Shell colour ontogeny and tubeworm mimicry in a marine gastropod *Littorina mariae*

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The intertidal prosobranch *Littorina mariae* has an adult shell colour polymorphism and also exhibits variation in the ontogeny of shell colour. Shells may be uniform in colour throughout their life (yellow or reticulate) or exhibit a discrete white-spiral juvenile phase prior to acquisition of the highly cryptic adult pigmentation. Laboratory reared clutches have the same juvenile colour phases and non-random associations with adult shell colour as those observed in the field. Juvenile shell colour may be controlled at a separate locus to that for adult colour and appears to show linkage disequilibrium with the yellow shell in some populations.

There is a visual resemblance between the white juvenile phase of *L. mariae* and the tubes of the polychaete *Spirorbis* which are found cemented to algal fronds. Several lines of evidence are consistent with a postulated mimetic relationship. Although *L. mariae* reaches an adult size of 14 mm, the white phase is rarely expressed on shells greater than 3.5 mm diameter; this approximates to the maximum size of the tubeworms. *Spirorbis* is found predominantly in the same intertidal zone as *L. mariae* and is found principally on *Fucus serratus* which is the major algal substrate of *L. mariae*. Individuals with the white phase were absent from a wave-exposed locality where the tubeworm was also absent; it occurred only in the yellow morph in habitats where the tubeworm was moderately common and occurred in both yellow and reticulate morphs where the tubeworm was very abundant (5–20 tubeworms/cm²). Predation experiments with the intertidal fish *Blennius pholis* indicated that individuals with the white phase had lower predation rates than yellow and reticulate shells, and that the difference was greater when *Spirorbis* was present. This represents the first reported example of gastropod-polychaete mimicry and provides further evidence for the overwhelming role of visual predators and natural selection in the evolution of shell colour among intertidal littorines.

KEY WORDS:—Crypsis – natural selection – adaptation – predation – intertidal – tubeworm – *Spirorbis* – polymorphism – littorine.

CONTENTS

INTRODUCTION

In the many studies of shell colour variation in pulmonates (Clarke *et al.*, 1975 for review) and prosobranchs (e.g. Giesel, 1970; Wanscher, 1971; Reimchen, 1979; Mercurio, Palmer & Lovell, 1985), one of the least investigated aspects is colour variation during early ontogeny. This is unexpected since, at least among prosobranchs, juvenile snails are subject to massive mortality during the first few months of life (Spight, 1975), and could potentially yield substantive evidence for natural selection and insight into population differentiation.

The intertidal prosobranch *Littorina mariae* is a useful species for analyses of early shell colour ontogeny as some shells exhibit a conspicuous white-spiral juvenile phase (visible on adults as a white apex) and this trait differs between adjacent populations (Reimchen, 1981). The two major shell colour morphs in this species, citrina (yellow) and dark reticulata (dark brown) exhibit remarkable background matching to the two dominant colour substrates on the algae; juveniles rather than adults are most closely associated with the appropriate background (Reimchen, 1979). The delayed expression of cryptic shell pigments by deposition of a white-spiral phase in early growth is puzzling, given that the snails occupy the same algal species where the usual colour morphs should have been favoured. My purpose here is to describe the juvenile colour ontogeny of *L. mariae* and examine potential habitat associations. I present evidence that this variability is heritable and that the white-spiral juvenile phase is a Batesian mimic of tubes of the polychaete worm *Spirorbis* which are found encrusted on the algae.

MATERIALS AND METHODS

Life history

L. mariae is found in the lower intertidal zone of rocky shores in the North Atlantic, principally on the macrophyte *Fucus serratus* where the snails spend their entire lives. A related species, *L. obtusata*, occasionally overlaps with *L. mariae* but is generally found higher on the shore on the fucoids *F. vesiculosus* and *Ascophyllum nodosum*. During reproduction, *L. mariae* egg masses are deposited directly on the algal frond. After hatching (*c.* 0.6 mm shell diameter), juveniles (miniature adults) disperse on the frond, ingesting both settled material and the algae itself. Adult size (6 to 14 mm shell diameter) is reached within 1 year (Reimchen, 1982). There are three major shell colours, citrina (yellow), light reticulata (light brown to orange) and dark reticulata (dark brown), the former predominating in sheltered localities and the latter on wave exposed shores (Reimchen, 1979).

