

MICROGEOGRAPHICAL VARIATION IN *LITTORINA MARIAE* SACCHI & RASTELLI AND A TAXONOMIC CONSIDERATION

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Abstract: In the intertidal prosobranch *Littorina mariae* Sacchi and Rastelli from Anglesey, Wales, there was a correlation between shell morphology and shell colour in several localities. Small (5-8 mm) and large (11-14 mm) adult shells differed in morph frequencies, lip and apex colour, and sculpturing on the periostracum, and were found in different microhabitats, the former on sandy run-off channels and the latter on exposed rock platforms. The two forms were relatively discrete over short distances where the habitats were distinct, but intergraded in all characters on intermediate habitats.

Functional aspects of this variation are discussed. These differences may represent the occurrence of several taxonomic groups within *L. mariae*.

INTRODUCTION

A bimodality of adult shell size in *Littorina obtusata* (L.) led Sacchi (1966) to suspect the existence of two co-existing groups in this highly polytypic species. On further examination of individuals of the two length modes, Sacchi and Rastelli (1966) found that there were correlated differences in sex ratio, penis morphology, colour morph frequencies and habitat. On this basis they separated *L. obtusata* into a smaller species, *mariae* (n. sp.) and a larger species *obtusata* (L. sensu stricto). Other studies confirmed these results (Sacchi, 1969) and provided additional distinctions including radula morphology (Reimchen, 1974; Goodwin and Fish, 1977) and biochemical markers (Reimchen, 1974).

L. mariae occurs primarily on lower intertidal Fucaceae, usually *Fucus serratus* and secondarily *F. vesiculosus* (Sacchi, 1969). It displays extensive variation in adult shell size between localities, with small adults occurring in sheltered conditions and large adults on exposed shores (Sacchi, 1969; Reimchen, 1974; Goodwin and Fish, 1977). It also demonstrates widespread variation in colour morph frequencies; a yellow morph predominates in protected bays and a dark brown morph on exposed headlands (Sacchi, 1969; Gratton, 1969; Reimchen, 1979).

Towards the conclusion of a study on *L. mariae* and *L. obtusata*, I noticed within several localities an unusually large amount of variation in adult shell size of *L. mariae*. Samples from one site in Anglesey, Wales, displayed a bimodality in size within each of the sexes, and associated with each length mode were characteristic morph frequencies, shell sculpturing and microhabitats. Collections from other sites provided several examples of similar variability. The magnitude and direction of these differences, which occurred over a distance of several meters, were equivalent to those detected when comparing samples from sheltered and exposed shores in geographical surveys.

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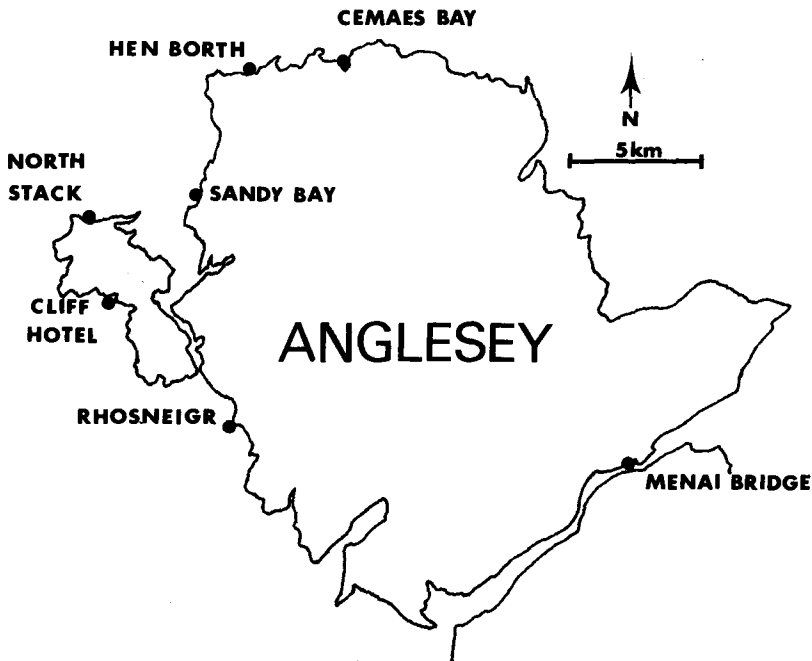


Fig. 1. Collecting areas in Anglesey, North Wales.

