OBSERVATIONS ON THE ADAPTIVE SIGNIFICANCE OF SHELL SHAPE AND BODY FORM IN DOGWHELKS (*NUCELLA LAPILLUS* (L.)) FROM N. WALES.

R. SEED

INTRODUCTION

Dogwhelks belonging to the gastropod family Thaisidae are important predators of barnacles and mussels on rocky shores throughout the world. Many species are exceedingly variable in their shell shape and body form e.g. *Nucella lapillus* (L.) from the Atlantic coasts (Moore 1936, Crothers 1975, Kitching 1977), various species of *Thais* from the N.W. Pacific (Spight 1973, Kitching 1976), *Dicathais* from Australia (Phillips, Campbell and Wilson 1973) and *Lepsiella* from New Zealand (Kitching and Lockwood 1974). Much of this recorded variation is considered to have survival value.

Whereas many marine organisms possess an effective dispersal phase dogwhelks emerge directly as juvenile stages from horny egg-capsules laid in crevices in the mid-low shore. The absence of a pelagic larval stage in their life history together with a general lack of any marked migratory behaviour enables dogwhelk populations to evolve quite independently in response to local selective pressures. In this paper the variability in shell shape and body form of *Nucella lapillus* from several shores in Wales will be examined and the possible adaptive advantages of such variability considered with respect to two potentially important selective forces — wave action and predation.

ABUNDANCE AND POPULATION STRUCTURE

Nucella populations on two quite dissimilar shores in N. Wales were studied in some detail during July 1977. Cable Bay on the W. coast of Anglesey is a very exposed wave-swept shore. It is relatively steep and supports dense populations of barnacles on which *Nucella* (density $101 \pm 52/m^2$) feeds. Small mussels are also present but these are restricted to cracks and crevices in the rock surface. Severe wave action and absence of refuge sites makes this type of shore extremely unsuitable for crabs and predation pressure from this source is probably minimal: no crabs were found at this site despite several prolonged searches. The shore at Menai Bridge, on the other hand, is sheltered from direct wave action and is dominated by a variety of macroalgae. The latter, together with the many loose stones and rocks, provide an ideal refuge for various species of crabs, notable *Carcinus maenas* (L.) and *Cancer pagurus L.* which are here present at high densities (25 ± 5/standard 10 min search). Barnacles occur on the steeper rocky outcrops and on the bridge supports but mussels are absent. Although *Nucella* is considerably less abundant at this site ($29 \pm 16/m^2$) those which do occur are here noticeably larger than at Cable Bay.

All observable dogwhelks in replicated $0.5m^2$ quadrats thrown at random in the mid-low shore were collected at these two sites. Shell height (Fig. 1) was measured to the nearest 0.1mm using sliding vernier calipers. Figure 2 shows the percentage size frequency distributions of *Nucella* from the two shores. In shelter small dogwhelks were uncommon and the population here consisted mainly of large individuals (>2.60cm in shell height) many of which were relatively thick-lipped with pronounced "teeth" immediately

