claw size (log manus length) for the six *Cancer* species studied (Fig. 3). Breaking forces were always greater than, and did not overlap with, either observed or estimated biting forces (Fig. 3). Therefore the estimated probability of failure for all claws for all six species was nearly zero.

Our analysis emphasized differences in slopes among regressions of force types against claw size because if slopes of two regression lines are parallel in a log-log plot, the ratio of two y-values associated with a given x-value will be constant. Therefore if the slopes of both breaking force and biting force versus claw size do not differ, safety factors (break force/bite force) do not vary with claw size. The slope of log breaking force against log manus length did not differ significantly from the slope of log estimated biting force against log manus length for any of the six *Cancer* species (Table 1). However, for four species—*C. antennarius*, *C. branneri*, *C. gracilis* and *C. productus*—the slopes of log breaking force and log observed biting force against log manus length did differ significantly (Table 1A). Therefore, safety

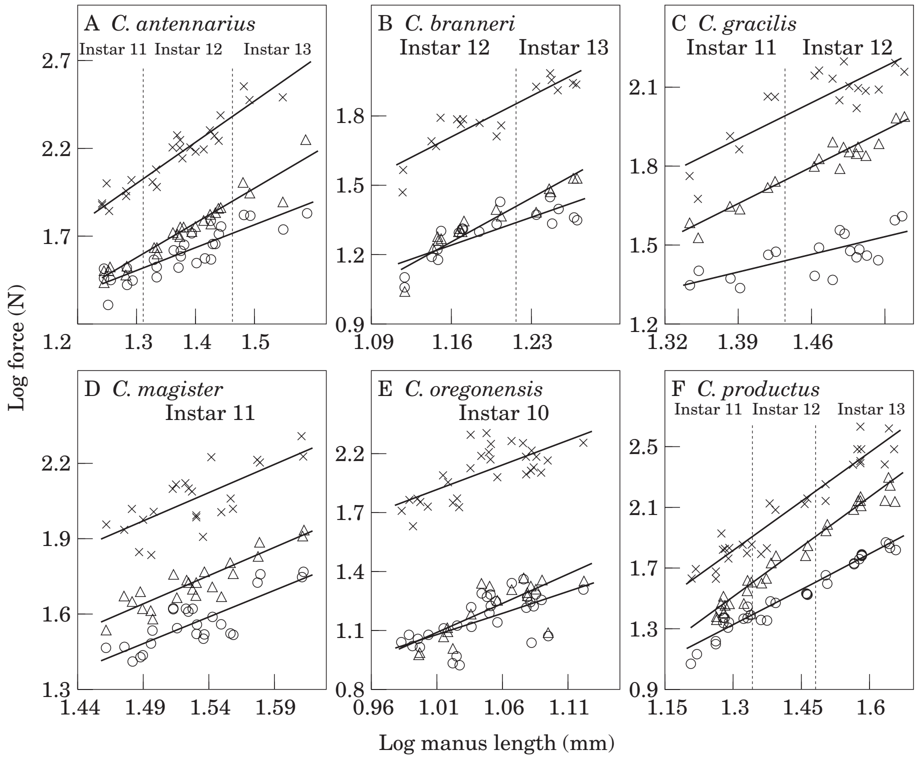

Figure 3. Association between manus length (mm) and each of the three force types – log pollex breaking force (×), log estimated biting force (△), log observed median-maximum biting force (○) – for individuals of all six *Cancer* species. Vertical dashed lines indicate estimated size-at-instar categories. Solid lines indicate least-squares linear regressions.

factors calculated using estimated biting force were similar over the range of manus lengths, while those calculated using observed biting forces varied (Table 1A). In these four species, biting-force slopes were less than breaking-force slopes, thus safety factors increased with increasing manus length (Fig. 3A, B, C, F & Table 1B) (Palmer *et al.*, submitted).

Differences in the range of instars sampled may explain why some species exhibited a more pronounced dependence of safety factor on size than others. With increasing claw size, biting force declined relative to breaking force in the four species for which we sampled more than one instar (Fig. 3A, B, C, F). In contrast, biting force did not decline relative to breaking force in those two species, *C. magister* and *C. oregonensis*, for which we had sampled only one instar (Fig. 3D, E). Later instars had significantly greater safety factors, however, safety factors among species were surprisingly similar within instars (Fig. 4 & Table 2C, D).

Both size-adjusted breaking forces and size-adjusted biting forces declined with later instars, though only the latter did so significantly (Fig. 5 & Table 2A, B). Because interaction effects (species x instar) were absent (Table 2A, B), the similar decline in breaking and biting force yielded safety factors that did not vary across instar categories (Fig. 4). The two species represented by only one instar (*C. magister* and *C. oregonensis*) were not included in the above analysis. Significantly, after the

TABLE 1. (A) Results from ANCOVAs for each of the six *Cancer* species testing the effects of force type (fixed effect) and sex (fixed effect; *C. branneri* and *C. gracilis* were excluded due to small sample sizes), with manus length as the covariate. The three force types are log pollex breaking force (N), log median biting force (N), and log estimated biting force (N). All mean squares (MS) were tested over the error MS. (B) Least-squares linear regressions for each force type and the results of significance tests for differences among slopes. Slopes sharing the same letter did not differ significantly via Tukey's test (Zar, 1984) (see Fig. 3 for data)

