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SAFETY FACTORS AND THE FUNCTIONAL PROPERTIES OF INTERTIDAL LIMPET SHELLS

by

RICHARD BRUCE LOWELL

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled SAFETY FACTORS AND THE FUNCTIONAL PROPERTIES OF INTERTIDAL LIMPET SHELLS submitted by RICHARD BRUCE LOWELL in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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Abstract

Load-bearing biological structures (e.g., tree limbs, vertebrate long bones) often seem to be stronger than they need to be to withstand the maximum forces or loads experienced during a functional lifetime. That is, they tend to have "built-in" safety factors (= structural strength/lifetime maximum load) that are greater than 1. A central question in studies of structural strength is "Just how large should these safety factors be?" Theory predicts that selection should act to increase the safety factor of a load-bearing biological structure as variability in either strength or maximum load increases. For limpet shells subject to prying forces by crab or bird predators, a safety factor can be measured as shell strength/foot tenacity because foot tenacity (= force required to detach foot) determines the maximum possible load on the shell margin. The safety factors of temperate eastern Pacific limpets were found to increase with increased variability in shell strength, thus providing the first direct support for the theory.

A comparison of the safety factors of tropical and temperate limpet shells in the eastern Pacific yielded two results of significance. First, on average, shell strength and foot tenacity for the tropical limpets were twice those for the temperate limpets. In contrast, the average safety

factors for the two groups were approximately equal. This comparatively narrow range of safety factors was due to a highly significant association of greater shell strengths with greater foot tenacities. The implication of this result is that selection has acted to closely link the mechanical performances of these two rather independent structures, the shell and the foot. Furthermore, this linkage appears to be maintained via the degree of allometry between foot area and the thickness of the shell margin.

Second, the presence of an additional class of predators that feed on the tropical limpets was reflected in the safety factors of their shells. Whereas the shells of both tropical and temperate limpets are exposed to predator-induced prying forces, the shells of the tropical group are also exposed to lateral crushing forces generated by fish predators. This additional selection pressure was associated with several deviations from the regression of safety factor versus variability in shell strength that had been calculated previously for the temperate limpets. As predicted, the magnitudes of these deviations were correlated with the degree of exposure to this additional selection pressure. Hence, the presence of more than one selection pressure appears to have influenced the precision with which the shells of these species have become adapted to a single selection pressure. The use of safety factor analysis provides a very useful methodology for identifying additional selection pressures or adaptive constraints on biological structures.

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In addition to those persons acknowledged in Chapters III and IV, a variety of other associates and friends have helped make this dissertation possible; although I haven't named many of them, I thank them all.

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The able assistance of the staff of three marine stations streamlined my work considerably: Bamfield Marine Station, Friday Harbor Laboratories, and the Naos Laboratory of the Smithsonian Tropical Research Institute. I would also like to acknowledge the financial support provided by a Killam Predoctoral Fellowship, a University of Alberta Dissertation Fellowship, and a Smithsonian Short-term Fellowship.

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I. INTRODUCTION

After a perceived period of stagnation during the early and mid parts of the twentieth century, functional morphology has seen a recent influx of new ideas and approaches (Mayr and Provine, 1980; Lauder, 1982). This renewal of interest in the field is apparent in the symposia published in recent issues of the *American Zoologist*. During the period 1980-1985, 20% (7 of 35) of the symposia were concerned primarily with form and function (Gaunt, 1980; Oxnard, 1980; Bock, 1981; Bryant, 1982; Liem and Lauder, 1982; Pough, 1983; Denny, 1984).

In particular, the field of biomechanics has recently received much attention. In addition to medical applications, biomechanical approaches have provided useful insights in at least four general fields of basic biology: 1) basic principles underlying the mechanical properties of biological materials and structures (Wainwright et al., 1976; Vogel, 1981; Alexander, 1983), 2) systematics (Lauder, 1981), 3) ecology (Witman and Suchanek, 1984; Denny et al., 1985), 4) evolution (Caple et al., 1983; Kingsolver and Koehl, 1985; Lowell, 1985; Norberg, 1985). The research presented in this dissertation falls primarily into categories 1 and 4.

In many cases, biomechanical analyses can be facilitated by choosing structures with easily quantified morphologies (Wainwright et al., 1976). Complex morphologies can be described mathematically, but this usually involves a large number of time-consuming measurements and calculations (Bookstein, 1978, 1982; Strauss and Bookstein, 1982). In a study of the number of terms required to describe the skeletal morphologies of several taxa of commonly fossilized organisms, Schopf et al. (1975) found that the taxa fell into three groups. These groups, in order of increasing morphological complexity, were 1) gastropods, bivalves, ectoprocts; 2) echinoids, foraminiferans, ostracods, nautiloids, corals, trilobites, brachiopods; and 3) mammals, ammonoids. Therefore, from a practical standpoint, the taxa in Group 1 are logical choices for biomechanical analyses.

Whole-animal skeletal morphology has been particularly well studied for gastropods (Vermeij, 1978). Their overall shell morphology can often be described using only four coiling parameters (Raup and Michelson, 1965; Raup, 1966), although mathematical descriptions of shell sculpture and the shape of the aperture require additional information (Vermeij, 1971; see also Illert, 1983).

Nevertheless, even within the gastropods, mechanical analysis is difficult for spirally-coiled shells (Wainwright et al., 1976). Consequently, I chose to focus on those gastropod species with patelliform (limpet-shaped) shells. For many purposes, these comparatively simple shells can be treated in a biologically meaningful way as elliptical cones

(Lowell, 1984 and references therein).

An additional advantage to using limpets was that their general biology had already been well studied. Branch (1981) has reviewed this extensive literature on a worldwide basis. Carlton (1981) has also provided an indexed bibliography for several of the limpet species examined herein.

Limpet ecology and shell morphology were studied in the eastern Pacific where I was based at the following marine laboratories: Bamfield Marine Station, Bamfield, British Columbia, Canada (operated by the Western Canadian Universities Marine Biological Society); Friday Harbor Laboratories, Friday Harbor, Washington, USA (operated by the University of Washington); Naos Laboratory, Balboa, Panama (operated by the Smithsonian Tropical Research Institute). I worked with a variety of common species of rocky intertidal limpets: 1) temperate eastern Pacific - Acmaeidae - *Acmaea mitra, Collisella digitalis, C. pelta, Notoacmea persona, N. scutum*; Fissurellidae - *Diodora aspera*; 2) tropical eastern Pacific - Acmaeidae - *Collisella pediculus, Lottia (= Scurria) stipulata*; Fissurellidae - *Fissurella longifissa, F. virescens*; Siphonariidae - *Siphonaria gigas, S. maura*. The shells of these species are commonly subjected to breaking forces by crabs and fish; this was reflected in the morphology and the mechanical properties of their shells (Chapters II and IV).

By using this information on predator attack technique and limpet shell morphology, it was possible to test a recently developed theoretical model dealing with the safety factors of load-bearing biological structures (Alexander, 1981; Lowell, 1985). All organisms are supported to varying extents by biological structures (e.g., cell walls, tree limbs, vertebrate long bones, limpet shells) that must withstand the forces or loads encountered in their environment. In studies of these load-bearing structures, a central and, in most cases, unanswered question is, "Just how strong should such structures be?" This question is similar to that faced by an engineer designing a bridge. If 1) there is a cost to further strengthening the bridge and 2) the maximum load on and strength of the bridge are entirely predictable, then the bridge should be designed so that it is exactly strong enough to support the maximum load it is likely to experience during its lifetime. Although the first assumption is almost invariably true, the second is not. The lifetime maximum load on the bridge will vary, depending upon factors such as unpredictable combinations of traffic use and wind patterns. Likewise, the strength of the bridge will vary since the materials, workmanship, and degree of deterioration can not be completely controlled. Engineers sometimes incorporate this variability into a probabilistic model used to decide on an optimal safety factor (mean strength/mean maximum load) for the bridge, where what is optimal reflects a compromise between the cost of failure and the cost of construction and maintenance.

Biological structures are also exposed to unpredictable environments which, as above, leads to variability in both the strengths of these structures and the loads they experience. Unlike man-made structures, however, they are "designed" (sensu Wainwright et al., 1976) over many generations via the process of natural selection. On average, selection should favor those individuals having structures with "optimal" safety factors. In any given organism, however, such structures must develop and function in concert with the other parts of the organism, and this interdependency may limit how closely the "optimal" safety factor will be approximated. The range of possible safety factors may be limited further by the evolutionary history of the organism. Hence, the observed safety factors of biological structures are likely to be a function of several variables, including not only the cost of failure versus the cost of production and maintenance, but also the constraints associated with development and evolutionary history.

Within these constraints, however, the safety factor model predicts that increased variability should lead to selection for increased safety factors. The results of my work on the safety factors of limpet shells support this prediction (Chapter III).

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II. CRAB PREDATION ON LIMPETS: PREDATOR BEHAVIOR AND DEFENSIVE FEATURES OF THE SHELL MORPHOLOGY OF THE PREY

INTRODUCTION

Selection to resist attacks by shell-breaking predators appears to have been a central feature in the evolution of the shell form of marine gastropods (Vermeij, 1977; Vermeij et al., 1980, 1981). Understanding of this selection pressure requires information on both the techniques of attack used by predators and the biomechanical properties of those parts of the shell that are most important in resisting these attacks. Previous studies of this kind have focused almost exclusively on gastropods with spirally-coiled shells (Kitching et al., 1966; Vermeij, 1974, 1976, 1978; Zipser and Vermeij, 1978; Palmer, 1979, 1985; Bertness and Cunningham, 1981). For these species, low spires, thickened shells, narrow or occluded apertures, and strong shell sculpture appear to reduce the probability of mortality due to attacks by shell-breaking predators such as fish and crustaceans. Very little information is available on those morphological attributes of gastropods with patelliform (limpet-shaped) shells that help to prevent predator-induced shell breakage (but see Chapin, 1968 and Lowell, 1985).

The three major groups of shell-breaking predators that feed on limpets are crabs (Chapin, 1968; R.B. Lowell, unpublished data), fish [only certain, mostly tropical, species generate shell-breaking forces before their limpet prey are detached from the substratum (Chapter IV; Garrity and Levings, 1983; S.D. Gaines, personal communication)], and birds (Feare, 1971; Hartwick, 1976, 1978, 1981; Frank, 1982; Hockey and Branch, 1983; Mercurio et al., 1985) (see also Branch, 1981 for general review). Of these three groups, crabs (or other functionally similar decapods) are perhaps the most geographically and temporally ubiquitous in the rocky intertidal areas where limpets are found in the eastern Pacific (Chapter IV, Ricketts and Calvin, 1968; Menge and Lubchenco, 1981; Frank, 1982).

To determine the influence these crab predators are likely to have had on the evolution of the shell form of rocky intertidal limpets, I recorded the techniques used by crabs to feed on limpets in the tropical and temperate eastern Pacific. The results of this study indicated that by far the most frequent feeding behavior was to attempt to pry the margin of the limpet's shell away from the substratum. Therefore, I measured the contribution of the characteristically thickened margin of the shell to the breaking resistance of the shells of several eastern Pacific limpet species which commonly co-occur with these crabs. I also determined the relationship between the breaking resistance of the shell and the attachment strength of the foot.

MATERIALS AND METHODS

Crab Feeding Behavior

Temperate Eastern Pacific

Two species of cancrid crabs, *Cancer productus* and *C. oregonensis*, were chosen to study the feeding behavior of temperate Pacific crabs. Both species commonly co-occur with and feed on limpets in the rocky intertidal and will readily attack limpets in the laboratory, often within seconds of being offered limpets for the first time (R.B. Lowell, unpublished data). *Cancer productus* attains fairly large sizes; the seven individuals (6 males, 1 female) used for this study ranged from 8.2cm to 11.5cm in maximum carapace width. *Cancer oregonensis* is a much smaller species; the two individuals (both female) used were 3.5cm and 5.3cm in maximum carapace width. No molts occurred during the course of the study. All *C. productus* and one *C. oregonensis* were collected two years prior to the study from Bamfield Inlet (48°49'N, 125°8'W) and Grappler Inlet (48°50'N, 125°7'W) near the Bamfield Marine Station, British Columbia, Canada. The other, smaller *C. oregonensis* was collected from the plankton adjacent to the marine station at the postlarval (megalops) stage two years prior to the study and raised to maturity in the laboratory. All crabs were fed only bivalves (mostly *Mytilus edulis* and

Protothaca staminea) and barnacles (mostly *Balanus glandula*) until 23 days before the first set of observations, after which they were fed only the four sets of limpets described below. Each crab was placed in one of nine 37.5ℓ glass aquaria (50x25x30cm) with a constant supply of fresh seawater and left undisturbed for 23 days before offering the first set of limpets, except for two *C. productus* which were placed in their aquaria 1 day before the first limpets were offered. These latter two crabs exhibited similar behavior to the other five *C. productus* throughout the study. To minimize disturbance, all aquaria were surrounded by black plastic sheets which admitted only dim light. The aquaria were situated in a room with a west-facing window. Although no attempt was made to regulate artificial lighting conditions exterior to the plastic enclosures, all crabs were most active during the late afternoon and through the night.

Four different size-shape classes of limpets were offered to each crab over a period of two months in 1984. To vary shape, the limpets were divided by species into a flat shell group (*Notoacmea scutum*) and a tall shell group (*Collisella pelta, N. persona*). To vary size, the limpets were further divided into small (18-23mm in shell length) and large (30-40mm) individuals. The four size-shape combinations were offered to the two crab species as follows: 1) five small, flat *N. scutum* per crab on 4 August;

2) four large, flat *N. scutum* per crab on 18 September; 3) five small, tall *C. pelta* per crab on 22 September; 4) four large, tall *N. persona* per crab on 24 September (*C. productus*) and 25 September (*C. oregonensis*). All crabs were offered each combination except that one *C. oregonensis* (3.5cm) was not offered combination 4.

The limpets were collected one day before each of the observational trials from the following locations near the Bamfield Marine Station: small *N. scutum* - Kirby Point (48°51'N, 125°12'W); large *N. scutum* and *N. persona* - Ross Islets (48°52'N, 125°9'W); small *C. pelta* - Prasiola Point (48°49'N, 125°10'W). Four or five limpets were placed on each of nine flat rocks (upper surface area approximately 100cm^2). The following day, one rock was placed in each of the nine crab aquaria during the late afternoon and, in most cases, the feeding behavior of the crabs was observed for 40-95 minutes. Following these direct observations, the limpets were left with the crabs and their fates (alive vs. dead, shell whole vs. shell broken) were recorded at 2-24 hour intervals over the next 1-5 days. Shells with minor chips that did not extend beyond the thickened part of the shell margin (such chips would not expose the soft parts of a live, attached limpet) were not recorded as broken. At the beginning of each new trial, all limpets from the previous trial were removed.

Although not studied in detail, several measurements were made of the prying forces generated by a small crab while attempting to detach a limpet. A small (5.9cm maximum carapace width) *C. productus* was collected in Grappler Inlet and held for several months in a shallow seawater tray (approximately 70x70x20cm) connected to the same seawater system as used for the aquaria described above. Prior to the prying force measurements, this crab was fed a combination of bivalves (mostly *P. staminea*) and limpets (mostly *N. scutum*). Although artificial lighting conditions were not controlled, this crab was also most active at night.

To measure prying force, the shell of a newly-killed *N. scutum* (30.6mm in length) was tethered by a strand of nylon filament (glued into the interior apex of the shell) running through a sheet of plexiglass to a force transducer. The force transducer, on the opposite side of the plexiglass sheet from the tethered shell, was positioned so as to hold the shell (via the tether) against the sheet with a force of 2.7N. The whole setup, with the plane of the plexiglass sheet oriented vertically, was then placed in the seawater tray at 21:30 and left until 12:30 the following day. The prying forces generated by the crab were recorded throughout this period on a strip chart recorder; the crab's behavior was also observed for the first three hours.

Tropical Eastern Pacific

Five species of xanthid crabs were chosen to study the feeding behavior of tropical Pacific crabs at the Naos Laboratory of the Smithsonian Tropical Research Institute in Panama. Two of these species (*Ozius verreuxii, Eriphia squamata*) are the most common predatory crabs co-occurring on intertidal bedrock or boulders with the tropical limpets studied (Lubchenco et al., 1984). The other three (*Eurypanopeus planus, Xanthodius sternburghii, Leptodius taboganus*) are more common on cobble beaches where these limpets, though present, are less common (J.H. Christy, R.B. Lowell, personal observation). All five species readily feed on limpets in the laboratory. Relative to *C. productus*, these crab species are all fairly small. The size ranges (maximum carapace width) and number of individuals used for each species were as follows: *O. verreuxii* - 3.9-7.1cm, 1 male, 3 females; *E. squamata* - 3.0-4.5cm, 3 males, 1 female; *E. planus* - 2.1-2.3cm, 3 males; *X. sternburghii* - 2.8-3.1cm, 10 males; *L. taboganus* - 2.7cm, 1 male. All crabs were collected from small islands (Naos, Culebra, 8°55'N, 79°32'W; Taboguilla, 8°48'N, 79°31'W) in the Bay of Panama (see Garrity and Levings, 1981 for descriptions of these islands) over several weeks prior to the observational trials.

The crabs were fed only the limpets used in these trials. For *O. verreuxii* and *E. squamata*, crabs were held individually, one in each of eight glass aquaria; individuals of each of the other three species were held together, one species in each of three glass aquaria. All aquaria (each approximately 12ℓ) were kept in outdoor tanks under transparent roofing where they received a constant supply of fresh seawater. No attempt was made to control artificial lighting conditions; nevertheless, the crabs were most active at night.

Three to four different size-classes (see Table 5) of one limpet species (*Fissurella virescens* - tall shells) were introduced into each aquarium over a one month period (20 March - 11 April, 1984). Each size class was offered separately in increasing order starting with the smallest class. Although no attempt was made to standardize hunger levels, each trial was separated by at least four days. All limpets were collected from Culebra Island. The procedures for collecting the limpets and offering them to the crabs were the same as those for the temperate Pacific study.

Mechanical Performance of the Shell

Shell Models

All limpet species used in this study from both tropical and temperate shores exhibited characteristically thickened shell margins (R.B. Lowell, unpublished data). To determine the contribution of the thickened shell margin to the strength of the shell when subject to a crab-induced prying force, I sought to compare shells with a natural thickness distribution to shells that were identical in all respects except for being of constant thickness throughout all regions of the shell. Of the several thousand eastern Pacific limpet shells that were handled during the course of this and other related studies, a shell was never once found to have a constant thickness distribution. Therefore, it was necessary to make this comparison by constructing naturally shaped models of limpet shells. By using a homogeneous material for these models, it was also possible to avoid differences in shell strength due to differences in the thicknesses of various shell microstructures (Currey, 1980).

These homogeneous models were composed of a "fiberglass" mixture of powdered glass embedded in Coating Resin P-18 which was hardened with Catalyst P-102 (Fiberlay, Inc., Seattle, WA, USA). I formed the models by using a silicone rubber cast of a real *N. scutum* shell (see Fig. II-2 for the dimensions and thickness profile of this shell). Four models with a natural thickness distribution were formed from full casts. Three models with a constant thickness distribution (approximately 0.8mm thick) were formed in the following manner. A positive cast, in the form of an epoxy plug, was made from the the original negative cast of the dorsal surface of the shell. By using a micromanipulator to move the positive and negative casts away from each other, it was possible to create an intervening space of any desired thickness which was of the same shape as the original shell. This space was filled with the "fiberglass" mixture to form the constant thickness models. The same amount of "fiberglass" was used to form both model types so that they differed only in their thickness profiles.

When a live limpet is subject to a crab-induced prying force, the force is transmitted from the shell to the foot (and, finally, to the substratum) via the horseshoe-shaped muscle scar where the foot muscle attaches to the shell. Therefore, I attached the shell models to fixed platforms with horseshoe-shaped strips of aluminum foil which were glued to the models along the ventral region of the model where this muscle scar would normally be found. A prying force, similar to that applied by a crab, was applied in a dorsal direction to the anterior margin of each model with a weighted 1.16mm diameter steel hook of circular cross section.

To determine the patterns of deformation of the shell models, each model was coated with a spray-on brittle lacquer (Tens-Lac TL-500-75A with Undercoat U-10-A, Measurements Group, Charlotte, NC, USA). This lacquer cracks easily and the crack patterns are useful for determining the patterns of tensile strain (deformation) in a rigid structure which is subject to a force acting to deform the structure (Preuschoft et al., 1975). The area where the lacquer first cracks indicates the area of greatest tensile strain. Since the shell models were made of a homogeneous material, the area of greatest strain would correspond to the area of greatest tensile stress (force/cross-sectional area). Mollusc shell material is much weaker in tension than in compression (Currey, 1980). Consequently, the area of greatest tensile stress is where the shell would be most likely to break.

Shell Strength and Foot Tenacity

I also measured the strengths of various sides of the margins of real shells for several eastern Pacific limpet species. In the temperate eastern Pacific, measurements were taken for six common species from the west side of San Juan Island, Washington, USA (Lime Kiln Lighthouse, 48°31'N, 123°9'W; False Bay, 48°29'N, 123°4'W): Acmaeidae - *Collisella digitalis, C. pelta, Notoacmea persona, N. scutum, Acmaea mitra*; Fissurellidae - *Diodora aspera* (Plate II-1). In the tropical eastern Pacific, measurements were taken for six additional common species from the south side of Taboguilla Island: Acmaeidae - *Collisella pediculus, Lottia* (*Scurria*; Lindberg and McLean, 1981) *stipulata*; Fissurellidae - *Fissurella longifissa, F. virescens*; Siphonariidae - *Siphonaria gigas, S. maura* (Plate II-2).

Plate II-1. Lateral (top) and dorsal (bottom) views of temperate eastern Pacific limpet shells. Anterior side of shell faces left. 15cm rule at top of figure.

