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The tissues of articulate brachiopods and their value to predators

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SUMMARY

The punctate brachiopods *Liothyrella neozelanica* and *Neothyris lenticularis* were compared with the impunctate *Notosaria nigricans* and the bivalve molluscs *Mytilus edulis* and *Lima colorata* in terms of the force needed to crush the shells, the time needed to drill through shells by a standard apparatus, the organic content of the internal tissues (ash-free dry mass, AFDM), the tissue density (AFDM per unit volume between the shell valves) and the inorganic content of the internal tissues and whole animals. At one site *M. edulis* needed greater force to fracture its shell (× 3.5), more time to drill through the shell (× 10.8) and contained more AFDM (× 6.2) than the brachiopod *L. neozelanica*. At a second site there was no significant difference between the brachiopods *N. lenticularis* and *N. nigricans* and the bivalve *L. colorata* in terms of force needed to crush the shells, but the bivalve was × 2 to × 30 harder to drill through and contained 10.7 times as much tissue AFDM as *N. lenticularis* and 4.2 times as much as *N. nigricans*. The impunctate *N. nigricans* had 2.6 times as much AFDM in its internal tissue as the punctate *N. lenticularis*. Cost–benefit ratios showed neither group to be consistently better prey items for predators in terms of reward (AFDM available) per unit effort. The punctate brachiopods had the lowest tissue densities (AFDM per internal volume) with values of 5–8 mg cm^{-3}, the impunctate *N. nigricans* was next at 12–16 mg cm^{-3} and the bivalve molluscs were highest with values of 45–120 mg cm^{-3}. Tissue inorganic contents were also markedly different. The punctate brachiopods had values of 47.3% (*N. lenticularis*) and 56.2% (*L. neozelanica*), whereas the figure for the impunctate *N. nigricans* was 30.2%, and the bivalves were much lower at 12.8% (*M. edulis*) and 14.2% (*L. colorata*). These results suggest that predation pressures may be low on articulate brachiopods because of the very low tissue density and high inorganic content (because of the presence of spicules) of the internal tissues, both of which are characteristics which are not consistent with the possession of potent chemical defences.

1. INTRODUCTION

Articulate brachiopods are sessile suspension-feeding benthic marine invertebrates. They live in all the oceans of the world from the tropics to polar latitudes and from intertidal areas to abyssal depths. They do, however, tend to inhabit specific areas, most of which are relatively inaccessible, such as the deep sea and in fiords. Because of this they have received little attention from, and are rarely seen by, biologists. In contrast to their current distribution and abundance, brachiopods were once the dominant group of all benthic filter-feeding organisms and they were a major component of marine faunas as far back as the early Cambrian period. Thus the phylum has existed for over 500 Ma, and some of the earliest taxa have survived to present times with little obvious change. Brachiopods also suffered greatly in some of the major mass extinction events, notably at the end of the Permian 250 Ma ago. They have, therefore, received a great deal of attention from palaeontologists, and much effort has been put into attempts to explain the success of some taxa and the decline of others. An obvious example of this is the replacement in many habitats of the brachiopods by bivalve molluscs, and many papers have been published on comparisons of the two groups (Steele-Petrovic 1975, 1979; Thayer 1985, 1986; Rhodes & Thayer 1991; Peck 1992), although there is doubt about whether brachiopods and bivalve molluscs were in direct competition at any time during the above events (Gould & Calloway 1980).

Over the past 10 years there has been a great deal of interest in the effects of predation on survival and evolution in fossil species. The theories of evolution and escalation, where traits are evolved in defence against some predation pressure only to be followed by an increase in effectiveness of the predators involved, put forward by Vermeij (1982, 1986, 1987), have been to the fore in this debate. Brachiopods have also received a large amount of attention in this respect in the recent past, with Stanley (1974, 1977, 1979) suggesting that predators limited brachiopod radiation after the Permo-Triassic mass extinction event. Donovan & Gale (1990) suggested that asteroids were the organisms responsible for the predation

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pressure, although there has been considerable disagreement over this (Blake & Guensberg 1990; Vermeij 1990). Alexander (1986, 1990) and Alexander *et al.* (1992) have also done detailed studies of the effects of durophagous (crushing) predators on both living and fossil brachiopod populations, as well as repair mechanisms used by brachiopods after the shell has been damaged.

Given the importance of brachiopods in the fossil record and to the understanding of evolutionary processes, the recent debate on interactions between brachiopods and species which prey on them has assumed a position of some importance. It is a common observation that there is little predation pressure on living brachiopod populations. However, there are many observations which show that brachiopods are taken by a range of predators including fish, asteroids and drilling gastropods (Stanley 1977; Witman & Cooper 1983; Fouke & LaBarbera 1986; James *et al.* 1992), although in some circumstances they may only be a by-product of feeding on other prey items. McCammon (1972) noted that brachiopods were very rarely taken by crabs and starfish in aquaria. Furthermore, Thayer (1985) showed that a range of potential predators preferred bivalve mollusc tissues to those of brachiopods, and Thayer & Allmon (1991) did experiments which showed that some brachiopod tissues were unpalatable to or not accepted by some fish and anemones, whereas 'control tissues' from mussels were readily eaten. This has led to the idea that unpalatability or some type of chemical defence mechanism was developed by the surviving brachiopod clades to overcome the escalating predation pressures since the Permo-Triassic extinction event, even though no toxic or repellent substances have yet been isolated from, or demonstrated to be present in, brachiopod tissues.

Many factors affect the selection of prey items by a given predator (Hughes 1980; Taylor 1984; Sibly & Calow 1986). Factors which are usually important are the return that is obtained from a prey item (the benefit) in relation to the costs involved with feeding on that prey. Cost–benefit ratios are often calculated in studies of predator–prey interactions, and the two parameters may be optimized under certain circumstances, often maximizing net energy gained per unit handling time or per unit cost. Foraging effort and prey size are often also very important in these types of analysis (Hughes 1986; Harris 1989; Hughes & Elner 1989; Hughes & Burrows 1990). At present there are no data for any brachiopod species on any of the above parameters which are known to affect predator–prey interactions strongly.

The present study estimates the relative effort required to drill through and crush shells of two punctate brachiopods (possessing mantle extensions, called caeca, which traverse the shell), one impunctate brachiopod (no caeca) and two bivalve molluscs. The organic content (estimated as ash-free dry mass (AFDM) of the tissues available to predators (excluding those in the caeca) was also measured, as was the volume between the shell valves and the inorganic content of the internal tissues and whole animals.

2. MATERIALS AND METHODS

Specimens studied were collected from two sites on the coastline of South Island, New Zealand (figure 1). Site 1 was at Campbells Kingdom in Doubtful Sound, Fiordland (45°25′ S, 167°07′ E) on the west coast. Specimens of the punctate brachiopod *Liothyrella neozelanica* and the bivalve mollusc *Mytilus edulis* were collected there from depths between 4 m and 18 m by SCUBA divers. At this site there was, as there was throughout most of Doubtful Sound, a thick layer of freshwater at the surface ranging between 1 m and 6 m in depth. The *M. edulis* occurring there were at, or slightly below, the junction between the fresh- and seawater layers, whereas the *L. neozelanica* did not occur shallower than 15 m. The rockface at the site was sheer, with a depth of 300 m being recorded within 40 m of the shoreline. The *M. edulis* were attached to the rock surface, whereas the *L. neozelanica* hung from the upper surfaces of crevices, often in clumps of five or more animals attached to each other.

Site 2 was on the east coast of South Island and was 14.9 miles east of Tiaroa Head at the mouth of Otago Harbour (45°50′ S, 171°50′ E). Specimens of the punctate brachiopod *Neothyris lenticularis*, the impunctate brachiopod *Notosaria nigricans* and the bivalve mollusc *Lima colorata* were collected by dredge from the *R.V. Munida* of the Portobello Marine Laboratory of the University of Otago. Animals were living in 160 m to 180 m of water on the edge of the continental shelf and were attached to gravel embedded in and lying on a clay substratum. After collection all specimens were placed in aquaria at the Portobello Marine Laboratory for up to 72 h before being used in experiments. *M. edulis* and *L. colorata* were chosen as

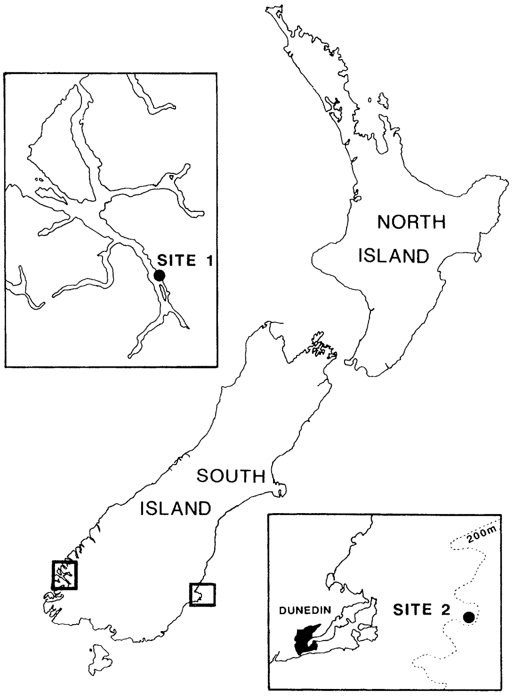

Figure 1. Map of New Zealand showing positions of sampling sites.

