

FATIGUE DAMAGE: REPEATED LOADING ENABLES CRABS TO OPEN LARGER BIVALVES

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ABSTRACT

Observations of behavior and direct measurements of force indicated that the cancrid crab *Cancer productus* could directly crush only the smallest specimens of *Protothaca staminea*, a venerid bivalve. Crabs opened larger *P. staminea* by repeatedly loading the same region of the bivalve's shell with a chela; we hypothesized that this repeated loading caused fatigue of the shell material. To test whether significant fatigue damage would accumulate in the number of cycles a crab was likely to exert, live bivalves and cleaned valves were cyclically loaded in a mechanical testing machine to loads of a constant maximum amplitude of 70–100% of the bivalves' predicted static strength. Failure frequently occurred in fewer than 200 cycles. Recordings from strain gauges attached to the chelae of crabs showed that during an attack on a bivalve a crab would squeeze more than 200 times and that failure of the bivalve could occur during a force pulse which was weaker than previous force pulses. We conclude that repeated loading enables crabs to open larger bivalves than could be crushed outright; by greatly increasing the maximum size of prey vulnerability this expands the size range of molluscan prey available to crabs.

INTRODUCTION

Crabs can be voracious predators on shelled molluscs and, where abundant, can deplete their preferred prey (Walne and Dean, 1972; Mackenzie, 1977). Hungry crabs will persist in attacking prey that require time-consuming handling techniques. For example, crabs will often open large gastropods by progressively peeling back the body whorl, a much slower method than the rapid crushing of the spire that is possible with smaller gastropods (Zipser and Vermeij, 1978).

Small red rock crabs (*Cancer productus*) can open relatively large venerid bivalves if given sufficient time (Boulding, 1984). The crab braces the bivalve against its body with one chela and uses the other chela to repetitively squeeze the ventral shell margin. The crab may release the shell for a period of time and then reapply its chela, repeating this until a chip breaks off. When a large enough hole has been chipped away, the crab forces one chela between the valves and pries them apart. A more efficient method can be used when the bivalve is small enough to fit within the crab's chela; small bivalves can be crushed outright although those with thick shells may require more than one contraction of the crab's chela. The crab behavior of repeatedly loading bivalve shells was first reported by Elnor (1978). He suggested that a shore crab (*Carcinus maenas*), faced with mussels (*Mytilus edulis*) it was not strong

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enough to crush outright, opened them by a cumulative process of extending micro-cracks that were present in the shell substructure.

The failure of a structure under repeated loading with subcritical loads is known as fatigue failure (Sandor, 1972). In structures made of brittle materials, such as concrete beams and bivalve shells, fatigue damage begins when small cracks are initiated or existing cracks are propagated by a load (Boresi *et al.*, 1978). If the structure is repeatedly loaded and unloaded, these cracks will grow until they reach a size where the structure fails; failure may occur during a load that is less than loads previously applied. Research on concrete beams has shown that the number of loading cycles a beam can withstand is a function of its static strength, but that other factors such as stress concentrations, environmental conditions, and load history can also be important (Anonymous, 1974).

A bivalve shell, like any structure, would be expected to fail if loaded a sufficient number of times (*i.e.*, high cycle fatigue, see Sandor, 1972). The interesting biological question is whether failure will occur within the number of cycles a crab is likely to exert during normal predatory behavior. To test our hypothesis that crabs weaken bivalve shells by fatiguing the shell material we must show that: (1) crabs apply force to bivalve shells in a manner that could cause fatigue damage, and that (2) bivalve shells are susceptible to low cycle fatigue. To do this we measured the magnitude and duration of the force pulses generated by a crab attacking bivalves and used mechanical testing machines to cyclically load bivalve shells under controlled conditions.

MATERIALS AND METHODS

Crab predation behavior

Bivalves [*Protothaca staminea* (Conrad)] and crabs [*Cancer productus* (Randall)] were collected in the vicinity of Bamfield Marine Station, Bamfield, British Columbia. The crabs were held in individual aquaria in free-flowing seawater and observed while preying on a range of sizes (shell lengths 5 mm to 65 mm) of the bivalves.