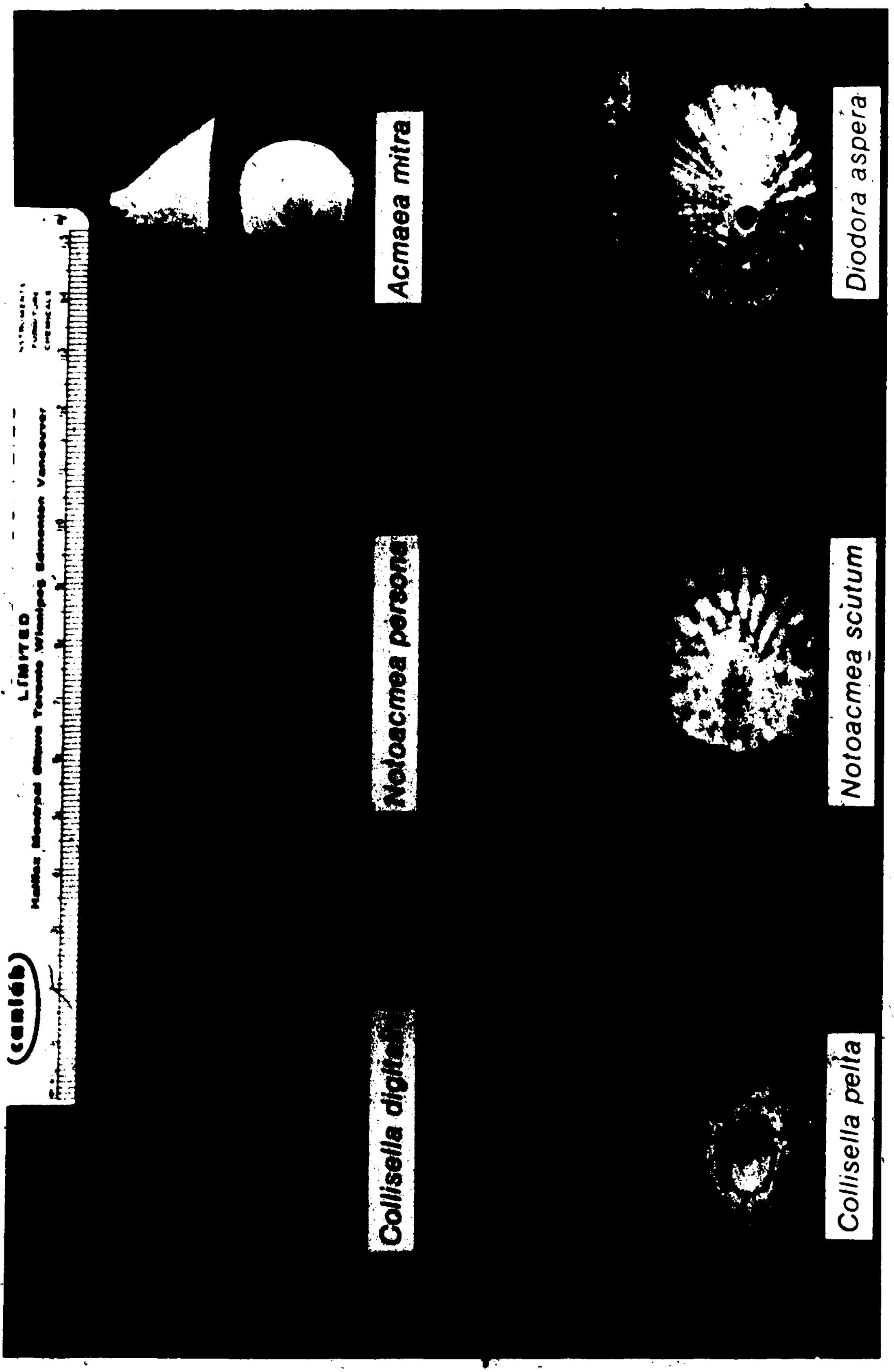
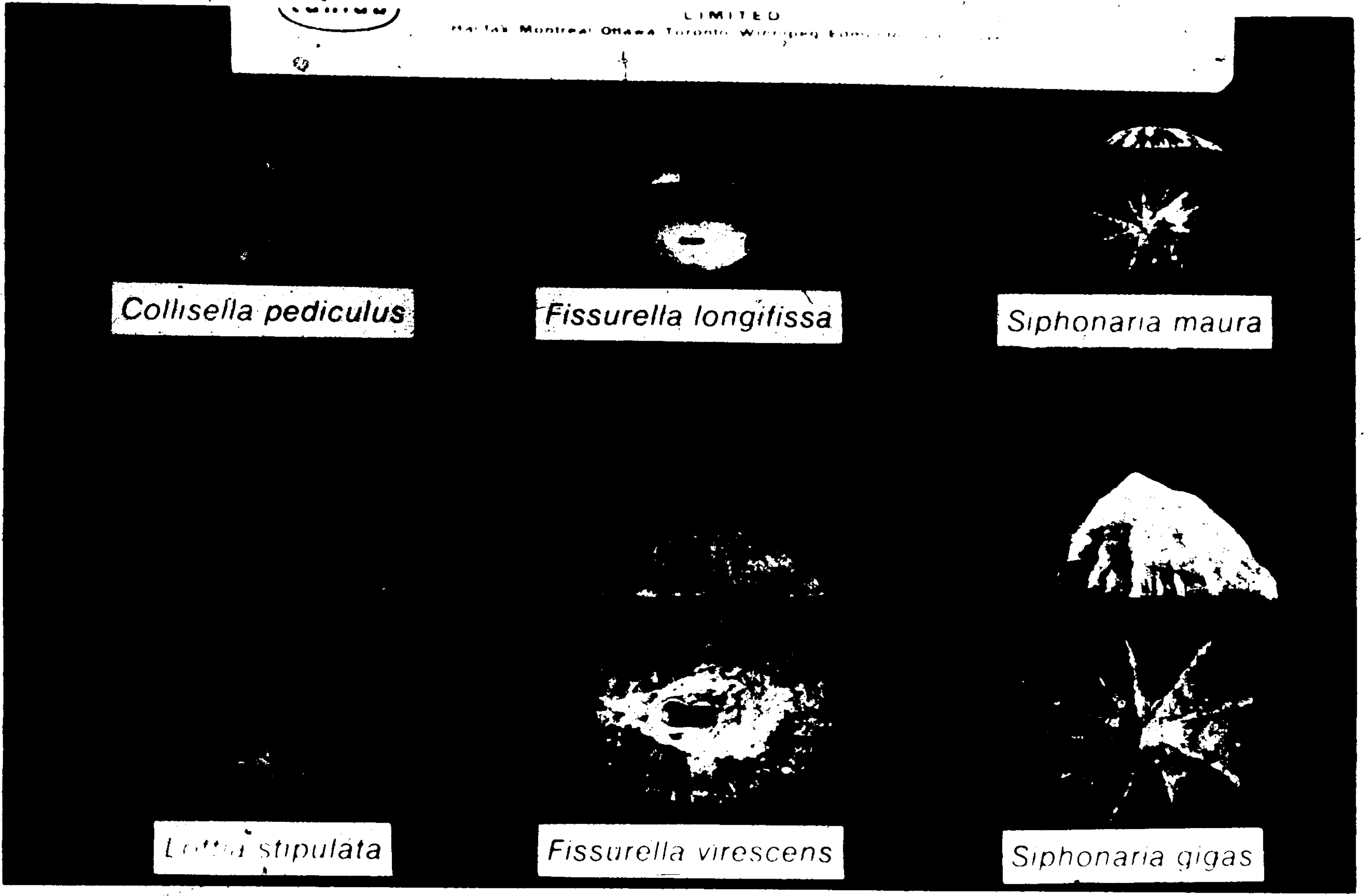

Acmaea mitra
Notoacmea persona
Collisella digitalis
Diodora aspera
Notoacmea scutum
Collisella pelta
canlab
LIMITED

Plate II-2. Lateral (top) and dorsal (bottom) views of tropical eastern Pacific limpet shells. See Plate II-1 legend for further information.

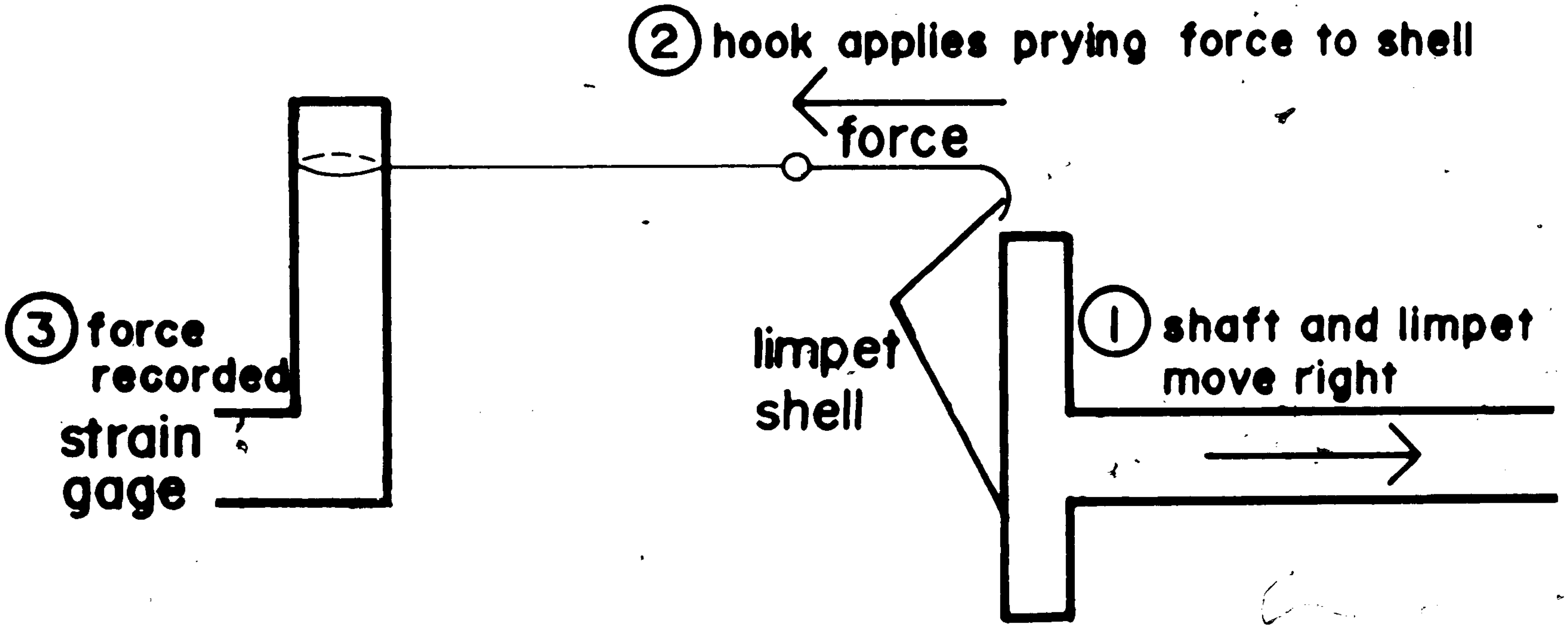

LIMITED
Halifax Montreal Ottawa Toronto Winnipeg
Collisella pediculus
Fissurella longifissa
Siphonaria maura
Lottia stipulata
Fissurella virescens
Siphonaria gigas

To measure the strengths of these real limpet shells, I used a procedure similar to that used for the shell models. The shells of newly killed limpets were mounted, while still wet, onto one shaft of a Monsanto (type W) tensometer (Fig. II-1). As for the shell models, a 1.16mm diameter steel hook (in this case, attached to the other shaft of the tensometer) subjected the edge of the shell to a prying force and the force required to break the shell was recorded. 0.67mm and 2.64mm diameter hooks were used for particularly small and large shells, respectively (Chapter IV); hook diameter had no significant effect on the force needed to break the shells (Lowell, 1985).

To mount the shells securely enough to withstand the force required to break the shell, it was necessary to provide a greater surface area for the glue to attach than the area of the muscle scar. Since the shell model experiment showed that the area of greatest stress in a shell subject to a prying force is at the point of force application at the margin of the shell (see Results), the real shells were mounted via two steel cables inserted into a pool of quick-setting epoxy put into the interior apical region of the shell dorsal to and overlapping the edges of the muscle scar. This method of mounting was double-checked by mounting lacquer-coated shell models (3 natural thickness, 4 constant thickness) in the same manner and subjecting them to prying forces. This mounting procedure

Figure II-1. Diagram of tensometer setup used to measure force required to break limpet shells. The force was recorded via a strain-gage force transducer.

MEASUREMENT OF BREAKING FORCE



yielded the same results as those reported for the more natural procedure of mounting the models with strips of aluminum foil attached only to the region of the model where the muscle scar would normally be. The quick-setting epoxy generated heat while setting; to minimize any potential effects of this heating on the strength of the real shells, the dorsal surface of each shell was kept immersed in seawater while the epoxy was setting. All shells broke at the shell margin rather than around the apical region.

The maximum possible prying force that the margin of a limpet shell can experience is set by the maximum strength of attachment of the foot to the substratum (maximum tenacity). Therefore, one would expect selection for the strength of the shell margin to be sensitive to maximum tenacity (Chapter IV; Lowell, 1985). I used spring scales to measure the maximum tenacity of previously undisturbed, healthy limpets on flat rock surfaces in the field (except for two *S. gigas*, see below). These measurements were made by subjecting the margin of the shell to a prying force in a manner identical to and on the same sides of the shell as for the shell strength measurements. In addition, the limpets used in the tenacity measurements came from the same populations as those used in the shell strength measurements. On average, the Panamanian limpets attain much higher tenacities than the northeastern Pacific limpets (Chapter IV) and, possibly in consequence, the incidence of damage to the foot during detachment was much greater for the Panamanian limpets.

Both shell strength and foot tenacity were measured for limpets of a variety of different sizes. Foot area, estimated from measurements of shell length and width, was chosen as a measure of size because of its relevance to tenacity. Tenacity was always measured after the foot had tightly clamped to the substratum. Therefore, maximum foot length (FL) and width (FW) were measured for several individuals (collected from the same populations used for the shell strength and foot tenacity measurements) of each species while they were tightly clamped to transparent glass plates (FL for both *Siphonaria* species included the length of the ventral surface of the head, which was also used for adhesion by these two species). The relationship of shell length and width to foot length and width was then calculated (Tables II-1, II-2). Foot area (FA) was calculated as the area of an ellipse: $FA=0.25\pi FL\cdot FW$ (Miller, 1974; Dimock, 1984).

One Panamanian species, *S. gigas*, is usually found on the backs of conspecifics when small. Therefore, the tenacities of the two smallest individuals used for this species were measured while on the backs of larger individuals. The two smallest *S. gigas* used for the shell strength measurements also came from the backs of larger individuals. Both the shell strengths and foot tenacities

Table II-1. Regressions of foot length (FL, in mm) against shell length (SL, in mm) for eastern Pacific limpet species. Range indicates maximum and minimum values for shell lengths used in regressions. n - sample size; r - correlation coefficient; p - probability that r=0

Species	Equation	range	n	r	p
TEMPERATE					
Acmaea mitra	FL=-2.13+0.755SL	10.5-33.5	12	0.9888	<0.0001
Collisella digitalis	FL=-1.61+0.743SL	11.8-25.2	10	0.9889	<0.0001
Collisella pelta	FL=0.38+0.689SL	13.1-33.9	10	0.9865	<0.0001
Notoacmea persona	FL=-2.55+0.753SL	10.0-31.8	11	0.9958	<0.0001
Notoacmea scutum	FL=1.07+0.612SL	23.1-49.7	11	0.9892	<0.0001
Diodora aspera	FL=1.98+0.757SL	21.2-52.5	11	0.9648	<0.0001
TROPICAL					
Collisella pediculus	FL=0.38+0.551SL	6.0-15.0	9	0.9318	0.0003
Lottia stipulata	FL=-2.13+0.761SL	13.3-21.1	10	0.9617	<0.0001
Fissurella longifissa	FL=0.67+0.662SL	10.2-19.2	10	0.9808	<0.0001
Fissurella virescens	FL=-0.85+0.716SL	13.9-40.4	10	0.9863	<0.0001
Siphonaria gigas	FL=-2.33+0.748SL	8.7-48.1	12	0.9904	<0.0001
Siphonaria maura	FL=-1.80+0.905SL	10.4-18.7	10	0.9742	<0.0001

Table II-2 Regressions of foot width (FW, in mm) against shell width (SW, in mm) for eastern Pacific limpet species. Range indicates maximum and minimum values for shell widths used in regressions.

Species	Equation	range	n	r	p
TEMPERATE					
Acmaea mitra	FW= 1 30+0 795SW	8 7-28 8	12	0 9729	<0 0001
Collisella digitalis	FW=-1.33+0 750SW	8 5-20 1	10	0 9613	<0 0001
Collisella pelta	FW=1 58+0 675SW	9 1-27 0	10	0 9827	<0 0001
Notoacmea persona	FW=-1 63+0 729SW	7 7-26 6	11	0 9878	<0 0001
Notoacmea scutum	FW=-1 29+0.761SW	17 8-39 5	11	0 9768	<0 0001
Diodora aspera	FW=-1 11+0 957SW	14 4-34 4	11	0 9530	<0 0001
TROPICAL					
Collisella pediculus	FW=-0 17+0 627SW	5 1-11 2	9	0 9455	0 0001
Lottia stipulata	FW=-0 99+0.795SW	9 5-15 6	10	0 9395	0 0001
Fissurella longifissa	FW=0.94+0 641SW	6 5-11 1	10	0 9720	<0 0001
Fissurella virescens	FW=0 99+0 622SW	9 1-29 1	10	0 9847	<0 0001
Siphonaria gigas	FW=-1 25+0 700SW	6 1-40 9	12	0 9976	<0 0001
Siphonaria maura	FW=0 21+0 640SW	7 1-14 5	10	0 9556	<0 0001

of these small *S. gigas* fell on the regression lines calculated for the larger *S. gigas*. Consequently, all sizes were pooled for the regressions given in Tables II-6 and II-7.

Statistics

The limpets used in the following regression analyses were chosen so as to provide a fairly even distribution of sizes within the size ranges tested. In some cases, the data were log-transformed before analysis to linearize the data and homogenize the variances. For those analyses where neither the X nor Y variable could be regarded as the independent variable and where the regression equation was to be used for functional (slopes and intercepts to be compared among regressions) rather than predictive (regressions used merely to predict Y for a given X) purposes, the reduced major axis was calculated rather than the standard least squares regression line (Ricker, 1973, 1984).

RESULTS

Crab Feeding Behavior

Direct Observations

The large temperate Pacific species, *C. productus*, exhibited four techniques for feeding on the limpets they were offered (Table II-3). 1)Pry - During this behavior, the tip of a chela or walking leg was inserted under the edge of a shell and an attempt was made to pry the shell away from the substratum. In most cases, the tip of the appendage was not fully under the edge of the shell and the attempt was unsuccessful. Although not quantified, none of the crab species showed an obvious preference for a particular side of the shell. Rather, they usually probed around the edge of the shell until they found a sufficiently large space under the shell margin to initiate a prying attack. All successful prying attacks which were directly observed resulted in the shell being detached whole. 2) Lateral slide - In one case, a *C. productus* successfully used its chela to slide a small, high-spired *C. pelta* off the rock in a lateral direction. 3) Crush at apex - Four attempts were made to crush the apex of large, tall *N. persona* between the two fingers of the chela. The apex of this species, though elevated, is rounded and provides a poor grip for an attacking crab; only one attempt was successful. 4) Crush at margins - Seven attempts by *C. productus* were made to crush the shells of small, steep-sided *C. pelta* between the fingers of one chela where each finger was placed at opposite margins of the shell. This technique was always

Table II-3. Direct observations of feeding techniques used by crabs. Dur Obs - Duration of observations in minutes; U - number of unsuccessful attacks observed; S - number of successful attacks observed; % - percent successful attacks observed; f - flat, t - tall.

Crab Species	Number of Crabs	Limpet Species	Limpet Size (mm)	Dur Obs	Feeding Technique											
					Prying			Lateral Slide			Crush at Apex			Crush at Margins		
					U	S	%	U	S	%	U	S	%	U	S	%
Cancer productus	7	*Notoacmea scutum* f	18-23	40	38	0	0	0	0	-	0	0	-	0	0	-
Cancer productus	7	*Notoacmea scutum* f	30-40	95	82	0	0	0	0	-	0	0	-	0	0	-
Cancer productus	7	*Collisella pelta* t	18-23	60	15	9	38	0	1	100	0	0	-	0	7	100
Cancer productus	7	*Notoacmea persona* t	30-40	90	284	8	3	0	0	-	3	1	25	0	0	-
				totals	419	17	4	0	1	100	3	1	25	0	7	100
Cancer oregonensis	2	*Notoacmea scutum* f	18-23	40	12	0	0	0	0	-	0	0	-	0	0	-
Cancer oregonensis	2	*Notoacmea scutum* f	30-40	95	28	0	0	0	0	-	0	0	-	0	0	-
Cancer oregonensis	2	*Collisella pelta* t	18-23	50	0	0	-	0	0	-	0	0	-	0	0	-
				totals	40	0	0	0	0	-	0	0	-	0	0	-

immediately successful. The prying technique was by far the most common feeding behavior observed for *C. productus* (prying vs. all other techniques, $\chi^2=441$, df=1, P<0.0001).

This latter tendency was even more pronounced for the smaller crab species. The prying technique was the only behavior observed for *C. oregonensis* (Table II-3). The Panamanian crabs were more reluctant to feed while being observed and direct observations of their feeding behavior were not quantified. Nevertheless, of more than fifty observed attacks by *O. verreuxii* and *E. squamata*, only the prying technique was seen.

Shell Remains

The high frequency of prying attacks may also be inferred from the high frequency of whole shells that were found during 1-8 days of feeding (Tables II-4, II-5). The only other observed feeding behavior which resulted in shells being removed whole, the lateral sliding technique, was very rare (Table II-3). Since all crab species frequently broke up limpet shells after they were removed, most of the % whole values less than 100 in Tables II-4 and II-5 probably greatly underestimate the frequency of successful prying attacks relative to other types of attacks. The shells of all or most of the limpets killed by the smallest crabs (*C. oregonensis, E. planus, X. sternburghii, L. taboganus*) were removed whole. The

Table II-4. Condition (whole vs broken) of shells of limpets offered to temperate crabs. Dur Obs - Duration of observations in days; Whole - number of shells known to be detached whole; Broken - number of shells broken either during or after detachment; Alive - number of limpets alive at end of feeding trial; % whole - percent known to be detached whole of those eaten; f - flat, t - tall.

