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The Biomechanics and Evolution of *Cancer* Crab Claws

By

Graeme Michael Taylor ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of *Doctor of Philosophy*

in

Systematics and Evolution

Department of Biological Sciences

Edmonton, Alberta

FALL 1999

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Date: Oct 1st 1999

" A sarcastic soul once observed that the primary function of our schools is to impart sufficient facts to make the children stop asking questions. Those with whom the schools do not succeed become scientists. I never made good grades in school, at times I nearly failed, and I never stopped asking questions."

Knut Schmidt-Nielsen, 1994

Edmonton, Alberta, December, 1966, 4 a.m.
When did I stop writing you?
The sandalwood is on fire in this small hotel on Jasper
Street.
You've entered the room a hundred times
disguises of sari and armour and jeans,
and you sit beside me for hours
like a woman alone in a happy room.
I've sung to a thousand people
And I've written a small new song
I believe I will trust myself with the care of my soul.
I hope you have money for the winter.
I'll send you some as soon as I'm paid.
Grass and honey, the singing radiator,
the shadow of bridges on the ice
of the North Saskatchewan River,
the cold blue hospital of the sky—
it all keeps us such sweet company.

Leonard Cohen

I see the ocean from my window
it is very dull
no whales today
no tidal wave
The fisherman fiddles
with his air conditioner
The sunset is slowly squashed
by the huge forces of night
I telephone my wife
We watch it in each other's arms

Leonard Cohen, 1968,
The Energy of Slaves

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *The Biomechanics and Evolution of Cancer Crab Claws* submitted by Graeme Michael Taylor in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Systematics and Evolution.

Dr. A. R. Palmer

Dr. J. I. Goldberg

Dr. B. S. Heming

Dr. J. W. Osborn

Dr. R. W. Elner

Date: Sept. 24, 1999

For Penny

Abstract

Although robust claws have evolved numerous times in clawed crustaceans, the biomechanical factors that contribute to or constrain claw performance have not been explored in a rigorous, comparative manner. For six species of *Cancer* crabs (*C. antennarius, C. branneri, C. gracilis, C. magister, C. oregonensis,* and *C. productus*), I examined natural breakage frequencies, maximum biting forces, maximum theoretical biting forces, and breaking strengths of claws, and interpreted these findings in terms of safety factor theory.

For all six *Cancer* species, claw safety factors (the ratio of breaking strength to maximum load) were not static ratios, but increased with claw size. Since crabs lose the ability to regenerate claws with increasing size (age), the increased safety factors with size appeared adaptive. Higher safety factors in larger crabs resulted primarily from lower relative biting force, perhaps due to behavioral restraint or to a constraint on muscle performance.

Relatively lower biting forces in larger crabs were due to lower maximum muscle stress (i.e., force per unit area of muscle), as observed by others in stone crabs (*Menippe mercenaria*) and lobsters (*Homarus americanus*). The lower maximum muscle stress in larger claws contrasted with the pattern in several other claw traits, which increased intraspecifically with increasing claw size: relative claw height, mechanical advantage, and sarcomere length of the closer muscle. This strongly suggests an unidentified constraint may be acting on maximum biting force in larger claws, and may be widespread in decapod crustaceans.

Interspecific variation in claw safety factors was correlated with claw shape. Particularly important were a) the height of the claw (i.e., manus), which correlated with closer muscle properties (sarcomere length and angle of pinnation) that affect performance,

and b) the length of the fixed finger (i.e., pollex), which influences how biting forces translate into stresses on the finger. The high correspondence between exoskeletal and performance traits offers a powerful predictive tool for interpreting wider biogeographical patterns in claw size and shape for both extant and extinct species of crabs.

Finally, a phylogenetic analysis suggested that claw form evolved rapidly in *Cancer* crabs because similar forms arose independently in separate lineages.

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I am truly indebted to Anise C. Barton who developed the method for assessing claw strength and was a colleague on the safety factor work. Also, I thank Judith Robertson who explored with me the notion of structural failure in crab claws, which was the precursor to the safety factor work. C.K. Govind hosted me in his lab for several months and taught me much about crab muscle physiology. I am very thankful for getting to know him as a researcher and as a friend. Also, during my stay in C.K.'s lab, I was assisted by Johanne Pearce and Tom Read, both of whom are truly skilled individuals in the laboratory and who often assisted me freely. Kent West provided me with computer programming making calculations of the second moments of area for irregular shapes possible. I thank Keith Jackson for computer advice, and Yazdan Keivany for the use of his computer. For art work, I thank Tom Saunders for superb drawings of the six *Cancer* claws (Chapter 4), and Dave Denning for photographing the *Cancer* crab crew.

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J. E. Gordon wrote a book titled 'Structures: or Why Things Don't Fall Down'. After several years of living and working at Bamfield Marine Station, I have the answer — STAFF. I am sure my research and my life would have slid into the ocean if not for the concerted effort made by all Bamfield Marine Station members to keep all within their grasp alive. I thank all of them.

Lab mates and crab people provided indispensable help in the field and lab, and I particularly thank Tim Rawlings, Stef Zaklan, Chris Cameron, Iain McGaw, Dave Smith,

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1. Introduction

Vermeij (1987) proposed an intriguing evolutionary hypothesis about the 'arms-race' between predators and prey: with time, prey increase their resistance to predation by increasing the safety of their armor, and predators counter this response by increasing the strength of their armament. For a co-evolved system, the dynamics between predator and prey appear to escalate with time, as older geographic regions tend to have prey populations with greater armor strength and also have predator populations with greater armament capabilities (Vermeij 1987). Vermeij (1977) applied his hypothesis to marine crabs and their benthic prey, and he concluded that crabs and their hard-shelled prey are highly co-evolved. Others were skeptical, and suggested the data could not support any firm conclusion, and the null hypothesis that the observed brachyuran diversity arose by chance was not rejected (Abele *et al.*, 1981).

The underlying premise of the evolutionary arms race assumes the evolution of the diversity of life arises by a highly organized deterministic process (Abele *et al.*, 1981). In other words, the patterns we observe can be explained by mechanistic rules of design (Thompson, 1917; Wainwright *et al.*, 1976) and more dynamic rules governing organismal interactions, such as competition and predator-prey dynamics (MacArthur, 1972; Alexander, 1982; Alexander, 1991). The alternative view sees the diversity of life forms as arising by less deterministic processes, such as random events and historical contingency (Gould *et al.*, 1977; Strong *et al.*, 1979; Gould, 1989). The general evolutionary question still remains unanswered, and is central to many evolutionary and ecological debates: can the variation in species diversity over evolutionary time be explained by rules of physics and of organismal interaction, or need we invoke a component of chance to truly account for diversity?

The views held by the two schools of thought on the diversity of life are not mutually exclusive, and it may be more important to find a method to assess the degree of order and the degree of stochasticity, underlying the variation within a given system (Losos & Miles, 1994). Within each of the two schools, the school of 'order' and the school of 'stochasticity', methods exist for formulating testable predictions (Losos & Miles, 1994). For the school of order, natural laws provide predictions about the kind of variation we expect to observe, and these methods are embodied in the study of biomechanics and are extended to the study of optimality theory (Alexander, 1982). For the school of 'stochasticity', laws of history explain the diversity of life, and phylogenetic trees provide the organizing principle. Studies of biomechanics and optimality tend to assume that patterns of variation in a morphological trait reflect adaptation to prevailing selective pressures (Alexander, 1982; Alexander, 1991). However, in the absence of historical information, the adaptive interpretation is problematic (Felsenstein, 1985; Harvey & Pagel, 1991; Losos & Miles, 1994). History may play more of a role than can be accounted for in a purely functional analysis among related species (Pagel & Harvey, 1988; Gould, 1989; Harvey & Pagel, 1991). Conversely, in the absence of sound biomechanical interpretation of design, the historical interpretation is problematic. Mapping of traits onto phylogenetic trees may underestimate the complexity of structural design, as simple aspects of morphology are often assumed to reflect performance (e.g., body size, brain size). The combined use of biomechanical models, supported with empirical data on performance and morphology, and phylogenetic information should provide insight on debates over the degree of order and the degree of stochasticity underlying organismal diversity.

Although most biological structures give the impression of being well designed for their respective functions, formal comparative studies of the mechanical and morphological differences among groups of closely related species are surprisingly rare (Wainwright & Reilly, 1994). I explore the evolution of claw performance and design by documenting its variation within species (size and sex) and among species within the genus *Cancer* (Decapoda: Brachyura, Cancridae) for six species: *C. antennarius*, *C. branneri*, *C. gracilis*, *C. magister*, *C. oregonensis* and *C. productus*. In interpreting the observed patterns of variation, I employ biomechanical models relevant to brachyuran claw design and performance. Others are presently constructing a molecular phylogeny of the group {23 morphologically distinct species (Nations, 1975)}, and a partial phylogenetic tree including the six *Cancer* species mentioned above has been published (Harrison & Crespi, 1999). My research program provides for a more complete understanding of the diversity of claw form with respect to performance, and makes some first steps in reconciling the degree of determinism and the degree of historical contingency underlying the diversity in this system.

The morphology and performance of decapod claws

The claws of durophagous predators and the shells of their prey both give the impression of being well designed for their functions and appear highly co-evolved. In part, crabs use their claws to crush the armor of their prey, and shells of prey resist being crushed. Slow and sedentary animals like gastropods, bivalves, and barnacles, clearly depend on the strength of their armor for survival. The force required to break the shells of gastropods are exceptional, up to 8,800 Newtons (Vermeij & Currey, 1980). Because hard-shelled prey abound in many benthic marine environments, claws capable of generating strong crushing forces should be favored by natural selection in many durophagous decapod crustaceans (Vermeij, 1987). Crab claws produce some of the highest biting forces reported for any group, and have been measured to produce a bite force of up to 800 Newtons (Vermeij, 1987; Blundon, 1988).

Crabs with claws adapted for feeding on hard-shelled prey appear to have larger claws relative to their body size than crabs specializing on other prey items (Vermeij, 1977; Smith & Palmer, 1994), however, we do not have a good sense of how claw size correlates with other 'strength' traits. If claws are adapted for strong bite-forces, then from a purely mechanical perspective, changes in performance should be paralleled by concordant changes in several traits affecting bite force (I develop this argument in Chapter 2, and explain the details of the properties of force in several subsections of the Introduction found below). For example, closing speed can be traded-off for biting strength, or *vice versa*, and the tradeoff will be reflected in claw design throughout, as seen in many species with dimorphic crusher and cutter claws (Alexander, 1968; Warner, 1977). The predicted correlations are apparent from the formula describing claw biting forces. The force a claw generates at the tip of the fingers depends upon several factors (Alexander, 1983). First, it depends on the force applied at the apodeme insertion point (**F_{in}**) and on the mechanical advantage (**MA**) or shape of the dactyl:

$$\mathbf{F_{out} = F_{in} * MA}$$

Second, the force generated at the tip of the apodeme (F_{in}) depends on the muscle stress (S), the area of the apodeme (A) and the angles the muscle fibers insert on the apodeme (Θ):

$$F_{in} = S * (A * \sin 2\Theta)$$

Thus increases in any of the factors **MA, S, A or sin2Θ** will yield an increase in maximum biting force. Therefore, for a given volume of muscle, a claw adapted for strong bite forces should show concordant directional changes in all of the above metric traits in order to maximize force over speed.

Claws appear to be designed for either strength or speed, since mechanically it is impossible to design a claw with both properties (Alexander, 1968; Warner, 1977). Observations on dimorphic clawed species support this posit since the right and the left claw tend to diverge in design. The larger claw is often termed the 'crusher' or 'strong', and the smaller claws is the 'cutter' or 'fast', because of the associated strength and speed properties. Crusher claws tends to have a higher mechanical advantage, a more molar-like occlusive surface, a larger closer apodeme, a greater angle of pinnation, and a closer muscle with a higher average sarcomere length (potential muscle stress) than cutter claws (Warner, 1977). In general, behavioral observations on claw use and measures of claw performance support the crusher and cutter claw dichotomy, since the crusher claw is often used preferentially to break the shells of prey, while the cutter claw is used to manipulate prey and to tear its soft-flesh once the shell has been crushed (Elner, 1978; Zipser & Vermeij, 1978; Elner, 1980; Hughes, 1989). In general, therefore claws do appear highly adapted to the functional tasks they perform.

For interspecific comparisons however, the co-variation between strength traits within crusher and cutter claws has not always been consistent (Warner & Jones, 1976; Brown, Cassuto & Loos, 1979; Govind & Blundon, 1985), suggesting either additional selection pressures (Elner & Campbell, 1981; Orensanz & Gallucci, 1988), or constraints (Elner & Campbell, 1981) or pure chance events (Abele *et al.*, 1981) may be effecting claw design. For example, *Macropipus depurator* showed intermediate sarcomere length fibers for both crusher and cutter claws (Warner & Jones, 1976). Similarly, the asymmetric chelae of the blue crab (*Callinectes sapidus*) are symmetrical in muscle morphology for both sarcomere length and histochemical composition (Govind & Blundon, 1985). Therefore, conclusions based solely upon intraspecific patterns of claw dimorphism cannot simply be extended to clawed crustaceans in general. A more systematic approach is required that a) quantifies claw shape for several dimensions, b) measures muscle properties for both sexes and for different sized individuals, and c) extends the analysis beyond a single species.

Sexual selection and other selection pressures acting on claw design

Because durophagous brachyuran claws can generate strong crushing forces, studies of claw function have focused mainly on foraging behavior (Ebling *et al.*, 1964; Elner, 1978; Elner & Hughes, 1978; Vermeij & Covich, 1978; Zipser & Vermeij, 1978; Elner, 1980; Hughes, 1989; Lee & Seed, 1992; Seed & Hughes, 1997) though other factors may also influence claw design. A primary hypothesis suggests the claw acts as the template upon which feeding habits and prey preferences are determined (Schafer, 1954; Elner, 1978; Elner, 1980; Lawton & Elner, 1985). However, other, less documented selection pressures, may determine claw size and form, such as defense and reproduction (Elner & Campbell, 1981; Orensanz & Gallucci, 1988; Lee & Seed, 1992; Orensanz *et al.*, 1995). Sexual selection acting on claw size is most apparent in species of the fiddler crab *Uca*, where the major claw is much larger than the minor and can account for as much as 50% of the male's total body weight (Crane, 1975; Levinton &Judge, 1993). Though less pronounced, sexual dimorphism exits in most crab genera (Shine, 1989), suggesting sexual selection as a fairly ubiquitous force acting on claw size. Identification of alternative selective pressures acting on claws should be improved by quantification of various exoskeletal traits and muscle traits. More detailed quantification of claw design will allow us to assess the degree of claw 'specialization' towards either a 'strong' or 'fast' claw, as mentioned above, and also allow us to assess subtle departures from the expected forms, suggesting alternative selection pressures or constraints.

The 'arms-race' between crabs and prey

Brachyuran predators and their hard shelled prey appear highly co-evolved system, and their interactions have escalated with evolutionary time (Vermeij, 1977). Vermeij (1977), speculating on the fossil record of crabs previous to the Tertiary, suggests that bite-force of crabs (as inferred by claw size relative to body size) did increase over time. Brachyuran crabs appear to originate in the Jurassic (213 million years ago, all numerical ages based on Harland *et al.*, 1982) or earliest Cretaceaous {see references in Vermeij, (1977)}. The claws of crabs during this time are slender and do not appear capable of subduing heavily armored prey, though molluscan shells also appear mechanically weak at this time. The ability of crabs to break large molluscan shells does not becomes apparent until Late Cretaceous (144 million years ago) or earliest Tertiary time (65 million years ago) (Vermeij 1977). In general, the appearance of crabs with 'strong' claws is correlated with the appearance of more effective shelled armored prey. The present diversity of brachyuran crabs with large claws took approximately 100 million years to appear. Furthermore, the diversity of durophagous crabs appears different among oceans, with the highest claw size in the Indo-West Pacific, intermediate in the Eastern Pacific, and lower in the tropical Atlantic and least in the temperate zones (Vermeij, 1977; but see Abele *et al.*, 1981). In general, older geographic regions tend to have crab predators with greater potential bite-force capabilities and prey populations with greater armor strength than younger regions (Vermeij, 1977).

Vermeij (1977) restricted his geographical comparison to crabs within the same genus, or, at most, within a group of closely allied genera, to avoid potentially confounding variation in claw muscle properties. However, variation in muscle architecture at the genus level, remains unknown in clawed durophagous crustaceans, thus making comparisons of claws based solely on external architecture, at any taxonomic level, unrealistic. I address this assumption and explore the variation in muscle architecture for six species of *Cancer* crabs in chapter 3 and also make wider comparisons with other decapod crustaceans in Appendix 2.

The significance of Cancer *crabs for studies of claw morphometrics and performance*

Cancer is a highly suitable genus for a comparative analysis of claw form and function and ecological adaptation, because it includes species from a variety of habitats, whose claw size and shape correlate with habitat type (Lawton & Elner, 1985; Orensanz & Gallucci, 1988). Within a relatively short period of time compared to the brachyurans as a group, the *Cancer* genus radiated into 23 extant species (Nations, 1975) representing a wide range of claw sizes (relative to body size) and shapes (Lawton & Elner, 1985), which suggests diversification of claw form can occur rapidly. The *Cancer* genus arose in the early Miocene, approximately 15 million years ago (Nations, 1975). The monogeneric Cancridae are one of the four brachyuran crab families — Cancridae, Portunidae, Xanthidae and Parthenopidae— containing species known to feed on shelled molluscs, as reported by Vermeij (1977). The six *Cancer* species studied here represent approximately 62% of the variation in relative claw size (i.e., relative to carapace width) measured for durophagous brachyurans (Fig. 1-1). Furthermore, almost 100% of the variation among brachyurans in the single claw shape variable, mechanical advantage, as measured by Vermeij (1977), is seen among claws of the six *Cancer* species studied here (see Table 3 in Vermeij, 1977 and Chapter 2 here). This wide range of variation permits an important test: does the variation in claw size, and mechanical advantage observed for *Cancer* crabs reflect variation in muscle attributes and claw bite-force performance?

Biomechanics, anatomy, and the potential performance of crab claws

Explaining the evolution of strong crushing forces and the diversity of claw design requires a clear understanding of claw biomechanics. Biomechanical models can make for robust predictions about how the claw should be designed and how it should perform. (Huxley & Niedergerke, 1954; Huxley & Hanson, 1954; Gordon, Huxley & Julian, 1966; Alexander, 1968; Josephson, 1975; Wainwright *et al.*, 1976; Alexander and Goldspink, 1977; Warner, 1977; Gordon, 1978; Alexander, 1983). Furthermore, safety factor models allow for robust predictions about how two independent, but related performance attributes should co-vary and evolve (Alexander, 1981; Lowell, 1985; Lowell, 1987; Biewener, 1993; safety factor models are discussed extensively in the introduction of Chapter 2). However, biomechanical models are limited, since they can only allow for speculations on the upper and lower boundaries of performance and anatomy. They do not reveal the actual relation between two or more traits, and therefore the power of such models to explain organismal diversity will ultimately be determined by the empirical data supporting them.

In the following sections I summarize the anatomy of the claw in relation to the various biomechanical models I have used throughout my thesis. The mechanical concepts I discuss here can be found in most general books on physics and in the biomechanical literature (cited above).

Lever mechanics and variation among decapods

Lever systems modify a force produced by the muscle and are important determinants of claw performance. Levers ranging from 1^{st}, 2^{nd}, and 3^{rd} order systems, defined by the relation of the pivot to the force and the load, can be found among skeletol-muscle systems of animals {see Fig. 1-2a and Alexander & Goldspink (1977) for a general discussion on levers}. Biomechanically, the claw represents a first-order lever system, with the pivot, or dactyl hinge, located between the force (closer muscle attachment site) and the load (teeth and/or tip of dactyl; Alexander 1968)(Fig. 1-2). The lever system of claws varies by modifying the distance of either the first lever arm (L_1) or the second (L_2). Changing the ratio of the distances between the pivot and the force and/or the pivot and the load alters the velocity ratio. If the pivot is frictionless, the mechanical advantage becomes equal to the velocity ratio. Therefore, for a given force, and a given load at the dactyl tip, a claw with a long lever-1 and a short lever-2 delivers a higher force than a claw with a short lever-1 and a long lever-2 (Warner, 1977).

Properties of the dactyl-lever system can be easily measured and used to predict the potential force delivered by the claw, and therefore can potentially predict the degree of diet specialization among clawed decapods (Warner, 1977). For a given closer muscle force, a claw with a high mechanical advantage closes slowly but with a strong closing force, while a claw with a low mechanical advantage closes quickly but with a weak closing force. Crabs with 'strong' claws are predicted to hunt slow moving, but well protected, prey like gastropods. Crabs with 'fast' claws are predicted to hunt fast moving prey like fish and other crustaceans (Warner, 1977). The lever system imposes a trade-off in design since a claw cannot be both 'strong' and 'fast' simultaneously. However, the trade-off only exists when lever-2 is measured from the pivot to the dactyl tip, since all crabs can position the prey more proximally along the occlusive surface and therefore all decapods have potentially 'strong' claws, as argued by Brown *et al.,* (1979). In general, the hypothetical 'fast' and 'strong' claw are extremes in a broad ranging continuum of claw lever system diversity, with each specialization suggesting a particular mode of feeding (Schafer 1954).

From a purely mechanical perspective however, claws are only 'intermediate' and 'fast' first order lever systems (Fig. 1-2b), since lever-1 is always less or equal to lever-2.

The mechanical advantage is therefore never greater than one, and any force produced by the muscle will be lower after being modified by the lever system of the claw. For claws of decapods, the reported mechanical advantages range from a high of 0.58 for *Carpilus spp.* to a low of 0.22 for the crayfish *Procambarus clarki* (Vermeij, 1987).

The ultrastructure of the sarcomere, the mechanics of force, and variation among the claw closer muscle of decapods

The performance of striated muscles depends on its structural organization and its chemical constituents, and both vary tremendously among the muscles of clawed decapods (Hoyle, 1967; Atwood, 1973; Warner & Jones, 1976; Hoyle, 1983; Govind, Mellon & Quigley, 1987). Metric traits involved in muscle performance have been termed 'extensive factors', while the chemical traits have been termed 'intensive factors' (Josephson, 1975). The primary focus of my thesis has been on the extensive factors of muscle, such as size, shape, angle of pinnation, and the sarcomere length rather than the 'intensive factors' (see Mykles, 1988). This emphasis is reasonable since the extensive factors are highly correlated with performance (Josephson, 1975). Variation in metric muscle traits, mainly the sarcomere length and the angle of pinnation, makes the simple, first order lever system of the claw design more complex and increases the potential to vary the force and speed of closure.

The sarcomere is the smallest unit of muscle contraction and understanding its role in generating biting forces is essential to understanding claw performance. The closer muscle is composed of fibers running in a specific direction that determines the direction of the contraction force (Fig. 1-3). A single muscle fiber consists of myofibers and these, in turn, are composed of myofibrils (Fig. 1-3). The myofibril is composed of sarcomere units lying in series. A sarcomere unit is defined by Z-bands, and the distance between two Z-bands is the length of the sarcomere. Directly attached to the Z-bands are the thin filaments. Indirectly attached to the thin filaments via contact by actin-myosin bridges are the thick filaments. The muscle contracts by the active process of breaking and reconnecting the actin-myosin bridges coupled with myosin head pivoting, which results in the thin and thick filaments sliding past each other (Huxley & Niedergerke, 1954; Huxley & Hanson, 1954; Gordon, Huxley & Julian, 1966; Huxley, 1969). The contraction force of the sarcomere is directly proportional to the number of actin-myosin bridges, which is determined by the length of the thick filament (A-band) (Huxley and Niedergerke, 1954; Jahromi & Atwood, 1966; Jahromi & Atwood, 1969). Therefore, for a given sarcomere length, the longer the A-band, the higher the potential contraction force.

How individual sarcomere units are arranged relative to one another (i.e., in series or in parallel) determines the overall force and the overall velocity acting on the load (Josephson, 1975). In general, for any structure under linear tension or compression, the force is the same at every cross-section along the length of the structure perpendicular to the direction of force. A sarcomere, which exerts its own tension, will act in the same way as any inert structure. In other words, for a sarcomere under its own tension, the force from its tension will be the same at every cross-section along the length of the sarcomere perpendicular to its length (Fig. 1-4a). When sarcomeres are added in parallel force is additive with respect to the number of sarcomere units, and therefore depends on the total cross-sectional area (Fig. 1-4b). Furthermore, with the addition of sarcomere units in parallel, distance between the load and the fixed end of the sarcomere does not change, and thus the velocity for a given contraction will not change (Fig. 1-4b). Alternatively, when sarcomere units are added in series, the force remains the same as it would be for a single sarcomere unit because the cross-sectional area remains unchanged (Fig. 1-4c). Furthermore, with the addition of sarcomere units in series, distance between the load and the fixed end of the sarcomere does change by the number of additional units, and thus the velocity for a given contraction will change proportionately (Fig. 1-4c). Therefore, how the sarcomeres are arranged, whether in parallel or in series, determines the performance of the muscle (Josephson, 1975).

Whole muscle design also affects contraction force and velocity (Alexander, 1968). The fibers of striated muscle are arranged in various ways, of which there are two main types, parallel and pinnate (see Alexander & Goldspink, (1977) for more detailed arrangements). The parallel muscle shortens over a greater distance than the pinnate muscle, but exerts a relatively lower force (Fig. 1-5a), since for a given volume of muscle the effective cross-sectional area is less than the effective cross-sectional area of a pinnate muscle (Fig. 1-5b; for a more detailed discussion see Alexander, 1968). Furthermore, in a pinnate muscle, as the angle between the fiber and apodeme increases the effective cross-sectional area increases (Fig. 1-5c), and thus the potential force for a given muscle volume increases. However, with increased angles of pinnation, there will be greater loss of net force in the direction of the load. This cost is best illustrated by the hypothetical maximum possible 90 degree angle of pinnation, which maximizes the effective cross-sectional area (Fig. 1-5d) yields no net force acting on the first lever arm of the dactyl. Because of this cost, most pinnate muscle arrangements are less than 45 degrees (Alexander, 1968). Thus for claws of decapods in general, by increasing the angle of pinnation (up to 45 degrees) decapods can increase the effective force acting on the dactyl, in a similar fashion as increasing the mechanical advantage of the claw (Alexander, 1968).

Overview of thesis

The general objectives of this study were: 1) To measure inter- and intraspecific variation in claw performance, particularly biting force and pollex breaking strength, for six sympatric *Cancer* species, 2) to integrate these two independent performance attributes by measuring inter- and intraspecific variation in claw safety factors, and 3) to relate claw exoskeletal and muscle morphology to claw performance.

In Chapter Two, I describe inter- and intraspecific variation in claw biting force, breaking strength, and safety factor for the six *Cancer* species. In Chapter Three, I examine the negative allometry of claw biting force, which is a result of declining muscle stress with increasing claw size. In Chapter Four, I investigate the potential for claw shape to explain interspecific variation in claw safety factors, and to this end examine the relations among claw exoskeletal morphology, internal muscle morphology, biting forces, and pollex breaking strengths among species. Appendix One examines the positive size-dependence of claw safety factors within species, and explores aspects of claw cuticular strength and is a general review of the size-dependence of safety factors for a wide range of taxa. Appendix Two is an interspecific scaling study of muscle stress and sarcomere length, based on my data from the six *Cancer* species and data from various other species compiled from the literature. Here I show that sarcomere length is indeed a good predictor of potential muscle stress.

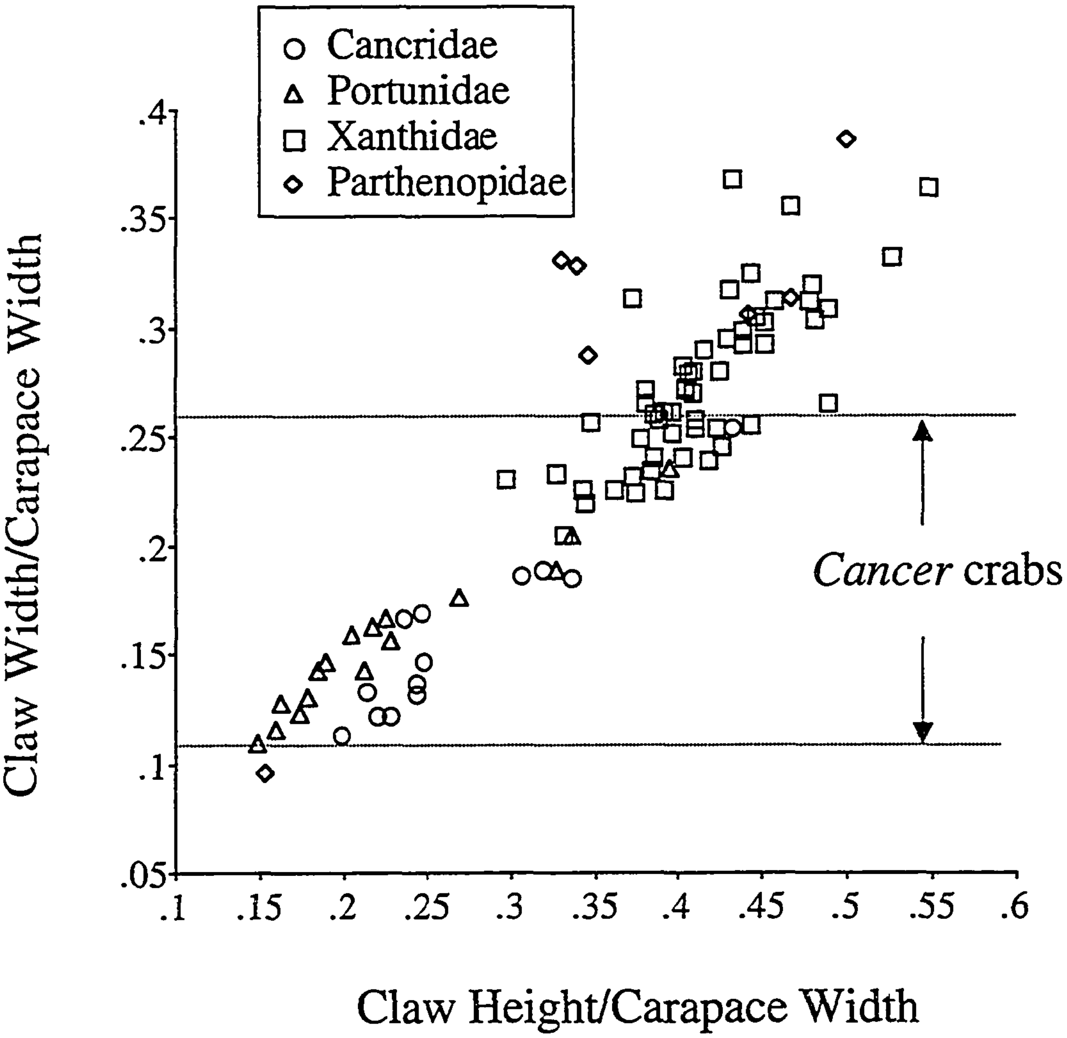

Figure 1-1. Association between relative claw height and relative claw width for four brachyuran families (data from Table 2 in Vermeij, 1977). The two dashed lines represent the lower and upper limits for *Cancer* species.

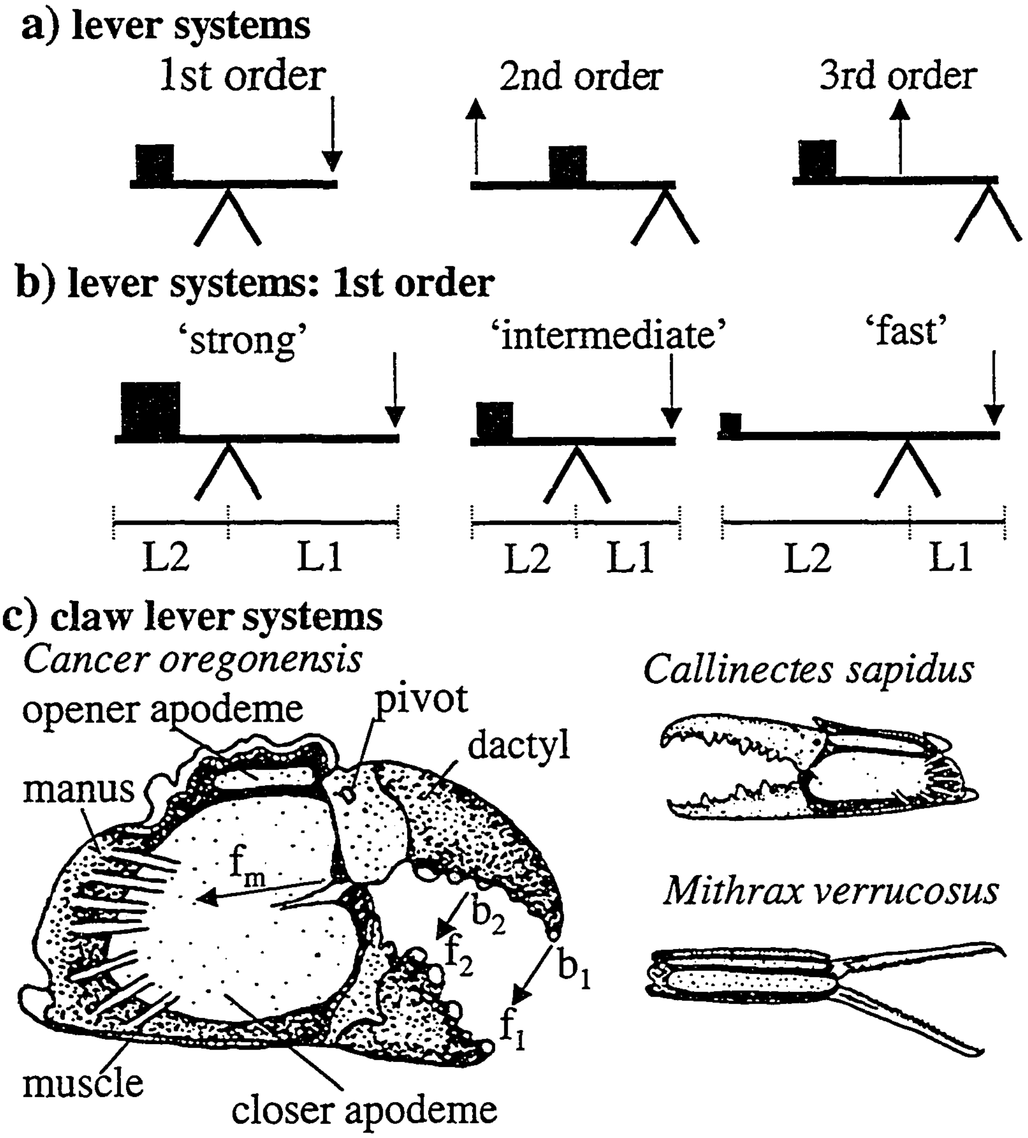

Figure 1-2. a) classification of lever systems based on position of the pivot (open triangle), relative to the load (solid square) and the force (arrow) for a given lever length (solid line),(Alexander & Goldspink, 1977). b) first order lever system with varying lengths of the levers relative to the position of the pivot. For a given force and for the system to remain balanced, the load must change in relation to the length of the levers. c) Variation in the lengths of the lever arms for claws (lever-1 = pivot to apodeme insertion and lever-2 = pivot to dactyl tip), of 3 species of crabs with first order lever systems. Manus cuticle and muscle mass (a few muscle fibers were left) have been removed to show apodeme placement and attachment to the dactyl. The contraction force f_m produced by the closer muscle results in (f_1) or (f_2) depending on position (b_1) or (b_2) of object to be grasped.

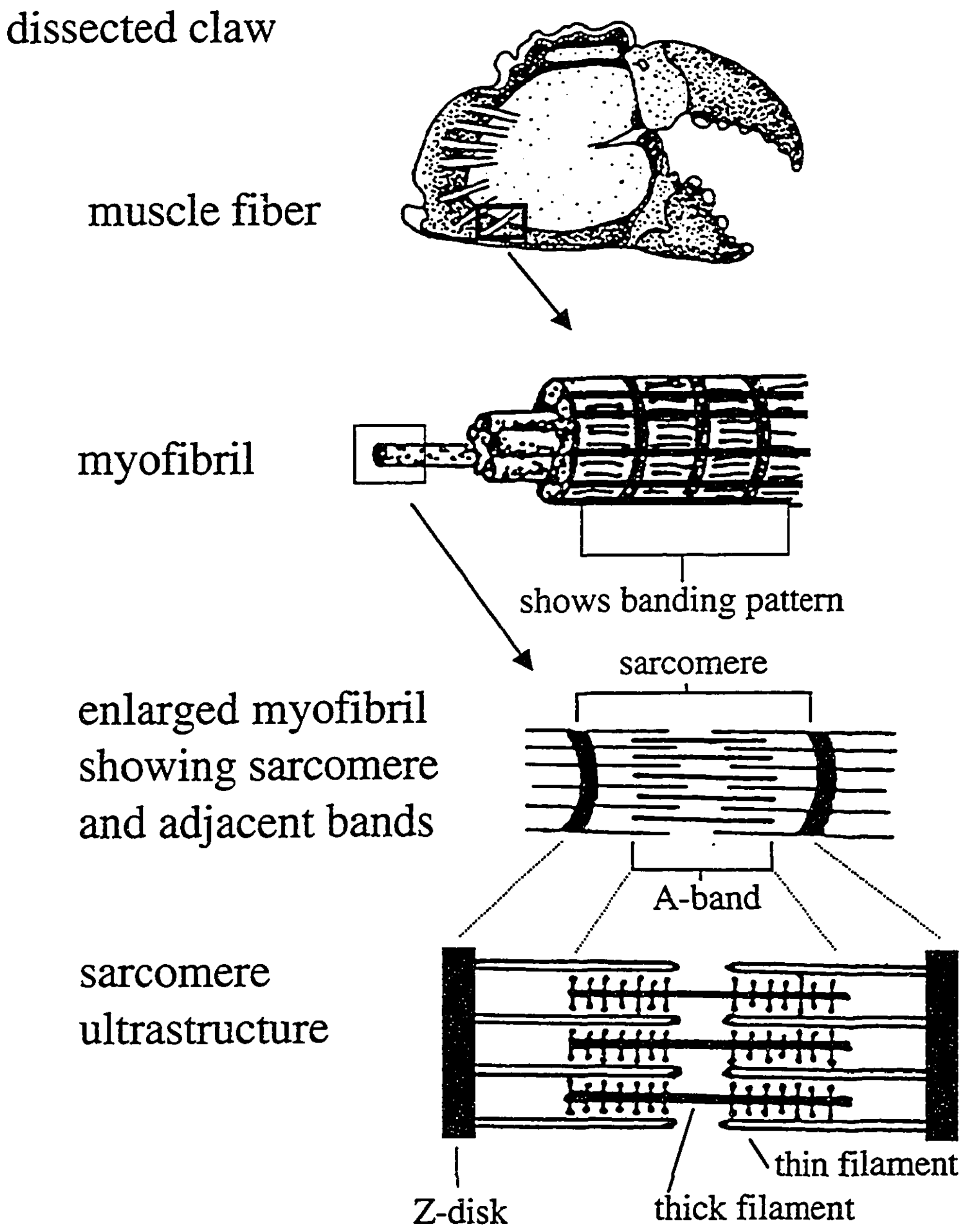

Figure 1-3. The general anatomy of muscle and the ultrastructure of the sarcomere (see text for discussion).

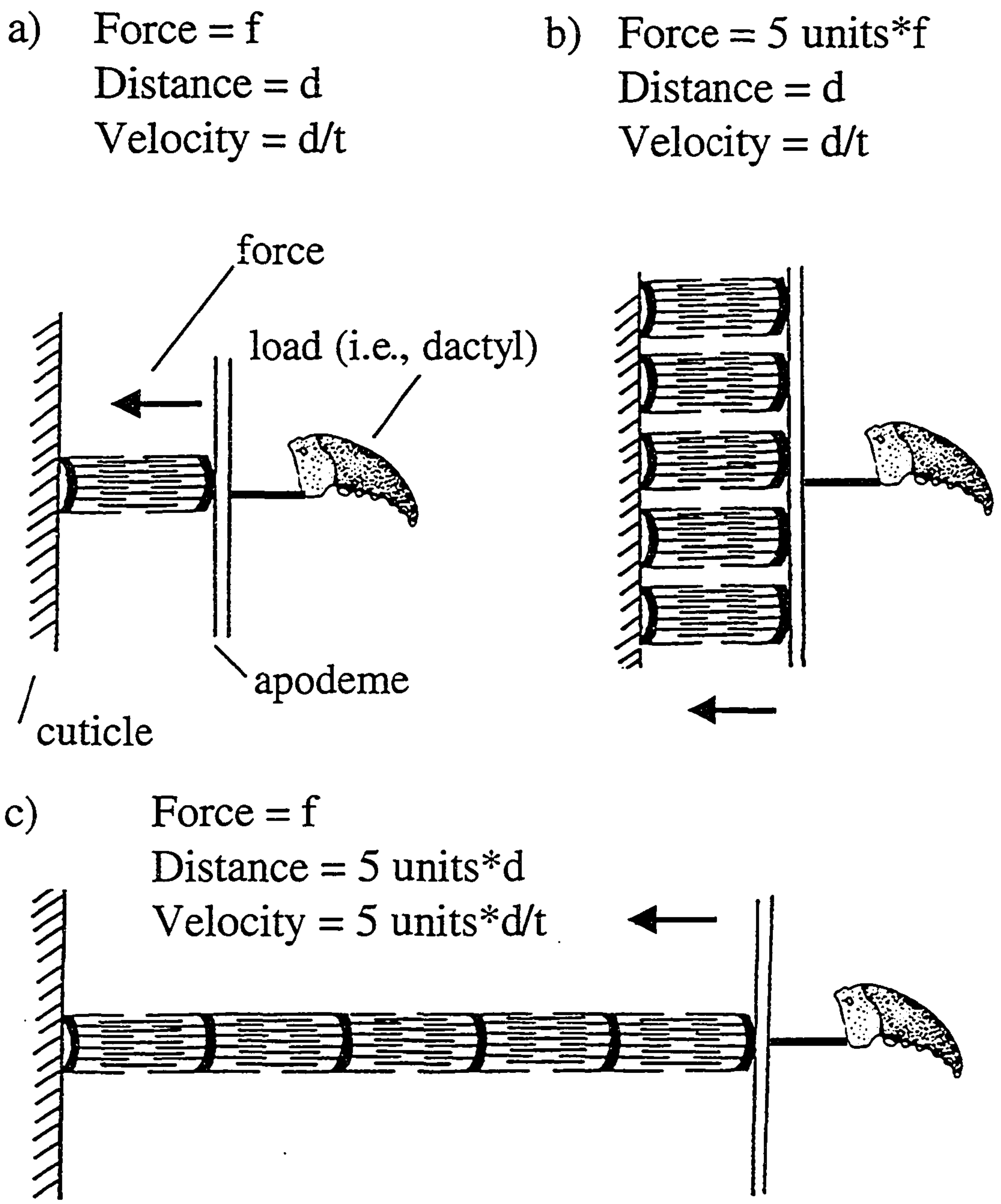

Figure 1-4. a) a hypothetical, individual contractile unit (i.e., sarcomere) attached to both claw-cuticle (fixed) and claw-apodeme (movable). The apodeme is attached to the dactyl. b) a set of 5 contractile units in parallel. c) A set of contractile units in series (modified from Josephson, 1975). The arrow represents the direction of force resulting from contraction of the sarcomere(s). t = time.

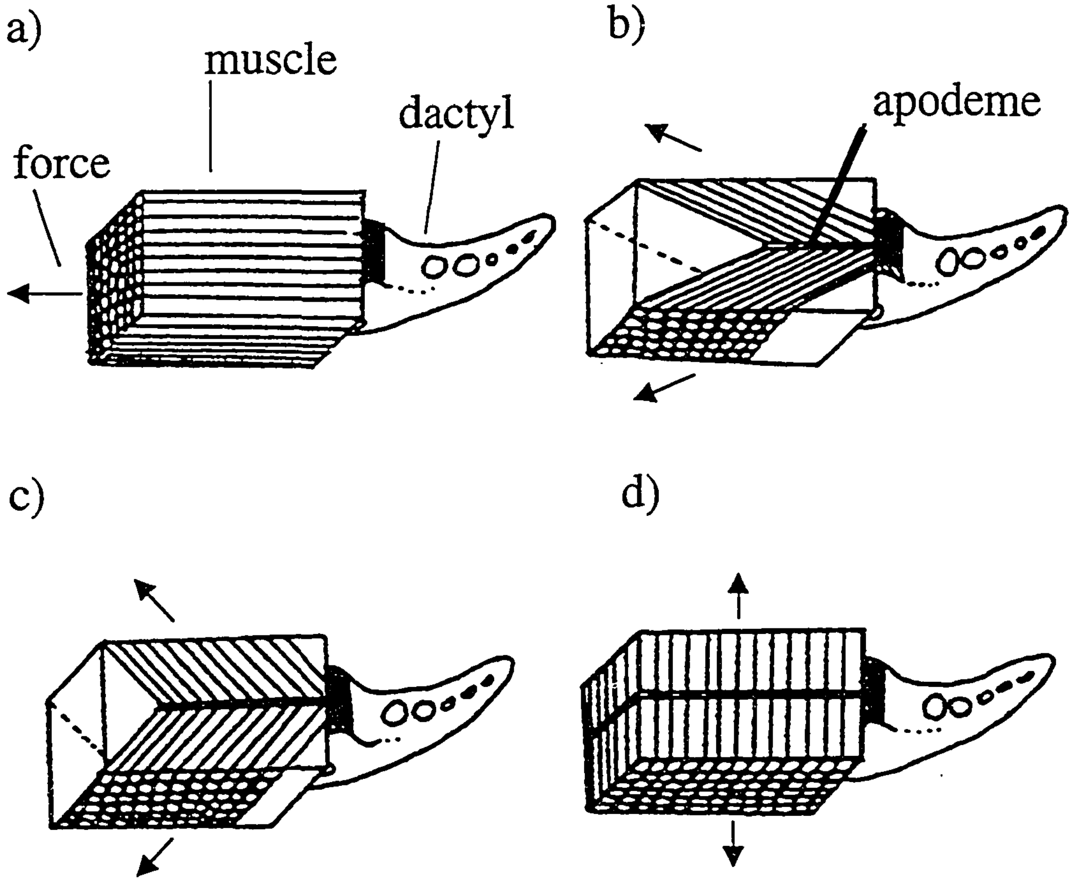

Figure 1-5. A hypothetical closer muscle associated with a dactyl lever system showing various fiber arrangements within a given volume of muscle. The arrows indicate the direction of muscle contraction. a) muscle fibers arranged in parallel. The entire effective cross-sectional area is shown. b) a fiber pinnation-angle of 20 degrees (typical for the cutter claw of the lobster), showing one side of the effective cross-sectional area. c) a fiber pinnation-angle of 40 degrees (typical for the claw of *C. oregonensis*), showing one side of the effective cross-sectional area. d) a fiber pinnation-angle of 90 degrees showing one side of the effective cross-sectional area.

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2. Variation in Safety Factors of Claws Within and Among Six Species of *Cancer* Crabs (Decapoda: Brachyura) *

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 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 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

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* A version of this chapter has been accepted for publication. Taylor, Palmer, and Barton. Biological Journal of the Linnean Society.

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 modeled 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) and 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 1). 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.

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. 2-9a). 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. 2-1a-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. 2-1b): an increase in safety factor may result from an increase in strength (Fig. 2-1b.i) or a decrease in maximum load (Fig. 2-1b.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. 2-1c.iii], or vice versa [Fig. 2-1c.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. 2-1d). 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).

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 molt 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 and which 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).

Materials 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° 08'30 W); *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 analyzed using the X^2-test (Sokal & Rohlf, 1995).

Experimental animals

To analyze claw performance, several mid-intermolt crabs of each species were selected based on 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 x 14 cm x 9 cm), which were fully submerged in running sea water (salinity ≈ 32 ‰, 10-12° C) in a large fiberglass aquarium (150 cm x 90 cm x 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, defense 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. 2-2) 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 forces 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 measurement, 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. 2-2). 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. 2-2). 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 - 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 $\mathbf{F_1}$ is the force where the closer apodeme inserts on the dactyl, ($\mathbf{F_1 = F_2 / MA}$ where $\mathbf{F_2}$ is the force measured at the dactyl tip and $\mathbf{MA = L_1 / L_2}$, where $\mathbf{L_1}$ is the proximal and $\mathbf{L_2}$ 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). $\mathbf{F_2}$ and **MA** were obtained 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 ($\sigma = 20$ N•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 N•cm^{-2} in stone crabs, *Menippe mercenaria* (Blundon, 1988), to a low of 43.0 N•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 N•cm^{-2}, at 15° C) is slightly lower than the one we obtained for all six *Cancer* species pooled (S*= 81.4 N•cm^{-2}, ±2.00 S.E., N = 135, at 10-12° C).

We then calculated the maximum potential biting force at the dactyl tip ($\mathbf{P'_{MA}}$) 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***):

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

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). For example, growth data for *C. magister* over the entire North American coast show that for a mean carapace width of 120 mm, an estimated individual instar could range from instar 10 to 14 (see Figure 7 in Orensanz & Gallucci, 1988). Our estimates of instar were necessarily approximate. However, instar values are presented only for those individuals measured here and all crabs were collected at the same time and from sites that where in close proximity to one another. Therefore, though our estimates of instar may not be completely accurate, they are reasonable indices of age relative to one another.