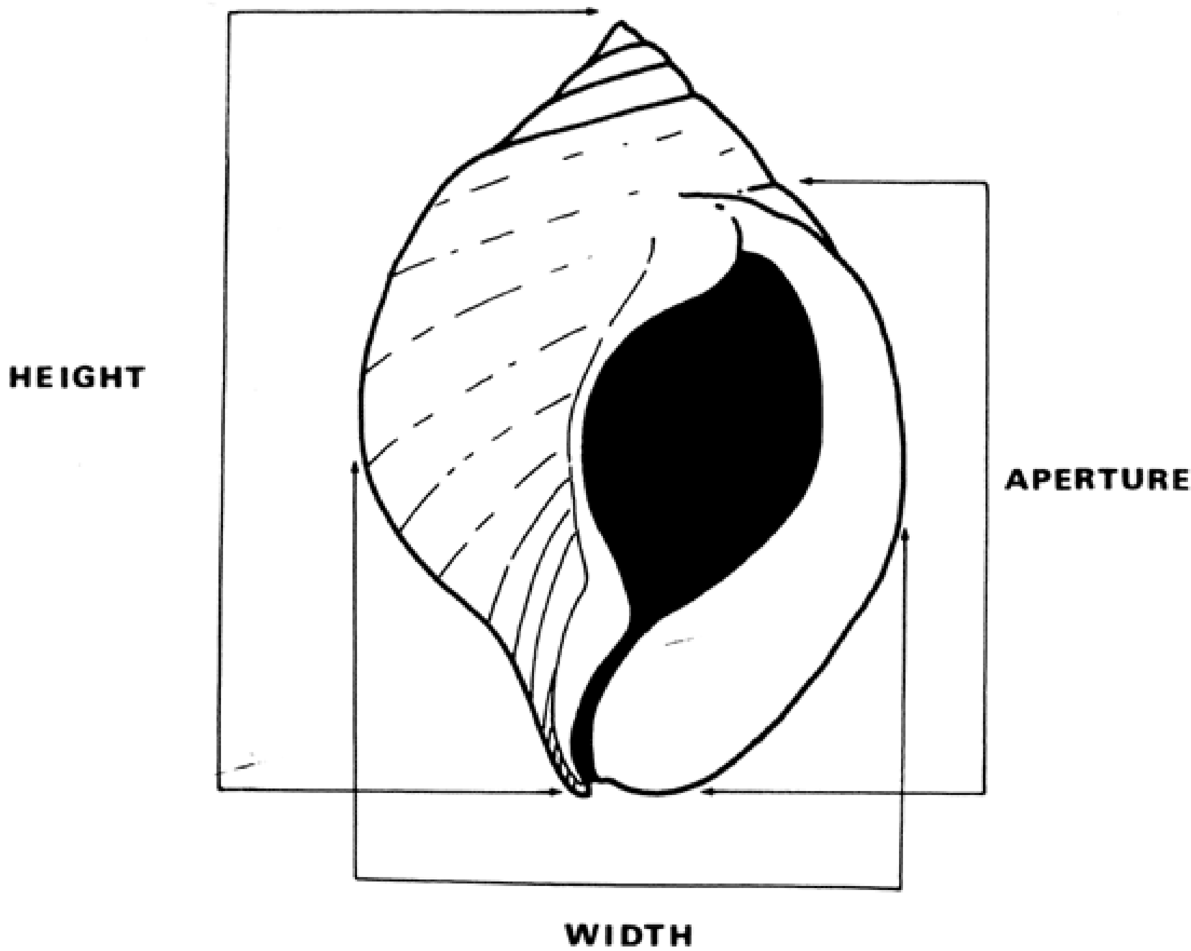

Fig. 1
Parameters of the dogwhelk shell measured in this investigation.

inside the shell aperture (for details of these "teeth" see Cowell and Crothers 1970, Crothers 1971). The Cable Bay population, on the other hand, consisted mainly of dogwhelks in the smaller and medium-size classes whilst individuals over 2.50cm in shell height were comparatively rare.

SHELL SHAPE

Samples of the *largest* occurring *Nucella* (n = 30) were collected at random at Cable Bay and Menai Bridge and additionally from several other rocky shores of comparable exposure. The height, width and aperture of each shell was measured (Fig. 1) and the height/aperture (H/A) and height/width (H/W) ratios calculated. These data, which are summarised in Table 1 indicate quite clearly that the findings for the Cable Bay and Menai Bridge populations are not inconsistent with the results obtained for other populations from shores of comparable exposure. Frequency distributions of the H/A and H/W ratios for each of the eight populations studied are illustrated in Figure 3. The lower values obtained for the exposed shore populations indicate that *Nucella* from these habitats have shorter, squatter (=wider) shells with somewhat larger apertures than those from shelter. It could perhaps be argued that these differences in shell proportions might be due to size effects since the dogwhelks from shelter were consistently larger than those from the more wave-swept sites. This explanation, however,