The purpose of this paper is to describe the microgeographical variation within these localities and to discuss briefly the possibility of a further taxonomic division within *L. mariae*.

STUDY AREA AND METHODS

Samples collected at Sandy Bay, Anglesey in March 1973 were used for a preliminary examination of adult shell size in *L. mariae*. This locality has a diversity of substrates including exposed bedrock platforms with modest cover of *F. spiralis*, *F. vesiculosus*, *F. serratus* and *Ascophyllum nodosum*, and sandy run-off channels with scattered clumps of *F. serratus*.

Resulting from this examination, horizontal transects were established along the shore at Sandy Bay and at 6 other localities around Anglesey (Fig. 1). These sites were chosen to include a sheltered area (Menai Bridge), a relatively exposed area (North Stack), and those with a diversity of substratum and exposure (Hen Borth, Cemaes Bay, Rhosneigr and Cliff Hotel). All snails found within a series of one meter squares were collected, first by extensive shaking of the fronds and retrieving the shells on the ground, and then by visual inspection of the fronds. Samples were preserved in 10% formaldehyde.

Adult shells, determined by the presence of a thickened lip, were measured for maximum diameter and scored for sex and colour phenotypes. In specimens from Sandy Bay, the penis was removed at the base and measured for total length and for length of the distal tubule. The major colour morphs represented were *citrina*, *light reticulata*, and *dark reticulata*, which correspond generally to yellow, pale brown, and dark brown respectively.

Mean adult shell size and morph frequencies from 85 localities in Ireland, Wales, Somerset, Cornwall, Devon and the Isles of Scilly were extracted from data appendices in Reimchen

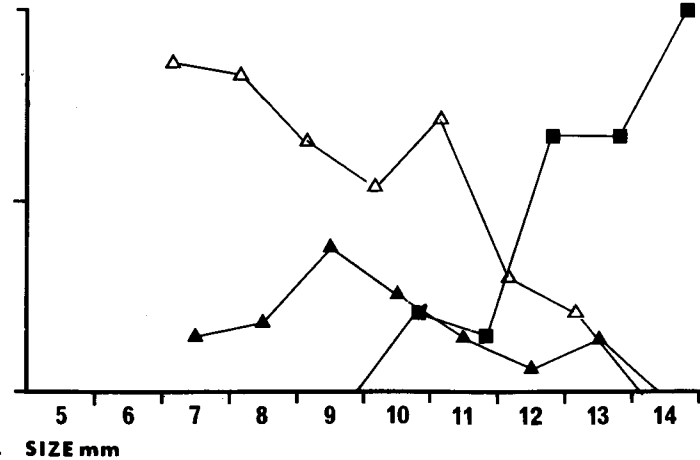
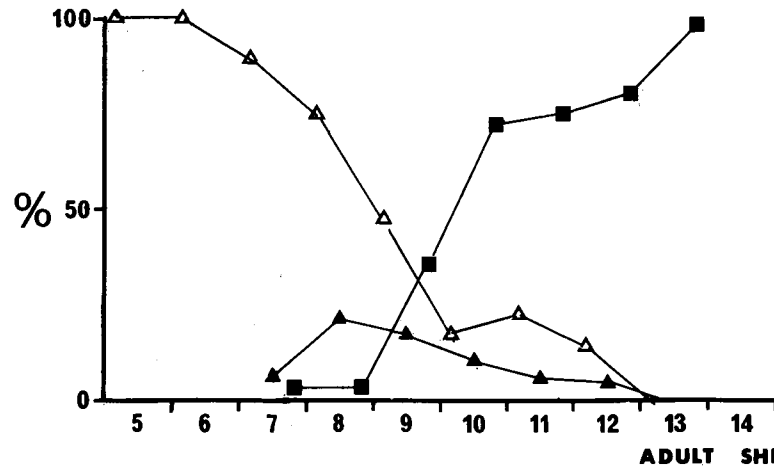
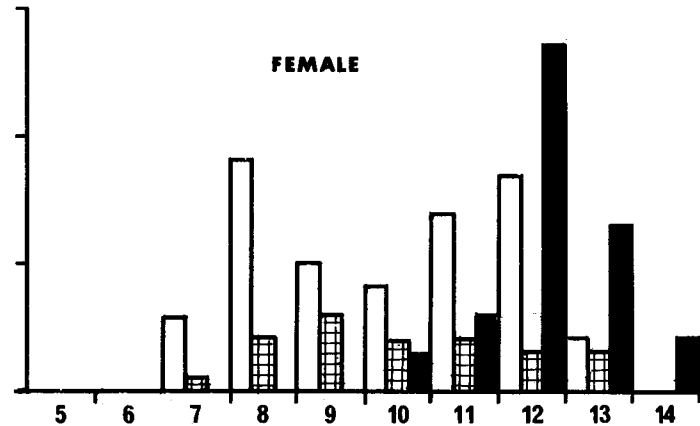
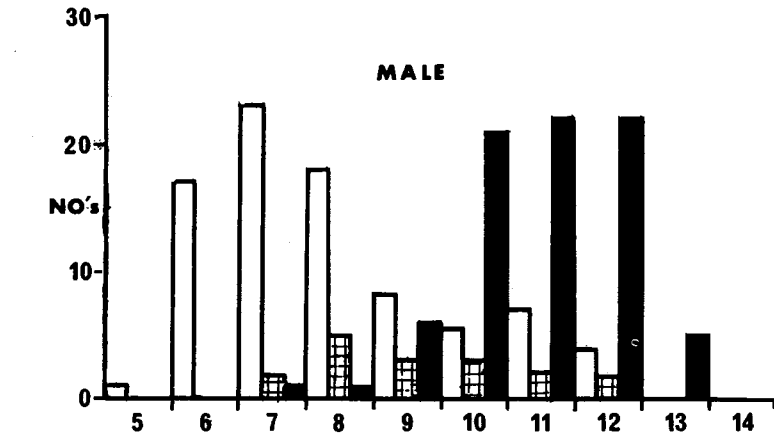