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 0.3X reducing lens was used. Claw dimensions (see Palmer *et al.*, 1999) were digitized from the calibrated drawings 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 hr of autotomy by clamping claws (see Palmer *et al.*, 1999), 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.*, 1999) and only 4% shattered along the lower margin of the pollex (these were excluded from the analyses, for details see Palmer *et al.*, 1999), 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 (X^2 test, $X^2 = 10.07$, $P = 0.073$), nor did it differ between males and females for all species pooled (X^2 test, $X^2 = 0.008$, $P = 0.978$). 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 (X^2 test, $X^2 = 2.27$, $P = 0.132$).

However, individuals with 'extreme wear' had a higher breakage frequency than those with 'no wear' or 'intermediate wear' (X^2 test, $X^2 = 15.32$, $P < 0.001$), suggesting that crabs later in the intermolt interval were more likely to break their claws (Fig. 2-3). 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 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' (X^2 test, $X^2 = 6.61$, $P = 0.037$). 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. 2-4). Breaking forces were always greater than, and did not overlap with, either observed or estimated biting forces (Fig. 2-4). 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 2-1).

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 2-1a). Therefore, safety factors calculated using estimated biting force were similar over the range of manus lengths, while those calculated using observed biting forces varied (Table 2-1a). In these four species, biting-force slopes were less than breaking-force slopes, thus safety factors increased with increasing manus length (Fig. 2-4a, b, c, f ; Table 2-1b) (see also Palmer *et al.*, 1999).

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. 2-4a, 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. 2-4d, e). Later instars had significantly greater safety factors, however, safety factors among species were surprisingly similar within instars (Fig. 2-5 , Table 2-2c,d).

Both size-adjusted breaking forces and size-adjusted biting forces declined with later instars, though only the latter did so significantly (Fig. 2-6 , Table 2-2a,b). Because interaction effects (species x instar) were absent (Table 2-2a, b), the similar decline in breaking and biting force yielded safety factors that did not vary across instar categories (Fig. 2-5). The two species represented by only one instar (*C. magister* and *C. oregonensis*) were not included in the above analysis. Significantly, after the 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. 2-5).

Among individual crabs, an analysis of residuals (deviations from regression against manus length in Fig. 2-4) revealed that claws with a higher-than-expected biting force also had a higher-than-expected breaking force (Fig. 2-7). In other words, for a given claw size breaking force was positively correlated with biting force (Fig. 2-7). This correlation was highly significant for all 6 species combined (Table 2-3a) as well as for 5 of the 6 species individually (Table 2-3b), and was not a statistical artifact of using the same covariate (manus length) to derive both sets of residuals. First, we 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 2-3a), 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. 2-8a , Table 2-4a). The size-adjusted breaking force for *C. 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. 2-7a). *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. 2-8b , Table 2-4b). 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. 2-8b). However, an almost significant interaction effect between species and sex (Table 2-4) 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. 2-8c, Table 2-4c). The high safety factor of *C. oregonensis* was due to a significantly higher-than-average pollex breaking force (Fig. 2-8a) rather than a lower-than-average median bite force (Fig. 2-8b). The low safety factor of *C. magister* resulted from a slightly lower-than-average biting force (Fig. 2-8a) coupled with a much lower-then-average pollex breaking force (Fig. 2-8b). Curiously, size-adjusted safety factors did not differ between the sexes within species (Table 2-4c,d), even for *C. oregonensis* where biting and breaking forces differed significantly between males and females (Table 2-4a,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 claw sizes. Therefore, the predicted probability of failure for the population was nearly zero (Fig. 2-4), 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 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 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.* 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. 2-3); 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. 2-3). 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. 2-9), which shows a consistent dependence of breaking force on biting force. When the effects of size were not 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. 2-9a). 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. 2-9b). 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. 2-9b). 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. 2-6) 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. 2-6b) did parallel the decline in claw strength (Fig. 2-6a), 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 - 18% (overall mean of ±12.2% for break force and ±14.6% for bite force) (Fig. 2-7). 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 molt 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 molt cycle.

These correlations between maximum load and breaking strength among claws as a function of age or stage in molt 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 favor 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* — were 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 behavior); 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. 2-8c). 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 defense. 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. 2-8c). 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 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 sapidus* 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.

Table 2-1. (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. 2-4 for data).

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

Spp = species, ANT = *C. antennarius*, BRA = *C. branneri*, GRA = *C. gracilis*, MAG = *C.* magister, ORE = C. oregonensis, PRO = *C. productus* ; ML = log manus length (mm);

Break = breaking force of pollex; EBite = estimated biting force of claw; Biting = claw biting force

Dif. = differences

Table 2-2. 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 break force				c) ANOVA; log safety factor			
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 bite force				d) ANCOVA; log safety factor			
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	--

Table 2-3. (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. 2-7 for data).

a) ANCOVA;
residual breaking force

Source	df	*MS*	*P*
Spp	5	0.001	0.957
Sex	1	0.002	0.495
Resid.BitF.	1	0.139	<0.001
Spp*Sex	5	0.010	0.046
Error	123	0.004	--

b) Regression;
break force residuals (*Y*) vs. bite force residuals (*X*)

Species	N	Intercept	Slope	r^2	*P*
ANT	28	$-3.74E^{-19}$±0.01	0.12±0.17	0.02	0.487
BRA	13	$-3.79E^{-20}$±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	$-1.36E^{-19}$±0.01	0.88±0.24	0.41	0.002
ORE	30	$3.3E^{-20}$±0.01	0.68±0.13	0.51	<0.001
PRO	30	$-3.57E^{-19}$±0.01	0.79±0.31	0.19	0.016

Spp = species, Resid. = residual, BitF. = Biting force.

ANT = *C. antennarius*, BRA = *C. branneri*, GRA = *C. gracilis*, MAG = *C. magister*, ORE = C. oregonensis, PRO = *C. productus*.

Table 2-4. 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. oregonensis* (see Fig. 2-8 for data).

Source	df	*MS*	*P*	Source	df	*MS*	*P*
a) ANCOVA; log breaking force				c) ANCOVA; log safety factor			
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							
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	--				

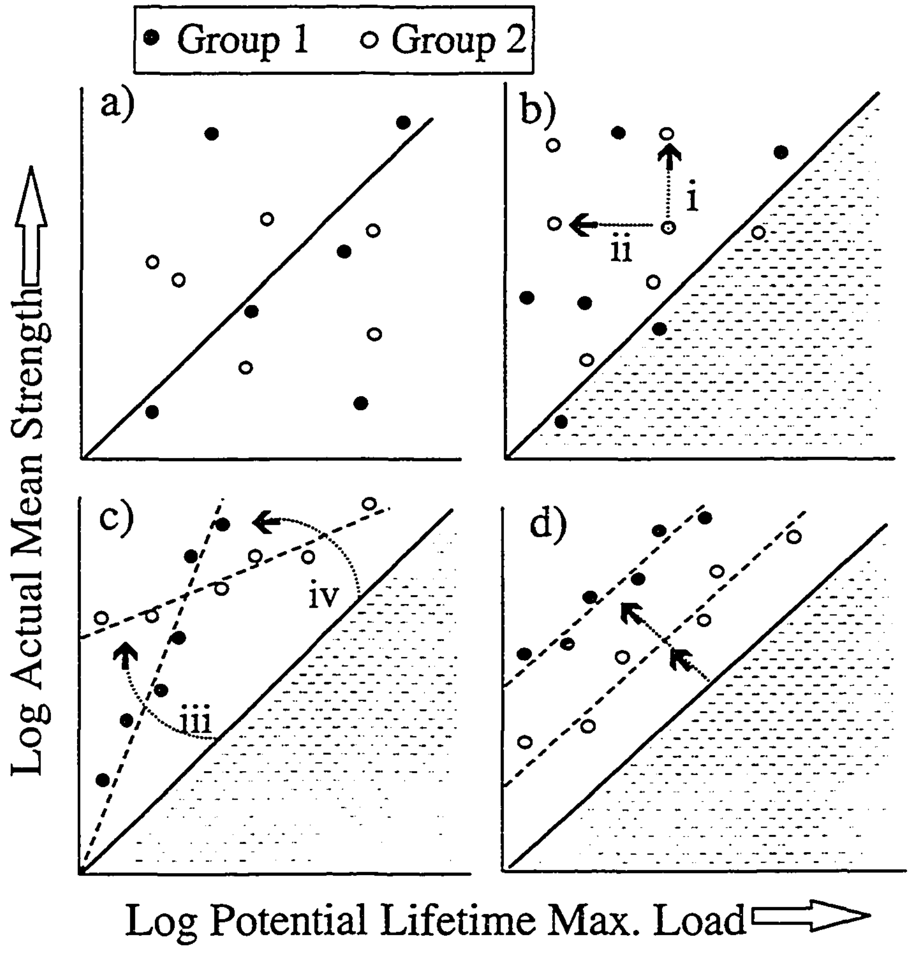


Figure 2-1. Hypothetical relation between mean strength and potential lifetime maximum load. The open and closed circles represent two groups within a hypothetical category (e.g., species, sex, or habitat type). The solid line in all graphs indicates a safety factor of 1.0. (a) Mean strength and potential 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 introduction for further explanation.

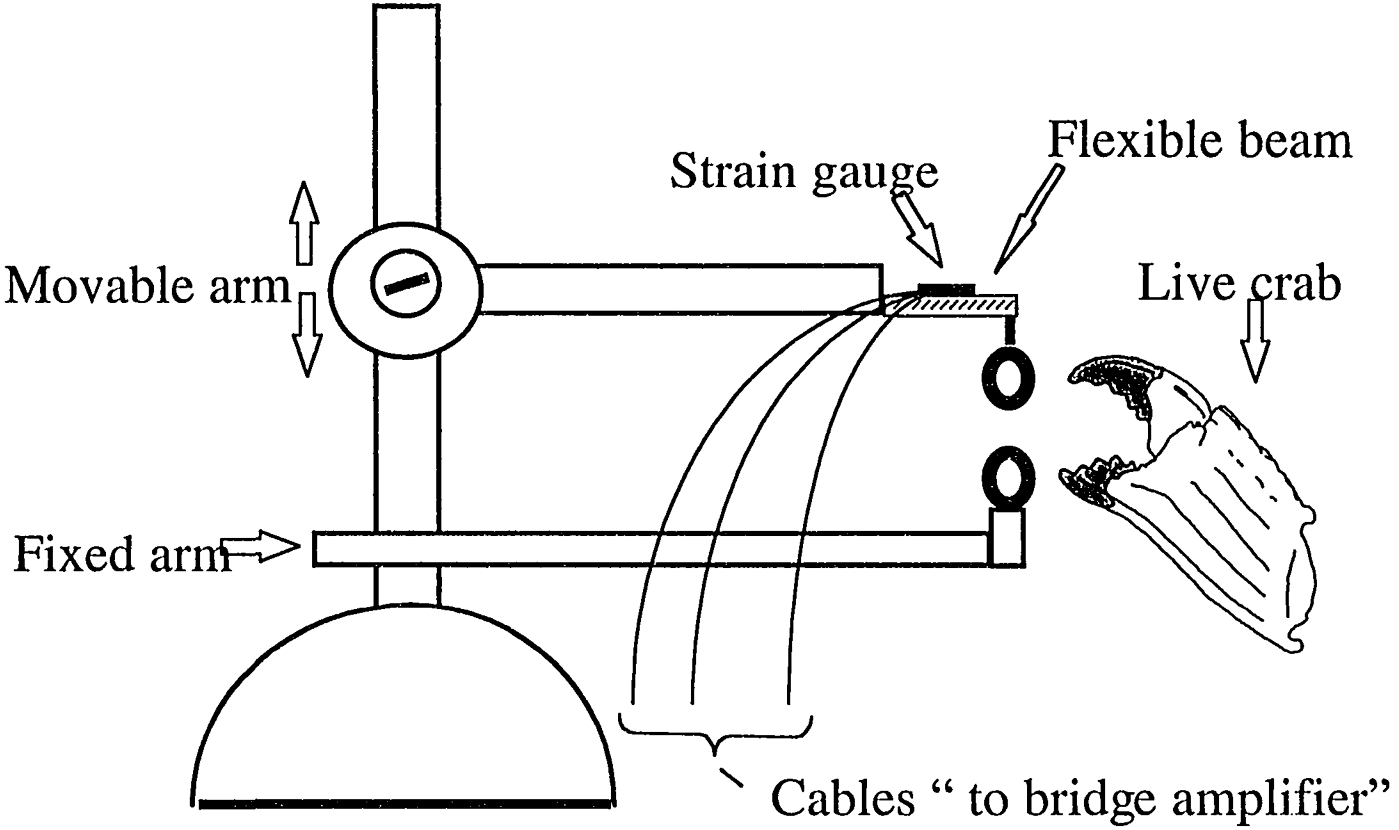


Figure 2-2. Apparatus used to measure bite-forces in live crabs. The flexible beam, with mounted strain gauge, was attached to a swing-arm microscope stand. The strain gauge was connected to a bridge-amplifier which was in turn connected to a chart recorder.

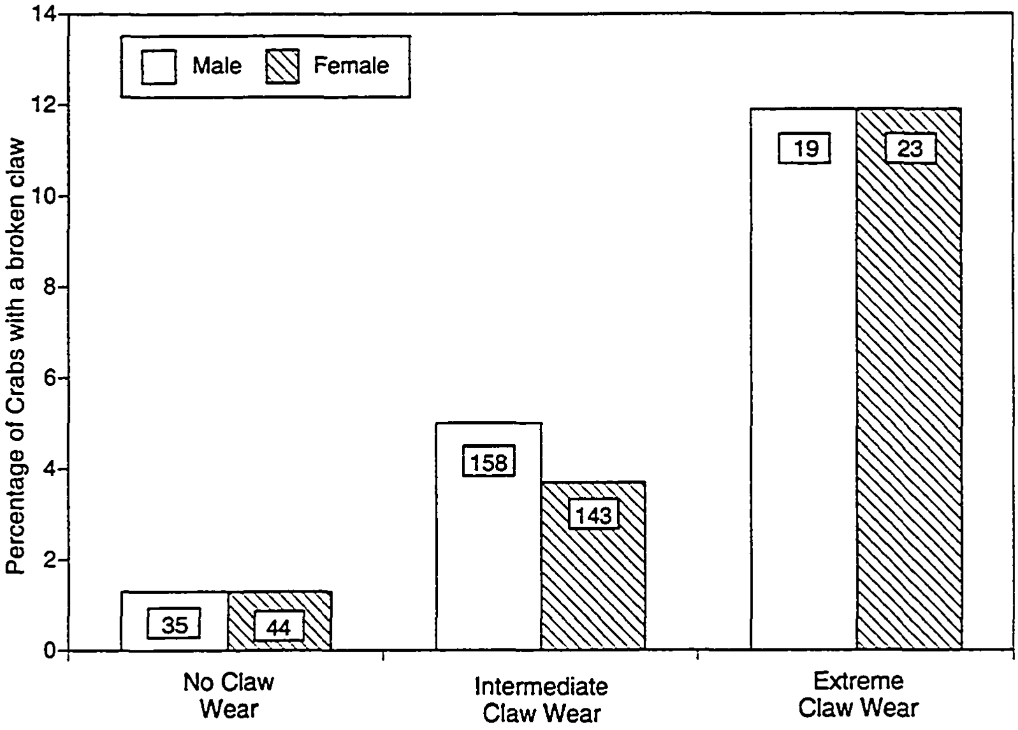
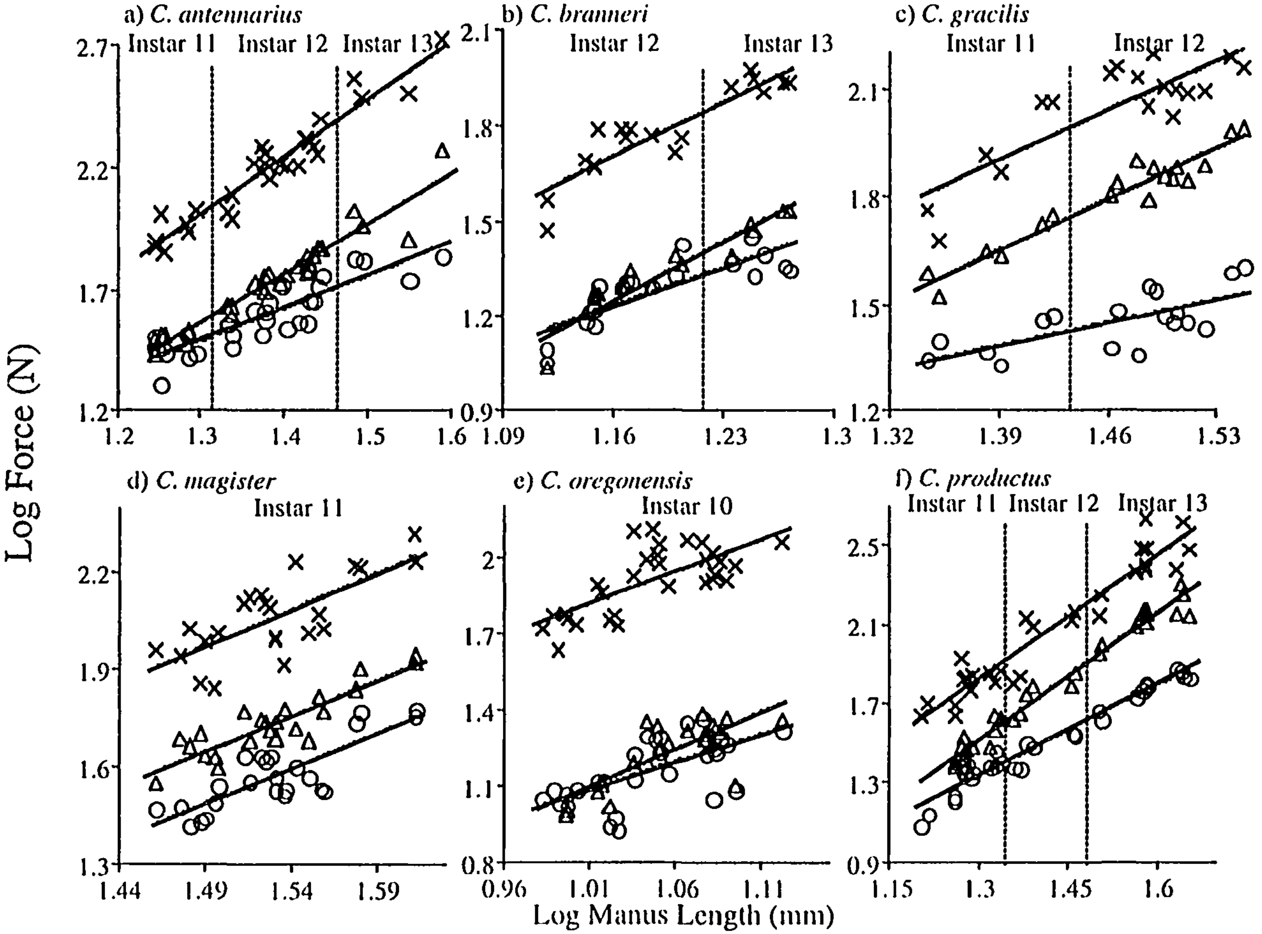


Figure 2-3. Pooled claw breakage frequencies for field-collected crabs from six *Cancer* species (*C. antennarius*, *C. branneri*, *C. gracilis*, *C. magister*, *C. oregonensis* and *C. productus*), grouped according to claw-wear categories and sex. The percentage of crabs with a broken claw was computed from the total in each category (the number inside each bar). See results for statistical analyses.



ΔFigure 2-4. Association between manus length (mm) and each of the three force types — log pollex breaking force (N)(X), log estimated biting force (N) (Δ), log observed median-maximum biting force (N) (O)— for individuals of all six *Cancer* species. Vertical dashed lines indicate estimated size-at-instar categories. Solid lines indicate least-squares linear regressions.

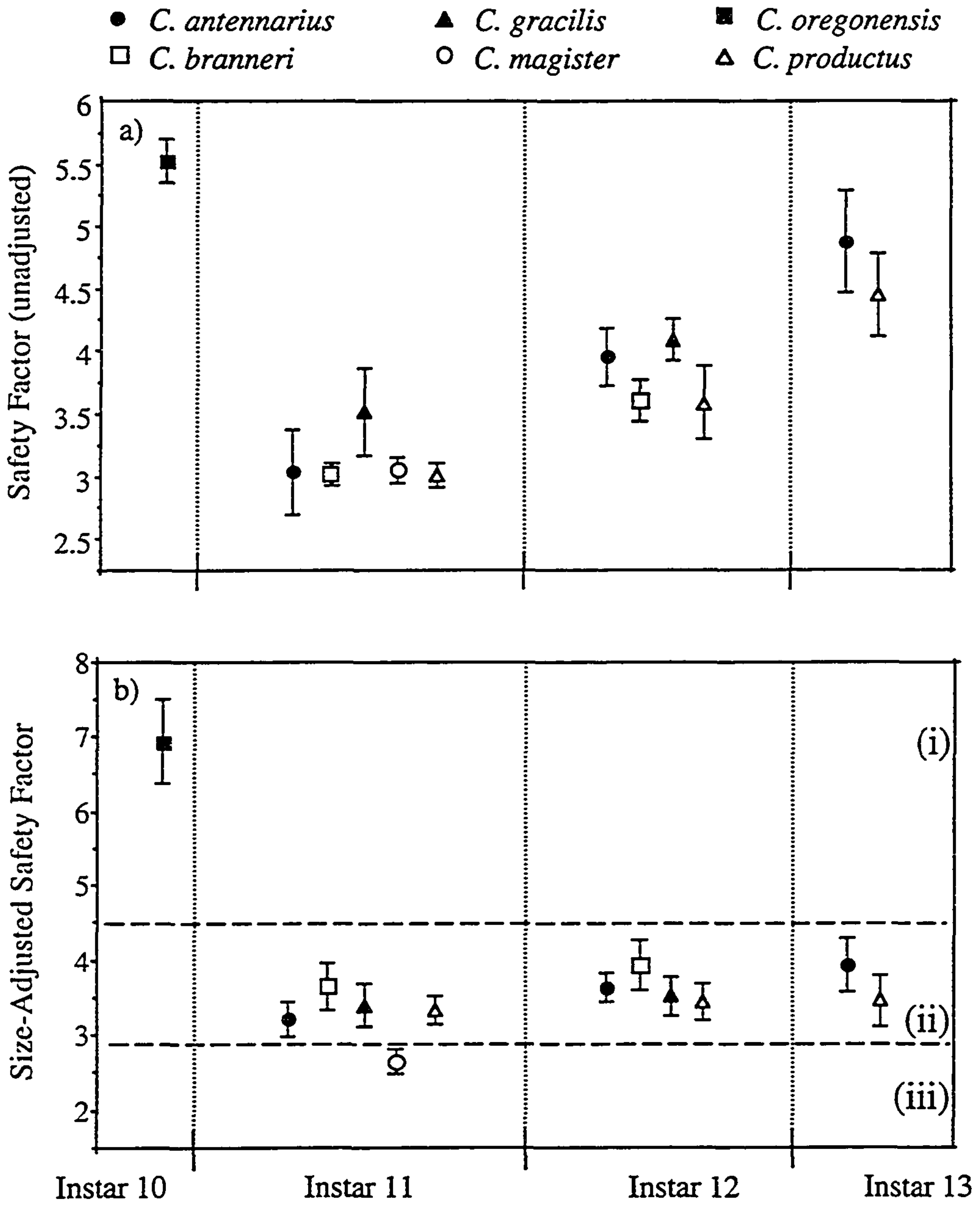


Figure 2-5. Safety factors as a function of instar number in six *Cancer* species. a) safety factors not adjusted for claw size effects. b) claw size effects on safety factors removed via least-squares linear regression [horizontal dashed lines separate groups — (i), (ii), and (iii) — within which mean safety factors did not differ significantly]. See Table 2-2 for ANCOVA results.

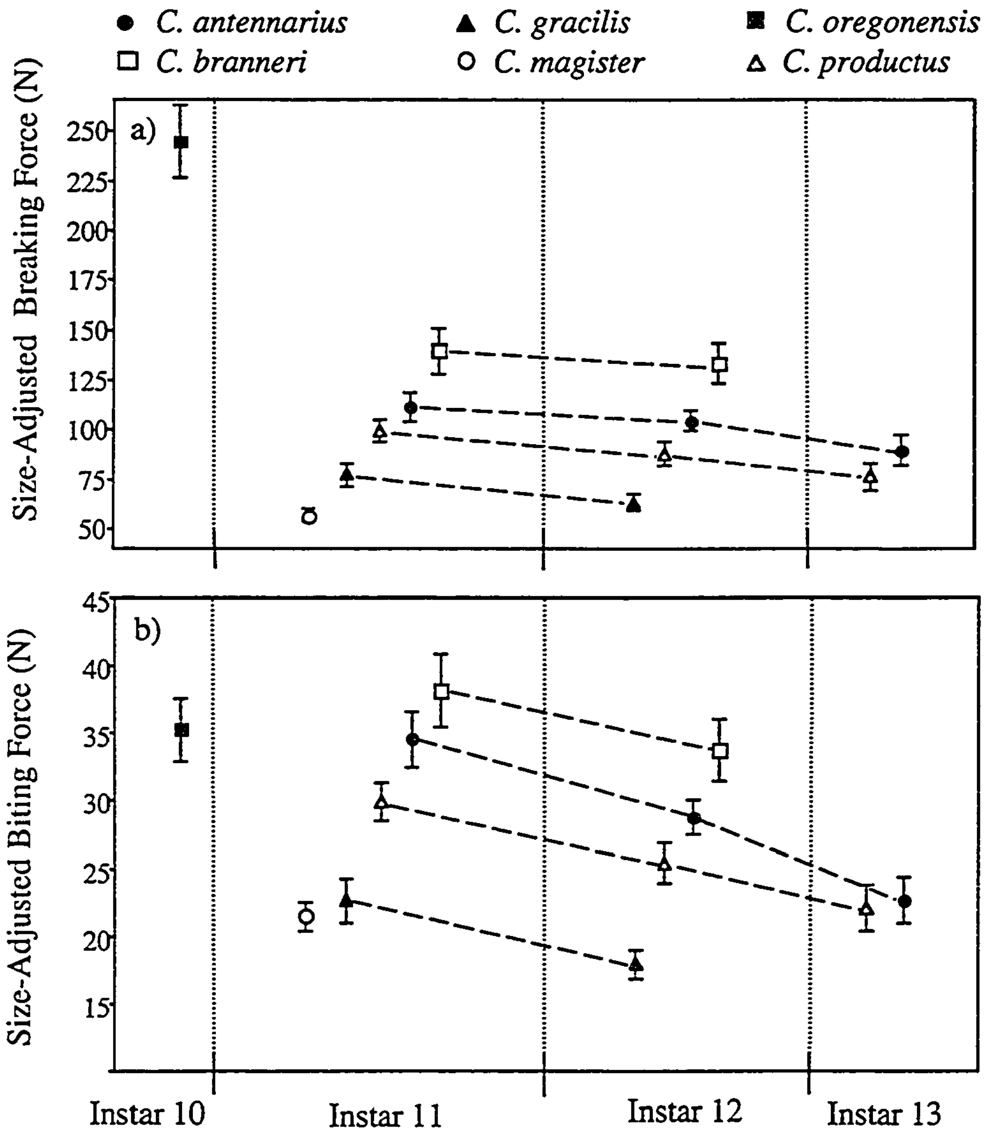


Figure 2-6. a) size-adjusted mean pollex breaking force (N) and b) size-adjusted mean biting force (N) as a function of instar number for each of the six *Cancer* species. Both were computed using linear regression techniques for a standard claw size of 4.94 wet-weight (g). Dashed lines connect different instars of the same species. See Table 2-2 for ANCOVA results.

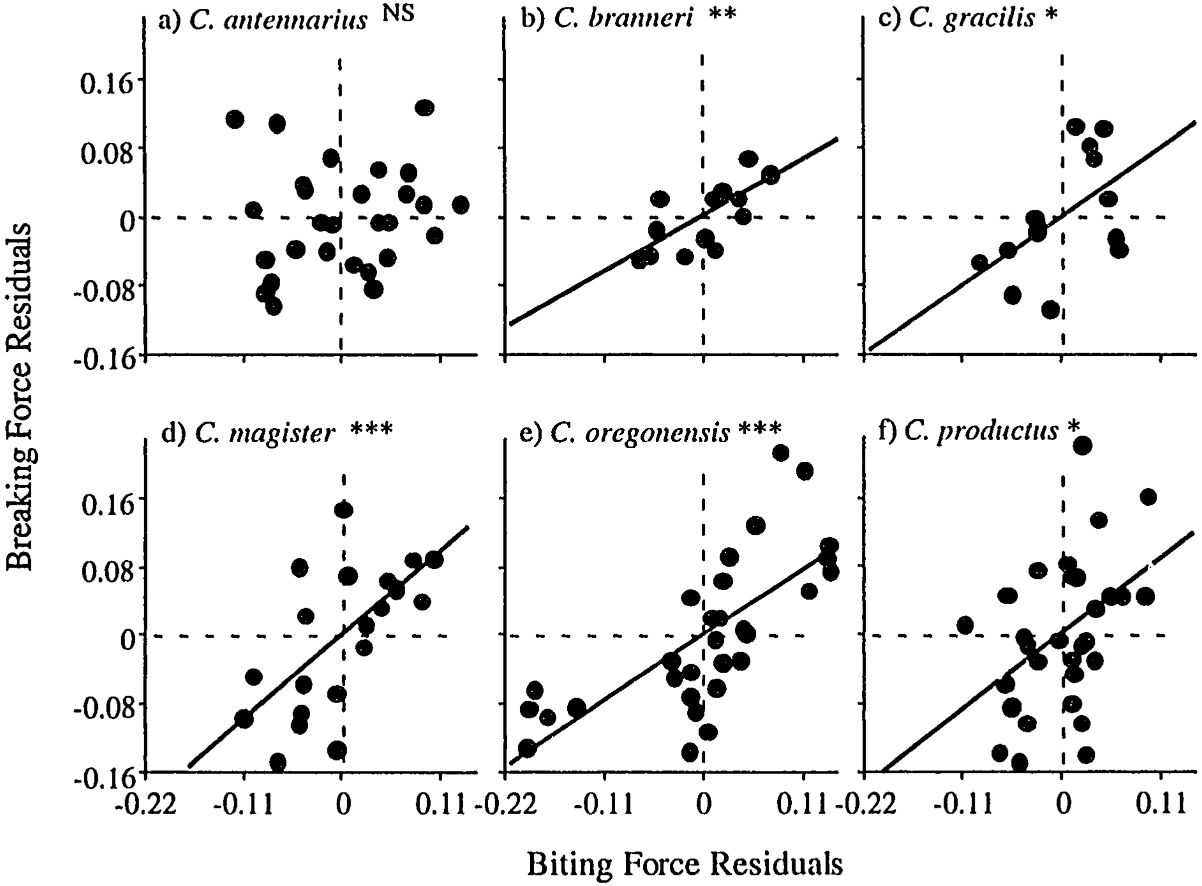


Figure 2-7. Correlations between breaking-force residuals and biting-force residuals for individual claws of all six *Cancer* species. Both residuals were obtained separately for each species as deviations from a from least-squares linear regression against log manus length (mm). Solid lines indicate least-squares linear regression fit (*P >0.05, ** P > 0.01, *** P > 0.001, NS = not significant). See Table 2-3 for statistics.

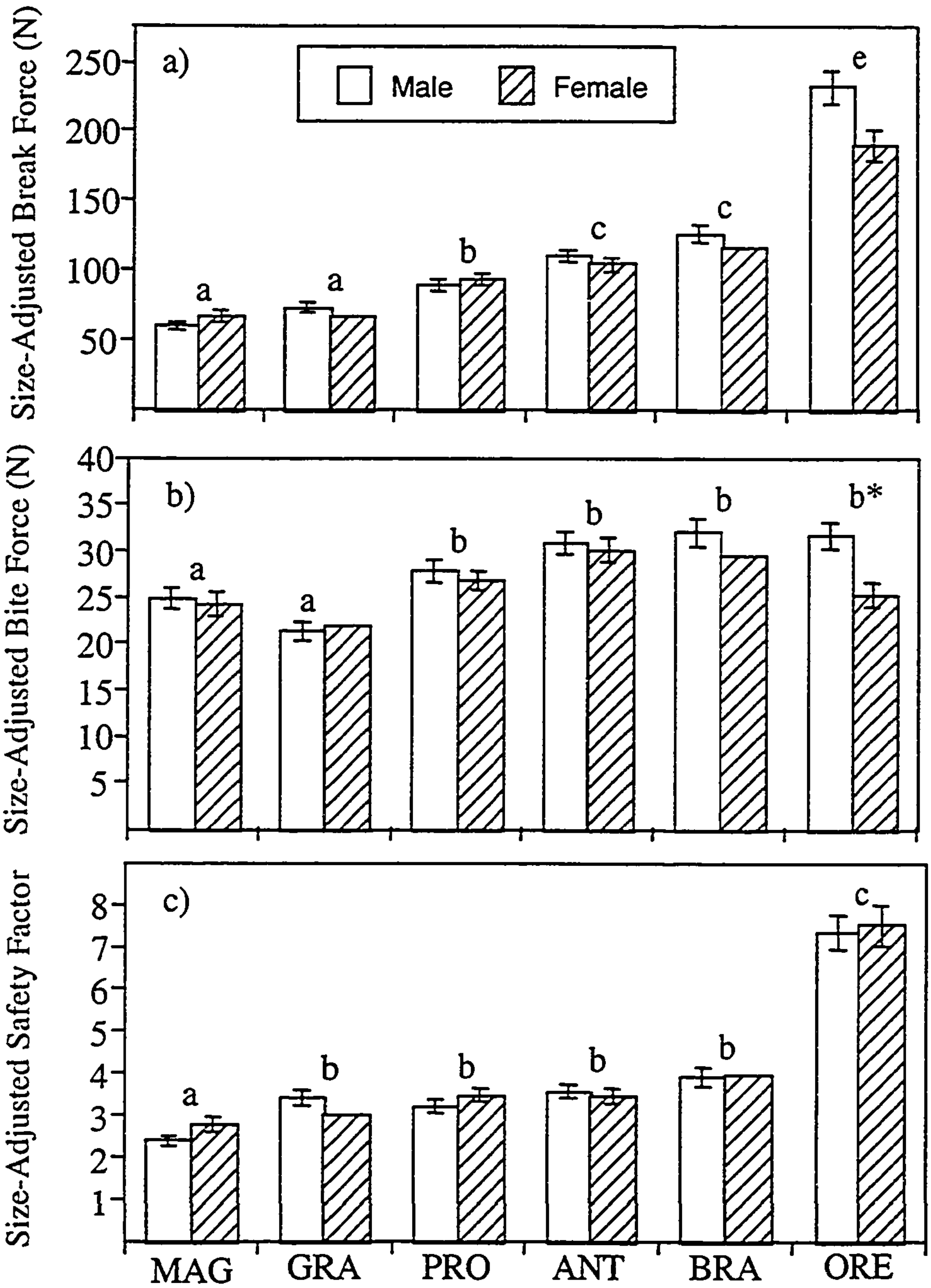


Figure 2-8. Size-adjusted means of a) pollex breaking force, b) biting force, and c) safety factors, for each sex and species of *Cancer* crab. All were computed using a single ANCOVA for a standard claw size 3.76 wet weight (g). Letters identify groups of means that did not differ significantly after 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*).

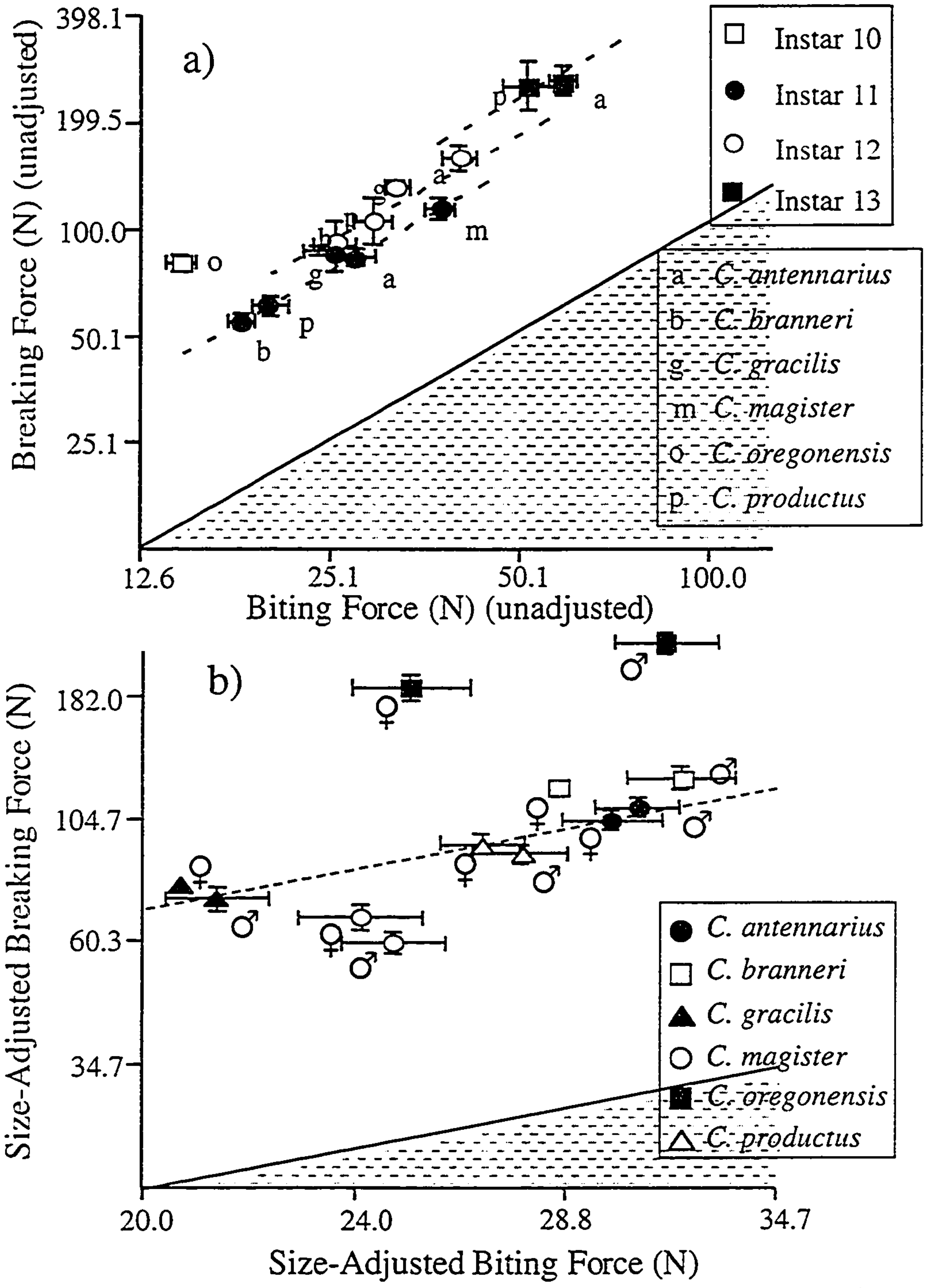


Figure 2-9. Breaking force (N) versus biting force (N), on a log scale, for all six *Cancer* species. The solid line indicates constant safety factor of 1.0 and the shaded area indicates safety factors < 1.0. (a) Strength versus load (not size-adjusted) for each species and instar. The dashed lines indicate 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*.

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3. The Evolution of Armament Strength: Evidence for a Constraint on Biting Performance of Claws of Durophagous Decapods.

Introduction

Adaptation to producing strong crushing forces has likely been a key feature in the evolution of clawed crustaceans, because hard-shelled prey are a ubiquitous food resource for benthic durophagous predators (Vermeij, 1977; Vermeij, 1987; West *et al.*, 1991). Numerous estimates of decapod claw biting forces have been reported, and the functional and evolutionary significance of these in feeding on hard-shelled prey discussed (Elner, 1978; Brown, Cassuto & Loos, 1979; Warner *et al.*, 1982; Boulding, 1984; Boulding & LaBarbera, 1986; Smith & Palmer, 1994; Freire *et al.*, 1996; Preston *et al.*, 1996). However, little attention has been paid to measuring the effect of claw size on biting force (Elner & Campbell, 1981; Blundon, 1988; Levinton & Judge, 1993; Chapter 2). Some have assumed an isometric relationship between claw size and claw performance when interpreting evolutionary patterns among decapods (Vermeij, 1977; Elner, 1980; Hughes & Seed, 1981; Lee & Seed, 1992; Lee, 1993). This is a fair initial assumption since, all else being equal, the force used to subdue armored prey should be directly proportional to the cross-sectional area of claw muscle (Gould, 1966; Emerson *et al.*, 1994). Surprisingly, however, maximum claw force is negatively allometric with claw size (Chapter 2 & Appendix I), apparently because maximum muscle stress (i.e., force per unit area of muscle) declines with increasing claw size (Elner & Campbell, 1981). It is not clear whether this decline in muscle stress represents a performance constraint or an adaptation, nor what the functional cause is. Here, I investigate the negative allometry of maximum claw biting force for six *Cancer* species. By measuring the effect of size on several claw traits involved in crushing performance, I ascertain whether declining muscle stress represents a constraint on claw performance. I also examine the implications of declining muscle stress for crabs feeding on hard-shelled prey by comparing claw biting force allometry to the allometry of gastropod shell breaking strengths, using data from the literature.

Crustaceans use claws to crush hard-shelled prey exert some of the highest forces known, for a given body mass (Alexander, 1985). Several traits allow decapods to be effective predators of hard-shelled prey (Vermeij, 1987). First, the weight of a claw relative to the body is exceptionally high {e.g., ca. 50% in *Menippe mercenaria* (Simonson & Steele, 1981)}, and seems to exceed the contribution to mass by a single limb in any other animal. Second, the claws of decapods are operated by muscles acting on lever systems with high mechanical advantages, as are the jaws of mammals and reptiles (Brown *et al.* 1979; Alexander, 1985). Third, the fibers of the claw-closer muscles are pinnate as opposed to parallel (Alexander, 1968), which increases the cross-sectional area of the muscle for a given volume. Fourth, the claw-closer muscle is composed of fibers that have predominantly long sarcomere lengths and produce the highest reported muscles stresses (forces per unit area of muscle) from 40 to 200 Ncm^{-2}, compared to other taxa that typically produce muscle stresses from 10 to 30 Ncm^{-2} (see Appendix 2). This suite of claw traits makes decapods unusually effective predators of armored prey.

Durophagous crustaceans possess muscle capable of generating exceptionally high stresses, yet stress declines rapidly with absolute claw size within species (Elner & Campbell 1977; Blundon 1988). Both results are surprising, since stress was believed to remain relatively constant among taxa and muscle types (Prosser, 1973; Hoyle, 1983; Wainwright, 1988; Pennycuick, 1992). This belief stems from extensive work on vertebrates. Their muscle stresses differ by only a factor of two, because the average resting sarcomere length of vertebrate muscle, an indirect measure of the length of the two sliding filaments (i.e., actin and myosin), only varies from 2.6 to 3.2 μm (Josephson, 1993). However, among invertebrates, muscle stress varies 20-fold and sarcomere length ranges from 0.84 to 25 μm (Hoyle, 1983). Average muscle stress increases with increasing sarcomere length (Jahromi & Atwood, 1969) because resting sarcomere length determines the number of myosin-actin cross bridges that are in parallel (Josephson, 1975). Though resting sarcomere length has been documented for many invertebrate species (Hoyle, 1983), little is known about how sarcomere length changes with size among related species or ontogenetically within species. I examine whether the decline in muscle stress with claw size in durophagous crustaceans is the result of a decline in average sarcomere length.

The decline in muscle stress with increasing claw size in decapods may have had an important impact on the evolution of claw size and form, and on the "arms race" of predator and prey, because it may have amplified allometric increases in claw size and simultaneously constrained absolute claw size. Declining muscle stress may provide a mechanism to account for the high positive allometry of claw size with body size, which has been observed for so many clawed decapods (Huxley, 1932; MacKay, 1943; Hartnoll, 1974). Assuming (1) that optimal prey size is proportional to predator body size (Elner & Hughes 1978), and (2) that the breaking strength of shells increases proportionately with increases in body size, then clawed predators should maintain a given force output relative to their body size to optimize foraging. In light of declining muscle stress, this will require disproportionate increases in claw size as body size increases. Furthermore, as claws become larger they become increasingly less efficient tools for crushing. Consider that a decapod claw greater than 5 centimeters in height will have, on average, muscle stress values of around 20 Ncm^{-2}, which is 10 fold less than a claw with a height of 4 centimeters and that is the typical value for vertebrate muscle (Prosser, 1973). This may impose an upper limit on claw size, beyond which the costs associated with claw construction and maintenance outweigh the increasingly marginal benefits of higher force production. In turn, the predator-prey "arms race" may be limited. Overall, the evolutionary impact of declining muscle stress in decapods is potentially quite significant.

The decline in muscle stress with increasing claw size may represent a constraint, which is some mechanical, developmental, or physiological limitation on the muscle stress that can be produced by larger claws. Or it may represent an adaptation to an environment that changes as decapods grow, conferring some fitness advantage on large-clawed individuals that are relatively weaker. Additional selection pressures, such as defense and sexual selection, may act on decapod claws (Darwin, 1859; Brown *et al.,* 1979; Christy & Salmon, 1984; Orensanz & Gallucci, 1988; Levinton & Judge, 1993), and enhance attributes other than crushing strength such as a) increased size without a necessary increase in strength or b) increased speed rather than strength. For example, mature males may possess large claws for display, and claw size may be inflated relative to actual closing force capabilities (Huxley, 1932). Also, performance demands may change with size such that strength is traded for speed.

We have a good understanding of claw biomechanics and of the traits involved in determining the claw closing force: mechanical advantage, angle of pinnation (Alexander, 1969; Alexander, 1983), and sarcomere length (Huxley & Niedergerke, 1954; Huxley & Hanson, 1954; Huxley, 1971; Josephson, 1975). One may therefore test whether selection has been for increased strength or rather for increased speed or increased 'display' size (Levinton & Judge, 1993). In brief, higher mechanical advantage, wider angles of pinnation (Alexander, 1968; Alexander, 1969), and longer sarcomeres increase strength at the cost of speed (Josephson, 1975). If the decline in muscle stress with increasing size is associated with increasing mechanical advantage, increasing angles of pinnation, and increasing sarcomere lengths with size, either among species or ontogenetically within species, then muscle performance is likely under a constraint. The alternative scenario would indicate changing selection pressures with increasing size.

Performance is context dependent (Bock, 1980; Koehl, 1996) and although muscle stress is the ultimate measure of muscle performance, the actual force delivered by the crab's claw against its prey, in association with the prey's ability to counteract the crab's closing-force with armor, determines the 'success' of the predator, and hence it's fitness. Therefore, I relate the allometry of predator weapon performance to that of prey armor performance using data on shell strength of thaidid snails (Vermeij & Currey, 1980; Currey & Hughes, 1982). A similar approach has been used to study the allometry of predator-prey size interactions among amphibians (Emerson *et al.*, 1994). The ratio of the allometric coefficient of prey armor strength to that of predator armament strength indicates how the prey's safety factor (ratio of mean strength of armor to maximum lifetime load delivered by predators) changes with size. Models of safety factors are powerful tools for studying the evolution of biological structures (Alexander, 1981; Lowell, 1985; Lowell, 1987; Alexander, 1997) and knowing how prey safety factors change with size can provide insights into how predator-prey interactions change with size and whether prey armor strength varies adaptively (Chapter 2 & Appendix I).

I studied the musculoskeletal properties of six sympatric species of *Cancer* crabs — *C. antennarius*, *C. branneri*, *C. gracilis*, *C. magister*, *C. oregonensis*, and *C. productus* — that vary in absolute body and claw size, and also in relative claw size (Lawton & Elner, 1985; Orensanz & Gallucci, 1988), to test the effects of size on muscle performance within the same guild of predatory crabs. Actual bite forces are reported elsewhere Chapter 2. Here, I emphasize the effects of absolute rather than relative claw size on claw traits, since absolute size determines strength and whether a particular shell can be broken lethally by a predatory crab (Abele *et al.*, 1981). I also emphasize muscle stress, since it is the ultimate measure of muscle performance and other traits, such as lever properties, simply modify muscle stress. Furthermore, because stress is functionally related to sarcomere length, I make intensive measures of this variable. My data on *Cancer* crabs are then compared with those from two other studies illustrating size-dependence of muscle stress of decapod claws (Elner & Campbell, 1981; Blundon, 1988). The Cancridae are one of the four brachyuran crab families — Cancridae, Portunidae, Xanthidae and Parthenopidae — that include many members that crush shelled molluscan and crustacean prey (Vermeij, 1977; Lawton & Elner, 1985). Among brachyurans, relative size of the crusher claw ranges from a claw height to carapace width ratio of 0.148 to 0.527, and claw mechanical advantage ranges from 0.300 to 0.548 (Vermeij, 1977; Vermeij, 1987), and 62% and 100% respectively of this variation is reflected by the six *Cancer* species I studied. Though these species are from a single genus, they represent a reasonable range of the variation in claw morphology observed for durophagous brachyurans.