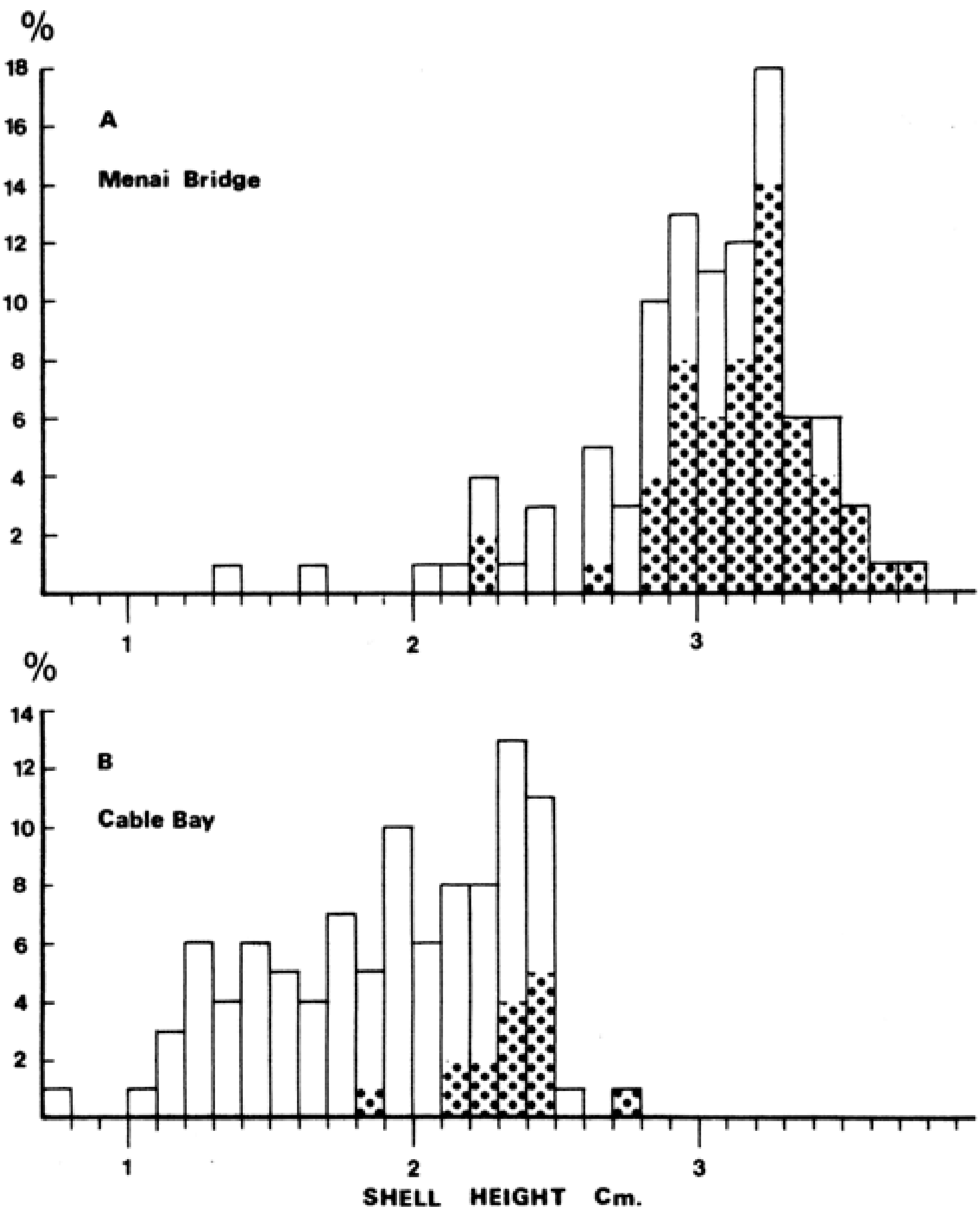

Fig. 2
Percentage size frequency distributions of *Nucella* from (A) Menai Bridge and (B) Cable Bay, Anglesey. Stippled areas indicate shells which are thick and dentate.

seems most unlikely as Table 2 demonstrates: *Nucella* from Cable Bay showed no significant or systematic change in shell proportions across the three selected size categories although small dogwhelks were noticeably thinner and more highly sculptured. Coefficients of variation (standard deviations expressed as percentages of the mean values) further indicate that the variability within this population is extremely low and does not change significantly with increasing shell height. Berry and Crothers (1968), on the other hand, found that in Pembrokeshire young dogwhelks from exposed sites (though not from shelter) were much more variable than older individuals implying that some degree of wave-induced selection probably does occur. However, they later showed (Berry and Crothers, 1970) that Somerset populations exhibited very little decrease in variability with age except at the most wave-swept sites.

TABLE 1 *Shell characteristics of Nucella from several rocky shores in Wales.*

	N	Height (cm)	Width (cm)	Aperture (cm)	Height / Width	Height / Aperture	% with "teeth"	Shell wt (g)
Exposed shores: (exposure rating = 2)[1]								
1. Cable Bay	30	2.31	1.63	1.80	1.42	1.28	15	2.75
2. Trearddur Bay	30	2.38	1.68	1.90	1.42	1.25	87	3.31
3. Llanddwyn Is.	30	2.40	1.66	1.83	1.45	1.31	53	2.93
4. West Dale Bay	30	2.66	1.81	2.09	1.47	1.27	92	4.50
Sheltered shores: (exposure rating = 7)[1]								
5. Menai Bridge	30	3.22	1.92	2.10	1.67	1.54	58	5.77
6. Plas Newydd	30	3.10	1.89	2.12	1.66	1.48	79	5.80
7. Caernarfon	30	3.14	1.92	2.12	1.64	1.48	43	4.76
8. Beaumaris	30	2.96	1.78	1.90	1.66	1.56	30	3.56

[1] Ballantine (1961)

Sites 1-3 are located on Anglesey, sites 5-8 in the Menai Straits, site 4 in Pembrokeshire