Fig. 2. A: Length distribution of adult shells from Sandy Bay among males and females for major colour morphs. Citrina—open; light reticulata—hatched; dark reticulata—solid. B: Percentage of morphs in relation to adult shell size. Citrina—open triangle; light reticulata—solid triangle; dark reticulata—solid square.

(1974). Since the sexes differ in shell size, data on shell length was restricted to males.

RESULTS

At Sandy Bay, there was a wide range of adult shell sizes (5–14 mm) in comparison to adjacent localities such as North Stack (10–13.5 mm) (variance-ratio test for males $P < 0.01$ and for females $P < 0.01$). Length distributions for each sex showed large differences between the colour morphs (Fig. 2a). Male *citrina* had a strong mode at 7 mm and a second weak mode at 11 mm; females were distinctly bimodal at 8 mm and 12 mm. In contrast, dark *reticulata* was unimodal at 10–12 mm in males and 12 mm in females.

A correlation is present between adult shell size and frequencies of the morphs (Fig. 2b). In both males and females, 5–8 mm adults were predominantly *citrina*, while 12–14 mm adults were primarily dark *reticulata* and secondarily *citrina*. The largest shells of males and females were entirely dark *reticulata*. Light *reticulata* were disproportionately common among the morphs in intermediate length classes.

When these shells were separated into two length groups, corresponding to the lower mode of *citrina* (5–8 mm) and the upper mode of *citrina* and dark *reticulata* (11–14 mm), other distinctions were evident. For convenience in discussion, these two length groups will henceforth be referred to as 'dwarf' and 'large' forms.

