Shell size divergence in *Littorina mariae* and *L. obtusata* and predation by crabs

T. E. Reimchen[1]
Department of Zoology, University of Liverpool, Liverpool, England

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On the British and Irish coasts, *Littorina mariae* and *L. obtusata* show geographical variation in adult shell size, the former decreasing and the latter increasing in localities with increased protection from wave action. Within some shores, *L. obtusata* is relatively small in upper tidal positions but increases in size towards the lower shore where it overlaps with the much smaller shelled *L. mariae*.

Characteristic signs of repair observed on the shells are considered to have resulted from unsuccessful attacks by crabs such as *Carcinus maenas*. High frequencies of these shell injuries were associated with the presence of large-shelled populations of *L. obtusata* both between localities and between different levels on the shore.

Experimental work showed that large-shelled *L. obtusata* (16–17 mm) were exceptionally resistant to breakage by large *C. maenas* while smaller adult shells of *L. obtusata* (13–16 mm) and those of *L. mariae* (6–13 mm) were very susceptible. Small *C. maenas* were unable to successfully crack the thickened outer whorl of adult shells of either species and could only break the thin shells of juveniles. It is argued that small adult size, as seen in *L. mariae*, could represent an adaptation for a contracted juvenile stage and thus early maturity where small crabs are important predators.

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Le long des côtes britannique et irlandaise, il existe des variations géographiques de la taille de la coquille chez les adultes de deux espèces de *Littorina*: la taille de la coquille de *L. mariae* augmente et celle de *L. obtusata* diminue dans les endroits protégés de l'action des vagues. Sur certaines rives, *L. obtusata* est relativement petit dans les zones supérieures de marée, mais augmente de taille sur les rives basses où elle cohabite avec *L. mariae* à coquille beaucoup plus petite.

Les coquilles portent des "cicatrices" qui sont probablement le résultat d'attaques ratées par des crabes tels que *Carcinus maenas*. La fréquence élevée de ces blessures est associée à la présence de populations à grande coquille de *L. obtusata*, à la fois dans les comparaisons entre différentes localités et les comparaisons entre différents niveaux sur la même rive.

Des expériences ont démontré que les *L. obtusata* à grande coquille (16–17 mm) sont particulièrement résistants au bris par les *C. maenas*, alors que les coquilles plus petit (13–16 mm) de *L. obtusata* adultes et celles de *L. mariae* (6–13 mm) sont très susceptibles au bris. Les petits crabes *C. maenas* sont incapables de casser complètement la couche externe épaissie des coquilles adultes de l'une ou l'autre espèce et ne peuvent briser que la coquille mince des littorines immatures. Il est possible que la petite taille au stade adulte, comme chez *L. mariae*, représente une adaptation par laquelle le stade juvénile serait raccourci conduisant à une maturité précoce, là où les petits crabes sont des prédateurs importants.

[Traduit par le journal]

Introduction

Intertidal prosobranchs in temperate oceans commonly display geographical varation in maximum size of shells (Fischer-Piette and Gaillard 1961; Ebling et al. 1964; Sacchi 1966; James 1968; Crothers 1974; Goodwin and Fish 1977). Populations from wave-swept shores have relatively small, smooth, and thin shells which are considered to be hydrodynamic adaptations for reducing projected surface area (Kitching et al. 1966; Guiterman 1971). Sheltered localities have snails with large and thickened shells; traditional interpretations for this trend have emphasized abiotic correlatives including increased calcium utilization, resistance to desiccation, and salinity differences (North 1954; Barkman 1956; Sacchi 1969).

By contrast, recent studies on diverse taxa of tropical gastropods have interpreted such characters as thick shells and narrow apertures primarily as defensive adaptations to shell-breaking predators (Vermeij 1978) for review). The large chelae present on many crabs appear to be used commonly for crushing molluscan shells, and their appearance in the paleontological record coincides with the general disappearance of open-whorled and thin-shelled taxa, which are particularly susceptible to breakage (Vermeij 1977). Apart from the seminal papers on *Nucella lapillus* (Ebling et al. 1964; Kitching et al. 1966), few authors have examined the extent of crab predation on temperate prosobranchs and its relationship to geographical variation in shell morphology.

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[1] Present address: Department of Zoology, University of Alberta, Edmonton, Alta., Canada T6G 2E9. Field address: Box 297, Port Clements, B.C., Canada V06 1R0.