	(A) ANCOVA				(B) Comparison of Slopes				
Species	Source	df	*MS*	*P*	Force-type	Intercept	Slope	Difference	r^2
ANT	Force-type	2	0.022	0.005	Breaking	−1.03 ± 0.14	2.34 ± 0.14	a	0.92
	Sex	1	0.001	0.577	Est. biting	−1.07 ± 0.12	2.03 ± 0.11	a	0.93
	Log ML	1	2.332	<0.001	Biting	−0.28 ± 0.16	1.36 ± 0.15	b	0.76
	Force-type* Log ML	2	0.054	<0.001					
	Error	76	0.004						
BRA	Force-type	2	0.004	0.123	Breaking	−0.72 ± 0.27	2.12 ± 0.24	ab	0.87
	Log ML	1	0.280	<0.001	Est. biting	−1.21 ± 0.20	2.15 ± 0.18	a	0.93
	Force-type* Log ML	2	0.006	0.048	Biting	−0.32 ± 0.32	1.36 ± 0.29	b	0.66
	Error	32	0.002						
GRA	Force-type	2	0.006	0.155	Breaking	−0.19 ± 0.36	1.54 ± 0.24	a	0.65
	Log ML	1	0.292	<0.001	Est. biting	−0.91 ± 0.15	1.85 ± 0.14	a	0.94
	Force-type* Log ML	2	0.010	0.042	Biting	0.08 ± 0.26	0.94 ± 0.24	b	0.56
	Error	36	0.003						
MAG	Force-type	2	0.000	0.920	Breaking	−1.52 ± 0.48	2.33 ± 0.45	–	0.58
	Sex	1	0.018	0.048	Est. biting	−1.61 ± 0.27	2.19 ± 0.25	–	0.81
	Log ML	1	0.561	<0.001	Biting	−1.81 ± 0.34	2.21 ± 0.33	–	0.71
	Force-type* Log ML	2	0.000	0.950					
	Error	55	0.004						
ORE	Force-type	2	0.010	0.188	Breaking	−0.75 ± 0.48	2.54 ± 0.47	–	0.51
	Sex	1	0.242	<0.001	Est. biting	−1.93 ± 0.60	2.99 ± 0.57	–	0.59
	Log ML	1	0.239	<0.001	Biting	−1.12 ± 0.50	2.18 ± 0.49	–	0.41
	Force-type* Log ML	2	0.005	0.408					
	Error	74	0.006						
PRO	Force-type	2	0.023	0.008	Breaking	−0.86 ± 0.12	2.07 ± 0.16	a	0.92
	Sex	1	0.000	0.884	Est. biting	−1.26 ± 0.08	2.13 ± 0.07	a	0.97
	Log ML	1	4.670	<0.001	Biting	−0.67 ± 0.06	1.54 ± 0.06	b	0.95
	Force-type* Log ML	2	0.063	<0.001					
	Error	82	0.005						

ANT = *C. antennarius*, BRA = *C. branneri*, GRA = *C. gracilis*, MAG = *C. magister*, ORE = *C. oregonensis*, PRO = *C. productus*; ML = manus length (mm); Breaking = breaking force of pollex; Biting = biting force of claw; Est. biting = estimated biting force of claw.

effects of claw size were removed, *C. magister* exhibited the lowest safety factor relative to any other species or instar category. In addition, regardless of the effects of size, the safety factor for *C. oregonensis* was greater than any other species or instar category (Fig. 4).

Among individual crabs, an analysis of residuals (deviations from regression against manus length in Fig. 3) revealed that claws with a higher-than-expected biting force also had a higher-than-expected breaking force (Fig. 6). In other words, for a given claw size breaking force was positively correlated with biting force (Fig. 6). This correlation was highly significant for all 6 species combined (Table 3A) as well as for 5 of the 6 species individually (Table 3B), and was not a statistical artifact of using the same covariate (manus length) to derive both sets of residuals. First, we

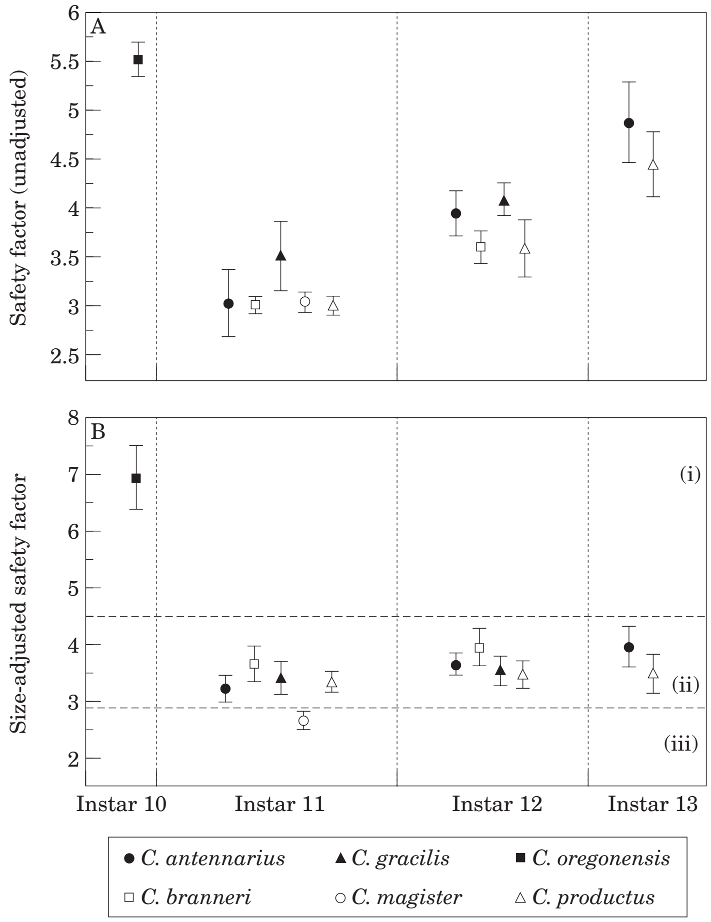

Figure 4. Safety factors as a function of instar number in six *Cancer* species. A, safety factors not adjusted for claw size effects. B, claw size effects on safety factors removed via least-squares linear regression [horizontal dashed lines separate groups – (i), (ii), and (iii) – within which mean safety factors did not differ significantly]. See Table 2 for ANCOVA results.

performed the same analysis using residuals derived from two other covariates of claw size (manus height and claw wet-weight). Second, we also regressed breaking and biting force residuals derived from different covariates (manus length, manus height and claw wet-weight) against one another. In all of these regressions a significant correlation between residuals was always detected (analyses not shown). In the ANCOVA, the species-by-sex interaction for breaking force residuals (Table 3A), was entirely due to *C. oregonensis*, for which the claws of males tended to break at higher loads and bite with greater force than the claws of females.