There were subtle differences in the expression of shell pigments between the two forms. Lip colour in 'dwarf' light *reticulata* was tinged with pink as opposed to white or violet among 'large' shells. This phenotype graded continuously into *citrina* among 'dwarf' shells, but represented a discrete morph among the 'large'. 'Dwarf' *citrina* occasionally merged into a white phenotype (var. *albescens*), a character not seen in the 'large' *citrina*. Additional differences occurred in developmental stages of shell colour. Shell pigmentation of juveniles can generally be determined from the apex on unabraded adult shells. On 'large' shells the apex was usually the same colour as the remainder of the shell, but occasionally on 'dwarf' forms there was a discrete white apex representing the first 3–4 mm of shell growth. That this variation represents early shell colour rather than abrasion was confirmed by collections of juveniles from 2–6 mm in size. Some of the shells less than 4 mm in length were white, while slightly larger individuals showed the first expression of the adult pigmentation on the new increments of shell growth.

With low magnification (10x) one can observe sculpturing on the periostracum composed of minute longitudinal ridges perpendicular to the lip (Fig. 3). On 'dwarf' shells there was a regular series across the outer whorl, composed of high ridges separated by 2 to 4 low ridges, all about equal distance from each other. On 'large' forms the differences between high and low ridges was less pronounced, with a marked irregularity in pattern, or grading into a uniform series with all ridges being the same height. I did not detect any characteristic pattern in the 'large' form as was possible in the 'dwarf'. On adults, these differences were occasionally indistinct due to the recurrent abrasion of the shells, but in juvenile and sub-adults, sculpturing was usually well developed. At Sandy Bay, the majority of juvenile *citrina* (4–6 mm) had a pattern like the 'dwarf' adults, while all dark *reticulata* (4–9 mm) had the irregular pattern of the 'large' adults.

Minor differences were evident in the morphology of the penis, specifically, in the relative length of the distal tubule. In the 'dwarf' form, the tubule constituted about 30–40% of the total length of the penis and in the 'large' form it represented 60–70%. However, this may represent allometric growth since a continuous gradation was present between small and large snails (Fig. 4).

There were consistent trends in the abundance of 'dwarf' and 'large' forms on different parts of the shore (Fig. 5). At Sandy Bay, 'dwarf' shells were most common on isolated clumps of *F.*

"DWARF"

"LARGE"



Fig. 3. Sculpturing on periostracum of 'dwarf' and 'large' shells.

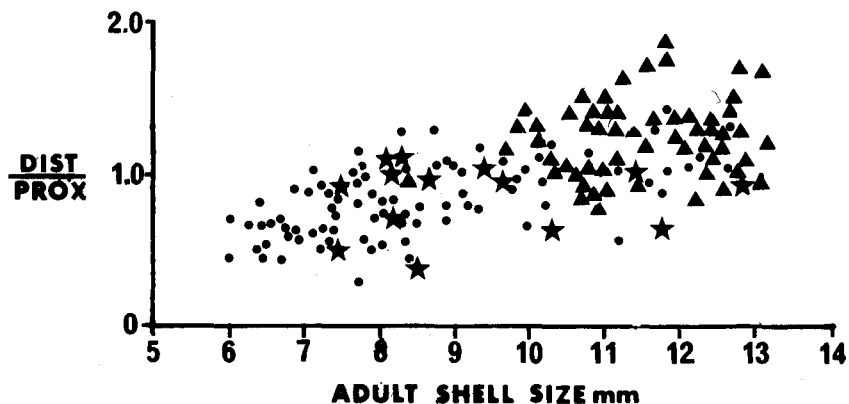
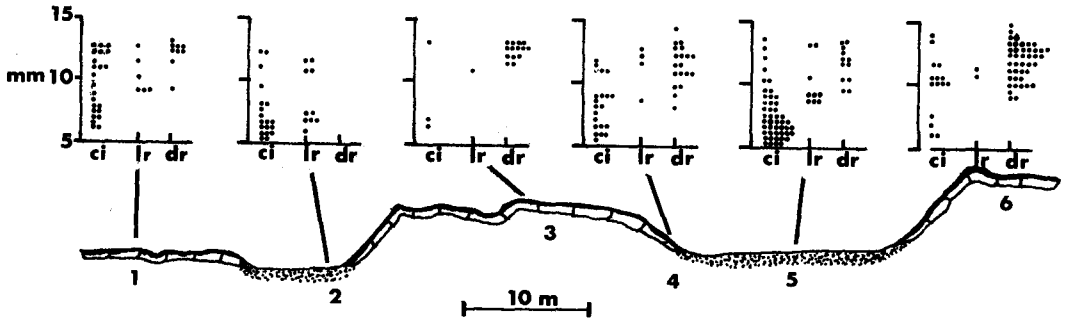