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There are numerous methodological difficulties in quantifying the extent of crab predation in the intertidal region. Large crabs such as *Cancer*, *Carcinus*, and *Macropipus* retreat to the sublittoral during low tide (Kitching et al. 1966) and, at least in *Carcinus*, remain there during winter months (Edwards 1958). The occurrence of alternate prey items in some localities or in particular seasons will result in differing proportions of gastropods in the diet. These data are not readily obtainable during wide geographical surveys. However, information on population life histories and evidence for crab attacks can be deduced from examining either the kinds of broken shells on the shore (Vermeij 1979) or the frequencies of repaired injuries incurred during growth of the shell (Reimchen 1974; Raffaelli 1978; Dudley 1980; Vermeij et al. 1980).

In this study I consider geographic patterns in shell size and frequencies of crab-induced injuries in two sibling species of intertidal snails, *Littorina mariae* and *L. obtusata*. These coexisting species occur on Atlantic shores in association with macrophytes such as *Fucus serratus*, *F. vesiculosus*, and *Ascophyllum nodosum*. The snails are generally zoned, with *L. mariae* occurring from mean low water (MLW) up to the middle shore position (MW) and *L. obtusata* occurring from just below MW up to mean high water (MHW) (Sacchi and Rastelli 1966; Reimchen 1974). Both species lack pelagic larvae; egg masses deposited on the fucoids hatch directly into young snails. This characteristic has resulted in very localized adaptations in color and shape of the shells (Reimchen 1979, 1981).

Study area and methods

Samples were obtained from 104 localities in the British Isles and Ireland (Fig. 1), representing a wide range of shore exposures and profiles, from sheltered inlets with mud substratum to exposed rocky headlands. General sampling techniques and estimates of shore exposure are described in Reimchen (1979). In summary, collections were made near MW and, in the case of *L. mariae*, below this level. Owing to the lower shore distribution, and hence reduced accessibility, sample sizes for *L. mariae* were generally smaller than those for *L. obtusata*. All adult snails, recognized by the presence of a thickened lip to the shell, were measured for maximum diameter (lip to opposite side of body whorl) and scored for sex. For estimating mean shell size in a sample, only males were used since there is a sexual dimorphism in size (Sacchi and Rastelli 1966).

Shell repairs on the body whorl were categorized according to the extent of injury, from minor disruptions of shell growth through to major breakages (Fig. 2). Only major injuries will be considered in this study. It is possible that some injuries may have been caused by factors other than crab attack, such as other predators, abrasion during storms or crushing from boulder movement. Three lines of evidence, however, point strongly for a predominance of crab-mediated injuries (see also Vermeij 1978). First, characteristic breakages of the outer whorl in field samples were indistinguishable from those seen in experiments with *Carcinus maenas*, the most commonly encountered crab in the intertidal region and a major predator on *Littorina* spp. (Pettitt 1975). An intertidal fish (*Blennius pholis*) is also an important predator; this species does not crush but, rather, swallows the entire shell (Reimchen 1979). Second, if the injuries were the result of wave action and boulder movement, frequencies should have been consistently higher on wave-swept shores. Yet the highest frequencies were found in sheltered bays and harbours with mud substratum. Third, during the geographical survey, I noted an exceptional abundance of *C. maenas* in 7 of the 104 localities. In six of these, the frequencies of repaired injuries were higher than in surrounding localities.

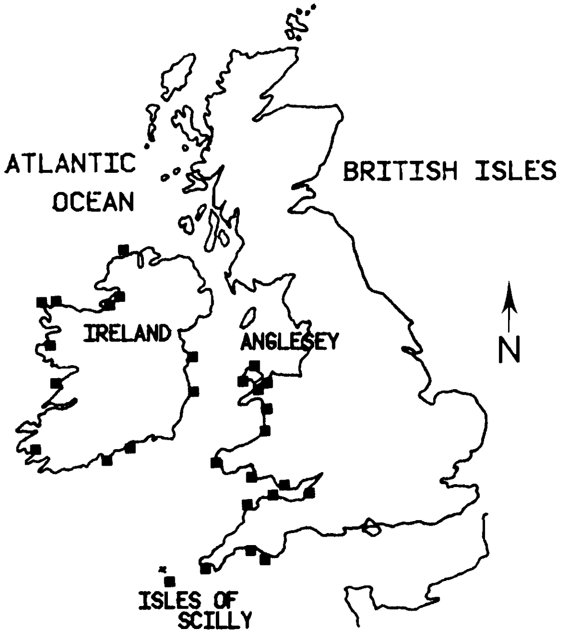

FIG. 1. Collection sites in the British Isles and Ireland.