Interspecific variation in claw performance

Breaking forces for a standardized claw size (3.76 g wet-weight) differed significantly among species (Fig. 7A & Table 4A). The size-adjusted breaking force for *C.*

TABLE 2. Results from ANCOVAs testing the effects of species (fixed effect) and instar (fixed effect) on the dependent variables (A) log pollex breaking force (N), and (B) log biting force. Claw-size effects were factored out using the covariate log claw wet-weight (g). (C) Results from ANOVA testing the effects of species (fixed effect) and instar (fixed effect) on log safety factor (dependent, effects of size not removed). (D) Results from ANCOVA testing the effects of species (fixed effect) and instar (fixed effect) on log safety factor [dependent, effects of size removed, covariate log claw wet weight (g)]. All mean squares were tested over the error MS (see Figs 4 & 5 for data)

Source	df	*MS*	*P*	Source	df	*MS*	*P*
(A) ANCOVA; log breaking force (dependent)				(C) ANOVA; log safety factor (dependent)			
Species	3	0.102	<0.001	Species	3	0.012	0.153
Instar	2	0.004	0.396	Instar	2	0.165	<0.001
Log claw weight	1	0.826	<0.001	Species* instar	4	0.001	0.929
Error	78	0.004	–	Error	75	0.007	–
(B) ANCOVA; log biting force (dependent)				(D) ANCOVA; log safety factor (dependent)			
Species	3	0.076	<0.001	Species	3	0.008	0.272
Instar	2	0.010	0.031	Instar	2	0.001	0.866
Log claw weight	1	0.490	<0.001	Log claw weight	1	0.051	0.005
Error	78	0.215	–	Species* instar	4	0.003	0.705
				Error	74	0.006	–

oregonensis (210 N) was nearly twice as great as the average of the other five species (90 N), whereas those for *C. magister* and *C. gracilis* (67 N) were significantly lower than those of the three remaining species (Fig. 7A). *C. antennarius* and *C. branneri* exhibited intermediate breaking forces (on average 114 N) that were not significantly different from each other.

Maximum biting forces for a standardized claw size (3.76 g wet-weight) fell into two groups (Fig. 7B & Table 4B). The biting forces of *C. antennarius*, *C. branneri*, *C. productus*, and *C. oregonensis* (average = 29.1 N) were significantly higher than those of *C. magister* and *C. gracilis* (average = 23.0 N) (Fig. 7B). However, an almost significant interaction effect between species and sex (Table 4) suggests that caution with this interpretation. The difference between *C. oregonensis* and both *C. magister* and *C. gracilis*, depended on the higher biting force of male *C. oregonensis*. The biting force of *C. oregonensis* females was only slightly, but not significantly, greater than that of *C. magister* and *C. gracilis* females.

Claw safety factors for a standardized claw size also differed significantly among the six *Cancer* species. *C. oregonensis* had the highest safety factor, *C. magister* the lowest, and the remaining four species were intermediate and did not differ (Fig. 7C, Table 4C). The high safety factor of *C. oregonensis* was due to a significantly higher-than-average pollex breaking force (Fig. 7A) rather than a lower-than-average median bite force (Fig. 7B). The low safety factor of *C. magister* resulted from a slightly lower-than-average biting force (Fig. 7A) coupled with a much lower-then-average pollex breaking force (Fig. 7B). Curiously, size-adjusted safety factors did not differ between the sexes within species (Table 4C, D), even for *C. oregonensis* where biting and breaking forces differed significantly between males and females (Table 4A, B).

DISCUSSION

Sources of claw failure in natural populations

In the six *Cancer* species we examined, the strength and load distributions (both the estimated and actual biting forces) did not overlap over the observed range of

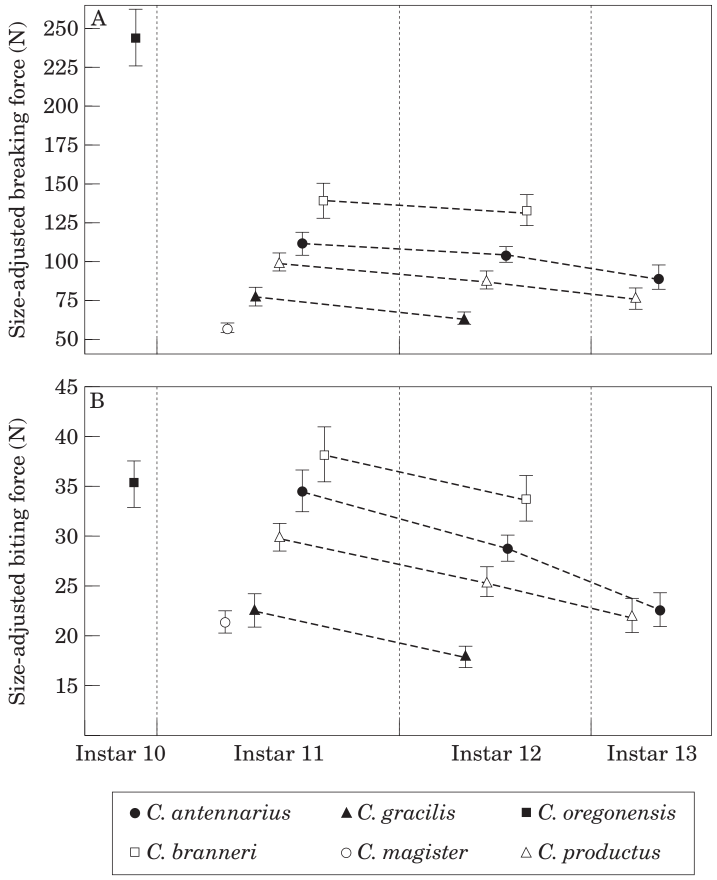

Figure 5. Size-adjusted mean pollex breaking force (A) and mean biting force (B) as a function of instar number for each of the six *Cancer* species. Both were computed using linear regression techniques for a standard claw size of 4.94 wet-weight (g). Dashed lines connect different instars of the same species. See Table 2 for ANCOVA results.

claw sizes. Therefore, the predicted probability of failure for the population was nearly zero (Fig. 3), and healthy crabs that bite hard-shelled prey with maximal force should not break their claws. However, our field data and those of others (Juanes & Hartwick, 1990) reveal that claws do fail in natural populations, so breakage must result from loads or conditions other than those experienced in the laboratory.