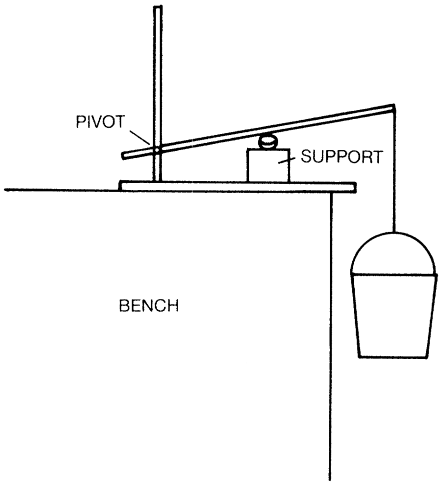

Figure 2. Apparatus used to measure force needed to fracture shells of species under investigation. Specimens were placed on a supporting block at the same height as the pivot. The bar was then placed on top of the shell and water added to the bucket until the shell collapsed. The mass of the bucket and contents then allowed the force used to be calculated.

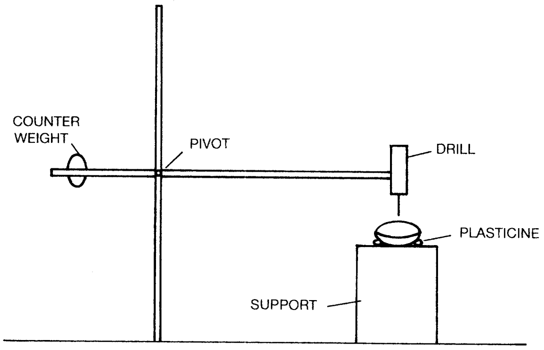

Figure 3. Apparatus used to estimate the relative effort needed to drill through brachiopod and bivalve mollusc shells. Shells were held in place using plasticine. The apparatus was set up so that the drill bit approached the shell perpendicularly to the tangent at maximum shell height. The drill was weighted in the same way for each specimen and the time taken to bore through the shell completely taken as a relative measure of resistance to drilling.

organisms for comparison with the brachiopods because of the similarities in their lifestyles. Both live attached to hard rock surfaces in close proximity to brachiopod populations and they also feed on suspended phytoplankton, as do brachiopods. The comparisons in this study were made on bivalves and brachiopods living in close proximity to each other from the same environments.

For each species the following parameters were measured: the force needed to crush shells, the relative effort required to drill holes through the shells, volumes occupied by various tissues and the AFDM of internal tissues. Crushing experiments were done using the apparatus shown in figure 2.

Animals were placed on a wooden support and an aluminium bar rested across the top of the shell. The bar was pivoted at one end and had a plastic bucket suspended from the other. The whole apparatus was sited on the edge of a bench so that the bucket could hang freely. Water was then poured into the bucket until the shell of the specimen collapsed. The bucket and contents were then weighed. Assessments were made at three positions along the bar: half-way from the pivot to the other end, one-quarter of the way, and one-eighth of the way, depending on animal size and robustness. The mass of the water was multiplied by the relevant factor and added to the force exerted by the mass of the bar to obtain the crushing force applied to the shell at the moment of collapse. Assessments were always made with the force being applied across the maximum height of the shell.

The relative effort needed to drill through shells was obtained by using a modeller's drill mounted on the end of another pivoted aluminium bar (figure 3). Specimens were again placed on a wooden support, but were now restricted from lateral movement by a plasticine ring. The wooden supports used were of varying thicknesses to allow the drill bit to contact the shell at 90° to the upper surface tangent. A counter weight was set on the other side of the pivot to the drill and was fixed in place after a variety of shells from all the species investigated had been used to indicate a suitable position. After the drill was fixed on a given setting, a stopwatch was used to measure the time needed for holes to be drilled through shells under investigation. Three drillings were made per shell and were each made as close as possible to the point of maximum shell height. Tungsten carbide drill bits of 1.0 mm diameter were used throughout. After a preliminary investigation it was found necessary to change a drill bit when it had been used on five animals. Before and after each animal was drilled a 'standard' shell was drilled. Thus allowances for errors resulting from slight variance in the performance of the drill bit, both during the drilling of an individual, between shells, and between bits, were possible. There were three 'standard' shells, which were specimens of *Liothyrella uva* (Broderip 1833) from Signy Island, Antarctica, of 45.1 mm, 45.2 mm and 45.4 mm in length. They were cross calibrated using new drill bits both before and after all the other assessments.

Volume assessments were made of whole, closed animals and shells with the internal soft tissues removed. Internal volume was obtained from the difference between the above measurements. Measurements were made by displacement, with animals or shells being placed on trays suspended freely in a 250 cm^3 beaker of seawater. Neither the trays nor the specimens being investigated touched the sides of the beaker. Thus changes in mass shown by a top-pan balance placed beneath the beaker showed the mass of water displaced by the animals or shells (Archimedes principle). Dividing by the density of the seawater used allowed volumes to be measured to an accuracy of 0.001 cm^3. Very tiny overestimates were made by this methodology, as when specimens were placed on trays the seawater rose in the beaker. The trays in the beakers were supported by thin wires and the seawater also rose up these, which displace a very small amount of extra water. The largest errors occurred when measuring the largest specimens, which had volumes of 10–15 cm^3, as they caused the largest rise in water level, and in these the error was less than 0.0015 cm^3. This process is described in more detail by Peck (1992) and is similar to that used by Rodhouse (1977*a*). AFDM values were obtained from the difference between masses of material oven dried for 48 h at 60°C and those of tissues ignited at 470°C for 24 h. After treatment, all tissues were cooled to room temperature in a desiccator before weighing. During drying, samples were cooled and weighed at intervals until no further change in mass was obtained. This indicated that a 48 h period was necessary to reach a stable dry mass for this material.