Supplementary collections of adult snails were obtained from Anglesey, North Wales, to determine whether gradients in shell size occurred within shores. Vertical transects were established between MHW and MLW at two of the localities to assess frequencies of injuries in relation to shore position, and

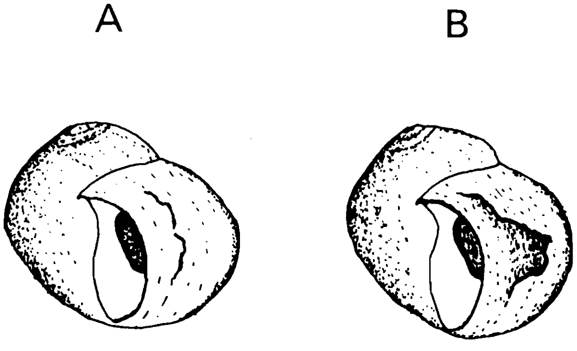

FIG. 2. Examples of minor (A) and major (B) shell injuries.

TABLE 1. Summarized distribution of adult shell lengths in *L. mariae* and *L. obtusata*. Significance of tests shown as NS, nonsignificant; * < 0.05; ** < 0.01; *** < 0.001. Sample sizes range from 2 to 110 ($\bar{x}$ = 25) for *L. mariae* and from 7 to 140 ($\bar{x}$ = 36) for *L. obtusata*. *s*, standard deviation; variance ratio computed as s^2 *mariae*/s^2 *obtusata*

Area	Species	No. of localities	$\bar{x}$ (mm)	*s*	Range of $\bar{x}$	Variance ratio (*F*)	Correlation coefficient (*r*)
Mainland Britain[a]	*L. mariae*	43	9.47	1.74	6.3–12.5	5.14***	−0.41**
	L. obtusata	52	15.87	0.77	14.1–17.3		
Isles of Scilly	*L. mariae*	22	10.04	2.19	5.1–13.5	10.44***	−0.08 NS
	L. obtusata	29	16.10	0.68	14.3–17.3		
Ireland	*L. mariae*	15	10.03	2.00	5.7–12.8	3.63**	−0.53*
	L. obtusata	22	16.65	1.05	13.0–17.7		

[a] Mainland Britain includes Wales, Somerset, Devon, and Cornwall.

for seasonal comparisons. Snails were scored for major injuries at the collection sites and then released.

For predation experiments, collections of *C. maenas* were obtained from Sandy Bay, Anglesey. They were placed in 20-L glass tanks containing fronds of *F. serratus* and *Ascophyllum nodosum* with circulating seawater at 11°C. Crabs were separated into three size classes, with maximum carapace widths of 15–25, 40–60, and 90–110 mm, and placed in separate tanks. For each size category, two replicate tanks were used, each containing three individuals. In the first series of experiments, five groups of *Littorina* were used: *L. mariae* adults (6–8 mm); *L. mariae* adults (10–13 mm); *L. obtusata* juveniles from MHW (6–8 mm); *L. obtusata* adults from MHW (13–15 mm); *L. obtusata* adults from MW (16–17 mm). Five individuals of each group were placed at the bottom of the tank whereupon the snails moved onto the algal fronds. Sand was placed around the perimeter of the tank to eliminate movement onto the sides of the tanks where the snails would be inaccessible to crabs. The tanks were left undisturbed for 12 h, after which the surviving snails were removed and scored. The cycle was repeated for 3 days with small crabs (15–25 mm) and for 7 days with larger crabs (40–110 mm).

In a second experiment, two groups of snails were added to the tanks: *L. mariae* adults (6–8 mm) and *L. obtusata* juveniles (6–8 mm); *L. mariae* adults (6–8 mm) and *L. mariae* juveniles (5–8 mm); *L. mariae* adults (6–8 mm) and *L. obtusata* adults from MW (16–17 mm); *L. obtusata* adults from MHW (13–15 mm) and *L. obtusata* adults from MW (16–17 mm). Numbers of crabs and conditions in the tank were the same as in the first experiments. During this series, observations were made on the method of shell breakage by crabs of different size classes.

Results

Adult shell size

Littorina mariae and *L. obtusata* both exhibited geographical variation in mean shell size, the former ranging from 5.1 to 13.5 mm and the latter from 13.0 to 17.7 mm among localities (Table 1). Within each of the larger sampling regions, *L. mariae* was significantly more variable among populations than *L. obtusata* ($P <$ 0.005, variance ratio test). Among localities where both species were obtained, there was also a significant negative correlation between mean adult sizes in two of the geographical regions (Table 1). This inverse size relationship is a consequence of the correlations between the amount of wave action on the shore and adult shell size in the two species, since *L. mariae* decreases and *L. obtusata* increases in size with decreasing wave action (Fig. 3). In *L. mariae*, the regression correlation was significant ($P < 0.001$) in each of the geographical regions, while in *L. obtusata* it was significant in mainland Britain ($P < 0.001$) and Ireland ($P < 0.01$) but not on the Isles of Scilly. Generally, therefore, the two species, while similar in size on exposed shores, are divergent in sheltered areas.