Methods

Experimental animals and claw biting force measurements

All six *Cancer* species were obtained from sites near Bamfield Marine Station (Bamfield, British Columbia, Canada). I measured several bite forces from each crab within 7 days of field collection because maximum force and consistency tend to decline with time in the laboratory (G.M.T., unpubl.). Several mid-intermolt crabs of each species were selected, based on estimated claw wear (claw index 2, as described in Chapter 2). Crabs were housed individually in plastic mesh containers (20 cm x 14 cm x 9 cm), which were submerged in large fiberglass aquaria supplied with running sea-water (salinity 32 ‰, 10-12°C). The method used to measure claw bite forces is described elsewhere (Smith & Palmer, 1994; Chapter 2 & in Appendix I). Actual bite-forces taken at the dactyl-pollex tips are also reported elsewhere (Fig. 2-2).

In brief, individual crabs were removed from the water and encouraged to grasp forcefully a strain gauge transducer (Blundon, 1988; Smith & Palmer, 1994). The 'finger-rings' grasped by the crab were adjusted to 60% of maximum gape for each claw. The transducer was calibrated before and after each session with known weights that covered the range of bite-forces. The average of these two calibration curves was used to calculate biting forces (Newtons) from of the original chart recordings. Each session included measurements from both the right and left claws, in succession, of 7 - 10 crabs. The first bite measured on an individual crab alternated between the right and left claw. The mean number of bites used to assess the biting-force of a claw ranged from 6.9 - 8.2 among species.

Muscle stress calculations

All claws used in the bite force experiment were autotomized (piercing through the soft membrane of the merus induced autotomy) from crabs and drawn via a camera-lucida attached to a dissecting microscope, in a view perpendicular to the plane of dactyl rotation (Fig. 3-1a). Chela (i.e., claws) were cut from the rest of the cheliped along the carpus propodus joint, with the cut edge separating the propodus cuticle and joint membrane around its entire circumference. Linear measurements, such as claw height and distances associated with mechanical advantage (e.g., lever length 1 (center of the pivot to the base of the dactyl) and lever length 2 (center of the pivot to the tip of the dactyl) were digitized from individual claw drawings (Fig. 3-1a). Closer and opener muscle tissue were removed and wet and dry weight, excluding apodemes, were measured. Apodeme surface areas were drawn and measured as described above for claw outlines. Muscle stress (S) was then calculated as

$$\mathbf{S = F_1/A\sin 2\Theta}$$

where $\mathbf{F_1}$ is the force applied to the base of the dactyl by the closer muscle, **A** is the area of one side of the apodeme and **Θ** is the mean acute angle of pinnation of muscle fibers (Alexander, 1969; Elner & Campbell, 1981). Stress will be underestimated by the degree of force lost in the fulcrum, since the formula assumes a frictionless fulcrum.

Angle-of-pinnation

Angle-of-pinnation of closer muscle fibers was measured in other similar-sized individuals of each *Cancer* species. Claws were dissected along a mid sagittal plane just below carinae number 5 (Fig. 3-1b) and the angles of six to eight fibers were measured from the outer mid section of the closer muscle for each claw (Fig. 3-1c). The angle of pinnation depends on the extent to which the muscle is contracted and therefore, on the angle of claw gape (Fig. 3-1a). Claws were fixed (10% buffered formalin) at approximately 60% of maximum claw gape to ensure that angles-of-pinnation were representative of those claws used in the biting-force measurements. This method is not precise, as the fixation process causes muscles to contract slightly reducing claw gape angle to less than 60% of their maximum. After fixation, the actual angle of claw gape (Fig. 3-1a) was then used to correct for variation in the degree of muscle contraction by using this angle as a covariate in a 2-factor (species and sex) ANCOVA. I examined the effect of size on angles of pinnation by performing a regression analysis on residuals. For each species, residual deviations from the regression of ‘angle-of-pinnation’ versus 'gape-angle' (i.e., the angle between the open dactyl and the pollex after the claw were fixed), were plotted against claw height; a significant correlation between these two variables would suggest angle-of-pinnation is size-dependent.

Muscle filament lengths

Resting sarcomere and A-band length measurements were obtained from other claws similar in size to those used for biting force measurements. Claw-closer muscles were fixed and filament traits measured as reported in the literature (Govind *et al.*, 1978). Sampling of fibers from the closer muscle of each claw was restricted to a section that ran dorsal-ventral mid-way along the manus (Fig. 3-1b). Histochemical analysis supported a restricted sampling regime, because closer muscles of 3 species (*C. productus*, *C. oregonensis*, and juvenile *C. magister*) stained at a uniform intensity over their lengths for both myofibrillar ATPase and NADH diaphorase (G.M.T. unpubl.). This section was divided into four smaller regions, which were defined by exoskeletal carinae running in a proximo-distal direction along the manus. Exoskeletal carinae are homologous structures in *Cancer* (Nations, 1975), and sampled sites were therefore consistent among species. From each of these four regions (M1-M4, Fig. 3-1b), 10 fibers were teased apart at random from wet mount preparations. From a fiber, a single sarcomere length and its A-band length were measured with a phase-contrast microscope (magnification 500x) via a camera-lucida and a calibrated digitizing tablet. Mean resting sarcomere and A-band length for a given claw thus refers to the average of 40 sarcomeres. Although resting sarcomere length is the filament trait often reported in the literature because of the ease of visualizing Z-bands, only A-band lengths were used in the analysis because resting sarcomere length is confounded by the degree of muscle contraction. Fiber traits were not measured if A-bands and I-bands were not clearly visible.

Claw bite-force data from the literature

Muscle stress and claw height data were compiled from the literature for two additional decapod crustaceans, *Homarus americanus* (Elner & Campbell, 1981) and *Menippe mercenaria* (Blundon, 1988) using the program 'dataThief' version 1.0.8 (K. Huyser & J. Laan, 1994). From Elner & Campbell (1981), mean muscle stress values for various crusher and cutter claw heights were from Figure 8 and apodeme areas relative to claw height were from Figure 4. Elner & Campbell (1981) derived stress values using two methods to measure claw bite forces, first, a static *in vivo* technique (Brown *et al.* 1979) and second, a dynamic *in vivo* technique (Elner & Campbell 1981). The dynamic *in vivo* values were excluded from the compilation because of limited data. From Blundon's (1988) paper, muscle stress versus manus length for crusher claws only (muscle stress was not size-dependent for cutter claws) were from Figure 4. Blundon's (1988) method of measuring claw bite-forces was similar to the method used here, except the grip size of the transducer was not adjusted to fit the size of the claw. Manus length was converted to claw height by taking the ratio of these two variables. A ratio was justified as manus length and claw height scaled isometrically over these ranges (Vermeij, unpubl. data). Blundon's (1988) Figure 4 included stress values for crusher claws from both tropical and temperature *M. mercenaria.* They were not significantly different from each other, and therefore I do not distinguish between them here. For claws of *H. americanus* and *M. mercenaria*, muscle stresses were plotted and analyzed, in association with the muscle stresses reported here for *Cancer* claws, to define a possible scaling relationship of muscle stress versus claw size for decapods in general.

Shell strength data from the literature

Thaidid snails are often attacked by *Cancer* crabs (Spight, 1976; Bertness, 1977; Zipser & Vermeij, 1978; Currey & Hughes, 1982; Palmer, 1985). I examined the scaling relation between armor-performance and size for temperate and tropical thaidid gastropods using data on shell strength (i.e., the force in newtons required to break the shell) and size (both mass and height) compiled from the literature (Vermeij & Currey, 1980; Currey & Hughes, 1982). Data points were obtained from figures using the program dataThief version 1.0.8.

Results

Muscle stress of claws—intraspecific patterns

Closer muscle stress decreased with increasing claw size in five of the six *Cancer* species (Fig. 3-2, Table 3-1a). This relation was highly significant for the two species (P = 0.009 for *C. antennarius* and P < 0.001 for *C. productus*) for which the range of sizes included both subadults and adults, and significant for *C. gracilis* and *C. oregonensis*, in spite of a limited size range (less than two fold). Also, stress declined with claw size in *C. branneri*, though the trend was not significant. In contrast, stress tended to increase with claw size in *C. magister* (Fig. 3-1a), though not significantly. Stress was slightly higher for females than for males for a given claw size [log least-square means (±SE) were 1.90 (0.016) and 1.87 (0.009), respectively], but this difference was not quite significant (ANCOVA; $F_{2,107} = 3.27$, $P = 0.073$). A common slope could not be computed for all six species, because slopes differed significantly among them (ANCOVA; $F_{2,105} = 3.08$, $P = 0.012$). When *C. branneri* and *C. magister* were excluded from the analyses, slopes did not differ among the remaining species (Table 3-2a). For these 4 species the coefficient of allometry for stress was proportional to claw height $^{-0.794\pm0.091}$ (Table 3-2a). The model explained 71% (coefficient of determination) of the variation in muscle stress among these 4 *Cancer* species (Table 3-1). Therefore, the null hypothesis that muscle stress is independent of size can be rejected for *Cancer* claws, and claw height, as a measure of claw size, accounted for much of the variation in closer muscle stress observed among claws.

The size-dependence of stress was not a spurious result arising from allometry in other claw traits, because these traits scaled isometrically with claw height or were positively allometric. First, claw height scaled isometrically with two other measures of claw size, manus length and wet weight (Table 3-2b, c). Furthermore, when claw wet weight was used as the covariate, closer muscle stress decreased with increasing claw size for five of the six *Cancer* species (Table 3-1b), as it did with claw height. Second, the mechanical advantage was positively allometric with claw height (see section below, and Table 3-3a). Third, apodeme area and muscle dry weight both increased isometrically with claw height (Table 3-2e,f). Thus, claw height was a reasonable scaling variable for claw size and, changes in muscle weight and apodeme area did not account for the observed size-dependence of muscle stress.

A-band length of claws—intraspecific patterns

Average A-band length increased with increasing claw size for all six *Cancer* species (Fig. 3-3; Table 3-3a). This relation was highly significant for *C. antennarius*, *C. gracilis*, and *C. magister*, and significant at alpha = 0.05 for *C. oregonensis*. The relation was non-significant for *C. branneri* and *C. productus*, but nevertheless the trend was positive (Fig. 3-3; Table 3-3a). The slopes did not differ among all six species ($P = 0.149$) so computing a common slope was justified. Overall, the coefficient of allometry for A-band length verses claw height was slightly positive (claw height 0.146±0.019), and significantly different from zero ($P < 0.001$). The model explained 77% (coefficient of determination) of the variation in A-band length among six *Cancer* species (ANCOVA; $F2,125 = 61.85$, $P < .001$). Therefore, average claw A-band length increased with claw size in a similar fashion for all of the six *Cancer* species and cannot provide an explanation for the observed decline in muscle stress with claw size.

Mechanical advantage and angles of pinnation—intraspecific patterns

Mechanical advantage increased with increasing claw size for five of the six *Cancer* species (Fig. 3-4, Table 3-3b). This increase was highly significant for *C. gracilis*, *C. oregonensis* and *C. productus*, significant at alpha = 0.05 for *C. antennarius*, and not significant for *C. branneri* (see Fig. 3-4 for actual *P* values). Mechanical advantage did not change with size in *C. magister*, although this may be due to sampling a limited size-range. For the other five species, all slopes were slightly positive ranging from 0.05 to 0.31 (Table 3-3b), yet a common regression could not be computed since slopes were significantly different from each other (ANCOVA; $F_{2,250} = 3.58$, $P < 0.004$). The increase in mechanical advantage (ratio of L_1/L_2) with claw height resulted from both a relative increase in L_1 and a relative decrease in L_2 with claw height (data not shown).

No relation was observed between average angle-of-pinnation and claw size for five *Cancer* species, though mean angle-of-pinnations did differ among species and between sexes (2-factor ANCOVA, $F_{4,95} = 9.28$, $P < 0.001$) (Table 3-4). Intraspecifically, larger claws did not have higher angles of pinnation than smaller claws, since no correlation was detected between residual angles-of-pinnation, from a regression with claw gape angle, with claw height for five of the six species (Fig. 3-5, Table 3-4). In contrast, a significantly negative correlation between residuals and claw height was detected for claws of *C. magister* ($N = 16$, $r^2 = 0.466$, $P = 0.003$), suggesting larger claws have lower angles-of-pinnation compared to smaller claws (Fig. 3-5d). In general, however, the null hypothesis that angle-of-pinnation does not change with claw size cannot be rejected.

Skeleto-muscular correlates of size — interspecific patterns

Maximum closer muscle stress differed among species. Mean closer muscle stress for claws of mature individuals was significantly different among species (ANOVA; $F_{2,107} = 36.56$, $P > 0.001$) and grouped by a sequential Bonferroni posthoc test (Rice, 1989) as follows: the highest stress values [means ±SE (Ncm^{-2})] were for *C. branneri* (102.41±4.98) and *C. oregonensis* (100.67±3.02), intermediate values were for *C. antennarius* (82.36±3.78) and *C. magister* (75.71±2.52), and the lowest were for *C.*

productus (54.96±3.76) and *C. gracilis* (50.88±3.01). For mature individuals, mean closer muscle stress decreased with increasing mean absolute claw size among species ($P = 0.039$, $r^2 = 0.70$, see Fig.3-2). Therefore, maximum closer muscle stress declined with increasing claw size both within and among species.

Similar analyses were conducted on the species means for the other three claw traits: mechanical advantage, A-band length, and angle-of-pinnation. These traits were not size-dependent (claw wet weight) among the six *Cancer* species ($P = 0.782$, $r^2 = 0.02$; $P = 0.147$, $r^2 = 0.20$; $P = 0.872$, $r^2 = 0.01$; respectively). Thus, the effect of claw size on mechanical advantage and A-band length was restricted to within species (see above), while angle-of-pinnation was independent of claw size both within (see above) and among species.

Claw height as a reference variable for claw biting force— patterns among decapod genera

The coefficient of allometry of muscle stress versus claw height differed significantly among genera and claw types of decapods (Fig. 3-6, Table 3-5). Claw type included the two general categories, 'crusher' and 'cutter'. Because *Cancer* claws do not exhibit pronounced dimorphism, both claws of five species were classified as 'crusher'-type. Both claws of *C. magister*, which are appreciably different from the other species in mechanical advantage, A-band length, and angles-of-pinnation, were classified as 'cutter'-type. Species from the two other genera have dimorphic claws. The steepest negative slope (±SE) was for crusher-claws of *Menippe* (-2.131 ±0.239), while the rate was nearly half for crusher-claws of *Homarus* (-1.289 ±0.107). Significantly, crusher-claws of *Homarus* had a slightly greater rate of stress decline than observed for crusher-claws of *Cancer* (-0.849 ±0.137), which were similar to *Homarus* cutter-claws (-0.690 ±0.096) (Fig. 3-6a,b, Table 3-5). There was no effect of size on stress for cutter claws of *Menippe* (Blundon, 1988). Therefore, although stress declines with increasing claw size in many species, a universal or general exponent of muscle stress versus claw height cannot be inferred for clawed crustaceans.

In the absence of a taxon grouping variable, a simple least-square linear regression produces a strong significant correlation ($r = 0.78$) for stress versus claw height among claws of decapods (Table 3-6). Although correlation coefficients are the most common method to asses the strength of bivariate relations, residual analysis gives direct information about the relation of one variable to the other without the confounding effects of range or sample size (Smith, 1984). For the among-decapod analysis, the linear regression of stress on claw height had a high prediction error (45%) and did not effectively predict claw performance. However, the ability to predict performance increased when the analysis was done at lower taxonomic levels and when claw type was included for the dimorphic species (Table 3-6); prediction error was only 14 and 32% for *Cancer* and *Homarus*, respectively, and was only approximately 20% when *Homarus* was divided by claw-type. Inspection of Figures 3-6 clearly shows claw height does not predict performance among decapods, however, this trait appears useful for predicting stress within genera and species.

Claw biting force in relation to breaking strength of thaidid snail shells

For *Cancer* crabs, the decline in muscle stress with size (Fig. 3-2, Table 3-1) results in a negative allometry of maximum bite force with size (Fig. 2-4). Bite force allometries appear to parallel those of breaking strength versus shell size for temperate thaidid snails (Fig. 3-7). When RMA (reduced major axis) slopes were compared, shell strength of temperate snails was positively allometric with shell mass for *Nucella lapillus* and for several thaidid species from various localities (Table 3-7). Alternatively, when the scaling variable shell height was used, the RMA slope of shell strength with shell height was isometric (Table 3-7). Regardless of the different slopes observed in Table 3-7, for temperate shell strength relative to temperate claw strength, differences in the rate of increase could not be distinguished between the two groups by an ANCOVA ($F_{2,250} = 0.058$, $P = 0.810$)(Fig. 3-7b). Therefore, with the present data, we cannot confirm the potential changes in 'success' of predation by crabs on hard shelled prey, is size dependent or not, primarily because the slope of shell-breaking strength against size for temperate snails remains undetermined.

As tropical thaidid shells increase in size, they also increase significantly more rapidly in relative strength than temperate shells (Table 3-7). Clearly, this slope was significantly different from slopes of strength versus mass for shells of temperate snails and bite-force versus mass for claws of temperate *Cancer* crabs (Table 3-7).

Discussion

Inferring bite force from claw size

Clearly, claw muscle stress decreased with claw size both within and among *Cancer* species, supporting and extending earlier results for lobsters (*Homarus*) and crabs (*Menippe*) (Fig. 3-2). Within species, stresses were higher for smaller claws than larger claws, for five of the six *Cancer* species studied here (Table 3-1). Because the decline in stress with size was consistent for species of different adult sizes the effect of age on muscle stress can be rejected. Likewise, stresses were exceptionally high for claws of small species (*C. branneri* and *C. oregonensis*) compared to those of large species (*C. antennarius*, *C. gracilis*, *C. magister* and *C. productus*). For 'mature' adults only, the mean stress of the smallest species (*C. oregonensis*, 101 Ncm^{-2}) was almost two-fold greater than that of the largest species (*C. productus*, 55 Ncm^{-2}). Furthermore muscle stress can be predicted from claw height with a high degree of confidence for the genus *Cancer* (Table 3-6). The consistent relationship between muscle stress and claw size among species means that claw height can be used as an acceptable indicator of maximum biting force in *Cancer* crab claws.

Muscle stress was negatively size-dependent for other decapods; however, claw height was not an acceptable indicator of claw biting force among genera (*Cancer*, *Homarus* and *Menippe*), since the rate of decline of stress with size was not consistent (Table 3-5). This precluded a statistical comparison of means, though stresses are clearly higher for smaller claws of *Menippe* than for smaller claws of either *Cancer* or *Homarus* (Fig. 3-6). The upper stress values reported for the relatively small crusher claws of *Menippe* are exceptional, being two-fold greater than the upper stress value for relatively small claws of *Cancer*, and four-fold greater than for both relatively small cutter and crusher claws of *Homarus*. These exceptional muscle stresses decline rapidly with size and larger claws of *Menippe* are similar to those of large *Cancer* and *Homarus* claws. Therefore, the relation between stress and claw height was unique for each genus, suggesting that both comparisons of stress among genera, and inferences of strength based on claw size (Vermeij, 1977; Vermeij, 1987), must be made with caution.

For claws of *Menippe*, *Cancer* and *Homarus*, the differences in the dependence of stress on claw height might have resulted from differences in methods used to assess bite forces. Future assessment of maximal bite force performance should attempt to standardize procedure. For claws of *Cancer* crabs, method of stimulation (i.e., behavior) was controlled by having claws bite at a specific mechanical advantage and gape-angle, and by limiting other movements of the animal's body so as not to add or counter bite-forces. This procedure may yield bite forces that are somewhat arbitrary (Elner & Campbell, 1981; Boulding, 1984; Boulding & LaBarbera, 1986). However, maximum bite forces reported here for *C. productus* (e.g., 194 Newtons for a carapace width of 130mm) agree with Boulding's (1984) measurements for a similar sized crab (174 Newtons), where she measured *in vivo* bite forces from a strain gauge mounted directly on the claw of a feeding crab. Furthermore, this procedure allows accurate determination of a standard claw closing performance, which can be replicated and used to make relevant comparisons among species and individuals.

Size-dependence of muscle stress — a constraint on claw biting force

The widespread negative size-dependence of muscle stress in decapod claws suggests a constraint (or a behavioral restraint) rather than an adaptation, because associated force-enhancing traits, such as mechanical advantage and sarcomere length, do not all decrease with increasing claw size in a similar fashion. From a purely mechanical perspective, the claw is a simple machine for applying closing forces, and changes in performance should be paralleled by concordant changes in several traits. For example, speed can be traded-off for strength, or *vice versa*, and the tradeoff will be reflected in claw design throughout, as seen in many species with dimorphic crusher and cutter claws (Schafer, 1954; Alexander, 1968; Warner & Jones, 1976; Brown *et al.*, 1979; Elner & Campbell, 1981; Warner *et al.*, 1982; Govind & Blundon, 1985; Govind, 1989). The predicted correlations are apparent from the formula describing claw biting forces. The force a claw generates at the tip of the fingers depends upon several factors. First, it depends on the force applied at the apodeme insertion point (**F_{in}**) and on the mechanical advantage (**MA**) or shape of the dactyl:

$$F_{out} = F_{in} M A$$

Second, the force generated at the tip of the apodeme (F_{in}) depends on the muscle stress (S), the area of the apodeme (A) and the angles the muscle fibers insert on the apodeme (Θ):

$$F_{in} = S * (A * \sin 2\Theta)$$

Therefore increases in any of these factors (**MA, S, A sin2Θ**) will yield an increase in maximum biting force.

Is the puzzling decline in maximum muscle stress with increasing size in *Cancer* claws adaptive, or does it reflect some hidden constraint on claw performance? If selection was acting to increase maximum force at the claw tip then most or all of the factors affecting claw performance, (S, A, **sin2Θ**, MA) should vary concordantly. Increases in S, MA, A and **sin2Θ** should parallel increases in maximum biting force. Although apodeme area (A) varies isometrically (Table 3-2e), both sarcomere length (Fig. 3-3) and mechanical advantage (MA, Fig. 3-4) show positive allometry with claw size in *Cancer* crabs, which suggests selection has acted to promote proportionally higher maximum biting forces in larger claws. Curiously, maximum muscle stress (S) declined with increasing claw size in nearly all *Cancer* species (Fig. 3-2), and clearly did not vary in a way that would enhance the maximum biting force in larger claws. This seemingly anomalous pattern suggests either a) that some physiological constraint acts on the muscle tissue of larger claws as suggested by (Elner & Campbell, 1981), or b) larger crabs behaviorally limit the maximum force they generate to avoid damaging their claws (Chapter 2), because of an upper limit to the cuticle strength of the claw (Appendix I)

The negative allometry of claw force in relation to relative claw size

Within *Cancer* species, as in many other decapods, claw size increases disproportionately as body size increases (Huxley, 1932; MacKay, 1943; Hartnoll, 1974). In addition, within some *Cancer* species, the coefficient of allometry of claw size versus body size actually increases in larger individuals, yielding allometric “phase shifts” (Orensanz & Gallucci 1988). These high positive allometries and phase shifts may be necessary to compensate for declining muscle stress with increasing claw size, to maintain a constant force output per unit body size, as discussed previously. The positive allometries of other traits that influence force production, such as sarcomere length and mechanical advantage, are also consistent with this hypothesis.

Interestingly, although the rate of decline of muscle stress with size is consistent among *Cancer* species, the allometry of claw size versus body size, and allometric phase shifts, are not consistent among species (Vermeij, 1977; Lawton & Elner, 1985; Orensanz & Gallucci, 1988). For example, the coefficient of allometry of claw size versus body size is much lower in *C. magister* than *C. oregonensis* (Vermeij, 1977; Lawton & Elner, 1985; Orensanz & Gallucci, 1988). Therefore, the allometries of claw size in *Cancer* crabs are not fully explained by declining muscle stress. This is not surprising given that the selection pressures affecting claw size are likely very complex (Chapter 2). A species' habitat and life history, as well as the uses to which it puts its claws, will affect how claw size changes with body size and age. In fact, the impact of declining muscle stress itself may be different for different species. For example, the impact will be far more severe for *C. oregonensis*, which inhabits rocky outcrops and whose diet is likely largely composed of hard-shelled prey (Chapter 2) than for *C. magister*, which inhabits open sandy areas and may have frequent opportunities to obtain soft prey items (Stevens *et al.*, 1982). Despite the complexity of factors that may influence claw allometries, the pervasiveness of declining muscle stress makes it an important factor to consider in future studies of claw evolution.

Implications for the coevolution of predator armament and prey armor

Investigation of the allometries of decapod crushing forces and gastropod shell breaking strengths yielded some surprising results. First, the allometric relation between shell breaking strength and size in temperate *Nucella* gastropods (Currey & Hughes, 1982) appears to parallel that between maximum biting force and claw size in temperate *Cancer* crabs, yet the true slope for breaking strength with size for *Nucella* may possibly be underestimated. However, for the temperate gastropod *Calliostoma ligatum*, LaBarbera & Merz (1992) also found a negative allometric relation between shell breaking strength and size. Thus, for temperate gastropods, shell safety factors (ratio of mean strength of shells to maximum load deliverable by predators) do not appear to change with size, and larger crabs are not disadvantaged relative to smaller ones when feeding on prey appropriate to their claw size.

Second, a very different situation was observed for tropical crabs and gastropods. Tropical gastropod shells appear to maintain isometry of breaking strength with size (Table 3-7). However, tropical crabs should still display negative allometry of maximum crushing force with claw size. Bite-forces of the tropical crab *Menippe* should increase with increasing claw size to an exponent less than the exponent of *Cancer* crabs, since muscle stress declined at a greater rate for claws of *Menippe* than for claws of *Cancer* (Fig. 3-6). Therefore, shell safety factors likely increase with size in tropical gastropods. Note that the isometric relation between shell strength and mass was derived from interspecific data (Vermeij &Currey, 1980) without controlling for intraspecific variation in the variables, so conclusions using these data must be held as speculative (LaBarbera, 1989; LaBarbera & Merz, 1992). However, several other lines of evidence support the suggestion that safety factors of tropical gastropods increase with size. First, for shells in general, safety factors should increase with increasing size (Palmer *et al.*, 1999) because shell weight or thickness increases disproportionately with increasing body size (Currey, 1977; Palmer, 1981; Palmer, 1992). Second, theory predicts that safety factors should increase with additional selection pressures (Alexander, 1981; Lowell, 1985; Lowell, 1987), and snails of tropical oceans do tend to have a more diverse range of predator types than temperate oceans (Vermeij, 1987; for evidence on geographic variation in durophagous fish see Palmer, 1979). Third, the presence of an additional class of predators on tropical limpets (i.e., prying forces from crabs and lateral crushing by fish) compared to temperate ones (i.e., prying forces only) was reflected in greater safety factors of tropical shells (Lowell, 1987). Furthermore, for *Nerita scabricosta*, a tropical gastropod, which is often subjugated by the crab *Ozius verreauxii*, the slope of shell breaking strength versus shell size is positively allometric (both shell mass$^{1.02}$ and aperture width$^{3.86}$) (Hughes, 1989). Combined, these lines of evidence strongly suggest that the safety factor of tropical shelled prey will increase with size.

Here, I have demonstrated that declining muscle stress with increasing claw size represents a performance constraint on the predatory armament of *Cancer* crabs. Interestingly, the realized performance of these temperate crabs, in terms of crushing hard-shelled prey, does not appear to be compromised as temperate gastropod shell strength follows a parallel allometry to *Cancer* biting strength. As such, the safety factor of the gastropod armor does not change with size. Allometric analyses of the strength of both predatory armament and prey armor provide very useful baseline information on the nature of the predator-prey interactions. Thus, this approach should prove fruitful in elucidating mechanisms of predator-prey coevolution.

Table 3-1. Size-dependence of maximum muscle stress for claws from six species of *Cancer*.

	Species	*n*	Slope (±SE)	Intercept	*r*	*P*
a) log(maximum muscle stress, Ncm^{-2}) (*Y*) vs. log (claw height, mm) (*X*)						
1)	*C. antennarius*	26	-0.619 (0.219)	2.738	0.501	0.009
2)	*C. branneri*	12	-0.953 (0.537)	3.048	0.489	0.106
3)	*C. gracilis*	14	-0.914 (0.358)	2.931	0.593	0.025
4)	*C. magister*	17	0.412 (0.354)	1.331	0.264	0.260
5)	*C. oregonensis*	21	-0.646 (0.285)	2.697	0.461	0.035
6)	*C. productus*	27	-0.866 (0.118)	2.980	0.827	<0.001
b) log(maximum muscle stress, Ncm^{-2}) (*Y*) vs. log (claw wet weight, g) (*X*)						
1)	*C. antennarius*	26	-0.189 (0.068)	2.068	0.493	0.011
2)	*C. branneri*	12	-0.289 (0.178)	2.052	0.457	0.135
3)	*C. gracilis*	14	-0.338 (0.121)	2.009	0.628	0.016
4)	*C. magister*	17	0.067 (0.138)	1.808	0.115	0.631
5)	*C. oregonensis*	21	-0.231(0.112)	2.002	0.428	0.053
6)	*C. productus*	27	-0.282 (0.035)	2.066	0.850	<0.001

Least-square linear regression equations; slopes correspond to coefficient of allometry.
Isometry for stress should be 0 (see text).
Abbreviations: ±SE = standard error, *r* = correlation coefficient, *n* sample size.

Table 3-2. Overall size-dependence of morphometric and performance traits for claws of *Cancer* crabs.

Slope$_{comm}$ (±SE)	Exp. Slope	P_{ES}	Range (n_s)*	Intercept	r^2_{comm}	P	P_{sp}
a) log(maximum muscle stress Ncm^{-2}) (Y) vs. log (claw height, mm) (X)†							
-0.794 (0.091)	0	<0.001	-0.91 to -0.62	2.886	0.707	<0.001	0.675
b) log(claw height, mm) (Y) vs. log (manus length, mm) (X)							
0.980 (0.016)	1.0	0.222	0.89 to 1.11	-0.0901	0.989	<0.001	0.592
c) log(claw height, mm) (Y) vs. log (claw wet weight, g) (X)							
0.325 (0.003)	0.33	0.090	0.31 to 0.35	1.0595	0.993	<0.001	0.530
d) log(maximum muscle stress Ncm^{-2}) (Y) vs. log (claw wet weight, g) (X)†							
-0.257 (0.027)	0	<0.001	-0.34 to -0.19	2.047	0.716	<0.001	0.501
e) log(apodeme area mm^2) (Y) vs. log (claw height, mm) (X)							
2.056 (0.050)	2.0	0.911	1.69 to 2.19	-0.377	0.980	<0.001	0.375
f) log(muscle dry weight, g) (Y) vs. log (claw height, mm) (X)							
2.829 (0.107)	3.0	0.112	2.05 to 4.29	-4.091	0.951	<0.001	0.088

†the common coefficient of allometry was calculated using only the four *Cancer* species with significant slopes in Fig. 3-2 — *C. antennarius, C. gracilis, C. oregonensis* and *C. productus.*

Slope$_{comm}$ = common slope from a two-factor ANCOVA (species and sex were the grouping variables).
Exp. Slope = expected slopes from isometry relative to the covariate (i.e., variable X).

P_{ES} = probability that the common slope did not differ from the expected slope of isometry.

Range (n_s)* = range of significant slopes among species.
Intercept = the y intercept of the common regression from an ANCOVA.
r^2_{comm} = coefficient of determination of the common regression from an ANCOVA.
P = probability that the common slope did not differ from zero.

P_{sp} = probability that slopes did not differ among species.

Table 3-3. Size-dependence of A-band length (a) and mechanical advantage (b) for claws from six species of *Cancer* crabs.

	Species	*n*	Slope (±SE)	Intercept	r^2	*P*
a) log(A-band length, μm) (Y) vs. log (claw height, mm) (X)						
1)	*C. antennarius*	27	0.156 (0.029)	0.707	0.535	<0.001
2)	*C. branneri*	10	0.459 (0.244)	0.331	0.308	0.096
3)	*C. gracilis*	15	0.293 (0.058)	0.479	0.664	<0.001
4)	*C. magister*	32	0.179 (0.055)	0.593	0.259	0.003
5)	*C. oregonensis*	24	0.101 (0.039)	0.844	0.234	0.017
6)	*C. productus*	18	0.088 (0.044)	0.791	0.201	0.062
7)	All combined†	126	0.146 (0.019)	0.720	0.771	<0.001
b) log(mechanical advantage) (Y) vs. log (claw height, mm) (X)						
1)	*C. antennarius*	53	0.055 (0.026)	0.284	0.286	0.038
2)	*C. branneri*	29	0.120 (0.082)	0.188	0.272	0.154
3)	*C. gracilis*	35	0.143 (0.045)	0.121	0.481	0.004
4)	*C. magister*	38	-0.014 (0.067)	0.272	0.036	0.831
5)	*C. oregonensis*	44	0.306 (0.075)	0.034	0.533	<0.001
6)	*C. productus*	52	0.096 (0.019)	0.254	0.589	<0.001

†the common coefficient of allometry was calculated using all six *Cancer* species
Abbreviations : *n* = sample size, SE = standard error, r^2 = coefficient of determination,
P = probability that the slope differed from zero.

Table 3-4. Least square mean angles of pinnation for an average claw gape of 38.6 degrees determined by a single ANCOVA.

Species	Male		Female		Size Dependence
	n	mean±SE	*n*	mean±SE	*P*
C. antennarius	12	37.8±1.07°	15	35.5±0.86°	0.244
C. branneri	14	36.6±0.91°	1	34.8±--	0.189
C. gracilis	8	34.6±1.17°	8	34.5±1.17°	0.705
C. magister	4	35.1±1.64°	12	32.0±0.97°	0.003
C. oregonensis	6	38.6±1.65°	8	35.4±0.92°	0.356
C. productus	10	31.6±1.04°	12	31.3±0.95°	0.737

Abbreviations: *P* = statistical significance of the correlation between pinnation-angle residuals (from the pinnation-angle vs. gape-angle regression) and claw height, *n* = number of claws, SE = standard error.

Table 3-5. Size-dependence of stress for claws from three genera of decapods.

Genus	n	Slope (SE)	Post-hoc Rank	Intercept	r^2	P
1) Menippe 'crusher'	38	-2.131 (0.239)	a	5.344	0.687	<0.001
2) Homarus 'crusher'	59	-1.289 (0.107)	b	3.425	0.717	<0.001
3) Cancer 'crusher' †	110	-0.849 (0.137)	c	2.940	0.63	0.002
4) Homarus 'cutter'	72	-0.690 (0.096)	c	2.638	0.426	<0.001

†Cancer 'crusher' does not includes C. magister (see text)
Abbreviations: n sample size, SE = standard error, r^2 = coefficient of determination, P = probability that the slope differed from zero.

Table 3-6. Correlation coefficients compared to % error of prediction for data on the size-dependence of stress for groups of decapods

Group	*n*	*r*	*P*	%Error of Prediction
All decapod genera	289	0.776	< .001	44.65
Homarus & *Cancer*	251	0.892	< .001	29.41
C. antennarius	26	0.500	0.009	15.30
C. branneri	12	0.489	0.106	12.84
C. gracilis	14	0.593	0.025	11.37
C. magister	20	0.264	0.26	16.50
C. oregonensis	21	0.461	0.035	10.07
C. productus	27	0.827	< .001	15.71
ALL *Cancer* spp	120	0.682	< .001	13.96
Menippe 'crusher'	38	0.829	< .001	27.35
Homarus 'crusher' & 'cutter'	131	0.744	< .001	32.55
Homarus 'crusher'	59	0.847	< .001	22.01
Homarus 'cutter'	72	0.653	< .001	18.62

Abbreviations : n = sample size, r = correlation coefficient, P = probability that the slope differed from zero. %Error of Prediction (see text)

Table 3-7. First, the breaking strength of shells (Newtons) in relation to mass (grams) for thaidid snails (Vermiej & Currey, 1980; Currey & Hughes, 1982) and the bite-force (Newtons) in relation to mass (grams) for claws for six *Cancer* species. Expected slope of isometry for log force versus log mass = 0.67 and for log force versus log length = 2.0. Second, the breaking strength of shells (Newtons) in relation to shell height (mm) for thaidid snails (Currey & Hughes, 1982) and the bite-force (Newtons) in relation to claw height for claws for six *Cancer* species.

Ref.	Trait	Location of specimens	n	Least Squared Slope (SE)	Size Range	Post-hoc Rank	Intercept	r^2	RMA Slope	P	$P_{isometry}$ (Allom.)
Log (Breaking Strength) vs. Log (Mass g)											
1	shell	tropical, VS	103	0.705 (0.040)	0.10 - 20.65	a	2.901	0.752	0.813	<0.001	<0.001 (Pos)
2	shells	temperate, VS	39	0.556 (0.067)	0.31 - 33.02	b	2.333	0.650	0.690	<0.001	0.769 (Iso)
3	shells	temperate W	103	0.513 (0.046)	0.42 - 11.27	b	2.494	0.549	0.692	<0.001	0.626 (Iso)
Log (Biting Force) vs. Log (Mass g)											
4	claws	temperate NEP	148	0.471 (0.017)	0.64 - 30.36	b	1.756	0.836	0.515	<0.001	<0.001 (Neg)
Log (Breaking Strength) vs. Log (Height mm)											
4	shells	temperate W	99	1.458 (0.165)	14.3 - 39.6	--	0.718	0.444	2.188	<0.001	0.257 (Iso)
Log (Biting Force) vs. Log (Height mm)											
3	claws	temperate NEP	150	1.494 (0.062)	9.5 - 34.4	--	0.175	0.797	1.673	<0.001	<0.001 (Neg)

Reference (Ref.); 1 = Vermeij & Currey (1980), 2 = Vermeij & Currey (1980), 3 = Currey & Hughes (1982), 4 = this study.

Abbreviations: n sample size, SE = standard error, r^2 = coefficient of determination, RMA = reduced major axis slope, P = probability that the slope differed from zero, $P_{isometry}$ = probability the RMA slope was different from isometry, VS = various sites, W = Wales, NEP = Northeast Pacific.

Allom. = the allometry of the RMA slope, which can be one of three, Iso = isometric, or Pos = positive allometry, or Neg = negative allomety.

Letters identify groups of least square slopes that did not differ significantly after a sequential Bonferroni adjustment on P values

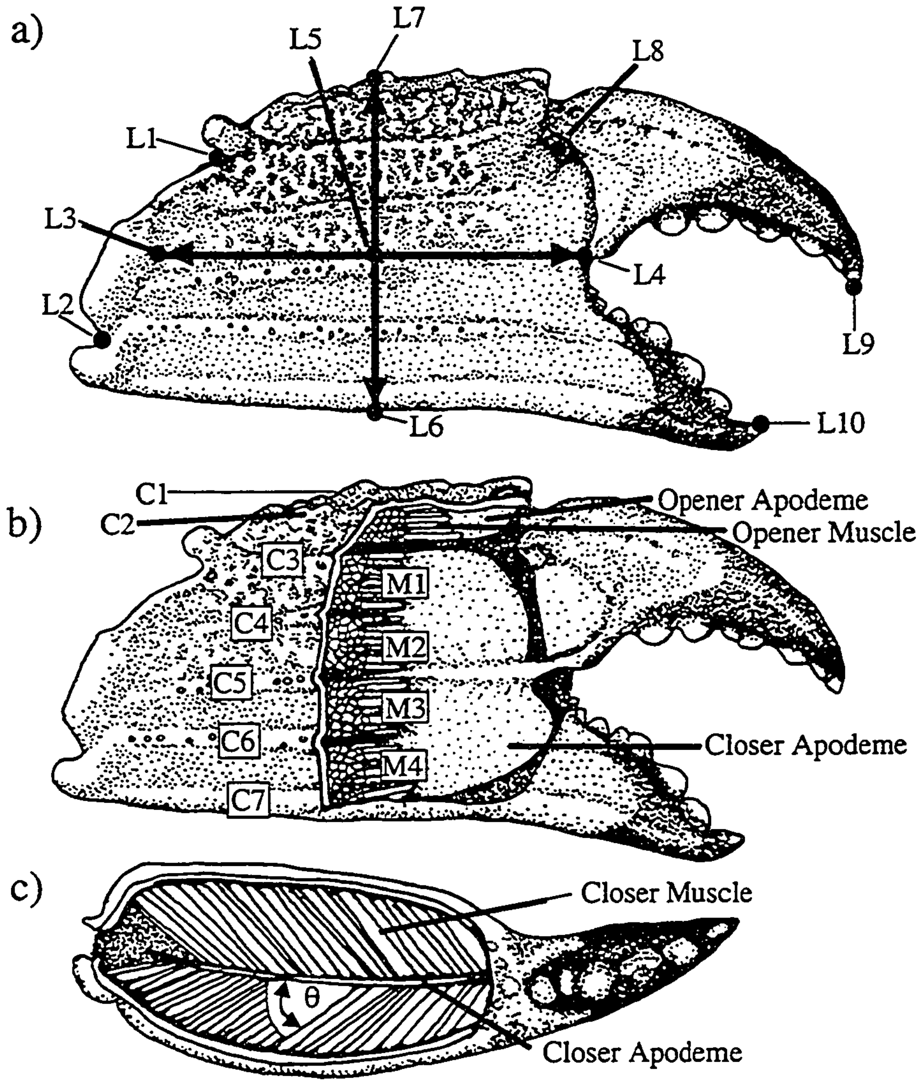

Figure 3-1. Measurements of exoskeletal and muscle morphology. a) Landmarks used for derived external linear measurements: L1 = upper manus hinge, L2 = lower manus hinge, L3 = mid-point between L1 and L2, L4 = intersection between the manus and the base of the dactyl, L5 = mid-point between L3 and L4, L6 and L7 = intersection between the manus ventral and dorsal edge respectively, and a perpendicular line to the line L3 to L4 with the base at L5, L8 = dactyl pivot, L9 = tip of dactyl, L10 = tip of pollex. Manus length is measured from L3 to L4, and claw height from L6 to L7. The first and second lever arms (L_1 and L_2) are measured from L4 to L8, and L8 to L9 respectively. The ratio of the two lever lengths L_1/L_2 is the mechanical advantage. 'Gape-angle' was measured at L8 and is defined by the triangle of the three landmarks, L10 to L8 to L9. b) A claw partially dissected with the closer and opener muscles revealed and their associated apodemes. The exoskeletal carinae, C1 to C7 {defined by Nations (1975)}, run in a proximo-distal direction along the manus and clearly define the muscle regions below the cuticle. The four closer muscle regions sampled were M1 to M4. c) A claw dissected along its mid-sagittal plane just below the fifth carina, in view is the ventral portion of the manus with the pollex. Θ = 'angle-of-pinnation'.

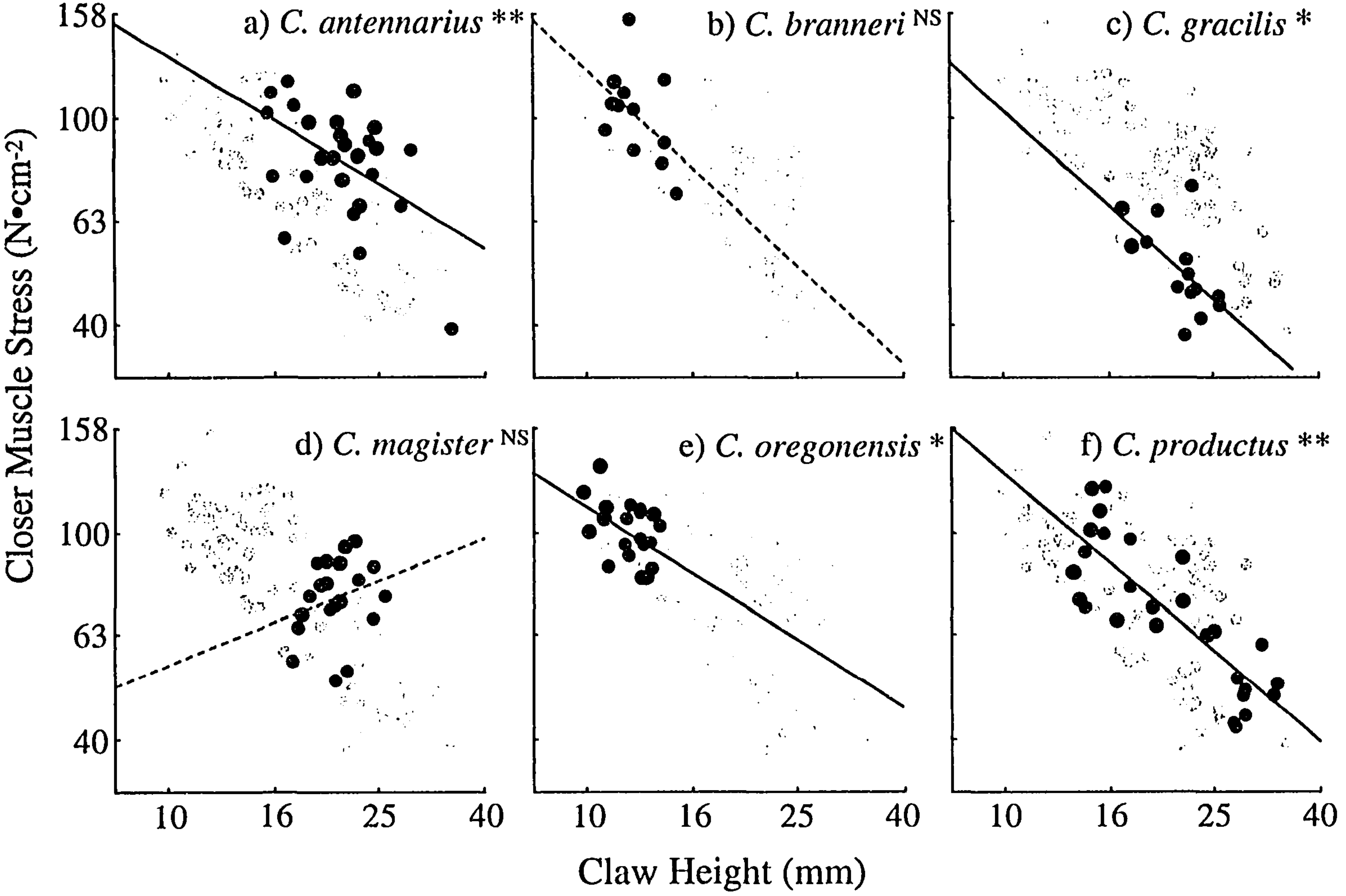

Figure 3-2. Size-dependence of claw muscle stress for six species of *Cancer* crabs. Each point (dark circles) represents an individual claw for the species indicated. Gray circles represent the other species for comparison. Solid lines indicate significant least-square regressions (see Table 3-1 for regression statistics and Table 3-2 for ANCOVA results). Broken lines indicate non-significant least-square regressions. NS = not significant, * $P < 0.05$, ** $P < 0.01$.

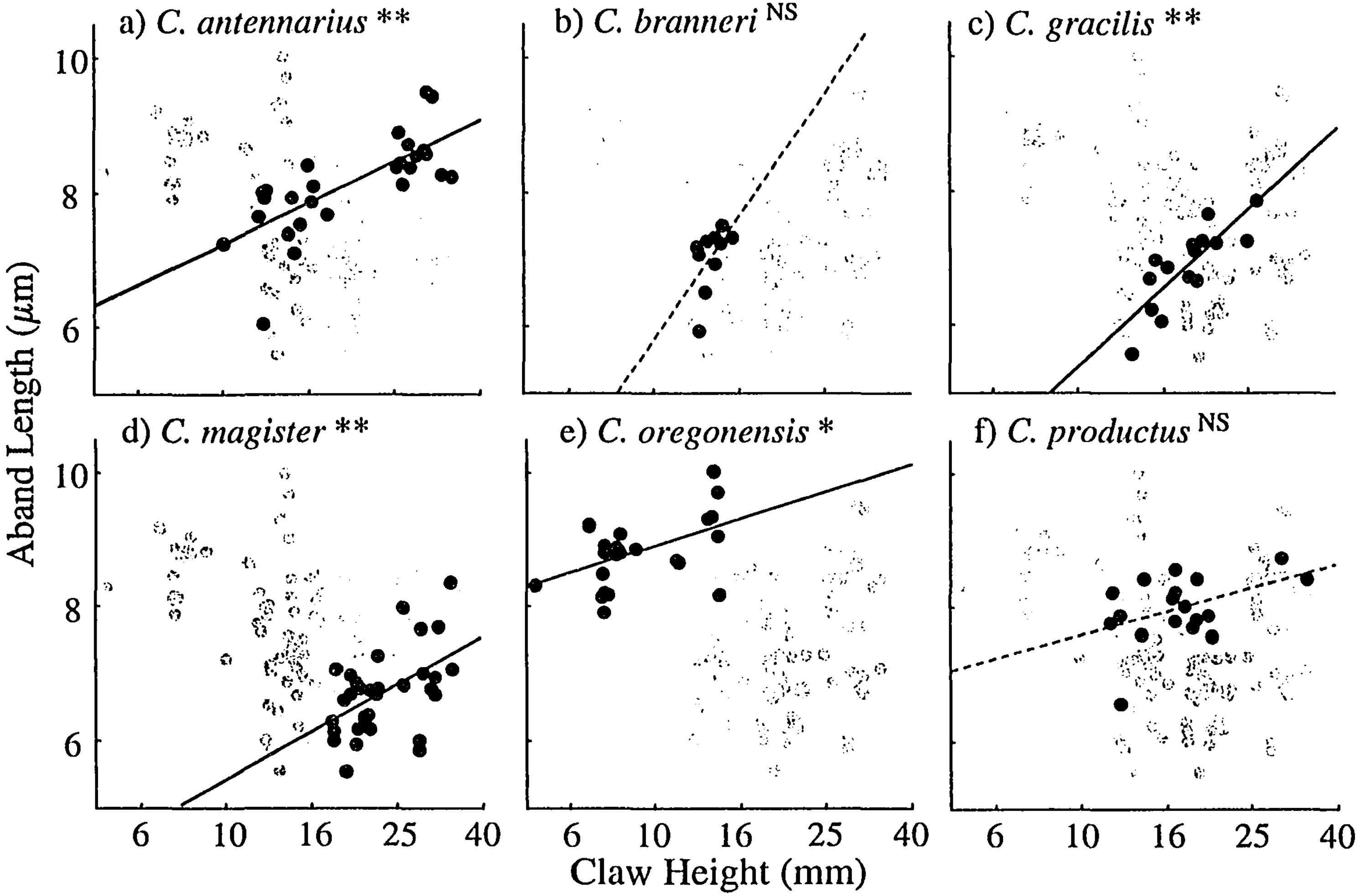

Figure 3-3. Size-dependence of claw muscle A-band length for six species of *Cancer* crabs. Each point (dark circles) represents a mean A-band length (N = 40) for a single claw for the species indicated. Gray circles represent the other species for comparison. Solid lines indicate significant least-square regressions (see Table 3-3 for regression statistics). Broken lines indicate non-significant least-square regression analysis. NS = not significant, * $P < 0.05$, ** $P < 0.01$.