Crab Species	Number of Crabs	Limpet Species	Limpet Size (mm)	Dur Obs	Whole	Broken	Alive	% Whole
Cancer productus	7	*Notoacmea scutum* f	18-23	2	0	11	24	0
Cancer productus	7	*Notoacmea scutum* f	30-40	3	8	10	10	44
Cancer productus	7	*Collisella pelta* t	18-23	1	13	22	0	37
Cancer productus	7	*Notoacmea persona* t	30-40	1	14	10	4	58
Cancer oregonensis	2	*Notoacmea scutum* f	18-23	2	4	1	5	80
Cancer oregonensis	2	*Notoacmea scutum* f	30-40	3	6	1	1	86
Cancer oregonensis	2	*Collisella pelta* t	18-23	4	10	0	0	100
Cancer oregonensis	1	*Collisella persona* t	30-40	5	4	0	0	100

Table II-5 Condition (whole vs. broken) of shells of *Fissurella virescens* offered to tropical crabs See Table II-4 legend for further information

Crab Species	Number of Crabs	Limpet Size (mm)	Dur Obs	Whole	Broken	Alive	% Whole
Ozius verreuxii	4	15-20	1	3	14	3	18
Ozius verreuxii	4	25-30	1	13	5	2	72
Ozius verreuxii	3	35-40	1	11	0	2	100
Ozius verreuxii	1	40-45	1	3	0	0	100
Eriphia squamata	4	15-20	1	1	17	2	6
Eriphia squamata	4	25-30	1	9	3	8	75
Eriphia squamata	4	35-40	1	5	1	10	83
Eurypanopeus planus	3	15-20	6	3	0	2	100
Eurypanopeus planus	3	20-30	6	3	0	2	100
Eurypanopeus planus	3	35-40	1	1	0	3	100
Xanthodius sternburghii	10	15-20	6	2	0	3	100
Xanthodius sternburghii	10	20-30	6	3	0	2	100
Xanthodius sternburghii	10	35-40	1	2	0	2	100
Leptodius taboganus	1	15-20	8	1	0	4	100
Leptodius taboganus	1	20-30	8	1	0	3	100
Leptodius taboganus	1	35-40	4	1	0	3	100

relative frequency of whole versus broken shells increased with increasing limpet size for the other crab species, although one comparison was not significant: *C. productus* - flat limpets (*N. scutum*), shell condition (whole or broken) vs. size, χ^2=6.75, df=1, P=0.0094; *C. productus* - tall limpets (*C. pelta, N. persona*), shell condition vs. size, χ^2=2.58, df=1, P=0.109; *O. verreuxii* - *F. virescens*, % whole vs. size (Spearman's Rank Correlation), r=0.8531, n=12, P=0.0047; *E. squamata* - *F. virescens*, % whole vs. size (Spearman's Rank Correlation), r=0.7937, n=12, P=0.0085. Most of the increased frequency of whole shells observed for the larger limpets was probably due to decreased breakage while manipulating the shell after being removed. Some of this increase in whole shell frequency, however, was probably also due to an increase in prying attacks as the ratio of limpet size to crab size increased.

Prying Force

Since no other food was available, the small *C. productus* used for the prying force measurements spent most of the night (22:30-09:30) attempting to pry the tethered shell away from the plexiglass sheet. During this period, 610 separate prying forces were recorded. Most were 1-5s in duration, although a few lasted up to 20s. The peak force recorded was 10.1N. The prying forces were generated with the tips of the walking legs or chelae and all sides of the shell were attacked. This left a record of tiny chips around the entire margin of the shell, although the thickened part of the margin remained intact.

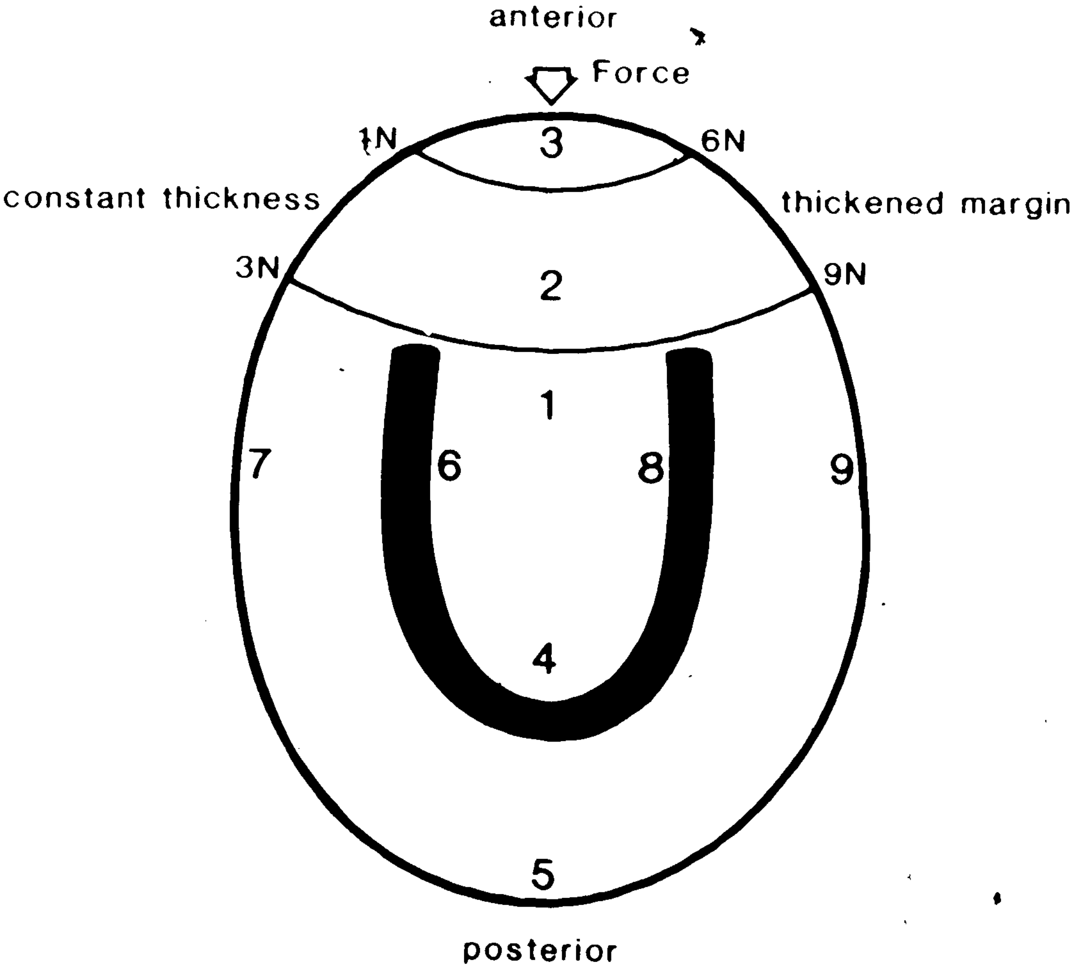
Mechanical Performance of the Shell

Shell Models

As the prying force was increased, the lacquer coating of all shell models first cracked on the ventral side of the shell at the point of force application. As the force was further increased, semicircular cracks formed farther from this point, creating the same concentric pattern on all models (Fig. II-2). This indicates that the greatest stress was at the point of force application. In a detailed study of scallop shells subject to point forces, Pennington and Currey (1984) also measured a tendency for shell deformation to be greater near the point of force application.

Figure II-2 also shows, for the two thickness distributions, the approximate force required to form cracks out to the indicated radial distances from the point of force application. The absolute magnitudes of these forces are unimportant since they are specific to the artificial material used for the models. Of significance is the result that much greater forces were required to cause a given degree of deformation or stress for the natural, thickened margin models as compared to the constant thickness models.

Figure II-2. Diagrammatic ventral view of interior of shell model. The thin semicircular lines show the extent of deformation (as indicated by cracks in the brittle lacquer) at two levels of loading at the anterior edge of the model (arrow indicates where force applied; direction of force is into plane of figure). The values on the left are the forces that were required to deform the constant thickness models to the indicated radial distances from the point of force application. Those on the right are the forces required to deform the thickened margin models a similar amount. The shaded, horseshoe-shaped region shows approximately where the foot muscle would attach to the shell. Numerals 1-9 indicate the locations where shell thickness was measured on the *Notoacmea scutum* shell used to make the models. Location 1 was the apex. Locations 2, 4, 6, and 8 were in the thin annular region surrounding the apex. Locations 3, 5, 7, and 9 were at the thickest part of the shell margin. Thicknesses: 1 - 0.67mm, 2 - 0.35mm, 3 - 1.23mm, 4 - 0.50mm, 5 - 1.10mm, 6 - 0.57mm, 7 - 1.31mm, 8 - 0.53mm, 9 - 1.38mm. Dimensions of whole shell: length - 38.7mm, width - 31.7mm, height - 11.5mm.


anterior
Force
1N
3
6N
constant thickness
thickened margin
3N
2
9N
1
7
6
8
9
4
5
posterior

Since the total amount of material used in each model type was equal, the constant thickness models had thicker apical regions and thinner shell margins than the natural thickness models. Therefore, these results indicate that, with respect to the strength of the shell when resisting prying forces, marginal thickness is of more importance than is thickness in more apical regions of the shell.

Shell Strength and Foot Tenacity

For each species and side of the shell tested, the natural logarithm (ln) of the force required to break the shell (shell strength) and ln of the force required to detach the foot (foot tenacity) were regressed against ln foot area. In all cases, shell strength and foot tenacity showed a highly significant increase with increasing size (Tables II-6, II-7).

DISCUSSION

Crab Feeding Behavior

Three major patterns were evident in the results of the feeding experiments. First, the prying technique was clearly the most frequently observed feeding behavior for all crabs, including the seven *C. productus* and one *C. oregonensis* which had not fed on limpets for at least two years. Furthermore, the other *C. oregonensis*, which had

Table II-6. Equations for shell strength (F, in newtons) as a function of foot area (FA, in cm²) for all species and sides of shell. Equations detransformed from linear regressions of ln F vs. ln FA (r and P values given for ln-ln regressions). Range indicates maximum and minimum values for foot areas used in regressions. Side A - anterior, R - right, P - posterior.

Species	Side	Equation	range	n	r	P
TEMPERATE						
Acmaea mitra	A	$F=54.4FA^{0.\text{[illegible]}}$	0.34-2.50	11	0.8131	0.0023
Collisella digitalis	A	$F=42.3FA^{0.\text{[illegible]}}$	0.28-1.80	12	0.7769	0.0030
Collisella digitalis	P	$F=33.2FA^{\text{[illegible]}}$	0.29-1.78	8	0.9231	0.0011
Collisella pelta	A	$F=11.8FA^{\text{[illegible]}}$	1.18-4.35	11	0.7948	0.0035
Collisella pelta	R	$F=13.6FA^{\text{[illegible]}}$	0.73-4.22	8	0.9709	0.0001
Collisella pelta	P	$F=10.1FA^{\text{[illegible]}}$	0.80-3.34	7	0.9501	0.0010
Notoacmea persona	A	$F=27.5FA^{0.\text{[illegible]}}$	0.19-2.95	8	0.8452	0.0012
Notoacmea scutum	A	$F=11.6FA^{0.\text{[illegible]}}$	0.76-8.04	20	0.9091	<0.0001
Notoacmea scutum	R	$F=13.0FA^{0.\text{[illegible]}}$	1.10-4.30	8	0.9077	0.0018
Notoacmea scutum	P	$F=9.0FA^{\text{[illegible]}}$	1.19-5.91	8	0.9652	0.0001
Diodora aspera	A	$F=14.0FA^{0.\text{[illegible]}}$	1.80-8.23	8	0.9180	0.0013

Table II-6 cont

Species	Side	Equation	range	n	r	p
TROPICAL						
Collisella pediculus	A	$F=76\ 5FA^{0}$ [illegible]	0 20-0 74	11	0 8306	0 0015
Lottia stipulata	A	$F=28\ 6FA^{0}$ [illegible]	0 41-1 49	12	0 7654	0 0037
Fissurella longifissa	A	$F=45\ 3FA^{1}$ [illegible]	0 37-1 65	12	0 9560	<0 0001
Fissurella virescens	A	$F=40\ 1FA^{1}$ [illegible]	0 25-4 13	12	0 9815	<0 0001
Fissurella virescens	R	$F=58\ 4FA^{0}$ [illegible]	0 34-6 37	12	0 9546	<0 0001
Fissurella virescens	P	$F=47\ 0FA^{1}$ [illegible]	0 21-4 19	12	0 9813	<0 0001
Siphonaria gigas	A	$F=62\ 0FA^{0}$ [illegible]	0 10-6 77	11	0 9873	<0 0001
Siphonaria maura	A	$F=36\ 3FA^{1}$ [illegible]	0 53-1 58	9	0 7845	0 0123

Table II-7 Equations for foot tenacity (F, in newtons) as a function of foot area (FA, in cm²) for all species and sides of shell See Table II-6 legend for further information

Species	Side	Equation	range	n	r^2	P
TEMPERATE						
Acmaea mitra	A	F=26 4FA[illegible]	0 25-4 29	10	0 9742	<0 0001
Collisella digitalis	A	F=21 9FA[illegible]	0 25-2 97	9	0 9782	<0 0001
Collisella digitalis	P	F=23 3FA[illegible]	0 32-1 52	8	0 8839	0 0036
Collisella pelta	A	F=7 6FA[illegible]	0 69-3 89	20	0 9278	<0 0001
Collisella pelta	R	F=8 8FA[illegible]	0 82-3 71	8	0 9600	0 0002
Collisella pelta	P	F=9 6FA[illegible]	0 91-3 36	8	0 9902	<0 0001
Notoacmea persona	A	F=21 1FA[illegible]	0 59-3 26	8	0 9[illegible]45	<0 0001
Notoacmea scutum	A	F=8 1FA[illegible]	0 32-5 93	23	0 9662	<0 0001
Notoacmea scutum	R	F=12 9FA[illegible]	0 64-5 98	10	0 9215	0 0002
Notoacmea scutum	P	F=12 6FA[illegible]	0 90-5 46	8	0 9524	0 0003
Diodora aspera	A	F=7 4FA[illegible]	1 45-9 20	12	0 8841	0 0001

Table II-7 cont

Species	Side	Equation	range	n	r	p
TROPICAL						
Collisella pediculus	A	$F=27.8FA^{0.[illegible]}$	0.17-0.73	13	0.7673	0.0022
Lottia stipulata	A	$F=26.0FA^{0.[illegible]}$	0.36-2.06	12	0.9652	<0.0001
Fissurella longifissa	A	$F=41.4FA^{1.[illegible]}$	0.48-1.01	8	0.8913	0.0030
Fissurella virescens	A	$F=33.1FA^{1.0[illegible]}$	0.49-4.23	14	0.9571	<0.0001
Fissurella virescens	R	$F=31.8FA^{1.0[illegible]}$	0.39-3.26	9	0.9669	<0.0001
Fissurella virescens	P	$F=33.4FA^{0.[illegible]}$	0.62-3.37	11	0.9806	<0.0001
Siphonaria gigas	A	$F=32.9FA^{1.0[illegible]}$	0.09-4.87	11	0.9834	<0.0001
Siphonaria maura	A	$F=25.7FA^{1.0[illegible]}$	0.42-2.00	10	0.9208	0.0002

been collected from the plankton, had never fed on limpets and was only observed to use the prying technique. These results indicate that the initial preference for prying attacks is not learned. Moreover, this pattern was maintained through two months of being fed only limpets, indicating that learning does not greatly change the strong preference for prying attacks (see Hughes, 1980, Lawton and Hughes, 1985, and references therein for discussions of the role of learning in the feeding behavior of crabs).

A second pattern observed was the increase in the relative frequency of prying attacks as the ratio of limpet size to crab size increased. When the ratio of limpet size to crab size is large, some of the other possible techniques (e.g., crush at margins) become physically impossible. Other techniques become very difficult (e.g., apex crush). In contrast, even small crabs can pry off large limpets if the limpet is caught before it has clamped down. This should also be true for lateral sliding attacks and the reason for the low frequency of this behavior is unknown. This low frequency may be related to the tendency for the edge of the shell to dig into the substratum when it is slid sideways. Undoubtedly, the prying forces generated by crabs include a lateral, in addition to vertical, component. A switch in feeding behavior as the ratio of gastropod size to crab size increases has also been observed for crabs feeding on spirally-coiled marine gastropods (Bertness and

Cunningham, 1981; Reimchen, 1982; ap Rheinallt and Hughes, 1985; Lawton and Hughes, 1985).

A third pattern emerging from these observations was an increase in the relative frequency of prying attacks for flat shells as opposed to tall shells. This was probably due to the difficulty of attaining a purchase on flat shells for non-prying attacks.

In addition to differences in the frequency of occurrence of attacks, the various feeding techniques also differed in the frequency of success (Table II-3). The potential for selection for defensive features of shell morphology is a function of both of these factors (Vermeij, 1985). For example, this point was illustrated in the one case where the crabs were large enough and the limpets small enough and of the right shape to enable the marginal crushing technique (*C. productus* - *C. pelta*). Combining all the attack techniques used in this case, over half the observed attacks were immediately successful (17 successful vs. 15 unsuccessful; Table II-3) and all limpets were eaten within four hours. For selection to favor a particular defensive feature of morphology, individuals possessing that feature must possess a higher probability of successfully surviving an attack than those lacking that feature. If the probability of surviving a series of attacks is vanishingly small regardless of morphology (as seems to be the case for marginal crushing attacks), selection is unlikely to occur.

(see Reimchen, 1980; Vermeij, 1982, 1985; Sih, 1985 for further discussion). The much higher probability of surviving a prying attack (Table II-3), coupled with the high frequency of this behavior, suggests that selection for morphological features of the shell which enhance resistance to prying forces is quite strong.

Mechanical Performance of the Shell

The results from the crab-behavior and the limpet-shell-model experiments emphasize the importance of the marginal thickness of limpet shells as a morphological defense against crab predation. This conclusion is further supported by the results of the strength measurements for real shells. For the strength measurements of the anterior side of *N. scutum*, thickness measurements at several locations on the shell were taken before the shells were broken. These locations corresponded to locations 1 through 7 of Figure II-2 and included three positions along the shell margin and four positions in the apical region. Due to the high correlations between these thickness measurements, particularly between the measurements of marginal thickness (Table II-8), it was not feasible to analyze the relationship between shell strength and thickness using a single multiple regression (Bendel, 1971). Therefore, shell strength was instead regressed separately against each measure of shell thickness. The correlation

Table II-8 Correlation matrix among thicknesses at several locations (1-7) on the shells of *Notoacmea scutum* n=20 for all correlations See Fig II-2 for positions of locations

	1	2	3	4	5	6	7
1	1.0000						
2	0.8043	1.0000					
3	0.4973	0.7444	1.0000				
4	0.7716	0.8838	0.5636	1.0000			
5	0.5288	0.7973	0.9642	0.6373	1.0000		
6	0.7397	0.9072	0.6867	0.9081	0.7562	1.0000	
7	0.5582	0.7938	0.9599	0.6595	0.9680	0.7568	1.0000

coefficients for these regressions indicate that marginal thickness accounted for more of the variation in the strength of these real shells than did any of the apical thicknesses (Table II-9).

The importance of marginal thickness to the strength of real limpet shells was further emphasized by comparisons among all the species tested. As for shell strength, marginal thickness also showed a highly significant increase with increasing size for all species and sides of the shell measured (Table II-10). These thickness measurements corresponded to the same sides of the shell for which shell strength and foot tenacity were measured. The measurements were made on the individuals used for the shell strength measurements (before breaking) and were supplemented with measurements made on additional individuals from the same populations. For those species with radial ribs extending to the shell margin, thickness was calculated as the average of the rib and adjoining furrow thicknesses.

These ln-ln regressions (Tables II-6, II-10) were then used to calculate shell strength and marginal thickness for each species and side of the shell at a single intermediate size (foot area=1cm^2) common to all species. These two sets of measurements were regressed against each other and shell strength showed a highly significant increase with increasing marginal thickness (Fig. II-3).

Table II-9. Equations for shell strength (F, in newtons) as a function of shell thickness (T, in mm) at seven locations on the shells of *Notoacmea scutum*. See Fig. II-2 for positions of locations. Equations detransformed from linear regressions of ln F vs. ln T (r and P values given for ln-ln regressions). Range indicates maximum and minimum values for shell thicknesses used in regressions. n=20 for all equations.