TABLE 2 *Relationship between shell shape and size in Nucella from Cable Bay, Anglesey.*

Height (cm) Range	Height (cm) Mean	Width (cm)	Aperture (cm)	Height / Width	Height / Aperture	n
1.20-1.69	1.41	0.99	1.12	1.43 (4.41)[1]	1.26 (3.97)	20
1.70-2.19	1.96	1.39	1.57	1.41 (3.40)	1.25 (3.28)	20
>2.20	2.40	1.71	1.88	1.41 (3.69)	1.28 (3.59)	20

[1] Coefficient of variation (Standard deviation expressed as a percentage of the mean)

BODY FORM AND OTHER VITAL STATISTICS

Samples of *Nucella* (n=30) of *varying* shell heights were also collected from Cable Bay and Menai Bridge. Although the size distributions of *Nucella* in these populations are quite dissimilar (Fig. 2) individuals of comparable shell height were deliberately selected wherever this proved practicable. Each dogwhelk was numbered for reference and its shell height measured. It was then allowed to become attached in a clear perspex aquarium, the outline of the foot of the crawling snail was traced and its area estimated. The shell was then cleaned and dried and a loop of strong thread attached using a spot of quick drying cement. It was then allowed to reattach in a finger bowl of fresh seawater and the force required to detach it recorded using a spring balance. After the cement was removed the dogwhelk was blotted dry and weighed on a top loading balance to the nearest 0.01g. The shell was then boiled in 10% KOH for 1 hr. in order to