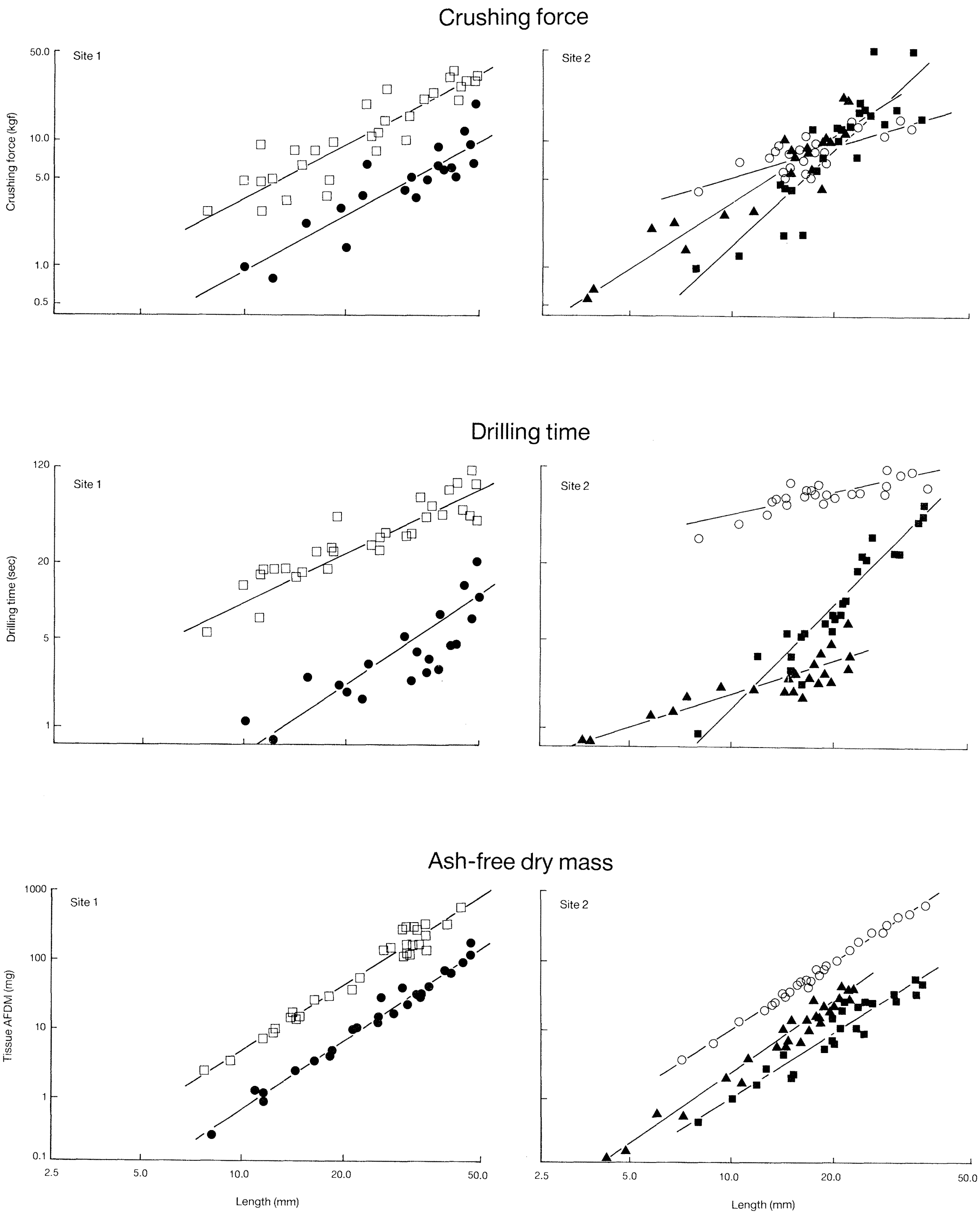

Figure 4. Graphs of crushing force (kgf) needed to fracture shells; time needed to drill through shells (s) and tissue ash-free dry mass (AFDM, mg), for brachiopods and bivalve molluscs from two sites. Filled symbols denote brachiopods, and open symbols are used for bivalve molluscs; *Mytilus edulis* (open squares), *Lima colorata* (open circles), *Liothyrella neozelanica* (filled circles), *Neothyris lenticularis* (filled squares), *Notosaria nigricans* (filled triangles). *L. neozelanica* and *N. lenticularis* are punctate species (possessing caeca), whereas *N. nigricans* is impunctate. Regression parameters are given in Appendix 1, comparisons of regression lines are given in table 1.

Table 1. *Slopes and statistics for comparisons of elevations of regression lines relating crushing force (CR), drilling time (DT) and AFDM to animal length*

(Where differences in intercept are given they were statistically significant at $p < 0.001$. Differences quoted are in logarithmic units ($\log_e$). Data for differences in intercept are only given where slopes are not significantly different. The parameters are for the relations shown in figure 4. Full regression parameters are given in Appendix 1.)

species	slope	*F*	d.f.	*p*	common slope	difference in intercepts
site 1						
CR						
L. neozelanica	1.47	0.06	1,46	0.80	1.44	1.26
M. edulis	1.43					
DT						
L. neozelanica	1.64	3.03	1,46	0.10	1.35	2.38
M. edulis	1.21					
AFDM						
L. neozelanica	3.25	0.56	1,50	0.46	3.19	1.83
M. edulis	3.11					
site 2						
CR						
N. lenticularis	2.44	13.04	2,63	0.001	—	—
N. nigricans	1.74					
L. colorata	0.80					
DT						
N. lenticularis	2.72	80.44	2,66	0.001	—	—
N. nigricans	0.88					
L. colorata	0.60					
AFDM						
N. lenticularis	3.08	1.53	2,67	0.223	3.24	2.37 (*L.c.* > *N.l.*) 0.94 (*N.n.* > *N.l.*) 1.44 (*L.c.* > *N.n.*)
N. nigricans	3.48					
L. colorata	3.19					

Manipulations of the data and statistical analyses were made on a VAX 8600 computer using the MINITAB release 7 statistical package (Ryan *et al.* 1985) and additional MACRO programs. Logarithmic ($\log_e$) transformations of the data were made where appropriate.

3. RESULTS

Plots of crushing force (CR), drilling time (DT) and organic content (AFDM) related to animal length for animals from site 1 show that all three parameters were greater in the bivalve *M. edulis* than the brachiopod *L. neozelanica* (figure 4). Comparisons of regression lines show that for each measure the slopes of the regressions are not significantly different (table 1). Differences in intercepts based on common slopes, therefore, show differences in elevation of the lines. On this basis it took 3.5 times as much force to crush the mollusc shell as the brachiopod, and 10.8 times the amount of time to drill through it, but it contained 6.2 times the amount of tissue AFDM.

At site 2 the situation was somewhat different. Measures of crushing force had significantly different slopes (table 1) and there was no clear pattern between species, although there was a trend for small *L. colorata* to be more difficult to crush than the brachiopods. Drilling times also showed different slopes for different species. However, the values for *L. colorata* were all higher than those for either of the brachiopods and there was no overlap in the data points. Differences in time required to drill through shells ranged from × 2 to × 30, depending on size. Relations between tissue organic content and length did not have significantly different slopes, and intercepts based on a common slope showed the bivalve to contain 4.2 times as much organic matter as the impunctate brachiopod *Notosaria nigricans* and 10.7 times as much as the punctate *Neothyris lenticularis*. The difference between the two types of brachiopod on this measure was × 2.6. It should be noted here that, in the case of punctate brachiopods, this is not an assessment of total animal organic content as the AFDM in the caeca has been deliberately ignored because it is not generally available to predators, although small amounts may be available to engulfing species.

(*a*) *Cost–benefit ratios*

At site 1 both the costs and benefits associated with feeding on the bivalve mollusc are clearly higher than those for the brachiopod. The same is true at site 2 for two of the three assessments. An important variable to predators is often the ratio of the benefits accrued to the costs expended during feeding. A simple measure

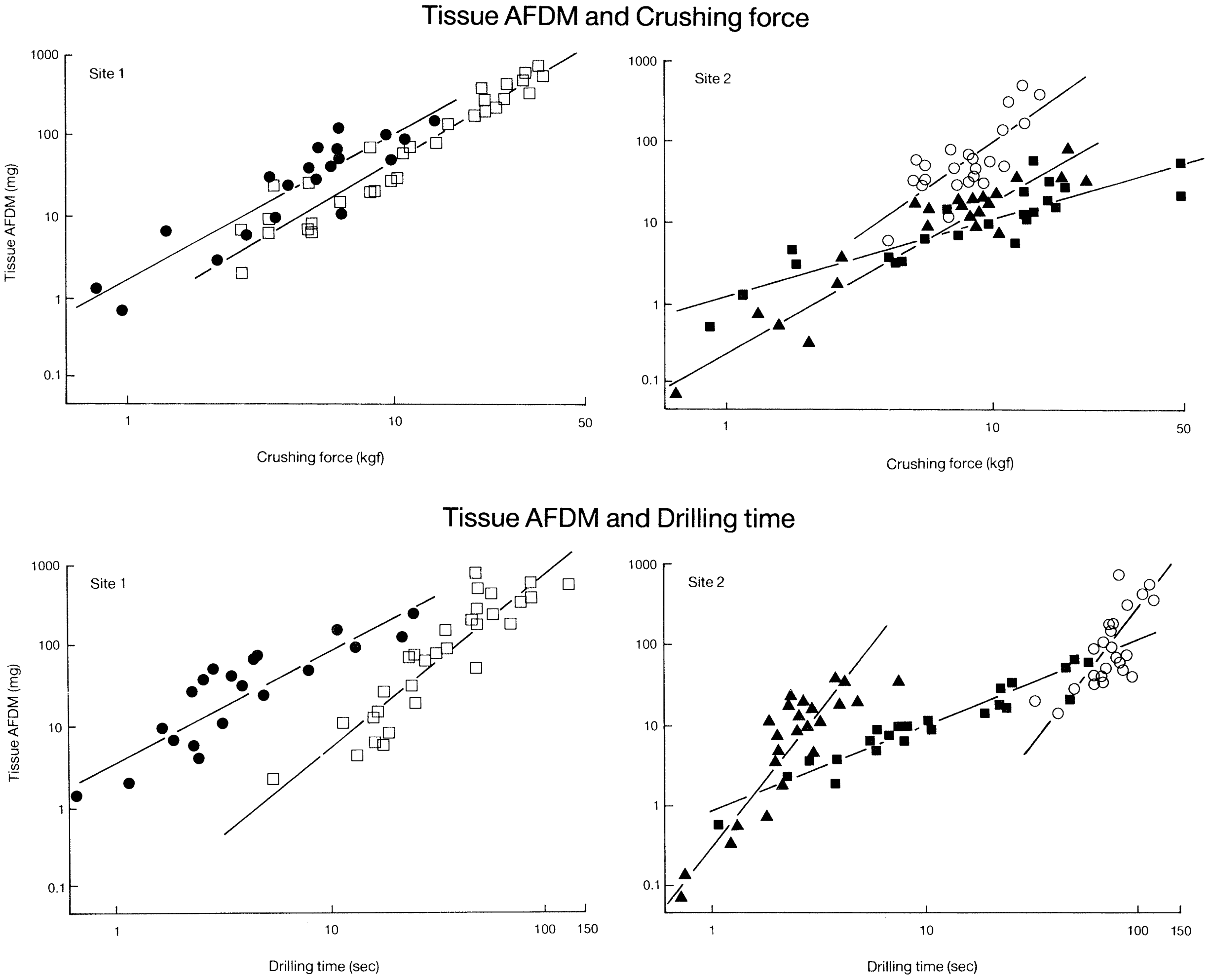

Figure 5. Returns for predators, measured as ash-free dry mass (AFDM), plotted against costs assessed as crushing force (kgf) and drilling time (s) needed to gain access to the tissues. Filled symbols denote brachiopods, and open symbols are used for bivalve molluscs; *Mytilus edulis* (open squares), *Lima colorata* (open circles), *Liothyrella neozelanica* (filled circles), *Neothyris lenticularis* (filled squares), *Notosaria nigricans* (filled triangles). Equation parameters are given in Appendix 1; comparisons of regression lines are given in table 2.