Location	Equation	range	r	P
1	$F=57.3T^{1.00}$	0.23-1.50	0.6581	0.0016
2	$F=160.3T^{1.}$[illegible]	0.15-0.66	0.7704	0.0001
3	$F=44.6T^{1.}$[illegible]	0.31-1.57	0.8966	<0.0001
4	$F=83.5T^{1.}$[illegible]	0.20-1.04	0.7030	0.0005
5	$F=35.4T^{1.}$[illegible]	0.33-1.94	0.9054	<0.0001
6	$F=92.1T^{1.}$[illegible]	0.20-1.07	0.7460	0.0002
7	$F=35.2T^{1.}$[illegible]	0.39-1.72	0.9260	<0.0001

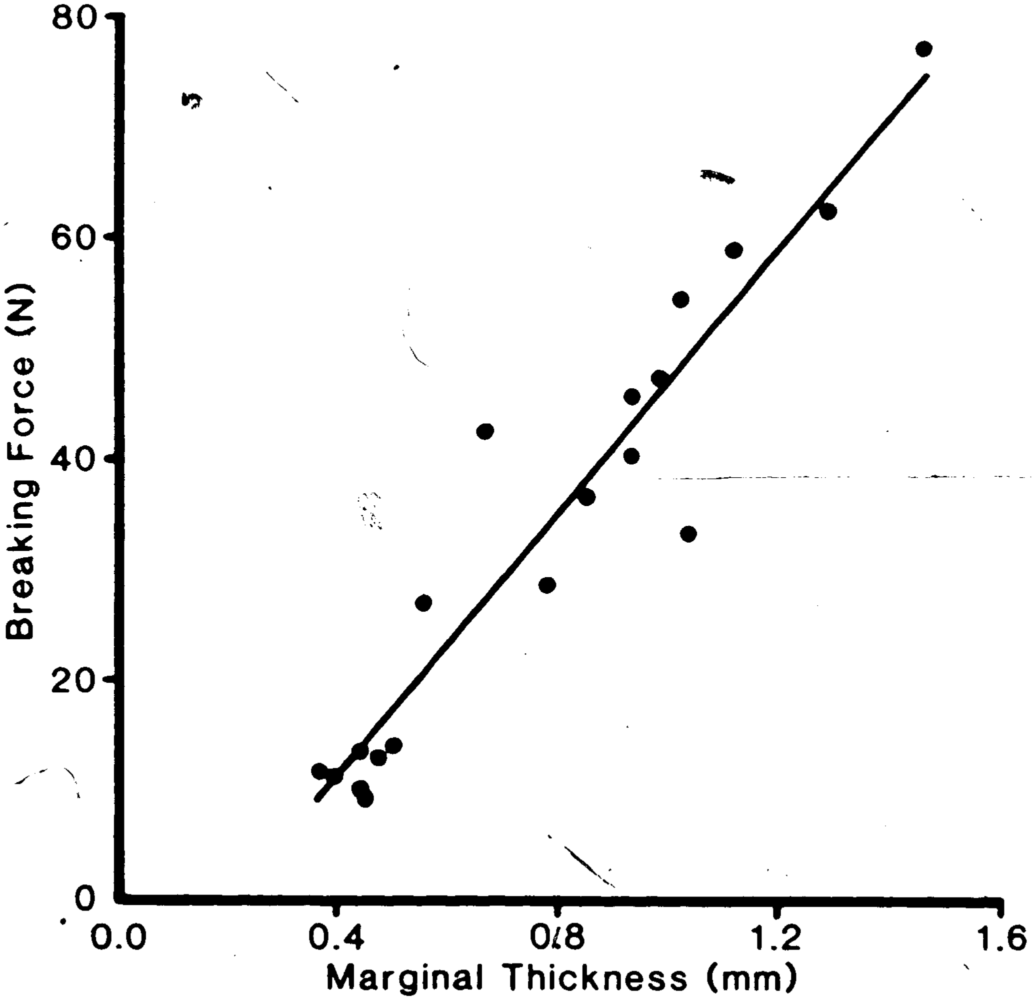
Table II-10. Equations for thickness at margin of shell (T, in mm) as a function of foot area (FA, in cm²) for all species and sides of shell. Equations detransformed from linear regressions (reduced major axis) of ln T vs. ln FA (r and P values given for ln-ln regressions). Range indicates maximum and minimum values for foot areas used in regressions. Side: A - anterior, R - right, P - posterior. * - indicates significant ($P<0.05$) allometric increase or decrease of marginal thickness with increasing foot area, as indicated by an exponent that is significantly greater or less than 0.5. See Clarke, 1980 for significance tests for slopes of reduced major axis regressions.

Species	Side	Equation	range	n	r	P
TEMPERATE						
Acmaea mitra	A	$T=1.03FA^{0.[illegible]}$	0.34-3.84	16	0.9221	<0.0001
Collisella digitalis	A	$T=0.67FA^{0.[illegible]}$	0.28-1.80	24	0.8153	<0.0001
Collisella digitalis	P	$T=1.04FA^{0.[illegible]}$	0.28-1.80	24	0.8939	<0.0001
Collisella pelta	A	$T=0.37FA^{0.[illegible]}$*	0.69-4.55	88	0.8263	<0.0001
Collisella pelta	R	$T=0.45FA^{0.[illegible]}$*	0.69-4.55	88	0.8765	<0.0001
Collisella pelta	P	$T=0.44FA^{0.[illegible]}$*	0.69-4.55	88	0.8875	<0.0001
Notoacmea persona	A	$T=0.57FA^{0.[illegible]}$*	0.19-2.95	8	0.8940	0.0027
Notoacmea scutum	A	$T=0.40FA^{0.[illegible]}$*	0.59-8.04	106	0.9180	<0.0001
Notoacmea scutum	R	$T=0.48FA^{0.[illegible]}$*	0.59-8.04	106	0.9239	<0.0001
Notoacmea scutum	P	$T=0.46FA^{0.[illegible]}$*	0.59-8.04	106	0.9234	<0.0001
Diodora aspera	A	$T=0.51FA^{0.[illegible]}$*	1.80-8.23	8	0.9752	<0.0001

Table II-10 cont

Species	Side	Equation	range	n	r	p
TROPICAL						
Collisella pediculus	A	$T=1\ 47FA^{0}$ [illegible]	0 16-0 80	19	0 8702	<0 0001
Lottia stipulata	A	$T=0\ 79FA^{0}$ [illegible]	0 41-1 49	15	0 7491	0 0013
Fissurella longifissa	A	$T=0\ 94FA^{0}$ [illegible]	0 30-1 65	13	0 9763	<0 0001
Fissurella virescens	A	$T=0\ 93FA^{0}$ [illegible]	0 21-6 37	43	0 9604	<0 0001
Fissurella virescens	R	$T=1\ 12FA^{0}$ [illegible]	0 21-6 37	43	0 9702	<0 0001
Fissurella virescens	P	$T=0\ 99FA^{0}$ [illegible]	0 21-6 37	43	0 9613	<0 0001
Siphonaria gigas	A	$T=1\ 29FA^{0}$ [illegible]	0 10-7 26	15	0 9720	<0 0001
Siphonaria maura	A	$T=0\ 85FA^{0}$ [illegible]	0 31-1 58	16	0 7296	0 0013

Figure II-3. Force to break shell (F, in newtons) versus marginal thickness (T, in mm) at intermediate size (foot area=1cm^2) for all species and sides of shell. Values calculated from equations in Tables II-6 and II-10. The regression line indicates the significant increase of shell strength with increasing marginal thickness: $F=-12.6+59.1T$; $n=19$; $r=0.9517$, $P<0.0001$.


80
60
40
20
0
Breaking Force (N)
0.0
0.4
0.8
1.2
1.6
Marginal Thickness (mm)

The prying forces exerted by crab predators on limpet shells differ from the breaking forces exerted by crabs on the shells of spirally-coiled gastropods in that the maximum possible prying force on a limpet shell is set by foot tenacity (Chapter IV; Lowell, 1985). This intrinsic limit does not apply to spirally-coiled gastropods, the shells of which still provide protection from predators even after the foot is detached. Therefore, limpets are unique in that one would expect selection to act to link the mechanical performances of the shell and the foot, given a cost to excessively strengthening the shell (Palmer, 1981). This linkage has been demonstrated in interspecific comparisons of limpets in the eastern Pacific (Chapter IV).

Further, intraspecific evidence for the linkage of the performances of the shell and foot is evident in comparisons of the slope of ln shell strength regressed against ln foot area to the slope of ln foot tenacity regressed against ln foot area for each species and side of the shell tested (slopes given in detransformed form as exponents; Tables II-6, II-7). These two slopes differed significantly in only one of nineteen cases (*F. virescens* - posterior side; Chapter IV). This means that, for the most part, the shell strength and foot tenacity ln-ln regressions were essentially parallel. Thus, the ratio of shell strength to foot tenacity remained fairly constant with increasing size. This linkage between shell strength and foot tenacity over a wide range of different slopes is further emphasized by the highly significant correlation between the slopes for shell strength and those for foot tenacity for all species and sides of the shell combined (Fig. II-4).

The linkage between shell strength and foot tenacity appears to be at least partially due to the degree of allometric increase of marginal thickness with increasing size. For an isometrically growing limpet, marginal thickness should increase as the square root of foot area due to simple geometric considerations. Several exponents in Table II-10 were significantly different than 0.5, indicating an allometric change in marginal thickness with increasing foot area. Furthermore, the exponents in Table II-10 (indicating degree of allometry) were highly correlated with the exponents for shell strength as a function of foot area in Table II-6 (Fig. II-5). In other words, the rate of increase of shell strength with increasing size appears to be linked to the rate of increase of marginal thickness with increasing size. This suggests that the limpets can control shell strength so that it parallels foot tenacity by controlling the degree of allometry in marginal thickness.

Taken as a whole, these data underscore the relationship between the localized forces generated by crabs feeding on limpets and the localized thickening (= strengthening) of a specific region of the limpet shell, the

Figure II-4. Slopes of shell strength ln-ln regressions (SS) versus slopes of foot tenacity ln-ln regressions (FT) for all species and sides of shell. Slopes given as exponents in Tables II-6 and II-7. The regression line (reduced major axis) indicates a significant tendency for greater slopes for shell strength to be associated with greater slopes for foot tenacity: $SS=-0.18+1.11FT$; $n=19$; $r=0.6708$; $P=0.0017$.

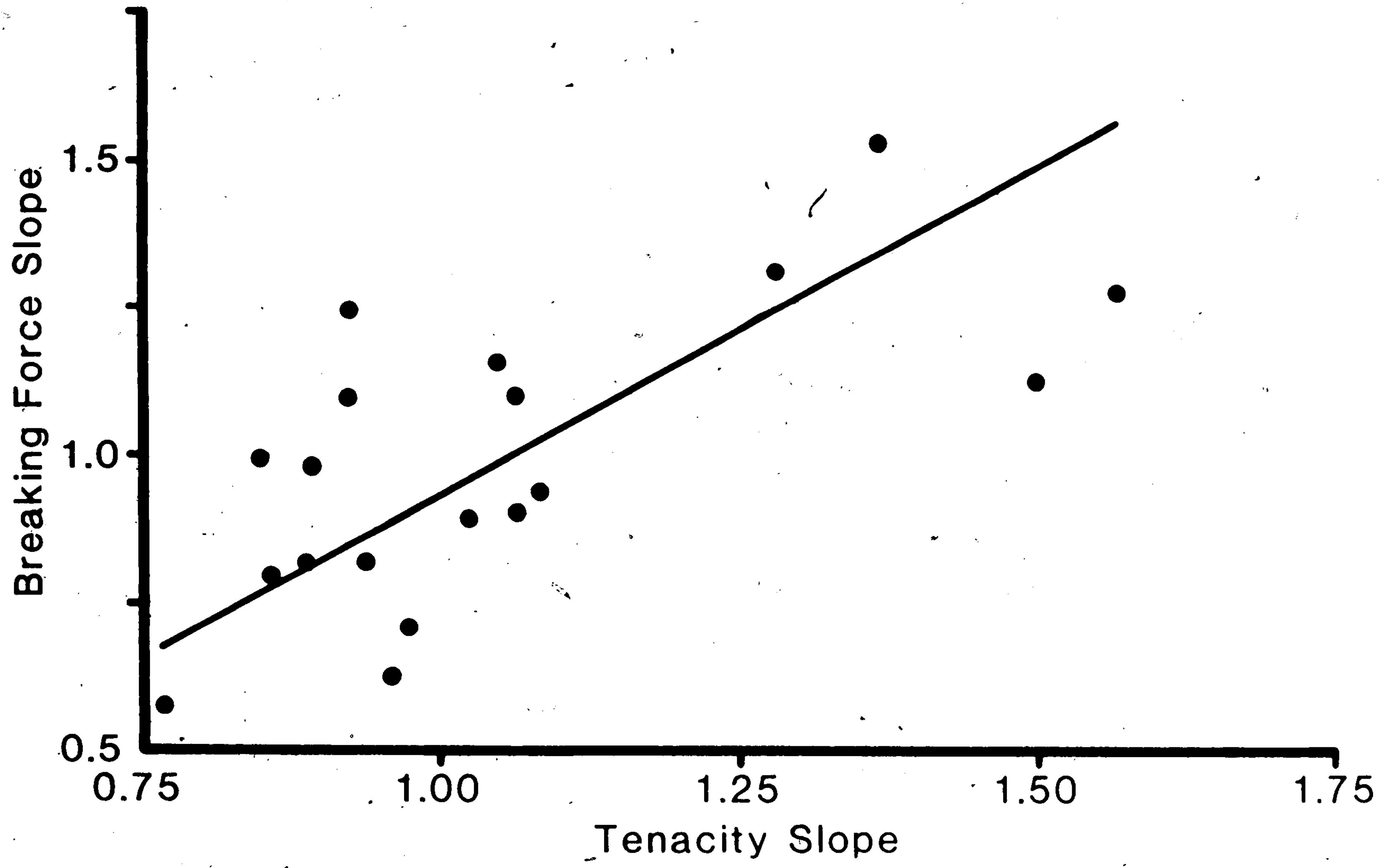
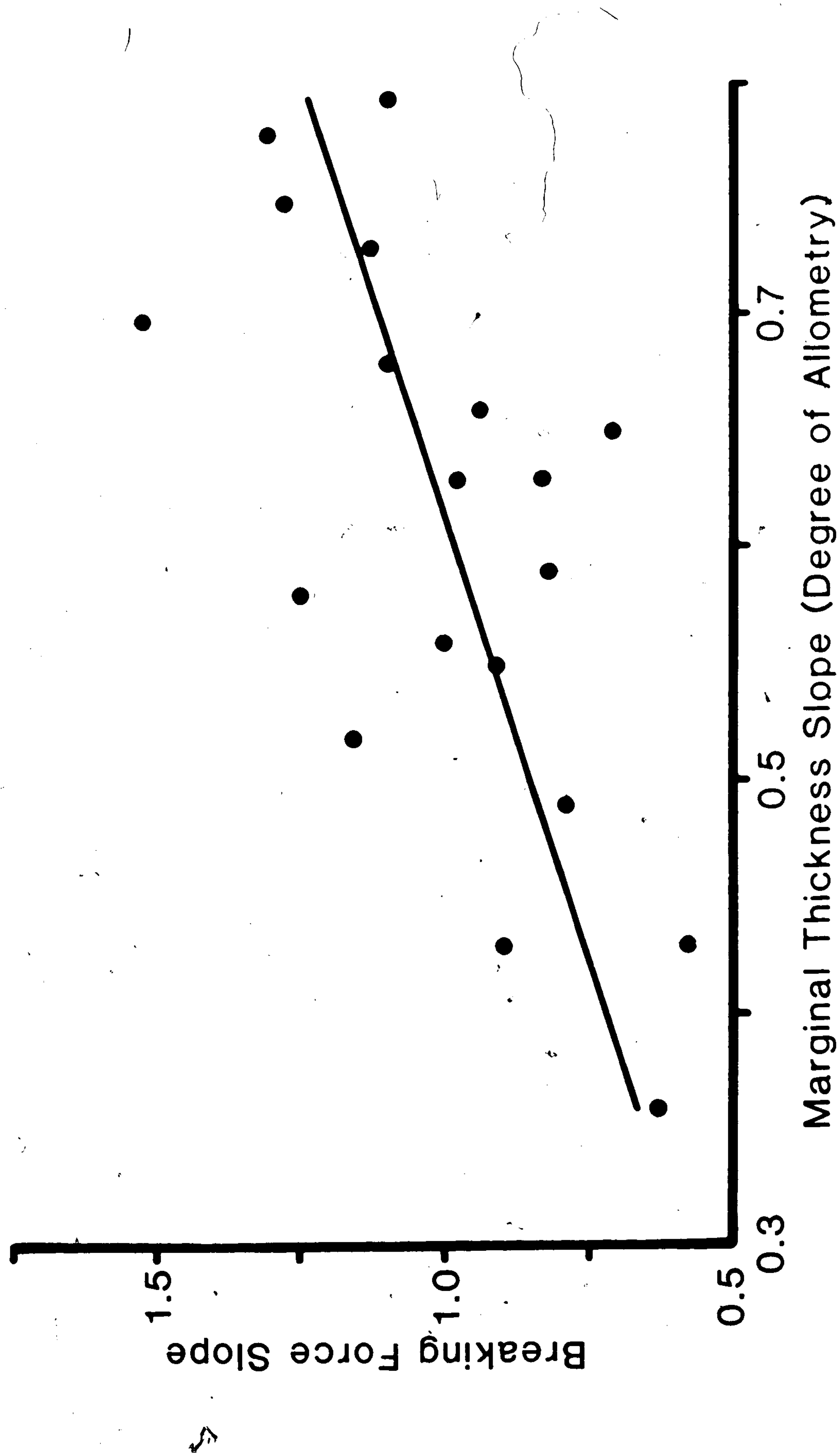

Breaking Force Slope
1.5
1.0
0.5
0.75
1.00
1.25
1.50
1.75
Tenacity Slope

Figure II-5. Slopes of shell strength ln-ln regressions (SS) versus slopes of marginal thickness ln-ln regressions (MT) for all species and sides of shell. Slopes given as exponents in Tables II-6 and II-10. SS represents the rate of increase of shell strength with increasing foot area. MT represents the rate of increase of marginal thickness with increasing foot area (= degree of allometry). SS and MT are positively correlated: SS=0.19+1.33MT; n=19; r=0.6589; P=0.0022.


Breaking Force Slope
0.5
1.0
1.5
Marginal Thickness Slope (Degree of Allometry)
0.3
0.5
0.7

shell margin. The strengths of whole shells have also been reported for a few species of bivalves (Elner, 1978; Currey, 1979; Blundon and Kennedy, 1982; Boulding, 1984) and spirally-coiled gastropods (Currey, 1979; Vermeij and Currey, 1980; Currey and Hughes, 1982; Blundon and Vermeij, 1983). These measurements were all made by crushing whole shells between planar or rounded surfaces. In most cases, the force was applied to opposite sides of whole shells (left and right valves still joined for bivalves) in various orientations across all or much of the entire width of the shell. This kind of "whole-animal" crushing force is generated by certain species of fish (Palmer, 1979) and crabs [when mollusc size/crab size is small (bivalves - Elner, 1978; Blundon and Kennedy, 1982; Boulding, 1984) (gastropods - Zipser and Vermeij, 1978; Bertness, 1981; Bertness and Cunningham, 1981; Reimchen, 1982; ap Rheinallt and Hughes, 1985; Lawton and Hughes, 1985)].

In contrast, the above studies on crabs have shown that, when the ratio of mollusc size to crab size is large, crabs exhibit a strong tendency to attack the edge of the valve for bivalves or the shell lip, apex, or similar narrow region of the shell for spirally-coiled gastropods. These studies have also shown that the probability of an unsuccessful attack is much greater when the ratio of mollusc size to crab size is large. As discussed earlier, this suggests that with respect to crab predation, the potential for selection for the strength of these localized regions of the shell may be greater than for the strength of other regions of the shell. Therefore, measurements of the force required to crush whole shells across the region of greatest width should be used with caution in discussions of the evolution of defensive shell morphologies. To the extent, however, that the thicknesses of different regions of the shell are correlated (as was found for *N. scutum*; Table II-8), such "whole-animal" strengths may be correlated with the strengths of the more critical regions of the shell.

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III. SELECTION FOR GREATER SAFETY FACTORS OF BIOLOGICAL STRUCTURES AS ENVIRONMENTAL UNPREDICTABILITY INCREASES

Most biological structures, from the cellular to organ system level, have evolved in environments that are, to a greater or lesser degree, unpredictable. In particular, using load-bearing structures as an example, one would expect lifetime maximum loads on such structures to vary in an unpredictable fashion. Through environmental effects on development and deterioration, the strength of these structures should also vary unpredictably. Therefore, selection for the strength of a structure, relative to the maximum load it must bear, should be sensitive not only to the average maximum load likely to be encountered, but also to <u>variability</u> in the strength of and/or maximum load on the structure (1). One measure of relative strength is "safety factor" (mean strength/mean lifetime maximum load) (2).

Figure III-1a illustrates, for a hypothetical load-bearing structure, the mean force required to break the structure ($\bar{S}$) and the mean maximum force that structure experiences during its lifetime ($\bar{L}_{mx}$), where these means are calculated for a population of individuals; safety factor equals $\bar{S}/\bar{L}_{mx}$. Since individual structures in the population will not all break at the same force (S), a variance in S will exist. Similarly, since individual structures will not

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A version of this chapter has been published. Lowell, R.B. 1985. *Science* 228:1009-1011.