Mortality occurs throughout the life history; the intertidal fish *Blennius pholis* takes primarily juvenile snails (1–5 mm) (Reimchen, 1979) and the crab *Carcinus maenus* all size classes of snails (Reimchen, 1982). Numerous other visual predators such as shorebirds are also known to consume littorines (Pettitt, 1975). The extent of crypsis of the shell colour morphs is a function of the substrate and of the foraging positions of predators. Dark reticulata is very cryptic to humans on the opaque stem of *Fucus serratus*; it is also very cryptic on the thin laminae when viewed from above, with reflected light (Fig. 1A), the common viewpoint of a surface forager such as birds looking downwards onto the fronds. Citrina is highly conspicuous on both of these substrates. However, when the shell is observed on the medial and distal parts of the lamina which is illuminated from behind (that

is, when the observer is within the algal clump looking upwards, which is a common foraging position of the blenny), the light transmitted through the lamina is bright yellow and citrina morphs are camouflaged while dark shells are conspicuous (Fig. 1B, C).

Study area and collections

Samples of *L. mariae* were examined from ten localities in Anglesey, North Wales (Reimchen, 1979, 1981); the localities represent a range of wave exposures including a sheltered site at Menai Bridge and an outer coast exposed site at North Stack. During these collections, I made notes on the shore habitat (sand *vs.* rock substratum) and rough abundance of *Spirorbis* tubes (absent, present and abundant, the latter occurring when the tubeworms covered at least 25% of the frond surface area and where densities could reach 5–20 tubes cm²). For each snail, I recorded general colour of the apex (which usually shows the colour of the shell at hatching), and noted changes in hue or intensity on successive increments on growth including the major whorl. Since pale apex colour on older adult shells may result from abrasion, particularly in those in which the periostracum was eroded, I also examined sub-adult and juveniles (characterized by a thin lip to the outer whorl) with intact and non-abraded periostraca. Samples of adult shells of the sibling species *L. obtusata* from these localities were also scored for the presence or absence of the white apex.

Breeding studies

I reared clutches from two populations which differed in shell colour ontogeny, Menai Bridge (all individuals lacked the white-spiral juvenile phase) and Porth Swtan (the white-spiral juvenile phase was restricted to the citrina morph), under similar conditions to determine whether the white juvenile phase was environmentally induced or heritable (Reimchen, 1974).

Snails from each locality were kept in separate tanks with fronds of *Fucus serratus,* their major food plant, and monitored for copulatory activity. When an egg clutch was produced, the clutch and associated frond were removed and placed in a separate 4 l glass tank. After hatching, juvenile snails dispersed on the frond. Filtered soil extracts in combination with sodium nitrate and di-sodium hydrogen orthophosphate dihydrate were added to the water in order to maintain algal growth (E. Burrows, personal communication). The water in each tank was replaced weekly and during this procedure I made notes on shell colour. Progeny from 29 crosses (Menai Bridge–3; Porth Swtan–26) were monitored from two to 16 months.

Ten crosses among *L. obtusata* (Menai Bridge–7, Porth Swtan–3) were also reared and scored for the presence or absence of the white-spiral juvenile phase.