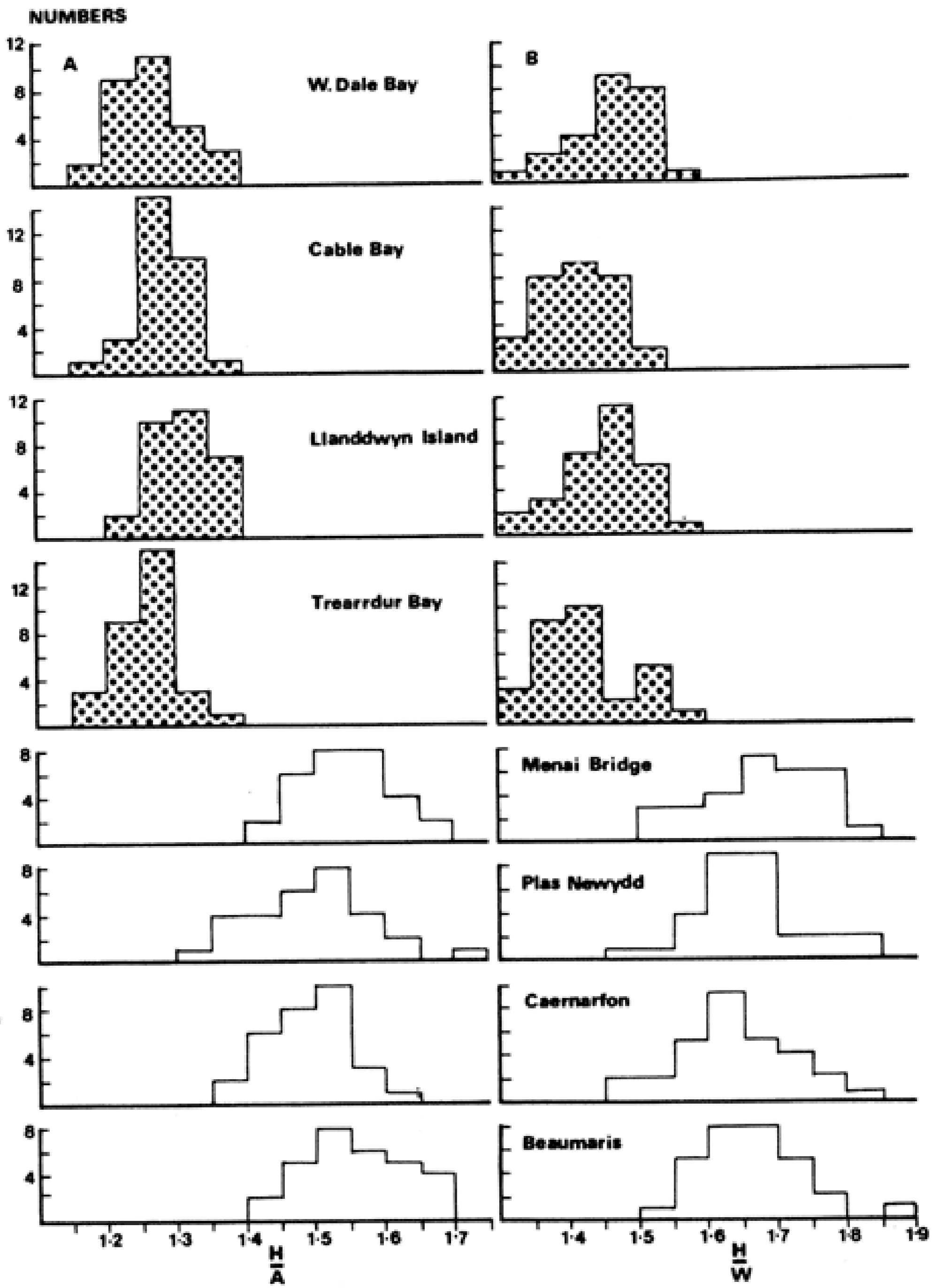

Fig. 3
Frequency distributions of (A) the height/aperture ratio and (B) the height/width ratio for several exposed (stippled) and sheltered *Nucella* populations.

remove the flesh and the empty shell reweighed. Wet tissue weight was estimated as the difference between these two weighings. Finally the shell was evacuated under water to remove all air bubbles and the shell carefully reweighed full of water. Shell volume (=capacity) was calculated as the difference between the weight of the empty shell and the weight of the shell full of water.