Within localities, there were regular differences in adult shell size which correlated with shore position. Samples of adult *L. mariae* obtained from *Fucus serratus* fronds in sandy runoff channels were composed of small individuals (5–10 mm), while those from

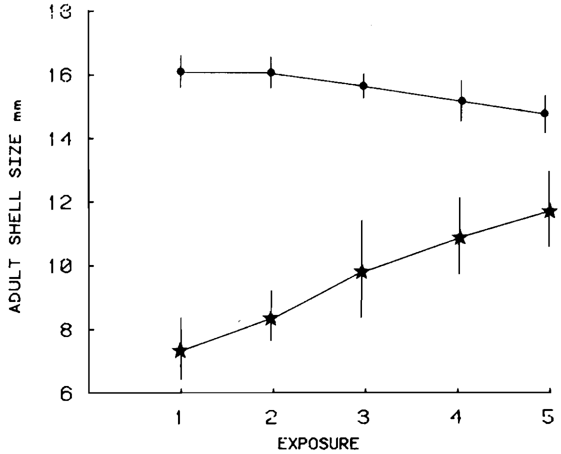

FIG. 3. Association between mean adult shell length and shore exposure. Localities arranged from most sheltered (1) to most exposed (5). ★, *L. mariae*; ●, *L. obtusata*. Vertical line shows one standard deviation.

adjacent rocky platforms at the same tidal height were larger (10–14 mm). This pattern was similar on other shores with comparable substrates and is discussed in detail by Reimchen (1981). For convenience, these two forms will be referred to as "dwarf" and "large" respectively. *Littorina obtusata* showed an increase in adult size from MHW down to near MLW in two of the three localities (Table 2). At Sandy Bay, where samples were obtained over a 2-year period, the trend was consistent between seasons and between years. At Cemaes Bay, which was the most sheltered locality, this relationship did not occur; there was extensive algal cover at this locality near MHW, which was not the case for Sandy Bay and Porth Swtan.

Shell injuries

Characteristic breakages of the body whorl occurred in the majority of localities on the British and Irish coasts, with a similar range of frequencies in each of the three collecting regions (Table 3). The highest frequencies occurred in sheltered bays and harbours in mainland Britain and on shores of intermediate exposure in the Isles of Scilly and Ireland (Fig. 4). Within each of these areas, the proportions of injuries was not significantly different between the species (paired *t*-test).

There was, however, an association between frequencies of injuries and size of adult shells in *L. obtusata* (Fig. 5). Localities with elevated injury rates generally had large-shelled populations; correlation coefficients were significant on mainland Britain and Ireland ($P < 0.02$ and $P < 0.05$ respectively) but not on the Isles of Scilly ($P < 0.5$). In *L. mariae* there were no distinctive trends (Fig. 6) except in mainland Britain where the highest injury rates were found with small-shelled adults ($P < 0.05$; for Ireland $0.10 < P < 0.15$; for Isles of Scilly ($0.05 < P < 0.10$).

TABLE 2. Mean shell length ($\bar{x}$) of adult *L. obtusata* on different shore levels. s = standard deviation

Locality	Date, month/year	Shore position	Sample size	$\bar{x}$ (mm)	s
Porth Swtan	2/71	MHW	30	14.6	0.81
		MLW	30	15.6	0.51
	3/73	MHW	30	14.3	0.27
		MLW	10	15.9	0.63
Sandy Bay	1/72	MHW	67	13.0	0.58
		MW	32	13.8	0.47
		MLW	29	15.4	0.47
	5/72	MHW	74	13.0	0.59
		MW	56	13.8	0.63
		MLW	36	15.4	0.76
	2/73	MHW	59	13.1	0.41
		MW	62	13.5	0.57
		MLW	52	15.5	0.38
	5/73	MHW	43	12.9	0.40
		MW	22	14.0	0.69
		MLW	49	15.8	0.70
Cemaes Bay	3/71	MHW	30	16.6	0.83
		MLW	30	16.9	1.18
	3/73	MHW	20	16.6	0.71
		MLW	40	17.0	0.67

TABLE 3. Mean percentage ($\bar{x}$) of injured shells among geographical regions. Paired *t*-test for means are nonsignificant in each region. s = standard deviation