of this is the organic content of the tissues gained as a function of the effort needed to crush or drill through the shell. When AFDM is plotted against crushing force or drilling time the results from site 1 are clear (figure 5). In both cases there is a greater return, in terms of AFDM per unit effort, from the brachiopod *L. neozelanica* than the bivalve mollusc *M. edulis*. For ratios involving crushing force, slopes were not different, and the difference in intercepts based on a common slope was ×2.3, or there was 2.3 times as much AFDM present for a given unit of crushing effort (table 2). Slopes for the AFDM to drilling time relation were slightly different, but the values were all higher for the brachiopod than the bivalve and differences ranged from 9 times to 25 times.

The situation is again less clear at site 2. Slopes were significantly different between species for both measures (table 2) and comparisons of intercepts are therefore inappropriate. For AFDM against crushing force the bivalve mollusc *L. colorata* appears to contain the greatest organic content per unit crushing effort, but there is almost total overlap between the two types of brachiopod on this scale. The plot of AFDM against drilling time is made difficult to interpret by the small ranges and complete lack of overlap in terms of drilling time exhibited by the impunctate *N. nigricans* and the bivalve *L. colorata*. *N. nigricans* is relatively easy to drill into, whereas the results for *L. colorata* all have long drilling times.

The pattern of results for site 2, with the bivalve data all having large x values, suggests that animal size may play an important role in the comparison of the variables. When cost–benefit ratios for predators (AFDM available per unit effort: AFDM/CR and AFDM/DT) are plotted against animal size, different results are obtained (figure 6). At site 1 the differences between *L. neozelanica* and *M. edulis* are reduced greatly, and for crushing force the mollusc has higher returns per unit effort than the brachiopod for an animal of given length. The slopes of the regressions relating these parameters to length at site 1 are not significantly different (table 3). Differences in intercepts based on a common slope show that for AFDM/CR *M. edulis* produces higher values than *L. neozelanica* by a factor of 1.5, whereas on the AFDM/DT measure the position is reversed, with the brachiopod being higher by a factor of 2.0. At site 2 the AFDM/CR measure shows that for a given-length individual the bivalve *L. colorata* has

Table 2. *Slopes and statistics for comparing elevations of regressions relating* AFDM *with crushing force and drilling time* (Abbreviations as in table 1; original data shown in figure 5. Full regressions given in Appendix 1.)

species	slope	F	d.f.	p	common slope	difference in intercepts
site 1						
AFDM and CR						
L. neozelanica	1.82	0.50	1,46	0.493	1.92	0.85
M. edulis	1.98					
AFDM and DT						
L. neozelanica	1.36	8.33	1,46	0.006	—	—
M. edulis	2.15					
site 2						
AFDM and CR						
N. lenticularis	0.98	46.74	2,65	0.001	—	—
N. nigricans	1.78					
L. colorata	2.36					
AFDM and DT						
N. lenticularis	1.06	28.67	2,64	0.001	—	—
N. nigricans	3.11					
L. colorata	3.39					

higher values than either brachiopod by factors ranging from 1.7 times to 23 times. The AFDM/DT measure at site 2 shows a similar pattern to the AFDM/CR plot, with the difference that the results for *N. nigricans* are higher than those for the bivalve *L. colorata*. Clearly unusual in the way these parameters scale to animal size is the punctate brachiopod *N. lenticularis*, as the slopes of these relations are much lower for this species than any of the others studied (table 3). In both measures (AFDM/CR and AFDM/DT) at site 2 the slopes of regressions are significantly different. The differences between figures 5 and 6 emphasize the large differences

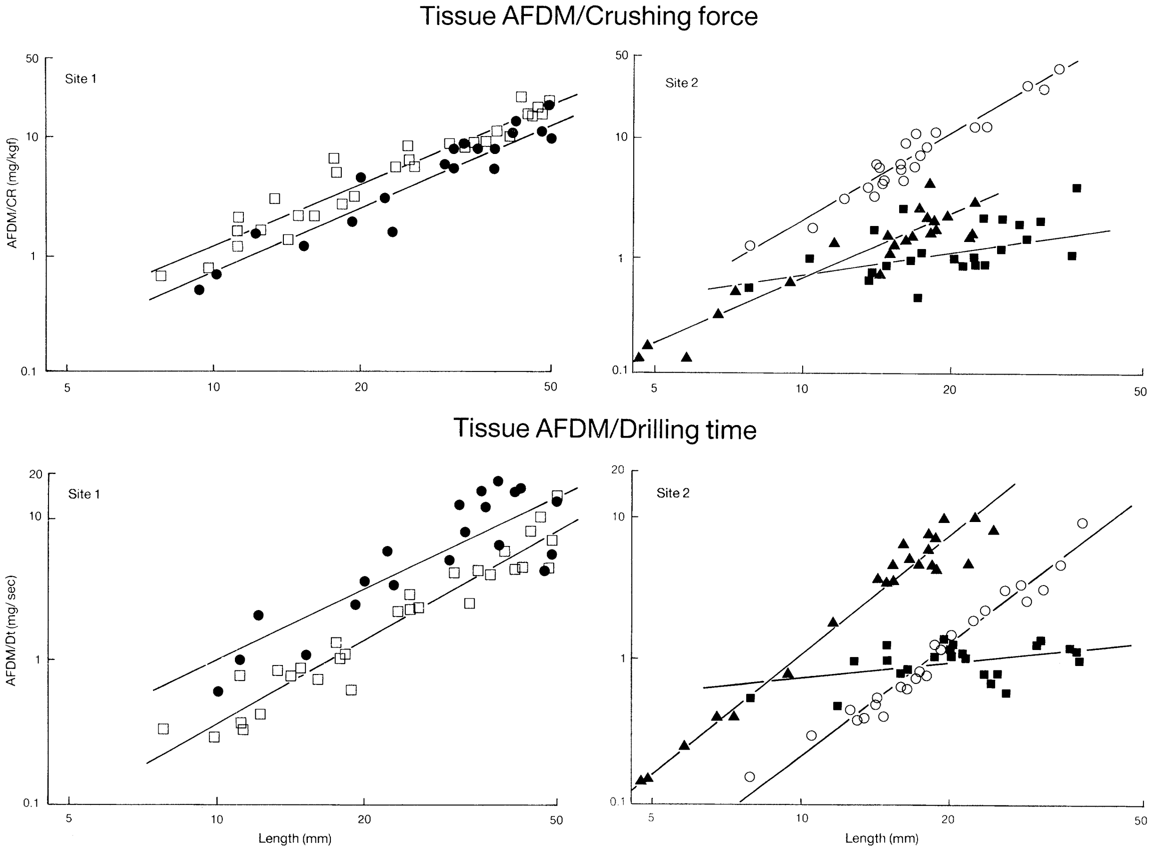

Figure 6. Benefit–cost ratio (AFDM/CR ($\mathrm{mg\,kgf^{-1}}$) and AFDM/DT ($\mathrm{mg\,s^{-1}}$)) plotted against animal length for brachiopods and bivalve molluscs from two sites. Filled symbols denote brachiopods, and open symbols are used for bivalve molluscs; *Mytilus edulis* (open squares), *Lima colorata* (open circles), *Liothyrella neozelanica* (filled circles), *Neothyris lenticularis* (filled squares), *Notosaria nigricans* (filled triangles). Equation parameters are given in Appendix 1 and comparisons of regression line are given in table 3.

