

Variations in the Shell-Flesh Relationships of *Mytilus*: The Value of Sea Mussels as Items of Prey

BY

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(1 Text figure)

OVER THE PAST DECADE or so there has been a growing interest in the different strategies adopted by predators in their search for food. An optimal foraging strategy represents the combination of those factors associated with maximising an organism's energy intake relative to the time and effort involved in acquiring food (*e.g.*, EMLEN, 1968; SCHOENER, 1971; CHARNOV, 1976; PYKE, PULLIAM & CHARNOV, 1977). A predator expends energy searching for and handling suitable items of prey and this must therefore be set against the amount of energy eventually yielded by the prey item. Predators feeding mainly on relatively sedentary species such as bivalves will generally select their prey on the basis of its size and availability (*e.g.*, ELNER & HUGHES, 1978; O'CONNOR & BROWN, 1977). *Mytilus*, however, which constitutes a major food resource for several contrasted predators (*e.g.*, sea-stars,

gastropods, crabs, birds) possesses a strong protective shell the size and strength of which will be a major factor in determining a predator's handling time. For practical reasons it is assumed that shell strength is proportional to shell weight (at least for mussels of similar size and shape) and the latter is known to vary not only from one locality to another but also with respect to tidal level (Table 1). Furthermore, the size and strength of the adductor muscle is also known to vary significantly even amongst mussels of comparable shell length (HANCOCK, 1965). This short communication considers the relationships between shell and flesh weights in *Mytilus* populations experiencing different degrees of aerial exposure and briefly comments on the possible importance of such considerations to studies of foraging behaviour in those predators that are known to feed extensively on sea mussels.

Table 1

Variations in Shell Weight in *Mytilus edulis*

Shell Length (cm)	Shell weight (g)					
	ⁱ High shore Filey Brigg	ⁱ Low shore Filey Brigg	ⁱⁱⁱ High shore Filey Bay	^{iv} Low shore Filey Bay	^v High shore Robin Hood's Bay	^{vi} Low shore Whitby Harbour
1.50	0.20	0.16	0.25	0.21	0.21	0.19
2.50	0.98	0.83	1.30	0.85	1.09	0.85
3.50	3.45	2.57	4.49	2.31	—	2.73
4.50	—	—	7.93	5.01	—	5.81
5.50	—	—	11.45	7.87	—	10.71
6.50	—	—	—	—	—	18.80
n	432	373	490	360	71	102

Filey Brigg and Robin Hood's Bay are high energy, waveswept shores.

Filey Bay and Whitby Harbour are low energy, protected shores.

All sites situated on the North Sea coast of N.E. England.

RAO (1953) demonstrated that shell weight in both *Mytilus edulis* Linnaeus, 1758 and *M. californianus* Conrad, 1837 decreased as exposure to air increased, the heaviest shells for any given flesh weight occurring amongst permanently submerged mussels. He attributed this relationship to the propensity of mussels for extracting calcium from seawater — thus the longer a mussel remained exposed to seawater the heavier its shell became. RAO (1953a) also noted an apparently similar phenomenon (though with somewhat different causes) in relation to high and low latitudinal mussel populations. FOX & COE (1943), however, found that *M. californianus* from the higher intertidal zone had thicker (and therefore presumably heavier) shells than conspecifics of similar length further down the shore, an observation which was subsequently corroborated by KOPP (1979) for *M. californianus* and by BAIRD & DRINNAN (1957) for *M. edulis*. Fast growing subtidal populations, by contrast, tend to have relatively thin rather brittle shells. BAIRD & DRINNAN (*op. cit.*) explained their findings in terms of requirements for basal metabolism. When mussels are exposed to air, basal metabolism reduces flesh weight at a greater rate than chemical erosion reduces the shell. Higher intertidal mussels will therefore have higher shell-flesh ratios than those from the lower intertidal zone. More recently, SEED (1973) obtained similar results for *M. edulis* from several contrasted localities. When mussels of similar shell length (though of differing age since growth rates also vary widely with intertidal height) were compared, those from the high shore had consistently heavier shell weights than those from the low shore (see also KOPP (1979) for *M. californianus*). Moreover, shell-flesh ratios generally increased with increasing shell length suggesting that as mussels age, their shells account for a progressively greater proportion of their total body weight. Figure 1 illustrates the relationship between shell and tissue weights as functions of intertidal height in mussels from 2 contrasted rocky shores on the NE coast of England. Mussels from the high shore consistently had heavier (=stronger) shells for any given weight of tissue than those from the low shore.