Predation experiments

The intertidal fish, *Blennius pholis,* an important predator on juvenile littorines (Reimchen, 1979), was collected from the field and kept in aquaria. Predation studies were carried out to examine relative mortality of different shell colour phenotypes on two substrates—*F. serratus* fronds on which *Spirorbis* tubes were
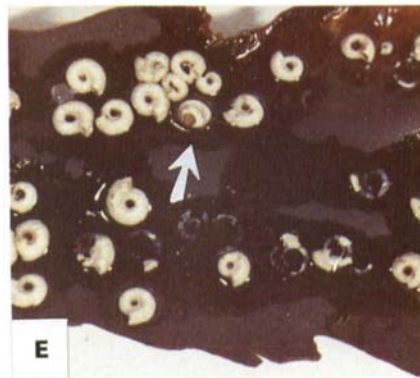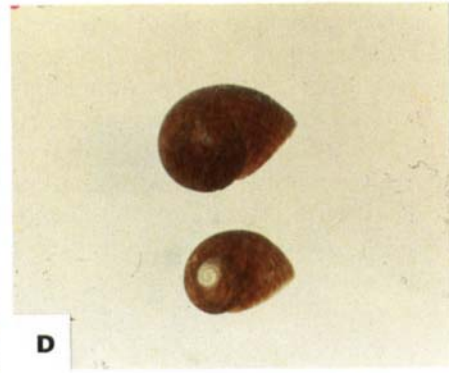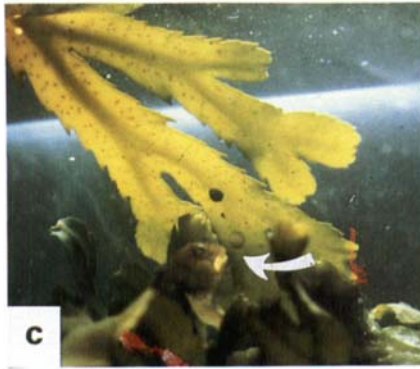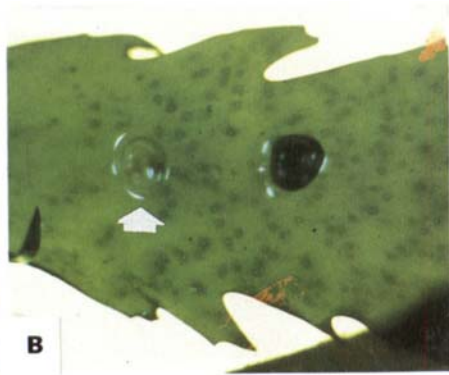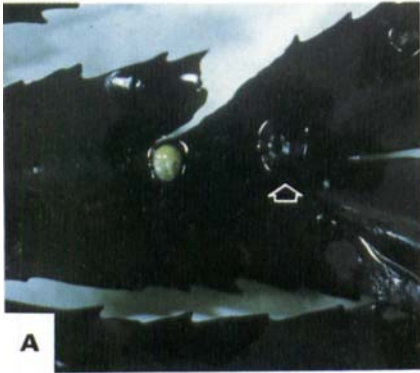
present, and other fronds devoid of tubes. Four tanks illuminated from above with a double filament fluorescent lamp were set up, each with a single *B. pholis*. Three juvenile *L. mariae* (*c.* 2.5 mm shell diameter), one of each colour phenotype (yellow, dark reticulata, white-spiral), were randomly positioned on a frond near the base of the lamina in the region where *Spirorbis* tubes were normally found. The frond was then lowered to the bottom of the tank. Within several minutes, a blenny approached and visually searched the frond; when a snail was detected, the blenny plucked it from the frond and swallowed the shell whole. I recorded the first snail taken. Four tests per blenny (separated by at least 1 h) per day were carried out over a period of 24 days.

RESULTS

Shell colour ontogeny among populations

The dominant shell pigmentation in *L. mariae* for each of the major colour phenotypes (citrina, light reticulata, dark reticulata) developed through one of two major ontogenetic pathways, either directly and rapidly to the adult shell colour or through a distinct juvenile phase (white-spiral) followed by the adult colour pattern. The former sequence was observed in all morphs in populations from Menai Bridge, Cemaes Bay and North Stack. At hatching, shells were very weakly pigmented and generally had an opaline appearance. In the citrina morph, initial increments of growth in the hatchling exhibited a gradual infusion of yellow pigment which reached full intensity by 3–4 mm shell size; this colour, which occasionally graded to orange, persisted throughout subsequent shell growth. A reticulate pattern was superimposed on the yellow or pale ground colour at different stages of growth. At Menai Bridge and Cemaes Bay, reticulations occurred on yellow shells near 3 mm shell size (range 2–5 mm), while at North Stack the pattern appeared to develop directly from the opaline phase (Fig. 2A).

At Porth Swtan, Sandy Bay and exposed regions at Hen Borth, Penrhynmawr, Cliff Hotel and Rhosneigr, both ontogenetic pathways were observed. Reticulata morphs developed directly into adult colouration from the opaline phase, as at North Stack. However, among citrina, new increments of shell growth in the hatchling, rather than showing a deposition of yellow pigment, exhibited white opaque banding perpendicular to the lip. These white bands were separated by several equivalent sized bands of non-pigmented (opaline) shell. Deposition of the white banding continued on further increments of growth until approximately