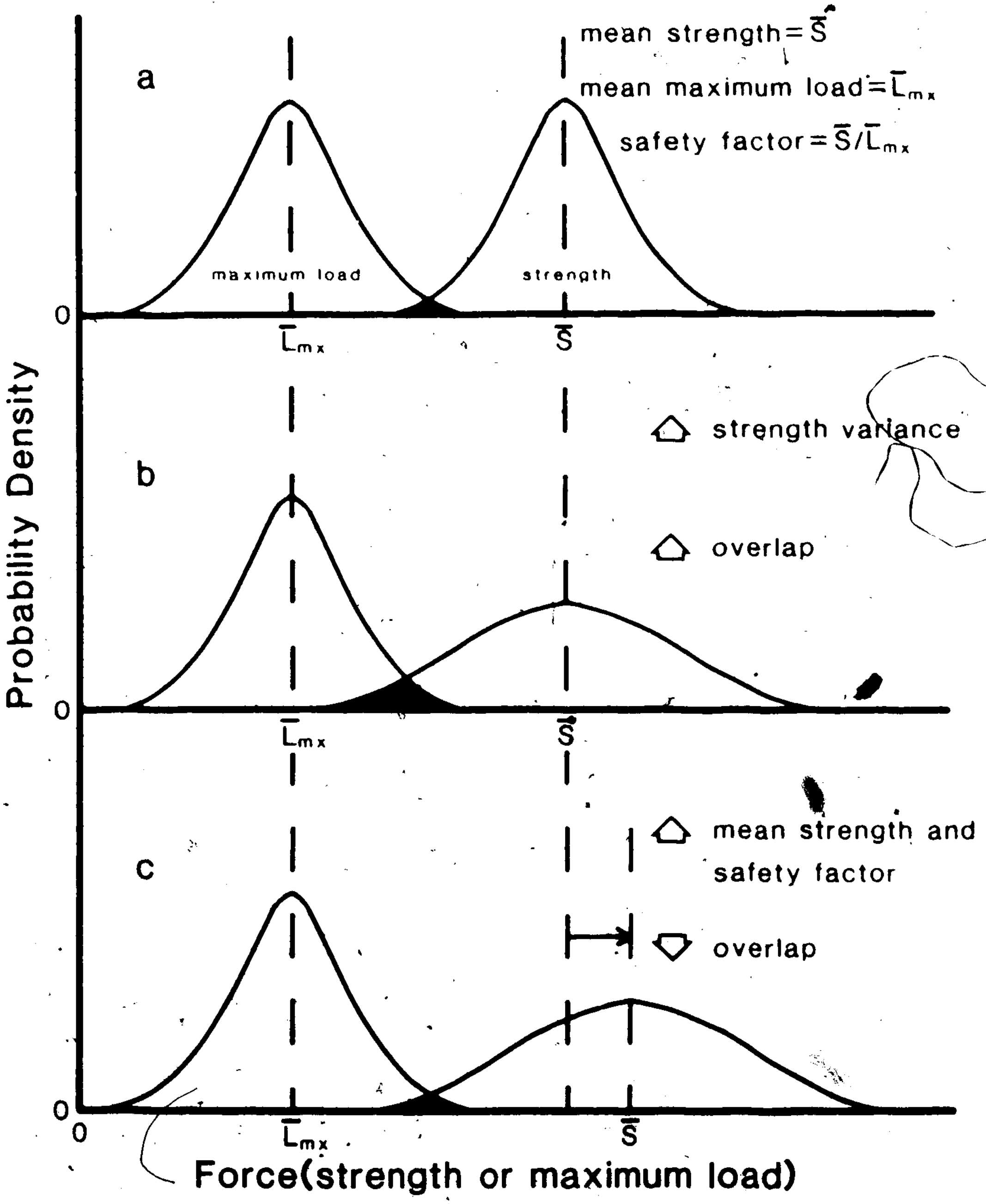
all experience the same lifetime maximum load (L_{mx}), a variance in L_{mx} will also exist. If the distribution of L_{mx} is described by function f and the distribution of S is described by function g, then the probability (PF) that an individual structure, chosen at random from the population, will fail sometime during its lifetime is:

$$PF = \int_0^\infty g(x)\int_x^\infty f(y)dydx$$

(relative magnitudes of PF are depicted as shaded overlap regions in Fig. III-1). If such a failure is deleterious, selection should act to minimize PF by increasing $\bar{S}$ when it is not possible to reduce $\bar{L}_{mx}$ or either variance. However, if there is a cost to strengthening the structure, PF may not be reduced to zero. If the variance in S or L_{mx} is increased without changing the means, the overlap, and thus PF, will increase (Fig. III-1b). Consequently, selectio[illegible] should act to increase the safety factor by increasing $\bar{S}$ [illegible] bring PF back down to a suitably low value (Fig. III-1c). Therefore, more variable systems should experience selection for greater safety factors - that is, greater relative strengths (3).

Testing this prediction requires a consistent measure of relative strength - that is, a measure of the relative positions of the two curves illustrated in Fig. III-1a using statistically fixed points (such as $\bar{S}$ and $\bar{L}_{mx}$ used to define

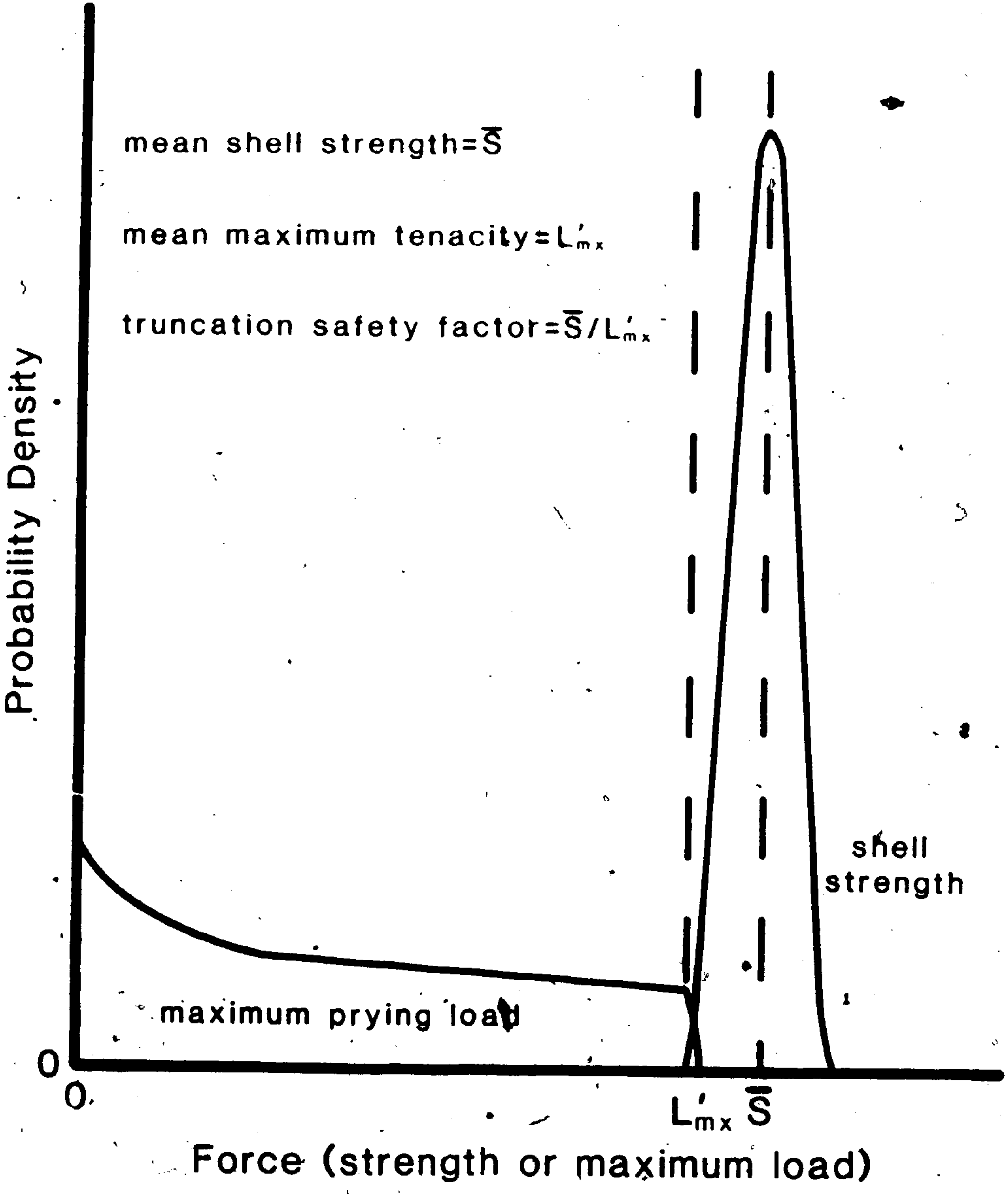
Figure III-1. Potential effect of increasing variance (unpredictability) on safety factor. The curves diagrammatically illustrate, for a given load-bearing, biological structure, the distribution of structural strengths and lifetime maximum loads for individuals within a single population as strength variance is increased. Increasing maximum load variance would have an analogous effect. See text for discussion.


mean strength = $\bar{S}$
mean maximum load = $\bar{L}_{mx}$
safety factor = $\bar{S}/\bar{L}_{mx}$
a
maximum load
strength
0
$\bar{L}_{mx}$
$\bar{S}$
b
△ strength variance
△ overlap
0
$\bar{L}_{mx}$
$\bar{S}$
c
△ mean strength and safety factor
▽ overlap
0
0
$\bar{L}_{mx}$
$\bar{S}$
Probability Density
Force(strength or maximum load)

a safety factor). The mean and variance of strength are readily obtained for many structures by measuring the force required to break several test specimens from the population of interest. The mean and variance of lifetime maximum load, however, are usually very difficult to measure under natural conditions due to the heterogeneous environment of forces most load-bearing structures experience. For example, $\bar{L}_{mx}$ for a given segment of an adult zebra femur would be a complex function of several parameters including the adult lifetime probabilities of a wide range of accelerations, decelerations, cruising speeds, falls, and collisions with predators and conspecifics. Biewener (4) has shown that a nonrigorous choice of $\bar{L}_{mx}$ can lead to the perhaps unreasonable conclusion that the limb bones of small mammals and birds have much greater safety factors than those of large mammals.

This problem sometimes can be avoided by using another statistically fixed point (L'_{mx}, Fig. III-2) from the maximum load distribution that <u>can</u> be measured for several kinds of structures. L'_{mx} is the maximum possible force a structure can experience under natural conditions - that is, the right hand edge or truncation of the maximum load distribution, and can be used to obtain an alternative measure of relative strength, "truncation safety factor" ($TSF = \bar{S}/L'_{mx}$). In general, more variable systems should also experience selection for greater TSF's since, on average, greater TSF's

Figure III-2. Truncation safety factor for hypothetical limpet population subject to prying forces. The shapes of the maximum prying load and shell strength distributions are meant to suggest 1) maximum load variance is likely to be greater than strength variance due to the heterogeneity of the intertidal environment, 2) many limpets probably live to reproduce and then die without ever having experienced a prying load, and 3) maximum tenacity determines the right hand truncation of the maximum load curve.


mean shell strength=$\bar{S}$
mean maximum tenacity=L'_{mx}
truncation safety factor=$\bar{S}/L'_{mx}$
Probability Density
shell strength
maximum prying load
0
0
L'_{mx}
$\bar{S}$
Force (strength or maximum load)

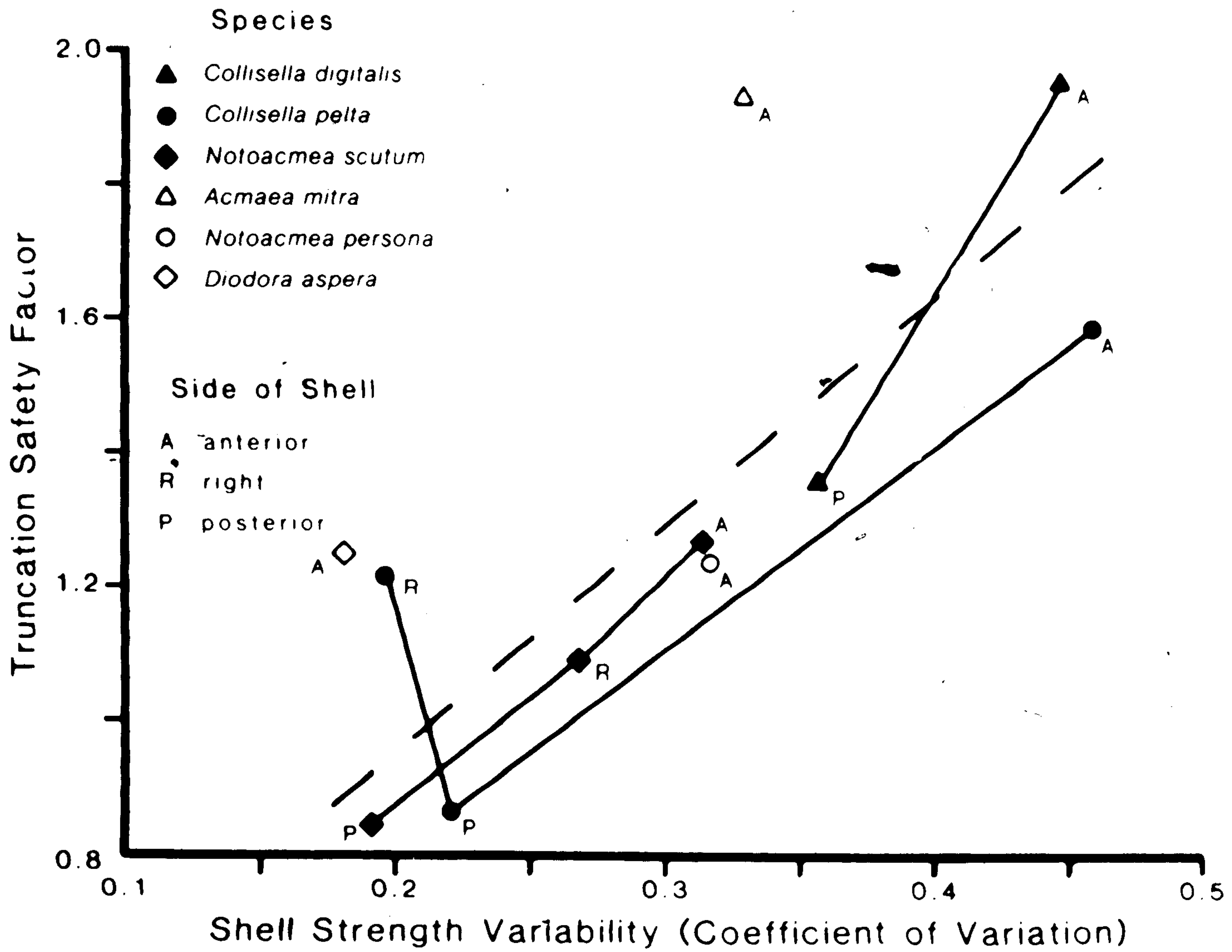
should be associated with greater safety factors. In particular, when the load distribution remains constant among the different structures being compared (see below), $\bar{L}_{mx}/L'_{mx}$ will also remain constant and TSF will, therefore, be a constant multiple of the true safety factor.

To test this prediction, I measured TSF's and shell strength variances for single populations of six species of northeast Pacific intertidal limpets, including five acmaeids (*Acmaea mitra, Collisella digitalis, C. pelta, Notoacmea persona, N. scutum*) and one fissurellid (*Diodora aspera*). The shells of these limpets are subjected to prying forces by predatory crabs (5) and birds (6). To find $\bar{S}$, I measured the prying force (shell strength) required to break various sides of wet shells from freshly sacrificed limpets (7). L'_{mx} could also be measured (8) since, in evolutionary terms, the maximum possible prying load that the edge of a limpet shell can experience equals the maximum force (maximum tenacity) required to detach the foot of a previously undisturbed, healthy limpet on a flat rock surface in the field. This is because after the foot is detached, the shell no longer affords any protection. Thus, TSF's could be assigned to those species and sides of the shell measured where $\bar{S}$ was mean shell strength and L'_{mx} was mean maximum tenacity. Fig. III-2 suggests strength and maximum load distributions for a hypothetical intertidal limpet population whose shells are subjected to prying forces. While the distributions illustrated in Figs. III-1 and III-2 are for the simplified case of a single structural size class, I actually measured shell strength and maximum tenacity for limpets of several sizes and used analysis of covariance to calculate TSF's and shell strength variances from adjusted means and residual variances (9).

Shell strength is strongly affected by shell thickness as well as by cracks and irregularities in the shell (Chapter II; R.B. Lowell, unpublished data). These parameters are, in turn, affected by several environmental factors such as infection by endolithic organisms, shell erosion, previous shell damage, and the particular microhabitats available to a limpet as it grows. For the most part, these environmental factors should be unpredictable to individual limpets and, consequently, the exact shell strength of any given individual would most likely also be unpredictable, resulting in the observed variability in shell strength. For example, *C. digitalis* is particularly susceptible to infection by the endolithic fungus *Pharcidia balani* (10) and also exhibits great variability in shell strength (Fig. III-3).

The TSF approach, as used here, assumes that the shape of the maximum load distribution is independent of strength variance. This assumption is very likely true for all the following comparisons since the shape of the maximum load distribution is presumably a function of limpet and predator

Figure III-3. Truncation safety factor (TSF) versus strength variability for the shells of northeastern Pacific limpets. The dashed line [reduced major axis (12) calculated for all species and shell sides combined, $r=0.7407$, $P=0.009$] illustrates the significant, average increase of TSF with increasing variability in shell strength. Solid lines connect the points for within-species comparisons of the different sides of the shell: *N[illegible]um*, $r=0.9987$, $P=0.032$; *C. pelta*, $r=0.8270$, $P=0.380$; *C. digitalis*, $t=1.648$, $df=31$, $P=0.109$, two-tailed t-test for ln anterior TSF versus ln posterior TSF (13).


Species
▲ Collisella digitalis
● Collisella pelta
◆ Notoacmea scutum
△ Acmaea mitra
○ Notoacmea persona
◇ Diodora aspera
Side of Shell
A anterior
R right
P posterior
Truncation Safety Factor
2.0
1.6
1.2
0.8
0.1
0.2
0.3
0.4
0.5
Shell Strength Variability (Coefficient of Variation)
A
R
P

distributions whereas strength variance is presumably an independent function of environmental effects on shell development and deterioration. Differently shaped maximum load distributions, as well as selective pressures other than prying forces that could independently affect shell strength as measured here, would tend to increase the noise (variance) about the expected average increase of TSF due to increased variability in shell strength. This noise should be reduced when the overlapping portions of the maximum load distributions are of approximately the same shape among the different structures or species being compared and when differences in selection pressures other than prying forces are minimal. These latter conditions are most likely to hold when comparing different sides of the shell within a single population.

I estimated single-population TSF's for the anterior, posterior, and right sides of *C. pelta* and *N. scutum* and for the anterior and posterior sides of *C. digitalis* where each side of the shell had its own characteristic shell strength variance. The causes for the within-population differences in strength variance among the different sides of the shell are unknown; one possibility is that these differences are due to interactions between shell asymmetry and environmental factors which weaken the shell. In any case, these differences exist and the results (points connected by solid lines, Fig. III-3) suggest a within-population increase in TSF with increasing variability in shell strength, although this trend was significant for only *N. scutum*.

Because the individuals of five of the six species came from populations along the same 50m stretch of shore and because all six species were exposed to the same suite of predators, the shapes of the overlapping portions of the maximum load distributions, as well as selective pressures other than prying forces, may also be similar for interspecific comparisons. For all species and sides of the shell combined (all points, Fig. III-3), TSF increased significantly with increasing variability in shell strength. Thus, the relationship holds even across four genera and two superfamilies of gastropods.

These results provide direct support for the hypothesis that the relative strength of load-bearing biological structures should increase as the variability of the system increases. The TSF approach should be useful for testing this hypothesis further for several other kinds of load-bearing structures such as 1) the stipes of those intertidal macrophytes where the maximum possible force on the stipe is determined by the strength of attachment to the substrate or 2) those tendons and apodemes where the maximum possible force on the tendon or apodeme is determined by maximal muscular contraction.

The safety factor-TSF approach described above can be generalized beyond load-bearing structures to make predictions about the relative performance of a much wider array of biological structures and systems by redefining safety factor as average realized performance $(\bar{S})$/average required performance $(\bar{L}_{mx})$ where, again, these averages are over a population of individuals. For instance, one would predict that the average maximum hormonal output of a given type of endocrine gland would be greater, relative to the average threshold output required during stressful conditions, for populations whose maximum hormonal outputs and/or threshold requirements are more unpredictable. An analogous prediction would be that the average nectar output of a given flower type would be greater, relative to the zero variance output required to attract pollinators away from another population, for populations whose nectar outputs are more unpredictable. There is already empirical evidence that bumblebee foraging decisions could provide the selective pressures required for the latter prediction (11).

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7. Using a Monsanto (Type W) tensometer, a force (measured in newtons) was applied in a dorsal direction perpendicular to the plane of the aperture by a 1.16mm diameter steel hook of circular cross section inserted under the edge of the shell to mimic the prying action of a rounded crab appendage; the breaking force did not differ significantly in pairwise comparisons among hooks ranging in diameter from 0.67mm to 2.64mm (smallest $P>0.15$, $n=7-20$, ANCOVA).

8. Spring scales were used to load (force measured in newtons) the edge of the shell in a manner identical to and on the same sides as the breaking force measurements. Limpets from Lime Kiln Lighthouse (all except *N. persona*) and False Bay (*N. persona*) on San Juan Island, Washington, USA were used both for strength and tenacity measurements.

9. Model I ANCOVA was used to calculate TSF and shell strength variance as follows. For each species and side of the shell, I regressed ln breaking force against ln foot area ($n=7-20$) and ln maximum tenacity against ln foot area ($n=8-23$). All ln breaking force-ln maximum tenacity regression pairs were parallel (no significant differences between the regression coefficients of each pair, smallest $P>0.05$). Hence, the TSF's were essentially constant over the size ranges tested. Therefore, $TSF=\exp(\ln\hat{S}-\ln L'_{mx})$ where $\ln\hat{S}$ was the ln breaking force adjusted mean and $\ln L'_{mx}$ was the ln maximum tenacity adjusted mean for each species and side of the shell. Shell strength variance equaled the residual variance (MSe) of the ln breaking force versus ln foot area regressions. MSe's are reported here as coefficients of variation (CV) where $CV=[\exp(MSe)-1]^{0.5}$ [P.N. Chalmer, *J. Zool., Lond.* 191, 241 (1980); R.C. Lewontin,

Syst. Zool. 15, 141 (1966); S. Wright, *Evolution and the Genetics of Populations* (University of Chicago Press, Chicago, vol. 1, 1968)]. ANCOVA, analysis of covariance; ln, natural logarithm; exp, base e antilogarithm.

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13. Ln TSF ± one standard error, CV ± one standard error for each point in Fig. 3: *C. digitalis* A, 0.67±0.147, 0.45±0.108; *C. digitalis* P, 0.30±0.161, 0.36±0.100; *C. pelta* A, 0.46±0.125, 0.46±0.117; *C. pelta* R, 0.20±0.128, 0.20±0.051; *C. pelta* P, -0.15±0.093, 0.22±0.062; *N. scutum* A, 0.23±0.086, 0.31±0.054; *N. scutum* R, 0.08±0.137, 0.27±0.072; *N. scutum* P, -0.17±0.102, 0.19±0.050; *A. mitra* A, 0.66±0.121, 0.33±0.077; *N. persona* A, 0.21±0.128, 0.31±0.086; *D. aspera* A, 0.22±0.134, 0.18±0.047; A, R, P as for Fig. 3.
14. I thank R.McN. Alexander, A.A. Biewener, G.M. Branch, J.D. Currey, D.H. Kelker, M. LaBarbera, A.R. Palmer, C. Strobeck, and two anonymous reviewers for their suggestions and the use of equipment. I also thank the staff and biomechanics group at the University of Washington's Friday Harbor Laboratories for

providing research space and facilities. Funding was provided by a Killam predoctoral fellowship to the author, NSERC operating grant A7245 to A.R. Palmer, and the Department of Zoology, University of Alberta.