The magnitude and duration of the forces generated when these crabs attacked the bivalves were recorded from strain gauges attached directly to the crabs' chelae (Elner and Campbell, 1981); in effect we used the cuticle of the crab's chela as a force transducer. These strain gauges were calibrated by provoking the crab to squeeze a calibrating device that had an output voltage directly proportional to the force being applied (see Boulding, 1984). Visual observations verified that only during the actual attack of a bivalve were the forces produced by the chela sufficient to deflect the pen of the recording apparatus.

Simulation of predation—live bivalves

The bivalves (*Protothaca staminea*) were collected from Wescott Bay and from Garrison Bay, San Juan Island, Washington. Only animals free of visible growth irregularities were used. Shell height (umbo to ventral margin), shell length (anterior to posterior), shell width (most distal point of each valve from the plane of the commissure, valve thickness (1 mm above the central ventral margin), and submerged shell weight (weight of live bivalve in seawater, correlation coefficient with shell weight in air = 0.9987, $P < 0.01$) were measured for each bivalve.

Force was applied to the shells through small brass columns bolted to the compression plates of a Monsanto tensometer. To insure that local stresses were proportional to applied loads, the area through which the force was transmitted to the shell was measured by placing carbon paper between the shell and the brass columns; vari-

ation in contact area was small ($\bar{X} = 18 \text{ mm}^2$; $SD = 1.8$). For the static loading tests the tensometer was manually operated so that the force increased at 33 N s^{-1} until failure occurred. The bivalves (shell lengths 20–60 mm) were oriented with the ventral margin down and the right and left brass columns touching the central region of the right and left valves, respectively, mimicking the crabs' "crushing outright" method of opening shells.

The usefulness of various shell measurements for predicting static strength was investigated using multiple linear regression with load at failure as the dependent variable and various combinations of the shell measurements as independent variables. All the variables were log-transformed to linearize the relationships.

To test whether bivalve shells fatigue significantly when loaded with a large load for a low number of cycles, bivalves were loaded with 80% of their static strength (as predicted from the regressions on the shell measurements) until they failed. Other bivalves were subjected to loads that had the maximum amplitude stepped up by 10% if no failure had occurred after 4 cycles at the same load.

Simulation of predation—cleaned valves

The valves of freshly killed *Protothaca staminea* were gently separated, cleaned, and glued to a wooden block with Devcon 5 minute epoxy so that the rim of the valve was in full contact with the block. Each valve was loaded at the center of its exterior surface using an Instron Universal testing machine (model TT-DM) at a head speed of 5 mm/min. This approximated the crabs' "crushing outright" method of opening shells as experienced by one valve of the shell. In order to keep the contact area constant and the contact surface smooth—so that the local stresses were proportional to the load applied—the force was applied through the molars of a cancrid crab chela glued to the upper plate of the Instron.

Each of 28 valves from 14 bivalves (shell length 52 to 58 mm) was loaded until failure occurred. The static strength of the left and right valves of the same shell were compared among shells using Analysis of Variance (ANOVA).

In order to predict static strength more accurately, the load at failure for one valve was used to predict the static strength of the other valve from the same shell. The second valve was then repeatedly loaded with a constant load of 70–100% of its predicted static strength using the automatic cycling control of the Instron. If no failure occurred within approximately 200 loading cycles the load was increased by 10% and the cyclic loading repeated. For some shells the load was increased and the cycling repeated four times before the shell failed. For three shells both valves were loaded cyclically with 80% of the predicted static strength for a shell with those dimensions from that site.

RESULTS

Crab predation behavior

Figure 1 shows the pulsed application of force by the chela of a *Cancer productus* to the shells of two bivalves. Failure of the shells does not necessarily occur during the greatest force pulse. Figure 1A (where failure probably occurred at F?) and other recordings (see Boulding, 1984) suggest that the magnitude of the force pulse at failure can be less than that of previous force pulses. These crabs load the shells at a rate of up to two force pulses per minute—one monitored crab continued to load a shell more than 265 times over a three day period before failure occurred—the number of