Fig. 4. Scatter plot of relative length of distal tubule and adult shell size from Sandy Bay. Vertical axis represents a length ratio of distal tubule to the proximal section. Citrina—dot; dark reticulata—triangle; reticulata with white apex—star.

serratus which were underlain and surrounded by sand or gravel, this habitat occurring in sheltered tidal run-off channels (site no. 5). In these areas, *F. serratus* had broad laminae, short narrow stems and often numerous tube-dwelling polychaetes (*Spirorbis* spp.). 'Large' shells were most abundant on *F. serratus* from elevated rock platforms, areas which were relatively exposed to wave action (sites no. 3 and 6). Fronds had narrow laminae, seldom with *Spirorbis*, and large broad stems which often constituted the major length of the frond. Samples from low rock platforms (site no. 1) and from intermediate areas (sites no. 2, 3 and 4) contained 'dwarf' and 'large' shells in roughly similar proportions.

There were suggestions of a length bimodality in citrina (sites no. 1, 4 and 6) and in each case, individuals from the lower mode retained the characteristic sculpturing of the 'dwarf' form

SANDY BAY



HEN BORTH

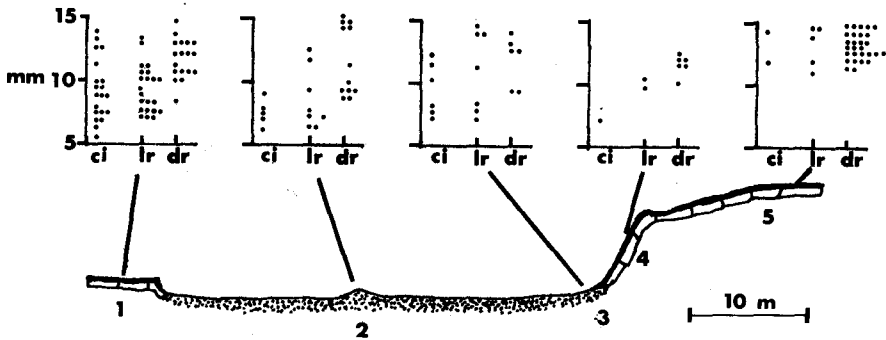


Fig. 5. Relationship between adult shell size, colour morph, and substrate at Sandy Bay and Hen Borth. Shoreline shown in cross-section with elevated rock platforms and sandy run-off channels (dotted). Graphs indicate size of all adult males in sample for each colour morph (citrina—ci; light reticulata—lr; dark reticulata—dr).

while those from the upper mode had sculpturing like 'large' dark reticulata. Light reticulata was often intermediate in size between the 'dwarf' and 'large' forms (sites no. 1 and 5). Sculpturing on these individuals was similar to the 'dwarf' form in having high ridges separated by several low ridges, yet the series was very irregular.

The trends described for Sandy Bay were also detected at Hen Borth, Rhosneigr and Cliff Hotel where there was an equivalent diversity in substrata. At Hen Borth (Fig. 5), light reticulata was again intermediate in size (site no. 1), but the smallest shells (site no. 2) and largest shells (site no. 5) had sculpturing characteristic of the 'dwarf' and 'large' forms respectively. A feature of this locality is the high incidence of the white apex. Dark reticulata phenotypes showing this character were generally similar to the 'dwarf' in sculpturing but in all of the samples, these shells were slightly larger than 'dwarf' citrina.

At Cemaes Bay, the diversity of substrata was reduced and snails were found only on several

exposed rock platforms and on a long band of intermediate habitat. Sheltered areas with isolated clumps of *F. serratus*, as at Sandy Bay, were absent. In the intermediate areas, *citrina* was highly variable in size but had a single mode near 11 mm, slightly lower than the 'large' dark *reticulata*. The majority of these *citrina* could not be reliably placed in either 'dwarf' or 'large' categories, as sculpturing was intermediate. However, all of the small *citrina* (6–8 mm) retained sculpturing of the 'dwarf' form.