Area	Species	$\bar{x}$	s	Range
Mainland Britain	*L. mariae*	10.4	10.4	0–44
	L. obtusata	10.6	11.4	0–37
Isles of Scilly	*L. mariae*	13.4	9.1	0–30
	L. obtusata	12.0	8.4	0–30
Ireland	*L. mariae*	7.7	7.4	0–23
	L. obtusata	12.8	10.5	2–47

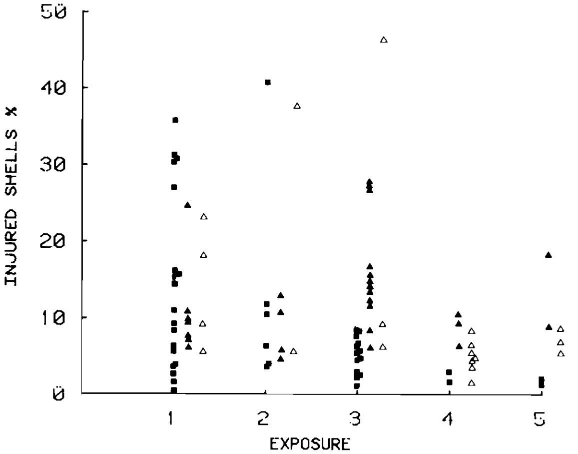

FIG. 4. Percentage of repaired shell injuries in relation to shore exposure. Injuries based on total sample (*L. mariae* + *L. obtusata*). ■, mainland Britain; ▲, Isles of Scilly; △, Ireland. Correlation coefficients for mainland Britain, $r = -0.44$ ($P < 0.01$); for Isles of Scilly, $r = 0.19$ ($P > 0.5$); for Ireland, $r = -0.37$ ($0.15 < P < 0.10$).

Injury rates varied according to the tidal zone occupied. On two shores in Anglesey, there was a general increase in the injury rate from high to low shore positions (Table 4). At Porth Swtan, injuries in *L. obtusata* increased from about 1 to 20% from MHW to MLW, a trend which was evident, as well, during winter months. However, at Cemaes Bay, where injuries were extremely common (>40%), frequencies were similar in upper and lower tidal zones. In *L. mariae*, which occurs below MW, injury rates along the vertical transect were similar, except at MLW where the frequency increased. Irrespective of position, *L. mariae*

TABLE 4. Percentage of shell injuries for *L. mariae* and *L. obtusata* in relation to shore position. Transects between upper (MHW) and lower (MLW) shore. χ^2 analyses for (*a*) between species for total injuries; (*b*) between species in region of overlap (positions where both species are present); and (*c*) between upper (1, 2, and 3) and lower (4, 5, and 6) shore *L. obtusata*. Fisher's exact probability calculated when expected values less than 5. NS = nonsignificant

Locality	Date, month/year	Shore position	*L. mariae*		*L. obtusata*		Probability		
			% injuries	*N*	% injuries	*N*	*a*	*b*	c
Porth Swtan	6/72	1 (MHW)	0	0	0.4	231	<0.001	NS	<0.001
		2	0	3	0.5	196			
		3	7.6	118	8.7	23			
		4	9.4	106	13.3	30			
		5	7.5	80	16.7	18			
		6 (MLW)	15.4	45	0	0			
	1/73	1	0	0	0	157	<0.001	NS	<0.01
		2	0	7	3.2	155			
		3	9.9	71	1.5	68			
		4	4.3	116	23.1	13			
		5	8.2	97	0	0			
		6	19.0	58	0	0			
Sandy Bay	6/72	1	0	0	0.5	795	<0.001	NS	<0.001
		3	0	0	0.8	366			
		5	5.3	39.6	6.6	182			
	1/73	1	0	0	1.1	440	<0.01	NS	<0.05
		3	0	0	1.8	221			
		5	7.1	652	4.8	147			
Cemaes Bay	6/72	2	0	0	42.7	192	NS	NS	NS
		5	46.1	167	50.0	50			