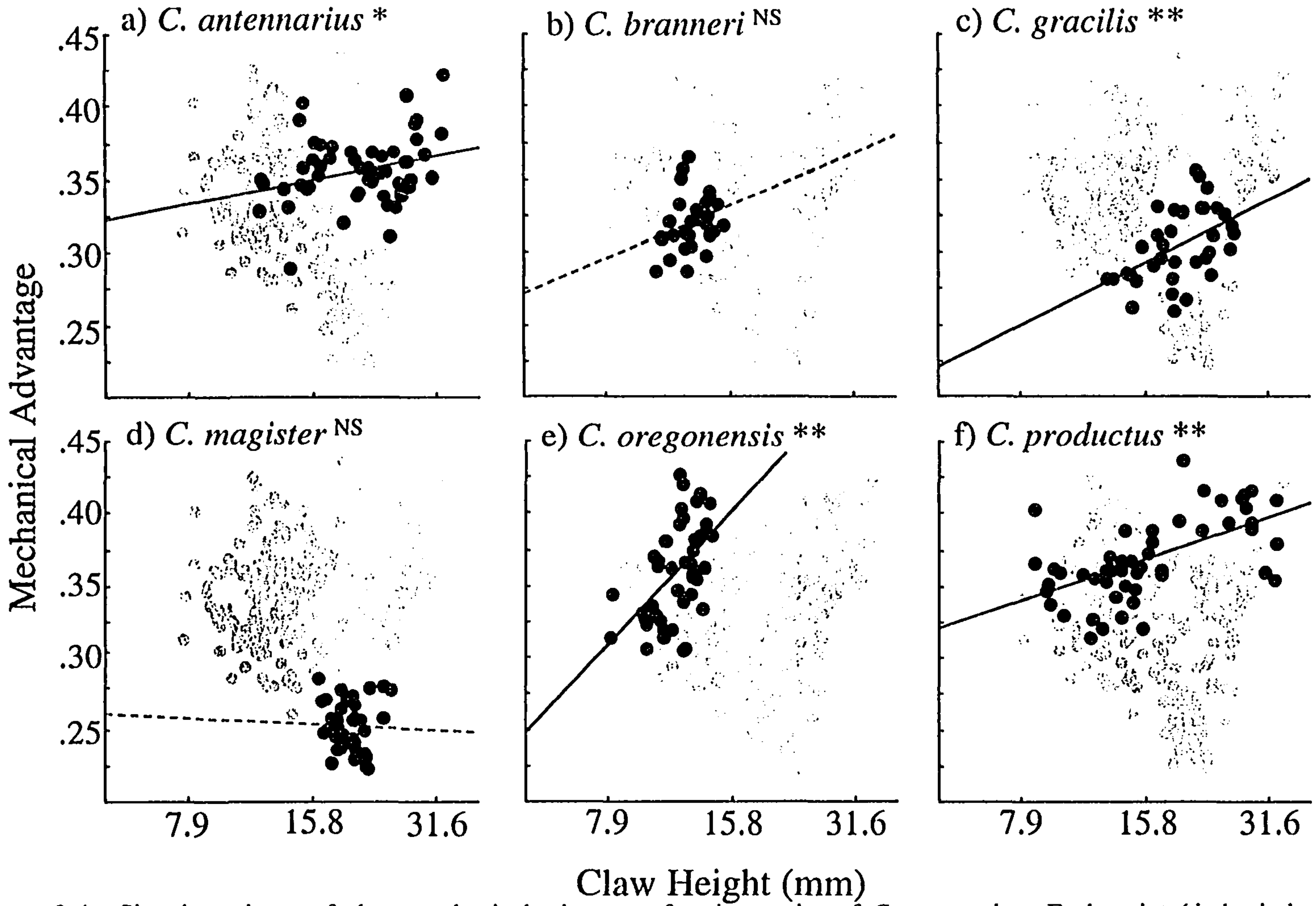

Figure 3-4. Size-dependence of claw mechanical advantage for six species of *Cancer* crabs. Each point (dark circles) represents a single claw for the species indicated. Data included are restricted to those individuals used in stress calculations. Gray circles represent the other species for comparison. Solid lines indicate significant least-square regressions (see Table 3-1 for regression statistics and Table 3-2 for ANCOVA results). Broken lines indicate non-significant least-square regression analysis. NS = not significant, * $P< 0.05$, ** $P< 0.01$

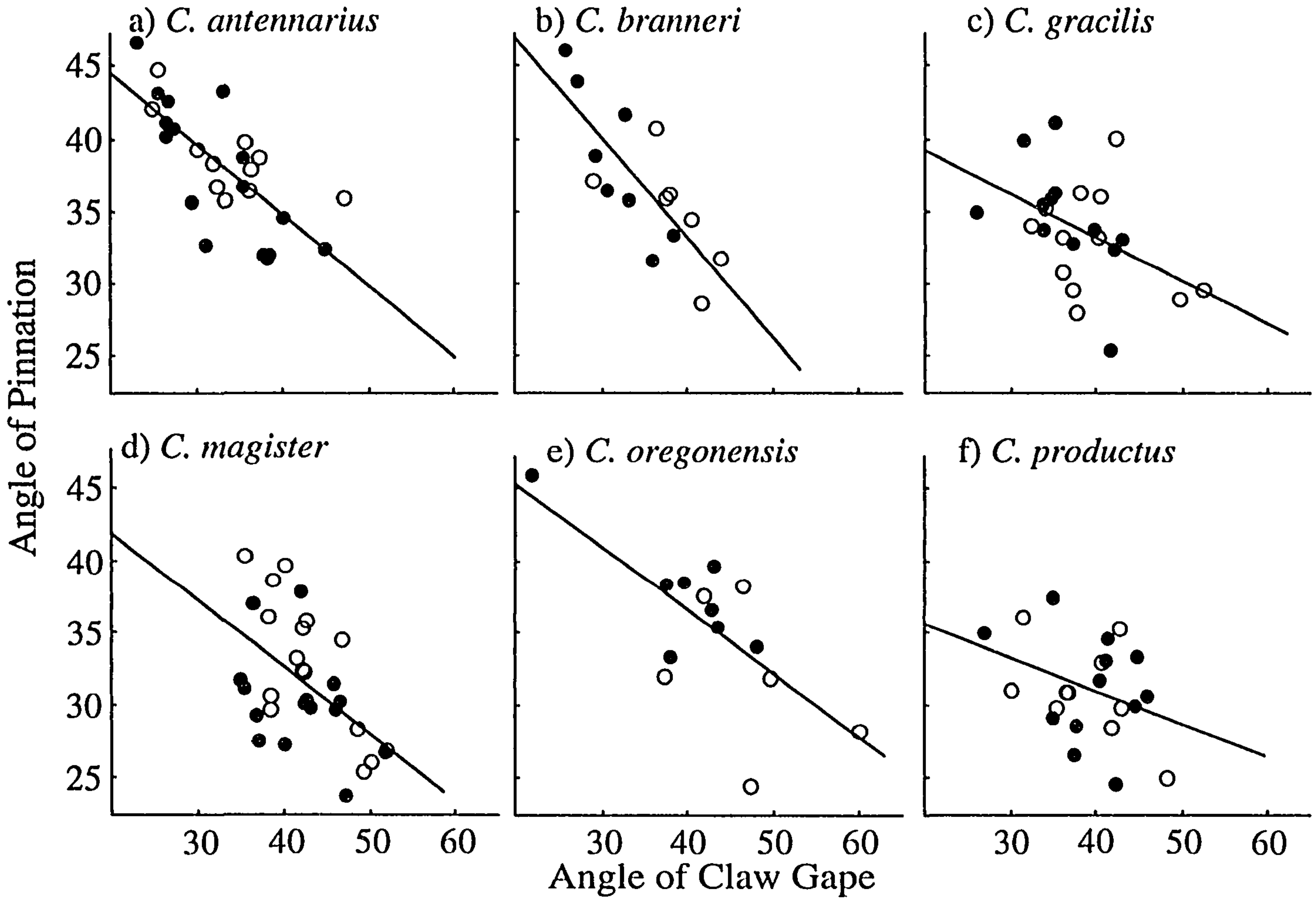

Figure 3-5. The lack of size dependence of angles of pinnation for six species of *Cancer* crabs. Each point (dark circle) represents a single 'larger' claw, and (open circle) represents a single 'small' claw, relative to the mean of the sample for each species treated separately. Lines indicate least-square regressions from which residuals were computed.

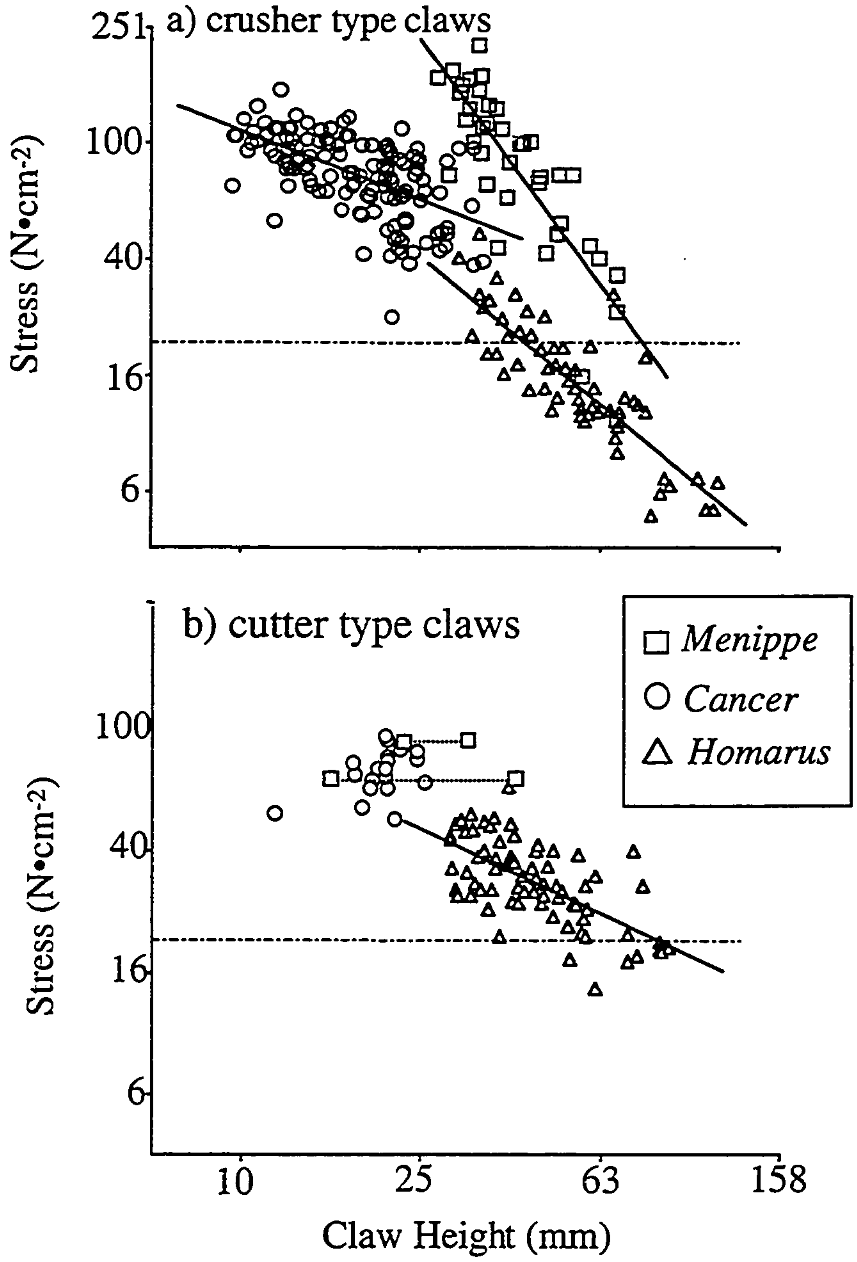

Figure 3-6. Size-dependence of claw muscle stress for a) crusher claws and b) cutter claws in three decapod genera. Claws of *C. magister* were classified as 'cutter', and those of the other five *Cancer* species were classified as 'crusher'. Data were compiled from the literature [*Menippe* (Blundon, 1988), *Cancer* (Fig. 3-2) and *Homarus* (Elner & Campbell, 1981)]. Lines indicate least-square regressions (see Table 3-5 for regression statistics and text for ANCOVA results). The single regression line for b) was assessed using only *Homarus* claws. The single horizontal dash-dot line in both parts a) and b) represents the typical stress of vertebrates (20 Ncm^{-2}). The dotted lines in b) represent the range of values for tropical (upper line) and temperate (lower line) *Menippe* 'cutter' claws, for which stress does not decline with claw size [see Blundon (1988) for details].

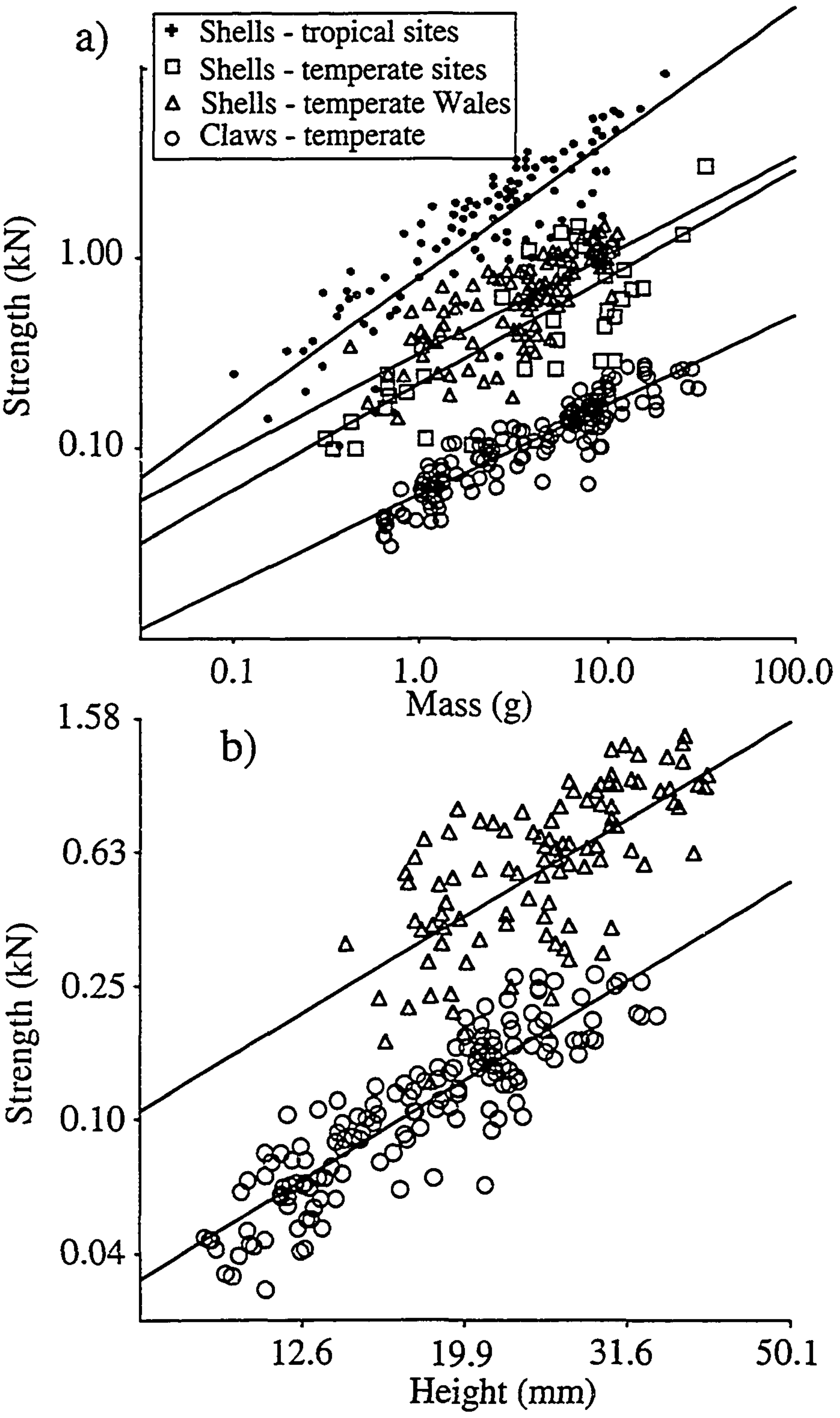

Figure 3-7. Breaking strength of thaidid snail shells versus size. a) Shell mass as the size indicator. Biting strength of *Cancer* claws versus claw mass are presented for comparison. Data for shell mass and load compiled from Fig. 1 of Vermeij & Currey (1980) and from Fig. 3 of Currey & Hughes (1982). b) Shell height as the size indicator. Biting strength of *Cancer* claws versus claw height is presented for comparison. Data for shell height and load compiled from Fig. 3 of Currey & Hughes (1982). See Table 3-7 for regression equations.

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4. The Shape of Strength: The Morphological Basis of Variation in Claw Safety Factors Among Six Species of *Cancer* Crabs.

Introduction

Safety factor theory provides an effective approach to investigate performance of biological structures, since it incorporates both the maximum lifetime load the structure will experience and its ability to resist breakage under such a load (Alexander, 1981; Lowell, 1985; Lowell, 1987; Alexander, 1997). Safety factors (i.e., breaking force of the claw's pollex/maximum claw bite force) depend on size within species of *Cancer* crabs, with larger claws having higher safety factors than smaller claws (Chapter 2 & Appendix I). However, claw size does not explain the variation in safety factors observed among the six *Cancer* species — *C. antennarius*, *C. branneri*, *C. gracilis*, *C. magister*, and *C. productus*. Within a species safety factors may range from approximately 3 to 5. The higher safety factors of larger claws appear adaptive because the cost of failure is assumed to increase with claw size, since older larger crabs lose the ability to regenerate damaged claws (Chapter 2 & Appendix I). Among species, safety factors ranged from approximately 2 to 7 (Chapter 2). The smallest species, *C. magister* had the highest mean claw safety factor (7.4), while the largest species, *C. magister*, had the lowest (2.6). The four other *Cancer* species, that vary in body size, have intermediate safety factors (average = 3.6). Therefore, claw safety factors cannot be completely 'size-driven', though most likely both the age of the claw (time spent in the intermolt) and the age of the crab plays a considerable role. Here I show that the most feasible, proximate explanation for among-species variation in claw safety factors is the shape of the claw independent of claw size.

Because a safety factor is a ratio, changes in either the numerator or the denominator can lead to variation in its values (Chapter 2). For claw safety factors, many variables can influence the numerator and the denominator. How these particular variables vary and co-vary ultimately determines whether safety factors differ among claws.

The safety factor denominator, the bite force, is determined jointly by the force of muscle contraction and the mechanical advantage of the claw. Differences in mechanical advantage (lever-1/lever-2, see Fig. 4-1), and closer- muscle properties such as angle of pinnation of the fibers and average sarcomere length, can change bite forces without changes in overall claw size. Fiber length does not affect the force of muscle contraction, however, a longer fiber will produce faster contractions (Alexander, 1968; Josephson, 1975). Thus, claws that bite harder tend to have higher mechanical advantages, shorter fiber lengths, greater angles of pinnation, and longer average sarcomere lengths. Alternatively, faster claws tend to have lower mechanical advantages, longer fiber lengths, lower angles of pinnation, and shorter average sarcomere lengths (Warner, 1977). For a given claw size, both the shape of the dactyl (i.e., the lever lengths) and the shape of the manus (i.e., height, length and width) should influence biting force of the claw because of their effect on mechanical advantage and closer muscle properties, respectively. The importance of dactyl shape is self evident as it defines the mechanical advantage of the claw, which has been well studied (Brown, Cassuto & Loos, 1979; Vermeij, 1987; Yamada & Boulding, 1998). The importance of manus shape is less obvious, since it does not directly influence the bite-force. However, the manus houses the muscle, and its shape likely reflects muscle properties such as angle-of-pinnation and fiber length. I therefore predict that manus shape will reflect underlying properties of muscle and hence muscle performance.

The safety factor numerator, the breaking strength of the pollex, should be determined by both material (Hahn & LaBarbera, 1993; Melnick, Chen & Mecholsky, 1996; Palmer, *et al.*, 1999) and beam properties of the pollex. The cuticle strength sets the upper limit of the beam's breaking strength, while beam shape determines how an applied stress will be distributed over its length (Wainwright *et al.*, 1976). Stresses acting on the beam are highest at the cross-sections that are furthest from the source of the applied load, and the distance from a cross-section to the applied load is the bending moment (Gordon, 1978). Therefore, for forces applied at the pollex tip, the area at the base of the pollex should have higher stress than any other area along its length. Selection for a 'strong' claw (i.e., ability to resist breaking) should maximize the second moment of area in the direction of bending at the base of the pollex, while minimizing the bending moment (i.e., the length of the pollex). For a detailed discussion of beam theory applied to biological structures, see Kitchener (1985; 1987). Optimally, the breaking strength of the pollex should covary with the bite-force of the claw, since any additional strength in either variable would mean that it was over-built, resulting in unnecessary loss of material or excessive potential bite-force {see Alexander (1997) for a general discussion of optimization of strengths}.

Most durophagous clawed decapods have dimorphic claws (Vermeij, 1977). One claw has a relatively larger size, higher mechanical advantage, and a blunter set of 'teeth' than the other (Warner, 1977). This claw is often referred to as the 'crusher', 'strong', or 'major' claw, while the other, smaller claw is referred to as the 'cutter', 'fast', or 'minor' claw. Minor claws tend to be more slender, have a lower mechanical advantage and sharper teeth than major claws. For the dimorphic clawed lobster, *Homarus americanus*, the shape of the claw is highly correlated with the underlying muscle properties (Govind *et al.*, 1987; Govind, 1989). In contrast, for brachyuran crabs, the correlation with underlying muscle, sarcomere length and angle of pinnation, is not always clear; some studies have shown a correlation while others have not (Warner & Jones, 1976; Govind & Blundon, 1985). When feeding on hard shelled prey, the major claw is used to crush, while the minor claw is used to manipulate and tear the soft flesh of prey once exposed (Elner, 1978). For crabs with dimorphic claws, this pattern of prey handling suggests that claw shape and design indicate dietary preferences and the associated performance demands (Elner, 1978).

In contrast to those of many other durophagous brachyurans, the claws of *Cancer* crabs are unusual in that the right and the left claws appear monomorphic in size and shape (Nations, 1975; Lawton & Elner, 1985). Both claws tend to have relatively high mechanical advantages compared to those of other crabs, and both are considered 'crusher' claws (Lawton & Hughes, 1985). *Cancer* crabs are molluscivores, and feeding observations suggest these crabs use their right and left claws equally when crushing hard-shelled prey (Lawton & Hughes, 1985; Juanes & Hartwick, 1990; Taylor, unpubl.observations). Symmetry in claw use thus reflects symmetry in claw shape. However, *Cancer* species can be grouped into two general categories based on claw size relative to body size (carapace width) and mechanical advantage (Lawton & Elner, 1985). The first group comprises species with 'strong' claws while the second comprises species with 'fast' claws (Lawton & Elner, 1985). Interestingly, therefore the dimorphism of claw size and shape seen within other brachyurans is not expressed within *Cancer* species but among them.

Claw form in decapods is not completely bimodal, but represents a continuum of patterns between the extremes of 'crusher' and 'cutter' (Schafer, 1954; Warner, 1977).

Classification of all claws into two narrow categories (Yamada & Boulding, 1998) is likely overly simplistic (Brown, Cassuto & Loos, 1979). Nevertheless, the underlying premise that external claw shape reflects internal properties and claw function is compelling. Here, I examine the relations between claw shape and claw performance attributes among six *Cancer* species. In this context, safety-factor theory provides a framework for integrating two different aspects of claw performance: biting force and breaking strength.

Methods

Claw safety factors

Claw safety factors were previously calculated for six *Cancer* species — *C. antennarius*, *C. branneri*, *C. gracilis*, *C. magister*, *C. magister*, and *C. productus* (Chapter 2 & Appendix I). The safety factor numerator was the force required to break the pollex by applying a load at its most distal portion, and the denominator was either the mean-maximum bite force or extreme-maximum bite force measured at the most distal end of the dactyl and pollex. Individual claw safety factors versus manus length are reported in Figure 2-3 and in Figure AI-4. The details of methods used to assess maximum bite force and break force of claws are also reported Chapter 2 and Appendix I.

Collection of crabs for morphological measurements

In addition to the crabs used in the safety factor experiment, other individuals of all six *Cancer* species were collected to measure morphological variables over a wider size range. Crabs were collected at approximately the same location and time as the crabs used in the safety factor experiments. All six *Cancer* species studied live parasympatrically, and were obtained from sites in close proximity to Bamfield Marine Station (Bamfield, British Columbia, Canada), which is located on the west coast of Vancouver Island, on the outer reaches of Barkley Sound. The life histories of *C. gracilis*, *C. magister*, *C.*

magister and *C. productus* have been well documented in Garrison Bay on the northwest coast of San Juan Island, North Puget Sound (Orensanz & Gallucci, 1988). Furthermore, a recent molecular phylogeny of the *Cancer* crabs, including the six species studied here, has been constructed (Harrison & Crespi, 1999). The combined knowledge of life history and phylogeny of this group, makes this guild of species ideally suited for allometric and biomechanical analyses.

Measurements of exoskeletal dimensions and claw weights

All claws used in the allometric analyses were cut from the rest of the cheliped along the carpus-propodus joint, with the cut edge separating the propodus cuticle and joint membrane around its entire circumference. Claws were drawn via a camera-lucida attached to a dissecting microscope (Wild M5A) with a 0.3X reducing lens, in a view perpendicular to the plane of dactyl rotation (Fig. 4-1a). For depictions of this view for representative claws, see Fig. 4-2. Linear measurements, such as manus height and the distances associated with mechanical advantage (i.e., lever lengths), were digitized (Summagraphics digitizing tablet, 20 dots per mm resolution) from individual claw drawings (Fig. 4-1a). Prior to drawing the perpendicular plane of the claw, claw wet weights (accurate to 0.001 grams), and digital caliper measurements (accurate to 0.01 mm) of claw width were taken. Throughout the text, I will refer to claw wet weight simply as claw weight. After drawing, closer and opener muscle tissue were removed and wet and dry weight, excluding apodemes, were measured. Apodeme surface areas were drawn and measured as described above for claw outlines.

For the analysis of claw shape, care was taken to exclude claws that were regenerating, damaged, or had worn occlusive surfaces. The regenerating claw differs in shape from the pristine claw and these shape differences can persist well into the 3rd and 4th molt, even when the claw approaches a similar size as that of the pristine claw (Taylor, unpublished observations).

Measurement of maximum and minimum moments of inertia

For some of the claws used in the previous safety factor experiment, the claw pollex and dactyl were cut at the base of the most proximal tooth along the occlusive surface (Lines L12-L13 and L15-L16, Fig. 4-1a). For both the pollex and dactyl, the direction of cut was made perpendicular to the horizontal plane of the occlusive surface. Cuts were made using a Dremel tool fitted with a circular blade (edge 0.1 mm, diameter 20 mm). Care was taken to avoid sectioning the pollex tooth, since the location of the pollex centroid would be influenced by additional 'tooth' material, which more likely functions to resist 'tooth-wear' rather than to increase beam strength. The cut surface was smoothed with emery-paper. Cross sections were drawn via a camera-lucida attached to a dissecting microscope (Wild M5A) with a 0.3X reducing lens, in a view perpendicular to the cut surface.

The axes of maximum and minimum moments of inertia (I_{max} and I_{min}), and their respective second moments of area, for both the dactyl and pollex beams, were measured using digital images of the cross-section drawings and custom software which calculates second moments of area for irregular, two dimensional shapes (programming was done by Kent West at the University of Alberta, Mechanical Engineering Department using Microsoft Visual Basic). A mathematical representation of the beam cross-sectional outline was obtained by digitizing both the inner and outer rings on the computer screen at regular intervals (approximately 40 to 50 dots per outline), then fitting cubic spline curves to these discrete points. The closed outline represented by the cubic spline curves was then numerically integrated to find the outline area, perimeter, centroid and 2nd moments of area. Regular geometric shapes (rectangles, circles and ellipses) were used to test the algorithm. A sample of claws were measured twice to determine the measurement error of second moments of area for I_{max} and I_{min}, which was found to be less than 2%.

Closer muscle fiber lengths and angles-of-pinnation

Claws were dissected along a mid sagittal plane just below carinae number 5 (Fig. 4-1b) and the angles of six to eight fibers were measured from the outer mid section of the closer muscle for each claw (Fig. 4-1c). The lengths of these fibers were also measured from the point of attachment on the apodeme to the point of attachment on the inside of the manus cuticle. Therefore, the average angle-of-pinnation and fiber length of each claw represents the mean of 6 to 8 fibers lengths from the mid outer region of the closer muscle. In measuring angles-of-pinnation, I corrected for variation in the degree of muscle contraction by using the actual angle of claw gape as a covariate in a 2-factor (species and sex) ANCOVA, as in Chapter 3. Within species, pinnation-angle does not change with size of the claw (Chapter 3).

Measurement of sarcomere lengths and A-band lengths

Resting sarcomere and A-band length measurements were obtained from other claws similar in size to those used in the safety factor experiment. Ten muscle fibers from each of four regions of the claw were teased apart from wet mount preparations and the resting sarcomere length and A-band length of each fiber were measured, as described in Chapter 3. Only A-band lengths were used in the analysis, since resting sarcomere length is confounded by the degree of muscle contraction, even though resting sarcomere length is the filament trait often reported in the literature because of the ease of visualizing Z-bands.

Statistical analysis

The use of ratios of linear variables to study shape is beset with potential problems when the variables used differ in their allometries (Gould, 1971; Abele *et al.*, 1981). However, ratios are useful tools for examining difference in shape and biomechanical properties that can often be overlooked by pure allometric studies (Pennycuick, 1992). I therefore used a combination of allometric analysis and ratios to examine variation in claw shape among six *Cancer* species.

For describing the allometries of safety-factors, I used $\log_{10}$-claw weight as the covariate rather than $\log_{10}$-manus length or $\log_{10}$-manus height, since claw weight should be the least confounded by claw shape differences in an among-species comparison. Also, $\log_{10}$-claw weight was used to remove the effects of size in order to test for manus height and length differences among species.

In reporting scaling coefficients, I report both a slope from the least-squares linear (OLS) regression and a slope from the reduce major axis (RMA) regression. The slope of the OLS can seriously underestimate the 'true' slope of the bivariate relation when the two variables are not highly correlated (LaBarbera, 1989). The RMA slopes were calculated by dividing the OLS slopes by the correlation coefficient.

Results

The relation between manus height, length and width

First, I examined the allometries of manus length, manus height and manus width versus claw weight, because if the allometric coefficients of the three linear variables differ, then taking ratios of these variables to express claw shape will be problematic, as the ratios will depend on claw size. For each species, all three regressions were tested simultaneously for an interaction effect by an ANCOVA (Table1). For each species, the slope of log manus length versus log claw weight did not differ significantly from the slope of log manus height versus log claw weight, nor from the slope of log manus width versus log claw weight. Likewise, the slope of log manus height versus log claw weight did not differ from the slope of log manus width versus log claw weight (Fig. 4-3 and Table 4-1). For each species, even though no interaction effect was detected between each shape variable regressed against claw weight by an ANCOVA (i.e. the 2-way interaction between shape and claw weight was not significant), examination of the slopes (OLS and RMA) for each regression indicates some degree of departure from isometry (Table 4-2). However, the regression lines, log manus length, height and width against log claw weight, do not cross and the relative ranks to one another, which are maintained over the size range of interest (Fig. 4-3) and therefore conclusions drawn from ratios are still valid.

Second, I examined differences among species in each linear 'shape' variable for a given claw weight. Manus length and manus height are often used as a measure of 'size' independent of 'shape'. I tested the effect of species (fixed) and sex (fixed) on each 'shape' variable — log manus length, log manus height and log manus width — using the covariate claw weight as a measure of size (Table 4-3). Claws of *C. branneri* were excluded from these analyses, because its presence produces a 3-way interaction between sex, species, and the covariate, which precludes calculation of least-square means (ANCOVA table not shown, see Table 4-2 for individual regression lines). Least square means for the three linear "shape" variables were then computed for the five remaining species.

Manus height for a standardized claw weight (9.17 grams) fell into three groups (Fig. 4-4a and Table 4-3): *C. magister* and *C. antennarius* (average = 19.2 mm) > *C. productus* and *C. gracilis* (average = 18.6 mm) > *C. magister* (average = 17.1). Manus length for a standardized claw weight (9.2 grams) fell into four groups (Fig. 4-4 and Table 4-3): *C. magister* > *C. gracilis* and *C. productus* (average = 24.9 mm) > *C. antennarius* > *C. magister*. Clearly, for a given claw weight, manus height and manus length differed among the species. Furthermore, species that had a relatively high manus height to other species also had a relatively low manus length, and vice-versa, suggesting a trade-off between these two dimensions of the claw in these *Cancer* species.

Residual analyses of the deviations of manus height, manus length and manus width, from the regressions with claw weight revealed that among species, claws with a higher-than-expected manus height had a lower-than-expected manus length (Fig. 4-5a). Claws with a higher-than-expected manus width also had a lower-than-expected manus length (Fig. 4-5b). And, claws with a higher-than-expected manus width had a higher-than-expected manus height (Fig. 4-5c). Clearly, for a given claw weight, manus height and manus width were positively correlated, and both were negatively correlated with manus length. In other words, as manus height increases, for a given weight, the manus becomes more 'box'-like instead of rectangular.

The mechanical advantage of the dactyl: The relation between lever-1 and lever-2

If there was strong selection on mechanical advantage of the dactyl, we would expect a strong negative correlation between the length of the first lever arm and the length of the second lever arm. If a high bite force was being selected for, then for a given claw size we would expect a longer lever-1 and a shorter lever-2, and if a 'fast' claw was being selected for, then we would expect a shorter lever-1 and a longer lever-2. Intraspecific variation in lever-1 and lever-2 supports this association, and mechanical advantage increases with claw size for all six species (Chapter 3).

However, patterns of interspecific variation in lever-1 and lever-2 differed from intraspecific ones. For a standardized claw weight (7.56 grams), lever-1 length fell into three groups (Fig. 4-6a and Table 4-4a): *C. productus* and *C. branneri* > *C. antennarius*, *C. magister*, and *C. gracilis* > *C. magister* (Fig. 4-6a). For a standardized claw weight (7.56 grams), the species grouped as follows based on lever-2 length (Fig. 4-6b and Table 4- 4b): *C. magister* > *C. gracilis* and *C. branneri* > *C. productus* > *C. antennarius* > *C. oregonensis*. Clearly, for a given claw weight, lever-1 length and lever-2 length differed among the species. Though a slight trend was observed between increased lever-1 length and decreased lever-2 length, the relation was not consistent and species that had a higher lever-1 length did not always have a lower lever-2 length. This suggests there is not a direct trade-off between these two dimensions of the dactyl among species.

For among species, I further examined the existence of a trade-off between lever lengths, by analysis of the residuals of lever-1 and lever-2 lengths from the regressions with claw weight (Fig. 4-7). Claws with a higher-than-expected lever-1 also had a lower-than-expected lever-2 (Fig. 4-7b). However, the explained variation was low (r^2 = 0.050). Therefore, lever-1 was not highly negatively correlated with lever-2 among-species.

The relation between manus exoskeletal shape and muscle properties

I investigated the associations between manus shape and various claw attributes that contribute to biting force among species, using the ratio of manus height to manus length as a general indicator of manus shape. First, claws with a higher manus height-to-length ratio also had a higher apodeme height-to-length ratio (Fig. 4-8a). Therefore, the shape of the manus directly reflected the shape of the closer apodeme. Furthermore, claws with a higher manus height-to-length ratio also had higher mechanical advantage (Fig. 4-8b), a higher closer-muscle angle of pinnation (Fig. 4-8c), and a higher average closer-muscle A-band length (Fig. 4-8d). Clearly, as manus height increased relative to manus length, attributes associated with a 'strong' bite force also increased.

For all six species, fiber length was proportional to claw weight$^{0.350\pm0.0475}$ (RMA mean, ±SE), which was not significantly different from a slope of isometry (0.33) (Student t-test, df = 121, P = 0.614). Further variation in fiber length was explained by claw gape angle. Residuals from the regression log fiber length versus log claw weight were significantly correlated with log claw gape angle (Fig. 4-9b), which was measured at the pivot after fixation of the closer muscle. Though closer-muscle fiber length was correlated with claw weight, it did not vary among species for claws of the same weight (ANCOVA; $F_{2,122} = 1.354, P = 0.247$) (Fig 4-9a). Therefore, there was no association between manus height-to-length ratio and fiber length.

The beam strength of the pollex: the relation between second moment of area and the bending moment

For all six *Cancer* species, the axis of maximum moment of inertia (I_{max}) always bisected the horizontal plane of the pollex cross-section and dactyl cross-section, while the axis of the minimum moment of inertia (I_{min}) always bisected the sagittal plane of the pollex cross-section and the dactyl cross-section (Fig. 4-10). The pollex centroid was always closer to the occlusive surface than the ventral surface (Fig. 4-10). Likewise, the dactyl centroid was always closer to the occlusive surface than the upper dorsal surface (Fig. 4-10). Therefore, biting forces will tend to be applied perpendicular to the axis of I_{min}, and it is the second moment of area about this axis which will determine the breaking strength of the pollex; from here on I will refer to this simply as the ‘second moment of area’, following the convention of Wainwright *et al.* (1976).

Pollex height was a good predictor of the pollex second moment of area (see methods for specific location of measurements) (Fig. 4-11a). For a given pollex height, the second moment of area at the base of the pollex did not differ among species (Fig. 4-11a). Additional variation in second moment of area was explained by differences in overall cuticle thickness (Fig.11b).

If there was strong selection on the beam strength of the pollex, we would expect a strong negative correlation between pollex height at the base (i.e., second moment of area) and pollex length (bending moment). Furthermore, if the main force applied to the pollex was from biting, then we would expect the manus height-to-length ratio to be correlated with the pollex height-to-length ratio, since this measure of manus shape was a good predictor of the claw potential bite-force (Fig. 4-8), while the pollex height-to-length ratio should be a good predictor of the claw's potential breaking strength. For claws of six *Cancer* species, the pollex height-to-length ratio was correlated with the manus height-to-length ratio (Fig.4-12a). For a standard claw weight, pollex height was not correlated with the average manus height-to-length ratio (Fig. 4-12b), but pollex length was (Fig. 4-12c). Therefore, the pollex length appears to be under strong selection from the potential bite-force of the claw, while the pollex height does not. Pollex height and pollex length did not appear strongly correlated, independent of size. I confirmed this by analysis of residual deviations from regressions of pollex height versus claw weight, and pollex length versus claw weight (Fig. 4-13a,b and Table 4-6). Claws with a higher-than-expected pollex height did not have a lower-than-expected pollex length (Fig. 4-13c). Therefore, selection for traits other than increased beam strength may be acting on pollex shape.

Interestingly, when residuals of pollex height versus claw weight, and pollex length versus claw weight, were plotted against each other, the six *Cancer* species tended to separate out among the four quadrats defined by the *X* and *Y* axes (Fig. 4-13c). *Cancer magister* and *C. productus* tended to have a higher than expected pollex height combined with a lower than expected pollex length. *Cancer gracilis* and *C. magister* tended to have a higher than expected pollex height combined with a higher than expected pollex length. *Cancer branneri* tended to have a lower than expected pollex height combined with a higher than expected pollex length. *Cancer antennarius*, tended to have a lower-than-expected pollex height combined with a lower-than-expected pollex length. The clear separation of species along these two different axes (Fig. 4-13c) suggests that the selection pressures acting on pollex shape are unique for each species. However, the strong correlation between the length of the pollex and the average manus height-to-length ratio (Fig. 4-12c), suggests that pollex length is primarily influenced by selection for pollex beam strength that is appropriate for the claw's biting force.

The relation between claw shape and claw safety factors

I used the ratio of manus height to pollex length as a general indicator of overall claw shape. For claws from the safety factor experiment, manus height was isometric with pollex length (Fig. 4-14a) and therefore the ratio of manus height to pollex length should not be unduly affected by size. This ratio explained 41% of the variation in claw safety factors (breaking force/ median biting force) (Fig. 4-14b).

Discussion

The size of an organism is perhaps its most apparent characteristic and the influence of body size on many aspects of biology has have been extensively explored (Peters, 1983; Calder, 1984; Schmidt-Nielsen, 1984; LaBarbera, 1986; LaBarbera, 1989), while shape, though recognized as being functionally important (Wainwright *et al.*, 1976), has attracted less attention. The claws of decapods are no exception. Many have quantified relative claw size, among individuals and correlated size with several aspects of performance, including bite force (Elner & Campbell, 1981; Blundon, 1988; Levinton & Judge, 1993; Smith & Palmer, 1994), feeding (Zipser & Vermeij, 1978; Elner, 1980; Lawton, 1983; Kaiser, Hughes & Reid, 1990), and mate choice (Stein, 1976; Govind *et al.*, 1992; Claxton, Govind & Elner, 1994). Claw shape has been recognized as functionally important, particularly since many species have dimorphic claws (Elner, 1980; Elner & Campbell, 1981; Govind & Blundon, 1985; Seed & Hughes, 1997). However, few have extensively documented shape variation in relation to performance among individuals for several species, with the exception of the mechanical advantage of the claw (for exception see (Brown, *et al.*, 1979)). The size of a claw influences its claw safety factor (i.e., breaking force of the claw's pollex/maximum claw bite force) and with larger claws having higher safety factors than smaller claws within species (Chapter 2 & Appendix I). However, I have shown that between species the shape of the claw influences safety factors, independent of size, suggesting that selection pressures acting on performance influence claw shape.

I identified the critical variables of claw shape affecting the performance of the claw, both for biting force and for breaking strength. Manus shape reflected internal properties of the claw closer muscle that in turn determine the safety factor denominator, biting force. The shape of the dactyl, as described by its mechanical advantage, did not vary predictably among species and cannot explain safety factor variation; dactyl shape is likely affected by selection for traits other than biting force. Pollex shape reflected beam properties that partly determine the safety factor numerator, the force required to break the pollex. Overall, the ratio of manus height and pollex length was a very good predictor of among-species variation in claw safety factors, suggesting that the selection pressures acting on claw performance particularly affect these two shape variables.

Manus shape and claw muscle characteristics

For a given claw size, the shape of the manus strongly reflected the potential bite force of the claw. Increases in manus height and manus width, and decreases in manus length, were associated with increased angles of pinnation and increased average sarcomere length. For a given volume of muscle, a higher angle of pinnation will increase the effective cross sectional area of the muscle (Alexander, 1968), thereby increasing bite force. In addition, for a given volume of muscle, longer sarcomere lengths will produce greater contraction forces because longer sarcomere lengths indicate more actin-myosin bridges acting in parallel (Gordon, Huxley & Julian, 1966; Jahromi & Atwood, 1969; Josephson, 1975) (see Appendix 2). Therefore, claws with higher manus heights and manus widths, and lower manus lengths, had higher potential bite-forces.

The association between increased manus height and the muscle properties which augment biting force may reflect the need to increase claw gape when there is selection for high biting force. The effective biting force of a claw can be increased by maximizing mechanical advantage, by placing the item to be crushed most proximally within the 'grip' of the claw (Elner, 1978; Brown, *et al.*, 1979). The ability to position the prey with the highest mechanical advantage 'grip', will depend on the claw gape. Claw gape, in turn, is limited by the manus height. Thus, under selection for high biting forces, we expect to see increases in sarcomere length and angle of pinnation concurrent with increases in claw gape which would, in turn, necessitate increases in manus height.

The positive correlation between manus height and manus width, and their joint association with increased potential biting force, may derive from a curious constraint: constant muscle fiber lengths. Increased manus width relative to other species was directly associated with increases in the angle of pinnation, since, for a give claw size, the fiber length remained constant among the six *Cancer* species. For a given claw weight, I predicted increases in fiber length to be correlated with longer manus lengths relative to other species, since 'slender' claws are considered 'fast' (Warner, 1977), and since increased fiber lengths will produce higher speeds of contraction (Josephson, 1975). However, fiber length remained constant among the six *Cancer* species. Under conditions of a constant fiber length, the only effective way of increasing the angle of pinnation will be to increase the width of the manus. And, under selection for strong biting forces and with constant fiber lengths, increasing angles of pinnation will be associated with increasing claw width. Therefore, for *Cancer* crabs, the external manus width predicts the angle of pinnation

Finally, I observed that manus height, manus width, and muscle properties, were negatively correlated with manus length. There is no direct biomechanical reason that decreasing manus length should be associated with increasing biting force. Likely, the negative correlation between manus length and biting force-enhancing properties simply reflects limits on the total claw size that can be achieved, for example because of energetic limitations, or because of declining muscle stress with increasing claw size (Chapter 3).

Thus, selection for high biting forces appears to result in greater sarcomere lengths and angles-of-pinnation, as well as higher manus height to increase claw gape. Constant fiber length necessitates that as angles-of-pinnation increase, so does manus width. Hence, there is a positive correlation between manus height and manus width. Finally, possibly because of constraints on total claw size, greater manus height and manus width are associated with reduced manus length.

Mechanical advantage of claws

Among the six *Cancer* species studied, variation in the mechanical advantage of the dactyl appears to result from selection pressures on factors other than maximal bite-force. Although mechanical advantage was correlated with other traits associated with strong bite forces, as noted for other decapod species (for review see Vermeij, 1987), the length of lever-1 was not highly correlated with the length of lever-2. In other words, for among species, crabs with a long lever-1 length did not necessarily posses a short lever-2 length. The lever-2 length is likely influenced by selection to increase the breaking strength of the claw dactyl. Both the dactyl and pollex will be under selection pressure not to break, since the cost of breaking a claw is high, and may include reduced feeding efficiency, reduced ability to obtain mates, and considerable time invested in regenerating a new claw (Juanes & Hartwick, 1990; Brock & Smith, 1998). Lack of correlation between the length of lever-1 and the length of lever-2 thus most likely arises because the length of lever-2 is influenced by a different, conflicting selection pressure: increasing resistance to failure.

In part, my results agrees with others (Brown *et al.*, 1979) who have argued against the use of simple categories, (i.e., ‘strong’ and ‘fast’) to infer bite-force for a given body size and to describe the morphological variation observed among decapod claws. Brown *et al.*, (1979) have shown qualitatively that the shape of the dactyl, and the contact areas between occlusive regions along the dactyl and pollex, can vary independently of the mechanical advantage. For a given muscle type, mechanical advantage determines the force at the end of second lever arm, however, the contact area between the occlusive regions of the dactyl and pollex determine the pressure of the resultant force (Brown, *et al.*, 1979). Occlusive surfaces vary tremendously among brachyuran crabs and do not fit into a simple dichotomy of 'crusher' and 'cutter' or 'strong' and 'fast'. Claws must be considered polyfunctional, rather than simple machines that either close with great force or with great speed. Likewise the claws of *Cancer* crabs are characterized by a continuum, lying somewhere between these two biomechanical extremes of 'strong' and 'fast'.

Beam strength of the pollex

Paralleling the variation seen in the dactyl lever lengths, the pollex height and the pollex length were not highly correlated among the six *Cancer* species. Therefore, the shape of the pollex is apparently not under the single selection pressure to resist breaking from a constant applied load perpendicular to the axis of minimum moment of inertia (as measured, see Fig. 4-1). Furthermore, the pollex height did not correlate with the manus height-to-length ratio, which serves as a measure of the potential biting force of the claw. Most likely, the height of the pollex is being limited by selection to maximize claw gape (as defined in 'Manus Shape and Claw Muscle Characteristics'). Increasing claw gape and pollex height simultaneously is not possible and crabs specializing on hard shell prey are faced with the following dilemma: either increase claw gape to maximize mechanical advantage, or increase pollex height to resist breaking under the reaction force from a 'strong' bite-force. This inherent conflict in claw design will be mitigated by the degree of specialization on hard-shelled prey, and by the alternative methods of attack employed by crabs. Thus, among species, the pollex height, relative to claw weight, appears to be influenced by unique selection pressures acting independently on each species (Fig. 4-13c).