Menai Bridge, a very sheltered locality, has a dominant substratum of loose sand and silt. Samples from this locality contained only 'dwarf' shells. At North Stack, a relatively exposed headland, the major habitat was sloping bedrock, with occasional rock shelves; all of the shells were the 'large' form.

In summary, within five localities there were consistent morphological differences in *L. mariae* on different parts of the shore (Fig. 6). Those found in sheltered and sandy areas had small adult size (5–9 mm), high frequencies of *citrina*, distinctive sculpturing of high and low ridges, a short distal tubule, and in three localities (Hen Borth, Rhosneigr, Cliff Hotel) a white apex. In contrast, elevated or exposed rock platforms had large shells (10–14 mm), high frequencies of dark *reticulata* and secondarily *citrina*, sculpturing with relatively uniform ridges, and a long distal tubule. A white apex was occasionally present, but was usually found on the smallest of these large shells. The 'dwarf' and 'large' forms were relatively discrete in areas where the substrata changed sharply from rock platforms to run-off channels, but intergraded when a large proportion of the habitat was intermediate between the two areas.

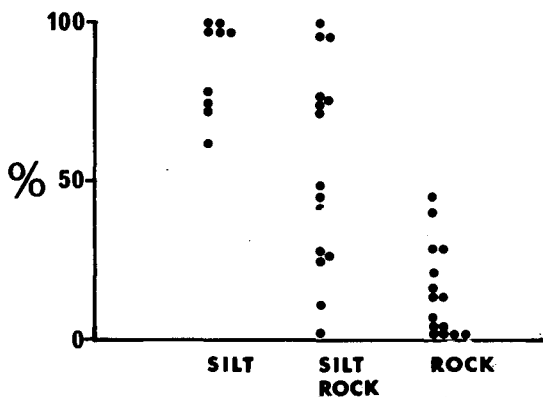


Fig. 6. Relative abundance of 'dwarf' shells according to substrate. Collections from all localities.

DISCUSSION

Many of the characters exhibited by the 'dwarf' and 'large' forms may represent functional adaptations to different selective pressures in each microhabitat. Crabs are widely distributed and are major predators on the littorines (Pettitt, 1975). Several studies document correlations between the intensity of crab predation and shell morphology (Ebling *et al.*, 1964; Kitching *et al.*, 1965; Guiterman, 1971; Vermeij, 1977). In a series of predation experiments with *Carcinus maenas*, Reimchen (1974) found that 'dwarf' and 'large' forms of *L. mariae* were differentially preyed upon. The adult 'dwarf' form had a thicker lip than juvenile 'large' forms of the same

shell length; this gave the 'dwarf' an advantage during predation by small *C. maenas* which breaks away successive parts of the outer whorl. In contrast, when adult shells were exposed to large *C. maenas*, the 'dwarf' were at a distinct disadvantage since their entire shell could be crushed by the major claw. It follows that local differences in the abundance and size distribution of crabs (cf. Ebling *et al.*, 1964; Raffaelli, 1978) will provide differing selective forces.

Differences in colour morph frequencies between localities have been interpreted as a response to visual predators such as *Blennius pholis* (Reimchen, 1979). In sheltered localities where *citrina* predominates, the majority of juvenile snails were found on the broad lamina of *F. serratus*. Since yellow is the dominant light transmitted through the lamina, *citrina* is the most camouflaged of the morphs. On exposed shores, where dark *reticulata* occurs, juveniles were found on the opaque brown stem of *F. serratus* where only dark *reticulata* is cryptic. It is unknown whether these differences between shores will apply as well to differences between run-off channels and adjacent rock platforms.