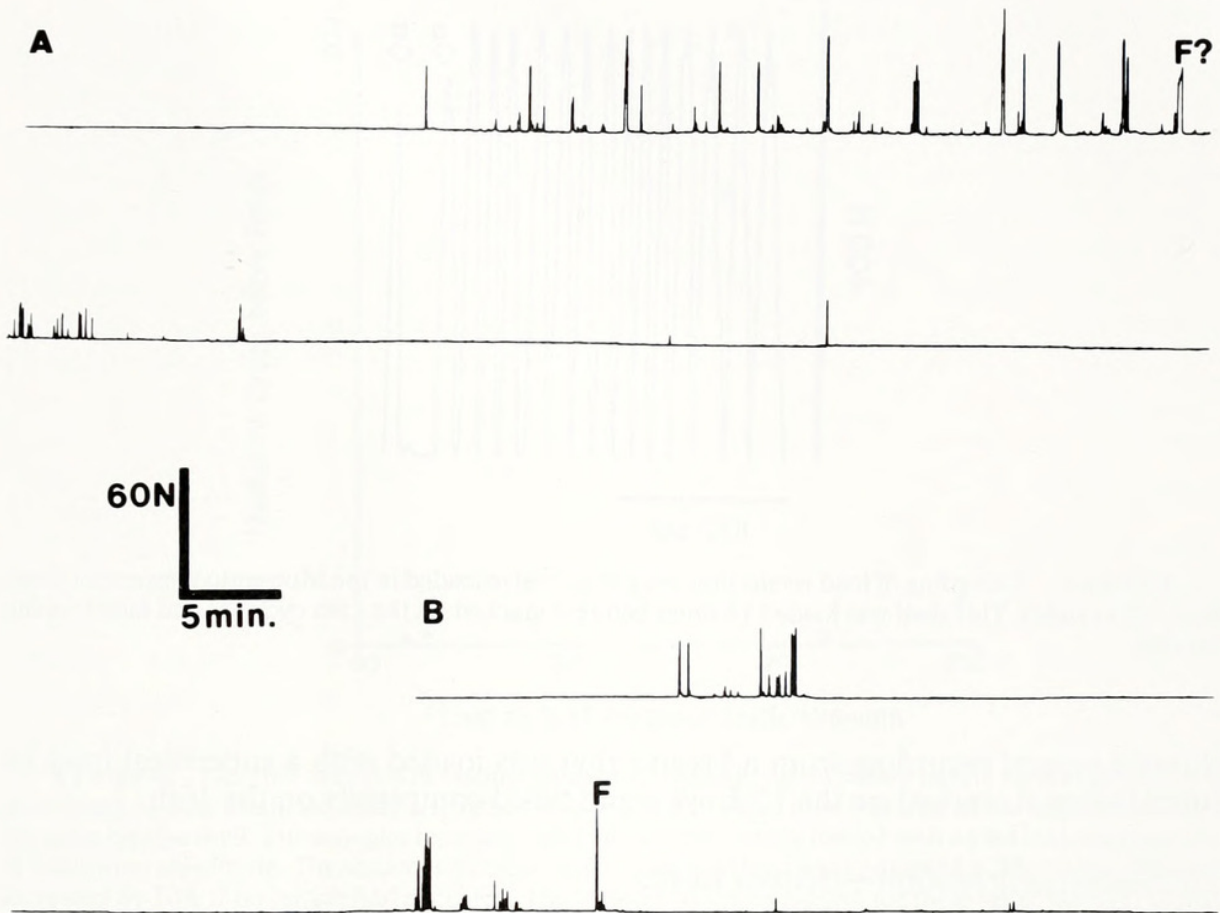


FIGURE 1. Continuous recordings (read from left to right) from a strain gauge glued directly to the chela of a female *Cancer productus* (carapace width 86 mm): in (A) which was not observed, the crab attacked a *Protothaca staminea* (thick-shelled morph; shell height 16 mm, shell length 18 mm) and in (B) which was directly observed, the same crab attacked a *P. staminea* (thick-shelled morph; shell height 14 mm, shell length 16 mm). In (B) the long interval between the two groups of force pulses occurred as the crab was disturbed by being photographed.

force pulses applied and the total handling time increased with the relative size of the bivalve (see also recordings in Boulding, 1984).