Figure 1. A, Citrina and dark reticulata morphs of *Littorina mariae* on *Fucus serratus* frond illuminated from above. Frond width *c.* 2 cm; B, citrina and dark reticulata morphs of *L. mariae* illuminated from behind (single 6W fluorescent tube) and therefore perceived with transmitted light. Frond width *c.* 2 cm; C, representative view of foraging position of *Blennius pholis* beneath *F. serratus* frond (illumination from behind) showing dark reticulata (upper snail) and citrina (lower). Length of exposed frond *c.* 20 cm; D, variation in apex colour of dark reticulata in adult shells of *L. mariae*. Upper figure—juvenile snail (initial whorls) with pigments similar to adults, lower figure—white-spiral juvenile phase. Upper shell 12 mm diameter; E, white-spiral juvenile of *L. mariae* shown amidst *Spirorbis* tubes. Frond width *c.* 2 cm; F, white shell of *Velutina*. Frond width *c.* 2 cm; G, translucent shell of *L. obtusata* (arrow, upper right), white-spiral of *L. mariae* (arrow, left) and dark reticulata of *L. mariae* (arrow, lower right). Frond width *c.* 2 cm; H, *Fucus serratus* fronds with and without *Spirorbis* collected from run-off channel and adjacent rocky platform respectively. Length of fronds *c.* 50 cm.
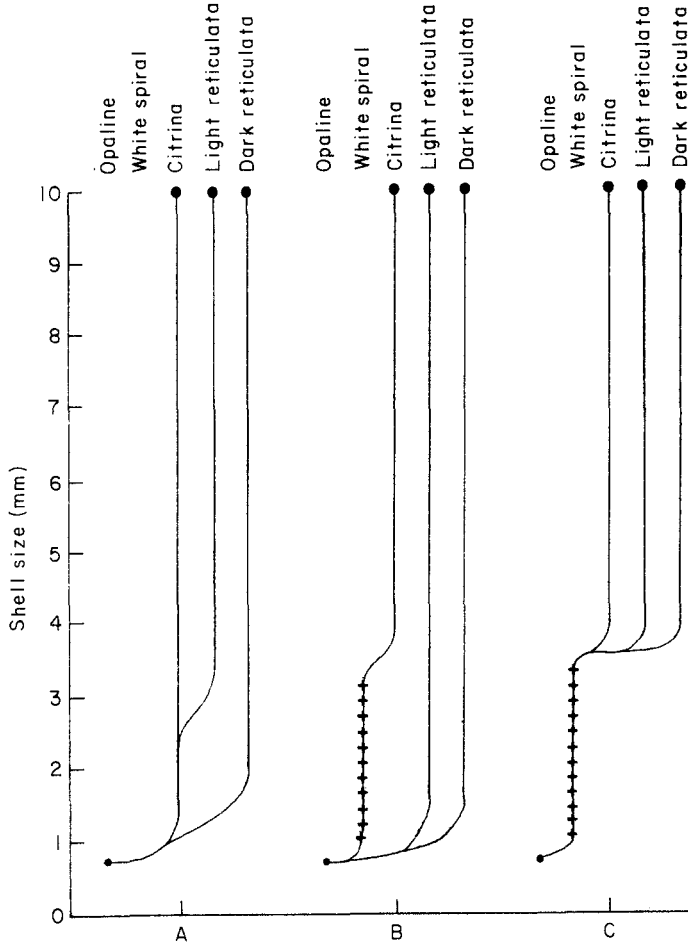
Figure 2. Representative ontogeny of shell colour in *Littorina mariae* against shell size from three groups of populations. A, Menai Bridge, Cemaes Bay, North Stack; B, Porth Swtan, exposed regions of Penrhynmawr; C, sheltered regions of Penrhynmawr Bay, Rhosneigr, Hen Borth. Shell colours (opaline, white-spiral, citrina, light reticulata, dark reticulata) are represented by different columns. All shells are opaline at hatch (*c.* 0.6 mm). Vertical lines indicate constancy of shell colour with increased shell size (vertical axis) while horizontal or diagonal lines show sizes at which shell colour changes to a different phenotype. Shells exhibiting white-spiral phase are shown emphasized (cross-hatching). Shell size at transitions between shell colours represents average values.

3 mm shell diameter, whereafter, new increments of lip growth showed an infusion of yellow pigment and reduced intensity of white banding (Fig. 2B). Full expression of the yellow pigment, which encompassed the entire lip, was reached by 4 mm shell size. This continued throughout the subsequent shell growth and produced a citrina morph that was indistinguishable from citrina at Menai Bridge, apart from increased apical whiteness.