IV. SAFETY FACTORS OF TROPICAL VERSUS TEMPERATE LIMPET SHELLS: MULTIPLE SELECTION PRESSURES ON A SINGLE STRUCTURE

INTRODUCTION

A major difficulty faced by functional morphologists attempting to determine the 'adaptedness' of biological structures is the identification of conflicting selection pressures or adaptive constraints that impinge upon these structures. In other words, how precisely can a structure respond to a single selection pressure against a background of additional selection pressures and adaptive constraints? Adaptive constraints can be due to developmental or phyletic history as well as to physical constraints placed upon the structure by its environment (Gould and Lewontin, 1979; Bonner, 1982; Mayr, 1983). A fruitful approach has been to make specific predictions about the way in which a particular structure would be expected to function when subject to a single selection pressure and then to measure how closely the structure approaches this ideal. Additional selection pressures or adaptive constraints may cause deviations from expected patterns that at first seem to be random. The heuristic value of this approach is that factoring out these "random" deviations helps to identify which additional selection

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pressures or adaptive constraints are most important.

The mechanical properties of load-bearing biological structures are often studied by functional morphologists since these structures are particularly amenable to recently developed techniques for measurement and analysis (Gaunt, 1980; Oxnard, 1980; Bock, 1981; Liem and Lauder, 1982; Denny, 1984). Load-bearing structures are those that must withstand externally or internally generated forces or loads (e.g., cell walls, tree limbs, mollusc shells, vertebrate long bones). Failure to withstand these loads may result in reduced fitness via breakage or critical deformation of the structure. A central question in such studies is "Just how strong should the structure be?" The simplest hypothesis is that it should be exactly strong enough to withstand the average maximum force it is likely to experience during its lifetime. As summarized below, a recently developed theoretical model predicts that this should not always be the case because of the effects of variability in structural strength and the forces which are experienced (Alexander, 1981, 1982; Lowell, 1985).

SAFETY FACTOR MODEL

Borrowing from the engineering literature (Kapur and Lamberson, 1977; Haugen, 1980; Johnson, 1980), a safety factor ($\bar{S}/\bar{L}_{mx}$) for a biological structure can be defined as the ratio of mean strength ($\bar{S}$ = average force required to break or critically deform the structure) to mean lifetime maximum load ($\bar{L}_{mx}$ = average maximum force the structure is likely to experience during its lifetime); these means are calculated over a population of individuals. Not all individual structures in the population would be expected to break at the same force (S). Therefore, a variance in S should exist. Likewise, not all individual structures in the population would be expected to experience the same lifetime maximum load (L_{mx}). Hence, a variance in L_{mx} should also exist. Theoretically, an increase in either of these variances should lead to selection for greater safety factors (Alexander, 1981; Lowell, 1985).

The rationale behind the prediction that the safety factor should increase with increased strength variance can be summarized verbally as follows for the cannon (lower leg) bones of a hypothetical population of deer. Due to the various costs associated with excessively strong long bones (Currey, 1984), selection should favor those cannon bones that are just strong enough to maintain a low probability of breakage. Assume that the strength variance of these cannon bones has been increased due to an increase in the variability of mineral availability (Wallach and Hoff, 1982). The resulting increase in the number of deer with diets that are particularly deficient in minerals should lead to an increased probability that an individual deer, chosen at random from the population, would have a particularly weak cannon bone. These weak bones would have a higher probability of experiencing a force great enough to cause breakage. Assuming that such a break would be deleterious, selection should act to reduce this higher probability of breakage. This could be accomplished via selection for a genetic propensity for a stronger cannon bone so that the probability of breakage remains small, even if an individual experiences an environment which is deficient in minerals. In other words, when it is not possible to decrease $\bar{L}_{mx}$ or the variance in either S or L_{mx}, a reduction in the probability of breakage is still possible by increasing the mean strength of the cannon bone ($\bar{S}$) - that is, by increasing the safety factor ($\bar{S}/\bar{L}_{mx}$). Therefore, on average, increased variability (strength variability in this example) should lead to selection for greater safety factors.

Due to the difficulty of measuring $\bar{L}_{mx}$ under natural conditions, I have proposed an alternative measure of relative strength, truncation safety factor (TSF; Lowell, 1985). TSF is defined as the ratio of mean strength ($\bar{S}$) to maximum possible load (L'_{mx}). $\bar{S}$ can be measured by breaking several test specimens in the lab. L'_{mx} can also be measured for certain structures when the maximum possible load on the structure of interest is set by the strength of another structure. For example, the maximum possible tensile load on some intertidal kelp stipes is set by the strength of attachment of the holdfast to the substratum. I have used this approach (Lowell, 1985) to measure the truncation safety factors of the shells of six common species of rocky intertidal limpets in the northeastern Pacific which are subject to prying forces by predatory crabs (Chapin, 1968; Chapter II) and birds (Frank, 1982; Lindberg and Chu, 1983). The maximum possible prying load on the edge of a limpet shell is set by the maximum strength of attachment of the foot to the substratum (maximum tenacity) since, after the foot is detached, the shell no longer affords any protection. Therefore, for a limpet shell subject to prying loads, TSF = mean shell strength/mean maximum tenacity.

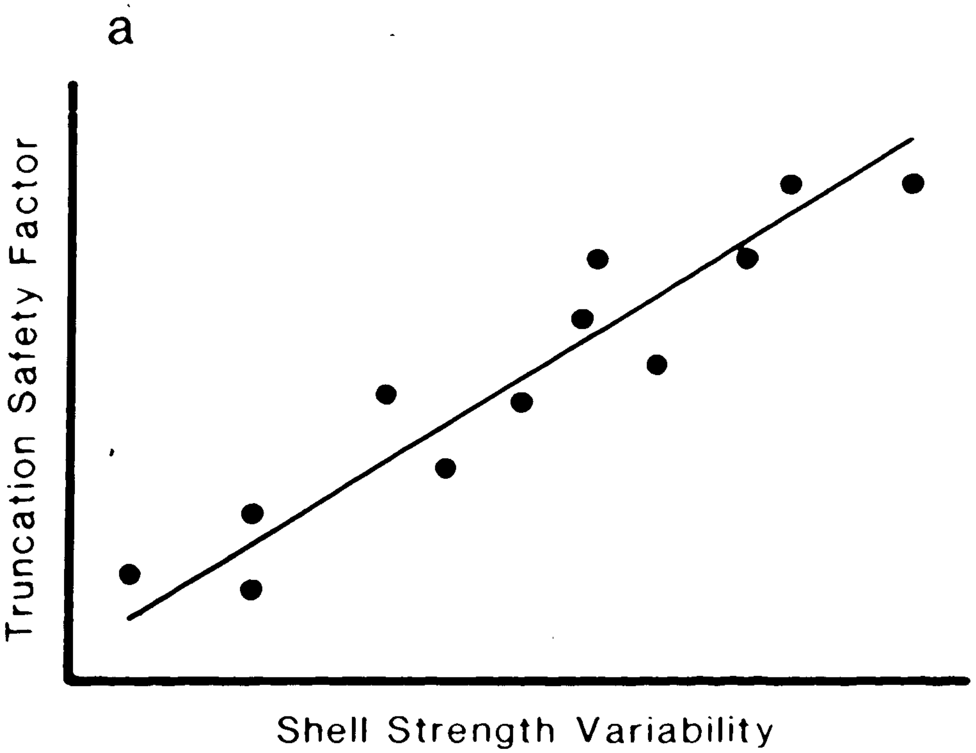
In this context, TSF should be considered in reference to that component of limpet shell strength which resists prying forces. This component of shell strength is largely a function of the thickness of the shell margin at the point where the load is applied to the shell (Lowell, 1986). Marginal thickness can vary greatly both among and within species in the eastern Pacific.

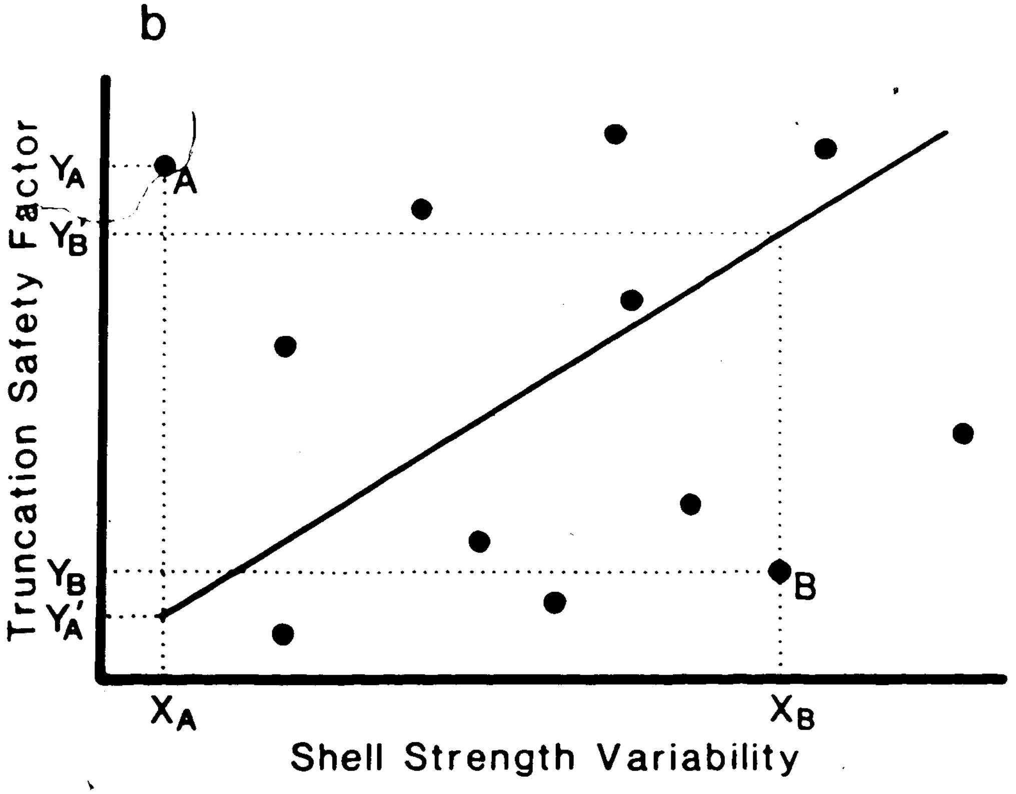
Part of this variation in marginal thickness appears to be due to genetic differences (Lowell, 1986, unpublished data). For example, the shell margin of *Acmaea mitra* is always much thicker (often more than three times thicker) than corresponding parts of the shell margin of *Notoacmea scutum* of equal size in the same microhabitat. Marginal thickness can also vary substantially between different sides of the shell within an individual. For instance, the posterior side of *Collisella digitalis* is always thicker (often over two times thicker) than the anterior side.

Variation in marginal thickness also has a nongenetic component. For example, reciprocal transplants indicate that individuals can deposit thicker or thinner shell margins depending upon microenvironmental conditions (R.B. Lowell, unpublished data). Thus, individual limpets show physiological flexibility in the thickness of the shell margins they deposit, although average thickness appears to be genetically determined as indicated by the consistent differences between different species and sides of the shell. This flexibility indicates that the strengths (and, therefore, the TSF's) of limpet shells are only loosely constrained by developmental and phyletic history.

For limpet shells subject to prying forces, the model predicts that selection should act to increase TSF with increased variability in shell strength. Therefore, a plot of TSF versus variability in shell strength for several different species and sides of the shell should yield a regression line with a positive slope (Fig. IV-1a). As with any bivariate regression, the potentially significant correlation between the dependent variable (TSF) and the independent variable (variability in shell strength) may be masked if other independent variables also have sufficiently great effects on the dependent variable. As already

Figure IV-1. Truncation safety factor (TSF) versus strength variability for the shells of a group of hypothetical limpet species subject to predator-induced prying forces. A) One predominant selection pressure (to resist prying forces). B) Several important selection pressures or adaptive constraints in addition to selection to resist prying forces. The solid line in both figures indicates the predicted relationship between TSF and shell strength variability (see text for discussion).


a
Truncation Safety Factor
Shell Strength Variability


b
Truncation Safety Factor
Y_A
Y_B'
Y_B
Y_A'
A
B
X_A
X_B
Shell Strength Variability

discussed, the potential effect of variability in shell strength on TSF would be expected to act via selection to resist prying forces. If, however, other selection pressures or adaptive constraints are also important, and if they vary independently of variability in shell strength, these additional independent variables may mask any correlation between TSF and variability in shell strength.

This latter situation is illustrated graphically in Fig. IV-1b. For example, hypothetical species A has strength variability X_A. The safety factor model predicts that for this species, TSF should equal Y'_A. But if species A uses the edge of its shell to bulldoze other limpets off its territory, this additional selection pressure might lead to selection for a stronger shell and greater TSF (Y_A) than predicted. Species B has strength variability X_B and a predicted TSF of Y'_B. The strength of the shell of this species, however, might be constrained by low calcium availability. Consequently, species B might have a weaker shell and lesser TSF (Y_B) than predicted. As these additional selection pressures and adaptive constraints become more prevalent, the predictions of the safety factor theory, when based upon a single variable, are likely to become less precise - that is, the variation about the expected relationship in Fig. IV-1b should increase.

Although some variation was present, TSF showed a highly significant increase with increasing variability in shell strength, as predicted, when combining the results for the six temperate eastern Pacific species mentioned above (Lowell, 1985). In the following discussion, these results are compared to a similar study involving several species of limpets in the tropical eastern Pacific. The presence of an additional selection pressure (lateral crushing forces generated by fish predators) in the tropics suggested that the safety factors of the tropical limpets would deviate in a predictable way from the pattern found for the temperate limpets.

Ideally, the positive identification of selection pressures requires direct data on the differential survival of heritable variants (Boag, 1983). In this study, this direct information was not available. Therefore, the importance of selection to resist prying forces generated by crab predators and lateral crushing forces generated by fish predators has been inferred based upon a variety of lab and field experiments (Garrity and Levings, 1983; Lowell, 1986, unpublished data). These studies included information on 1) the statistically significant mortality caused by these predators in the field, 2) predator feeding techniques, and 3) the functional significance of the thickened margin of limpet shells in resisting predator attacks.

MATERIALS AND METHODS

TSF and shell strength variability were measured for six common species of rocky intertidal limpets on the Pacific coast of Panama. These included representatives of the same two families used in the northeastern Pacific study: Acmaeidae - *Collisella pediculus, Lottia (Scurria) stipulata* (see Lindberg and McLean, 1981 for recent generic revision for this species); Fissurellidae - *Fissurella longifissa, F. virescens*. Also included were two pulmonate species of the family Siphonariidae: *Siphonaria gigas, S. maura*. Though only distantly related to the archaeogastropod limpets (Acmaeidae, Fissurellidae), the genus *Siphonaria* is remarkably convergent in gross shell morphology. All limpets were collected from or measured on a 10m stretch of shore on the south side of Taboguilla Island in the Bay of Panama (see Garrity and Levings, 1981; Menge and Lubchenco, 1981; Garrity, 1984; Lubchenco et al., 1984 for detailed descriptions of the physical and biotic characteristics of this shoreline).

The Panamanian limpets appear to be subject to the same kinds of prying forces experienced by the northeastern Pacific limpets. *Ozius verreauxii* and *Eriphia squamata* are the two most common large, predatory crabs in the rocky intertidal of Taboguilla Island (Lubchenco et al., 1984). Both species subject limpet shells to prying forces (Chapter II). Although not present on Taboguilla Island, American oystercatchers (*Haematopus palliatus*) do feed on limpets in the nearby Pearl Islands (Garrity and Levings, 1983), where they sometimes use the same prying technique used by the black oystercatchers (*H. bachmani*) of the northeastern Pacific (R.B. Lowell, personal observation).

I used the same techniques for measuring TSF and variability in shell strength as used in the northeastern Pacific study (Lowell, 1985). In brief, the shells of newly killed limpets were mounted, while still wet, on a Monsanto (type W) tensometer. Shell strength was measured by using a 1.16mm diameter steel hook to subject the edge of the shell to a prying force in a dorsal direction perpendicular to the plane of the aperture, thereby mimicking the prying action of a rounded crab appendage. A 0.67mm diameter hook was used for particularly small shells (<12mm in length) and a 2.64mm diameter hook was used for particularly large shells (>35mm in length); hook diameter had no significant effect on the measured values of shell strength (Lowell, 1985).

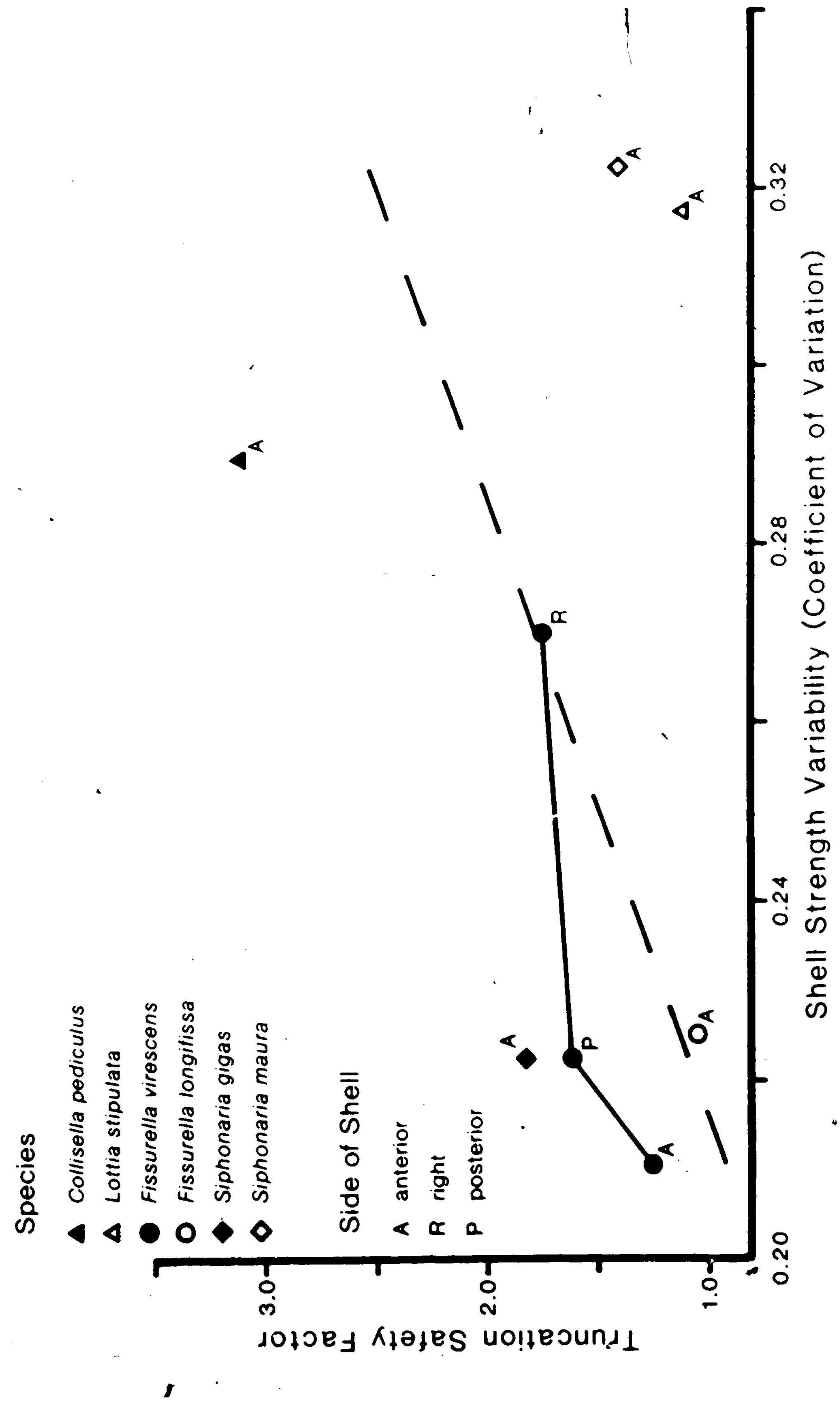
Maximum tenacity was measured by using a spring scale to load the edge of the shell of a previously undisturbed, healthy limpet in the field in a manner identical to the measurements of shell strength. To ensure that tenacity was measured while at its maximum, the following three precautions were taken. 1) All measurements of tenacity were made while the limpets were inactive on the home sites they occupied during high and low tides, this being where tenacity appeared to be at its maximum. For the acmaeids, siphonariids, and some of the fissurellids, these sites were distinctive home scars. 2) Tenacity was always measured on falling tides within one hour after emergence and while the limpets were still wet. This was necessary because tenacity sometimes decreased dramatically after several hours of exposure to the sun. 3) All limpets were allowed to clamp down before a prying force was applied.

Since shell strength and maximum tenacity were calculated over a range of different sizes, TSF was calculated via analysis of covariance (ANCOVA). For each species and side of the shell, I calculated regression equations for ln shell strength (force in newtons) as a function of ln foot area (n=9-12) and ln maximum tenacity (force in newtons) as a function of ln foot area (n=8-14). This yielded a ln shell strength-ln maximum tenacity regression pair for each species and side of the shell - that is, shell strength on the anterior side of *C. pediculus* was paired with maximum tenacity on the anterior side of *C. pediculus*, shell strength on the right side of *F. virescens* was paired with maximum tenacity on the right side of *F. virescens*, and so forth. All ln-ln regression pairs were parallel (no significant differences between the regression coefficients of each pair; smallest P>0.1), except for the posterior side of *F. virescens* (P=0.014). Therefore, with this one exception, the TSF's were essentially constant with increasing size. Consequently, TSF was calculated as TSF = $\exp(\ln\bar{S}-\ln L'_{mx})$ where $\ln\bar{S}$ was the adjusted mean (from ANCOVA) of the ln shell strength regression and $\ln L'_{mx}$ was the adjusted mean of the ln maximum tenacity regression for each species and side of the shell. This yielded an average (over the size range tested) TSF for the posterior side of *F. virescens*, since TSF changed with increasing size for this one case. Variance in shell strength was calculated as the residual variance (MSe) of the ln shell strength versus ln foot area regressions. MSe was converted to coefficient of variation (CV) as follows: $CV = [\exp(MSe)-1]^{0.5}$ (Lewontin, 1966; Wright, 1968; Chalmer, 1980).