Simulation of predation—live bivalves

Although a wide size range of bivalves was used, a large part (>35%) of the variation in the static strength of the shells could not be explained by a multiple linear regression using shell height, shell length, and shell weight as the independent variables ($r^2 = 0.646$, $N = 30$, $P < 0.01$). If shell height alone was used to predict static strength the equation: static strength = $97.5 \times$ shell height was obtained ($r^2 = 0.401$, $N = 30$, $P < 0.01$).

This latter equation was not a good predictor of static strength for a second group of 30 bivalves from the same site; when these bivalves were repeatedly loaded with 80% of their predicted static strength, 16 out of the 30 failed on the first loading cycle. Of the 14 remaining shells, 6 continued to be loaded repeatedly with 80% of their predicted static strength while 8 were subjected to stepped loads that were increased by 10% if no failure occurred after 4 cycles. All 14 of these bivalves ultimately failed under loads less than or equal to loads that had been previously applied. Figure 2

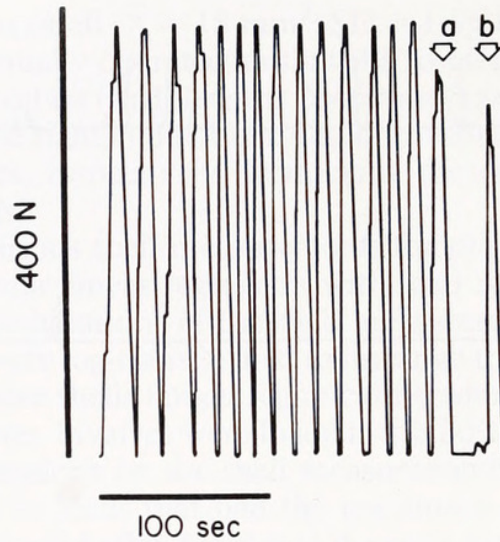


FIGURE 2. Recording of load *versus* time for a live bivalve loaded in the Monsanto tensometer (read from left to right). This shell was loaded 14 times before it cracked on the 15th cycle (a) and failed on the 16th (b).

shows a typical recording from a bivalve that was loaded with a subcritical load 14 times before it cracked on the 15th cycle and failed completely on the 16th.

Simulation of predation—cleaned valves

The static strengths of isolated valves from the same bivalve shell were more similar to each other than to the mean for all valves (ANOVA, $N = 14$, $P < 0.01$) even though the dimensions of all these shells were very similar (shell length 52 to 58 mm). There was no significant difference in the static strength of the right and left valves (sign test $P < 0.05$).

The fatigue life of two valves from the same shell could be appreciably different. For one shell, the right valve withstood 15 cycles while the left withstood 4 cycles of the same load. In another case the right valve failed after 261 cycles while the left withstood 579 cycles without failing. In a third case the right valve failed after 226 cycles while the left valve sustained 1666 cycles without failing.

In a group of 30 bivalves that had one valve loaded statically and one valve loaded

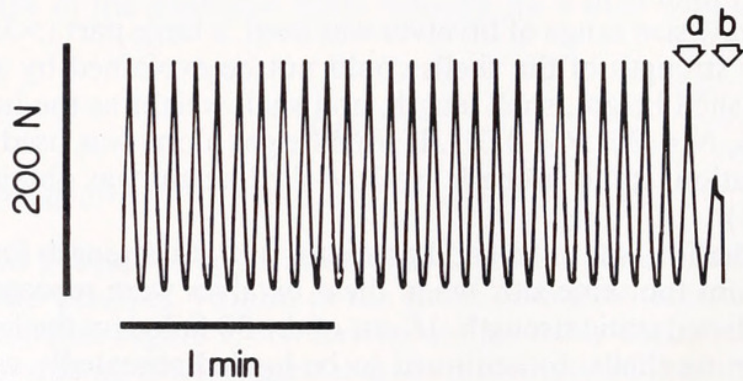


FIGURE 3. The final portion of a recording of load *versus* time for a valve loaded in the Instron (read from left to right). The shell failed after 143 cycles of a load of 176.4 N. The valve cracked at (a) and failed at (b).