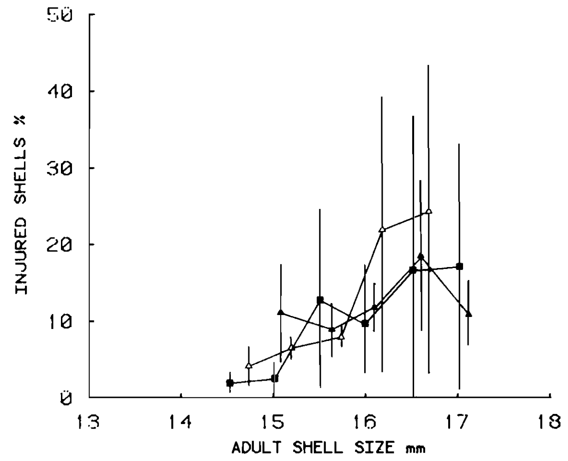

FIG. 5. Relationship between percentage of repaired injuries and mean adult shell length in *L. obtusata*. ■, mainland Britain; ▲, Isles of Scilly; △, Ireland. Vertical line shows one standard deviation. Each point represents the average injury rate among populations having characteristic shell lengths (15.0–15.5, 15.5–15.9, etc.). Populations with mean shell lengths less than 15 mm were uncommon and have been grouped. Correlation coefficients for mainland Britain, $r = 0.40$ ($P < 0.02$); for Isles of Scilly, $r = 0.07$ ($P > 0.5$); for Ireland, $r = 0.51$ ($P < 0.05$). Injury rate based on total sample (*L. mariae* + *L. obtusata*).

exhibited significantly more injuries than *L. obtusata* at Porth Swtan and Sandy Bay. However, in the zone of overlap there were no significant differences between the species.

In summary, localities with high frequencies of shell injuries were occupied by large-shelled populations of *L. obtusata* and by small-shelled populations of *L. mariae*. This trend also occurred over small distances; the increases in injury rate from MHW to MLW were associated with a comparable increase in shell size of *L. obtusata* (Table 2).

Predation experiments

The results summarized in Tables 5 and 6 indicate that small-shelled snails were most susceptible to breakage for each size class of *C. maenas* and that for snails of similar size, those with thinner shell lips were most susceptible. Considering the relative numbers consumed, the groups can be ranked in order of increasing resistance to successful attacks: (*i*) juvenile *L. obtusata* and *L. mariae* (6–9 mm); (*ii*) adult *L. mariae* (6–9 mm); (*iii*) adult *L. obtusata* (13–15 mm); (*iv*) adult *L. mariae* (10–13 mm); (*v*) adult *L. obtusata* (16–17 mm).

An important variable in assessing relative resistance of each group was the size of *C. maenas* and their methods of manipulation. Small crabs were successful

TABLE 5. Percentage of snails (five groups) consumed by three crabs in single aquaria. Adult snails were used in each group except for juvenile *L. obtusata* (6–8 mm). Mean lip thickness (millimetres) shown in parentheses

			% of each group consumed				
Carapace width of *Carcinus* (mm)	Tank	No. added per group	*L. obtusata* 6–8 mm (0.45)	*L. mariae* 6–9 mm (0.95)	*L. mariae* 10–13 mm (1.40)	*L. obtusata* 13–15 mm (0.84)	*L. obtusata* 16–17 mm (1.49)
15–25	1	20	45.0	0	0	0	0
	2	20	40.0	0	0	0	0
40–60	3	75	62.7	34.7	0	0	0
	4	75	60.0	28.0	2.7	1.3	0
90–110	5	75	73.3	89.3	40.0	73.3	2.7
	6	75	89.3	82.7	53.3	53.3	1.3

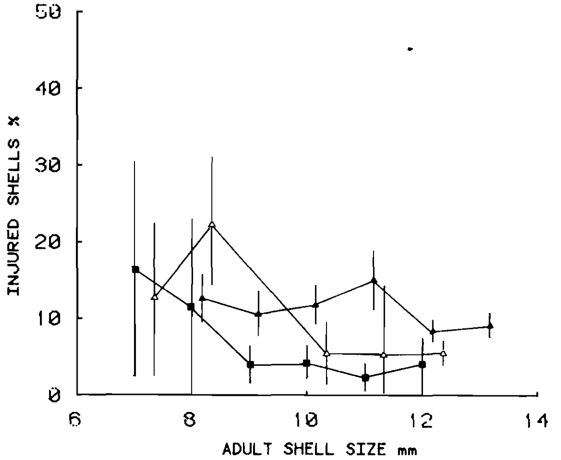

FIG. 6. Relationship between percentage of repaired injuries and adult shell length in *L. mariae*. ■, mainland Britain; ▲, Isles of Scilly; △, Ireland. Vertical line shows one standard deviation. Populations grouped into length categories 6–8, 8–9, 9–10, 10–11, 11–12, and 12–14 mm. Correlation coefficients for mainland Britain, $r = -0.41$ ($P < 0.05$); for Isles of Scilly, $r = -0.44$ ($0.05 < P < 0.10$); for Ireland, $r = -0.44$ ($0.10 < P < 0.15$). Injury rate based on total sample (*L. mariae* + *L. obtusata*).

at breaking and consuming only juvenile snails, which are characterized by a thin outer lip to the aperture. These *C. maenas* held the shell with one chela and with the other prised or peeled away successive portions of the outer whorl starting at the lip until the body of the snail was exposed. The thicker lip of adult snails, even in "dwarf" *L. mariae*, could not be chipped by small crabs and the snails were dropped after several minutes of manipulation. Intermediate-sized *C. maenas* also used a peeling method, taking primarily juvenile shells, but because of their larger chelae, they were also capable of breaking the thicker lip of "dwarf" *L. mariae*.