Claws may fail for three general reasons that are not independent of each other. First, extrinsic loads, such as those experienced during an attack by a predator or during battles between conspecifics for resources (mates, food, or space), may exceed the intrinsic loads (i.e. individual biting forces) we measured. Second, failure may result from fatigue [i.e. accumulation of microcracks from previous loading history (Boulding & LaBarbera, 1986)] or wear [i.e. cross-sectional area is reduced by excessive abrasion (Wainwright *et al.*, 1976] and scratches [i.e. local stress concentration that lower the theoretical strength of a structure (Gordon, 1978)] accumulated over an intermolt interval. Third, claw failure may occur just after ecdysis

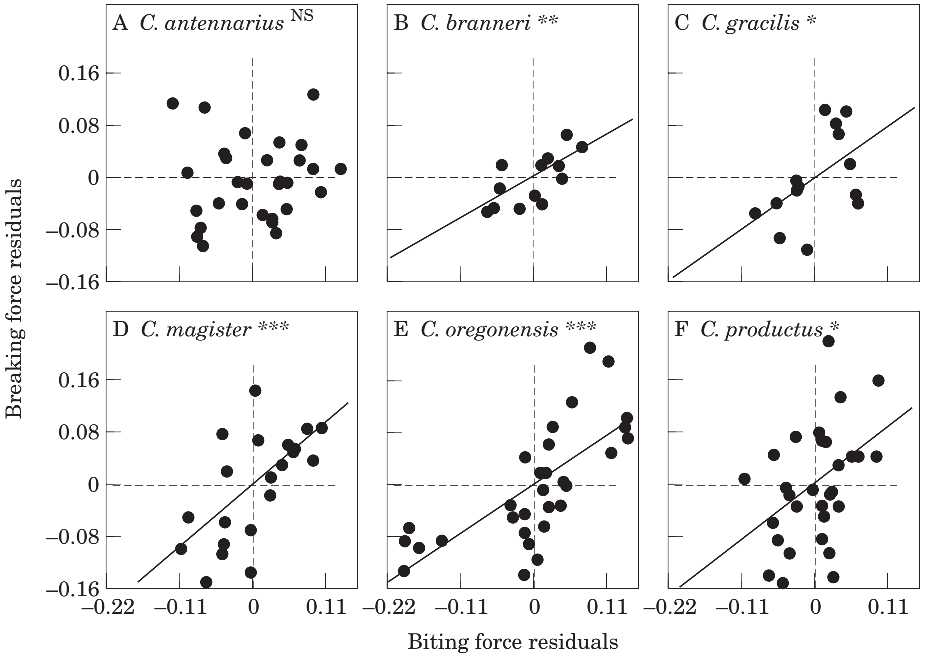

Figure 6. Correlations between breaking-force residuals and biting-force residuals for individual claws of all six *Cancer* species. Both residuals were obtained separately for each species as deviations from a from least-squares linear regression against log manus length (mm). Solid lines indicate least-squares linear regression fit (**P*>0.05, ***P*>0.01, ****P*>0.001, NS = not significant). See Table 3 for statistics.

Table 3. (A) Results from ANCOVA testing the effect of species (fixed effect) and sex (fixed effect) on the residual breaking force, with residual biting force as the covariate. (B) Least-squares linear regressions for residual biting forces against residual breaking forces for each of the six *Cancer* species. Residuals for each species were derived from independent analyses of log pollex breaking force (N) versus log manus length (mm) and log claw biting force (N) versus log manus length (mm) (see Fig. 6 for data).

(A) ANCOVA;
tresidual breaking force (dependent)

Source	df	*MS*	*P*
Species	5	0.001	0.957
Sex	1	0.002	0.495
Residual BitF.	1	0.139	<0.001
Species* Sex	5	0.010	0.046
Error	123	0.004	–

(B) Regression;
breaking force residuals (Y) vs. biting force residuals (X)

Species	N	Intercept	Slope	r^2	*P*
ANT	28	$-3.74\mathrm{E}^{-19} \pm 0.01$	0.12 ± 0.17	0.02	0.487
BRA	13	$-3.79\mathrm{E}^{-20} \pm 0.01$	0.58 ± 0.18	0.48	0.008
GRA	9	0.0106 ± 0.02	0.83 ± 0.35	0.44	0.049
MAG	21	$-1.36\mathrm{E}^{-19} \pm 0.01$	0.88 ± 0.24	0.41	0.002
ORE	30	$3.3\mathrm{E}^{-20} \pm 0.01$	0.68 ± 0.13	0.51	<0.001
PRO	30	$-3.57\mathrm{E}^{-19} \pm 0.01$	0.79 ± 0.31	0.19	0.016

ANT = *C. antennarius*, BRA = *C. branneri*, GRA = *C. gracilis*, MAG = *C. magister*, *ORE* = *C. oregonesis*, PRO = *C. productus*; BitF. = Biting force.

before the cuticle can attain its original strength. As argued below, we suspect fatigue or wear/scratches, in association with feeding on hard-shelled prey during the later part of the intermolt interval, is the most likely cause. Since, unlike humans (Osborn, 1996) or ungulates (Radinsky, 1985) that use weak bite forces to process prey, crabs are known to exert exceptionally high claw bite-forces while subduing hard shell