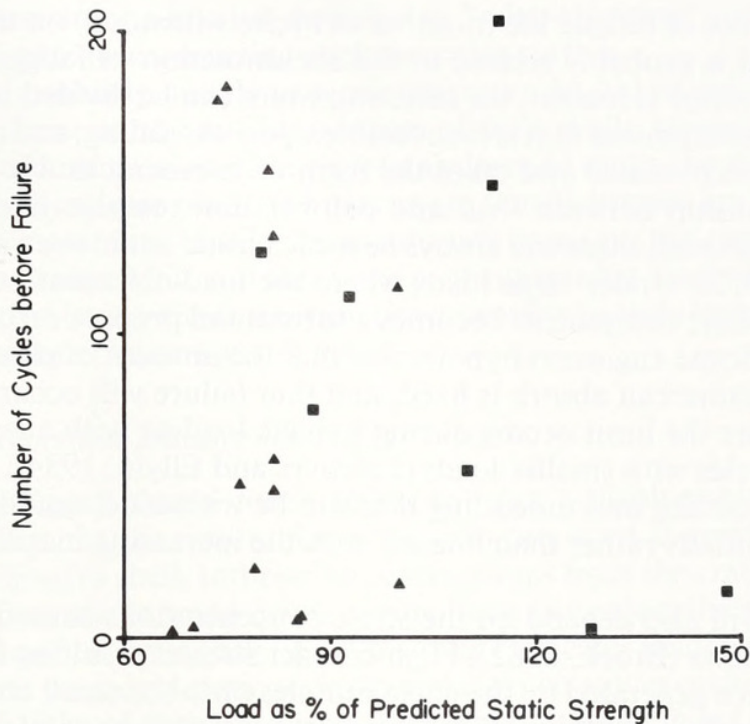


FIGURE 4. Number of cycles of loading withstood by single valves before failure *versus* the load as a percentage of their predicted static strength. The predicted strength used was that of the other valve from the same bivalve shell. The triangles represent valves that were repeatedly loaded with a load that was constant in maximum amplitude. The squares represent valves where the load was constant for 200 cycles, then was increased by 10% if no failure had occurred. The number of cycles plotted for these latter (square) points is the number of cycles since the last increase in the maximum amplitude of the load.

cyclically (Fig. 3), 12 of the cyclically loaded valves failed on the first load, 10 withstood between 4 and 182 cycles before failing, and 8 withstood at least 200 cycles before failing and had their maximum loads increased by 10% up to four times.

There was no evident relationship between the load applied, measured as a percentage of the static strength of the other valve from the same shell, and the number of cycles withstood (Fig. 4). This was probably a reflection of the low precision with which it is possible to predict the static strength of whole shells. Only loads close to the actual static strength of the valve seemed to appreciably weaken the shell; the position of the stepped valves (squares) along the y-axis of Figure 4 relative to those loaded at a constant amplitude (triangles) suggests that the previous cycles of loading at lower maximum loadings had little effect on the number of cycles withstood at the greatest maximum loading.

DISCUSSION

Low cycle fatigue of bivalve shells

Literature on low cycle fatigue of structures made of brittle materials is scarce, and primarily concerns structures made of concrete. Concrete beams can show appreciable fatigue damage within a low number of cycles when loaded with more than 75% of their predicted static strength (J. G. MacGregor, pers. comm.). Low cycle fatigue has been reported for human leg bones (see Wainwright *et al.*, 1976) and for strips of pearl oyster nacre for loads above 60% of the predicted static strength (Currey and Brear, 1984).

The dependence of fatigue life (number of cycles withstood) on the magnitude of the loads applied is probably related to the accumulation of fatigue damage. Each time a brittle structure is loaded, the resulting strain can be divided into two components: an elastic component that is recoverable upon unloading, and a plastic component that is not recoverable and takes the form of microcracks. Under small loads, while the relationship between load and deformation remains linear, most of the strain is elastic although there will always be some plastic strain even if it is unmeasurable (Sandor, 1972). Under large loads where the load-deformation relationship is nonlinear, the plastic component becomes a substantial proportion of the total strain (Sandor, 1972). Some engineers hypothesize that the amount of plastic strain energy that a given structure can absorb is fixed, and that failure will occur when this limit is reached whether the limit occurs during a single loading with a large load or after many loading cycles with smaller loads (Lefebvre and Ellyin, 1984). Thus, the number of cycles of loading and unloading that can be withstood would be predicted to decrease exponentially rather than linearly with the increasing magnitude of the load applied.