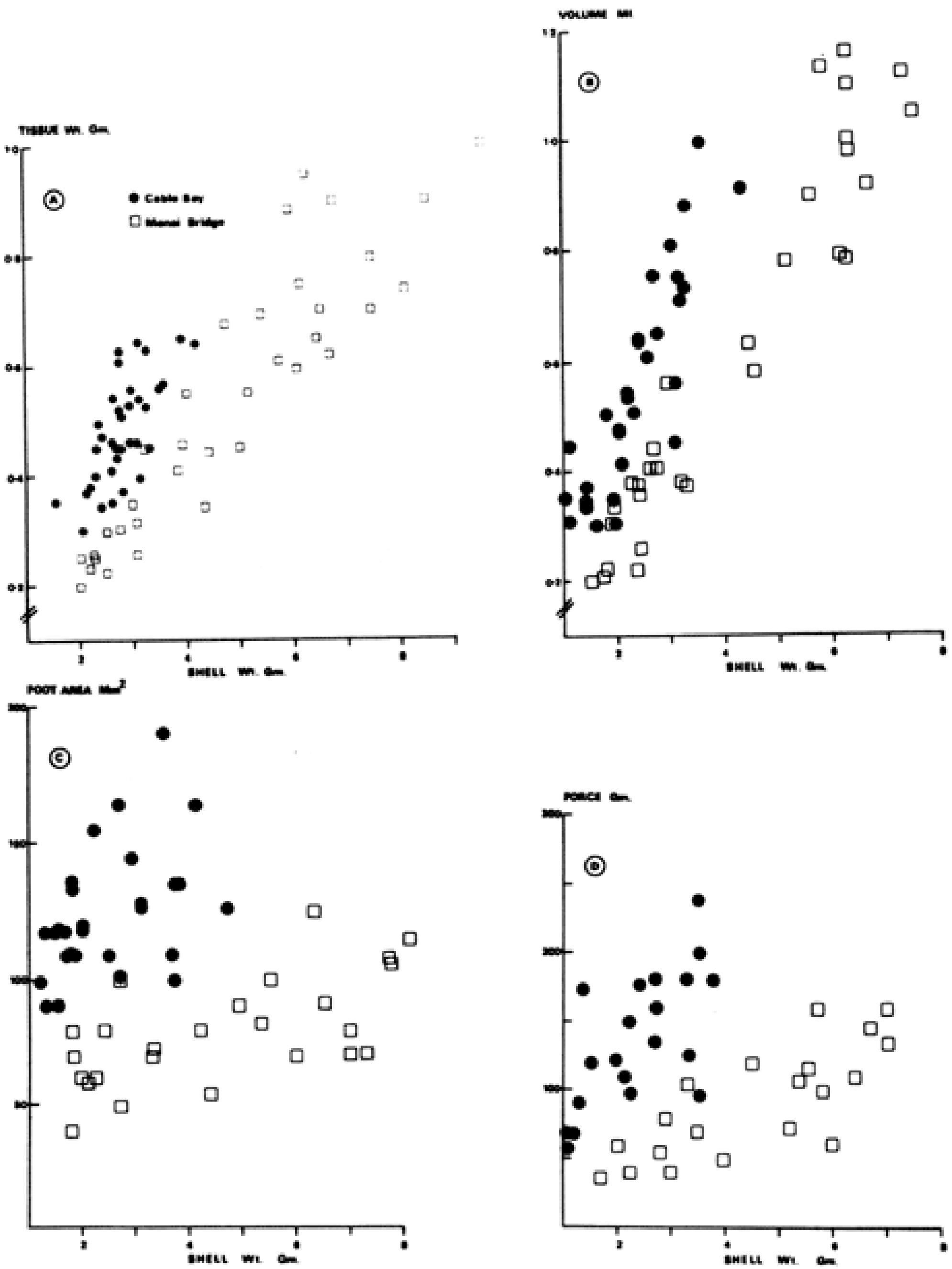

Fig. 4
Plots of (A) tissue weight (B) internal shell volume (C) foot area and (D) force required to detach the shell as functions of shell weight in the Cable Bay and Menai Bridge *Nucella* populations.

For animals of *comparable shell weight*, tissue weight, shell volume and foot area were consistently greater amongst *Nucella* from Cable Bay (Fig. 4a-c) despite the fact that those dogwhelks were somewhat smaller in terms of shell height than those of similar shell weight from Menai Bridge (Fig. 5). It should be remembered, however, that dogwhelks from the exposed shore had relatively wider shells than their conspecifics from shelter as demonstrated by their lower H/W ratios (Table 1). Associated with their greater internal volume and foot area *Nucella* from Cable Bay also appear to have rather greater powers of adhesion (Fig. 4d). These results are broadly in