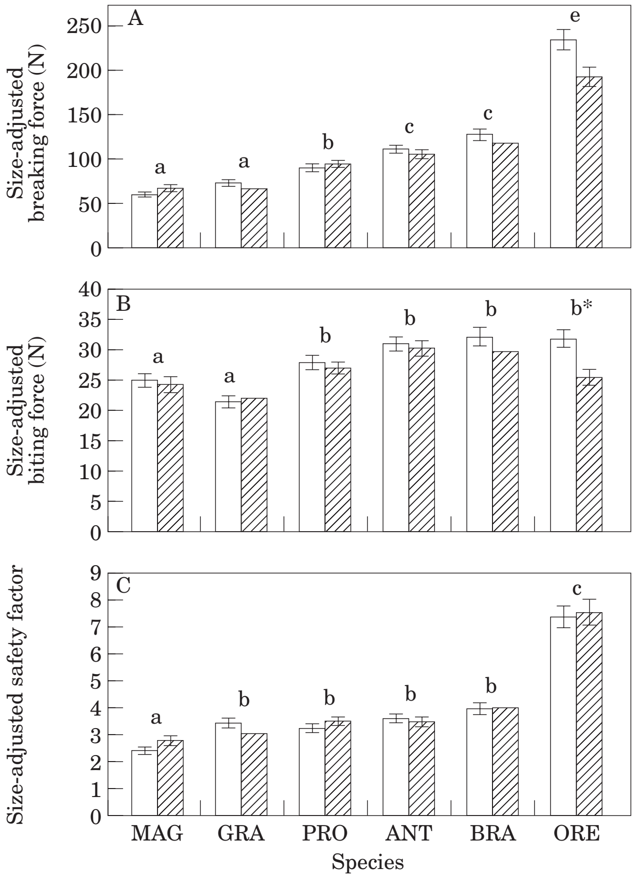

Figure 7. Size-adjusted means of (A) pollex breaking force, (B) biting force, and (C) safety factors, for each sex and species of *Cancer* crab. (□) male; (▨) female. All were computed using a single ANCOVA for a standard claw size 3.76 wet weight (g). Letters identify groups of means that did not differ significantly after the least-square means of each species were tested using a sequential Bonferroni adjustment on *P* values. b* indicates that male *C. oregonensis* were more similar to the group labelled b whereas females were more similar to group a. (see Table 5 for ANCOVA results). (MAG-*C. magister*; GRA – *C. gracilis*; PRO – *C. productus*; ANT – *C. antennarius*; BRA-*C. branneri*; and ORE – *C. oregonensis*).

prey (Boulding & LaBarbera, 1986, Preston *et al.*, 1996), similar to bone crushing carnivores (Van Valkenburgh, 1988).

Claw breakage by predators seems unlikely, because the force required to break a claw is greater than the force required to induce autotomy. For the six *Cancer* species studied, the average force to break a claw was 132 N. Such a force, if delivered by a predator on intact cuticle, would tend to induce autotomy (McVean, 1982). Furthermore, autotomy frequencies correlate with the intensity of predation (for review, see Juanes & Smith, 1995), and all such studies suggest that autotomy is more likely than breakage during an attack. Overall, predation does not appear to account for the high frequency of claw breakage in natural populations.

Agonistic interactions between males for sexually receptive females may also have little bearing on the claw-breakage frequencies observed in natural populations, because of the ritualized nature of these encounters (Christy, 1987; Orensanz *et al.*,

Table 4. Results from ANCOVAs testing the effects of species (fixed effect) and sex (fixed effect) on three dependent variables: (A) log pollex breaking force (N), (B) log median maximum biting force and (C) log safety factor. Size effects were factored out using the covariate log claw wet-weight (g). The significant interaction in the ANCOVA (A) was entirely the result of a sex effect on breaking force of *C. oregonesis* (see Fig. 7 for data).

Source	df	*MS*	*P*	Source	df	*MS*	*P*
(A) ANCOVA; log breaking force (dependent)				(C) ANCOVA; log safety factor (dependent)			
Species	5	0.324	<0.001	Species	5	0.239	<0.001
Sex	1	0.007	0.213	Sex	1	0.001	0.698
Log Claw Weight	1	3.585	<0.001	Log Claw Weight	1	0.337	<0.001
Species* Sex	5	0.014	0.009	Species* Sex	5	0.006	0.404
Error	123	0.005	–	Error	123	0.006	–
(B) ANCOVA; log biting force (dependent)							
Species	5	0.037	<0.001				
Sex	1	0.013	0.071				
Log Claw Weight	1	1.724	<0.001				
Species* Sex	5	0.009	0.055				
Error	123	0.004	–				

1995). Furthermore, if male-male competitive encounters were responsible for claw damage, males should show a higher frequency of claw breakage than do females. Our pooled results for all six species did not reveal any difference between males and females (Fig. 2); therefore, male agonistic interactions seem unlikely to account for the claw damage rates observed in natural populations of *Cancer*.

In addition, neither agonistic interactions over territory nor food seem likely to account for the injuries observed in wild *Cancer* crabs, because the type of claw damage we observed differed from that in other crabs known to defend a territory. Territorial crabs appear to suffer wounds predominantly on the manus reflective of extrinsic loads from conspecific or predatory attacks (Jones, 1980; Jensen & Armstrong, 1991), while damage to the fingers would likely reflect extreme self-loading. Of the 1346 claws we sampled from the six *Cancer* species, only two had manus wounds while 81 had broken fingers. Therefore, because *Cancer* crabs mainly exhibited damage to the fingers rather than to the manus, damage due to agonistic interactions seems unlikely.

Collectively, these observations suggest that breakage caused by extrinsic loading (predatory attack, agonistic conspecific interaction, and territorial defense) is unlikely. However, as Juanes & Hartwick (1990) hypothesized, the high breakage frequencies in natural populations of *Cancer* may result from excessive biting forces that 'hunger-motivated' crabs exert on hard-shelled prey. Furthermore this breakage event most likely occurs at the end of the intermolt interval, when the cumulative effects of wear and fatigue are maximal (Fig. 2). Therefore, food abundance and type (i.e. hard-bodied versus soft-bodied) near the end of the intermolt interval may significantly influence the probability of claw breakage.