Collections from sheltered regions of Penrhynmawr Bay, Hen Borth, Cliff Hotel and Rhosneigr also showed both ontogenetic sequences, but the white-spiral phase occurred not only in citrina but also in both reticulata morphs (Fig. 2C). Presence of this phase on dark-coloured shells produced a conspicuous white apex on adult specimens (Fig. 1D). The proportion of reticulata morphs with the

white-spiral juvenile phase varied with shore habitat. At Penrhynmawr, it ranged from 4% (N = 30) on bedrock platforms to 83% (N = 48) on sandy substratum outwash channels. At Rhosneigr, white-spiral was absent on an outer rocky platform (N = 18) and increased to 67% (N = 45) on a sandy substratum 200 m distance from the former. At Hen Borth, frequency increased from 10% (N = 41) on a rocky substrate to 56% (N = 36) on a sandy substratum over a distance of 30 m. However at Sandy Bay and Cliff Hotel, where white-spiral was uncommon (< 5%), I observed no change in frequency between rocky platforms and sandy habitats.

Shell colour ontogeny in laboratory crosses

Laboratory reared clutches yielded ontogenetic patterns similar to those observed in the field. In *L. mariae* from Menai Bridge (3 crosses), none of the progeny expressed the white-spiral phase and the citrina morph developed directly from the opaline phase. Crosses from Porth Swtan (citrina × citrina, dark reticulata × citrina, dark reticulata × dark reticulata) exhibited early differentiation into two phenotypes—white-spiral and reticulata, the former developing into citrina near 3 mm shell diameter (range 2–4 mm). No reticulate individuals exhibited the white-spiral phase. Crosses in *L. obtusata* (citrina × citrina; dark reticulata × dark reticulata) produced progeny all with an extended opaline phase (*c.* 0.6–3 mm), thereafter developing into a pale yellow or pale olive shell with reticulations as observed in field collections. The white-spiral phase was not observed on any individuals.

Evidence for Spirorbis mimicry

Various lines of evidence are consistent with a mimetic relationship between the white-spiral phase of *L. mariae* and the intertidal tubeworm *Spirorbis*. There is a modest visual resemblance between the two groups. When the white-spiral juveniles are viewed against the algal substrate, the brownish colour of the protoconch and the translucent areas between the white bands merge with the background and the white bands appear as two adjacent white spirals, similar to the white tube of *Spirorbis* (Fig. 1E). It is useful to emphasize that a uniform white shell, as in *Velutina* (Fig. 1F) or a translucent shell as in *L. obtusata* (Fig. 1G, upper right) does not produce a comparable mimetic resemblance.

Diameter of juvenile *L. mariae* shells exhibiting the white-spiral phase is similar to tubeworm diameter. Measurement of 100 *Spirorbis* tubes at Porth Swtan yielded a maximum diameter of 3.5 mm ($\bar{x} = 2.6$ mm) which coincides with the maximum size of the white-spiral phase (4 mm).

Intertidal zonation of the white-spiral phase and the tubeworm is congruent. *Spirorbis* is found in a narrow zone in the lower intertidal habitat (Lewis, 1964 and personal observation), which is also the zonation of *L. mariae* (Reimchen, 1974). Within this zone, *Spirorbis* is principally found on *F. serratus*, the dominant food plant and substrate of *L. mariae* (Reimchen, 1979). *Spirorbis* was rare or absent from adjacent macrophytes such as *F. vesiculosus* and *Ascophyllum nodosum;* these fucoids are usually occupied by *L. obtusata* which appears to lack the white-spiral phase.

While average densities of *Spirorbis* tubes were not quantified, there is a broad association between the relative occurrence of the white-spiral phase and the

abundance of tubeworms. *Spirorbis* was rare or absent from the wave-exposed locality at North Stack; white-spiral did not occur at this site. On shorelines of intermediate exposures such as Hen Borth, Porth Swtan and exposed areas of Penrhynmawr, *Spirorbis* occurred at low densities (*c.* $1/cm^2-5/cm^2$), principally on low-lying *F. serratus* fronds and less commonly on bedrock platforms; white-spiral shells were present in these localities but occurred only in the citrina morph. In wave-protected localities at Penrhynmawr Bay, Hen Borth and Rhosneigr, *Spirorbis* reached higher densities ($20/cm^2$) on fronds in silty run-off channels (Fig. 1H). In these habitats, the white-spiral phase occurred also among reticulata morphs (up to 83% of reticulata shells). I rarely obtained more than 5–10 juvenile snails per frond in any locality yet single fronds could commonly have 300–500 *Spirorbis* tubes indicating major differences in the relative densities, consistent with expected trends in a mimetic relationship.