Large *C. maenas* used two methods of shell breaking and took a greater range of prey sizes. Among the large-shelled snails, these crabs used the peeling method and with their large chelae broke the shells of upper shore *L. obtusata* and the very thick shells of "large" *L. mariae*. However, the lower shore *L. obtusata* were largely resistant to breakage. Several of these shells had broken segments which extended 6 mm back from the lip (15% of the body whorl), yet the animal within was uninjured and later showed shell regeneration in the laboratory. A second method of shell breaking was used on juvenile snails and "dwarf" *L. mariae*. The crabs were unable to insert the large chelae into the relatively small aperture of these shells, and instead, held the shell between the apex and aperture and with sustained pressure completely crushed the shells, exposing the body tissues. Since juvenile *L. obtusata* and "dwarf" *L. mariae* were consumed with similar frequencies by large crabs, it is apparent that the increased lip thickness of the adult *L. mariae* did not offer protection against this size class of *C. maenas*. For smaller crabs, however, which used the peeling method, lip thickness provided increased resistance to breakage.

Discussion

Littorina mariae and *L. obtusata* show extensive geographical variation in the frequencies of repaired shell injuries and, in some localities, 50% of the population have incurred sublethal attacks by predators. These frequencies provide no information on the mortality rate from crabs (Zipser and Vermeij 1978; Vermeij et al. 1980), but are useful for comparing the prevalence of unsuccessful crab attacks between localities. The quantitative field surveys described above indicate that populations of *L. mariae* and *L. obtusata* from sheltered areas incurred relatively higher levels of crab attack compared with those from exposed shores. This conclusion is supported by the general distribution of *C. maenas*, which is found commonly on sheltered beaches

TABLE 6. Numbers of snails (two groups) consumed by three crabs in single aquaria. Mean lip thickness (millimetres) shown in parentheses. χ^2 test shows departure from 1:1 ratio. Probabilities are * < 0.05 and *** < 0.001

Carapace width of *Carcinus* (mm)	No. added per group	No. of snails consumed		χ^2
		L. mariae 6–9 mm (0.95)	*L. obtusata*[a] 6–8 mm (0.45)	
15–25	20	1	11	6.7*
40–60	20	6	14	2.4
90–110	20	14	17	0.1
		L. mariae 6–9 mm (0.95)	*L. mariae*[a] 6–8 mm (0.72)	
15–25	20	0	9	7.1*
40–60	20	8	15	1.5
90–110	20	19	18	0.0
		L. mariae 6–9 mm (0.95)	*L. mariae* 10–13 mm (1.40)	
15–25	20	0	0	—
40–60	20	8	0	6.12*
90–110	20	20	8	4.32*
		L. mariae 10–13 mm (1.40)	*L. obtusata* 16–17 mm (1.49)	
15–25	20	0	0	—
40–60	20	0	0	—
90–110	20	15	0	13.1***
		L. obtusata 13–15 mm (0.84)	*L. obtusata* 16–17 mm (1.49)	
15–25	20	0	0	—
40–60	20	0	0	—
90–110	20	17	0	15.1***

[a] Juvenile snails.

and estuaries but is uncommon or absent on wave-swept shores (Ebling et al. 1964). Within localities, injuries were most common near MLW and generally decreased toward MHW. This coincides with the distribution of *Carcinus*, *Cancer*, and *Macropipus*, which occur primarily in subtidal zones or in lower and middle intertidal regions (Edwards 1958; Barrett and Yonge 1958). However, in localities with extensive rock or algal cover, *C. maenas* can occur up to MHW and are active during submergence (Edwards 1958; and personal observation). Such a pattern was inferred at Cemaes Bay where injury rates were also high at upper shore positions.