Fatigue life will also depend on the stress concentrations caused by pre-existing cracks or other flaws (Broek, 1982). High contact stresses resulting from concentration of all the force generated by the chela muscles onto the small area of the shell in contact with the chela molars could hasten the development of fatigue damage. Things are further complicated because the important stresses in a bivalve shell loaded on the apices of its two valves by a crab are probably not just those from simple bending. In simple bending, the greatest tensile stresses would be immediately below the loading points on the inside of each valve and the greatest compressive stresses would occur immediately below the loading points on the outside of each valve. The domed shape of *Protothaca* could result in unidirectional tensile stress on the inside of the valves being replaced by a two dimensional (membrane) stress field, especially if the shell margins are restrained from splaying out by friction along the ventral margins (Timoshenko and Woinowsky-Kreiger, 1959), and thus increase the amount of force a domed shell can withstand relative to that which a flat shell could withstand.

The dependence of fatigue life on stress concentrations was one reason we used whole shells instead of standardized test strips cut from shells to test for susceptibility to low cycle fatigue; because the geometries of whole shells and test strips are different their patterns of force concentration are different too. In addition, microcracks can result from the machining of test strips (Currey and Kohn, 1976) which could confound the results of fatigue tests made with test strips. By not using test strips we avoided these complications at the cost of precision in our estimates of static strength.

We could not use a mechanical testing machine to satisfactorily mimic the "edge-chipping" method that crabs use to open bivalves too large to fit entirely within a chela, but we believe that fatigue damage may also be involved in the chip formation seen in this mode of attack. During "edge-chipping," the crab's chela slips ventrally on the shell as the crab squeezes its chela around the ventral margin of the shell. The net force at a given chela molar can be resolved into two vectors: a large compressive vector normal to the shell surface and a smaller shearing vector parallel to the shell surface. A theoretical analysis (Boresi *et al.*, 1978) suggests that if the coefficient of friction of the chela on the shell is greater than $1/10$, the region of greatest tensile stress will move from the inside of the valve to the outer valve surface. These contact stresses can be the most significant stresses in the structure—particularly when the surfaces do not remain in fixed contact—and would be expected to lead to a type of fatigue failure that takes the form of pitting (Boresi *et al.*, 1978). Thus the formation of chips

at the ventral margin of a bivalve shell during “edge-chipping” may result from the repeated slipping of the contracting chela over this surface.

Bivalves are probably unable to repair microcracks out of reach of their mantle such as would occur on the outside surfaces of their shells; microcracks would thus be expected to accumulate on these regions and would make the shell especially vulnerable to loading regimes where the maximum tensile stresses are on these surfaces. Even when the maximum tensile stresses do not occur on the outer surfaces of the shell, the greater vulnerability of this layer is obvious; after loading and unloading a shell in the Instron many times we sometimes saw the outside layer crumbling away even though the inner layer was still intact.

Importance of repetitive loading behavior to crabs

Our results suggest that a crab's ability to open a bivalve shell is not simply a matter of whether the maximum force the crab can exert is greater than the static strength of the bivalve shell. Indirect force recordings from the crab's chela indicated that failure of prey shells could occur during force pulses less than or equal to those that had been applied previously. Live bivalves cyclically loaded in the tensometer with 80% of their predicted static strength and cleaned valves cyclically loaded in the Instron with 70–90% of their predicted static strength often failed in fewer than 200 loading cycles. This supports the hypothesis that bivalve shells are susceptible to low cycle fatigue if repeatedly loaded by crabs with a high proportion of the shells' static strength.