RESULTS AND DISCUSSION

The variation about the expected increase of TSF with increasing variability in shell strength should be less when comparing different sides of the shell within a single population of one species than when comparing shells among species. This is because, although some differences would be expected due to shell asymmetry, the selection pressures and adaptive constraints should be similar between different sides of the shell. In conjunction with the results for the northeastern Pacific limpets (Lowell, 1985), the results for *F. virescens* (points connected by solid lines, Fig. IV-2) suggest a within-population increase of TSF with increasing variability in shell strength, although the correlation

Figure IV-2. Truncation safety factor versus strength variability for the shells of Panamanian limpets. The dashed line is the reduced major axis (Ricker, 1973, 1984) for all species and sides of the shell combined (r=0.1628, P=0.700). The solid lines connect the points for a within-species comparison of different sides of the shell for *F. virescens* (r=0.8209, P=0.387).

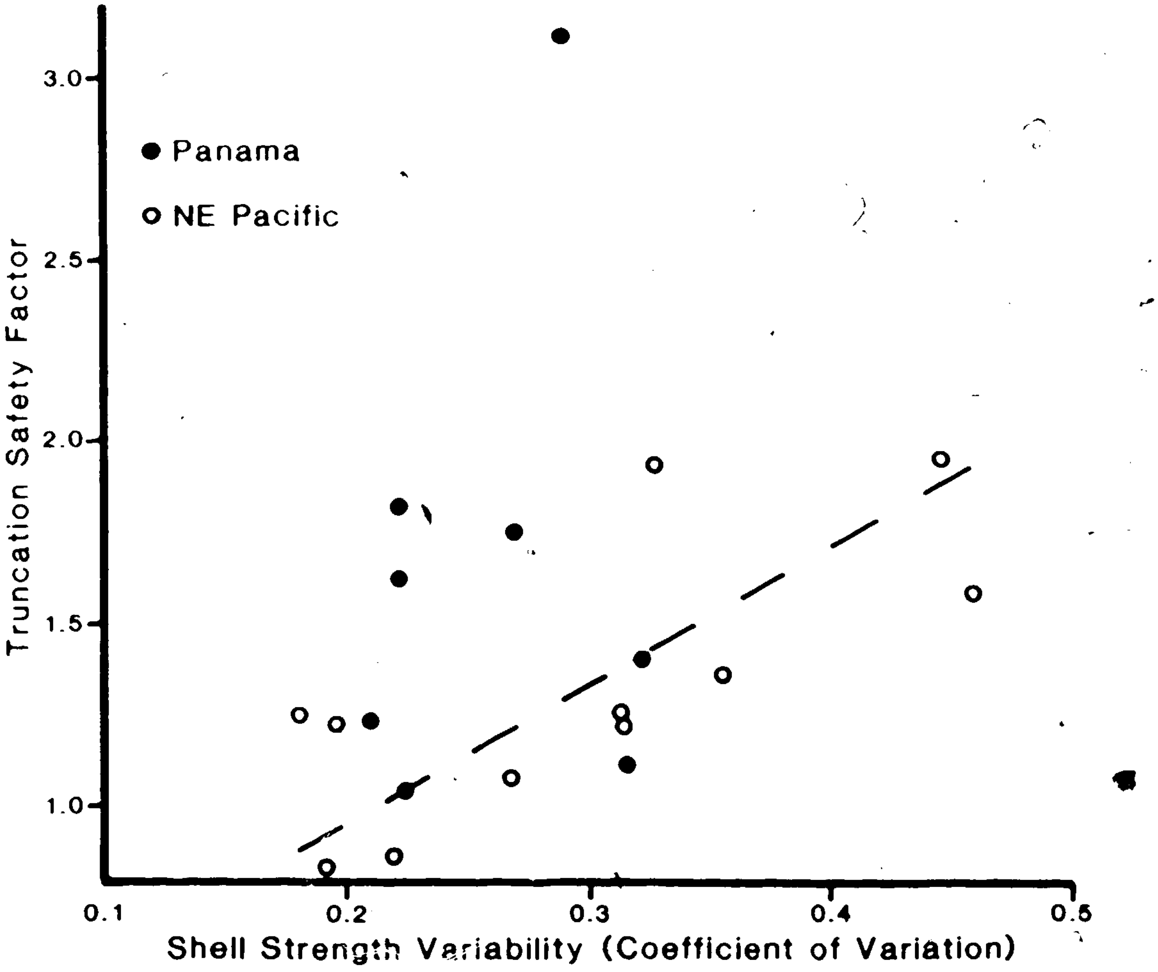

Species
▲ Collisella pediculus
△ Lottia stipulata
● Fissurella virescens
○ Fissurella longifissa
◆ Siphonaria gigas
◇ Siphonaria maura
Side of Shell
A anterior
R right
P posterior
Truncation Safety Factor
1.0
2.0
3.0
Shell Strength Variability (Coefficient of Variation)
0.20
0.24
0.28
0.32
A
P
R
A
A
A
A
A

coefficient was not significant. When all species and sides of the shell were combined, the scatter of points about the still positive regression line became even greater (Fig. IV-2). The Panamanian limpets exhibited a narrower range of values for variability in shell strength than did the northeastern Pacific limpets (Fig. IV-3). This likely contributed to the lack of statistical significance for the Panama regression (Fig. IV-2). Nevertheless, as will be discussed, other factors were probably also involved in this lack of significance.

Constancy of Safety Factors

The values of TSF for the Panamanian limpets tended to be equal to or greater than those for the northeastern Pacific limpets after correcting for differences in variability in shell strength (Fig. IV-3). Disregarding variability in shell strength, mean TSF for the Panamanian species as a group (1.64) was approximately equal to that for the northeastern Pacific species (1.32); the difference between the two groups was not statistically significant (Mann-Whitney U=32.0, P=0.322, n=8,11). At the extremes, the TSF's for the two groups fell within a factor of 4 of one another (most fell within a factor of 2). This degree of similarity is quite surprising when the extreme range of values for maximum tenacity and shell strength are considered.

Figure IV-3. Truncation safety factor versus strength variability for the shells of Panamanian (see Fig. IV-2) and northeastern Pacific (see Lowell, 1985) limpets. The dashed line is the reduced major axis for the northeastern Pacific limpets alone (r=0.7407, P=0.009).


● Panama
○ NE Pacific
Truncation Safety Factor
3.0
2.5
2.0
1.5
1.0
0.1
0.2
0.3
0.4
0.5
Shell Strength Variability (Coefficient of Variation)

Mean maximum tenacity for the Panamanian limpets (31.5N), at a standardized, intermediate size, exceeded that for the northeastern Pacific limpets (14.5N) by a factor of 2.2 (Fig. IV-4), this difference being highly significant (Mann-Whitney U=2.0, P=0.0005, n=8,11). The tenacities of the species at the extremes differed by a factor of 6. The northeastern Pacific species fell into a low tenacity group (*Collisella pelta, Notoacmea scutum, Diodora aspera*) and an intermediate tenacity group (*Acmaea mitra, C. digitalis, N. persona*). The tenacities for the Panamanian species ranged from intermediate to high.

As for tenacity, mean shell strength for the Panamanian limpets (49.3N) exceeded that for the northeastern Pacific limpets (21.9N) by a similar factor of 2.3 (Fig. IV-5), the difference again being significant (Mann-Whitney U=9.0, P=0.0039, n=8,11). The range of values for shell strength was particularly great, with the shell strengths of the species at the extremes differing by a factor of 9. In addition, the ranking of values for shell strength followed a pattern very similar to that for maximum tenacity (Figs. IV-4 and IV-5). As before, *C. pelta, N. scutum,* and *D. aspera* fell into a low shell strength group while *A. mitra, C. digitalis,* and *N. persona* fell into an intermediate shell strength group. And again, the shell strengths for the Panamanian limpets ranged from intermediate to high.

Figure IV-4. Maximum tenacities for northeastern Pacific and Panamanian limpets at standardized size (foot area = 1 cm^2) common to all species. Means (±1 standard error) calculated from intercepts of regressions of ln maximum tenacity versus ln foot area for each species and side of shell. Genera: *A.* - *Acmaea*, *C.* - *Collisella*, *D.* - *Diodora*, *N.* - *Notoacmea*, *F.* - *Fissurella*, *L.* - *Lottia*, *S.* - *Siphonaria*. Sides of shell: A - anterior, R - right, P - posterior.

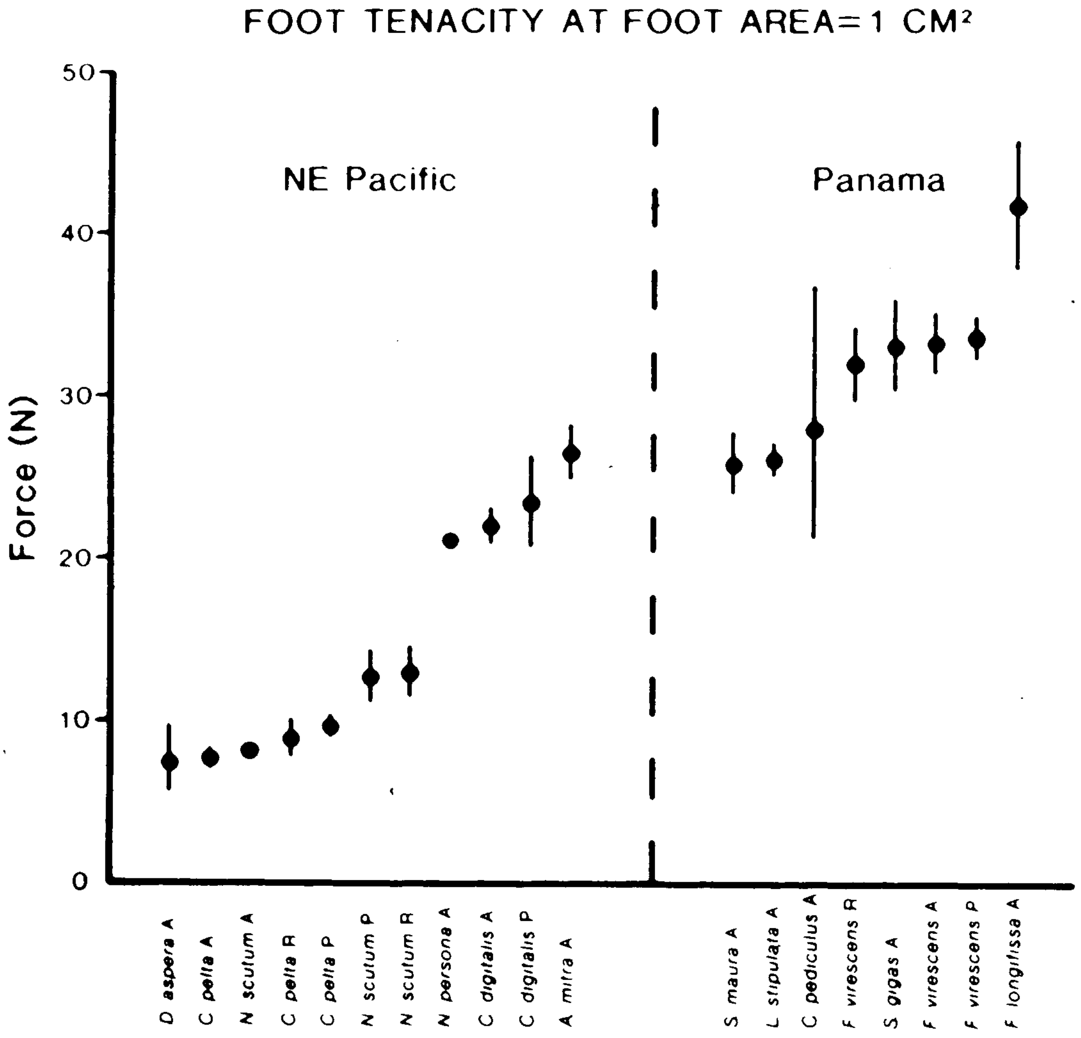
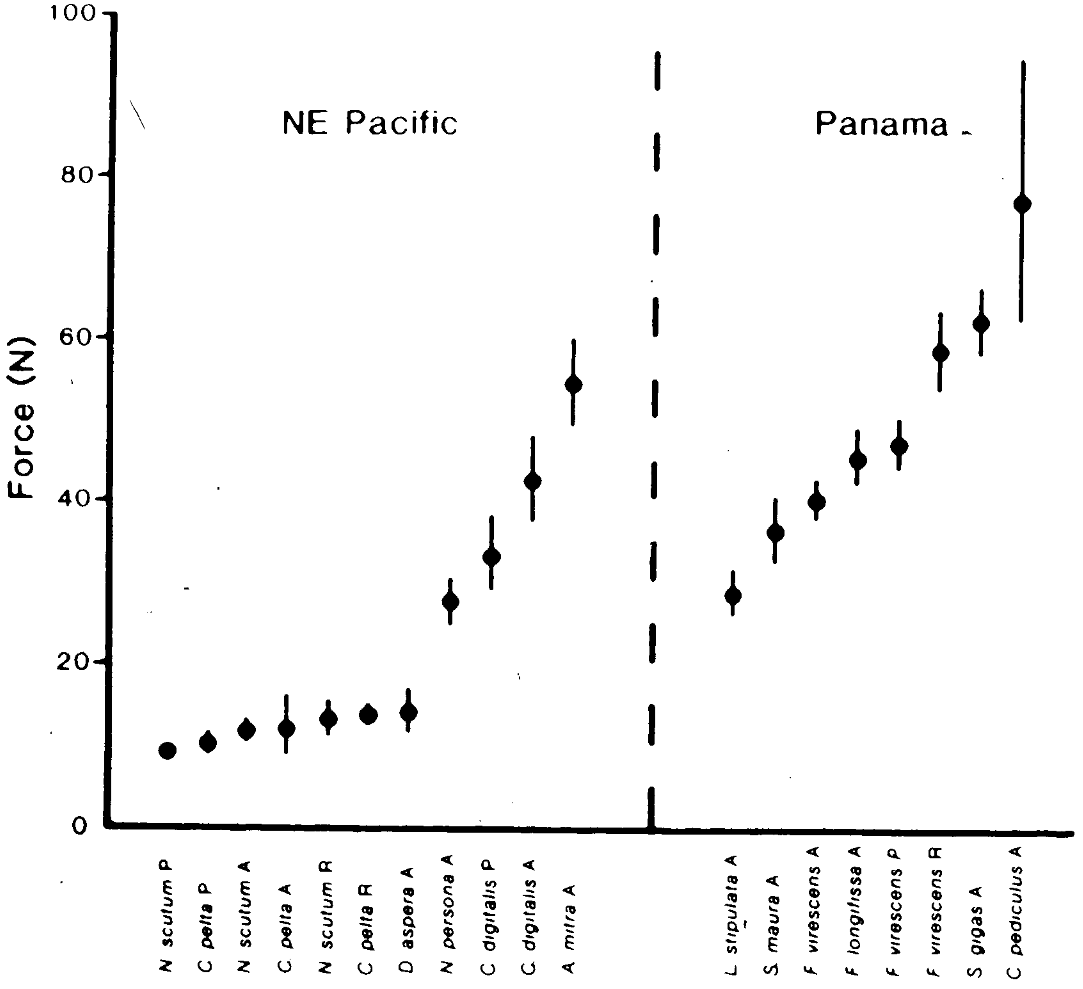

FOOT TENACITY AT FOOT AREA=1 CM²
Force (N)
0
10
20
30
40
50
NE Pacific
Panama
D aspera A
C pelta A
N scutum A
C pelta R
C pelta P
N scutum P
N scutum R
N persona A
C digitalis A
C digitalis P
A mitra A
S maura A
L stipulata A
C pediculus A
F virescens R
S gigas A
F virescens A
F virescens P
F longitissa A

Figure IV-5. Shell strengths for northeastern Pacific and Panamanian limpets at standardized size (foot area = 1 cm^2). Means (±1 standard error) calculated from intercepts of regressions of ln shell strength versus ln foot area for each species and side of shell. Abbreviations as for Fig. IV-4.

SHELL STRENGTH AT FOOT AREA=1 CM²



This highly significant association of greater shell strengths with greater foot tenacities (r=0.8221, P<0.0001, n=19) explains why the TSF's all fell within a comparatively narrow range. Since TSF is the ratio of shell strength to maximum tenacity, the TSF's remained remarkably similar between Panama and the northeastern Pacific, despite the large differences in shell strength and maximum tenacity.

As previously discussed, the ln shell strength versus ln foot area and the ln maximum tenacity versus ln foot area regressions were parallel in seven of eight cases for the Panamanian limpets. In addition, the ln-ln regression pairs were parallel in eleven of eleven cases for the northeastern Pacific limpets. These data, coupled with the relative constancy of TSF from the temperate to tropical eastern Pacific, suggest that the mechanical performances of two strikingly distinct structures, the foot and the shell, are quite closely coadapted in these limpets spanning two subclasses of gastropods.

The great shell strengths which the Panamanian limpets attain are probably largely due to their particularly thick shell margins (Chapter II). The manner in which the Panamanian limpets attain such high tenacities is less clear. Branch and Marsh (1978) have measured several morphological and physiological features which appear to increase the tenacity of certain species of South African limpets. In general, higher tenacity is associated with low mucus secretion, small number of mucocytes, inflexibility of the foot, large area of muscle attachment, and fewer and smaller basal haemocoelic spaces. These features have not been measured for Panamanian limpets. It is also possible that the Panamanian limpets invest more energy in foot musculature or that the composition of their pedal mucus differs from the northeastern Pacific limpets (see Grenon and Walker, 1978, 1981 for a discussion of the adhesive functions of different kinds of limpet pedal secretions).

In addition, the tenacities of all the limpets used in the Panama study were measured while they were on their home sites or scars. In contrast, none of the species used in the northeastern Pacific study consistently exhibit homing behavior. Limpets on home scars can probably resist greater lateral forces due to the "lock and key" fit of the shell to the substratum (Lindberg and Dwyer, 1983). They may also resist greater prying forces (the force measured in this study) through modifications of the substratum. For example, surface roughness and wetting properties can affect limpet foot adhesion (Grenon and Walker, 1981). The presence of an algal film between the foot and the substratum may also affect tenacity. These surface properties are likely to be affected by the formation of home scars. For instance, some limpets are able to modify the surface of their home scar, apparently via acidic secretions and subsequent abrasion with the radula (Lindberg and Dwyer, 1983).

Diodora aspera, a keyhole limpet, exhibited the lowest tenacity measured (Fig. IV-4). Northeastern Atlantic keyhole limpets also exhibit relatively low tenacities (Fretter and Graham, 1962). Fleure (1904) has argued that a perforation in the shell weakens the force of pedal attachment and was, therefore, eliminated from some limpet groups via natural selection. Yonge (1947) discounted this evolutionary scenario using an argument based on the relative positioning of the gills. Since keyhole limpets (*F. longifissa, F. virescens*) also attained the highest tenacities measured for the eastern Pacific limpets as a whole (Fig. IV-4), the presence of a perforation in the apex of the shell apparently does not prevent high tenacities.

Additional Selection Pressures Or Adaptive Constraints

The temperate and tropical eastern Pacific differ dramatically in the presence of large, predatory fish that forage in the rocky intertidal (Menge and Lubchenco, 1981). These fish are much more abundant and diverse in the tropical eastern Pacific and several species feed on molluscan prey by breaking their shells using powerful jaws and specialized oral surfaces. The presence of these fish has been linked to defensive features in the shell morphology (increased thickness, strong sculpturing) of several species of spirally-coiled gastropods in the tropical eastern Pacific (Bertness et al., 1981). In fact, the frequent occurrence of defensive shell morphology associated with shell-crushing predation by fish appears to be a worldwide phenomenon in the tropics (Vermeij, 1978; Palmer, 1979).

The intertidally foraging fish at Taboguilla Island include several shell-crushing species that potentially prey on limpets. *Pseudobalistes naufragium* (triggerfish), *Arothron hispidus* (smooth puffer), and *Scarus perrico* (parrotfish) have been observed preying on transplanted limpets in the field (S.D. Garrity, R.B. Lowell, personal observation). In addition, *Diodon holocanthus, D. hystrix* (spiny puffers), and *Arothron meleagris* will feed on limpets in the lab (Garrity and Levings, 1983; R.B. Lowell, personal observation). Furthermore, limpets have been found in the stomachs of *Diodon spp., Sufflamen verres* (triggerfish), and *Bodianus diplotaenia* (wrasse) (S.D. Gaines, S.D. Garrity, personal communication), although the wrasse may not subject the limpet shell to a crushing force until after the limpet is detached, at which time selection for shell strength would have ceased to operate. Another shell-crushing fish present in the intertidal at Taboguilla Island that may also feed on limpets is *Balistes polylepis* (triggerfish) (Lubchenco et al., 1984).

These fish feed on limpets by biting them from the substratum. In doing so, they subject the margin of the shell to a lateral crushing force. This kind of force is qualitatively different from a prying force in that it is entirely decoupled from tenacity. In other words, the maximum lateral crushing force the shell margin will experience is no longer set by foot tenacity as was the case for a prying force. Rather, the maximum force is limited only by the maximum crushing force that the fish jaw can generate. So, when resisting a lateral crushing force, there will always be an advantage to having a thicker, stronger shell (within the constraints of the cost of adding extra shell material) regardless of the strength of pedal attachment.

Large, predatory fish also feed on rocky intertidal limpets in the northeastern Pacific. Most notable among these are two common species of seaperch, *Damalichthys vacca* and *Embiotoca lateralis* (DeMartini, 1969; Alevizon, 1975; Ellison et al., 1979; Haldorson and Moser, 1979; Lowell, 1984). These fish, however, feed on limpets by sucking them from the substratum (Mercurio et al., 1985). This feeding technique is quite efficient and fairly large limpets (>35mm in length) can be removed in this way when they are caught before clamping down. Nevertheless, suction feeding does not subject the shell margin to breaking forces and so is not an important direct selection pressure on the strength of the shell margin. Furthermore, suction-feeding fish are unlikely to generate pressures much more negative than that required to cause cavitation (roughly $-7N/cm^2$; Lauder, 1983). Cavitation of water occurs at low pressures when water vapor comes out of solution to form small vapor-filled cavities. The clearly audible, sharp sounds heard during field observations of suction-feeding on limpets by *D. vacca* and *E. lateralis* suggests that cavitation was occurring and that these two fish species have reached this limit in the negative pressure that can be effectively generated (R.B. Lowell, personal observation). Since most of the limpets attained tenacities greater than $7N/cm^2$ (sometimes much greater; Fig. IV-4), it seems unlikely that suction feeding has led to direct selection for the maximum tenacities attained by the more tenacious limpet species.