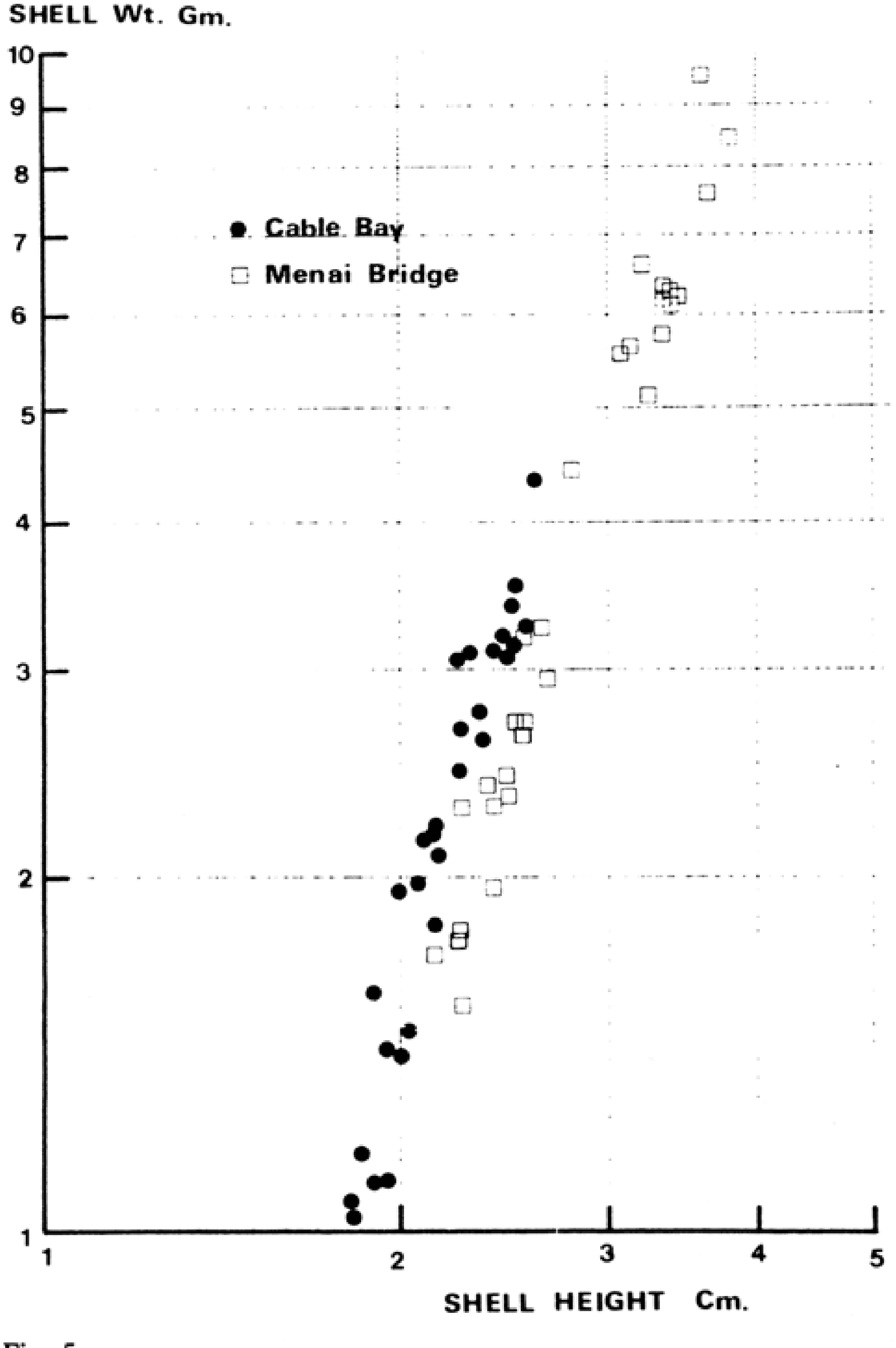

Fig. 5
Logarithmic plots of shell weight as a function of shell height in the Cable Bay and Menai Bridge *Nucella* populations.

agreement with those previously found by Kitching, Muntz and Ebling (1966) for *Nucella* from Lough Ine in S. W. Ireland.

VULNERABILITY TO CRAB PREDATION

In the first of two laboratory experiments, crabs collected from the shore at Menai Bridge were given a choice of *Nucella* of three different size ranges — small (1.0-1.4cm in shell height) medium (1.5-1.9cm) and large 2.0cm).

TABLE 3 *Feeding behaviour of crabs on Nucella of different size from Cable Bay.*

	Size groups of *Nucella* offered (cm) Small 1.0-1.4	Medium 1.5-1.9	Large >2.0 (thin)[1]	>2.0 (thick)[1]
i *Carcinus* (55, 51, 47, 51)[2]				
No. *Nucella* offered	5	5	5	5
No. smashed	4	0	0	0
No. with damaged or missing operculae	1	5	3	1
ii *Carcinus* (64, 66)[2]				
No. *Nucella* offered	5	-	5	5
No. smashed	5	-	3	0
No. with damaged or missing operculae	0	-	1	2
iii *Carcinus* (58, 61)[2]				
No. *Nucella* offered	5	-	5	5
No. smashed	5	-	2	0
No. with damaged or missing operculae	0	-	2	1
iv *Cancer* (60, 78, 113)[2]				
No. *Nucella* offered	5	-	5	5
No. smashed	2	-	2	0
No. with damaged or missing operculae	0	-	0	2

1 Thin or thick lipped *Nucella*
2 Carapace width of crabs (mm)

Duration of experiment — 3 days

Since many of the larger (=older?) dogwhelks had thicker shells with dentate apertures the largest size class was further subdivided into thick and thin-lipped types. After three days the number of *Nucella* which had been either cracked open or had badly damaged or missing operculae were recorded. Since one of the functions of the gastropod operculum is to resist desiccation (Gibson, 1970) those individuals with damaged operculae would almost certainly perish under natural conditions. The results, presented in Table 3, show that virtually all of the small and medium-sized *Nucella* (88%) as well as many of the large thin-lipped individuals (55%) had some

TABLE 4 *Feeding behaviour of crabs on Nucella: wide mouthed versus narrow mouthed Nucella.*

	Origin of the *Nucella* offered[1] Cable Bay	Menai Bridge
i *Carcinus*		
(55, 54, 45, 47)[2]		
No. *Nucella* offered	5	5
No. smashed	0	0
No. with damaged or missing operculae	3	0
ii *Carcinus*		
(52, 62)[2]		
No. *Nucella* offered	5	5
No. smashed	1	1
No. with damaged or missing operculae	3	0
iii *Carcinus*		
(55, 61)[2]		
No. *Nucella* offered	5	5
No. smashed	1	1
No. with damaged or missing operculae	1	0
iv *Carcinus*		
(66, 63)[2]		
No. *Nucella* offered	5	5
No. smashed	1	0
No. with damaged or missing operculae	2	0

1 All *Nucella* used in this experiment were 2.0-2.5 cm in height
2 Carapace width of crabs (mm)
Duration of experiment — 3 days

form of damage. By contrast, none of the large thick-lipped group had been broken although several (30%) did show evidence of opercular damage.

In the second experiment crabs were given a choice of *Nucella* from Cable Bay and Menai Bridge. All the animals chosen for this particular experiment were of similar shell height (2.0-2.5cm) and, as far as could be ascertained, of similar shell thickness. The results, summarised in Table 4, indicate that the wide mouthed form from exposure was far more susceptible to crab predation than the more slender dogwhelks from shelter with their comparatively narrow shell apertures: of the 20 *Nucella* from Cable Bay which were offered at the outset of the experiment 12 (60%) had been damaged in some way after three days compared with only 2 (10%) of those from Menai Bridge.

All of the above experiments were carried out at exactly the same time under identical conditions in laboratory aquaria supplied with running seawater.