Although the white-spiral phase was observed only in habitats where *Spirorbis* was present, the converse did not occur. At Menai Bridge, *Spirorbis* was present on *F. serratus*, yet I observed no individuals of the white-spiral phase in field samples or in laboratory crosses.

Predation experiments with Blennius pholis

Observations of the foraging behaviour of *B. pholis* indicate that *Spirorbis* is an acceptable but not a preferred prey item relative to *L. mariae*. When starved for several days and then presented with a *F. serratus* frond densely covered with *Spirorbis*, a blenny searched the frond and occasionally attempted to pluck a tubeworm from the frond. However, I saw no instances where a blenny successfully pulled one from the surface. When gastropods (*L. mariae, L. obtusata*) of comparable diameter to the tubeworms were placed on fronds amid tubeworms, a blenny found and ingested a snail within several minutes and then proceeded to eat additional littorines among the *Spirorbis* tubes.

The predation experiments with *B. pholis* allow several predictions in accordance with conspicuousness of the shells and proposed mimicry between white-spiral juveniles and *Spirorbis:* 1) the morph dark reticulata is highly cryptic and should have the lowest overall predation rate, 2) yellow shells and white-spiral shells, which are both conspicuous on dark brown algal substrates, should both have similar but much higher predation rates than dark reticulata on fronds lacking *Spirorbis* and 3) white-spiral shells should have an advantage over citrina on fronds with *Spirorbis*. Results of the experiments are summarized in Table 1. Since samples are small and results from different tanks are homogeneous (heterogeneity $\chi^2 = 1.5$, 6 d.f., $P > 0.5$), the data were pooled. Contrary to predictions 1 and 2, white-spiral, rather than dark reticulata had the lowest number of attacks (white-spiral–16.1%, dark reticulata–20.3%, yellow–63.5%). Consistent with prediction 3, the reduction in attacks on the white-spiral was greater on fronds with *Spirorbis* than on fronds without *Spirorbis* (9.4% *vs.* 22.9%, $\chi^2 = 6.6$, 2 d.f., $P < 0.05$).

DISCUSSION

The case for a mimetic relationship between the white-spiral juvenile phase of *L. mariae* and *Spirorbis* tubes, while speculative, is consistent with habitat and

TABLE 1. Susceptibility of shell colour phenotypes in *Littorina mariae* to predation by *Blennius pholis* in the presence and absence of *Spirorbis* tubes. Results show the number of times that a particular phenotype was the first snail consumed. Each fish had 48 different 3-choice presentations, 24 with each substrate. White-spiral and dark reticulata juveniles collected from Porth Swtan and yellow shells collected from Menai Bridge. Chi-square tests (2 × 3 with Yates correction) shown with 2 d.f. whsp = white-spiral; yell = yellow; dkret = dark reticulata

| | *Spirorbis* present | | | *Spirorbis* absent | | | | |
| | Shell colour phenotype | | | | | | | |
Tank	whsp	yell	dkret	whsp	yell	dkret	χ^2	P
A	2	15	7	6	13	5	1.24	>0.5
B	4	13	7	7	10	7	0.61	>0.5
C	1	21	2	3	16	5	1.25	>0.5
D	2	20	2	6	14	4	2.03	>0.1
Total	9	69	18	22	53	21	6.59	<0.025

experimental data and conforms to the general criteria for mimic and model (Vane-Wright, 1980; Robinson, 1981). Several aspects of the relationship are equivocal and merit additional investigation. The predation experiments, while consistent with the hypothesis, were somewhat puzzling since predation rate on the mimic was very low and comparable to the highly cryptic form (dark reticulata) even in the absence of the model. It is possible that apostatic selection is occurring such that the white-spiral phase has an advantage because of its phenotypic difference from the other morphs rather than to its resemblance with *Spirorbis* tubes. Yet if this was true, one would expect to find the white-spiral phase in localities where *Spirorbis* tubes were absent; this was not observed, which supports, therefore, a mimetic interpretation. Probably the most reasonable explanation for the pattern was that the blennies retained the visual signal of the model from previous experience (either in the field or in the aquaria) and accordingly were deceived by the single mimic on the substrate. A second possible difficulty to the proposal is whether *Spirorbis* tubes act as a model. While all of the aquaria observations were consistent with this, stomach analyses of field captured blennies (Qasim, 1957) showed evidence of predation on tubeworms (26% of the stomachs with tubeworm remains), although these were primarily serpulid rather than spirorbid taxa. In many Batesian systems, the model has toxins or other defences resulting in reduced predation (Cott, 1940; Wickler, 1968). With *Spirorbis*, the principal defence against *B. pholis* predation appears to be the strong adhesion of tubes to the substrate; major investment of foraging time required to remove the tubes would limit suitability of *Spirorbis* as a food item. In particular, tubes may be unoccupied and subsequent removal would yield little caloric benefit. A third difficulty with the proposal was that the white-spiral juvenile phase was not detected at Menai Bridge where *Spirorbis* tubes were present. I am not able to account for this pattern with the limited habitat data available. Since juvenile snails at this locality occur principally near the distal parts of the laminae (Reimchen, 1979), this may result in selection for crypsis against the laminae rather than mimicry of *Spirorbis* tubes, which are usually more abundant near the basal parts of the laminae.