Table 3. *Slopes and statistics for comparisons of elevations of regressions relating cost–benefit ratios (AFDM/CR and AFDM/DT) to animal length for potential predators feeding on brachiopods and bivalve molluscs*

(Abbreviations as in table 1. Original data shown in figure 6, full regression parameters in Appendix 1. *L. colorata* and *N. nigricans* had significantly different slopes for the AFDM/CR comparison ($F = 4.79$, 1,42 d.f., $p < 0.05$); however, they were not significantly different for the AFDM/DT comparison ($F = 0.14$, 1,42 d.f., $p = 0.85$). On this basis the difference in intercepts was 1.88 on a logarithmic scale ($= \times 6.55$).)

species	slope	F	d.f.	p	common slope	difference in intercepts
site 1						
AFDM/CR						
L. neozelanica	1.77	0.23	1,46	0.634	1.72	0.414
M. edulis	1.69					
AFDM/DT						
L. neozelanica	1.61	1.50	1,46	0.226	1.82	0.705
M. edulis	1.91					
site 2						
AFDM/CR						
N. lenticularis	0.63	16.22	2,64	0.001	—	—
N. nigricans	1.74					
L. colorata	2.38					
AFDM/DT						
N. lenticularis	0.36	105.73	2,64	0.001	—	—
N. nigricans	2.61					
L. colorata	2.58					

between species seen in figure 4 in terms of tissue AFDM content.

(*b*) *Body volumes and inorganic content*

Other factors which would be expected to affect the value of a given prey item to a predator, in excess of the usual cost–benefit ratio analyses, are how difficult the tissues are to extract (once entry through the shell has been gained) and the presence of any structural inorganic material in the tissues. Plots of tissue AFDM against internal volume show the same results at both sites (figure 7). At site 1 the mollusc *M. edulis* has a much higher organic content per unit internal volume (between the shell valves) than the brachiopod *L. neozelanica*. At site 2 the picture is the same with the mollusc *L. colorata* higher than the brachiopods. These results also show that for tissue AFDM against internal volume the impunctate brachiopod *N. nigricans* is consistently higher than the punctate *N. lenticularis*. The data in figure 7 suggest that there are strong differences in tissue density (that is, organic content per unit volume between the shell valves). Plots of AFDM per unit of internal volume against animal length show that this is the case (figure 8). The bivalve molluscs have much higher tissue densities at both sites than the brachiopods, and the impunctate brachiopod has a higher density than either punctate brachiopod. None of the slopes are significantly different from zero (Appendix 1), showing that the density of tissue between the shell valves does not change with size (age). None of the slopes are significantly different from each other (table 4). At site 1 the difference in intercepts based on a common

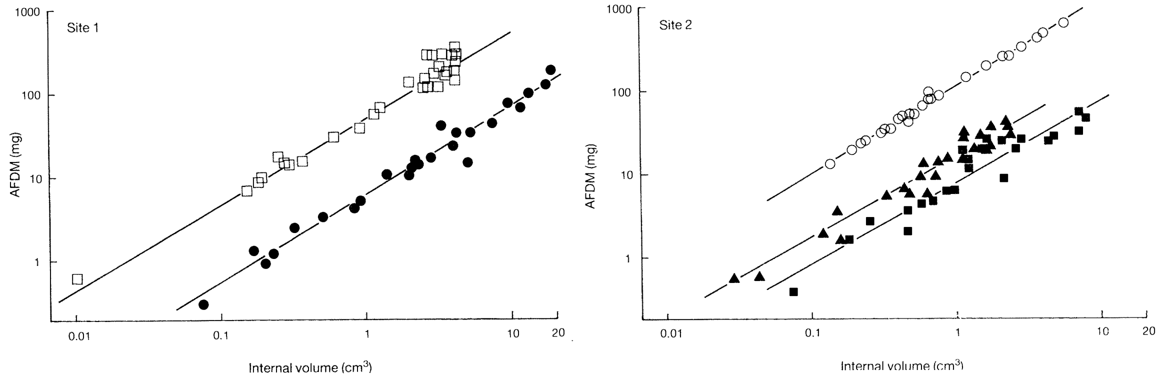

Figure 7. Tissue ash-free dry mass (AFDM (mg)) plotted against the internal volume (volume between the valves (cm^3)) for *M. edulis* and *L. neozelanica* from site 1 and for *L. colorata*, *N. lenticularis* and *N. nigricans* from site 2. Filled symbols denote brachiopods, and open symbols are used for bivalve molluscs; *Mytilus edulis* (open squares), *Lima colorata* (open circles), *Liothyrella neozelanica* (filled circles), *Neothyris lenticularis* (filled squares), *Notosaria nigricans* (filled triangles). Regression parameters in Appendix 1.

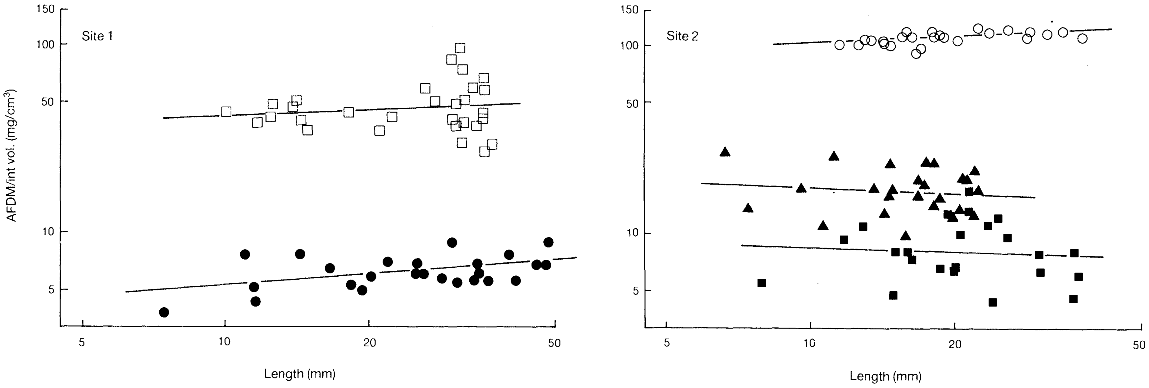

Figure 8. Tissue density as ash-free dry mass per unit internal volume (AFDM/internal volume (mg cm^{-3})) plotted against animal size (length (mm)). Filled symbols denote brachiopods, and open symbols are used for bivalve molluscs; *Mytilus edulis* (open squares), *Lima colorata* (open circles), *Liothyrella neozelanica* (filled circles), *Neothyris lenticularis* (filled squares), *Notosaria nigricans* (filled triangles). Regression parameters are given in Appendix 1; comparisons of regression lines are given in table 4.

slope for tissue density is × 7.2. At site 2 on the same basis the bivalve *L. colorata* is 6.6 times higher than the impunctate *N. nigricans* and has a tissue density which is 14.0 times greater than that of the punctate *N. lenticularis*. The difference between the two types of brachiopod is 2.1 times.

Data on the inorganic (ash) content of the tissues show large differences between brachiopods and bivalve molluscs (table 5). The values for *M. edulis* of 12.8% and 14.5% for *L. colorata* are much lower than the punctate brachiopods which fall in the range 34.5% to 82.3% (minimum and maximum individual values). The impunctate *N. nigricans* falls between these two data sets with a mean of 34.2%. In three of the species the inorganic content of the tissues did not change with animal size, whereas the other two species (*L. neozelanica* and *L. colorata*) showed very small but significant reductions of tissue ash content with increased length (Appendix 1). Despite this, all of the mean values for this measure are significantly different from each other (*F* test and *t*-tests, $p < 0.05$ in all cases). Thus the punctate brachiopods have between 3.3 times and 4.4 times the tissue ash content of the bivalves and 1.4 times to 1.6 times that of the impunctate *N. nigricans*.

Ash content values on a whole animal basis (including the tissues in the caeca in the shell) also show large differences between bivalves and brachiopods (table 5). Values for the brachiopods ranged from 93.9% to 97.5% inorganic, with the results for the impunctate *N. nigricans* lying between those of the punctate species, whereas the values for the bivalves were 85.6% (*M. edulis*) and 68.9% (*L. colorata*). The data for the molluscs were significantly lower than the brachiopods (no overlap of 95% confidence intervals, $p < 0.05$), and were also significantly different from each other ($t = 11.09$, $p < 0.0001$).

Shell dry mass assessments showed that at site 1 *M. edulis* had significantly heavier shells than *L. neozelanica* (10 mm animal, $t = 2.53$, $p < 0.01$; 20 mm animal, $t = 3.67$, $p < 0.01$; 30 mm animal, $t = 2.75$, $p < 0.01$; table 6). At site 2, 10 mm bivalves had heavier shells than the brachiopods (*t*-tests all $p < 0.05$), while in specimens of 20 mm and 30 mm length the brachiopods all had heavier shells (*t*-tests all $p < 0.05$). Differences between sites were consistent, with brachiopods at site 2 having shells which were heavier than those at site 1 by factors of × 1.8 to × 2.8 (*t*-tests, all differences significant at $p = 0.05$), whereas shells of the bivalves at site 2 were × 1.5 to × 1.9 heavier than at site 1 (*t*-tests, all differences significant at $p = 0.001$).