DISCUSSION

In sheltered localities like the Menai Straits various species of crabs are abundant both intertidally and subtidally and predation from this source is probably intense. This is almost certainly an important factor contributing to the considerably reduced densities of *Nucella* on such shores though other factors such as food supply are also probably implicated. Small, more easily predated dogwhelks in particular are uncommon in shelter and the population here consists mainly of large *Nucella* which have probably grown too large to be eaten by their predators. Having 'escaped' predation by virtue of their size these large dogwhelks then probably enjoy a considerably enhanced longevity.

Apart from their generally smaller size and higher population densities *Nucella* from wave beaten shores also have comparatively wider shells with larger apertures than those from shelter. In addition they have a greater internal volume and foot area associated with which is their increased powers of adhesion, clearly an advantage in habitats experiencing considerable surf action. Dogwhelks with large apertures are, however, much more easily predated by crabs and on sheltered shores, where crab predation is more severe, *Nucella* restricts the size of the shell opening for protection. Differences of opinion have been expressed concerning the relationship between shell thickness and habitat in *Nucella*. In Pembrokeshire, Crothers (1973) showed that the short squat forms from exposed shores were thicker shelled than the taller shells from shelter, apparently quite the opposite situation to that previously described by Kitching *et al* (1966) for dogwhelks from S. W. Ireland. Kitching's conclusions concerning shell thickness, however, were based largely on the relationship between shell weight and internal capacity but in view of the marked differences in shape between the Cable Bay and Menai Bridge populations no such inference could be made in the present investigation. Data presented in Table 1 strongly suggest that thickness is probably not related directly to wave action since thick shelled dentate *Nucella* were approximately equally distributed on both types of shore. This variability from one shore to another suggests that shell thickness is probably more a function of a combination of factors such as age, local feeding conditions and the degree of abrasion rather than to any direct effect of wave action. Nevertheless, a thick shell especially when associated with pronounced tooth development, does probably serve as an effective antipredator device (see also Vermeij 1976).

Whilst short squat shells can be shown to be adapted to exposed conditions Crothers (1973) argues that no one has yet demonstrated any selective advantage associated with tall narrow shells. He suggests that the presence of an elongated spire may make such forms less acceptable to gulls which frequently swallow gastropods whole whilst the smaller apertures of these dogwhelks *may* discourage crabs. He also argues that the increased surface/volume ratio of these shells may be an advantage in the muddier conditions which frequently prevail in more sheltered habitats. However, two further possibilities ought perhaps to be considered. Firstly the development of a tall, relatively narrow, many-whorled shell may be the most efficient (possibly the only) way in which a shell with a restricted aperture (and thus a restricted growing edge) can increase its body size, i.e. this particular shape may simply accrue directly as a response to restricting the size of the aperture as an antipredator device and it is conceivable that these tall narrow shells do not in themselves have any particular adaptive significance. In shelter, however, they may be at no selective disadvantage though in more exposed localities they would probably be readily dislodged. Little is known concerning the relative abilities of the two shell forms in withstanding the mechanical stresses of wave action.

Secondly, although exposed shore dogwhelks can accommodate a relatively greater volume of tissue than shells of similar size from shelter, much of this weight is taken up by the foot and it is possible that the taller narrower shells more typical of sheltered habitats can in fact house a greater volume of digestive and reproductive tissue thereby enabling them not only to grow faster but also to produce relatively more offspring than their conspecifics from exposure.

Although chromosomal differences have been described in populations of *Nucella* (Staiger 1957, Bantock and Cockayne 1975) other workers (e.g. Moore 1936, Spight 1973, Phillips *et al.* 1973) believe that habitat-specific shapes are probably phenotypic. Thus although shell shape and body form in *Nucella* does appear to be highly adaptive, the precise sources of this variation, whether genetic or environmental, are at present far from completely understood.

SUMMARY

1. *Nucella* is much less abundant in habitats sheltered from wave action and populations here consist mostly of larger (older?) individuals. The scarcity of smaller dogwhelks in such habitats is probably attributable to intense crab predation.

2. *Nucella* from exposed shores have shorter broader shells with larger apertures than those from shelter. The relatively greater internal capacity and foot area further endows these dogwhelks with improved powers of adhesion — clearly an advantage in wave-swept conditions. In shelter, *Nucella* restricts the size of its shell aperture as an antipredator device and develops a taller narrower shell with more body whorls.

3. Field observations and laboratory experiments strongly suggest that habitat-specific differences in the shape and body form of *Nucella* are adaptive though at present it is still largely uncertain as to precisely what extent such differences are genetically or environmentally controlled.

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Department of Zoology, University College of North Wales, Bangor, Gwynedd.