In contrast, the unique selection pressure acting on the pollex length was identifiable, since pollex length was strongly correlated with the manus height-to-length ratio, which reflects biting force properties (i.e., angle of pinnation and sarcomere length). With increased potential bite force of the claw there was a corresponding decrease in the length of the pollex, which would minimize stresses experienced under bending. Therefore, the length and beam-strength of the pollex were strongly influenced by the potential bite-force of the claw.

The shape-dependence of claw safety factors

Clearly, manus height and pollex length are important shape variables that predict overall claw performance. The ratio of the two was strongly correlated with the claw safety factors (Fig. 4-14b); claws with higher manus heights and lower pollex lengths relative to claw weight had higher claw safety factors. It may be possible to take any length and any height measure of the claw, which would appropriately reflect a 'stout' or a 'slender' claw, and produce a correlation with the observed safety factors. However, manus height has a functional relationship with the bite-force of the claw, and pollex length has a functional relationship with the breaking strength of the claw, independent of size. Thus, the ratio of these two variables is the best morphological indicator of claw performance.

First, manus height is a good predictor of bite force among six *Cancer* species, as manus height measures the overall size of the muscle (Chapter 3). In addition, as shown here, manus height relative to claw weight also reflected angles of pinnation and sarcomere lengths. Variation in the size, shape and type of muscle will result in different contraction forces that can be described as:

$$\mathbf{F_{in} = S * (A * \sin 2\Theta)}$$

where the force generated at the tip of the apodeme ($\mathbf{F_{in}}$) depends on the muscle stress (S), the area of the apodeme (A), and the angles the fibers insert on the apodeme (Θ). Most importantly, the apodeme area (A) describes both a component of size and a component of the effective cross sectional area. The effective muscle cross-sectional area is determined by both the apodeme area (A) and the angle of pinnation (Θ). The muscle stress (S) is directly proportional to the resting sarcomere length, both for isolated muscle preparations (Gordon, Huxley & Julian, 1966; Jahromi & Atwood, 1969; Atwood, 1973; West, Humphris & Stephenson, 1992), and over a wide range of taxa and muscle types

(Appendix 2)(but see Chapter 3 for the effects of size on stress). Therefore, both absolute and manus height relative to body size were good predictors of biting strength, because they were highly correlated with apodeme area (A), and with angle of pinnation (Θ) and potential muscle stress (S), respectively.

The length of the pollex only describes one aspect of the beam strength of the pollex. However, it appears to be one of the most critical factors in determining pollex breaking strength in an among species analysis. The beam strength of the claw can be described as:

$$\sigma = \underline{F}_b * \underline{r}_c * \underline{M}_P\ \underline{I}^{-1}$$

where the bending stress (force per unit area) generated at the base of the pollex (σ) depends on the bending force ($\underline{F}_b$), the location of the force along the length of the pollex (bending moment, $\underline{M}$), the second moment of area of the cross sectional area of the pollex base ($\underline{I}$) and the radius of the second moment of area taken from the center of the centroid to the outer circumference towards the occlusive surface. For a given cuticle strength, 'strong' claws should minimize σ by maximizing $\underline{I}$ and minimizing $\underline{F}_b$, $\underline{r}_c$, and $\underline{M}$. Consider the claws of *C. magister*: for a standard claw size of 6 grams, average bite force of 41.2 Newtons, centroid radius of 3.3 mm, bending moment of 16.0 mm, and second moment of area of 80.7 mm^4, the bending stress at the base of the pollex would be 27.0 N mm^{-2}. Now consider the stress if a similar-sized claw of *C. magister* had the same pollex length relative to claw weight as a claw of *C. oregonensis*, and all other factors remain constant. For a 6 gram claw, a male *C. oregonensis* was predicted to have a pollex length of 5.0 mm, which was about 3 times less than the pollex length of *C. magister*. The resulting bending stress of a *C. magister* pollex with the length of a *C. oregonensis* claw would be 8.4 N mm^2, which is about a 3.4 fold reduction in bending stress acting on the base of the pollex. Thus, changes in pollex length alone can lead to significant, and disproportionate, changes in bending stress.

Furthermore, consider the safety factor of the pollex as the ratio of the calculated ultimate cuticle stress which induces breaking (Palmer *et al.*,1999) to the experienced bending stress for the mean bite force. Notice that by varying only the pollex length, and keeping all other factors constant, calculated pollex safety factors can vary tremendously. And, the variation reflects that observed among safety factors of the six *Cancer* species calculated using actual bite-forces and actual breaking strengths of the pollex (Chapter 2). Thus, for claws of *C. magister* for a standard claw weight of 6 grams (approx. 30 mm manus length), the approximate ultimate cuticle stress would be about 70 N mm^{-2} (see Figure AI-3, in Appendix I) and the stress experienced under mean biting forces would be 27.0 N mm^{-2} (as calculated previously). Therefore, the safety factor of the pollex would be 2.6. For a *C. magister* claw with the equivalent pollex length of *C. magister*, the estimated stress experienced under mean biting forces was 8.4 N mm^2, producing a safety factor of 8.3. Actual mean, size-adjusted safety factors for *C. magister* and *C. magister* were 2.6 and 7.4 respectively, as calculated from individual variation in bite-force and break force for claws (Chapter 2). Thus, variation in pollex length likely plays an important role in determining claw safety factors. Overall, the manus height to pollex length ratio is the best measure of claw shape which reflects claw performance and explains interspecific variation in claw safety factors.

Conclusion

Others working on crab foraging behavior have suggested that the size and shape of the claw is a template determining feeding habits and prey preferences (Elner, 1978; Elner, 1980; Lawton & Elner, 1985). This suggestion derives from the observation that for species of crabs that are dimorphic in claw size and shape, differences in exoskeletal traits of claws have been correlated with differences in underlying muscle properties (Govind & Lang, 1974; Warner & Jones, 1976; Elner, 1978). In addition, differences in exoskeletal traits are correlated with behavioral differences, such that ‘strong’ claws are used for crushing and ‘fast’ claws are used for manipulating and tearing flesh (Elner, 1978; Elner, 1980). My work supports this proposition, and provides a more in-depth, quantitative approach to defining the claw-template. Clearly, future assessment of the decapod claw ‘template’ must measure manus properties independent of finger (i.e., pollex and dactyl) properties, since the manus shape reflects underlying muscle properties, while the dactyl and pollex reflect lever and beam-strength properties respectively.

Claw design appears very specific for each *Cancer* species, but varies in a highly predictable fashion along a ‘strong’ and ‘fast’ claw continuum. However, over the continuum there was an ‘envelope’ by which variation in claw properties could vary. For example, claws of *C. productus* had a very high mechanical advantages compared to the other five species, yet they also had relatively low angles of pinnation. Does this suggest that claws are polyfunctional as suggested by Brown *et al.*, (1979) and Lee & Seed, (1992)? Or, does it mean we should look beyond the 'crusher'-'cutter' dichotomy, at the variety of feeding tactics used by crabs in association with variation in claw design? Now that we have identified some of the critical traits involved in defining a claw template we can look more closely at feeding behavior in association with these traits to discriminate among these possible hypotheses.

Table 4-1. Results from ANCOVAs testing the effects of shape variable and sex on linear measures of claw size, with claw weight as the covariate.

Species Source	df	*MS*	*P*	Species Source	df	*MS*	*P*
1) *C. antennarius*				2) *C. branneri*			
SHP	2	0.201	<0.001	SHP	2	0.260	<0.001
Sex	1	0.001	0.024	CWt	1	0.179	<0.001
CWt	1	2.401	<0.001	SHP*CWt	2	0.000	0.526
SHP*Sex	2	0.000	0.836	Error	90	0.000	
SHP*CWt	2	0.000	0.205				
Sex*CWt	1	0.001	0.030				
SHP*Sex*CWt	2	0.000	0.824				
Error	153	0.000					
3) *C. gracilis*				4) *C. magister*			
SHP	2	0.052	<0.001	SHP	2	0.022	<0.001
Sex	1	0.000	0.177	Sex	1	0.000	0.394
CWt	1	0.223	<0.001	CWt	1	0.132	<0.001
SHP*Sex	2	0.000	0.712	SHP*Sex	2	0.000	0.610
SHP*CWt	2	0.000	0.137	SHP*CWt	2	0.000	0.631
Sex*CWt	1	0.000	0.400	Sex*CWt	1	0.000	0.244
SHP*Sex*CWt	2	0.000	0.702	SHP*Sex*CWt	2	0.000	0.695
Error	99	0.000		Error	147	0.000	
4) *C. oregonensis*				6) *C. productus*			
SHP	2	0.340	<0.001	SHP	2	0.140	<0.001
Sex	1	0.000	0.936	Sex	1	0.000	0.109
CWt	1	0.073	<0.001	CWt	1	1.804	<0.001
SHP*Sex	2	0.001	0.007	SHP*Sex	2	0.000	0.906
SHP*CWt	2	0.000	0.737	SHP*CWt	2	0.000	0.639
Sex*CWt	1	0.000	0.629	Sex*CWt	1	0.000	0.914
SHP*Sex*CWt	2	0.000	0.564	SHP*Sex*CWt	2	0.000	0.375
Error	99	0.000		Error	81	0.000	

SHP = the shape variables ($\log_{10}$ -manus length, $\log_{10}$ -manus height,& $\log_{10}$ -manus width), Sex = male and female, CWt = $\log_{10}$-claw wet weight (g; the covariate)

Table 4-2. Scaling of 3 linear claw measures with claw weight.

		OLS		RMA		
Species	n	Slope(±SE)	Intercept	Slopes	P	r^2
a) log (manus height) (Y) vs. log (claw weight) (X)						
1. *C. antennarius*	55	0.328(0.005)	1.065(0.004)	0.329	<0.001	0.994
2. *C. branneri*	32	0.295(0.016)	1.048(0.004)	0.308	<0.001	0.921
3. *C. gracilis*	37	0.345(0.031)	1.046(0.018)	0.349	<0.001	0.978
4. *C. magister*	52	0.296(0.052)	1.042(0.047)	0.302	<0.001	0.960
5. *C. oregonensis*	37	0.363(0.026)	1.077(0.004)	0.378	<0.001	0.921
6. *C. productus*	64	0.336(0.004)	1.060(0.002)	0.336	<0.001	0.997
7. All combined*	245	0.328(0.002)	1.063(0.003)	0.329	<0.001	0.993
b) log (manus length) (Y) vs. log (claw weight) (X)						
1. *C. antennarius*	55	0.323(0.006)	1.117(0.005)	0.324	<0.001	0.992
2. *C. branneri*	32	0.309(0.015)	1.144(0.004)	0.319	<0.001	0.933
3. *C. gracilis*	37	0.335(0.025)	1.170(0.015)	0.338	<0.001	0.987
4. *C. magister*	52	0.321(0.039)	1.222(0.035)	0.325	<0.001	0.976
5. *C. oregonensis*	37	0.318(0.020)	1.059(0.003)	0.330	<0.001	0.928
6. *C. productus*	64	0.339(0.003)	1.172(0.002)	0.340	<0.001	0.998
7. All combined*	245	0.331(0.002)	1.175(0.002)	0.331	<0.001	0.997
c) log (manus thickness) (Y) vs. log (claw weight) (X)						
1. *C. antennarius*	55	0.332(0.007)	0.853(0.005)	0.334	<0.001	0.9899
2. *C. branneri*	32	0.323(0.020)	0.828(0.005)	0.340	<0.001	0.8982
3. *C. gracilis*	37	0.295(0.029)	0.837(0.17)	0.298	<0.001	0.9774
4. *C. magister*	52	0.265(0.041)	0.852(0.037)	0.269	<0.001	0.9719
5. *C. oregonensis*	37	0.305(0.003)	0.847(0.003)	0.314	<0.001	0.9413
6. *C. productus*	64	0.325(0.003)	0.825(0.002)	0.325	<0.001	0.9975
7. All combined*	--	--	--	--	--	--

OLS = ordinary least square; RMA = reduced major axis

*Common slope from a two-factor ANCOVA with species and sex as the grouping variable

Table 4-3. Results from ANCOVAs testing effects of species (fixed effect) and sex (fixed effect) on the dependent variables a) $\log_{10}$-manus height (mm), b) $\log_{10}$-manus length and c) $\log_{10}$-manus width. The covariate was $\log_{10}$-claw wet weight (g).

a) $\log_{10}$-manus height (mm)

Source	df	*MS*	*P*
Spp	4	0.007	<0.001
Sex	1	0.000	0.762
CWt	1	2.943	<0.001
Spp*Sex	4	0.000	0.078
Error	113	0.000	

b) $\log_{10}$-manus length (mm)

Source	df	*MS*	*P*
Spp	4	0.077	<0.001
Sex	1	0.000	0.512
CWt	1	3.043	<0.001
Spp*Sex	4	0.001	0.006
Error	132	0.000	

c) $\log_{10}$-manus width (mm)

Source	df	*MS*	*P*
Spp	4	0.007	<0.001
Sex.a	1	0.000	0.159
CWt	1	0.701	<0.001
Spp * Sex	4	0.001	0.003
Spp*CWt	4	0.000	0.023
Sex*CWt	1	0.001	0.017
Spp*Sex*CWt	4	0.001	0.001
Error	185	0.000	

Spp = *C. antennarius, C. gracilis, C. magister, C. oregonensis, and C. productus.*

Sex = male and female

Table 4-4. Results from ANCOVAs testing effects of species (fixed) and sex (fixed) on the depedent variables a) $\log_{10}$-Lever 1, and b) $\log_{10}$-Lever 2, using $\log_{10}$-claw weight as the covariate.

a) $\log_{10}$-Lever 1				b) $\log_{10}$-Lever 2			
Source	df	*MS*	*P*	Source	df	*MS*	*P*
Spp	5	0.062	<.001	Spp	5	0.062	<.001
Sex	1	0.007	0.000	Sex	1	0.007	0.000
CWt	1	4.725	<.001	CWt	1	4.725	<.001
Spp*Sex	5	0.002	0.004	Spp*Sex	5	0.002	0.004
Error	273	0.001		Error	272	0.001	

Spp = *C. antennarius, C. branneri, C. gracilis, C. magister, C. oregonensis, C. productus.*

Sex = male and female

CWt = $\log_{10}$-claw wet weight

Table 4-5. Results from ANCOVAs testing effects of species (fixed) and sex (fixed) on the depedent variables a) log10-pollex height, and b) log10-pollex length for six Cancer species. c) Results from an ANCOVA, 2 species (*C. gracilis* and *C. productus*) removed from the ANCOVA model in b)(see Table 4-6 for species and common regression equations).

a) log-pollex height (mm)

Source	df	MS	P
Spp†	5	0.059	<0.001
Sex	1	0.000	0.440
CWt	1	3.870	<0.001
Spp†*Sex	5	0.001	0.361
Error	270	0.001	

b) log-pollex length (mm)

Source	df	MS	P
Spp†	5	0.039	<0.001
Sex	1	0.000	0.449
CWt	1	0.004	0.019
Spp†*Sex	5	0.012	<0.001
Spp†*CWt	5	0.005	<0.001
Sex*CWt	1	0.000	0.834
Spp†*Sex*CWt	5	0.002	0.018
Error	261	0.001	

c) log-pollex length (mm)

Source	df	MS	P
Spp¥	3	0.413	<0.001
Sex	1	0.012	<0.001
CWt	1	1.057	<0.001
Spp¥*Sex	3	0.022	<0.001
Error	175	0.001	

Spp† = *C. antennarius, C. branneri, C. gracilis, C. magister, C. oregonensis, & C. productus*

Spp¥ = *C. antennarius, C. branneri, C. magister, & C. oregonensis.*

Sex = male and female

CWt = $\log_{10}$-claw wet weight

Table 4-6. Regression statistics for the association between claw weight and pollex height and length for six species of *Cancer* (Isometry = 0.333).

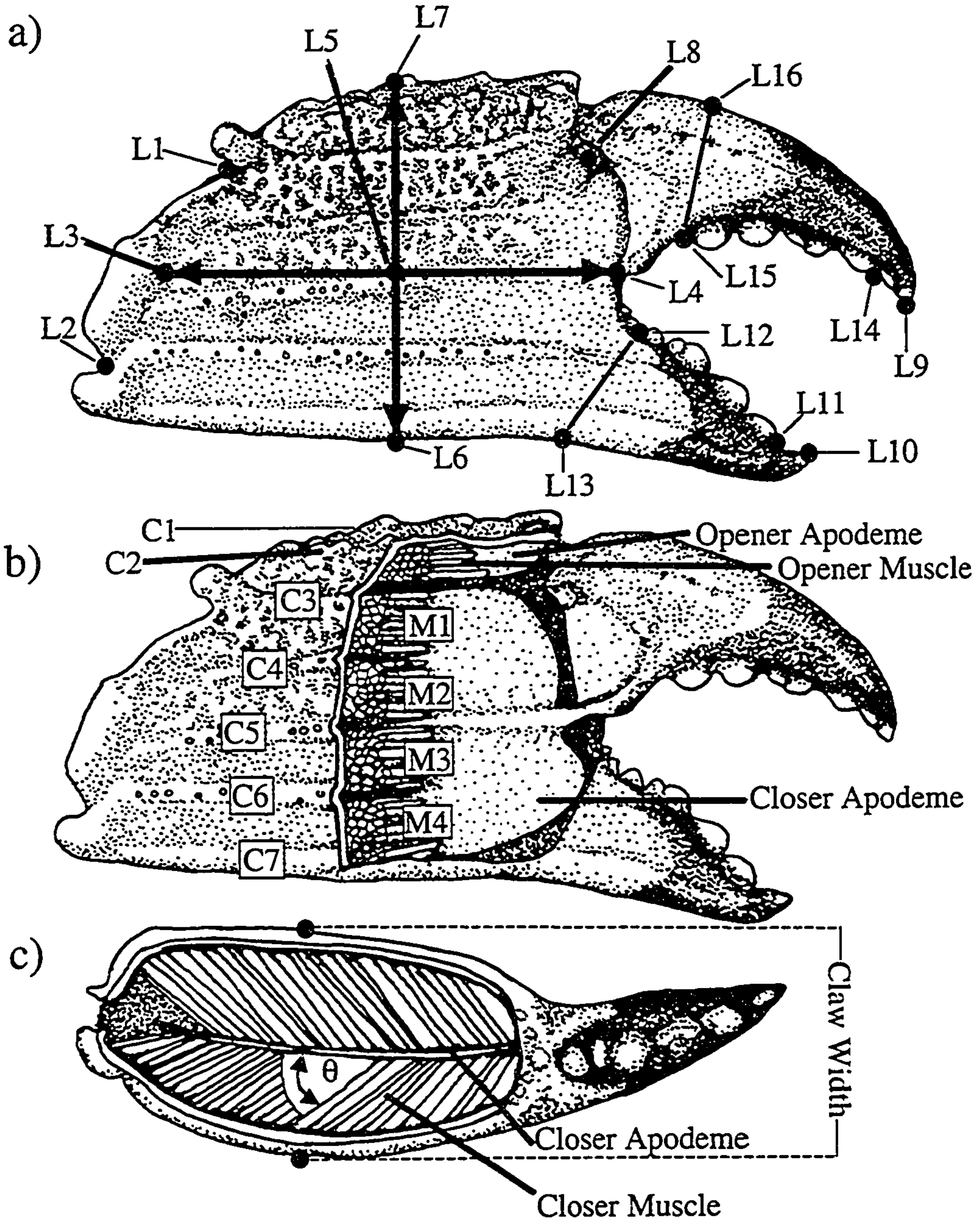
Species	*n*	Slope (±SE)	P_{OLS}	Intercept (±SE)	r^2	RMA	P_{RMA}	Allometry
a) log (pollex height) (<u>Y</u>) vs. log(claw weight) (<u>X</u>)								
1) *C. antennarius*	55	0.311(0.009)	<0.001	0.633(0.008)	0.979	0.325	0.370	Isometric
2) *C. branner*	32	0.214(0.044)	<0.001	0.621(0.011)	0.443	0.321	0.791	Isometric
3) *C. gracilis*	37	0.351(0.010)	<0.001	0.664(0.008)	0.972	0.356	0.027	Positive
4) *C. magister*	52	0.338(0.013)	<0.001	0.673(0.013)	0.936	0.350	0.188	Isometric
5) *C. oregonensis*	43	0.296(0.032)	<0.001	0.723(0.005)	0.673	0.361	0.396	Isometric
6) *C. productus*	64	0.334(0.005)	<0.001	0.662(0.004)	0.988	0.336	0.577	Isometric
7) Common†	283	0.328(0.004)	<0.001	0.665(0.004)	0.975	0.332	0.803	Isometric
b) log (pollex length) (<u>Y</u>) vs. log(claw weight) (<u>X</u>)								
1) *C. antennarius*	55	0.280(0.011)	<0.001	0.776(0.009)	0.927	0.291	<0.001	Negative
2) *C. branner*	32	0.267(0.025)	<0.001	0.856(0.006)	0.793	0.300	0.192	Isometric
3) *C. gracilis*	37	0.365(0.011)	<0.001	0.846(0.008)	0.970	0.371	<0.001	Positive
4) *C. magister*	52	0.329(0.011)	<0.001	0.934(0.012)	0.943	0.338	0.637	Isometric
5) *C. oregonensis*	45	0.177(0.058)	0.004	0.655(0.010)	0.180	0.418	0.149	Isometric
6) *C. productus*	64	0.348(0.005)	<0.001	0.740(0.005)	0.987	0.350	<0.001	Positive
7) Common¥	184	0.295(0.009)	<0.001	0.707(0.007)	0.985	0.297	<0.001	Negative

N = sample size; SE = standard error; Slope = slope of the ordinary least square (OLS); P_{OLS} = probability that OLS slope deviates from zero; Intercept = intercept of the ordinary least square; r^2 =coefficient of determination; RMA slope of the reduced major axis; P_{RMA} = probability that ovserved RMA slope deviates from isometry (t-test)

Common† = regression equation for all of the six *Cancer* species combined

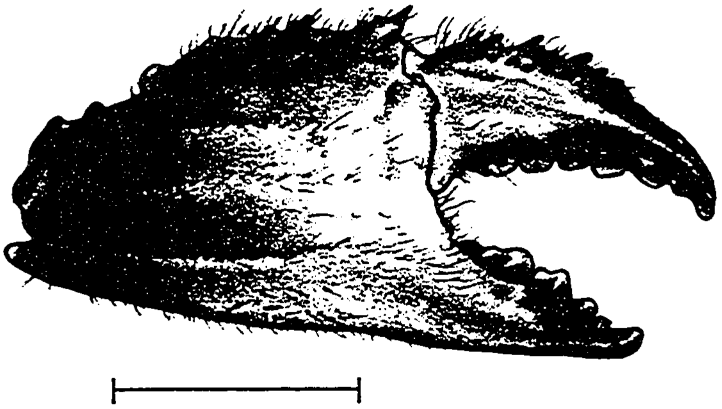
Common¥ = regression equation for *C. antennarius, C. branneri, C. magister,* & *C. oregonensis.*

Figure 4-1. Measurements of exoskeletal and muscle morphology. a) Landmarks used for derived external linear measurements: L1 = upper manus hinge, L2 = lower manus hinge, L3 = mid-point between L1 and L2, L4 = intersection between the manus and the base of the dactyl, L5 = mid-point between L3 and L4, L6 = intersection between the manus ventral edge and a perpendicular line to the line L3 to L4 with the base at L5, L7 = intersection between the manus dorsal edge and a perpendicular line to the line L3 to L4 with the base at L5, L8 = dactyl pivot, L9 = tip of dactyl, L10 = tip of pollex, L11 = first occlusive valley behind tip of pollex, L12 = valley of last active tooth on pollex, L14 = first occlusive valley behind tip of dactyl, L15 = valley of last active tooth on dactyl. Manus length is from L3 to L4. Manus height is from L6 to L7. The first lever arm (L_1) is from L4 to L8 and the second lever arm (L_2) is from L8 to L9. The ratio of these two lever lengths L_1/ L_2 is the mechanical advantage of the claw. The 'gape-angle' of the claw is measured at L8 and is defined by the triangle of the three landmarks, L10 to L8 to L9. The length of the pollex was measured from L11 to L12. The pollex height L12 to L13 refers to the perpendicular line to the line represented by L11 to L12. The dactyl height L15 to L16 refers to the perpendicular line to the line represented by L14 to L15. The lines for pollex and dactyl height indicate where cuticle cross-sections were taken. b) A claw partially dissected with the closer and opener muscles revealed and their associated apodemes. The exoskeletal carinae, C1 to C7 {defined by Nations (1975)}, run in a proximo-distal direction along the manus and clearly define the muscle regions below the cuticle. The closer muscle regions sampled are M1 to M4. c) A claw dissected along its mid-sagittal plane just below the fifth carina. In view is the ventral portion of the manus with the pollex. Θ = 'angle-of-pinnation'. Claw width was measured at the approximate mid region of the claw represented by the line L6 to L7 in a).


a)
L7
L5
L8
L16
L1
L3
L2
L4
L15
L12
L14
L9
L11
L10
L6
L13
b)
C1
C2
Opener Apodeme
Opener Muscle
C3
C4
C5
C6
C7
M1
M2
M3
M4
Closer Apodeme
c)
θ
Claw Width
Closer Apodeme
Closer Muscle

a) *C. antennarius*

b) *C. branneri*



c) *C. gracilis*

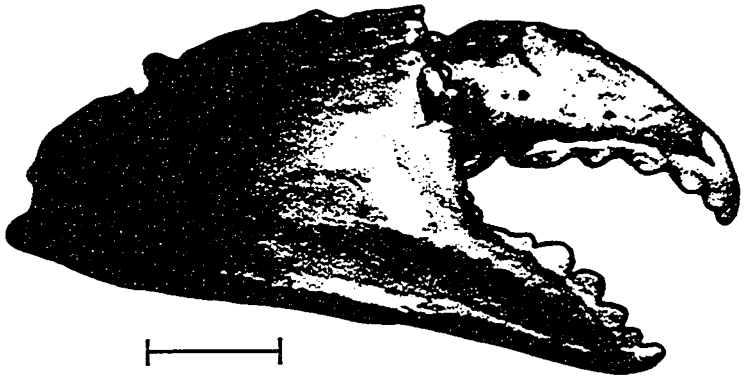
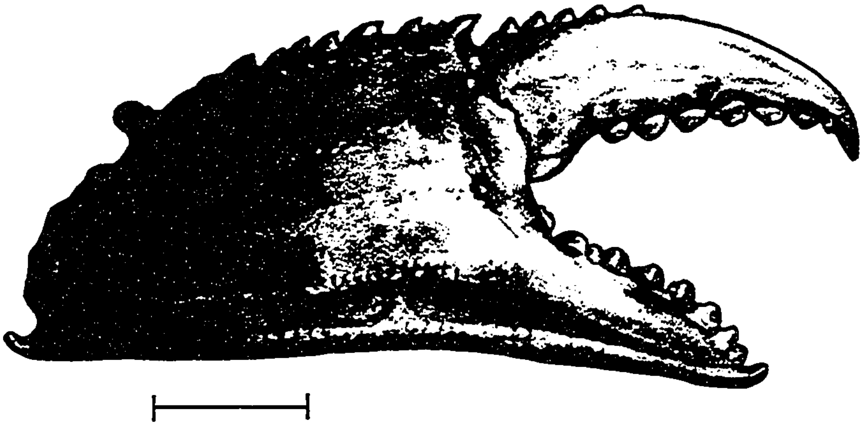
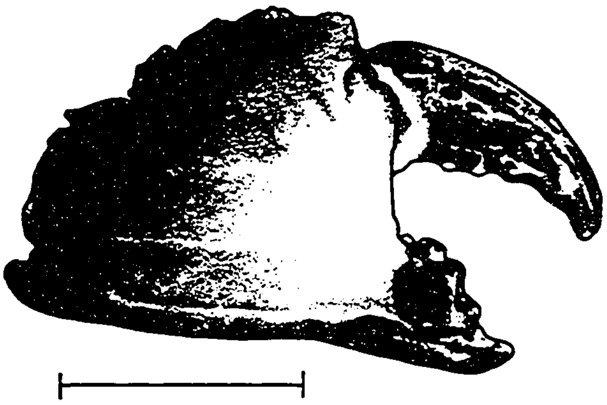


Figure 4-2. Diagrams of claws of the six species of Cancer crabs (see also following page). Scale bars are 10 mm.

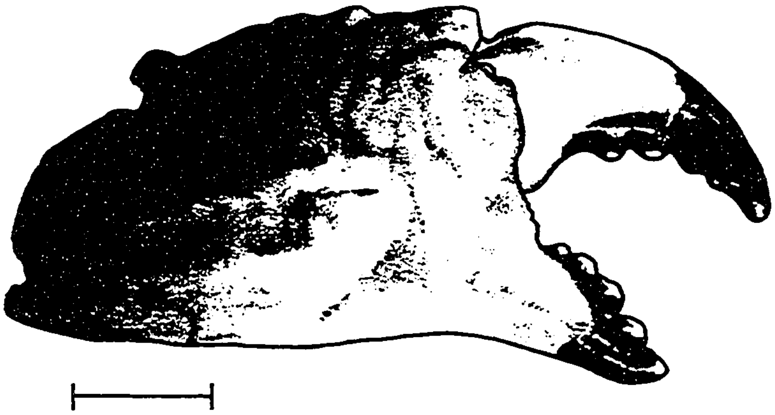
d) *C. magister*



e) *C. oregonensis*



f) *C. productus*



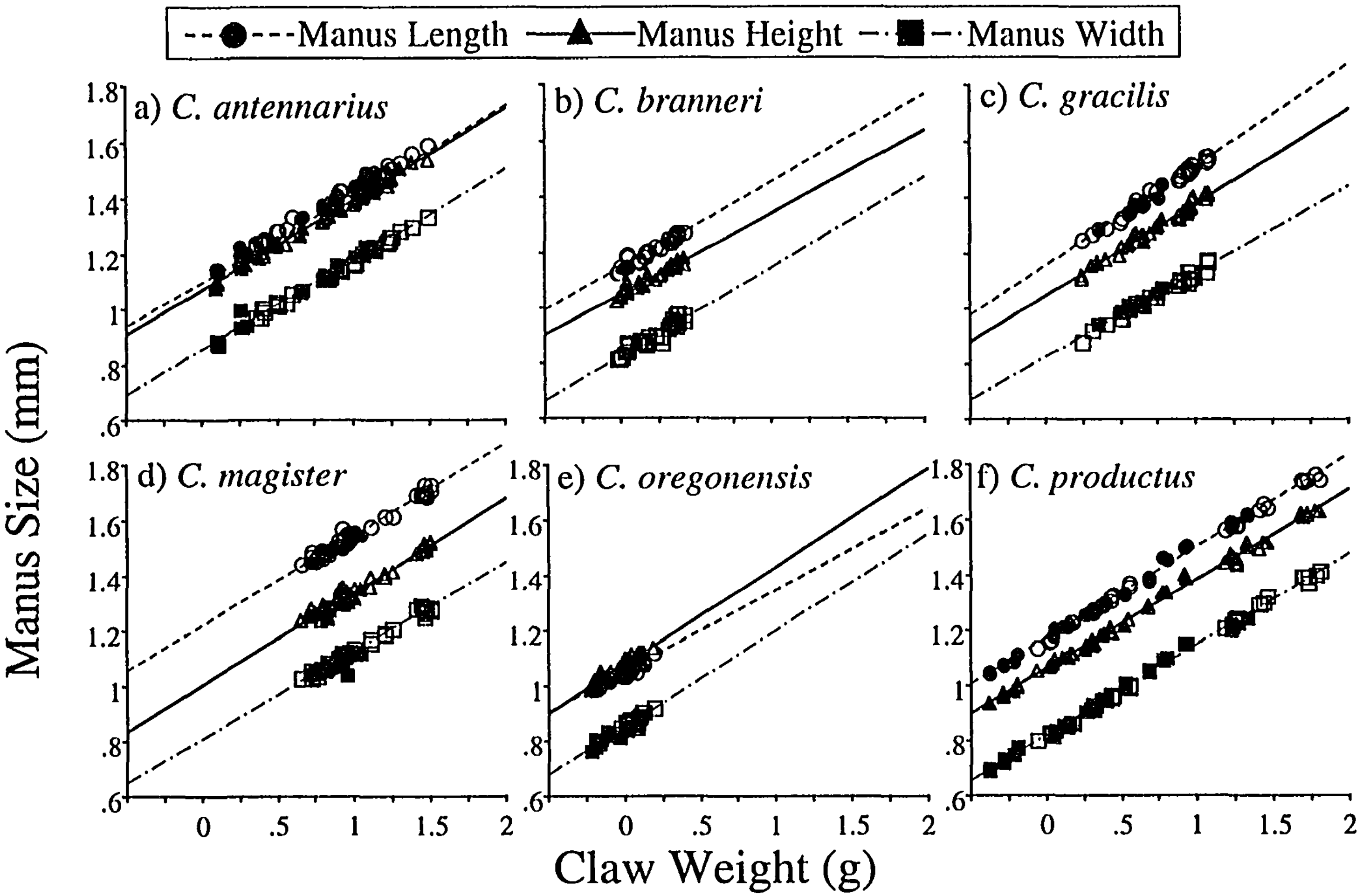


Figure 4-3. Association between log-claw wet weight (grams) and 3 linear measures of the manus: log-manus length (mm), log-manus height (mm) and log-manus width (mm), for claws of all six *Cancer* species. Open symbols are female and closed symbols are male. All lines are least square linear regressions. See Table 4-2 for regression statistics.

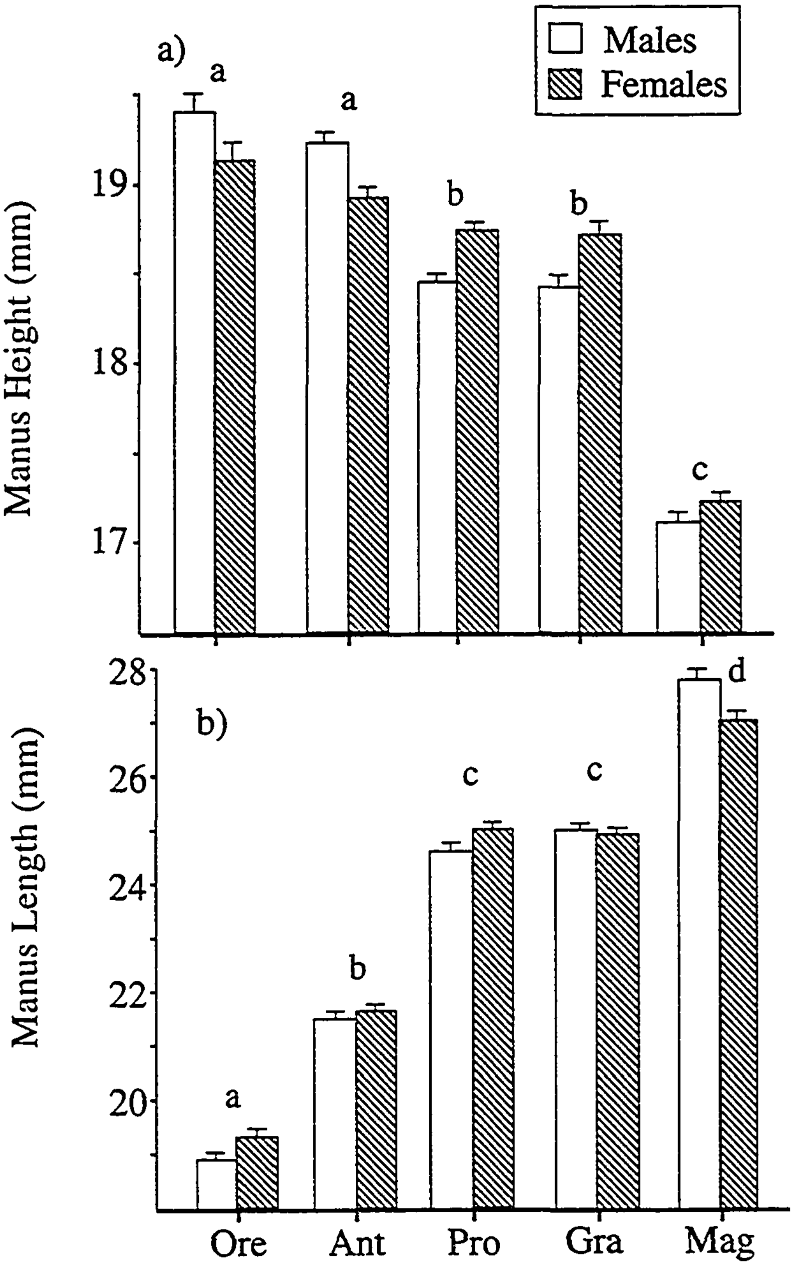


Figure 4-4. Size-adjusted means of a) manus height, and b) manus length, for each species and sex, excluding *C. branneri*. All were computed using a single ANCOVA with a common slope for a standard claw weight of 9.17 grams. For species effects only, letters identify groups of least-square means that did not differ significantly after a sequential Bonferroni adjustment on *P* values. Ore = *C. oregonensis*, Ant = *C. antennarius*, Pro = *C. productus*, Gra = *C. gracilis*, Mag = *C. magister*.

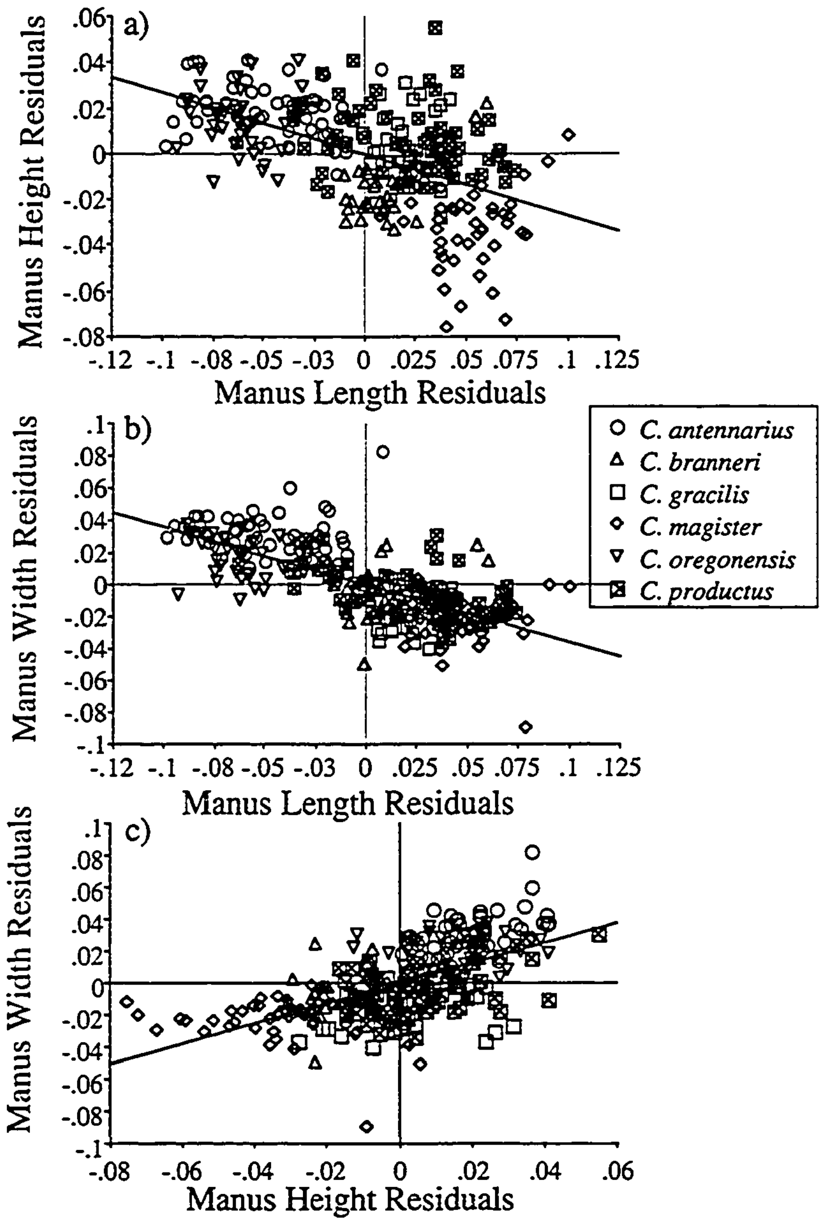


Figure 4-5. Correlations between a) manus height residuals and manus length residuals ($P < 0.001$, $r^2 = 0.313$), b) manus width residuals and manus length residuals ($P < 0.001$, $r^2 = 0.509$) and c) manus width residuals and manus height residuals ($P < 0.001$, $r^2 = 0.369$) for claws of all six *Cancer* species. All residuals were computed as deviations from a single regression fit to pooled data of all six species. Solid lines indicate least square linear regressions.

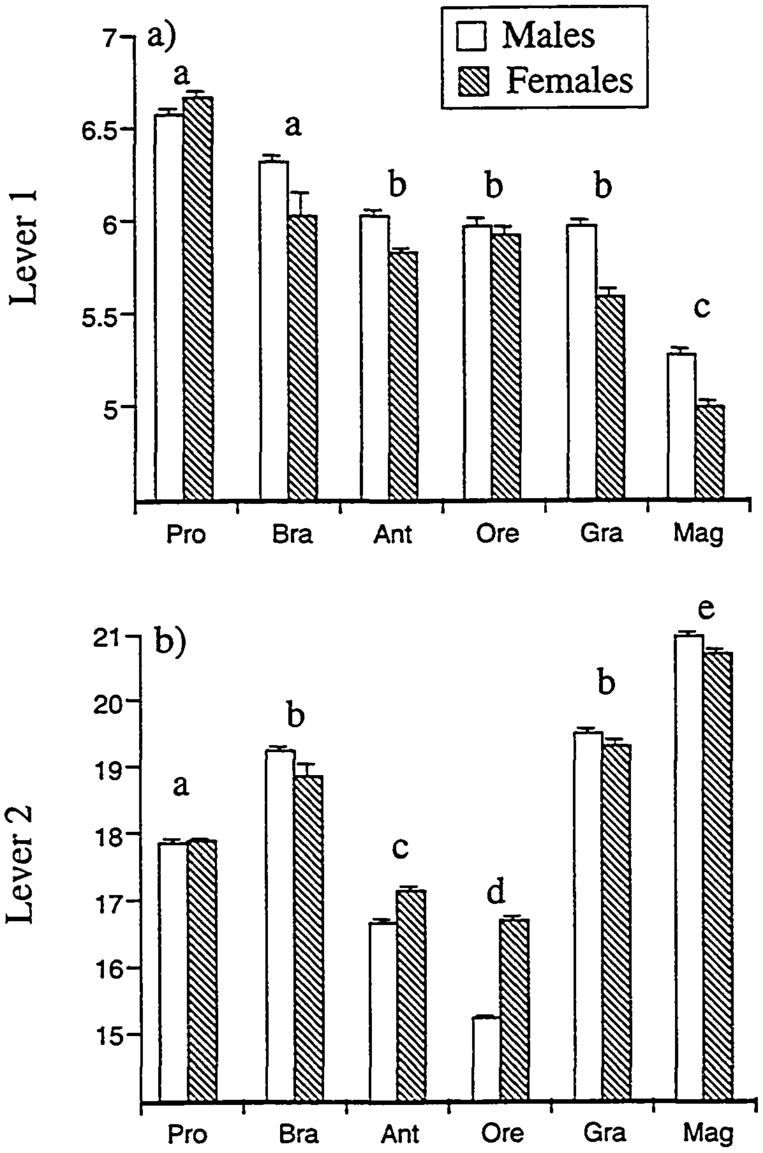


Figure 4-6. Size-adjusted means of a) lever-1 lengths, and b) lever-2 lengths, for each species and sex. All were computed using a single ANCOVA and a common slope for each of the lever lengths for a standard claw weight of 7.56 grams. For species effects only, letters identify groups of least-square means that did not differ significantly after a sequential Bonferroni adjustment on *P* values. Pro = *C. productus*, Bra = *C. branneri*, Ant = *C. antennarius*, Ore = *C. magister*, Gra = *C. gracilis*, Mag = *C. magister*.

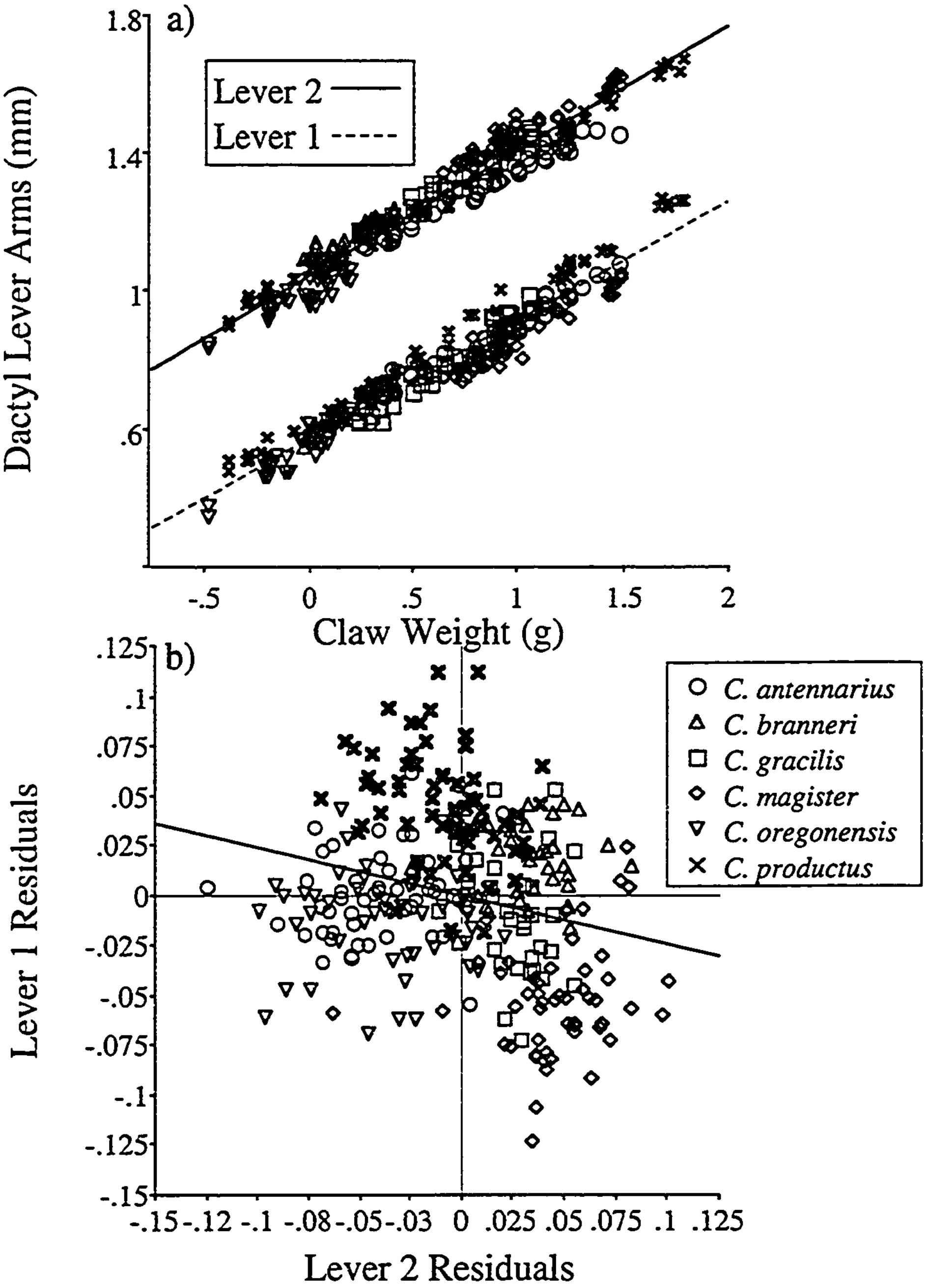


Figure 4-7. a) association between log-claw weight (grams) and lever-1 lengths ($P < 0.001$, $r^2 = 0.984$), and lever-2 lengths ($P < 0.001$, $r^2 = 0.989$) for claws of all six *Cancer* species. b) correlation between lever-1 residuals and lever-2 residuals for claws of all six *Cancer* species ($P < 0.001$, $r^2 = 0.050$). All residuals were computed as deviations from a single regression fit to pooled data of all six species. Solid lines indicate least square linear fits.