4. DISCUSSION

(*a*) *Costs and benefits*

At site 1 the mollusc *Mytilus edulis* is more resistant to crushing and drilling and contains significantly more organic material for any predator than the brachiopod *Liothyrella neozelanica* (figure 4). The results from site 2 show the same pattern for drilling time and tissue content, but there was no measurable difference between the effort needed to crush the shells of either type of brachiopod or the bivalve mollusc. The overall picture is thus one where bivalves have higher costs for predators feeding on them by factors of 2 to 30, but they also provide returns which are up to 10 times those of the brachiopods. Alexander (1990) used similar methods to those used here to measure the forces needed to crush the shell valves of eight species of articulate brachiopod. The forces needed to fracture shells which he registered ranged from 1.6 kilograms-force (kgf) to 19 kgf for animal sizes which ranged from 15 mm to 42 mm in length. These results and the spread of his data are remarkably similar to those obtained here, even though he was working with dried or alcohol-preserved material, whereas this study was based on fresh material. Alexander (1990) had one impunctate species, *Hemithyris psittacea*, in his study and, as was also the case here, results fell well within the range of those for the punctate species. This shows that the presence or absence of punctae does not have large effects on the strength of a brachiopod shell. Alexander did not show a significant relation between animal size (length) and resistance to breakage, but that was almost certainly due to the small size ranges used for any given species. Major effects on shell

Table 4. *Slopes and statistics for comparisons of elevations of regressions relating tissue density (AFDM/internal volume) and animal length*

(Abbreviations as in table 1; original data shown in figure 7; full regression parameters in Appendix 1. None of the slopes are significantly different from each other ($F = 1.05$, 4,117 d.f., $p = 0.39$).)

species	slope	F	d.f.	p	common slope	difference in intercepts
site 1						
L. neozelanica	0.19	0.27	1,50	0.607	0.15	1.97
M. edulis	0.10					
site 2						
N. lenticularis	−0.07	0.63	2,69	0.535	0.016	0.75 (*N.n.* > *N.l.*) 2.64 (*L.c.* > *N.l.*) 1.89 (*L.c.* > *N.n.*)
N. nigricans	−0.10					
L. colorata	0.13					

strength were increasing biconvexity and increased shell valve thickness.

The amount of material present in a shell certainly affects how resistant it is to attacks from predators, as it should reflect shell thickness. At site 1 the shell of *M. edulis* was heavier than that of the brachiopod *L. neozelanica* (table 6). However, the shells of the bivalve were only × 1.2 to × 1.3 heavier than those of *L. neozelanica*, whereas *M. edulis* was × 3.5 more resistant to crushing and × 10.8 more resistant to drilling than the brachiopod (table 1). At site 2 large brachiopods had heavier shells than the bivalve *L. colorata*, but the situation was reversed in small specimens (table 6). This may be consistent with the results for resistance to crushing, but does not match the data for resistance to drilling, where *L. colorata* was up to 30 times as resistant as *N. lenticularis* or *N. nigricans* (figure 4). This suggests that other factors such as shell composition must have powerful effects on shell physical characteristics.

There were, however, consistent differences between sites for both brachiopods and bivalve molluscs in terms of shell dry mass. Shells at site 2 were × 1.5 to × 2.5 heavier than at site 1 (t-tests, all cases $p < 0.001$). These differences probably reflect the different requirements of living suspended on rock faces (site 1, lighter shells) than sitting on sediments (site 2, heavier shells), and the relative accessibility of

Table 5. *Mean ash contents (ash mass/dry mass as a percentage) of internal tissues and whole animals for brachiopods and bivalve molluscs*

(For the internal tissues comparisons all means are significantly different ($F = 129.8$, 4,123 d.f., $p < 0.001$; t tests between close species: *M. edulis* against *L. colorata* ($t = 2.70$, 48 d.f., $p = 0.009$); *N. lenticularis* against *N. neozelanica* ($t = 3.03$, 41 d.f., $p = 0.004$); *N. lenticularis* against *N. nigricans* ($t = 4.15$, 40 d.f., $p < 0.001$). Some species have ash contents which change with size, for these species slopes (b), F values and significances (p) are quoted (see Appendix 1). Slopes quoted as 0.00 denote values less than 0.005.)

species	mean	s.e.	minimum value	maximum value	b	F	p	n
Internal tissues								
punctate brachiopods								
L. neozelanica	56.2	2.43	35.5	82.4	−0.01	18.6	0.001	25
N. lenticularis	47.3	1.64	34.6	63.0				23
impunctate brachiopod								
N. nigricans	30.2	2.58	19.0	53.1	—	—	—	25
bivalve molluscs								
M. edulis	12.8	0.51	6.1	18.8				30
L. colorata	14.5	0.33	12.1	18.4	−0.00	10.65	0.003	25
Whole animals								
punctate brachiopods								
L. neozelanica	93.9	0.36	89.7	93.8	−0.00	12.87	0.002	25
N. lenticularis	97.5	0.07	96.9	97.7				22
impunctate brachiopod								
N. nigricans	95·5	0.19	92.8	94.9	—	—	—	24
bivalve molluscs								
M. edulis	85.6	0.47	77.0	89.2				30
L. colorata	68.9	1.43	50.5	78.6	−0.01	39.08	0.001	25

Table 6. *Shell dry mass measurements for brachiopods and bivalve molluscs*

(Data are presented for animals of 10 mm, 20 mm and 30 mm length and were generated from regressions of shell dry mass (g) against animal length (mm). Regressions (see Appendix 1) were made on logarithmically transformed data for both variables; n = number of specimens in regression analysis.)

	animal length						
	10 mm		20 mm		30 mm		
species	mean	s.e.	mean	s.e.	mean	s.e.	*n*
site 1							
L. neozelanica	0.056	0.003	0.400	0.012	1.258	0.039	25
M. edulis	0.073	0.006	0.492	0.022	1.495	0.077	30
site 2							
N. lenticularis	0.102	0.008	0.894	0.036	3.185	0.177	23
N. nigricans	0.104	0.014	1.135	0.058	—	—	25
L. colorata	0.138	0.008	0.809	0.021	2.270	0.097	25

the latter site for predators, especially drilling species. However, although the data suggest that animals at site 2 may be slightly more resistant to crushing and drilling than those from site 1, results do overlap and there is no significant difference between them (figure 4).

The estimates of crushing effort required to fracture shells generated in this study should be robust; however, the commonest predatory gastropods (Muricaceans and Naticaceans) use acid secretions from an accessory boring organ to soften shells while drilling through them with the radula (Hughes 1986). This may reduce the actual physical effort required to gain access to tissues, but could increase the amount of time needed to drill through the shell valves. Some thick-shelled prey may take days for naticids to penetrate (Hughes 1985). Clearly, more information is needed to elucidate the characteristics of shells which are important in conferring resistance to crushing and drilling by predators.

In this study the tissue content measurements for the impunctate *N. nigricans* were higher than for the punctate brachiopods by a factor of 2.5. However, it should be noted that this comparison is limited to tissues between the valves, which are available to predators, and excludes caecal contents, which may be as much as 50% of the total animal AFDM of adults of some punctate species (Curry & Ansell 1986; Peck & Holmes 1989; Curry *et al.* 1989), and may possibly be much higher than this in small juvenile individuals (Peck *et al.* 1987*a*). This factor obviously has a major effect on the value of a punctate species to any potential predator.

These results are consistent with the idea that predation pressures are very important to the balance between physical defences and tissue contents in vicinal populations of brachiopods and bivalve molluscs. They are not what would be expected if the brachiopods had evolved potent chemical defences. Chemical defences would be expected to allow animals to contain large amounts of organic matter with relatively light physical defences, as exhibited by some nemerteans and nudibranchs. Brachiopods clearly do not fit this pattern.