Although previous explanations for the observed differences in shell-flesh relationships amongst vertically separated mussel populations appear to have been sought in physiological terms, other possibly equally important factors such as longevity and population stability¹ ought perhaps also be considered. Stability and longevity in rocky shore mussel populations are known to increase

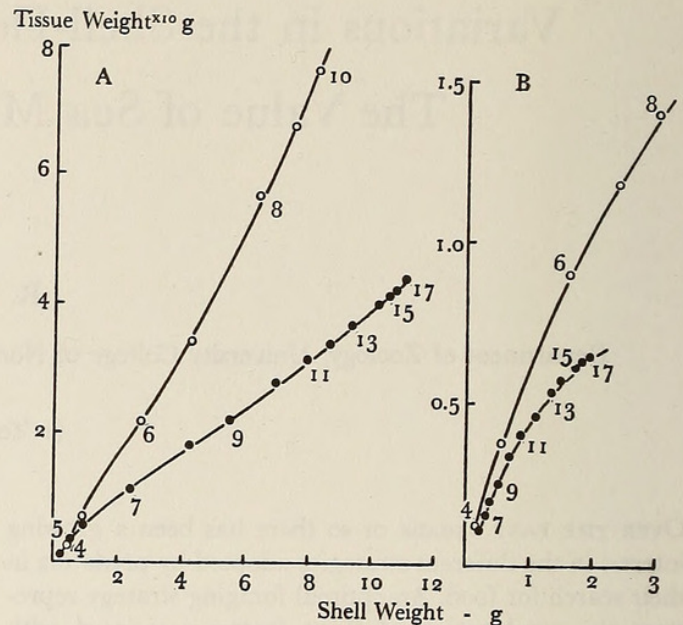


Figure 1

The relationship between shell and tissue weights as functions of intertidal height in mussels of known age and size from (A) Filey Bay — a comparatively low energy shore and (B) Filey Brigg — a severely wave exposed high energy shore. Solid symbols represent high shore populations; open symbols, low shore populations. Numbers indicate the estimated age of mussels of known size

progressively with increasing intertidal height (SEED, 1976; see also LEWIS, 1972). In the low shore, heavy settlement and rapid growth are generally accompanied by exceedingly intense predation resulting in a rapid turnover of mussels and wide oscillations in population density. By contrast, the higher intertidal area provides a spatial refuge largely free of mussel predators and although recruitment and growth are here substantially reduced, enhanced longevity confers considerable long term population stability. High shore populations are therefore frequently characterised by relatively high proportions of old, slow-growing mussels with typically high shell-flesh ratios. It is by no means unusual for many of these upper shore populations to consist of 20 or more year classes even though the largest mussels in such populations may measure only 2–3 cm in shell length (SEED, 1969).

On certain shores, however, mussels can also attain substantial immunity from predation by way of large body size, thereby surpassing the ability of any single predator to consume them (PAINE, 1976). This will be partly determined by local predation pressure but it will also be considerably enhanced in habitats which are optimal for

¹ I use the term 'stability' to denote the absence of any marked temporal change in population structure

mussel growth, *e. g.*, the low shore and subtidal regions. Size-limited predation may conceivably be more characteristic of *Mytilus californianus* populations since this species appears to be rather less attractive than *M. edulis* to certain predators, probably by virtue of its strong, heavily ribbed shell and its ability to grow to a much larger body size (HARGER, 1972). However, low shore populations of unusually large and sometimes apparently very old *M. edulis* are occasionally encountered, more especially in habitats sheltered from wave action where local growth rates may be substantially improved. Although these large bodied, apparently predator-free mussels will increase the stability and structural diversity of such populations thereby enabling both predator and prey to coexist in close proximity, their presence will also substantially alter the microenvironment available to newly recruited mussels. Small mussels which settle in amongst these larger individuals will experience severe intraspecific competition for food and their growth rates can therefore be greatly reduced (*e. g.*, SEED, 1969). At the same time, however, the matrix of large mussels will offer substantial protection from predators and many of these populations could therefore exhibit many of the characteristic features more generally associated with high shore mussel populations (*i. e.*, greater stability, enhanced longevity, and high shell-flesh ratios). Consideration of the structure and relative stability of mussel populations can therefore go some way towards explaining the apparently contradictory literature regarding shell-flesh relationships in mussels collected from different local habitats. It may therefore be relevant to note that the subtidal mussels (*M. edulis*) studied by RAO (1953) came from the underside of floats, a habitat in which mussels may be substantially protected against predation. More recently, size-limited predation has been demonstrated in subtidal *Modiolus modiolus* (Linnaeus) (SEED & BROWN, 1978) and these populations too exhibit considerable long term stability.

From this brief account it will perhaps be appreciated that sea mussels vary considerably in their shell-flesh characteristics according to the very local nature of both the physical and biological environment. Accordingly, the amount of time a predator might spend handling mussels of comparable size but different shell strength could vary within quite broad limits as indeed could the eventual food value yielded by such mussels. Furthermore, many of the common predators of sea mussels forage over relatively wide areas whilst some also exhibit regular tidal

and seasonal migrations. Since an extremely wide range of mussel types could therefore be encountered by these foraging predators, rigorous investigations of the size structure and shell-flesh characteristics of locally occurring mussel populations will clearly be fundamental to any proper understanding of the foraging behaviour of those predators known to utilise mussels as a major food resource.

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