In those localities where injury rate was high and extensive predation by crabs was implicated, populations of *L. obtusata* had relatively large shells. As well, over short distances within shores the largest shells are found where the injury rate was highest. Abiotic influences such as temperature, salinity, and calcium utilization may be important factors in shell variation in *L. obtusata* (cf. Barkman 1956; Sacchi 1969), although the correlations with injury rate suggest that large shell size may be a defensive adaptation to shell-breaking predators. Such an advantage was demonstrated in the predation experiments which showed 6- to 9-mm *L. mariae* most susceptible, 10- to 14-mm *L. mariae* and 13- to 15-mm *L. obtusata* less so, and 16- to 17-mm *L. obtusata* largely resistant to successful attack by large *C. maenas*. Similar results were reported by Guiterman (1971) who found that lower shore *L. obtusata* were larger and thicker than upper shore individuals and were more resistant to attack by crabs. In *Nucella lapillus*, where *Carcinus*, *Macropipus*, and *Cancer* were significant predators, the largest shells were most resistant to breakage (Ebling et al. 1964; Kitching et al. 1966). As well, large thick-shelled populations of *Lepsiella* sp. occurred where the shore crab *Hemigrapsus* was common and were more resistant to breakage than adjacent thin-shelled populations where the crab was absent (Kitching and Lockwood 1974).

Among the gastropods on the British and Irish shores, maximum size of shells generally increases from upper to lower shore positions. These range from 5 mm (*L. nertoides*) in the splash zone, to 20 mm (*L. saxatilis* complex, *L. obtusata*, *N. lapillus*) on midshore, to 30 mm (*L. littorea*) near MLW, and to 100 mm (*Buccinum*, *Ocenebra*) in subtidal levels, the latter groups being extensively thickened (Barrett and Yonge 1958). Although zonation of gastropods is generally treated as a response to differential desiccation (Lewis 1964; Butler

1979), these gradients in maximum size may also represent a response to the vertical zonation in crushing capabilities of crabs (see also Vermeij 1978), or perhaps may allow survival in habitats where large individuals of *C. maenas* (up to 110 mm), *Macropipus* (up to 125), and *Cancer* (up to 250 mm) are prevalent.

In apparent contrast to the above trends is the occurrence of the small-shelled *L. mariae* near MLW and the reduction in mean shell size in sheltered localities (which often had high frequencies of injuries). While this species has a relatively thick lip and narrow aperture in comparison with *L. obtusata* (Goodwin and Fish 1977), representing a general adaptation of gastropod shells to shell-breaking predators (Vermeij et al. 1980), the results of the predation experiments showed *L. mariae* to be much more susceptible than *L. obtusata* to attacks by large *C. maenas*. Furthermore, small shells would appear to be at a distinct disadvantage in the presence of lower tidal or subtidal fish (Palmer 1979; Reimchen 1979).

A possible advantage to small shell size is suggested by the breaking techniques employed by different length classes of crabs. Small *C. maenas* (15–25 mm) used the peeling technique and were only able to consume juvenile snails, i.e., thin-lipped shells. After hatching, and with additional size increment during growth, snails have a relatively thin shell which becomes progressively thickened when maximum size is reached (Moore 1936). Small *C. maenas* appeared unable to break the thickened outer whorl of any adult snails, including that of "dwarf" *L. mariae*. Thus, the most susceptible species to attack by small crabs will be the group with the most extended juvenile stage. Growth rates have not been determined for these sibling groups of *Littorina*. However, in *Murex*, small- and large-shelled species exhibited comparable growth rates as juveniles and, consequently, large-shelled species had longer juvenile periods than smaller forms (Spight et al. 1974). If these findings are applicable, *L. obtusata*, maturing near 16 mm in size, will retain the thin-lipped juvenile stage for about 1.5 times longer than will "large" *L. mariae* and about 2.5 times longer than "dwarf" *L. mariae*. Under these conditions, the order of decreasing susceptibility to predation by small *C. maenas* is *L. obtusata*, "large" *L. mariae*, and "dwarf" *L. mariae*. This pattern is the inverse of that observed for predation by large *C. maenas* and could result in a selective regime favoring early maturity, and therefore small size, if small crabs represent a primary source of mortality.

Such a selective regime could occur if small rather than large crabs were prevalent in the particular habitat where "dwarf" *L. mariae* occur. These snails are found on isolated *F. serratus* clumps in sandy runoff channels, while "large" *L. mariae* occur on *F. serratus* from rocky platforms (Reimchen 1981). In contrast, juvenile *L. obtusata* occur higher on the shore on *F. vesiculosis* and *Ascophyllum nodosum* and are often found sheltered within the partially eroded air bladders of these fucoids (Reimchen 1974). At present, no quantitative data are available on the distribution of crabs among these areas which would allow assessment of the prediction.

This study has shown that *L. mariae* and *L. obtusata* exhibit regular differences in adult shell size both between and within localities. Resulting from the examination of shell injuries and the predation experiments, it is proposed that some of these size gradients are a response to different relative intensities of predation by different length classes of crabs. Examination of the frequencies of shell injuries among juveniles of the three forms and documentation of the feeding preferences and habitats of each length class of crabs will determine the validity of these interpretations.

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