(*b*) *Cost–benefit ratios*

Plots of cost to benefit assessments as AFDM against effort (figure 5) are difficult to interpret. This is because at site 1 the data suggest that the brachiopod *L. neozelanica* would be a better prey item than the mollusc *M. edulis* for both crushing and drilling predators. The lower efforts required to gain access to the tissues outweigh the reduced rewards accrued. However, at site 2 the reverse seems to be the case for crushing (durophagous) predators, with the bivalve *L. colorata* giving better rewards than either brachiopod, and no species is clearly better for drilling predators at this site. With the exception of the values for *N. lenticularis*, the slopes of all of these relations are significantly greater than 1 (table 2). This shows that the returns for predators in relation to effort increase with animal size, and large animals in any species should be taken, if possible, in preference to small individuals. Replotting these results as cost–benefit ratios related to animal size (figure 6, table 3) changes some of the conclusions obtained, with the results at site 1 showing *M. edulis* to be a better prey item than *L. neozelanica* for crushing species and the reverse to be the case for drilling predators. At site 2, the mollusc *L. colorata* clearly provides better returns than the brachiopods for crushing species while again there is no species which is obviously better for drilling predators. The slopes for drilling predators feeding on *L. colorata* and *N. lenticularis* are less than unity (table 3), suggesting that rewards for such predators decline with prey size. It is also the case that increased size per se may reduce the potential risk from predators, by taking a given animal out of the size range of prey that certain predators are capable of taking (Connell 1972; Hughes 1980). Peck (1992) has shown that articulate brachiopods are significantly more globose than bivalves from nearby populations. This in itself may pose significant problems for some predators, especially those crushing species with limited distances over which they can bring force to bear. Thus the results of the cost to benefit assessments undertaken here show that the differences between bivalve molluscs and brachiopods on these criteria are small; that

Table 7. *Proximate protein, lipid and carbohydrate contents for the brachiopod* Liothyrella uva *and the bivalve molluscs* Mytilus edulis, Crassostrea virginica, Ostrea gigas *and* Donax vittatus

(Values quoted are percentage dry mass, and energy contents were calculated from figures quoted by Schmidt-Nielsen (1979).)

	tissue dry mass (%)				
species	protein	lipid	carbohydrate	energy content of tissue/(kcal g^{-1})	Reference
bivalve molluscs					
Mytilus edulis	50	10	20	3.93	Pieters *et al.* (1979)
Crassostrea virginica	42	8	26	3.65	Giese (1966)
Ostrea gigas	50	11	11	3.65	Giese (1966)
Donax vittatus	60	9	11	3.89	Ansell (1972)
brachiopod					
Liothyrella uva	43.6	9	4	2.91	Peck *et al.* (1987*b*)

taking animal size into account affects the conclusions obtained; that the data are not consistently in favour of one group compared with the other; and they do not suggest that in terms of energy maximization either bivalves or brachiopods as a group should be favoured.

The amount of organic material available to a predator is a relatively crude indicator of the value of a prey item. Energy contents and energy maximization over time are usually expected to be the important criteria for predators faced with choices between prey (Hughes 1986; Sibley & Calow 1986). On this basis the composition of the organic matter contained between the valves of brachiopods and bivalve molluscs is important, as lipids contain more energy than carbohydrates or proteins. From the limited data available, lipid levels in brachiopod tissues appear to be similar to those in bivalve molluscs, but protein contents may be lower and the carbohydrate levels are much lower (table 7). The energy contents calculated per gram of tissue on the basis of these protein, lipid and carbohydrate levels suggest that brachiopod tissues may have only 75% to 80% of the energy content of bivalve mollusc tissues. If these data are representative of brachiopods as a whole, the cost–benefit ratios would be changed slightly, but the conclusions drawn here would not be significantly altered. However, it should be noted that at present there are only data for one species of brachiopod, and more data are needed on brachiopod tissue composition.

Other factors which alter the value of prey items to predators include the digestibility of the tissues. The tendinous parts of brachiopod muscles are often not digested by animals feeding on them (C. W. Thayer, personal communication). If these tendons form a significant proportion of the AFDM of brachiopod tissues then the returns to predators would again be reduced. All of these factors combined may significantly alter the cost–benefit ratios obtained. They would reduce the value of brachiopods to predators and may provide one reason why predation pressures are light on brachiopod populations. However, data on the digestibility of various brachiopod tissues are not currently available. It is also possible that predators taking the species studied here may have techniques which reduce the costs involved, either by drilling in areas which are softer than those used here in a 'standard comparison', or crushing shells along a different axis from that used in this study. Observations of predator–prey interactions involving brachiopods would clearly be of value.

(*c*) *Body volumes and inorganic contents*

Other factors than cost–benefit ratios also affect the value of a prey item to be eaten, and information affecting foraging costs such as animal distributions, population densities and patchiness would be of value. Handling costs themselves are not merely the effort required to gain access to the tissues, but also include parameters such as time taken and effort needed to consume and digest the tissues obtained (Hughes & Elner 1989). In this context the volume in which the internal tissues are housed is important, as the larger the space to be cleared of tissue, the longer it will take to eat the contents, which may also increase the chances of losing some of the tissue to the surrounding seawater or other predators (Hughes 1986). Tissue densities in the bivalve molluscs are higher than the punctate brachiopods by factors of 7 to 14, whereas that of the impunctate *N. nigricans* is only twice that of the punctate species. These differences are consistent over the whole size range of animals studied and should reduce the relative value of brachiopods to all predators. It will mean drilling predators will have much more difficulty reaching distal tissues than in the bivalves and that crushing predators will be more likely to lose tissue fragments when processing brachiopod prey. This argument also suggests that an impunctate brachiopod should be a better prey item than a punctate one (figures 7 and 8, table 4). Making significant amounts of tissue relatively inaccessible to predators (by placing it in caeca) is clearly of great importance when considering tissue availability to predators.

There have been no detailed reviews of spicule contents of brachiopod tissues, and most authors merely state that they may be densely developed in the tissues of some species (see, for example, Williams

Table 8. *Ash content values, as percentage dry mass, for tissues from a range of marine invertebrates*

(Values for Crustacea and Polychaeta are for whole animals, including exoskeleton. na = data not available.)

species	ash (%)	s.e.	*n*	authority
Porifera				
Antarctic sponges	64.2	12.9	15[a]	Dayton *et al.* (1974)
Spongilla lacustris	58	na	4	Paine (1964)
Brachiopoda				
articulate				
Liothyrella neozelanica	56.2	2.43	25	this study
Neothyris lenticularis	47.3	1.64	23	this study
Liothyrella uva	46–53	na	95[b]	Peck *et al.* (1987)
Terebratulina retusa	46	na	10	Curry & Ansell (1986)
Terebratella inconspicua	19.7	na	12[c]	Curry & Ansell (1986)
Notosaria nigricans	30.2	2.58	27[d]	this study
inarticulate				
Crania anomala	18.6	na	9	Curry & Ansell (1986)
bivalve molluscs				
Lima colorata	14.5	0.33	27	this study
Mytilus edulis	12.8	0.51	30	this study
Mytilus edulis	10–22	na	630	Rodhouse *et al.* (1984)
Ostrea edulis	18–25	na	2662	Rodhouse (1977*b*)
Baltic sea bivalves	18.7	1.1	22[a]	Rumohr *et al.* (1987)
Gastropod molluscs				
Nacella concinna	15.7	—	117[e]	Nolan (1991)
Baltic sea gastropods	16.3	1.0	27[a]	Rumohr *et al.* (1987)
Clione limacina	18.9	na	2	Ikeda (1970)
Crustacea				
Calanus cristatus	35.2	na	5	Ikeda (1970)
Notocrangon antarcticus	27.9	0.63	29	Clarke, personal communication
Eualus gaimardii	23.1	0.20	69	Clarke, personal communication
Chorismus antarcticus	25.7	0.21	113	Clarke, personal communication
Euphausia superba	18.0	0.17	34[f]	Ikeda & Kirkwood (1989)
	17.3	0.27	14[g]	
Baltic sea crustacea	28.3	1.72	35[a]	Rumohr *et al.* (1987)
Polychaeta				
Tomopteris septentrionalis	23.9	na	2	Ikeda (1970)
Baltic sea polychaetes	24.8	1.70	48[a]	Rumohr *et al.* (1987)

[a] Mean value quoted for the number of species quoted, not individuals in a sample.

[b] % ash changed with animal size over the range 46–53%.

[c] *T. inconspicua* has far fewer supporting spicules than the other punctate articulate brachiopods investigated.

[d] *N. nigricans* is impunctate.

[e] Value calculated from equations relating dry mass and ash-free dry mass to animal length for 25 mm animal (mid point of size range).

[f] Value for males.

[g] Value for females.

& Rowell 1965; Rudwick 1970; James *et al.* 1992). Foster (1974), working on Antarctic brachiopods, stated that spiculation of the tissues varied greatly between individuals, populations and species. This is borne out by the data in table 5 for *L. neozelanica*, *N. lenticularis* and *N. nigricans* which are highly variable. It is further enhanced by the data for *Terebratella inconspicua* from Curry & Ansell (1986) which at 19.7% has an inorganic content well within the range of other taxa (table 8). These authors also provided data for the inarticulate *Crania anomala* which was low, at 18.6%, but this might be expected as inarticulate lophophores do not have the spicule supports of the articulates (Williams & Rowell 1965).

Spicules provide mechanical support for the soft tissues, especially the lophophore (Fouke 1986). They may also fulfil a potent antipredator function. When assessing the value of a prey item or palatability of a given tissue to a predator, the spicule or other inorganic content may be very important. This is especially so when the inorganic contents are high, as in the brachiopods studied here. The measurements made in this study show that the punctate species had much higher inorganic contents in the tissues than the impunctate *N. nigricans* and were higher than the bivalve mollusc values by a factor of around 4 (table 5). General comparisons with molluscs, crustacea, polychaetes and sponges (table 8) show that articulate brachiopods may have higher tissue inorganic contents, by factors of 2 to 3, than all those groups except sponges. On this criterion certain brachiopods may appear to some predators to be sponges with shells on.