The relation between claw strength and load

All claws exhibited safety factors clearly above 1.0 (Fig. 8), which shows a consistent dependence of breaking force on biting force. When the effects of size were not

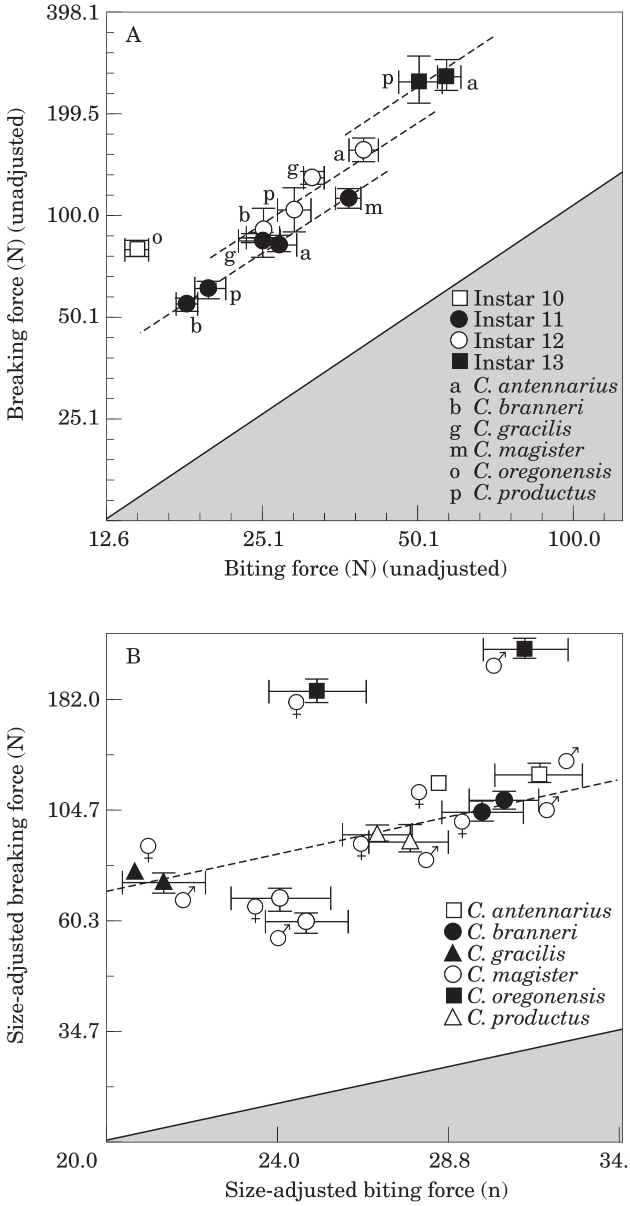

Figure 8. Breaking force versus biting force, on a log scale, for all six *Cancer* species. The solid line indicates constant safety factor of 1.0 and the shaded area indicates safety factors <1.0. A, strength versus load (not size-adjusted) for each species and instar. The dashed lines indicate a constant safety factor for each instar for all species (instar 11, safety factor = 3.1; instar 12, safety factor = 3.9; instar 13, safety factor = 4.6). B, size-adjusted strength versus size-adjusted load for each species and sex. The dashed line represents an average constant safety factor of 3.6 for *C. antennarius*, *C. branneri*, *C. gracilis* and *C. productus*.

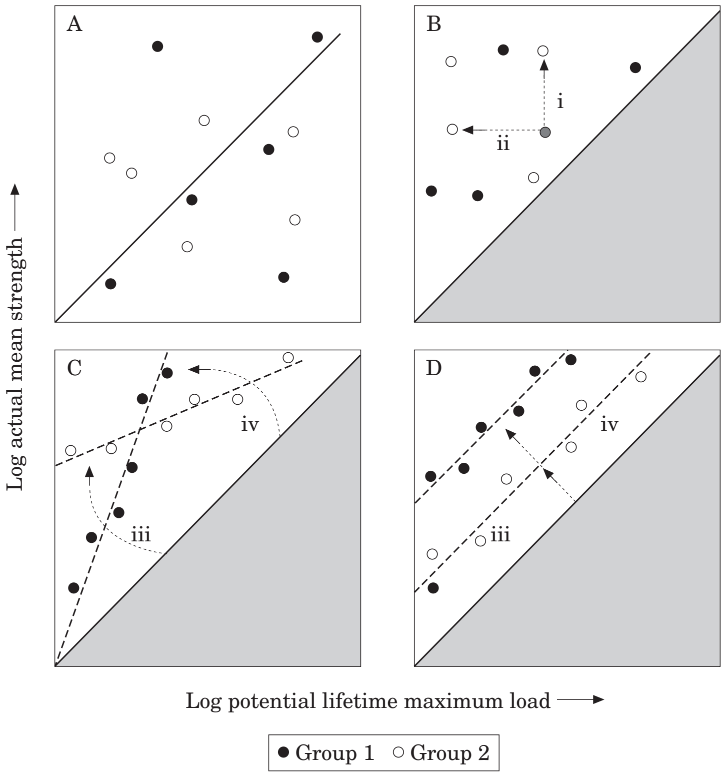

Figure 9. Hypothetical relation between mean strength and potential lifetime maximum load. The open and closed circles represent two groups within a hypothetical category (e.g. species, sex, or habitat type). The solid line in all graphs indicates a safety factor of 1.0. A, mean strength and potential lifetime maximum load vary independently because selection pressures on them differ. B, mean strength exceeds maximum load because these variables are functionally related, but are not tightly coupled or constrained. Note that the safety factor may increase due either to an increase in strength (i) or to a decrease in maximum load (ii). C, mean strength and maximum load are tightly coupled and vary allometrically relative to each other because one or the other may be constrained for geometrical or functional reasons (i.e. mean strength may either increase at a greater rate (iii) or at a lesser rate (iv) than potential lifetime maximum load). D, mean strength and maximum load are tightly coupled but vary isometrically relative to each other, as would be expected if a single selection pressure exerted a proportional effect on both variables. See Appendix for further explanation.

removed, breaking and biting forces varied among all species and instars in a positive allometric fashion, in contrast, when instars were examined separately, the relation between breaking and biting force appeared isometric (Fig. 8A). Similarly, when the effects of claw size were removed, size-adjusted breaking and biting forces for four species (*C. antennarius*, *C. branneri*, *C. gracilis*, and *C. productus*) yielded a stable size-adjusted safety factor of 3.6 (dashed line, Fig. 8B). However, *C. oregonensis* and *C. magister* did not fall on this line and had size-adjusted safety factors of 7.4 and 2.6 respectively (Fig. 8B). Nonetheless, the difference between the sexes for *C. oregonensis* also resembled the isometric pattern among the four species (*C. antennarius*, *C. branneri*, *C. gracilis*, and *C. productus*). Clearly, safety factors cannot be considered static ratios.