Mimetic systems in marine invertebrates seem to be relatively uncommon compared with terrestrial taxa but have been observed between nudibranchs (mimic) and coelenterates and between an amphipod (mimic) and a gastropod (Crane, 1969; Field, 1974; Carter & Behrens, 1980). The present study represents to my knowledge the only evidence for gastropod–polychaete mimicry and differs from other relationships in being restricted to an exceptionally narrow segment of the life history of the mimic. As mimetic systems frequently involve multiple-character states integrated into a co-adapted gene complex (Sheppard & Cook, 1962), additional characters associated with the white-spiral phase may be expected. For example, the possible linkage disequilibrium between citrina and the white-spiral phase at several localities and in the laboratory is evidence for such associations. As well, in localities such as Penrhynmawr Bay, 'dwarf' and 'large' adult shells are found on the same fronds and it is principally the 'dwarf' shells which exhibit the white-spiral phase (Reimchen, 1981). It would be of interest to examine whether there are differences among the two forms in their average proximity to *Spirorbis* tubes. Limpets exhibit microhabitat preferences on heterogeneous backgrounds which maximize shell crypsis (Giesel, 1970; Mercurio *et al.*, 1985).

It seems unlikely that *L. mariae* would be the only species among the numerous intertidal gastropods able to exploit such a mimetic relationship. Conceivably the flat spire in *L. mariae*, in contrast to other high spired gastropods, facilitates the potential for mimicry of a planar spiral tube. Although I observed no instances of the white-spiral phase in *L. obtusata* in the present study, the species shows major overlap with *L. mariae* in some shores, including convergence in colour morph frequencies (Reimchen, 1974) and accordingly might be expected to exhibit a white-spiral phase where the model is common on the corresponding algal species.

Previous studies of shell colour in *L. mariae* have yielded extensive evidence for the influence of crypsis and visual predators on the polymorphism (Reimchen, 1979). The degree of crypsis was strongly affected both by the characteristics of the *Fucus serratus* substrate and by the foraging positions of the predator. Therefore, under what conditions would the delayed expression of the cryptic pigmentation in juvenile shells be advantageous? On wave-exposed shores, relatively few juveniles were found on distal segments of *F. serratus* lamina where citrina is cryptic; most occurred on the basal parts of the frond on which citrina juveniles are conspicuous against the dark substratum (Reimchen, 1979). Delayed expression of the yellow pigment and its replacement with a white-spiral mimic of encrusting tubes would be advantageous in juvenile snails in these habitats if *Spirorbis* tubes were present. This would account for the close association of the white-spiral juvenile phase with the citrina morph rather than the cryptic reticulate morphs. Termination of the white-spiral juvenile phase and activation of the adult shell pigmentation occurs when the shells reach approximately 4 mm in size. This size-dependent change from a mimetic to a cryptic phase occurs near the maximum size of the *Spirorbis* tubes and may be an adaptation resulting from reduced likelihood of predator deception by the mimic.

In localities where *Spirorbis* tubes were very abundant, even the cryptic dark reticulata exhibits the white-spiral juvenile phase. Presumably, this represents a situation where the strategy of being detected and ignored is more advantageous that a strategy of evading detection. The predation experiments suggested that the white-spiral had a marginal advantage over dark reticulata and accordingly,

it is not unrealistic that at high tubeworm densities, mimicry would be advantageous over crypsis. Conceivably, the juvenile littorines, simply as a consequence of the reduced surface area of algal substrates, might regularly crawl on the white tubes on which reticulata shells are conspicuous. A white-spiral phase could be advantageous for two reasons. It could be mimetic if the predator was deceived by the resemblance of the white-spiral phase to an individual tubeworm, but also cryptic if the predator did not detect the white-spiral phase amid the high tubeworm densities. Thus, there will be a graded series between mimetic and cryptic functions where classification becomes difficult since it will depend on the visual acuity and relative distances of the forager from the prey. Comparable problems exist in defining whether leaf and stone resemblances in insects are cryptic or mimetic (Endler, 1981 for review). Since distinct colour phases of the littorine occur during a brief part of the ontogeny on the same algal substrate and have a common predator, this could provide a useful experimental system for examining further conceptual aspects of crypsis and mimicry.