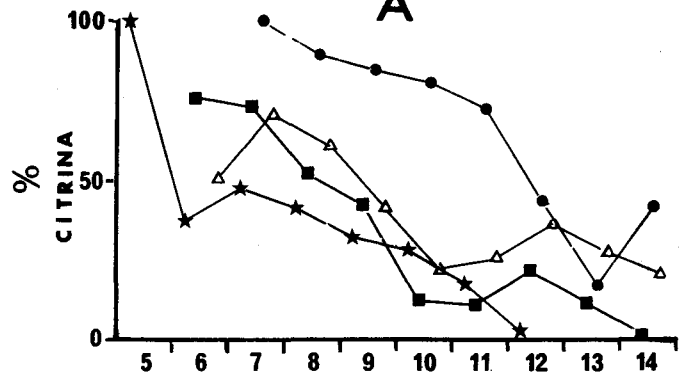
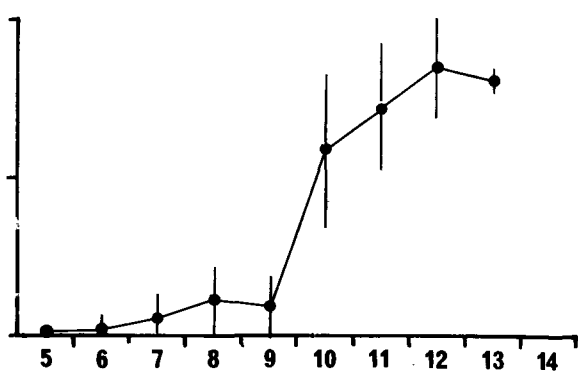
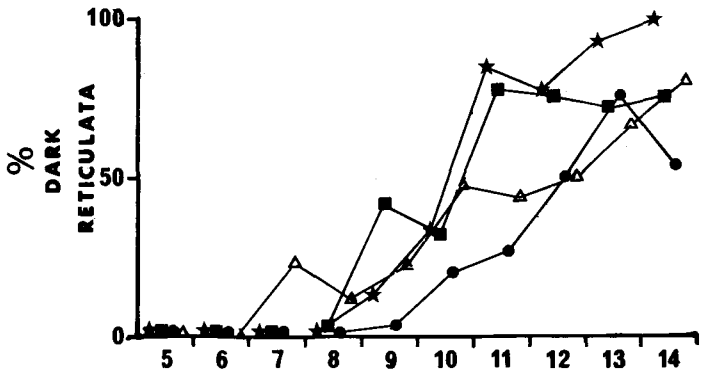
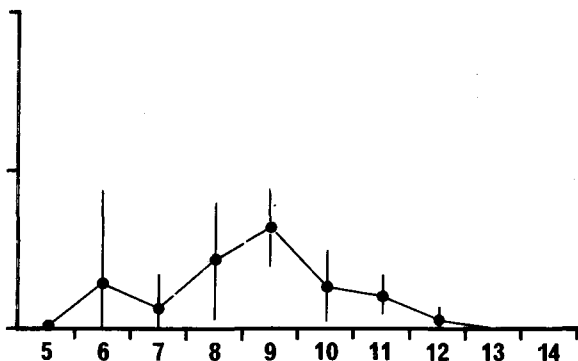
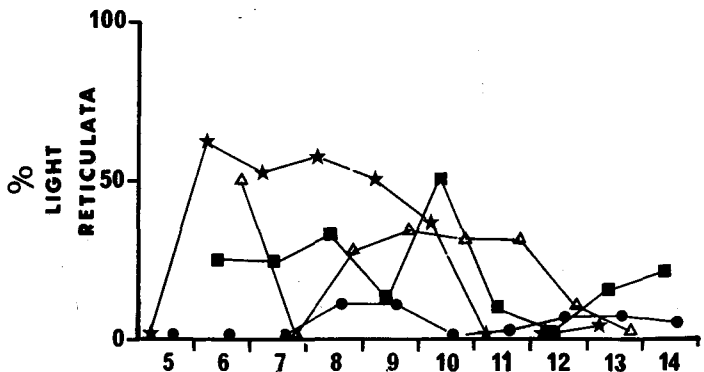
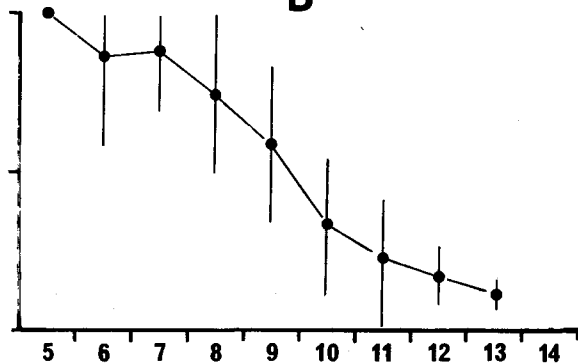
The white apex on 'dwarf' *reticulata* phenotypes was associated with fronds of *F. serratus* densely covered with tube-dwelling polychaetes. After hatching and during the first 4 mm of shell growth, some snails have a white-banded shell which closely resembles the white tubes of *Spirorbis*. In predation experiments with *Blennius pholis*, white shells were consumed less frequently than equivalent sized yellow or brown shells (Reimchen, in preparation).