Among-individual variation in safety factors

The evolutionary response of safety factors depends on, among other things, the overlap between the strength and load distributions in a population: the greater the overlap, the greater the probability of failure (Alexander, 1981). However, estimates of the probability of failure may be confounded if both strength and load co-vary in a predictable fashion among individuals (Biewener, 1993). Should such correlations go undetected the probability of failure in natural populations could be significantly overestimated.

Our data revealed two ways in which among-individual variation in strength and load was positively correlated. First, later instars of four of the six *Cancer* species exhibited lower size-adjusted biting and breaking forces than earlier instars (Fig. 5) in a manner that suggests crabs may regulate their maximum biting force behaviorally as they age. The decline in breaking force with inferred age was expected, because the amount of fatigue and wear on the claws (Juanes & Hartwick, 1990) should increase as the length of the intermolt interval increases (Orensanz & Gallucci, 1988). However, the decline in size-adjusted biting force was not expected, because size-adjusted muscle mass and apodeme area remained constant across instars (G.M.T., unpublished). Significantly, the decline in size-adjusted biting force in later instars (Fig. 5B) did parallel the decline in claw strength (Fig. 5A), which suggests that individuals may behaviorally adjust their biting force as relative claw strength declines with increasing age.

Second, among similar sized crabs maximal biting forces were lower in claws with weaker fingers in all six species of *Cancer* crabs even though intraspecific variation only ranged from 8 to 18% (overall mean of ±12.2% for break force and ±14.6% for bite force) (Fig. 6). These among-individual differences could be due either to behavioural differences or to physiological differences. A closer inspection of our data revealed that relative cuticle dry weight and relative closer muscle dry weight also varied among individuals within a species (±9.0% and ±15.6% respectively). In addition, this variation was significantly correlated with variation in relative biting and breaking force ($P<0.001$ for all four correlations, data not shown), and all four factors were highly correlated between the right and left claws among individuals ($P<0.001$, data not shown). Collectively, these correlations all suggest that the among-individual variation we observed among similar sized crabs was due to physiological and anatomical changes over the moult cycle, rather than to behavioral differences. Regardless, individual safety factors remained surprisingly similar because of the covariation between maximum biting and breaking force, a pattern which maintains a relatively constant probability of claw failure over the moult cycle.

These correlations between maximum load and breaking strength among claw as a function of age or stage in moult cycle complicates traditional calculations of the probability of failure (Alexander, 1981). Individuals with a low breaking strength, compared to others in the population, may not actually be at as high a risk of failure as would be expected from the breaking-force distribution for the population. Therefore, increased variability in strength or load within a population need not favour an evolutionary increase in safety factor—as would be expected in the traditional view (Lowell, 1985)—if among-individual variation in strength and load are correlated.

Phylogenetic patterns in safety factors

Among the six species of *Cancer* crabs we studied, the average safety factor for the claws of four of them—*C. antennarius*, *C. branneri*, *C. gracilis*, and *C. productus*—was surprisingly similar (safety factor = 3.6). The two remaining species differed significantly from this group. *C. magister* had a lower safety factor (2.6), where as *C. oregonensis* had an exceptionally high safety factor (7.4), not only compared to the other five species, but also compared to other arthropod structures and vertebrate bone (safety factor = 1.6 to 5.6; Alexander, 1981). These differences among species might be due to phylogenetic effects, or to ecological differences (diet, habitat, or mating behaviour); we consider several alternative hypotheses below.

The four species—*C. antennarius*, *C. branneri*, *C. gracilis*, and *C. productus*—have different mating systems (Orensanz *et al.*, 1995), use different habitats (Orensanz & Gallucci, 1988), and almost certainly have different diets [as reflected by their claw shape (Lawton & Elner, 1985)]; however, size-adjusted safety factors were indistinguishable among them (Fig. 7C). Do these similar safety factors represent common ancestry or convergence resulting from a common selection pressure?

A recent phylogeny inferred from sequence variation in the cytochrome oxidase I gene (Harrison, 1997), and consistent with the fossil record (Nations, 1975; Harrison, 1997), suggests safety factors of claws for *C. antennarius*, *C. branneri*, *C. gracilis*, and *C. productus* are similar because of common ancestry. Among the six species examined in this study, *C. productus* (intermediate safety factor) was the sister group to the other five. *C. oregonensis* (high safety factor) occurs in a clade with *C. branneri* and *C. gracilis* (both with intermediate safety factors), whereas *C. magister* (low safety factor) occurs in a clade with *C. antennarius* and *C. novaezealandiae* (intermediate safety factor and unknown safety factor respectively). Parsimony suggests that the most plausible safety factor of a hypothetical ancestor would be ‘intermediate’, and that the relatively high safety factor of *C. oregonensis* and the relatively low safety factor of *C. magister* are derived.

Although the similarity of safety factors among the other four species is most easily interpreted as the result of common ancestry, these species may nonetheless still be experiencing a common selection pressure. However, the rather substantial differences in claw form and life-history among them (Lawton & Elner, 1985; Orensanz & Gallucci, 1988) suggests the similarity of safety factors is greater than would be expected given their ecological diversity.

Effects of relative claw size on safety factors

According to theory, biological structures that have a high contribution to fitness, or that are costly to produce, should have a high safety factor (Alexander, 1981). An increase in relative claw size should indicate an increase in the cost of claw production. Therefore, species with relatively larger claws should have higher safety factors. Our data support this prediction. Among the six species studied. *C. oregonensis*, which has the largest claw size relative to body size (Lawton & Elner, 1985; Orensanz & Gallucci, 1988), had the highest safety factor while *C. magister* had the smallest claw size relative to body size and the lowest safety factor. The relative claw sizes and safety factors for the other *Cancer* species were intermediate, suggesting a positive correlation between claw size and safety factor.

Following the same reasoning, the claw safety factors of males and females of sexually dimorphic species should differ. The consequences of failure should be higher for males than for females, because male crabs tend to have relatively larger claws, and rely on their claws for combat with other males over the acquisition of mates (Smith & Hines, 1991) as well as for feeding and defence. Therefore, we would expect higher safety factors for males of species with male-biased claw dimorphism. *C. oregonensis*, which had the highest overall safety factor, exhibited the greatest male-biased claw dimorphism. However, the size-adjusted claw safety factors of the two sexes were almost identical (Fig. 7C). Of the other five *Cancer* species, all except *C. magister*, show varying degrees of sexual dimorphism in claw size (Lawton & Elner, 1985; Orensanz & Gallucci, 1988). However, safety factors did not differ between the sexes in those species for which we had large enough samples of both males and females: *C. antennarius*, *C. oregonensis* and *C. productus*.