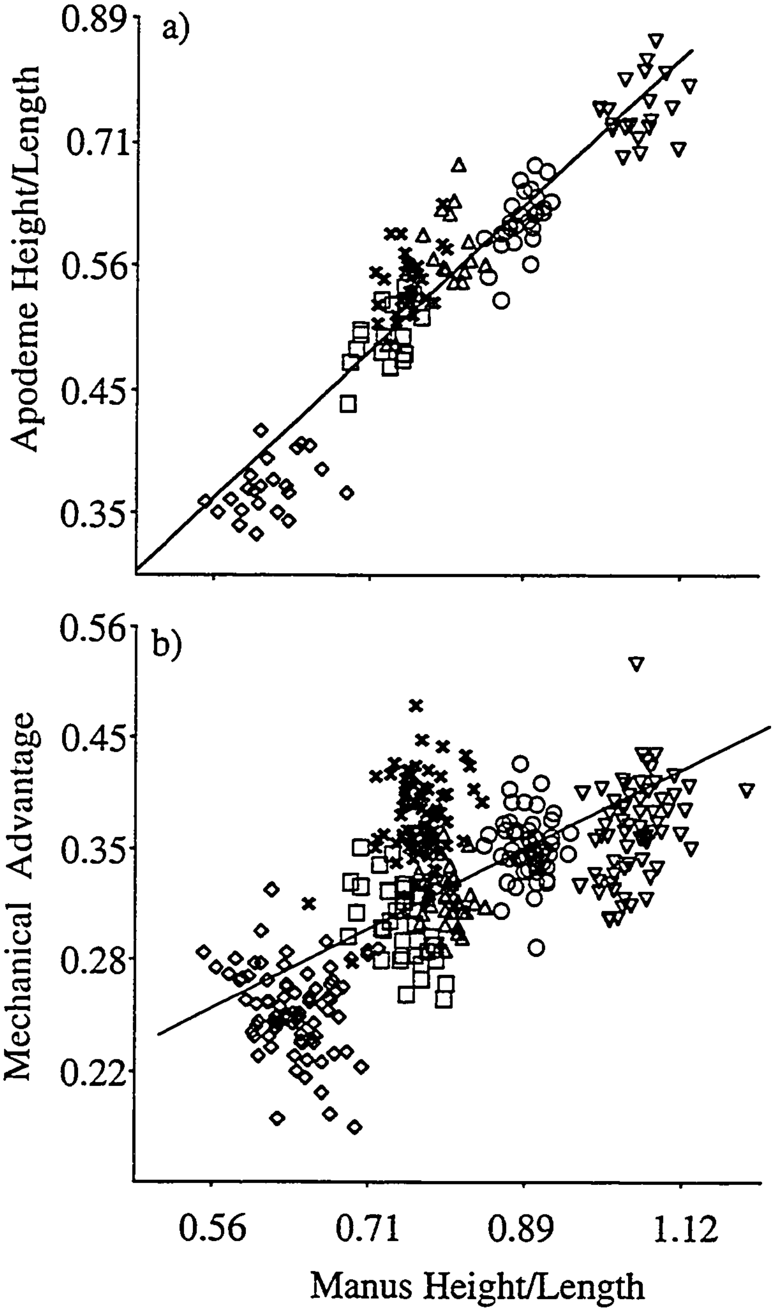
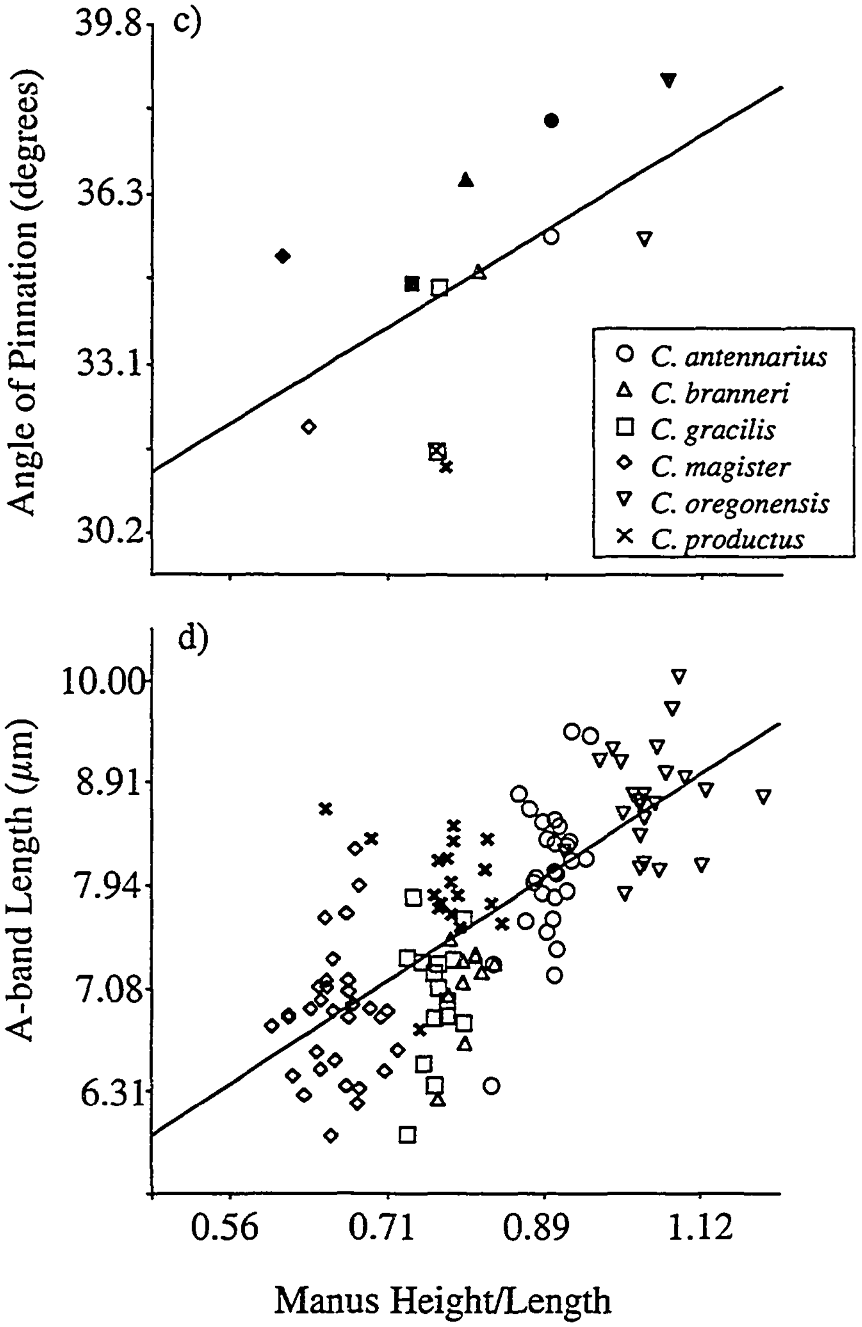


Figure 4-8. Associations between the log of the ratio of manus height to manus length and four (log) metric traits related to bite force: a) ratio of apodeme height to apodeme length ($P < 0.001$, $r^2 = 0.893$) b) mechanical advantage ($P < 0.001$, $r^2 = 0.472$), c) (see following page) mean angle of pinnation ($P = 0.034$, $r^2 = 0.375$), d) A-band length ($P < 0.001$, $r^2 = 0.554$). All lines are least square linear regressions.


c)
Angle of Pinnation (degrees)
39.8
36.3
33.1
30.2
○ C. antennarius
△ C. branneri
□ C. gracilis
◇ C. magister
▽ C. oregonensis
× C. productus
d)
A-band Length (μm)
10.00
8.91
7.94
7.08
6.31
0.56
0.71
0.89
1.12
Manus Height/Length

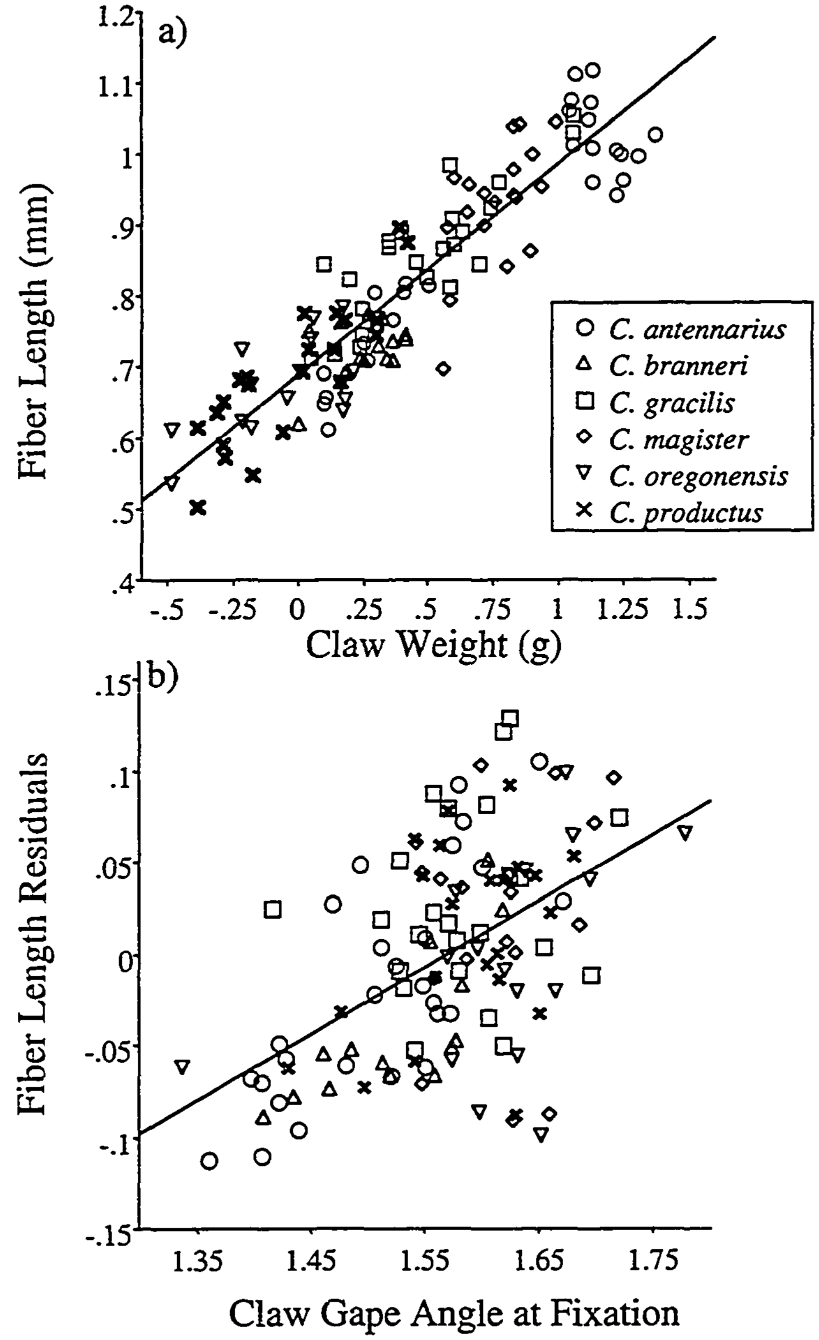


Figure 4-9. a) association between log-fiber length and log-claw weight (grams) for claws of all six *Cancer* species ($P < 0.001$, $r^2 = 0.866$). Each point represents a mean of 6 – 8 fibers from the mid region of the closer muscle. b) correlation between residual mean claw fiber lengths and the log-angle of claw gape (degrees) at the dactyl pivot, after the claw was fixed ($P < 0.001$, $r^2 = 0.245$).

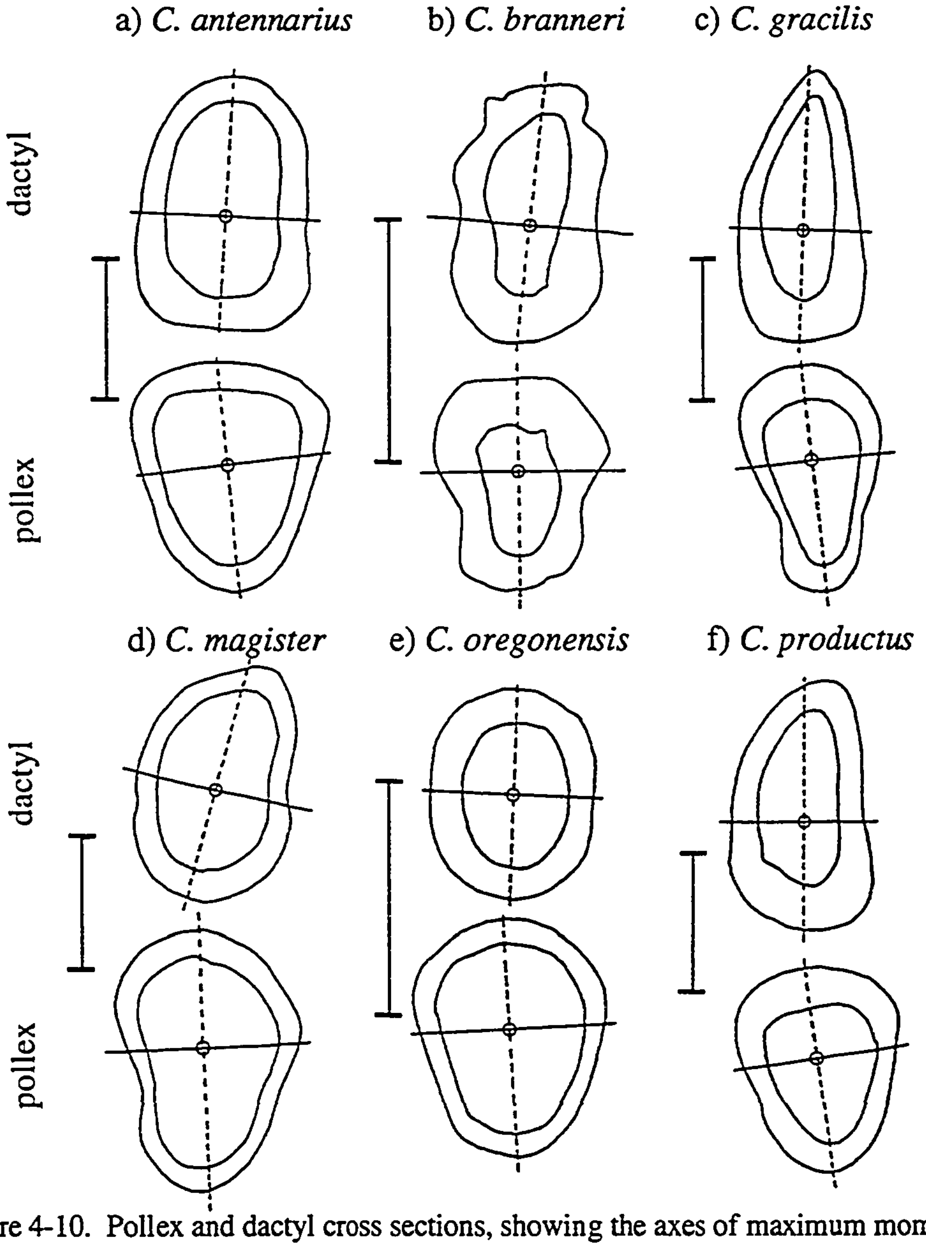


Figure 4-10. Pollex and dactyl cross sections, showing the axes of maximum moment of inertia (solid line) and minimum moment of inertia (broken line), and the centroids (small open circle), for representative claws of each *Cancer* species. Scale bars are 5 mm. For specific locations along the lengths of where the pollex and dactyl cross sections were sampled see Figure 4-1a.

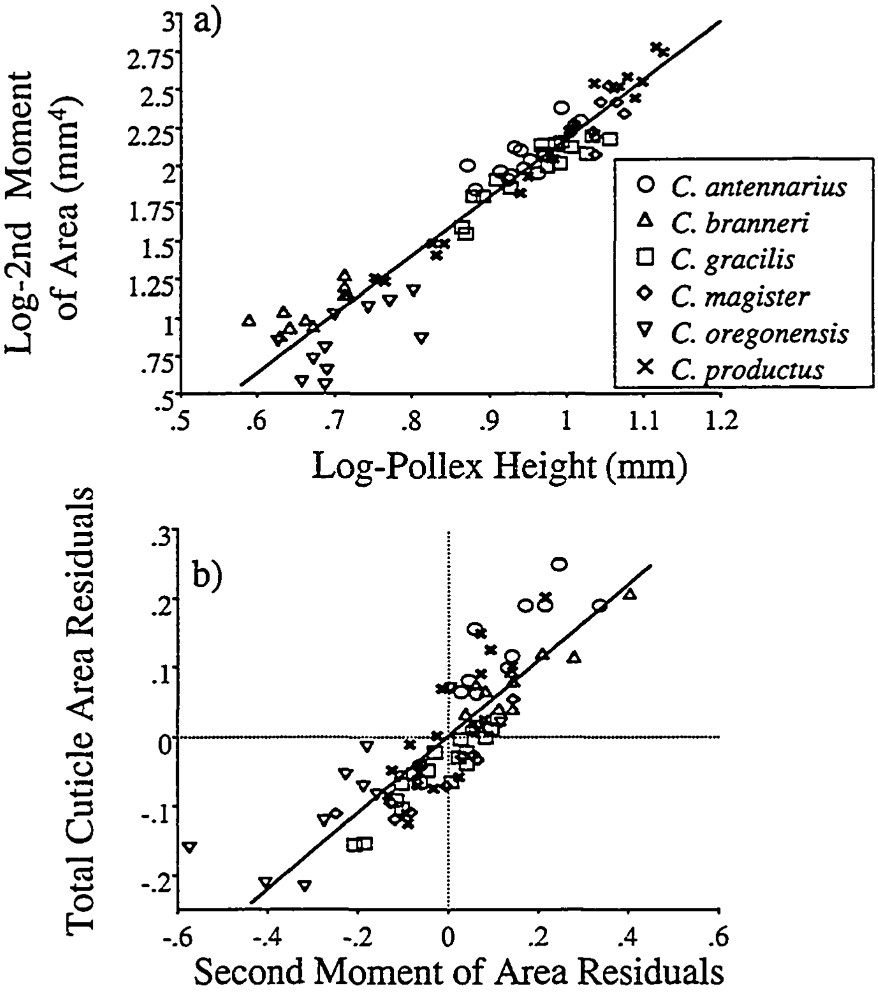


Figure 4-11. a) association between log-pollex height and log-second moment of area about the axis of I_{min} for all six *Cancer* species ($P < 0.001$, $r^2 = 0.970$)(ANCOVA; $F_{2,59} = 0.850$). The coefficient of allometry (4.012±0.123)(mean±SE) was not significantly different from isometry (4.0) (t-test, $P = 0.862$). b) correlation between log-second moment of area residuals and total cuticle cross sectional area residuals for claws of all six *Cancer* species ($P < 0.001$, $r^2 = 0.734$). Both the Y and the X residuals were obtained from least-squares linear regressions against log-pollex height by using a common slope for all six *Cancer* species. Solid lines indicate least square linear regressions and each symbol indicates a single claw value.

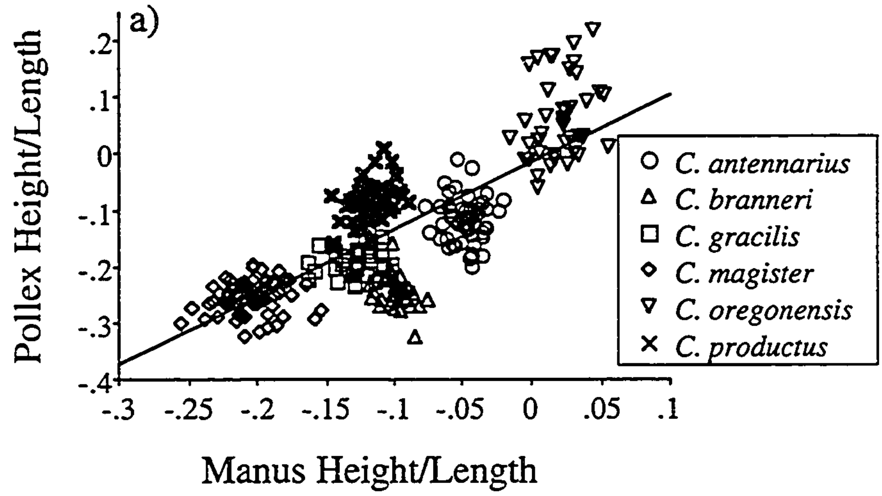
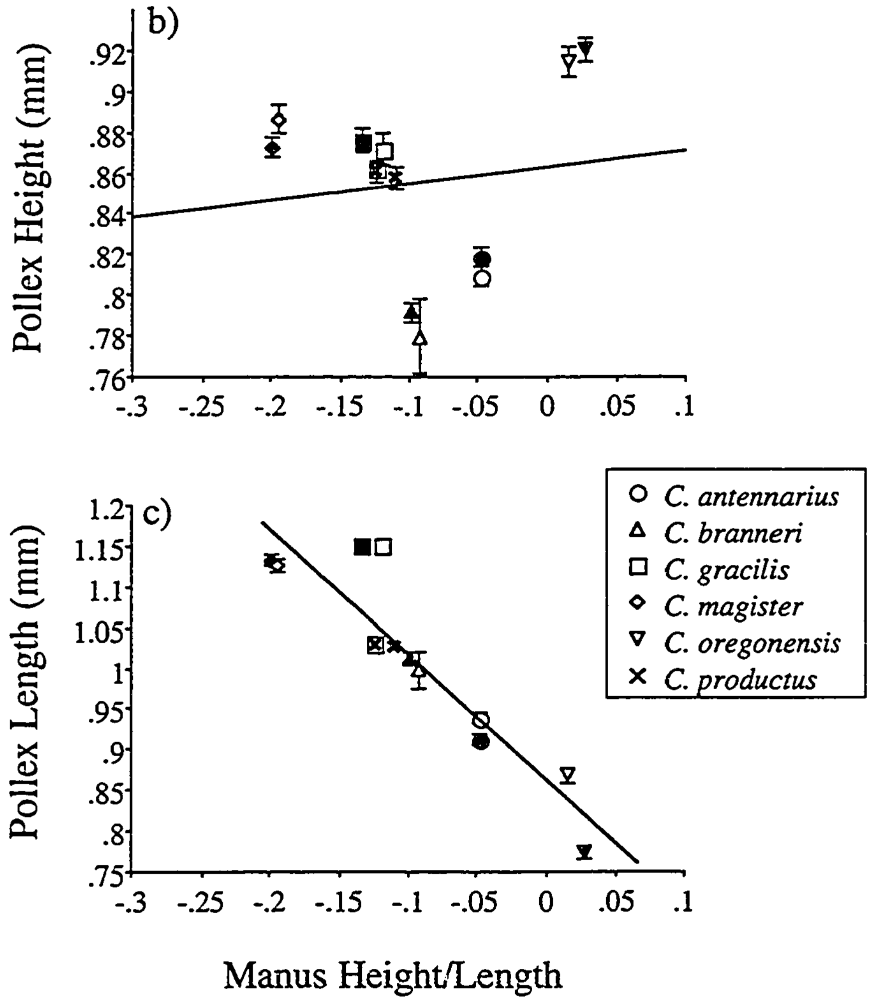


Figure 4-12. a) correlation between log of pollex height to pollex length ratio and log of manus height to manus length ratio (*P* <0.001, r^2 = 0.605). Each symbol indicates a single claw value. b) (see following page) correlation between mean size-adjusted log-pollex height and log of manus height to manus length ratio (*P* = 0.694, r^2 = 0.016). For a standard claw weight of 7.20 grams, least-square means were obtained by a single ANCOVA using a common slope, with species (fixed) and sex (fixed) as grouping variables and log-claw weight (grams) as the covariate (see Table 5). c) correlation between mean size-adjusted log-pollex length (species by sex) and log of manus height to manus length ratio (*P* < 0.001, r^2 = 0.847). For a standard claw weight of 6.54 grams, for four species: *C. antennarius*, *C. branneri*, *C. magister*, and *C. productus*. Least square means were obtained by a single ANCOVA with species (fixed) and sex (fixed) as grouping variables and log-claw weight (grams) as the covariate (see Table 5). For a standard claw weight of 6.54 grams, means of *C. gracilis* and *C. productus* were estimated by individual regressions of log-pollex length against log-claw weight (see Table 6 for species regressions). Solid symbols (bars = SE) indicate mean male values and the open symbols (bars = SE) indicate mean female values. Solid lines indicate least square linear regressions.


b)
Pollex Height (mm)
.92
.9
.88
.86
.84
.82
.8
.78
.76
-.3 -.25 -.2 -.15 -.1 -.05 0 .05 .1
c)
Pollex Length (mm)
1.2
1.15
1.1
1.05
1
.95
.9
.85
.8
.75
-.3 -.25 -.2 -.15 -.1 -.05 0 .05 .1
Manus Height/Length
○ C. antennarius
△ C. branneri
□ C. gracilis
◇ C. magister
▽ C. oregonensis
× C. productus

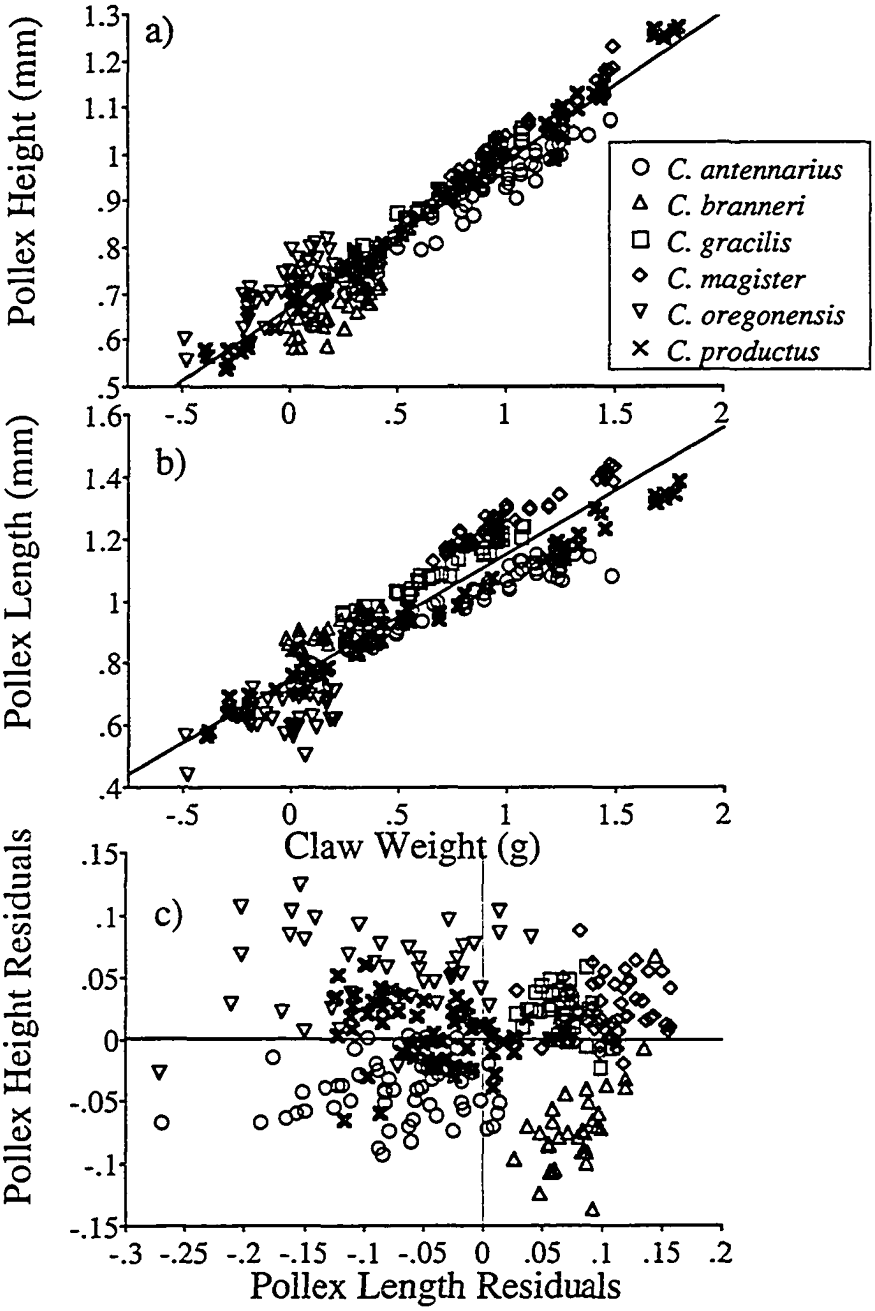


Figure 4-13. Correlation between a) log-pollex height and log-claw weight (P<0.001, r^2 = 0.923), and b) log-pollex length and log-claw weight (P <0.001, r^2 = 0.843) for individuals claws of six *Cancer* species (for individual species regression equations see Table 6). c) correlation between pollex height residuals and pollex length residuals (P = 0.866, r^2 <0.001), for individual claws of all six *Cancer* species. All residuals were computed as deviations from a single regression fit to pooled data of all six species. Solid lines indicate least square linear regressions. See Table 6 for regression statistics for a) and b).

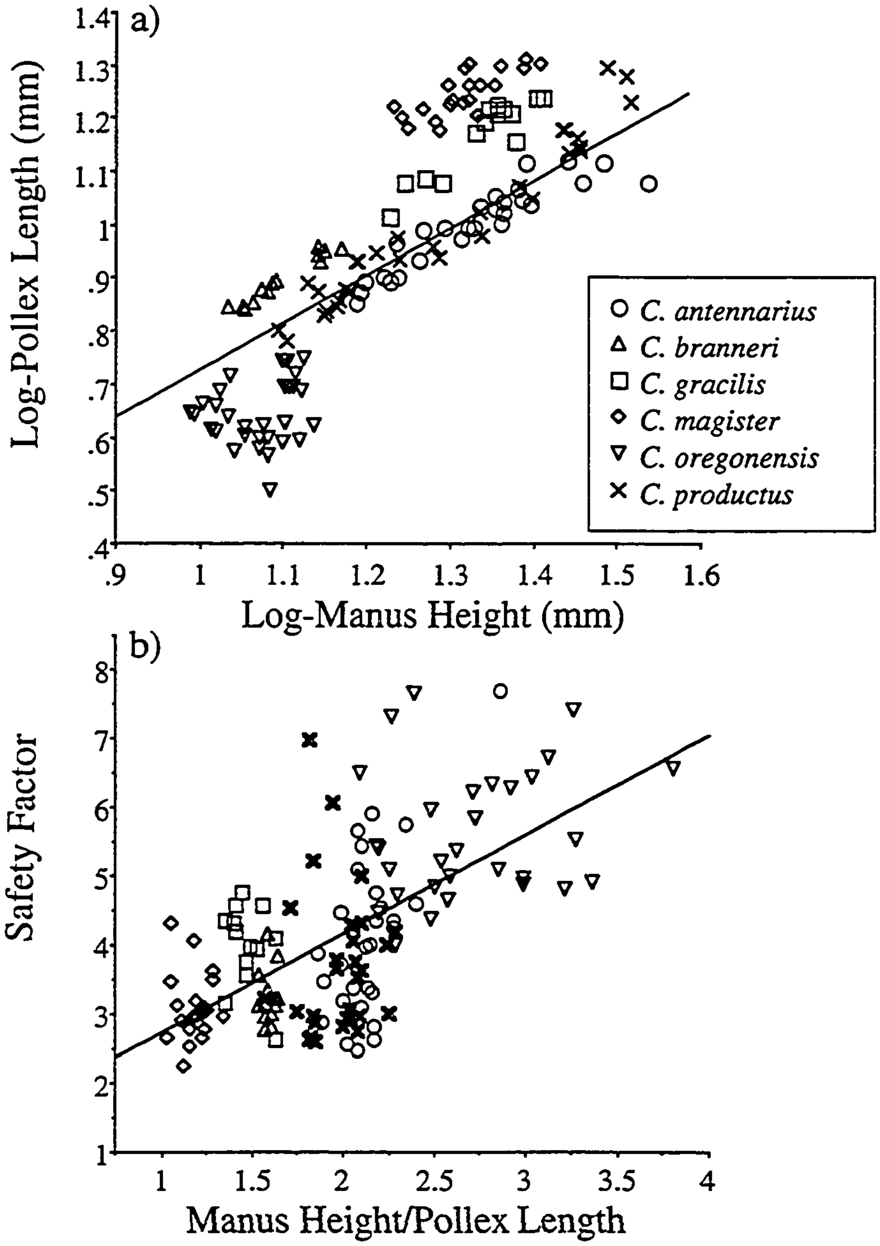


Figure 4-14. a) association between log-manus height and log-pollex length ($P < 0.001$, $r^2 = 0.716$) for claws of six *Cancer* species. Values are from claws used in safety factor experiment only (see Palmer *et al.*, 1999; Taylor *et al.*, in press). Solid line indicates the RMA common slope from an ANCOVA (1.06±0.039)(mean±SE), which was not significantly different from isometry (1.0) (t-test , $P = 0.119$). b) correlation between claw safety factor (breaking-force/median bite-force) and claw pollex length to manus height ratio ($P < 0.001$, $r^2 = 0.411$). For b), solid line indicates the least square linear regression.

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5. Discussion

Patterns in claw size and shape: The geography of crushing for decapod claws

The work I have done on *Cancer* claw biomechanics represents a quantitative and data-rich approach to understanding claw design, and conclusions drawn here should allow for more complete ecological and evolutionary interpretation of claw diversity and its relation to crab behavior. I was inspired by the intriguing evolutionary 'arm-race' hypothesis proposed by Vermeij (1987). Vermeij (1977) applied the notion of escalation to the armament of crabs, though with little success, as his speculation was seriously criticized by others (Abele *et al.*, 1981). Though some criticisms were certainly valid, I am afraid that some of Vermeij's very intruiging and worthwhile hypotheses may have been overlooked in the process. Outside of the work by West, Cohen & Baron, (1991) and West & Cohen, (1996) on Lake Tanganyikan gastropods and their predatory crabs, little research has been done on larger biogeographic comparisons of crab claw size and shape in relation to the prey they hunt, since Vermeij's (1977) initial investigation. I hope my work here will inspire more research on wider taxanomic comparisons of patterns of claw size and shape, since the underlying muscle properties of claws appear predictable from claw size and shape (i.e., manus dimensions, mechanical advantage, and pollex dimensions), as I have discussed in Chapters 3 and 4, and in Appendix 2.

The use of safety factor models and the performance of decapod claws

Although the theory of safety factors is robust, and makes definitive predictions about how safety factors should vary under changing environmental conditions, few empirical data exist that test these predictions. The simple question stated by Lowell, 1987 " just how large should a safety factor be?" appears unanswered for many groups, and the reason for its dormancy may be lack of an appropriate system. I suggest that the decapod claw system is ideal for addressing predictions arising from safety factor theory. Knowing how claw safety factors vary among individuals, populations and species in decapods, should prove fruitful.

Based on my work with *Cancer* species, there appear to be two plausible hypotheses to explain patterns of interspecific variation in safety factors. The first hypothesis is one of 'cost-of-investment'. Theory predicts that 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 claw-size relative to body size should indicate an increase in the cost of claw production. Therefore, species with larger claws relative to body size should have higher safety factors. The second hypothesis is one of 'mobility' (Chapter 2). The actual cost of damaging a structure may depend on complex ecological variables and on the ability of the organism to compensate for the damage. In particular, the cost of losing a claw may be less for a crab that is highly mobile compared to one that is restricted to foraging within a certain range (Chapter 2).

Future work on safety factors of decapod claws should focus on the above two hypotheses, ‘cost-of-investment’ and ‘mobility’ (cost of claw loss or damage). Data from *Cancer* crabs support both hypotheses; claw safety factors vary as predicted with claw size relative to body size and with inferred mobility (Chapter 2). Similar studies in groups of crabs within which claw size and mobility are not confounded, would allow one to tease apart these hypotheses. Although the hypotheses are not mutually exclusive, determining which of the two factors primarily drives the evolution of claw safety factors adds to our understanding of biogeographical patterns of claw size and shape.

The biting performance of claws of durophagous decapods

The puzzling question of why maximum muscle stress declines with claw size remains unsolved. In other words, larger claws have relatively weaker bite-forces than would be predicted by the size of the muscle, independent of changes in average sarcomere length and angles of pinnation (Chapter 3 and Appendix 2). In fact, sarcomere length and mechanical advantage were found to increase with claw size, suggesting that bite force should be higher than expected based on size. Therefore, maximum bite-force performance does appear to be under a functional constraint. We are clearly in need of more sophisticated models of maximum claw biting performance to interpret variation in claw shape and size among brachyurans.

Furthermore, we are in need of more empirical data on the maximum bite forces of crabs from different durophagous brachyuran families, such as Xanthidae, Parthenopidae and Portunidae. Tropical-temperate stone crab, *Menippe mercenaria*, (Xanthidae) appears to have higher bite forces than the *Cancer* and *Homarus* species (Chapter 3). The exceptionally high maximum muscle stress of about 215 N mm^2 observed for these smaller individuals is in need of replication in other xanthid species of both tropical and temperate origins. Overall, many questions remain concerning the maximum bite force performance of durophagous brachyurans. Xanthids appear to have relatively larger claws than cancrids and portunids (Fig.1-1) (data from Vermeij, 1977)- does this result in actual performance differences? For a given claw size, stone crabs appear to have the highest bite forces yet reported (Vermeij, 1987; Blundon, 1988) - are additional muscle properties required to explain these bite forces, such as exceptionally long average sarcomere lengths or high angles of pinnation? Are the high bite forces of the stone crab a result of history, reflecting its relation to other xanthids, or do they reflect geographical differences between tropical and temperate crabs arising from the evolutionary arms race (Vermeij, 1987)?

Further thoughts on the size-dependence of closer muscle stress

The decline in muscle stress with increasing claw size (Chapter 3) is a highly significant yet puzzling pattern. The cause of this decline remains unclear. For closer muscles of claws within six *Cancer* species, I clearly demonstrate that sarcomere length increases with claw size, which soundly rejects the hypothesis that declining sarcomere length explains the decline in muscle stress with increasing claw size.

Several other possible non-behavioral explanations for the negative size-dependency on muscle stress exist (Elner & Campbell, 1981) and should be tested in future studies on claw performance. Primarily, as proposed by Elner and Campbell (1981), the negative size-dependency of stress may result from larger muscles containing a higher proportion of vascular and connective tissues than smaller muscles. Extending this hypothesis, larger muscles may contain a higher proportion of any structure that is involved in muscle function other than contractile filaments, such as cytoskeletal components, mitochondria, sarcoplasmic reticulum, and transverse tubules. Another muscle contraction property, twitch duration, is affected by proportional changes in cellular composition. Increases in the relative sarcoplasmic reticulum and T-tubules in the muscle tissue have been negatively correlated with twitch duration of the forwing muscle of tettigoniids (*Neoconocephalus robustus*) (Josephson & Young, 1987). Therefore, changes in the proportion of muscle contractile units relative to other structures with increasing size of the closer muscle could potentially explain the decline in muscle stress with size.

Alternatively, behavior may be the cause of the puzzling decline in muscle stress with increasing claw size (Chapter 3). As discussed in Chapter 2, direct evidence from individual variation within instars does demonstrate that individual behavior plays a role in modifying safety factors (via individual bite forces). Extending this argument, it is possibile that large crabs may bite with less force than small crabs as a result of differences in behavior (possible reasons for differences in behavior among small and larger crabs are discussed in Chapter 2 and in Appendix I). MacMillian and Dando, (1972) found that the apodemes of *C. magister* are supplied with tension receptors capable of registering the forces of muscle contraction throughout ongoing motor activity. Furthermore, it is most likely that crabs possess proprioceptors within the cuticle of their pollex, which suggests that crabs possess a physiological mechanism that would allow them to adjust their biting-force according to the strength of their claws. Therefore, behavior differences among large and small crabs must be considered as a possible reason for the observed decline in muscle stress with size.

Thus, there are several testable hypotheses that could form the basis for future work on the decline in muscle stress with claw size (i.e., manus height) for within species comparison of individuals.

Muscle stress and bite forces for other animal groups

Muscle stress (force per unit area) is a useful variable for comparing performance among divergent groups of animals, since it removes the effects of size (Josephson, 1993). By looking at the variation in mean maximum muscle stress among vertebrates, insects and crustaceans (Appendix 2), I was able to show that the unusually high bite forces of crabs were mostly explained by resting sarcomere length since, as predicted by the sliding filament model of muscle contraction, mean maximum muscle stress scaled isometrically with mean resting sarcomere length.

However, size is an important ecological and evolutionary variable (Schmidt-Nielsen, 1984), and to truly understand performance for whole animals, size must also be considered. For example, the occurrence of negative allometry in bite forces should be investigated in other animal groups. In general, information on bite forces in other animals is in short supply. Hylander (1985), in a paper on mandibular function and biomechanical stress and scaling of vertebrates, discusses the lack of data for primates. Several maximum bite forces have been reported for humans (upper maximum bite forces range from 600 to 700 N), but mainly in association with the effects of sex or in relation to jaw design (Osborn, 1996), with little concern for the effects of size on maximum bite forces. It would be most interesting to determine if the constraint on maximum bite force observed in *Cancer* crabs is universal.

The shape of strength

My data strongly support the notion that claw form reflects claw performance. I observed a surprisingly strong correlation between manus shape and muscle attributes (sarcomere length and angle of pinnation) that are associated with the potential bite force of the claw (Chapter 4). A similar analysis was conducted in Appendix 2, where I correlated average resting sarcomere length with mechanical advantage of the claw for 11 brachyuran species (7 cancrids, 3 portunids (both crusher and cutter claws), and 1 majid). Though the data are biased towards claws of *Cancer* species, the correlation strongly suggests that external morphology of the claw does predict muscle attributes for brachyurans generally, and hence the potential bite force of the claw may be predictable (but see Chapter 3). Furthermore, two linear measures of the claw (manus height and pollex length) could be used to explain variation in claw safety factors among *Cancer* species, further justifying that morphometric analysis of claw shape can predict performance.

The monomorphic claws of Cancer *crabs*

Why do *Cancer* crabs have monomorphic claws when many other durophagous brachyurans are asymmetrical in claw size and shape? Some have speculated on this (Smith & Palmer, 1994; Smith et al. 1999), but no real data exist that provide a convincing answer. One possible mechanism whereby asymmetrical claws might begin to evolve from symmetrical progenitors, preferential use of one claw over the other in feeding, was suggested by Smith & Palmer (1994). Applied to *Cancer,* this hypothesis assumes that the genus was derived from a symmetrical clawed ancestor. Alternatively, there could be selection for monomorphic claws (ancestor asymmetrical or symmetrical), for example, via selection for proficiency in digging for soft shelled prey (Smith *et al.*1999). *Cancer productus* digs large pits to access deeply buried bivalves in a manner analogous to a bulldozer, using both its chelipeds to push the sand forward. Symmetrical chelipeds may make for more efficient 'bulldozing' than asymmetrical chelipeds (Smith *et al.*, 1999). However, *C. magister* (a large *Cancer* species) is not known to dig large pits like that of *C. productus*, yet it also displays monomorphic claws. Furthermore, the ancestor to the *Cancer* crabs was probably symmetrical in claw size (Palmer, 1996) and therefore the suggestion that 'bulldozing' selects for symmetrical claws in a derived species is likely a spurious conclusion. Until more detailed observations of foraging behavior in association with morphometric analysis are made for more *Cancer* species and until claw form and function can be measured in those species most closely related to *Cancer* species, the mechanism driving claw symmetry in this group will remain unknown.

Cancer crabs of the northeast Pacific: Are they the 'Darwin's finches' of the marine world?

The principles determining and organizing organic diversity have been elucidated by focusing on diverse yet recently evolved lineages, such as Darwin's finches of the Galápagos (Grant, 1986). Researchers focusing on these finches have gained considerable knowledge about how organic diversity, in terms of form, function and behavior, has arisen via natural selection (Grant, 1986). The recently evolved sympatric guild of *Cancer* crabs along the northeast Pacific (Nations, 1975; Harrison, 1997; Harrison & Crespi, 1999), mostly represented by the six species studied here, offers a similar system in which form, function, and behavior can be explored. Within the short evolutionary time span since *Cancer* crabs have appeared (15 million years ago)(Harrison, 1997; Harrison and Crespi, 1999), compared to other durophagous predatory crabs (Xanthidae), they have diversified into numerous niches and show a tremendous amount of variation in claw size and shape (Fig. 5-1). Therefore, investigation of the principles determining diversity in claw design and performance within the *Cancer* genus should continue to prove fruitful.

Before firm conclusions can be drawn regarding the role that historical and deterministic processes play in the evolution of claw diversity in *Cancer* crabs, a more complete phylogeny than is currently available will be required. However, based on the available information (Harrison, 1997; Harrison and Crespi, 1999), deterministic processes appear to predominate over historical ones. Within this recently evolved clade, a wide diversity of claw form is observed, and even within smaller, internal clades rapid divergence in claw design has occurred (Fig. 5-2). The rapid divergence between species with respect to claw design suggests that species are responding to unique selection pressures acting on claws. Therefore, deterministic processes, rather than historical ones, appear to predominate in this system.

Conclusion

In this thesis, I have attempted to elucidate some complex relationships between morphology and performance, to gain insight into the evolution of claw form in *Cancer* crabs. I feel this study has advanced our understanding of claw design in decapods, and I hope it will contribute to future studies of the evolution and ecology of this group. Many intriguing questions have arisen during the course of my investigations, some of which I have summarized in this chapter. I also hope that they may provide a basis for fruitful research in the future.

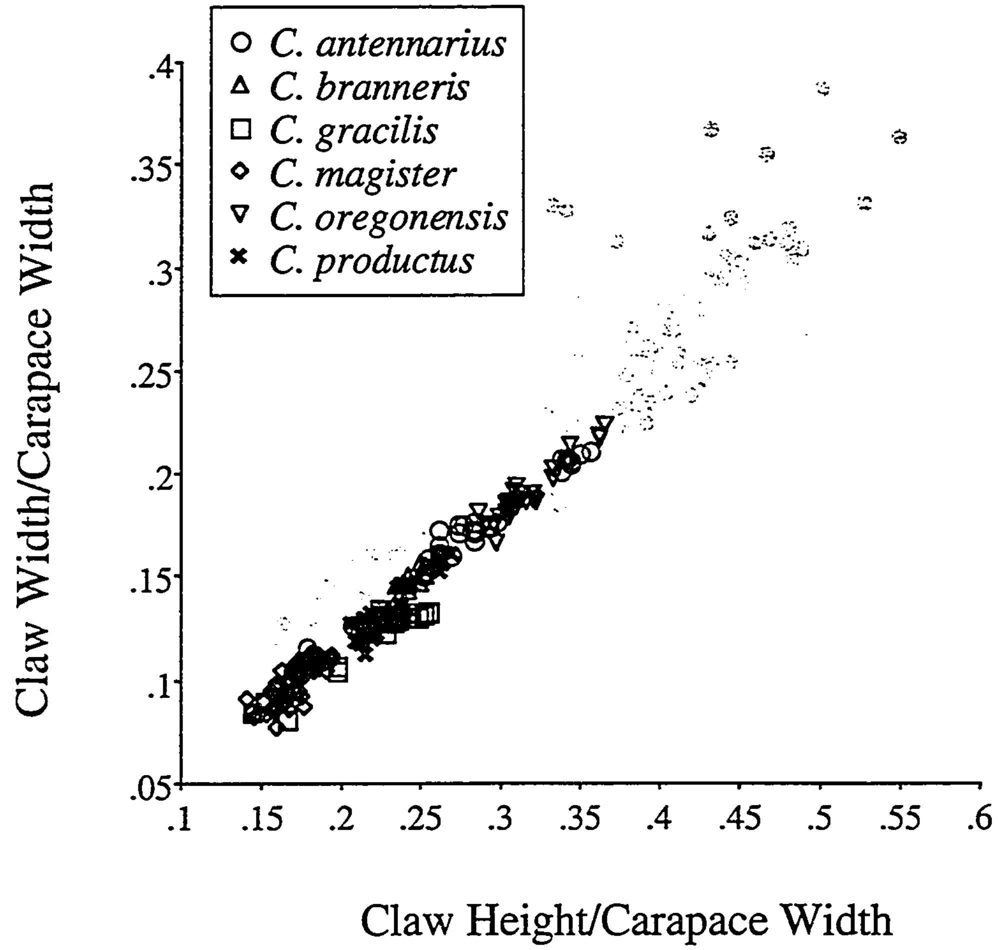
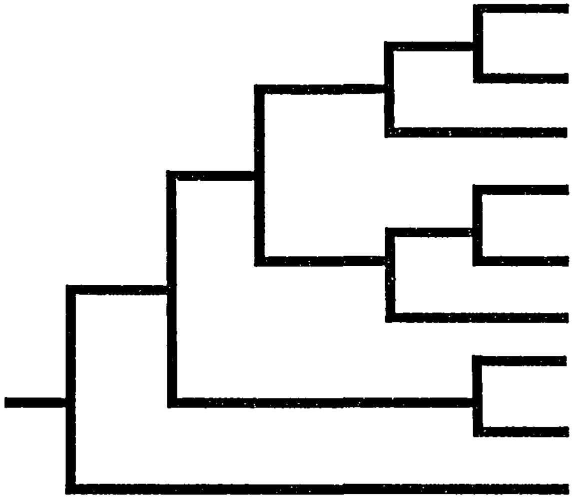


Figure 5-1. Association between claw height to carapace width ratio, and claw width to carapace width ratio, for six *Cancer* species (black circles). Gray circles indicate Vermeij's (1977) data for the four brachyuran families, Cancridae, Portunidae, Xanthidae, and Parthenopidae (see Fig.1-1 for details).