As a group, the six species of northeastern Pacific limpets used in this study range from southern Alaska to Baja California (Morris et al., 1980; Lindberg, 1981). The two seaperch species have an identical range (Hart, 1973). The six species of Panamanian limpets range from Baja California to Peru (Keen, 1971). Following a similar pattern of overlap, the nine species of Panamanian fish discussed above range from Baja California to Chile, except for *B. polylepis* which is present, though rare, as far north as northern California (Thomson et al., 1979; Gotshall, 1982; Eschmeyer and Herald, 1983). Hence, each of the two limpet groups co-occurs with only one of the two predator groups throughout most of its range. More importantly for this discussion, the northeastern Pacific limpets are, for the most part, free from fish-induced, lateral crushing forces. Consequently, the dashed line (= average TSF as a function of variability in shell strength for northeastern Pacific limpets) in Figure IV-3 could be viewed as an approximate TSF baseline expected in the absence of fish-induced, lateral crushing forces.

A thick shell margin that can resist greater prying forces is also likely to resist greater lateral crushing forces. Therefore, the imposition of this additional selection pressure on the Panamanian limpets would be expected to lead to stronger shells than would be anticipated based on consideration of prying forces alone. Those species which are more accessible to fish predators would be expected to lie farther above the northeastern Pacific TSF baseline than those which are less accessible.

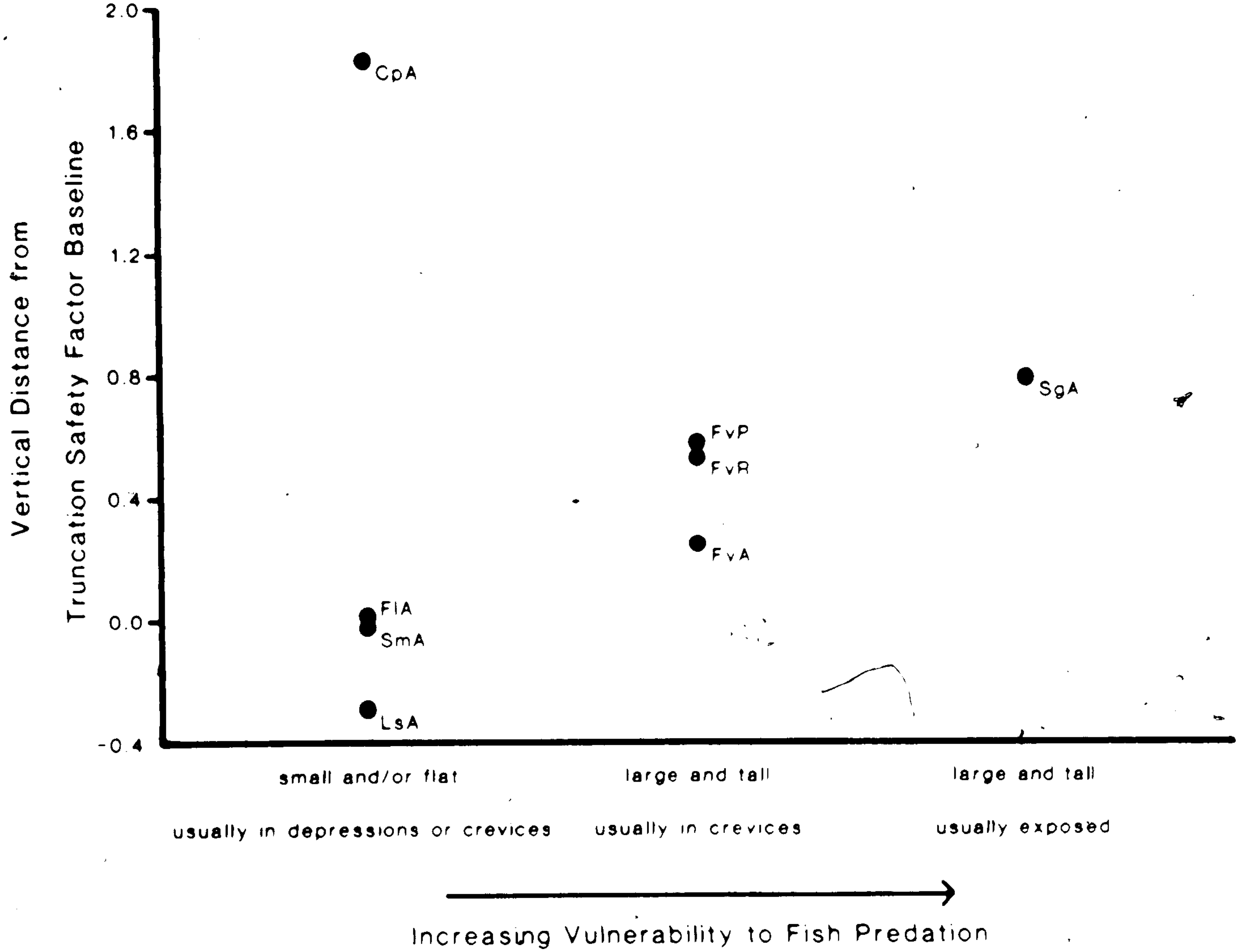
Benthic prey along the Pacific coastline of Panama reduce their vulnerability to fish predators both behaviorally and morphologically. For example, many species of snails and crabs remain within crevices or depressions during high tide, particularly during the day, where visually hunting fish can not reach them (Bertness and Cunningham, 1981; Garrity and Levings, 1981; Levings and Garrity, 1983; Lubchenco et al., 1984). The flat morphology (sometimes coupled with small size) of several barnacle species also appears to reduce vulnerability to fish predators due to the difficulty of gaining a purchase on the shell plates (Menge and Lubchenco, 1981). Limpets, too, benefit from these behavioral and morphological defenses (Bertness et al., 1981; Menge and Lubchenco, 1981; Gaines, 1983; Garrity, 1984; R.B. Lowell, unpublished data).

I have ranked the six species of Panamanian limpets used in this study into three broad categories according to their relative vulnerability to fish predation. These categories are based on 1) typical maximum size attained [small (length < 30mm), large (length > 50mm)], 2) shape (flat, tall), and 3) microhabitat occupied during high tide (protected - usually in depressions or crevices, exposed - usually on relatively homogeneous surfaces exposed to fish predators). In general, small, flat, protected limpets are less vulnerable than large, tall, exposed limpets. The least vulnerable category includes all three families studied. *Collisella pediculus*, *L. stipulata*, and *S. maura* are all small, flat, and protected. *Fissurella longifissa*, though not flat, is also small and protected. In the next most vulnerable category, *F. virescens* is both large and tall, although it, too, is usually found in crevices that somewhat protect it from fish predators. This species will, however, remain in the open in areas of high wave exposure where fish are less able to forage in the intertidal (Ortega, 1985; B.A. Menge, personal communication). Finally, in the most vulnerable category, *S. gigas* is large, tall, and usually exposed during high tide.

The relationship of TSF to fish predation may be seen by comparing the vertical distances above the northeastern Pacific TSF baseline for the Panamanian limpets in each of the three vulnerability categories (Fig. IV-6). With the notable exception of *C. pediculus*, this vertical distance increased with increasing vulnerability to fish predation. This supports the prediction that the prevalence of fish-induced lateral crushing forces in the tropical eastern Pacific has led to selection for limpet shells that are stronger than would be expected if only one selection pressure (resistance to prying forces) were considered. In other words, this additional selection pressure (lateral crushing forces) appears to explain a good deal of the scatter in Figure IV-2.

Collisella pediculus is an outlier by a wide margin which suggests that this species is subject to selection pressures or adaptive constraints that have not yet been identified. At least two hypotheses may be proposed to explain why its shell, which has a particularly thick margin, is much stronger than predicted even after taking into account variability in shell strength and susceptibility to lateral crushing forces. 1) The thick shell margin creates a pronounced lip along the ventral edge of the region where the foot muscle attaches to the shell. Since *C. pediculus* has an extremely flat shell, this lip may

Figure IV-6. Differences between Panama truncation safety factors (TSF) and northeastern Pacific TSF baseline (dashed line in Fig. IV-3). Species: Cp - *Collisella pediculus*, Fl - *Fissurella longifissa*, Fv - *F. virescens*, Ls - *Lottia stipulata*, Sg - *Siphonaria gigas*, Sm - *S. maura*. Sides of shell: abbreviations as for Fig. IV-4.


Vertical Distance from
Truncation Safety Factor Baseline
2.0
1.6
1.2
0.8
0.4
0.0
-0.4
CpA
FlA
SmA
LsA
FvP
FvR
FvA
SgA
small and/or flat
usually in depressions or crevices
large and tall
usually in crevices
large and tall
usually exposed
Increasing Vulnerability to Fish Predation

facilitate muscle insertion on the shell which appears to be an important factor in the strength of attachment to the substratum (Branch and Marsh, 1978). 2) Alternatively, a particularly thick, strong shell becomes more feasible when the cost of shell production is reduced. One potential cost of shell production is the reduced rate of body growth associated with thick shells when the rate of shell production is limiting (Palmer, 1981). If *C. pediculus* has adopted a life history strategy characterized by slow body growth, more time would be available for the production of a particularly thick shell. This negative correlation between growth rate and shell thickness has been noted for the *Purpura columellaris - P. pansa* species complex, a snail which co-occurs with *C. pediculus* (Wellington and Kuris, 1983). In any case, the identification of *C. pediculus* as a particularly unusual species deserving of more study further emphasizes the heuristic value of the safety factor approach.

Safety factor analysis suggests that the strength of the shell margin of eastern Pacific limpet shells is influenced by at least two (probably more than two) important selection pressures. These are 1) lateral crushing forces generated by fish predators on tropical shores and 2) prying forces generated by crab and bird predators on both tropical and temperate shores. The effects of the latter selection pressure are reflected in the apparent close coadaptation of the mechanical performances of the shell and the foot.

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V. DISCUSSION

In the preceding chapters, I have emphasized the relationship between predator-induced prying forces acting to break limpet shells and the safety factors of those shells. I have argued 1) that variability in shell strength has led to selection for greater safety factors and 2) that additional and potentially conflicting selection pressures and evolutionary constraints have also had important effects on shell morphology (e.g., selection for particularly thick shells which can resist greater crushing forces generated by fish predators; Chapter IV). My results have underscored the particular significance of certain features of shell morphology including, most notably, the thickness of the shell margin. This chapter focuses on some of the other components of limpet shell morphology not discussed in the previous chapters. Some of these other components are only indirectly related to the strength of limpet shells subjected to prying forces. Nevertheless, they all potentially affect limpet survival under certain environmental conditions. The chapter concludes with some final comments on the generality of the safety factor model.

COMPONENTS OF LIMPET SHELL MORPHOLOGY

Although they are all interdependent, for the purposes of discussion, overall limpet shell morphology can be broken down into five components of particular significance: 1) relative shell height, 2) streamlining, 3) thickness, 4) sculpture, 5) microstructure. Each of these components may be evaluated in terms of the various morphologies exhibited by limpet shells and their potential advantages and disadvantages.

Relative Shell Height

Relative shell height (RSH) refers to shell height with respect to basal dimensions and can be defined as RSH = $H/(LW)^{0.5}$ where H = perpendicular distance from base to dorsal-most part of shell (usually the apex), L = anterior-posterior length of shell, and W = maximum width at base of shell (Vermeij, 1973).

Tall shells (RSH relatively large) offer at least six possible advantages. 1) When subjected to a predator induced prying force (Chapter II), the side of a tall, steeply-sided shell is more likely to be loaded in compression than a flat shell because, for a tall shell, the lines of force would be more nearly parallel to a plane tangent to the side of the shell. In contrast, a flat shell is more likely to experience significant tensile forces on its ventral surface. Since shell material is much stronger in compression than in tension (Currey, 1980), tall shells are likely to withstand greater prying forces than flat ones, all else being equal.

2) Limpets producing tall shells should experience reduced desiccation relative to limpets of equal volume having a flatter shell. Water loss in limpets has been shown to be proportional to the ratio of aperture circumference (proportional to area available for water loss) to internal shell volume (proportional to water stores) (Lowell, 1984). This ratio decreases with increasing RSH.

3) Tall, more highly-domed shells provide a greater surface area for insertion for the foot retractor muscle and this increased area is correlated with increasing tenacity (Branch and Marsh, 1978).

4) A more highly-spired shell would provide more volume for the viscera, which are located on the dorsal surface of the foot (Fretter and Graham, 1962), given that the volume of the foot and related musculature is more closely proportional to the basal area of the shell than to overall shell volume. This increased volume could enable the development of larger gonads and, hence, increased reproductive output. A positive correlation between a measure analogous to RSH and gonadal volume has been found in a comparison of chitons with tall shells (*Lepidozona spp.*) to those with flat shells (*Mopalia spp.*)

(S.S. Rumrill, unpublished data).

5) Tall shells permit a larger body volume to be covered by a given amount of shell material. Due to geometrical considerations, the amount of shell material required to enclose a conical space of fixed volume can be minimized if 1) the cone is circular rather than elliptical, 2) the apex is central, and 3) the ratio of the height of the cone to the radius of its base equals 2° '. *Acmaea mitra* shells fit this description quite closely (R.B. Lowell, unpublished data). *A. mitra* was the tallest of all the species I worked with and its shell was thicker than any of the temperate Pacific species. Given a limit to the rate of shell deposition (Palmer, 1981), this suggests that *A. mitra* may minimize slow growth due to depositing a thick shell by depositing the minimum surface area of shell material required to enclose a given internal body volume. Minimizing the amount of shell material required to produce a thick shell is probably also energetically less costly (Palmer, 1983).

6) During midday when solar radiation is most intense, tall shells will minimize the projected area available for absorption of solar radiation relative to the total surface area available for heat loss due to convection and to longwave emittance by the shell (Campbell, 1977). This may minimize heat stress to the animal (Vermeij, 1973).

Flat shells (RSH relatively small), on the other hand, offer at least four possible advantages. 1) Crab predators have more difficulty obtaining a grip on the shells of flat limpets, even when their shells are small enough for a crab to crush them from the sides (Chapter II).

2) Flat shells subjected to wave-induced forces experience both lower horizontal drag and lower vertical lift than tall shells of comparable internal volume (Denny et al., 1985; R.B. Lowell, unpublished data). Denny et al. also suggested that the forces due to the "acceleration reaction" are lower for flat organisms in the intertidal, although this remains to be measured for limpet shells. These latter forces, which are in addition to the drag and lift forces generated during constant flow, are due to the acceleration of water around a stationary object on a wave-beaten shore. This reduction of drag, lift, and the acceleration reaction is advantageous in two ways. First, it reduces the probability of dislodgement. Second, it reduces the metabolic cost of the muscular contraction which is required to remain attached (Houlihan and Newton, 1977).

3) Flat shells can accommodate a larger foot area, in contrast to a greater internal shell volume available for gonads in tall shells. Larger foot area, in turn, enables increased foot tenacity (Chapter II).

4) Maximum speed also seems to increase with increasing foot area (Miller, 1974). This would be advantageous in

escaping slow moving predators such as seastars or snails.

RSH can also change during ontogeny. For most limpets, RSH increases allometrically with increasing size due to doming of the shell (caused by a curving inward of the shell margin as the limpet grows; Lowell, 1984). This means that the shells are changing shape as they grow; in other words, an originally flat shell can become a more highly-spired one. Furthermore, the degree of doming can change with changing growth rate (Vermeij, 1980; R.B. Lowell, unpublished data). Therefore, individuals may be able to take advantage of being flat or tall at different times during ontogeny.

Streamlining

In certain environments, limpets are subjected to drag forces by seawater flowing in predictable directions. One such environment is the wall of a surge channel. Another is the stipe of a flexible kelp in an area of steady current where the kelp is free to orient parallel to the current (Vahl, 1971; Warburton, 1976). Such environments offer limpets the opportunity to orient parallel to the flow and thereby take advantage of a streamlined overall shell shape.

In addition to reduced RSH (see above), overall shell shape can be streamlined in two ways (Warburton, 1976; Branch and Marsh, 1978; Dudley, 1985). 1) The "fineness ratio" (ratio of length parallel to flow to width perpendicular to flow) can be increased. For a given internal shell volume, this decreases the frontal area of the shell facing into the flow, resulting in reduced drag. 2) "Apex eccentricity" (displacement of the apex toward the anterior of the shell) can be increased. When the limpet is oriented with its anterior end facing into the flow, this eccentricity provides a tapering downstream tail which, at the flow velocities experienced by most limpets, may reduce wake formation and, in consequence, may also reduce drag (Vogel, 1981).

Thickness

The potential advantages (shell strengthening) and disadvantages (reduced growth rate and greater energetic costs; Palmer, 1981, 1983) of thickened shell margins have already been discussed (Chapters II, III, IV). Limpets are also capable of secondarily thickening the interior layers of the apical region of the shell (R.B. Lowell, unpublished data). In some cases, this may reduce the probability of breakage due to crushing forces from above caused by predators (Chapin, 1968) or by objects thrown about by wave action. Apical thickening may also deter drilling gastropod or octopus predators (Black, 1978; Wells, 1980; Moran, 1985). In addition, thickened shells may provide thermal insulation (Vermeij, 1973), although any differences due to thickness may be negligible for small animals the size of limpets (G.S. Campbell, personal communication).

Sculpture

The most common shell sculpturing exhibited by limpet shells is radial ribbing. This ribbing can be either advantageous or disadvantageous, depending on which selection pressures are most prevalent. 1) Ribbing would increase the strength of the shell when subjected to a bending force because, for a given cross-sectional area of shell material, ribbing increases the second moment of area (Wainwright et al., 1976). This increase in strength is similar to that shown by a flat sheet of iron or plastic that has been formed into a corrugated shape. 2) Ribbing may minimize heat stress to the animal (Vermeij, 1973). As for tall shells, ribbing will minimize the ratio of projected area (proportional to absorption of solar radiation) to total surface area (proportional to heat loss due to convection and longwave emittance). 3) Ribbing is also likely to increase the turbulence of the fluid boundary layer around limpets subjected to onrushing waves. This increased turbulence may increase drag at low and at high Reynolds numbers but may decrease drag at intermediate Reynolds numbers (Branch and Marsh, 1978; Vogel, 1981). Branch and Marsh (1978) argued that certain kinds of ribbing decreased drag at the intermediate water velocities (intermediate Reynolds numbers) generated in their lab experiments. The effects of ribbing under the high velocity (high Reynolds numbers) conditions generated by waves in the field have not yet been measured. 4) Radial ribs provide a gripping-surface which appears to facilitate shell-crushing or shell-removal by crab predators (R.B. Lowell, personal observation) and, most likely, by some fish predators.

Microstructure

MacClintock (1967) has reviewed the shell microstructures of the individual acmaeid species included in my investigations. Boggild (1930) has also given general group descriptions of the shell microstructures of fissurellid and siphonariid limpets. According to these descriptions, all of the species used in my studies possess one or more crossed-lamellar layers. In addition, the acmaeid species have one to two outer prismatic layers (including fibrillar microstructures). One species, *Acmaea mitra*, also has an intermediate foliated layer.

The functional properties of these microstructures are only beginning to be understood. Currey (1976, 1977) has shown that nacre is the strongest molluscan microstructure in terms of tension, compression, and bending. He argues, though, that the precise geometry of the crystals make nacre more costly to produce, perhaps requiring more time for deposition. Nacre also may be more energetically expensive to produce because of its higher organic matrix content

(Palmer, 1983). In any case, none of the limpet taxa produce nacre. Of those microstructures that they do produce, none shows a clear advantage in terms of strength. The prismatic microstructure comprising the outer layers of the acmaeid species is, however, more resistant to chemical attacks of the types that may be used by boring predators (Currey, 1980). As for nacre, the prismatic microstructures have a high organic matrix content (Palmer, 1983). Currey and Kohn (1976) have also shown that the orientation of the crystals within crossed-lamellar layers has an important effect on shell strength. The significance of these results for the functional properties of limpet shells has not been measured.

GENERALITY OF SAFETY FACTOR MODEL

As originally outlined by Alexander (1981, 1982), the arguments of the safety factor model are based on optimality theory. Specifically, the cost of failure of a load-bearing biological structure is weighed against the costs of production and maintenance of the structure. Due to the variability induced by unpredictable environments, the cost of failure is associated with a particular probability of occurrence. For the case where mean strength exceeds mean maximum load as seems to be the case for limpet shells subjected to prying forces, this probability should be reduced either 1) by increasing the safety factor or 2) by decreasing the variance in either strength or maximum load (Chapter III). Although Prediction 1 still holds true, Prediction 2 is reversed for the case where mean strength is less than mean maximum load. In this case, the structure would more likely fail than not. This high probability of failure should, however, be reduced by <u>increasing</u> the variance. This is because a greater variance in either strength or maximum load would increase the chance of being particularly strong or of experiencing a particularly low lifetime maximum load, resulting in a reduced probability of failure.

These arguments are very similar to those developed in risk-aversion theory dealing with the mean-variance tradeoff (Caraco, 1980, 1983; Caraco and Lima, 1985; Real, 1980, 1981; Real et al., 1982). In their work with foraging birds (Caraco) and bees (Real), Caraco and Real have measured average food intake (analogous to mean strength) and have assumed a constant food requirement (analogous to mean maximum load). By experimentally manipulating variance in food intake (analogous to variance in strength), both workers have obtained results supporting the above predictions associated with the condition of mean strength > mean maximum load. Furthermore, Caraco has obtained results supporting the above predictions associated with the condition of mean strength < mean maximum load. Thus, the predictions of the safety factor model have been supported by evidence from a variety of different organisms. In addition, the safety factor model has the advantage over the models proposed by Caraco and Real of taking into account variance in food requirements (analogous to variance in maximum load).

The important effects of environmentally-induced variability on the relative performance of biological structures or whole organisms has only recently received serious attention. Judging by these preliminary results, this line of investigation holds much promise.

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