The close relationship between shell size and frequencies of colour morphs within these localities is also applicable to the general parameters of populations between localities. Using data from Reimchen (1974) involving 85 localities around Britain and Ireland, mean adult shell length in each locality was plotted against the percentage of each morph. Localities were then grouped and a mean percentage obtained from 1 mm length categories (5–6 mm, 6–7 mm, etc.). The resulting graph (Fig. 7) shows that both within and between localities the small length classes (5–8 mm) were characterized by high frequencies of *citrina*, intermediate length classes (9–11 mm) by similar proportions of the three morphs, and large shells (11–15 mm) by dark *reticulata* and secondarily *citrina*. Furthermore, small adult shells were found in sheltered localities, often with sand substratum, and large shells on exposed shores generally with rock substratum. When these samples were reexamined, those from sheltered shores in Ireland, Isles of Scilly and South England with small adult shells and high frequencies of *citrina* contained characteristic 'dwarf' sculpturing.

It is probable that the majority of these shell characters in the 'dwarf' and 'large' forms and those observed between sheltered and exposed localities represent very localized adaptation resulting, in part, from differential predation by *C. maenas* and *B. pholis*. Since sandy run-off channels and elevated rock platforms or shelter and exposure merge through a series of intermediate areas the gradation of shell characters may represent an adaptive response to 'intermediacy' in the selective regimes.

These data raise several difficulties concerning the genetic structure of the variation whereby a complex of characters can differ over several meters in a manner parallel to that of wide geographical distances. If this indicates genetic variations within a single species, it would require numerous linkage groups between adult shell size and the following characters: habitat, shell colour (bimodal in *citrina*, intermediate in light *reticulata*, and large in dark *reticulata*), presence or absence of a white juvenile phase, shell sculpturing, and the ability to express these characters in any complex of intermediate states according to the intermediacy of the habitat. While it is possible to incorporate a multiple-character association within a polymorphic

Fig. 7. A: Frequencies of colour morphs and adult shell size of males within localities from Anglesey. Rhosneigr (N = 59)—star; Hen Borth (N = 58)—square; Cemaes Bay (N = 80)—dot; Cliff Hotel (N = 67)—triangle. See Fig. 2 for data from Sandy Bay. B: Frequencies of colour morphs and mean adult shell size for males from localities in Ireland, Wales, Somerset, Devon, Cornwall, and Isles of Scilly. Vertical line shows one standard deviation from mean frequencies for localities with the corresponding mean adult shell size. Data from sites in Anglesey (Part A) excluded.

A**B**

ADULT SHELL SIZE mm

context (cf. Ford, 1964), the magnitude of the changes suggests a basic difference in the genome, and the occurrence of several taxonomic groups. If only two general groups are conceived, a 'dwarf' and a 'large' form, the frequent morphological intermediacy in light reticulata, both within samples and between localities, remains problematic. A second interpretation for the correlation between shell characters and microhabitat is that it represents an environmental rather than a genetic response. Until heritability is estimated for each character, this interpretation cannot be excluded. However, where breeding experiments were performed (Reimchen, 1974), expressions of the major colour morphs and the white-banded phase of juvenile shells were genetically determined.

The existing data do not justify a taxonomic division within the species. However, because of occasional bimodality in characters and very sharp clines, they do provide sufficient cause for an informal separation in further work. Multivariate analysis and electrophoretic variants may provide means of distinguishing between an exceedingly complex polymorphism and the occurrence of sibling species within *L. mariae*.

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