CW	MA	MH/ML	SF	
115	0.30 (.004)	0.74 (.005)	3.6	*C. gracilis*
58	0.32 (.003)	0.80 (.003)	3.6	*C. branneri*
53	0.37 (.005)	1.05 (.005)	7.4	*C. oregonensis*
160				*C. novaezealandiae*
178	0.36 (.003)	0.90 (.003)	3.6	*C. antennarius*
230	0.25 (.002)	0.64 (.004)	2.6	*C. magister*
180				*C. borealis*
267				*C. pagurus*
200	0.37 (.004)	0.76 (.003)	3.6	*C. productus*

Figure 5-2. Various morphometric traits and claw safety factors of six *Cancer* species mapped onto a phylogenetic tree. The tree is based on maximum-parsimony analysis of the cytochrome oxidase I gene from nine *Cancer* species (from Harrison & Crespi, 1999). CW = maximum male carapace width (mm) (from Harrison & Crespi, 1999). MA = mean claw mechanical advantage (standard error). MH/ML = mean manus height to manus length ratio (standard error). SF = mean, size-adjusted claw safety factor.

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Appendix 1: Cuticle Strength and the Size-Dependence of Safety Factors in *Cancer* Crab Claws *

Introduction

Rather unexpectedly, structures as diverse as mollusc shells (Vermeij, 1982; Brandwood, 1985), crab claws (Juanes and Hartwick, 1990; Chapter 2), the teeth of living and extinct carnivorous mammals (Van Valkenburgh, 1988; Van Valkenburgh and Hertel, 1993), the antlers of ungulates (Kitchener, 1991), and the limbs of birds and mammals (Buikstra, 1975; Currey, 1984; Brandwood *et al.*, 1986) exhibit high rates of non-lethal failure in natural populations. The skeletons of many organisms therefore appear to operate near their upper performance limits under normal living conditions, and safety factors (e.g., breaking strength / maximum load) should be under constant pressure to evolve. Yet enhanced durability bears a price and, like most attributes of organisms, must reflect a balance between the benefits of increased performance and the costs of construction, maintenance, and possible failure (Alexander, 1982).

Because explicit predictions exist for how safety factors should vary under different situations (Alexander, 1981, 1997), tests may be conducted to assess how closely biological structures approach theoretical design optima. Compared to analyses of among-species differences, those of size-dependent variation within species offer even more rigorous tests because fewer potentially confounding factors vary and predictions are therefore more precise (Currey, 1977; Niklas, 1994). For example, for the brachyuran crabs we studied, larger crabs should exhibit higher claw safety factors for several reasons: a) stress cracks and wear have more time to accumulate between molts, which increases the unpredictability of claw strength in larger crabs, b) the negative ecological impact of lost or damaged claws (Juanes and Smith, 1995) will be more prolonged or severe for larger crabs, and c) larger crabs may experience a greater range of extreme forces because claws are used increasingly for aggression (Juanes and Smith, 1995).

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* A version of this appendix has been published. Palmer, Taylor, and Barton 1999. Biological Bulletin. 196: 281-294.

Intraspecific size-dependence of safety factors may also reveal unexpected geometrical or ontogenetic constraints that preclude an optimal design. For example, if cuticle thickness scales proportional to body mass within a species, the critical buckling loads of walking legs must greatly exceed the likely maximal loads experienced in smaller insects to ensure an appropriate critical buckling load at larger body size (Prang, 1977). Similarly, the stems of small horsetails, *Equisetum*, are mechanically 'overbuilt' by roughly 10 times compared to larger plants (Niklas, 1989). In both of these examples of narrow, tubular support-systems, mechanical and growth considerations appear to conflict.

Unfortunately, biologically realistic strength and particularly load distributions are difficult to measure with confidence for most structures, so estimates of safety factors of individual organisms are often indirect. Typically, safety factors are estimated either a) by computing or measuring maximal loads on aggregate samples and then comparing these to standard estimates of material properties or theoretical estimates of failure strengths (Alexander, 1981; Biewener, 1990; Niklas, 1994; Biewener and Dial, 1995; Claussen and Maycock, 1995), or b) by computing an average maximum load and an average breaking force measured on different samples of individuals (Lowell, 1985, 1987; Friedland and Denny, 1995). Crab claws offer a particularly attractive opportunity to study directly the intraspecific size-dependence of safety factors because both maximal closing forces and breaking forces can be measured on an individual claw. In addition, because the entire cuticle is assembled anew following a molt, the intermolt interval may be considered a 'lifetime' for a claw (Chapter 2) in the same way as ungulate antlers that are also renewed annually (Kitchener, 1991). Therefore we could examine intraspecific variation that would otherwise not be apparent using indirect approaches.

We examined the size-dependence of safety factors in the claws of six closely related species of *Cancer* crabs, to test whether safety factors varied in a manner more consistent with adaptation or constraint: do claw safety factors increase with increasing crab size — as would be expected because of increased unpredictability of cuticle strength, increased costs of failure, and possibly increased unpredictability of load distribution (Juanes and Smith, 1995) — or do they decrease with increasing crab size, because geometric or ontogenetic constraints associated with the growth of 'external' tubular support systems yield structures that must be disproportionately strong at smaller sizes to retain function at larger sizes, as suggested for insect legs (Prang, 1977) and the shoots of horsetails (Niklas, 1989).

Throughout the paper, we apply the verb *'to bite'* to the action of claws. Although most commonly used in reference to mouthparts, we invoke it here because anyone attacked by a large crab would surely exclaim that they had been 'bitten' rather than squeezed, grasped, pinched or nipped, and because in carnivorous brachyuran crabs claws function to crush prey, or to tear apart the flesh, much like vertebrate jaws.

Methods

Experimental animals

Crabs collected from various shallow-water sites near Bamfield, BC, Canada (see Table A1-1 for size ranges) were held in running seawater aquaria and fed shucked mussels daily (*Mytilus* spp.). Biting forces of claws were measured within seven days of collection, as maximum force and consistency declined with time in the laboratory (G.M. Taylor, unpublished obs.). Crabs with damaged or regenerating claws were not used, nor were crabs suspected as early or late intermolt (Chapter 2) because biting forces (Kaiser *et al.*, 1990) and cuticle properties (Horst and Freeman, 1993) may vary substantially over the intermolt interval.

To minimize among-investigator variation, all biting force measurements were measured by GMT and all claw morphometrics and breaking strengths were done by AB.

Biting force measurements

Crabs were encouraged to grasp a force gauge with their claw and bite as hard as possible while held firmly in the air by the proximal portions of both chelipeds so other movement would not affect the biting force measurements. The pollex (fixed finger) was inserted into a lower fixed steel ring, and the dactyl into an upper ring mounted on a flexible 2 mm thick steel beam bearing two strain gauges (Bean BAE-13-250BB-350TE; 350Ω) that were connected to a Wheatstone bridge and a chart recorder (Fig. 2-2). The rings were positioned at the same point for all claws: just inside the tip of the dactyl and pollex, distal to the first tooth (i.e., the same position as the 'load' when breaking the claw, Fig. A1-2, Table A1-1). To ensure comparable biting forces among claws of different size, the distance between the inner margins of the rings was adjusted to approx. 60% of the maximum gape at this position for each claw. Before and after each session of 7 - 10 crabs, deflections of the upper ring were calibrated with five known weights (4.6 - 112 N) that exceeded the full range of observed maximum biting forces. The average of these two curves was used to digitize calibrated biting forces after each session.

Biting forces were measured on both claws of each crab in succession. To avoid possible biases, the first measurement alternated between the right and left claw on successive trials. At most, two measurements were obtained per claw per day, separated by at least four hours. Mean number of trials per claw varied from 6.9 - 8.3 among species (Table A1-1); claws with fewer than four trials were excluded from the analyses. Though median-maximum biting force exhibited less statistical noise, the allometric coefficient was statistically indistinguishable from that for extreme-maximum biting force (see Table A1-5e vs. Vf below), so extreme-maximum biting forces were used to permit comparison with previously published biting force values.

Morphometry and breaking force

Claw and cuticle dimensions (Fig. A1-1) were digitized with a Summagraphics drawing tablet (20 dots/mm resolution) from enlarged (8 - 12X), calibrated camera-lucida drawings of autotomized claws (Wild M5A dissecting microscope with a 0.3X reducing lens if necessary). This method is accurate to within ±1% (Smith and Palmer, 1994).

Claws were broken by within 1 hr of autotomy and held in seawater or kept wet continuously until broken. Breaking forces were typically measured within 2 - 3 days of the last biting force, and never more than 14 days after the last biting force. To obtain breaking forces, claws were clamped rigidly and a container suspended from the tip of the pollex by a loop of 4 mm diam. steel wire (Fig. A1-1). Lead weights to approx. 80% of the estimated breaking force were gently added, and then sand was poured into the container at a constant rate (approx. 5 g/s) until the claw broke. The container and contents were then weighed to the nearest gram.

After the claw failed, the location of the load wire and the fracture margin were recorded on each claw drawing. Cuticle thickness at the point of failure was measured by orienting the fracture surface of the broken pollex towards the viewer so that the line of sight was parallel to the occlusal surface of the pollex (line u, Fig. A1-1). Pollex width (*W*), as well as cuticle thickness at the dorsal (*f*), ventral (*g*), medial (*h*) and lateral (*i*) margins, was digitized from enlarged drawings of this orientation. In addition, the height of the pollex immediately below the point of crack initiation and perpendicular to the occlusal surface was also digitized (*H*, along the vertical dashed line labeled '*crack*', Fig. A1-1). The actual fracture plane was not always perpendicular to the occlusal surface, so stresses were calculated twice, once using all the data and once using only breaks that were within ±30° of the vertical dashed line labeled '*crack*' (Fig. A1-1).

Analyses

Regression analyses, and analyses of variance were conducted with StatViewII (ver. 1.03, Abacus Concepts). Tests for differences in slopes between sexes and among species, and common slopes, were computed via analysis of covariance (ANCOVA; SuperANOVA ver. 1.11, Abacus Concepts). A full analysis of differences between sexes and among species is presented elsewhere (Chapter 2).

Ultimate stress (σ_b, MNm^{-2}) of the cuticle surface at the point of fracture — '*extreme fiber stress*' in the engineering literature — was estimated via linearly elastic theory (Biewener, 1982)

$$\sigma_b = F_b \, r \, c \, I^{-1} \qquad \text{Eq. (1)}$$

where

F_b = breaking force (in Newtons, N).

r = moment arm (center of the load wire to the point of crack initiation, in mm; Fig. A1-1).

c = distance from the neutral axis of the pollex to the upper surface ($H/2$, where H= height of the pollex parallel to the load vector immediately below the point of crack initiation, in mm; Fig. A1-1). Ideally, c should be computed from the centroid (the presumed neutral axis) of the pollex cuticle in a plane perpendicular to the occlusal surface at the point of crack initiation, but we did not have sufficiently detailed measurements of the distribution of cuticle to do this, so we assumed that the neutral axis was at the midpoint of the cross-section of the pollex (H, Fig. A1-1).

I = second moment of area (mm^4) computed parallel to the load vector immediately below the point of crack initiation as $I = (I_u + I_l)/2$, where $I_u = (\pi/64)\ \{(WH^3)\text{-}[(W\text{-}h\text{-}i)(H\text{-}2f)^3]\}$ and $I_l = (\pi/64)\ \{(WH^3)\text{-}[(W\text{-}h\text{-}i)(H\text{-}h\text{-}i)^3]\}$ (see Fig. A1-1 for cuticle dimensions and Alexander (1983) for the formula). I was computed separately for the upper (I_u) and lower (I_l) half of the cross section of the pollex because the upper cuticle margin was approximately twice as thick as that of the sides or bottom. Side thicknesses (h and i of Fig. A1-1) were used to compute I_l instead of measured bottom thickness (g) because bottom thickness varied with fracture angle, and because in claws where the bottom thickness could be measured reliably, it did not differ from the side thickness (data not shown).

Ultimate stress (σ_b) could not be computed for all claws for which we obtained safety factors because a few claws broke at the base of the pollex adjacent to the opening where the dactyl inserted, so dimension (f) could not be measured.

Breaking force variability of different sized crabs was assessed by: a) computing residuals from a least-squares linear regression of untransformed breaking force (Y) on untransformed manus length (X) for each species separately (sexes were pooled), b) dividing the sample for each species into two roughly equal-sized groups (smaller and larger) based on carapace width, and c) conducting a Levene's test on the absolute values of the residuals (2-way ANOVA: species x size group). This analysis was also repeated using log-transformed variables.

Least-squares linear regressions were used to obtain coefficients of allometry throughout the analyses, even though such coefficients may be underestimated as the goodness-of-fit to a line declines (LaBarbera, 1989). They were nonetheless preferred over alternative Model II regressions in our study for two reasons. First, for our analyses the uncontrolled variation in the 'dependent' variable was substantially greater than that in the 'independent' variable (e.g., Table A1-2 and 4 below), so a Model I analysis was more appropriate. Second, we wished to compare both slopes and intercepts among species via ANCOVA (e.g., Table A1-3 and 5 below), and the validity of P-values from such comparisons based on Model II regressions is open to question.

The statistical significance of differences between pairs of model coefficients was computed via two-sample *t*-tests for unequal sample sizes (Sokal and Rohlf, 1995).

Results

Breaking force and breaking-force variability

Although claws broke at many different locations along the pollex, most breaks tended to fall either towards the base (0.2 - 0.4 of standardized pollex length), near the proximal margin of the tanned cuticle (the black ends to the fingers of many brachyuran crab claws), or towards the tip (0.6 - 0.8 of standardized pollex length, Fig. A1-2a). Nonetheless, even though pollex diameter varied substantially from the base to the tip, the location of the break had no effect on the force at which the pollex broke after controlling statistically for the effects of claw size (Fig. A1-2a). Only five claws out of 141 shattered along the lower margin of the pollex, as would occur when failure was due to local buckling (Wainwright *et al.*, 1976), and these were excluded from the analyses.

The fracture plane, however, was not always perpendicular to the upper pollex surface (i.e., parallel to the load vector). Most commonly, cracks deflected proximally towards the pollex base. In some cases, the fracture plane deviated by more than 30° from the load vector. Such cracks tended to be concentrated towards the tip of the pollex and yielded somewhat more variable estimates of breaking strength (Fig. A1-2b).

Larger crabs exhibited significantly more variable breaking forces ($P= 0.036$, Levene's test), but this difference was not significant when computed for log-transformed size and biting force ($P= 0.67$). Therefore in absolute terms, breaking forces were more variable for larger claws, but the variability appeared to be proportional to claw size.

Under natural conditions, claws may fail mechanically in ways other than the breakage of the pollex that we examined in this study. For example, claws might fail because the dactyl tip breaks, rather than the tip of the pollex, or because the dactyl condyles become disarticulated from their sockets. Among the 81 injured claws we observed in field-collected crabs, the dactyl tip was broken more frequently than the pollex tip (46 vs. 33), however none exhibited a dislocated dactyl. Disarticulated dactyls are occasionally observed in field-collected crabs (G.M. Taylor, unpublished obs.), but mode of failure appears quite rare. Therefore we believe our study has focused on the most biologically relevant form of claw failure: fracture of one of the fingers.

Cuticle strength of claws- patterns

Although breaking force did not vary along the pollex, the ultimate stress (force per unit area, σ_b) — a measure of the ability of claw cuticular material to resist failure in tension — did (Fig. A1-2b). When data for all species were considered together, ultimate stress increased distally from a mean of 53 at 0.1 to a mean of 78 MNm^{-2} at 0.9 of the standardized pollex length (Fig. A1-2b; $P< 0.001$, Table A1-2a-7). Ultimate stress (σ_b) of claws that fractured along a line deviating by more than 30° from the load vector (Fig. A1-2b) were somewhat more variable because of increased uncertainty about the true cuticle thicknesses below the crack initiation site. However, exclusion of these points did not significantly alter the slope or intercept of this relationship ($P= 0.75$; compare row a-8 to row a-7 in Table A1-2). Because ultimate stress (σ_b) declined with increasing claw size (see below), the effect of claw size might have confounded the effect of crack location. Here again, though, an analysis of the residuals, where residuals were computed separately for each species from a regression of log(ultimate stress) vs. log(manus length), also yielded a slope that did not differ significantly from the original untransformed data ($P= 0.50$; compare row a-9 to a-7 in Table A1-2). Slopes of this relationship appeared to vary among species (rows a1-a6, Table A1-2), however, these differences were not significant statistically ($P= 0.2$; see Table A1-5a below). Therefore, regardless of how the analysis was conducted, the cuticle was nearly 50% stronger at the pollex tip compared to the base (0.9 vs. 0.1 of standardized pollex length, respectively).

For all six *Cancer* species, breaking or ultimate stress (σ_b) declined with increasing claw size (Fig. A1-3, Table A1-2b). This decline was significant statistically only for *C. antennarius* and *C. productus* (Table A1-2b-1,6) when species were analyzed separately because of the smaller size ranges for the other species. However, a 1-factor ANCOVA with species as the grouping variable, revealed that slopes did not differ significantly among species ($P= 0.96$; see Table A1-5b below) and that the common slope was highly significant ($P< 0.001$) (Table A1-2b-7). To control for possible effects of crack location (Fig. A1-2b), an ANCOVA was also conducted on residuals from the regression of Table A1-2a-7. This too revealed no significant difference in slopes among species ($P= 0.97$; see Table A1-5b below). The common slope from ANCOVA was also highly significant statistically ($P< 0.001$) and did not differ significantly from the slope obtained for the original untransformed data ($P= 0.52$; compare row b-8 to b-7 in Table A1-2). Therefore, regardless of how the analysis was conducted, cuticle strength decreased by approximately 40% with a doubling of claw size (measured as manus length).

This decline was not simply an artifact of our computations for intact claws because, if it was, all claws should fall upon the same regression line and *C. oregonensis* clearly does not (Fig. A1-3). This decline was also not an artifact of using manus length as the arbitrary measure of claw size because nearly identical results were obtained using total claw wet weight as the covariate (results not shown).

Finally, size-adjusted breaking or ultimate stress (σ_b) differed up to twofold among *Cancer* species ($P< 0.001$, ANCOVA; Table A1-3). For a given claw size, *C. magister* had the strongest pollex cuticle and *C. oregonensis* the weakest. *Post-hoc* tests, however, revealed that most of the statistical support for interspecific variation arose from the unusually low value for *C. oregonensis*, although *C. magister* did differ from *C. antennarius* when standardized by manus length. Unfortunately, we cannot say with much confidence whether the significantly lower cuticle strength of *C. oregonensis* would also obtain for pristine, unworn claws because *C. oregonensis* are undoubtedly older, for a given body size, than the other *Cancer* species and their claws may simply have accumulated more fatigue or wear in the field prior to measurement.

Differences in our estimates of cuticle strength among species were potentially complicated by differences in cuticle thickness. Even though *Cancer oregonensis* claws have a much larger area of black cuticle at the pollex tip (G.M. Taylor, unpublished), and even though this material is likely considerably stronger than cuticle on the remainder of the claw (Melnick *et al.*, 1996, this study), *C. oregonensis* claws exhibited the lowest cuticle strength of all the *Cancer* species we examined (Table A1-3). *C. oregonensis* also had the thickest cuticle on the occlusal surface of the pollex (1.9 mm). It was nearly 2.5 times thicker than that for *C. magister* (0.7 mm), which had the highest cuticle strength (adjusted means from ANCOVA for a standard manus length of 20.9 mm, data and analysis not shown). Because the tanned and harder cuticle at the pollex tip forms only the outermost layer of the cuticle, and an additional layer of 'normal' cuticle appears to lie underneath it (G.M. Taylor, unpublished obs.), our estimates of cuticle strength, which were based on the total thickness of the cuticle, may underestimate the actual strength of this tanned cuticle and therefore potentially confound some of the differences we observed among species.

Cuticle strength of claws- assumptions

To compute ultimate tensile strength of cuticle based on failure of intact claws, we were obliged to make several simplifying assumptions. The indirect method we used, based on linearly elastic theory applied to cantilevered beams (Young, 1989), assumes: I) that the pollex or fixed finger of the claw exhibited a constant cross-section along its length, II) that the cuticle is isotropic and homogeneous, III) that shape variation along the length of the pollex, such as caused by teeth, does not create local points of stress concentration, and IV) that tensile strength was less than compressive strength (i.e., that the cuticle failed in tension).

The taper of the pollex (violation of assumption I) undoubtedly introduced some error, however Young (1989, p. 181) notes that tapers of 30° - 40°, similar to those observed in the pollex of *Cancer* claws, would only cause extreme fiber stress to be overestimated by 5% - 10%, so while our estimates of tensile strength may be somewhat high, this overestimate should be less than 10%.

Crustacean cuticle is undoubtedly neither isotropic nor homogeneous (violation of assumption II), because of its composite structure (Wainwright *et al.*, 1976). In addition, the stronger tanned material found at the tips of the fingers of many brachyuran crab claws (Melnick *et al.*, 1996) is limited to the outer layer of the cuticle in *Cancer* crabs (G.M. Taylor, unpublished obs.). Unfortunately, we cannot assess how these attributes influenced our estimates. This assumption, however, also applies to estimates of cuticle strength by others based on excised pieces of cuticle (Wainwright *et al.*, 1976; Melnick *et al.*, 1996).

Rather surprisingly, cracks did not appear to start preferentially at the base of adjacent teeth where stress might be expected to be concentrated (violation of assumption III); for example, for 22 of the 136 breaks we observed, cracks started at a point between the tip and base of a tooth, rather than at the top (where wear would have been greatest) or the base of a tooth (where fatigue might have been highest). In addition, breaking force exhibited no apparent predictable variation along the length of the pollex other than to increase towards the tip (Fig. A1-2a).

Finally, we were confident that the pollex failed in tension on the upper surface (assumption IV) because all but five of 141 claw tips fractured cleanly in one piece, indicating failure in tension of the upper margin, rather than buckling of the lower margin as observed in crab walking legs (Hahn and LaBarbera, 1993). Therefore, in spite of the potential errors introduced by estimating material properties from the behavior of a complex, intact structure, we believe our estimates are biologically realistic.

Safety-factor allometry

Pollex safety factors increased with increasing claw size for all six *Cancer* species, regardless of whether manus length (Fig. A1-4, Table A1-4a) or claw wet weight (Table A1-4b) was used as the measure of claw size. This increase was highly significant statistically for the two species for which the range of sizes was the largest ($P \leq 0.002$; *C. antennarius* and *C. productus*), and nearly significant for a third species ($P \leq 0.072$; *C. branneri*) (Table A1-4). Although the intercepts differed among species (see below), the slopes did not differ significantly (Table A1-5c,d), so we were therefore justified in computing a common slope (i.e., coefficient of allometry) via ANCOVA.

When all six species of *Cancer* crabs were analysed simultaneously via ANCOVA, claw safety factors increased $\propto$manus length$^{0.65\pm0.094}$ (mean±SE) or $\propto$claw wet weight$^{0.22\pm0.030}$ (Fig. A1-4, Table A1-5c,d). Viewed another way, the allometric coefficients for maximum biting force were significantly less than for breaking force. Maximum biting force increased $\propto$manus length$^{1.49\pm0.082}$ (Table A1-5f), while breaking force increased $\propto$manus length$^{2.13\pm0.0814}$ (Table A1-5g), yielding a difference in the coefficients of 0.64 (= 2.13 - 1.49). Therefore, regardless of how they were computed, safety factors increased approximately $\propto$manus length$^{0.6}$. If breaking force and biting force varied isometrically then the scaling coefficient for safety factors (a ratio of the two) should have been zero, so the observed coefficient was significantly greater than expected for isometry. Size-adjusted safety factors also differed among species, but these results are presented in detail elsewhere (Chapter 2).

Both relatively thicker cuticle and relatively weaker biting forces contributed to the higher safety factors of larger *Cancer* claws. When all six species were analysed together, lateral cuticle thickness of the pollex (dimensions *h* and *i*, Fig. A1-1) increased $\propto$manus length$^{1.31\pm0.078}$ (Table A1-5h), so cuticle cross-sectional area would increase $\propto$manus length$^{2.6}$. Since breaking force should scale $\propto$cross-sectional area for linearly elastic structures loaded in bending and of constant material properties and shape (see Eq. 1 in methods), this coefficient significantly exceeded that for breaking force ($\propto$manus length$^{2.13}$; $P < 0.001$). Furthermore, because of the longer time between molts, the cuticle of larger claws in our samples would likely have accumulated more stress cracks and wear than smaller ones, so the observed coefficient of 2.13 likely underestimates that for pristine claws. Therefore, the allometric increase in cuticle thickness alone would be sufficient to yield a significant positive allometry for safety factors in pristine claws even if relative biting force did not decline with increasing size, and we would expect an even higher positive allometry than the 0.6 actually observed had we been able to use pristine claws.

The lower than expected scaling coefficient for maximum biting force was not an artifact of size-dependence in our measurement protocol because: a) the gape angle at which biting force was measured was kept constant for all claw sizes, b) the location of the load wire scaled isometrically ($\propto$manus length$^{0.96\pm0.025}$) (data not shown), c) the transducers were re-calibrated before and after each set of measurements, and d) the scaling coefficients did not differ among species, even though average claw length differed among species by more than three-fold. Nor was it due to size-dependent changes in mechanical advantage. In all but one species, mechanical advantage did not vary significantly with size. In *C. productus*, mechanical advantage actually increased with increasing size, so the lower-than-expected coefficient of allometry for maximum biting force was even more puzzling.

Potential limitations due to small sample sizes and narrow size ranges

Coefficients of allometry based on small sample sizes or narrow size ranges can be misleading because of statistical uncertainties (LaBarbera, 1989). For only two species we studied did the size range approach or exceed a factor of two (*Cancer antennarius* and

C. productus) and, perhaps unsurprisingly, we most commonly obtained statistically significant associations with claw size for these two species (Table A1-1 and IV). We may thus be premature in concluding that safety factors increase allometrically, and in the same fashion, in all six *Cancer* species.

However, for all six species coefficients of allometry for safety factors were nonetheless positive in spite of small sample sizes and size ranges for four of them (Table A1-4), and for one of the remaining species the slope was nearly significant ($P < 0.072$, *C. branneri*). In addition, we could not reject the hypothesis that the slopes were statistically indistinguishable using ANCOVA (Table A1-5c,d), even for the species for which we had reasonable size ranges. Therefore, with the present data we are obliged to accept the simpler hypothesis that safety factors increase similarly with increasing claw size for all six *Cancer* species.

Discussion

Cuticle strength in Cancer crab claws

In spite of the functional significance of claws (Warner, 1977; Brown *et al.*, 1979; Seed and Hughes, 1995), and the impact that claw failure has on feeding ability (Juanes and Hartwick, 1990; Juanes and Smith, 1995), little is known about their mechanical properties other than biting force or mechanical advantage (Warner and Jones, 1976; Elner, 1978; Elner and Campbell, 1981; Blundon, 1988; Kaiser *et al.*, 1990; Levinton and Judge, 1993; Levinton *et al.*, 1995; Preston *et al.*, 1996). In addition, we are aware of only three reports of tensile strength in crustacean cuticle, and only one was for claw cuticle. The tensile strength of carapace cuticle reported for two portunid crabs is approximately 30 MNm^{-2} [Wainwright *et al.* (1976, Table 5.3) for *Carcinus maenas*, and Hepburn *et al.* (1975) for *Scylla serrata*], and Melnick *et al.* (1996) report fracture strength in three-point bending of 109 MNm^{-2} in the black cuticle of the claw tips and 32 MNm^{-2} ($N = 10$) in the lighter-colored cuticle of the manus in the stone crab (*Menippe mercenaria*). Although we computed stress on intact claws, as opposed to excised pieces of cuticle loaded in three-point bending, our estimates of breaking strength in *Cancer* claws (40 - 120 MNm^{-2}) nonetheless agree quite well with those of Melnick *et al.* (1996), in spite of the simplifying assumptions we were obliged to make (see *Cuticle strength of claws- assumptions* in the Results).

Our results (Fig. A1-2b, Table A1-2a) also support the conclusion of Melnick *et al.* (1996), that the distal cuticle on the fingers of brachyuran claws, often black in color, is a stronger material than other claw cuticle. This stronger material towards the claw tip ensures that the force at which the pollex breaks remains roughly constant along its length (Fig. A1-2a), even though the cross-sectional area declines distally. It may also increase the abrasion resistance of the claw tip, since crabs forced to feed for extended times on hard-shelled prey often exhibit severe wear of the teeth and tip of both the dactyl and pollex (A.R. Palmer, unpublished obs.). Material properties of the claw cuticle therefore appear finely tuned to the mechanical demands placed upon it.

Within- and among-species variation in cuticle strength

Unlike previous studies of cuticular properties, we were able to assess cuticle-strength variation as a function of claw size, both within and among closely-related crab species. Somewhat surprisingly, cuticle strength decreased with increasing claw size both within and among the six *Cancer* species we examined (Fig. A1-3).

Two observations suggest this decline may reflect increased wear and fatigue that larger claws experienced before we measured breaking strengths. First, the intermolt interval increases with increasing size in *Cancer* crabs (Orensanz and Gallucci, 1988) and although we attempted to use crabs in mid-intermolt throughout, larger crabs may have been further away from their most recent molt and their claws may thus have experienced more wear or fatigue. Second, *C. oregonensis*, whose claws exhibited generally lower cuticle strength for a given claw size (Fig. A1-3), matures at a considerably smaller body size (<25 mm carapace width) than the other *Cancer* species we studied (generally > 60 mm carapace with) (Orensanz and Gallucci, 1988). Here again, because intermolt intervals are longer for older crabs, claws of *C. oregonensis* may have accumulated more wear or fatigue before we measured their breaking strength, compared to similar-sized claws in presumably younger individuals of the other species. Regardless of the cause of this relationship, conclusions about differences in cuticle strength among species must take into account the effect of claw size.

Indeed, after controlling for the effects of claw size, cuticle strength varied by up to 100% among the six *Cancer* species we examined (Table A1-3). Even though potentially confounded by differences in cuticle thickness (see *Cuticle strength of claws-patterns* in the Results), these interspecific differences in size-adjusted cuticle strength correlated significantly with interspecific differences in size-adjusted safety factors (Fig. 7c of Taylor *et al.*, in press): species with weaker cuticle had higher safety factors ($N= 6$, $r= 0.92$, $P = 0.008$ when standardized by manus length, and $r= 0.82$, $P= 0.045$ when standardized by claw weight). Therefore differences in safety factors among species appear to have evolved at least in part in response to differences in mechanical properties of their cuticle.

Allometry of skeletal safety factors in crab claws

The higher safety factors we observed in larger claws of all six *Cancer* species were consistent with theoretical predictions. Larger claws were expected to have larger safety factors because: a) unpredictability of claw strength should increase in larger crabs due to the longer time to accumulate stress cracks and wear between molts, b) the costs of lost or damaged claws (Juanes and Smith, 1995) will be more prolonged or severe for larger crabs, and c) larger crabs likely experience a greater range of extreme forces because claws are used increasingly for aggression (Juanes and Smith, 1995). Therefore this size-dependence appears adaptive.

But why does maximum muscle stress, which has the biggest impact on the size-dependence of safety factors, decline with increasing claw size? Similar declines with increasing claw size in stone crabs (Blundon, 1988), male fiddler crabs (Levinton and Judge, 1993) and lobsters (Elner and Campbell, 1981) suggest a general pattern that remains a significant unsolved phenomenon in our understanding of claw mechanics and evolution. Perhaps larger crabs actively restrain the maximum stress they generate to avoid damaging their claws, as suggested by Taylor (Chapter 2). Alternatively, larger claws may generate lower stresses because of some as yet unidentified physiological constraints. The former would support our interpretation that higher safety factors in larger claws are adaptive, whereas the latter would not.

The scaling relation between maximum force and a linear claw dimension might possibly be influenced by the bipinnate arrangement of muscles in crustacean limbs (Warner and Jones, 1976), but we believe this is unlikely. In bipinnate muscles, twice as many muscle fibers attach per unit area of apodeme (the crustacean tendon) because they attach on both sides. Bipinnate muscles therefore generate more force per unit volume than linear muscles (Goldspink, 1977). In addition, muscle fibers attach to the apodeme at an angle, so their per-fiber contribution to the final biting force is less than in typical vertebrate skeletal muscle where fibers lie roughly parallel to the tendon (Goldspink, 1977). Nonetheless, these two factors only affect the force produced *per unit area of apodeme*. They do not affect the expected allometric relation between maximum force and claw length unless they too vary allometrically. Maximum biting force should therefore still increase $\propto$apodeme area (i.e., $\propto$claw length$^{2.0}$) for bipinnate muscles, just as it should for linear muscles.

The higher safety factors we observed in larger claws did not appear to affect the probability of failure in the field. Among the six *Cancer* species we examined 9.2% of crabs had injured claws and 28.9% were missing or regenerating one or both claws (N= 671). As injuries leading to death would have been under-represented, actual injury rates were probably higher. Significantly, in the two species for which we had adequate sample sizes, neither the incidence of regenerating or injured claws varied significantly with claw size: *P*= 0.44 and 0.94 respectively for *C. productus* (N= 285 crabs: one or both claws missing/regenerating- 33.0% or injured- 8.4%) and *C. gracilis* (N= 99 crabs: one or both claws missing/regenerating- 41.4% or injured- 17.2%) (Chapter 2). However, because larger claws should accumulate more wear during their longer intermolt intervals and thus be more likely to fail, their higher safety factors nonetheless appear to have reduced the probability of failure to levels similar to those of smaller crabs.

Allometry of skeletal safety factors in other taxa

In other taxa, safety factors vary in many ways with increasing body size or age. As body size or age increases within species, safety factors may either increase, decrease, or exhibit a U-shaped pattern (Table A1-6a). Within many molluscs species shell weight or thickness increases disproportionately with increasing body size (Currey, 1977; Palmer, 1981, 1992), suggesting that safety factors also increase with body size (Preston *et al.*, 1996) since the sizes of shell-breaking predators, and hence potential load distribution, should remain approximately the same. Only for bovid horns do safety factors appear not to change with increasing body size (Kitchener, 1991).

Rather few extensive studies of interspecific variation have been conducted, but safety factors appear to vary less with size among species of mammals and trees than within species (Table A1-6b). Only for non-woody plants and palm trees do safety factors appear to vary substantially with size among species.

These patterns raise an obvious question: to what extent is intraspecific variation in safety factors adaptive? Although the data are too few to draw any generalities with confidence, the patterns in Table A1-6a suggest that increases in safety factors with increasing size may more commonly reflect adaptive variation (the outcome of selection for genotypes that specifically induce changes in safety factors) whereas decreases in safety factors may signal some form of constraint (non-adaptive variation resulting from peculiarities of the ways in which organisms grow). The evidence for crab claws seems clear: longer intermolt intervals at larger size, increased variability in cuticle strength due to wear and fatigue, and increased cost of failure, should all favor higher safety factors (this study). Similarly, for many molluscs and other organisms whose defensive skeletons permit an *'escape in size'* (Paine, 1976; Palmer, 1990), larger size results in lower vulnerability, therefore higher safety factors appear adaptive.

In contrast, safety factors decline with increasing size in the walking legs of insects and arachnids (Prang, 1977) and in the *'rind-core'* type stems of many non-woody plants (Niklas, 1989, 1995). Indeed, for both arthropod limbs (Currey, 1967) and 'rind-core' type plant stems (Niklas, 1994), mechanical limits to strength appear to determine the upper limit to body size, which strongly implies that safety factors decline with increasing proximity to a 'critical' size and that this decline is not adaptive. One might also expect the safety factors of long bones in the walking legs of large-bodied vertebrates to decline non-adaptively with increasing body size, because of an unavoidable tradeoff between the mechanically necessary allometric increases in cross-sectional area required to support a greater body mass and the increased cost of producing and transporting heavier skeletal elements (Schmidt-Nielsen, 1984). Similarly, any time the future contribution to fitness declines with increasing size or age, safety factors might decrease non-adaptively, as observed in the long bones of human females (Table A1-6a, Biewener, 1993).

Two relations in the preceding discussion require additional comment. First, the argument for adaptive size-dependence in the safety factors of molluscan shells is not entirely untainted by potential constraints. In marine gastropods, and likely many heavily skeletonized marine invertebrates, the maximum rate of body growth at small size may be constrained by the maximum rate of calcification, which in turn may be limited by the physical chemistry of crystal growth (Palmer, 1981). This *'calcification-rate constraint'* imposes a cruel tradeoff on small individuals: rapid growth is incompatible with increased skeletal defense. So, while the increase in relative shell thickness with increasing size observed in so many molluscs is likely adaptive, because it reduces vulnerability to shell-breaking predators, the lower relative shell weight at small size, which is responsible for the observed trend, may be strongly influenced by the 'calcification-rate constraint'. Therefore, perhaps unsurprisingly, not all positive correlations between safety factors and body size may arise for purely adaptive reasons.

Second, whereas declines in safety factors with increasing size may typically signal some kind of constraint, such declines might be adaptive under unusual situations where controlled failure may enhance fitness. For example, fragmentation of corals may actually promote dispersal and colonization (Highsmith, 1982) but at small size competitive interactions may favor larger colonies (Sebens, 1983). Under these conditions, selection should favor reduced vulnerability to fragmentation at small size but enhanced vulnerability at larger size. Clearly, this type of adaptive decline in safety factors would be limited to colonial organisms.

Table A1-1. Crab size, load position* and number of bites obtained per claw for six species of *Cancer* crabs.

Species	n_i	Carapace width (mm) Mean (SE, min., max.)	n_c	Load position (±SE)*	Mean # bites per claw (±SE)
C. antennarius	14	76.1 (3.20, 56.4, 99.1)	28	0.89 (0.005)	7.8 (0.07)
C. branneri	8	51.0 (1.30, 44.9, 55.5)	16	0.92 (0.003)	6.9 (0.48)
C. gracilis	9	91.4 (3.13, 74.9, 103.8)	18	0.94 (0.002)	7.1 (0.75)
C. magister	12	122.6 (2.58, 111.4, 139.2)	23	0.94 (0.004)	7.8 (0.42)
C. oregonensis	15	33.1 (0.76, 29.4, 39.9)	30	0.86 (0.004)	7.4 (0.18)
C. productus	16	89.6 (6.26, 60.1, 130.1)	31	0.91 (0.006)	8.3 (0.20)

n_i = number of individual crabs, n_c = number of claws for which biting force measurements were obtained; not all claws were included in all analyses (see methods). *Position at which biting force or breaking strength was measured, expressed as a proportion of the pollex length (line d - e, Fig. A1-1).

Table A1-2. Size-dependence of pollex cuticle-strength for claws from six species of *Cancer* crabs.* See Fig. A1-2b and Fig. A1-3 for data.

Species	*n*	Slope (±SE)	Intercept (±SE)	*P*	*r*
a) log(ultimate stress, MNm-2) (*Y*) vs standardized pollex position (*X*)					
1- *C. antennarius*	28	0.178 (0.0953)	1.715 (0.0200)	0.073	0.344
2- *C. branneri*	12	0.427 (0.1537)	1.817 (0.0325)	0.019	0.66
3- *C. gracilis*	12	0.195 (0.1100)	1.684 (0.0285)	0.106	0.49
4- *C. magister*	17	0.262 (0.2060)	1.630 (0.0563)	0.223	0.312
5- *C. oregonensis*	28	0.198 (0.1334)	1.712 (0.0256)	0.151	0.279
6- *C. productus*	28	0.618 (0.1363)	1.377 (0.0250)	<0.001	0.664
7- All pooled	125	0.213 (0.0582)	1.702 (0.0136)	<0.001	0.313
8- All pooled**	60	0.178 (0.0971)	1.716 (0.0171)	0.073	0.234
9- All pooled§	125	0.162 (0.0478)	-0.095 (0.0112)	0.001	0.292
b) log(ultimate stress, MNm-2) (*Y*) vs log(manus length, mm) (*X*)					
1- *C. antennarius*	28	-0.615 (0.2023)	2.642 (0.0183)	0.005	0.512
2- *C. branneri*	12	-1.123 (0.8404)	3.352 (0.0399)	0.211	0.389
3- *C. gracilis*	12	-0.433 (0.4542)	2.408 (0.0313)	0.363	0.289
4- *C. magister*	17	-1.146 (1.3504)	3.562 (0.0578)	0.409	0.214
5- *C. oregonensis*	28	-0.575 (0.7015)	2.448 (0.0263)	0.42	0.159
6- *C. productus*	28	-0.811 (0.1776)	2.926 (0.0250)	<0.001	0.667
7- All combined†	125	-0.751 (0.1447)	2.842 (0.2042)	<0.001	0.573
8- All combined††	125	-0.624 (0.1352)	0.820 (0.1908)	<0.001	0.591

* Least-squares linear regression equations. **- excluding claws that broke at more than 30° from the load vector (Fig. A1-2b). §- based on residuals from separate regressions of log(ultimate stress) vs. log(manus length) for each species. † and ††- common slope from a one-factor ANCOVA with species as the grouping variable. ††- ANCOVA recomputed using residuals from a single regression of log(ultimate stress) vs. standardized pollex position for all species combined. ±SE- standard error. *r*- correlation coefficient.

Table A1-3. Average, size-adjusted pollex cuticle-strength for claws from six species of *Cancer* crabs.

Species	Mean (SE)*log (ultimate stress)	Detransformed mean ultimate stress (MNm-2) by length*	Post-hoc**	by weight†	Post-hoc**
C. magister	1.967 (0.0444)	92.7	a	80.7	a
C. branneri	1.919 (0.0434)	83.0	ab	83.6	a
C. gracilis	1.884 (0.0447)	76.6	ab	70.2	a
C. productus	1.851 (0.0281)	71.0	ab	66.1	a
C. antennarius	1.839 (0.0271)	69.0	b	71.7	a
C. oregonensis	1.641 (0.0474)	43.8	c	50.8	b

* Adjusted means (±SE) from a one-factor ANCOVA (species was the grouping factor; see Table A1-2b-7 for regression statistics) for a common manus length of 20.9 mm. Differences among adjusted means were highly significant ($P < 0.001$). ** Results from a Tukey-Kramer post-hoc test (Sokal & Rohlf, 1995) on adjusted means (prior to detransformation); letters indicate means that were not significantly different from each other at a table-wide significance level of 0.05. † detransformed means for a standard claw wet weight of 3.6 g from a similar one-factor ANCOVA using claw weight as opposed to manus length as the covariate (regression statistics not shown).

Table A1-4. Size-dependence of pollex safety-factors for claws from six species of Cancer crabs.*

Species	*n*	Slope (±SE)	Intercept (±SE)	*P*	*r*
a) log(safety factor) (*Y*) vs log(manus length, mm) (*X*)					
1- *C. antennarius*	28	0.827 (0.2393)	-0.673 (0.0215)	0.002	0.561
2- *C. branneri*	13	0.900 (0.4513)	-0.692 (0.0230)	0.072	0.515
3- *C. gracilis*	14	0.609 (0.3645)	-0.430 (0.0228)	0.121	0.434
4- *C. magister*	21	0.203 (0.3507)	0.079 (0.0153)	0.57	0.132
5- *C. oregonensis*	30	0.178 (0.3646)	0.446 (0.0138)	0.63	0.092
6- *C. productus*	30	0.633 (0.1520)	-0.483 (0.0223)	<0.001	0.618
b) log(safety factor) (*Y*) vs log(claw wet wt., g) (*X*)					
1- *C. antennarius*	28	0.247 (0.0734)	0.269 (0.0218)	0.002	0.551
2- *C. branneri*	13	0.307 (0.1514)	0.328 (0.0230)	0.067	0.522
3- *C. gracilis*	14	0.211 (0.1400)	0.282 (0.0233)	0.157	0.399
4- *C. magister*	21	0.103 (0.1175)	0.292 (0.0150)	0.392	0.197
5- *C. oregonensis*	30	0.060 (0.1138)	0.633 (0.0138)	0.599	0.1
6- *C. productus*	30	0.216 (0.0485)	0.256 (0.0218)	<0.001	0.645

* Least-squares linear regression equations; slopes correspond to coefficients of allometry. Safety factor- ratio of breaking force / maximum bite force; isometry for safety factors should be 0 (see text). ±SE- standard error. *r*- correlation coefficient.

Table A1-5. Overall size-dependence of mechanical and morphological attributes of *Cancer* crab claws.*

Slopecomm (±SE)	Range (n_s)†	r^2_{comm}	*P*	P_{sp}
a) log(ultimate stress, MNm-2) (*Y*) vs standardized pollex position (*X*)				
0.30 (0.059)	0.43 - 0.62 (2)	0.32	<0.001	0.2
0.21 (0.055)**	(none significant)	0.11	<0.001	0.98
b) log(ultimate stress, MNm-2) (*Y*) vs log(manus length, mm) (*X*)				
-0.75 (0.144)	-0.81 - -0.62 (2)	0.32	<0.001	0.96
-0.62 (0.135)**	-0.64 - -0.58 (2)	0.35	<0.001	0.97
c) log(safety factor) (*Y*) vs log(manus length, mm) (*X*)				
0.65 (0.094)	0.63 - 0.83 (2)	0.58	<0.001	0.72
d) log(safety factor) (*Y*) vs log(claw wet wt., g) (*X*)				
0.22 (0.030)	0.22 - 0.25 (2)	0.59	<0.001	0.83
e) log(median-maximum biting force, N) (*Y*) vs log(manus length, mm) (*X*)				
1.52 (0.072)	0.95 - 2.21 (6)	0.9	<0.001	0.045
f) log(extreme-maximum biting force, N) (*Y*) vs log(manus length, mm) (*X*)				
1.49 (0.082)	0.93 - 2.36 (6)	0.88	<0.001	0.081
g) log(breaking force, N) (*Y*) vs log(manus length, mm) (*X*)				
2.13 (0.081)	1.54 - 2.54 (5)	0.88	<0.001	0.35
h) log(lateral cuticle thickness of pollex‡, mm) (*Y*) vs log(manus length, mm) (*X*)				
1.31 (0.078)	1.20 - 1.92 (5)	0.76	<0.001	<0.001

* $n = 136$ claws (usually two per crab) for all analyses except a and b, for which $n = 125$. Safety factor- ratio of breaking force / maximum bite force. Slope_{comm}- common slope from a one-factor ANCOVA (species was the grouping factor); expected slopes for isometry relative to manus length are: 1.0 for ultimate stress (b), 0.0 for safety factors (c,d), 2.0 for biting force (e,f), 2.0 for breaking force (g), and 1.0 for cuticle thickness (see text). ±SE- standard error. n_s= number of statistically significant slopes for individual *Cancer* species out of six. r^2_{comm} - coefficient of determination for common slope from ANCOVA. *P*- probability that the common slope did not differ from zero. P_{sp} - probability that slopes did not differ among species. † Range of slopes among species exhibiting a significant slope. ** the same ANCOVA design but conducted on residuals obtained separately for each species from the regressions in Table A1-2. ‡ average of dimensions **h** and **i** in Fig. A1-1. See Tables A1-2, A1-3 and A1-4 for regression statistics for individual species.

Table A1-6. Dependence of safety factors on size or age in various taxa and structures.