The inorganic content of whole animals (including shell) of the punctate and impunctate species was the same (table 5). This is also true of whole-animal organic contents (AFDM). However, the organic content of the internal tissues alone (which the assessments of cost–benefit ratios were based on) showed dramatic differences. The differences between these data emphasize the advantages of making large amounts of organic matter inaccessible to predators by placing them in the punctae. The very high whole-animal inorganic content figures of 93.9% to 97.5% of the dry mass for brachiopods found here may also help to explain the results of Thayer & Allmon (1991), who found that there was no significant difference in preference exhibited by the anemone *Entacmea* for whole untreated specimens of the brachiopod *Thecidellina* compared with inert clasts (pebbles or sand).

Clearly, even though there is little difference between brachiopods and bivalve molluscs in terms of cost–benefit ratios for predators, the low organic content of brachiopod tissues in relation to the volume between the valves combined with high inorganic contents because of the presence of spicules will dramatically affect their value and palatability to predators. This will be true for all predatory species, not only the crushing and drilling types studied here. These results may also explain the rejection of some brachiopod tissues by carnivores without invoking chemical defence mechanisms, although it might be expected that chemical defences would be present in some species inhabiting areas of high predation pressure. If proven, the presence of chemical defences in animals with the attributes of brachiopods would clearly be of great interest.

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Appendix 1. *Regression parameters from equations for relations shown in figures 4–8 and tables 5 and 6*

Relations were obtained after logarithmic ($\log_e$) transformation of both variables, except those marked * in the dependent variable column, which were calculated on untransformed data; b = slope, F tests the significance of the slope (H_0: $b = 0$). CR = crushing force (kgf); DT = drilling time (s); LTH = length (mm); AFDM = tissue ash-free dry mass (g); IV = internal volume (cm^3); SDM = shell dry mass (g); tiss%ash = ash content of tissues as a percentage of dry mass; tot%ash = ash content of whole animals (including shell) as a percentage of dry mass.

species	dependent variable	independent variable	b	s.e.	intercept	r^2	n	F	p (<)
L. neozelanica	CR	LTH	1.47	0.16	3.41	0.82	30	85.0	0.001
M. edulis	CR	LTH	1.43	0.09	4.81	0.90	30	265.1	0.001
N. lenticularis	CR	LTH	2.44	0.28	1.68	0.78	25	74.5	0.001
N. nigricans	CR	LTH	1.74	0.13	4.09	0.89	23	174.9	0.001
L. colorata	CR	LTH	0.80	0.14	6.70	0.60	23	31.1	0.001
L. neozelanica	DT	LTH	1.64	0.26	−4.17	0.68	20	38.7	0.001
M. edulis	DT	LTH	1.21	0.10	−0.40	0.84	30	142.7	0.001
N. lenticularis	DT	LTH	2.72	0.15	−5.91	0.94	24	316.0	0.001
N. nigricans	DT	LTH	0.88	0.10	−1.41	0.79	23	77.0	0.001
L. colorata	DT	LTH	0.60	0.10	2.51	0.64	24	39.0	0.001
L. neozelanica	AFDM	LTH	3.25	0.12	−14.78	0.91	25	1283.6	0.001
M. edulis	AFDM	LTH	3.11	0.16	−12.69	0.94	30	402.2	0.001
N. lenticularis	AFDM	LTH	3.08	0.22	−13.08	0.90	24	3351.7	0.001
N. nigricans	AFDM	LTH	3.48	0.18	−14.16	0.94	26	357.9	0.001
L. colorata	AFDM	LTH	3.19	0.06	−11.87	0.99	27	2043.8	0.001
L. neozelanica	AFDM	CR	1.82	0.20	−19.11	0.83	20	85.0	0.001
M. edulis	AFDM	CR	1.98	0.12	−21.30	0.90	30	265.1	0.001
N. lenticularis	AFDM	CR	0.98	0.11	−13.52	0.78	23	74.5	0.001
N. nigricans	AFDM	CR	1.78	0.13	−20.51	0.89	23	174.9	0.001
L. colorata	AFDM	CR	2.36	0.42	−24.13	0.60	23	31.1	0.001
L. neozelanica	AFDM	DR	1.36	0.22	−5.65	0.68	20	38.7	0.001
M. edulis	AFDM	DT	2.15	0.18	−10.20	0.84	30	142.7	0.001
N. lenticularis	AFDM	DR	1.06	0.06	−7.07	0.94	23	316.0	0.001
N. nigricans	AFDM	DT	3.11	0.35	−7.85	0.79	23	77.0	0.001
L. colorata	AFDM	DT	3.39	0.54	−17.04	0.64	24	39.0	0.001
L. neozelanica	AFDM/CR	LTH	1.77	0.16	−18.18	0.87	20	124.3	0.001
M. edulis	AFDM/CR	LTH	1.70	0.09	−17.49	0.93	30	374.4	0.001
N. lenticularis	AFDM/CR	LTH	0.64	0.28	−15.62	0.19	23	5.02	0.036
N. nigricans	AFDM/CR	LTH	1.74	0.13	−18.23	0.89	23	174.4	0.001
L. colorata	AFDM/CR	LTH	2.38	0.15	−18.60	0.93	23	263.2	0.001
L. neozelanica	AFDM/DR	LTH	1.61	0.26	−10.64	0.68	20	37.4	0.001
M. edulis	AFDM/DT	LTH	1.91	0.10	−12.27	0.93	30	354.1	0.001
N. lenticularis	AFDM/DT	LTH	0.36	0.15	−8.02	0.21	23	5.56	0.028
N. nigricans	AFDM/DT	LTH	2.61	0.13	−18.22	0.89	23	174.4	0.001
L. colorata	AFDM/DT	LTH	2.58	0.10	−14.41	0.97	24	721.2	0.001
L. neozelanica	AFDM	IV	1.04	0.04	−5.14	0.97	25	828.7	0.001
M. edulis	AFDM	IV	0.94	0.04	−2.91	0.95	30	540.6	0.001
N. lenticularis	AFDM	IV	0.98	0.07	−4.83	0.91	23	216.3	0.001
N. nigricans	AFDM	IV	0.97	0.05	−4.10	0.95	25	407.8	0.001
L. colorata	AFDM	IV	1.04	0.01	−2.18	0.99	25	6985.3	0.001
L. neozelanica	AFDM/IV	LTH	0.14	0.11	−5.55	0.06	25	1.51	0.232
M. edulis	AFDM/IV	LTH	0.09	0.14	−3.24	0.01	30	0.40	0.532
N. lenticularis	AFDM/IV	LTH	−0.07	0.21	−4.62	0.00	23	0.11	0.740
N. nigricans	AFDM/IV	LTH	−0.11	0.17	−3.79	0.01	25	0.37	0.548
L. colorata	AFDM/IV	LTH	0.13	0.04	−2.59	0.35	25	12.2	0.002
L. neozelanica	SDM	LTH	2.83	0.06	−9.40	0.99	25	2304.7	0.001
M. edulis	SDM	LTH	2.75	0.09	−8.94	0.97	30	863.3	0.001
N. lenticularis	SDM	LTH	3.14	0.11	−9.51	0.98	23	856.9	0.001
N. nigricans	SDM	LTH	3.45	0.13	−10.22	0.97	25	733.3	0.001
L. colorata	SDM	LTH	2.55	0.08	−7.85	0.98	25	1102.2	0.001
L. neozelanica	tiss%ash*	LTH	−0.01	0.00	0.75	0.45	25	18.6	0.001
M. edulis	tiss%ash*	LTH	0.00	0.00	0.11	0.03	30	0.99	0.329
N. lenticularis	tiss%ash*	LTH	0.00	0.00	0.56	0.17	23	4.21	0.053
N. nigricans	tiss%ash*	LTH	−0.00	0.00	0.36	0.00	25	0.01	0.908
L. colorata	tiss%ash*	LTH	−0.00	0.00	0.17	0.32	25	10.65	0.003
L. neozelanica	tot%ash*	LTH	−0.00	0.00	0.96	0.36	25	12.87	0.002
M. edulis	tot%ash*	LTH	0.00	0.00	0.83	0.15	30	4.73	0.038
N. lenticularis	tot%ash*	LTH	0.00	0.00	0.97	0.14	22	3.25	0.087
N. nigricans	tot%ash*	LTH	−0.00	0.00	0.96	0.00	24	0.04	0.840
L. colorata	tot%ash*	LTH	−0.01	0.00	0.85	0.63	25	39.08	0.001