The results of the static loading investigations suggest that it would be difficult for crabs to predict the static strength of a bivalve's shell on the basis of its physical measurements. Shell height, shell length, and shell weight accounted for only 65% of the variation in static strength of these *Protothaca staminea* (shell length 20–60 mm); adding other variables such as valve thickness did not substantially increase the variation accounted for. Indeed, in a detailed study of scallop shells only 64% of a shell's tensile compliance could be predicted from the physical measurements of the shell such as thickness and corrugation amplitude (Pennington and Currey, 1984). We suspect that the remaining 35% or so of the variation in static strength is due primarily to historical factors such as wear or previous loading history. Indeed, the predicted fatigue life of standard concrete test specimens is usually given in probabilistic terms—cumulative probability of failure after a given number of loading cycles (Anonymous, 1974)—rather than as a simple function of the load applied. Our interpretation is supported by the relative similarity in the static strength of two valves from the same shell when compared with valves from other bivalves with similar physical measurements. Our results suggest that the fatigue life of a bivalve shell under a given loading regime would be even more difficult to predict than static strength unless the crab could somehow detect minute increases in compliance.

Given the unpredictable nature of the fatigue life of bivalve shells, it would seem at first a poor strategy for a crab to persist in squeezing a bivalve on the chance it might fail. However even if a crab can only exert a maximum of 70% of the force necessary to crush a given shell the microcracks propagated by the larger force pulses could be propagated by the smaller force pulses (Sandor, 1972). We will show that under certain circumstances it pays for crabs to persist in attacking a shell.

Crabs prefer small bivalve prey which they can open easily and rapidly (Boulding, 1984), and when crabs are abundant such prey may become scarce. By repeatedly loading shells, crabs greatly increase the size range of prey available to them. For example if a 60 mm male *Cancer productus* used only a single contraction of the

chelar muscles, the largest *Protothaca staminea* (thick-shelled morph) opened was one of 11 mm shell length, whereas if the crab used repeated loading of the ventral margin it could open bivalves greater than 49 mm (E. G. Boulding, pers. obs.). Periods of low prey abundance could result in selection for crab behavior and morphology that increased the size range of prey accessible to the crabs. Very high selection coefficients have been documented for Darwin's finches when a drought markedly reduced seed availability and selective consumption by predators increased the average size and hardness of those seeds that remained (Boag and Grant, 1981).

Crabs have demonstrated sophisticated predatory behavior that involves prolonged attack with repeated loading of the same region of a mollusc shell. The tropical crab *Carpilius maculatus* has been observed to persistently apply force pulses to the same region of tropical gastropod shells (Edith Zipser, pers. comm.). *Carcinus maenas* has been observed to repeatedly apply its chela to same spot on a mussel (Elner, 1978) and has been observed to squeeze bivalves for more than 20 minutes (Elner and Hughes, 1978) at a rate of 10 pulses per minute (Elner, 1978), approximately 200 loading cycles. *Cancer productus* has been observed to persistently attack the same region of the ventral margin of a *Protothaca* shell even after the crab had put down the shell and picked it up again; we have recorded a crab of this species continuing to squeeze the shell at the rate of 1 to 2 pulses per minute for three days (albeit with some pauses). *C. productus* will sometimes alternately attack a bivalve and walk around the aquarium searching for other prey, and this sequence often continues until the crab successfully opens the bivalve (Boulding, 1984).

Although smaller bivalves are much more quickly opened and are preferred in the laboratory (Boulding, 1984), crabs may reduce their risk of predation by carrying a large prey item to a safe place and repeatedly loading it until it fails. Tropical crabs were often found under boulders or large chunks of corals in association with the shell fragments of massively thick shells which are known from laboratory observations to require prolonged attack (Zipser and Vermeij, 1978; E. G. Boulding, pers. obs.). The recovery location of characteristically chipped shell fragments of previously marked *Protothaca staminea* implied that crabs were transporting these large, difficult-to-open bivalves from the intertidal to subtidal eelgrass beds (Boulding and Hay, 1984) where the crabs were presumably safer from predators.

Thus there is evidence that crabs persistently attack bivalves and gastropods, and that the prey shell is progressively weakened by fatigue damage until it fails. If the cost of continuing the attack is low, the risk of leaving the refuge high, and alternative prey scarce, then crabs may benefit most by continuing the attack.

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