Presence of the white apex on adult *L. mariae* marginally reduces the degree of crypsis they achieve and presumably represents one of the costs of a distinct juvenile colour phase. The increased conspicuousness is greater for dark reticulata than it is for citrina. This could be disadvantageous to the adult snail (at least on fronds devoid of *Spirorbis*) when exposed to visual predators such as brachyuran crabs or shorebirds which forage on adult littorines (Pettitt, 1975; Reimchen, 1982). Such predation could produce selection against the occasional ontogenetic association between the white-spiral phase and dark reticulata.

Results of the present study suggest possible avenues for further investigations of juvenile shell colour. Ontogenetic shifts in early shell pigmentation may be relatively common in gastropods. In land snails such as *Cepaea nemoralis*, individuals heterozygous for shell colour occasionally express the pigment of the recessive allele for a short period after hatching (Cain *et al.*, 1960). In *Partula taeniata*, juvenile colour is often darker than the adult shell and controlled at a separate locus from major shell colour (Murray & Clarke, 1976). This could reflect differences of microhabitat during the ontogeny. Among prosobranchs, such as *Nerita picea*, juvenile colour is white but subsequent growth is increasingly dark, possibly associated with a habitat change from light to dark substrates (J. Buckland-Nicks, personal communication). *Thais emarginata* exhibits an abrupt transition during early shell growth from white to dark shells. This trait is heritable and geographically variable (A. R. Palmer, personal communication).

Evidence for visual selection and background matching have been found in investigations of shell colours in pulmonates (Cain & Sheppard, 1950; Cain *et al.*, 1960; Parkin, 1971) and in prosobranchs (Giesel, 1970; Heller, 1975; Smith, 1976; Reimchen, 1979; Mercurio *et al.*, 1985). Commonly, however, no associations were detected between colour and background among populations and alternate mechanisms have been suggested such as climatic selection (Cain & Currey, 1963; Parkin, 1972; Jones, 1973; Heller & Volokiti, 1981) as well as linkage and other non-functional interpretations to shell colour (Clarke & Murray, 1971; Grüneberg, 1978, 1980; Raffaelli, 1979; Berry, 1983). Several major factors emerge from the present study which are relevant to general investigations of molluscan shell colour. Visual selection by predators appears to be operating during the earliest stages of shell growth and consequently the background of these early age classes is relevant to the interpretation of adult population

variation. The early age classes and their precise substrates have been neglected in most previous studies of shell colour variation but where they were considered (Giesel, 1970; Reimchen, 1979), major evidence for background matching was detected. Also, selection by visual predators can produce abrupt transitions in shell colour (white-spiral to citrina or dark reticulata) during a short segment of the life which are associated with exceptionally small differences in the microhabitat of the snails. One of the reasons that visual selection is occasionally rejected as a mechanism is that morph frequencies show sharp changes in habitats where no obvious ecological boundary occurs (Clarke & Murray, 1971). These clines could be functional changes in shell colour and potentially result from differences in age-specific microhabitats among populations rather than as a consequence of differing genetic backgrounds (Clarke *et al.*, 1975 for review).

There seems little reason to believe that shell colour or its ontogeny in *L. mariae* is non-functional in any meaningful sense. To the contrary, the evidence suggests that the adaptations are very precise, as emphasized by Cain (1964), and that selection by visual predators is the overwhelming factor in the evolution of shell colour in this species. Such a unitary theme is not consistent with recent attacks on the adaptationist programme advocating a more pluralistic balance of functional and non-functional variation (Gould & Lewontin, 1979). Nor does the theme necessarily imply comparable mechanisms in other taxa where investigations have detected no associations between shell colour and background. However, since these studies did not consider some of the fundamental aspects of life histories such as sources of mortality, foraging positions of predators, and age-specific microdistributions, their abandonment of the role of visual selection is premature.

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