Taxon & trait	Safety factor Load type	Dependence		Reference
a) Intraspecific variation				
Human female long bones	locomotion	A	decrease*	1
Bovid horns	fighting	S/A	none**	2
Spider walking legs	locomotion	S/A	decrease	3
Cockroach walking legs	locomotion	S/A	decrease	4
Crab claws	biting force	S/A	increase†	5
Mollusc shells	break force	S/A	increase††	6
Kelp stipe	wave stress	S	none	7
Equisetum stems	self-loading	S	decrease	8
Shade-intolerant tree trunks	self-loading	S/A	decrease	9
Early-successional tree trunks	self-loading	S/A	decrease	10
Shade-tolerant tree trunk	self-loading	S/A	U-shaped	11
Late-successional tree trunks	self-loading	S/A	U-shaped	12
b) Interspecific variation				
Mammalian long bones	locomotion	S	none§	13
Tree trunks	self-loading	S	none††	14
Tree trunks	self-loading	S	none§§	15
Various non-woody plant stems	self-loading	S	decrease¶	16
Herbaceous plant stems	self-loading	S	decrease¶¶	17

S- explicitly tests for size-dependence, A- explicitly tests for age-dependence, S/A- size- and age-dependence were confounded. * due to osteoporesis; inferred assuming load distributions were not age-dependent. ** true for 8 species. † true for 6 species. § interspecific variation over >3 orders of magnitude of body mass. †† many species. §§ 56 species. ¶ multiple species: mosses (N=40), pteridophytes (N= 16), dicot herbs (N= 120, palms (N= 17). ¶¶- for 76 species. References: 1-Biewener (1993), 2-Kitchener (1991), 3-Prang (1977), 4-Prang (1977), 5-this study), 6-Preston et al. (1996, see text), 7-Friedland & Denny (1995), 8-Niklas (1989), 9-King (1991), 10-Claussen & Maycock (1995), 11-King (1991), 12-Claussen & Maycock (1995), 13-Biewener (1990), 14-McMahon & Kronauer (1976), 15-Niklas (1994), 16-Niklas (1994), 17-Niklas (1995)

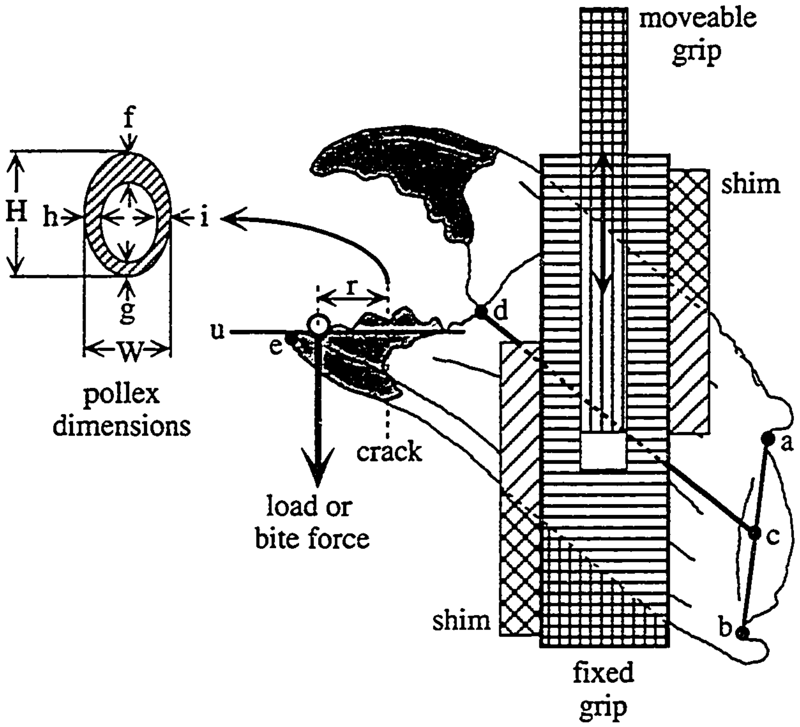

Figure A1-1. Clamping orientation and dimensions of a Cancer claw. (a) and (b) are the dorsal and ventral hinge points of the manus, and (c) is the midpoint between them. Manus length: line-segment (c)-(d) (i.e., chela length excluding the pollex). Pollex (=fixed finger) length: line-segment (d)-(e). Moment of the load at failure: the double-headed arrow labelled r. Moveable (vertical shading) and fixed (horizontal shading) pieces of plexiglass gripped the claw at approximately the midpoint of the manus and softer wooden shims (angled-shading) reduced the risk of twisting and unwanted damage to claws under load; cross-hatching indicates the plexiglass or shim was solid at that point. These plexiglass pieces and shims had notches cut in them to fit either the right or left claw as snugly as possible (not visible in the figure as they were parallel to the plane of view). Claws were aligned so the load was oriented perpendicular to the 'gum line' (=occlusal surface) of the pollex (line u; a best-fit line through the bases of the teeth). The load was applied just inside the tip of the pollex (open circle). Pollex height (H) and width (W), as well as cuticle thickness at the dorsal (f), ventral (g), medial (h) and lateral (i) margins, was measured at the point of fracture ('crack') in a plane parallel to the load vector and perpendicular to the long axis of the pollex.

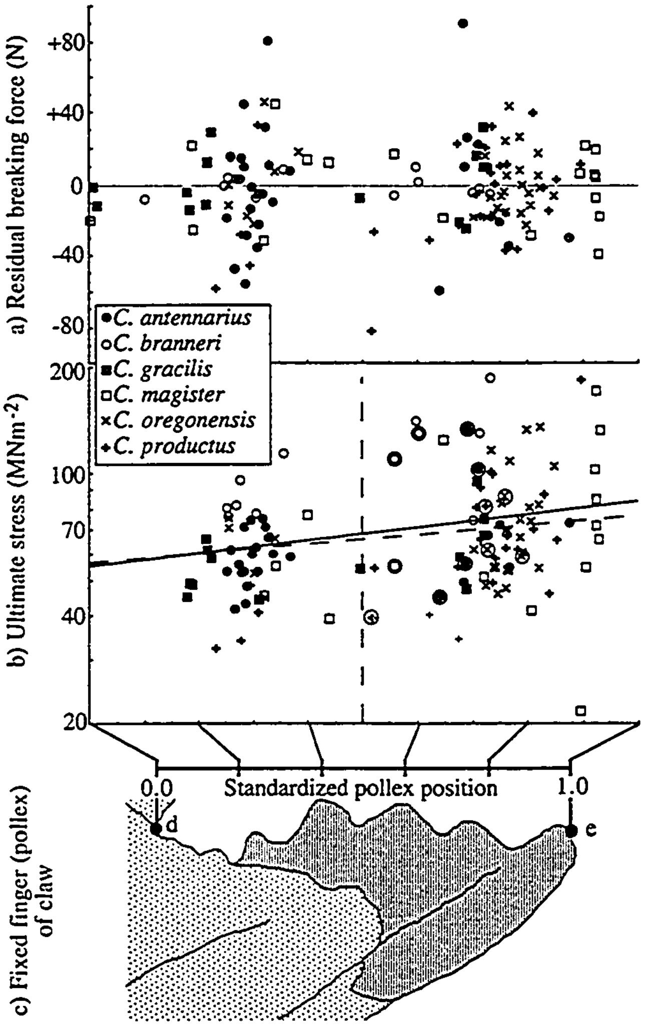

Figure A1-2. a) Deviation of breaking force from that expected for a given claw size (manus length), and b) the computed ultimate stress (sb; mega-Newtons per meter squared, MNm^{-2}) at which the cuticle failed, both as a function of standardized position along the upper margin of the pollex between the insertion point of the closer apodeme (landmark d) and the tip (landmark e) for six species of *Cancer* crabs. (c) The pollex, or fixed finger, of a *C. productus* claw illustrating how 'standardized position' was determined; claws of other *Cancer* species differ in shape and number of teeth (Nations, 1975). The darker portion of the finger is often black in life, and both harder and stronger (Melnick et al., 1996). Points surrounded by circles above 0.5 standardized pollex length indicate claws for which the fracture plane did not deviate by more than 30° from the load vector (see methods). The solid line in (b) indicates a least-squares linear regression through all the data, whereas the dashed line applies only to claws for which the fracture plane did not deviate by more than 30° from the load vector (see Table A1-2a7,8 for regression statistics).

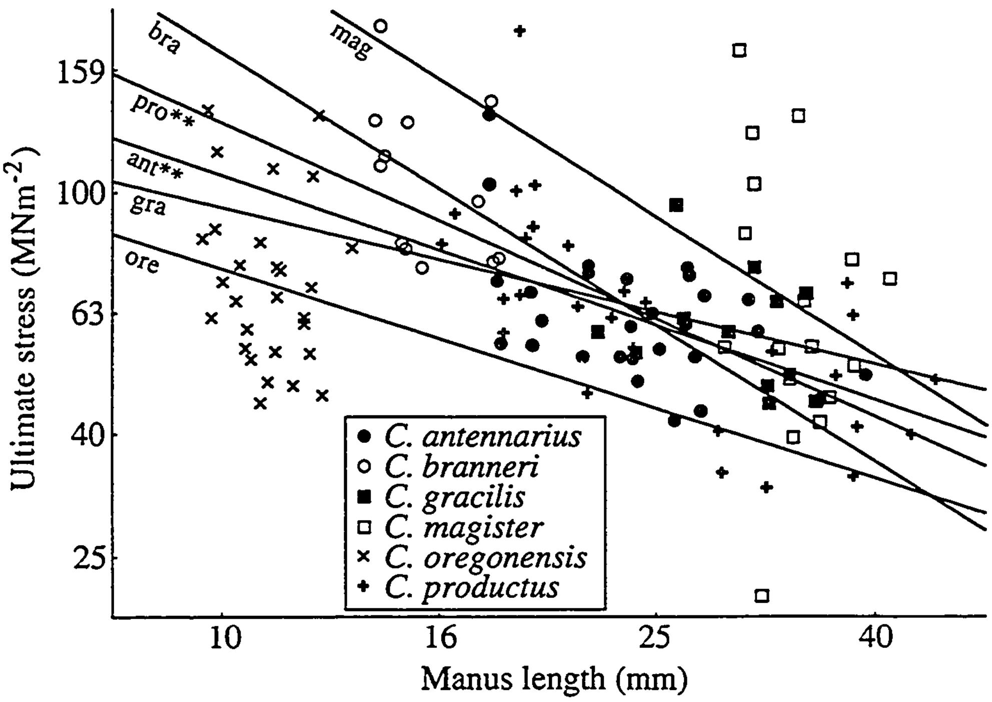

Figure A1-3. Cuticle ultimate stress (sb; mega-Newtons per meter squared, MNm-2) as a function of claw size (manus length, mm) for six species of Cancer crabs. Solid lines indicate least-squares linear regressions for each species. See Table A1-2 for statistics. ** P< 0.01. Note that both axes are on a logarithmic scale. Three letter abbreviations adjacent to each line indicate the first three letters of each species' name.

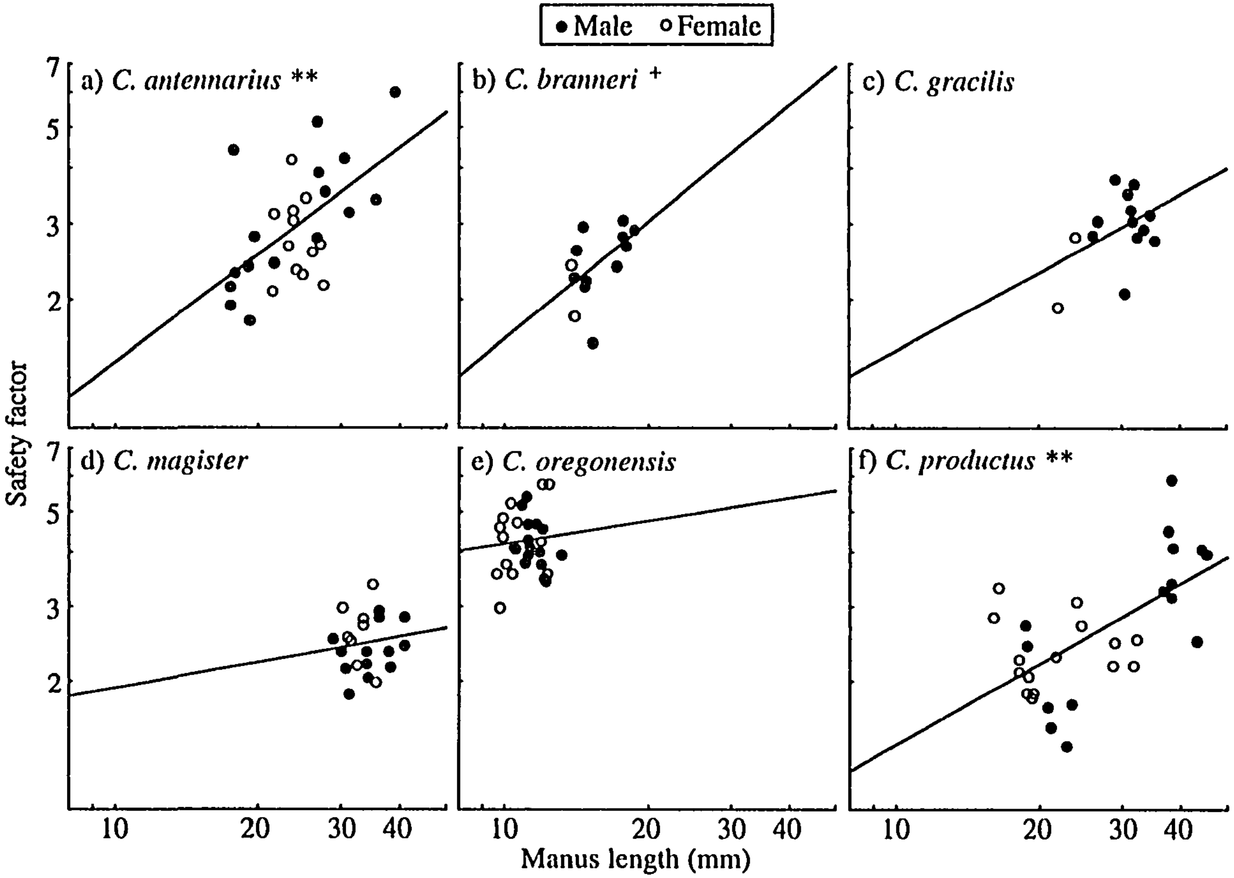

Figure A1-4. Size-dependence of claw safety factors [breaking force (N) / extreme-maximum biting force (N)] for six species of Cancer crabs. Each point represents an individual claw. Lines indicate least-squares linear regressions [see Table A1-4a for regression statistics and Table A1-5c for ANCOVA results; + P< 0.07, ** P< 0.005]. Note that both axes are on a logarithmic scale.

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Appendix 2. Interspecies Scaling of Resting Sarcomere Length and Maximum Muscle Stress *

Introduction

Huxley and Niedergerke (1954) predicted nearly fifty years ago that muscle stress (force per unit area) should increase with increasing resting sarcomere length (SL). Among species, this prediction has not been tested rigorously because studies tend to focus on vertebrate or insect-flight skeletal muscle, which exhibit little variation in resting SL. Unlike vertebrate and insect-flight muscles, which yield stresses from 10 - 30 Ncm^{-2}, the muscle in decapod crustacean claws can generate stresses from 40 to 200 Ncm^{-2} (refs. 1-8). Whether these high stresses result from simple differences in resting SL, or from other differences in the contractile machinery such as filament geometry and kinetics, remains a matter of debate[8,9]. I report here that for the claws of six species of *Cancer* crabs, maximum muscle stress increased with increasing resting SL. A more extensive analysis, incorporating additional data from the literature[1], revealed that stress scales isometrically with resting SL among species, as predicted by the sliding filament model[10-12]. Therefore other muscle or filament traits need not be invoked to explain the high stresses generated by crustacean claws.

The sliding filament model of muscle contraction[10,11] makes a simple prediction: when other factors are equivalent, maximum muscle stress should increase isometrically with resting SL[12]. It should increase because force is proportional to the number of myosin-actin crossbridge sites that can form within each half-sarcomere and additional active myosin heads are assumed with increasing filament length. The increase should be isometric with changes in sarcomere length because stress changes linearly with overlap of thick and thin filaments[12] and structural distance between myosin heads is uniform along the thick-filament backbone[13]. Although the sliding filament model has been widely accepted as it portrays the dependence of active tension on changing SL with contraction[12,14], empirical evidence for a dependence of maximum muscle stress on resting SL among species has remained elusive.

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* A version of this appendix has been submitted for publication. Taylor. Nature.

Methods

Experimental animals

Six northeastern Pacific *Cancer* species — *C. antennarius*, *C. branneri*, *C. gracilis*, *C. magister*, *C. oregonensis*, and *C. productus* — were collected from various shallow water sites in the vicinity of the Bamfield Marine Station, Bamfield, British Columbia, Canada. To analyze claw bite force performance, several mid-intermolt crabs of each species were selected based on estimated claw wear (claw index 2, as described in Chapter 2). Crabs were housed individually in plastic mesh containers (20 cm x 14 cm x 9 cm), which were submerged in large fiberglass aquarium supplied with running sea water (salinity 32 ‰, 10-12°C). Biting forces were measured within 7 days of collection, because maximum force and consistency tended to decline with time in the laboratory (Chapter 3).

Claw biting force measurements

This was done as previously described[22], with minor modifications and actual bite-force values are reported elsewhere (Chapter 2). In brief, individual crabs were removed from the water and encouraged to grasp forcefully a strain gauge apparatus[22], which was adjusted to 60% of maximum gape for each claw. The apparatus was calibrated before and after each session with known weights that covered the range of bite-forces. The average of these two calibration curves was used to digitize biting forces in Newtons from the original chart recordings. Each session included bite measurements from both the right and left claws, in succession, of 7 - 10 crabs. No more than two bite-force measurements were obtained for a single claw on any given day, and the mean number of bites used to asses the biting-force of a claw ranged from 6.9 - 8.2.

Muscle stress calculations

Claws were autotomized from crabs and drawn via a camera-lucida attached to a dissecting microscope, in a view perpendicular to the plane of dactyl rotation. All linear measurements, such as manus height and lever length 1 and 2 of the dactyl, were digitized from individual claw drawings. Apodemes were dissected and surface areas measured by digitizing projected outlines. Muscle stress was then calculated by the formula **$S = Fl/A\sin 2\Theta$**, where **Fl** is the force applied to the base of the dactyl by the closer muscle, **A** is the area of one side of the apodeme and **Θ** is the mean angle of pinnation of fibers[5]. Angle of pinnation measurements were taken from other similar-sized individuals of each *Cancer* species. To ensure representative angles of pinnation of those claws used in the biting-force measurements, claws were fixed (10% buffered formalin) at approximately 60% of maximum claw gape. Angles of six to eight fibers were measured from the mid section of the closer muscle for each claw. Average (±SE) angles of pinnation were: *C. antennarius* (36.7±0.71°, N = 27), *C. branneri* (36.6±0.91°, N = 14), *C. gracilis* (34.6±0.82°, N = 16), *C. magister* (33.6±0.96°, N = 16), *C. oregonensis* (37.0±0.92°, N = 14), and *C. productus* (31.5±0.70°, N = 22).

Measurement of filament lengths

Sarcomere and A-band length measurements were obtained from other crabs similar in size to those used for biting forces measurements. Claw-closer muscles were fixed as described in ref. 5. Sampling of fibers from the closer muscle of each claw were restricted to a section that ran dorsal-ventral mid-way along the manus. Histochemical analysis supported a restricted sampling regime, because closer muscles of 3 species (*C. productus*, *C. oregonensis*, and juvenile *C. magister*) stained at a uniform intensity over its length for both myofibrillar ATPase and NADH diaphorase (G.M.T. unpubl.). The mid section was divided into four smaller regions, which are defined by exoskeletal carinae running in a proximo-distal direction along the manus. Exoskeletal carinae are homologous structures in *Cancer*[23], and therefore sampled sites were consistent among species. From each of these four regions, 10 fiber were teased apart at random from wet mount preparations. From a fiber, a single resting SL and its A-band length was measured with a phase-contrast microscope (magnification 500x) via a camera-lucida and a digitizing tablet. Therefore, a mean SL for a given claw is the average of 40 randomly sampled sarcomeres within 4 predetermined regions (Table A2-2).

Determination of the scaling coefficient of allometry

Data from the literature were compiled, plotted and analyzed to define the scaling relationship shown in Fig. A2-2. Data and their sources are available from the author. I restricted my survey on Vertebrata to a recent review[1], except for three stress values calculated indirectly for 3 human muscles[24]. SLs were not reported, so an average SL (2.7 μ m) was estimated from mammalian muscle reported in ref.1. In spite of the considerable variation in SL displayed by the Uniramia[20], muscle performance data in the literature were sparse (N = 8). All uniramian stress values were from insect-flight muscle, also reported in ref. 1, except for a single high stress value of 70.5 (Ncm^{-2}) for the hind leg tibia extensor of *Schistocerca gregaria*[25].

Results and Discussion

Within all six species of *Cancer* crabs examined, SL increased with A-band length (Fig. A2-1). Therefore the resting SLs reported here were not significantly confounded by differential contraction of the muscles, and provide a reliable estimate of the size of the fundamental contractile unit. A-bands correspond to thick filaments and thus provide a more reliable measure of the size of the contractile unit (i.e., number of potential myosin-actin crossbridge sites), but most studies tend to report SLs because, although they will vary depending on the state of muscle contraction, they are easier to measure.

Among species of *Cancer* crabs, maximum muscle stress increased with increasing SL (Fig. A2-2, open circles) (see Table A2-1 & A2-2). This same relation was observed when published values for claws from other crustaceans were included (Fig. A2-2, solid symbols). Significantly, when all crustaceans were considered together, the slope of this relationship did not differ from isometry (Fig. A2-2). Therefore, for crustacean claws, maximum muscle stress, and as a consequence maximum biting force, both increased with SL as predicted by the sliding filament model. Increased maximum biting force therefore not only evolved via increases in relative claw size[15] and mechanical advantage[16], but also via changes in muscle properties.

Crustaceans are able to generate higher maximum muscle stresses than vertebrates and most insects[1]. However, the physiological basis of this difference has remained unresolved: are the higher stresses due simply to increases in resting SL or is it necessary to invoke other associated fiber-traits, such as density of myosin filaments[8, 9], arthropod 'catch-like' effects[17], myofibrillar bundle diameter[18], differences in actin-myosin filament ratios[8,9], and potential differences in actin-myosin cross-bridge duty factors[14]. Because of the heterogeneous nature of crustacean muscle[19] and because of the vast diversity of muscle types within the animal kingdom[20], the sliding-filament hypothesis was believed to offer little more than a qualitative description of the relationships between structural differences and performance[9, 20]. However, examination of the values of muscle stress for crustacean claws along with those for vertebrates and insects revealed that, within and among all three subphyla, 83% of the variation in muscle stress can be explained by resting SL (Table A2-3a).

When differences in method of muscle preparation were accounted for, and the effects of SL on muscle stress were removed, there was an almost significant difference in muscle performance between vertebrates and crustaceans (Table A2-3b) (limited data on uniramian muscle stress prevented this group from being entered into this analysis). Contrary to expectations, vertebrates tended to produce greater stresses than crustaceans for a given sarcomere length; adjusted least square means (±SE) are 38.37±1.14 and 22.56±1.19 Ncm^{-2}, respectively. The majority of the stress values reported for vertebrates are isolated fiber preparations under isometric conditions, and as such, higher stress values are expected for two reasons: 1) because of higher densities of contractile units within a given cross sectional area for a fiber verses a whole muscle preparation1 and 2) because of the researchers' ability to control for pure isometric contractions of isolated fibers[24]. A closer analysis did reveal that stresses produced by single-fiber preparations were consistently higher than those produced by whole-muscle preparations for crustaceans and vertebrates [adjusted least square means (±SE): crustacean-whole = 21.18±1.20 (N = 18), crustacean-fiber = 24.03±1.18 (N = 6), vertebrate-whole = 32.66±1.23 (N = 6), and vertebrate-fiber = 45.07±1.21 (N = 14)]. Also, the interaction between subphylum and method of muscle preparation was not significant, so regardless of muscle preparation, vertebrates tended to produce higher stresses for a given sarcomere length (Table A2-3b). Clearly, the higher muscle stresses reported here and elsewhere[1-8] for crustacean claws result almost entirely from differences in resting SL and other differences in muscle characteristics need not be invoked.

In brachyuran claws, muscle stress also correlated significantly with mechanical advantage (Fig. A2-3) a morphological attribute of claws known to affect maximum biting force[21]. Mechanical advantage is often used as a surrogate for maximum biting force because it is easy to measure[16]. The direct observations of SL reported here reveal that 84 % of the variation in SL can be explained statistically by variation in mechanical advantage. SLs for both living and fossil brachyurans species may thus be inferred with reasonable confidence based on measurements of mechanical advantage.

Table A2-1. Maximum closer-muscle stress of claws from various *Cancer* crab species.

	Stress (Ncm^{-2})			Mean Claw height (mm)
Species	Mean (±SE)	Range	*n*	
C. antennarius	86.57 (3.48)	55.10 - 118.20	24	20.7
C. branneri	103.15 (6.19)	71.34 - 153.57	12	12.5
C. gracilis	52.55 (2.87)	38.28 - 74.26	14	21.7
C. magister	75.60 (2.82)	51.94 - 96.29	20	20.8
C. oregonensis	100.67 (3.02)	81.67 - 134.58	21	12.1
C. productus	79.21 (6.00)	42.14 - 122.39	15	19.2

Table A2-2. Sarcomere lengths of the closer-muscle of claws from various *Cancer* crab species

Species	Sarcomere length (μm)			Mean Claw height (mm)
	Mean (±SE)	Range	*n*	
C. antennarius	13.7 (0.32)	10.7 - 17.1	27	22.9
C. branneri	12.7 (0.27)	11.5 - 13.7	9	13.2
C. gracilis	12.7 (0.36)	9.6 - 14.7	15	20.3
C. magister	12.2 (0.26)	10.0 - 15.3	26	20.7
C. oregonensis	16.5 (0.36)	14.2 - 17.1	9	10.7
C. productus	16.1 (0.26)	14.4 - 17.8	13	20.8

Table A2-3. Effects of subphyla and sarcomere length on maximum muscle stress.

Source	df	*MS*	*P*	Source	df	*MS*	*P*
a) ANCOVA; log maximum stress				b) ANCOVA; log maximum stress			
subphyla	2	0.617	0.148	subphyla	1	0.113	0.061
log SL	1	1.424	<0.001	MMP	1	0.061	0.164
Error	48	0.031		MMP *subphyla	1	0.014	0.501
				log SL	1	0.945	<0.001
				Error	39		

MMP = method of muscle preparation [i.e., either whole or isolated fiber(s)]

Table A2-4. Muscle stress and sarcomere length values for species used in the scaling analysis

Taxa				Sarcomere Length (μm)			Maximum Stress (Ncm-2)			
Species	Ref.	Body Region	Muscle	Mean (SE)	Range	*n*	Mean (SE)	Range	*n*	Method
Crustacea										
Cancer antennarius	1	chela crusher	dactyl closer	13.7 (0.32)	10.7 - 17.1	27	86.6 (3.5)	55.1 - 118.2	24	*vv,w,s*
Cancer branneri	1	chela crusher	dactyl closer	12.7 (0.27)	11.5 - 13.7	9	103.2 (6.2)	71.3 - 153.6	12	*vv,w,s*
Cancer gracilis	1	chela crusher	dactyl closer	12.7 (0.36)	9.6 - 14.7	15	52.6 (2.9)	38.3 - 74.3	14	*vv,w,s*
Cancer magister	1	chela crusher	dactyl closer	12.2 (0.26)	10.0 - 15.3	26	75.6 (2.8)	51.9 - 96.3	20	*vv,w,s*
Cancer oregonensis	1	chela crusher	dactyl closer	16.5 (0.36)	14.2 - 17.1	9	100.7 (3.0)	81.7 - 134.6	21	*vv,w,s*
Cancer productus	1	chela crusher	dactyl closer	16.1 (0.26)	14.4 - 17.8	13	79.2 (6.0)	42.1 - 122.4	15	*vv,w,s*
Cancer pagurus	2	chela crusher	dactyl closer	12.8 (0.39)	9 - 14	5	49.6 (32.1)	32 - 72	18	*vt,w,c*
M. mercenaria (temp)‡	3	chela crusher	dactyl closer	--	--	--	109.4 (9.5)	15.7 - 218.7	26	*vv,w,s*
M. mercenaria (temp)‡	3	chela cutter	dactyl closer	--	--	--	67.3 (10.0)	--	7	*vv,w,s*
M. mercenaria (trop)‡	3	chela crusher	dactyl closer	--	--	--	71.1 (13.5)	11.0 - 170.2	12.0	*vv,w,s*
M. mercenaria (trop)‡	3	chela cutter	dactyl closer	--	--	--	89.6 (9.0)	--	6	*vv,w,s*
Carcinus maenas	4	chela chrusher	dactyl closer	13.1 (--)	--	2	66.7 (58.0)	28.6 - 105.7	16	*vt,w,e*
Carcinus maenas	4	chela cutter	dactyl closer	9.5 (--)	--	2	47.4 (41.0)	17.2 - 77.9	15	*vt,w,e*
Macropipus spp	2	chela crusher	dactyl closer	8.9 (0.23)	7 - 9	4	27.5 (42.2)	--	6	*vt,w,c*
Macropipus spp	2	chela cutter	dactyl closer	7.5 (0.21)	3 - 5	4	26.8 (24.6)	--	7	*vt,w,c*
Callinectes sapidus	5	chela crusher	dactyl closer	11.2 (0.03)	6 - 15	3	63.8 (17.8)	--	18	*vv,w,s*
Callinectes sapidus	5	chela cutter	dactyl closer	10.5 (0.09)	6 - 15	3	51.4 (14.3)	--	18	*vv,w,s*
C. opilio (mature)	6	chela cutter	dactyl closer	10.4 (--)	4 - 17	--	55.2 (2.4)	--	12	*vv,w,s*
C. opilio (immature)	6	chela cutter	dactyl closer	9.5 (--)	4 - 17	--	44.4 (2.9)	--	13	*vv,w,s*
Homarus americanus	7 & 8	chela crusher	dactyl closer	7.6 (--)	6 - 10	--	30.2 (--)	25.3 - 39.0	3	*vv,w,s*
Homarus americanus	7 & 8	chela cutter	dactyl closer	4.2 (--)	2 - 10	--	27.2 (--)	18.2 - 42.6	8	*vv,w,s*
Cherax destructor	9	chela cutter	dactyl closer	8.6 (0.11)	6 - 10	49	30.5 (1.7)	10.0 - 57.1	49	*vt,f,c*
Cherax destructor	9	chela cutter	dactyl closer	3.3 (0.32)	2 - 5	64	18.6 (0.8)	5.7 - 27.8	64	*vt,f,c*
Astacus fluviatilis	10	walking leg	extensor	10.5 (0.3)	--	--	64.8 (--)	0.0 - 80.4	--	*vt,f,c*
Homarus americanus	11	adominal	MSE	6.8 (0.37)	6 - 10	25	44.3 (7.6)	--	4	*vt,b,c*
Homarus americanus	11	adominal	LDE	2.4 (0.19)	2 - 4.5	25	8.2 (1.5)	--	3	*vt,b,c*
Homarus americanus	12 & 13	2nd antenna	slow remotor	10.5 (--)	8 - 13	20	27.5 (--)	--	--	*vt,w,e*

(Table A2-4 continued)

Taxa				Sarcomere Length (µm)			Maximum Stress (Ncm-2)			
Species	Ref.	Body Region	Muscle	Mean (SE)	Range	*n*	Mean (SE)	Range	*n*	Method
Uniramia										
Schistocerca gregaria	15	hindwing	flight	3.9 (--)	3.1 - 4.1	--	15.7 (--)	--	--	*vt,b,e*
Schistocerca gregaria §	16	wing	metathoracic	3.9 (--)	--	--	29.5 (2.3)	--	12	*vv,w,e*
Schistocera americana §	17	wing	metathoracic	3.9 (--)	--	--	36.3 (1.4)	--	5	*vv,w,e*
N. robustus ¥	18	singing/wing	mesothoracic	3.3 (0.3)	--	3	10.9 (--)	--	7	*vv,w,e*
N. robustus ¥	18	wing	metathoracic	3.1 (0.3)	--	3	24ç (--)	--	5	*vv,w,e*
N. triops §¥	18	singing/wing	mesothoracic	3.3 (--)	--	--	12.4ç (--)	--	6	*vv,w,e*
N. triops §¥	18	wing	metathoracic	3.1 (--)	--	--	21.4ç (--)	--	6	*vv,w,e*
Schistocerca gregaria †	19 & 20	hind leg	tibia extensor	11.0 (--)	--	--	70.5 (--)	66.0 - 75.0	--	*vv,w,e*
Vertebrata										
Scyliorhinus canicula	21	postanal	myotomal white	2.6 (--)	2.3 - 2.8	--	24.1 (2.2)	--	7	*vt,b,e*
Cyprinus carpio	22	mid-line	myotomal red	2.1 (--)	--	--	11.6 (0.4)	10.2 - 12.5	5	*vt,b,e*
Makaira nigricans	23	trunk	myotomal white	2.3 (--)	--	--	17.6 (0.2)	--	13	*vt,f,c*
Makaira nigricans	23	trunk	myotomal red	2.3 (--)	--	--	5.7 (0.9)	--	11	*vt,b,c*
Xenopus laevis	24	hind leg	IL (1N fibres)	2.3 (--)	--	--	39.6 (5.4)	--	10	*vt,f,e*
Xenopus laevis	24	hind leg	IL (2S fibres)	2.3 (--)	--	--	33.7 (3.8)	--	12	*vt,f,e*
Xenopus laevis	24	hind leg	IL (2F fibre)	2.3 (--)	--	--	31.2 (3.6)	--	6	*vt,f,e*
Xenopus laevis	24	hind leg	IL (2N fibres)	2.3 (--)	--	--	30 (4.9)	--	8	*vt,f,e*
Pseudemys scripta	25	hind leg	IL (fast glycolytic)	2.3 (--)	--	--	18.3 (0.5)	--	17	*vt,f,s*
Pseudemys scripta	25	hind leg	IL (fast oxidative)	2.3 (--)	--	--	12 (0.3)	--	16	*vt,f,s*
Pseudemys scripta	25	hind leg	IL (slow oxidative)	2.3 (--)	--	--	7.1 (0.3)	--	19	*vt,f,s*
Rattus spp.	26	hind leg	EDL	2.5 (--)	--	--	20.9 (1.07)	--	8	*vt,b,e*
Rattus spp.	26	hind leg	soleus	2.5 (--)	--	--	19.8 (1.9)	--	8	*vt,b,e*
albino mice	27	extraocular	inferior rectus	2.6 (0.12)	--	6	10.2 (1.1)	--	6	*vt,w,e*
albino mice	27	hind leg	EDL	3.1 (0.14)	--	6	24.9 (1.0)	--	6	*vt,w,e*

(Table A2-4 continued)

Taxa				Sarcomere Length (µm)			Maximum Stress (Ncm-2)			
Species	Ref.	Body Region	Muscle	Mean (SE)	Range	*n*	Mean (SE)	Range	*n*	Method
Vertebrata										
albino mice	27	hind leg	soleus	2.8 (0.08)	--	6	17.7 (2.2)	--	6	*vt,w,e*
albino mice	27	diaphram	hemidiaphram	2.7 (0.09)	--	6	21.1 (0.9)	--	6	*vt,b,e*
Homo sapien ¶	28 & 29	hind leg	triceps surae	2.7 (--)	--	--	12 (0.4)	10.1 - 15.1	5	*vv,w,s*
Homo sapien ¶	28 & 29	hind leg	quadriceps	2.7 (--)	--	--	23.94 (0.8)	19.1 - 27.7	5	*vv,w,s*
Homo sapien ¶	28 & 29	hind leg	hip extensors	2.7 (--)	--	--	12.74 (0.8)	7.4 - 18.7	5	*vv,w,s*

Method symbols: vv = in vivo, vt = in vitro, w = whole muscle, b = bundle of fibres, f = single fibres, e = stimulated electrically, c = stimulated chemically, s = self stimulated. Muscle abreviations: MSE = medial superficial extensor, LDE = lateral deep extensor, IL = iliofibularis, EDL = extensor digitorum longus. Species abreviations: *M. mercenaria = Menippe mercenaria, C. opilis = Chionoecetes opilio, N. robutus = Neoconocephalus robustus, N. tripos = Neoconocephalus triops.*

‡ sarcomere length measurements are not available for claws of M. mercenaria crabs. However, mean claw mechanical advantage is reported at 0.390 (N = 77) for the crusher and 0.304 (N = 29) for the cutter (Blundun, 1988). Using the regression in figure A2-3 (MA verses SL; y = 25.858x + 4.8104), an average SLs of 14.9 µm for the crusher and 12.7 µm for the cutter-claw were predicted. Assuming these SL's are reasonable estimates, the mean stress of both claw types are within the 95% confidence limits of the regression, resting SL verses maximum stress (Fig. A2-2).

§ sarcomere length assumed to be the same as found for a closely related species.

¥ stress has been corrected for myofibril area.

† only A-band length measured, therefore sarcomere length estimated by doubling this value.

¶ sarcomere length estimated by taking the mean sarcomere length for mammalian muscles referenced in Josephson (1993).

Ref.= references, temp = temperate, trop = tropical

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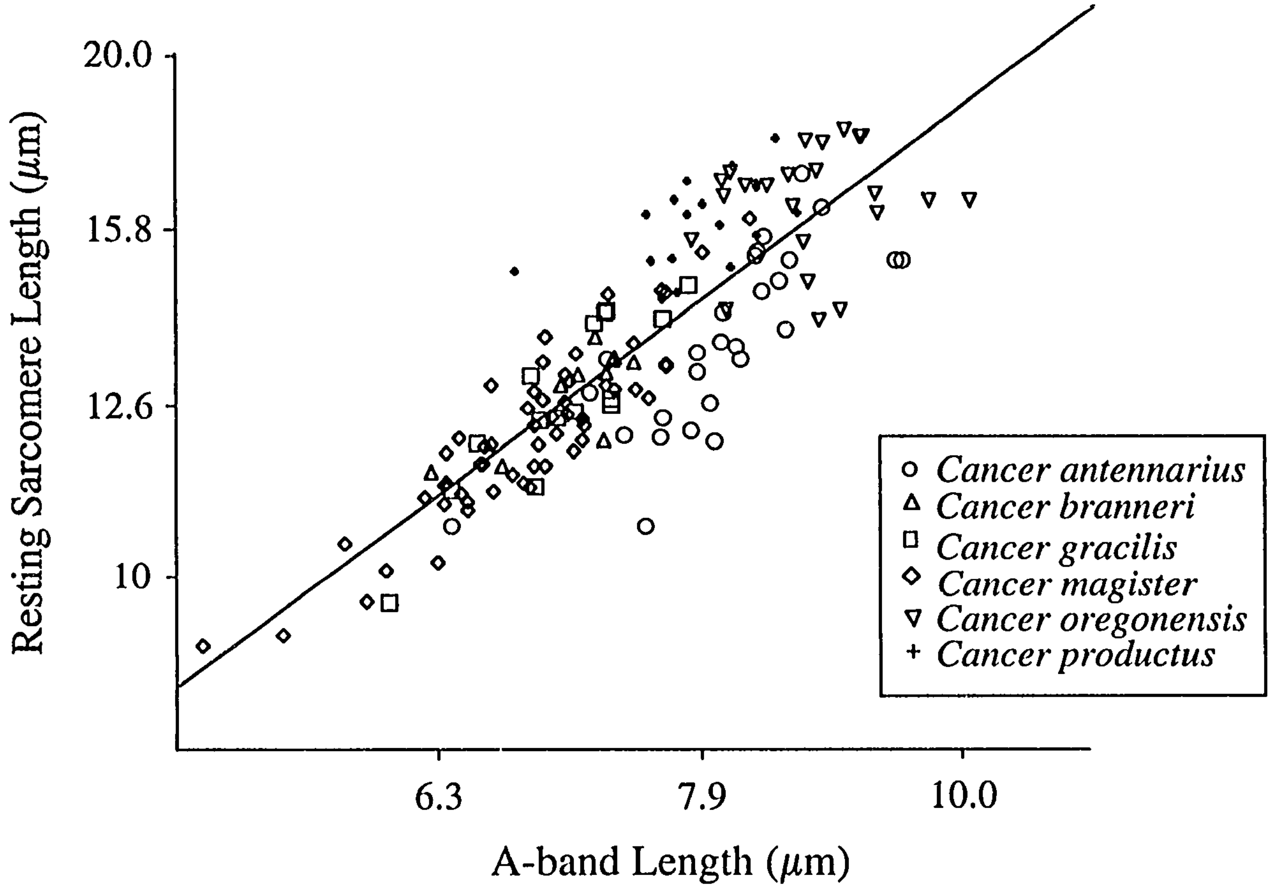

Figure A2-1. Correlation of mean claw resting sarcomere length and A-band length ($y = 1.119x + 0.151$; $r^2 = 0.747$; $P < 0.001$). Each point corresponds to a mean value for a single claw closer-muscle and axes are logarithmic.

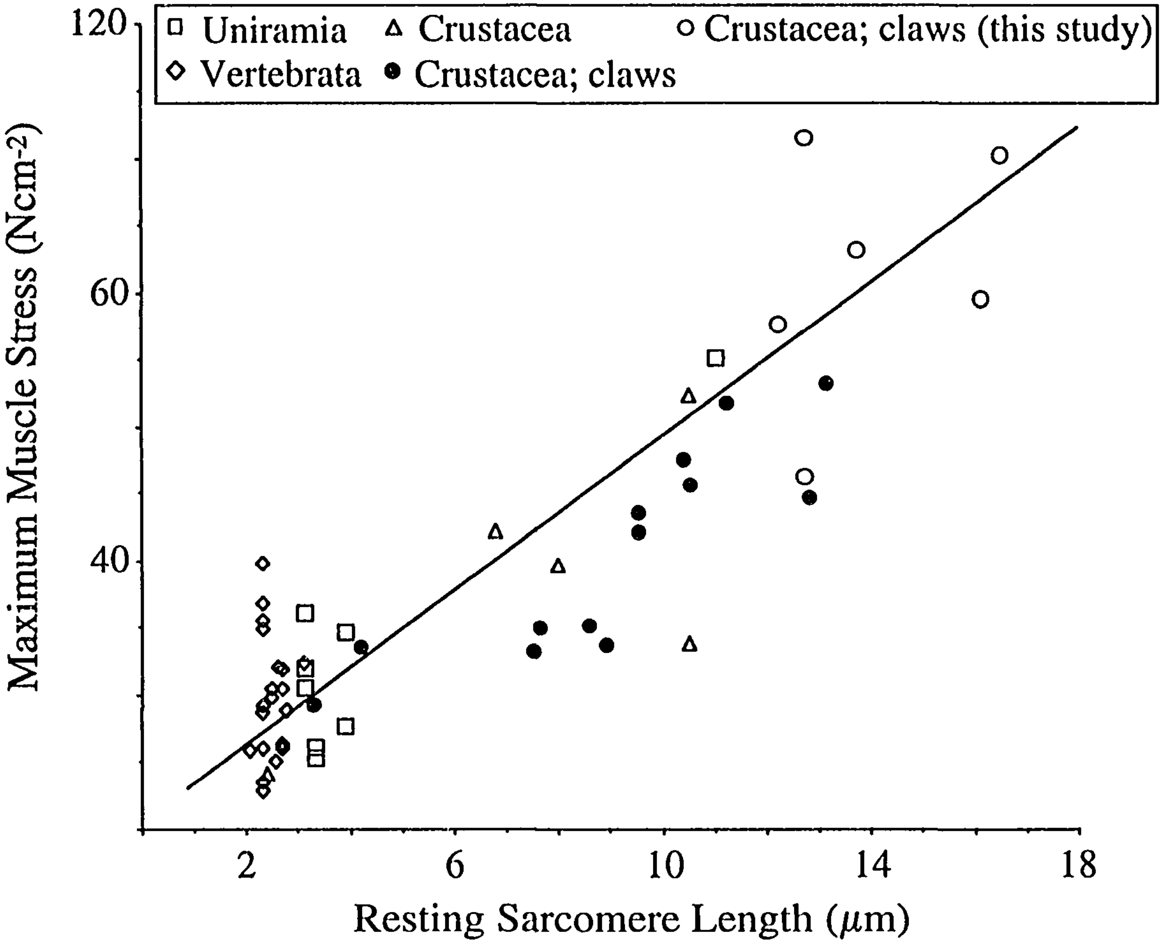

Figure A2-2. Regression of muscle resting sarcomere length against mean maximum stress for data compiled from the literature, representing three subphyla (Vertebrata, Uniramia, and Crustacea). The slope of the reduced major axis model (RMA) (β = 1.134), r = 0.889) did not differ significantly from an expected slope of 1.0 ($P < 0.05$).

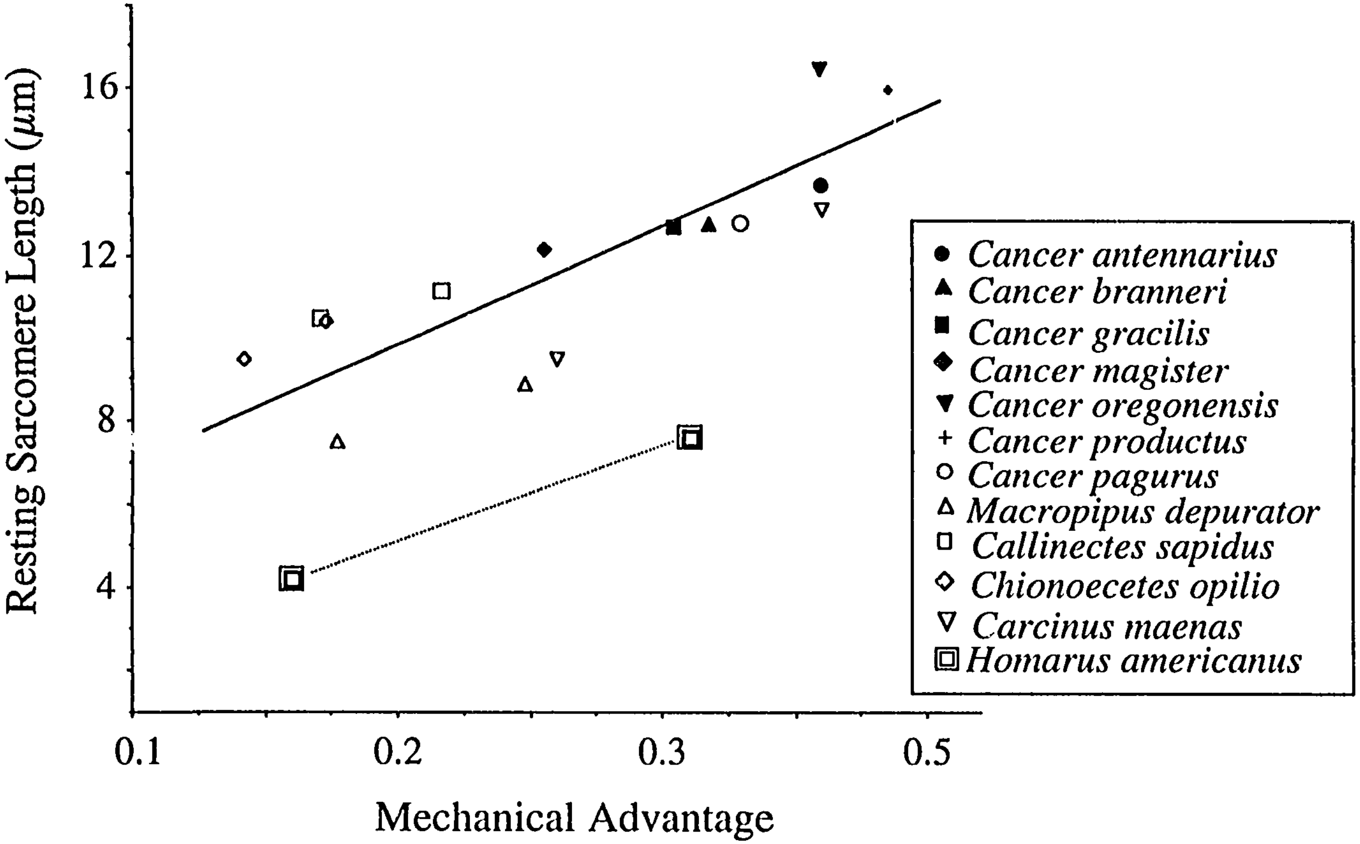

Figure A2-3. Correlation of mean claw sarcomere length with mean claw mechanical advantage for several decapod species, which were compiled from the literature. Values for both cutter and crusher claws of *Homarus americanus* are plotted, but were not included in the analyses restricted to brachyurans ($r = 0.836$; df = 13; $P < .001$). The solid line is a least square best fit, while the dashed line connects the lower-cutter and upper-crusher values of the lobster.

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Appendix 3. Catching *Cancer* Crabs in Barkley Sound

Mostly, *Cancer antennarius* is a southern species, but is quite common in Barkley Sound area, as reported by Jensen (1995). I had the most success hunting along the shore of the north facing bay on the Kirby Point Indian reserve. I hunted these crabs by turning over boulders. Larger individuals are further down the shore, and a low tide is required to obtain a wide size range of individuals. At the same location, trapping of *C. antennarius* with regular commercial crab traps proved unsuccessful.

Individual *C. branneri* were caught by hand by Chris Cameron and Steve Oaks using scuba equipment. Successful catches were made at the Ross Islets, specifically in waters between Sandford Island and Fleming Island. These crabs hide under rubble and sea urchins, and as such, a rake of some sort is useful. When back at the lab, keep these crabs separate from one another, as they seem highly cannibalistic.

As reported elsewhere (Jensen, 1995), *C. gracilis* likes the muddy flats associated with eel-grass beds. Densities can be very high at the right location , and at the right time of the year (see Orensanz & Gallucci 1985). *Cancer gracilis* can be found sporadically throughout Bamfield and Grappler Inlets. It is most abundant at the upper end of Bamfield Inlet; specifically, you must go through the narrows of Burlo Island. These crabs can be caught using regular commercial traps. I covered the commercial traps with fishing net, so as to catch all size ranges. Check traps on a regular basis to avoid having individuals of *C. gracilis* attacked by other caught *C. productus*. *C. productus* is rare in this area, but one big one can do much damage.

I have little to report on hunting *C. magister*, except, as when hunting anything, keep the bait fresh and keep it out. I set commercial crab traps in the deepest waters of upper Bamfield Inlet.

Cancer oregonensis can be found in abundance within small holes on the rock face along the shores of the native reserve located on Mills Peninsula. Tweezers can be used to pull individuals from their dens, however, this often leads to many individuals being punctured by the instrument. After many hours of collecting on a hot sunny day, and drinking coffee between catches, I was overcome by the urge to urinate. To my amazement, a small *C. oregonensis* came running out from the exact spot my shower hit the earth. I had discovered the best collecting tool. When short of urine, use highly diluted vinegar in an old spray bottle. After crabs have been exposed to these toxic attacks, quickly get them into a bucket with clean fresh water. This advice also extends to your hands.

Cancer productus can be trapped or hunted at low tide by turning over rocks. I found the best method for obtaining numerous mid-sized individuals was to hunt them on a returning tide at night. My sampling location was upper Grappler Inlet on the south facing shore of the largest Island (number 51 on the Barkley sound chart). I use a head lamp and run about in about three feet of water and when I see one, I just plunge in after them with my hands. Be careful! You will need most of your fingers to write up.

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