Overall, safety factor increased with increasing claw size among the six species of *Cancer* studied. However, this pattern did not hold with for intraspecific differences between sexes. Clearly, relative claw size, as a single variable reflecting cost of investment, is not adequate to explain the observed variation in safety factors among species.

Effects of diet and habitat on safety factors

We cannot easily separate the effects of diet and habitat on claw safety factors. A diet of harder-shelled prey [as inferred from absolute and relative claw size and leverage properties (Brown *et al.*, 1979; Elner & Campbell, 1981; Smith & Palmer, 1994; Yamada & Boulding, 1998)] need not promote a higher safety factor, since both biting force and breaking strength may increase in parallel. However, the consequences of claw damage or loss may be much higher for species that depend upon hard-shelled prey than for those that feed mainly on softer bodied prey. For example, *Cancer magister* with a damaged and/or a worn claw cannot feed efficiently on hard-shelled prey (Juanes & Hartwick, 1990) whereas claw loss appears to have little impact on the feeding efficiency of *Callinectes spaidus* when feeding on soft-shelled clams (Smith & Hines, 1991).

Significantly, prey toughness is often correlated with habitat type: soft-sediment environments typically offer a greater diversity and abundance of soft-bodied prey that tend to bury themselves to escape predators instead of relying on shell strength (Boulding, 1984), whereas prey from hard-bottom environments are usually more well defended morphologically. As a consequence, crabs such as *C. magister* (low safety factor), which tend to occupy open inlets having a sandy substrate (Orensanz & Gallucci, 1988) and to feed on a wide range of prey items other than hard-shelled prey, such as shrimp, small soft-shelled clams, and carrion (Bernard, 1979), may be less affected by claw injury than *C. oregonensis* (high safety factor), which is restricted to rocky substrata and feeds primarily on hard-shelled prey (Lawton & Elner, 1985). In addition, *C. magister* and *C. oregonensis* avoid predation in different ways: *C. magister* escapes predators by crypsis, by fleeing when attacked, and by achieving a large size through a high growth rate during the juvenile stages (Orensanz & Gallucci, 1988) whereas *C. oregonensis* escapes predators by defending a shelter, by feeding nearby and only at night, and by maturing at a small size (Orensanz & Gallucci, 1988; Jensen, 1995). The remaining four species (intermediate safety factors)—*C.*

antennarius, *C. branneri*, *C. gracilis*, and *C. productus*—occupy intermediate habitat types, and each depends partially on some structure in its environment for protection (Lawton & Elner, 1985; Orensanz & Gallucci, 1988; Jensen, 1995). Clearly, the effects on safety factors of differences in diet type, habitat, and life-history are difficult to disentangle, however the consequence of damaging a claw may be predictably different in different habitat types, which in turn should promote the evolution of different safety factors.

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APPENDIX

The performance of two traits may be tightly coupled, slightly coupled, or have a limited relation to one another. If the performance of one trait does not depend on the performance of a second, then strength and load may not be correlated (Fig. 9A). Typically, safety factors are studied for traits for which performance is correlated. In dogs, for example, the strength of the limb bones is highly correlated with the load that can be exerted by the muscles attached to these bones (Alexander, 1974). However, over evolutionary time the performance of two previously coupled traits may become uncoupled. For example, the shell strength and foot tenacity of limpet species appear to be tightly coupled functionally, because the shell offers protection only as long as the foot can resist prying forces by predatory crabs or birds (Lowell, 1987). If this selection pressure persists, we would expect the performance of the shell and foot to remain tightly coupled. However, if prying forces cease to be relevant, then the performance of the shell and foot might become uncoupled. For example, shell strength would contribute little to fitness of limpets preyed on by the surfperch *Damalichthys vacca* and *Embiotoca lateralis*, which feed by sucking limpets from the substratum (Mercurio *et al*., 1985). Where limpets are exposed only to predation by these fish, shell strength would become uncoupled from foot tenacity.

In general, if two traits are tightly coupled functionally, and both strength and load are highly predictable, the mean strength of the structure should exceed the lifetime maximum load only slightly (safety factor ≅ 1.0; solid line, Fig. 9A–D). Safety factors close to 1.0 may also persist in a structure because conflicting selection pressures result in trade-offs. For example, in dogs and kangaroos, an increase in tendon strength conflicts with an increase in tendon elasticity (Alexander, 1981). A detached tendon is a serious injury in mammals, so natural selection should minimize the probability of failure by increasing tendon strength, which would yield a greater safety factor. However, tendons in several taxa exhibit remarkably low safety factors (close to 1.0 and always below 2.0), apparently because of the trade-off between strength and the capacity to store elastic energy (Alexander, 1981).

More commonly, though, strength is not as tightly constrained as in tendons and safety factors may vary in a number of ways. For example, if selection pressures are unique for different species and both the mean strength and the potential lifetime maximum load are free to vary, then strength and load may not be tightly coupled (Fig. 9B): an increase in safety factor may result from an increase in strength (Fig. 9B.i) or a decrease in maximum load (Fig. 9B.ii). However, if one trait is somehow constrained while the other is free to vary, then strength and load may vary in one of two ways: mean strength may be free to vary while maximum load is constrained [Fig. 9C.iii], or vice versa [Fig. 9C.iv]. Such a relation has been reported for cuticle thickness and buckling resistance in insect walking legs (Prange, 1977). However, additional information is required to determine whether such curves are shaped by adaptation or constraint.

Finally, the performance of two structures may be tightly coupled so as to maintain a constant safety factor (Fig. 9D). This occurs in the limbs of terrestrial mammals, where safety factors remain constant over a wide range of adult body sizes, because mammals appear to adjust their posture to compensate for increased load (greater body mass) on their limbs (Biewener, 1989).