Substratum heterogeneity, crypsis, and colour polymorphism in an intertidal snail (*Littorina mariae*)

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On the British and Irish coasts, *Littorina mariae* showed extensive shell colour variation; the brown morph, dark reticulata, was common in exposed conditions, and the bright yellow morph, citrina, was common in shelter. *Fucus serratus*, the major substratum of *L. mariae*, contained a number of discreet colour backgrounds when viewed from the hunting position of *Blennius pholis*, a predator on juvenile *L. mariae*. These backgrounds corresponded closely to the colours of the principal morphs. The opaque stem is dark brown, while the lamina, when viewed with reflected light, is olive–brown. With light transmitted through the lamina, that is, when viewed from beneath the fronds, it appears a brilliant yellow. In predation experiments with *B. pholis*, citrina was taken preferentially to dark reticulata on the stem and on the lamina perceived by reflected light; with transmitted light, dark reticulata was preferred.

Examination of microdistributions showed juveniles prevalent on the lamina in sheltered shores but located on the stem and holdfast in exposed shores. The differences in adult morph frequencies between shores corresponded to the abundance of specific backgrounds on which juveniles were found. Stability in frequencies is discussed with reference to the heterogeneous backgrounds and density-dependent predation.

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Il y a beaucoup de variation dans la coloration de la coquille chez *Littorina mariae* des côtes d'Angleterre et d'Irlande: la forme brune, reticulata sombre, est commune dans les régions exposées, alors que la forme jaune clair, citrina, est commune dans les endroits protégés. *Fucus serratus*, principal substrat de *L. mariae*, comporte plusieurs zones de colorations distinctes lorsqu'on le regarde du point de vue de *Blennius pholis*, prédateur des formes immatures de *L. mariae*. Ces couleurs correspondent à celles des formes principales de *Littorina*. La tige opaque de l'algue est d'un brun foncé, alors que la lame, à la lumière réfléchie, est d'un brun olivâtre. Lorsque la lumière traverse la lame, c'est-à-dire vue de dessous, l'algue est d'un jaune brillant. Dans les expériences de prédation, *B. pholis* préfère la forme citrina à la forme reticulata sombre sur la tige et sur la lame lorsque la lumière est réfléchie, alors que, si la lumière passe à travers l'algue, le prédateur préfère la forme reticulata.

L'examen des microrépartitions a démontré que les gastropodes immatures se tiennent surtout sur les lames sur les rivages protégés, et surtout sur les tiges et les crampons, sur les rivages exposés. Les différences de fréquences des formes adultes entre les types de rivages correspondent à l'abondance des substrats spécifiques fréquentés par les formes immatures. La stabilité des fréquences est étudiée en fonction des substrats hétérogènes et de la prédation reliée à la densité.

[Traduit par le journal]

Introduction

Studies of discontinuous phenotypes or polymorphisms have provided some understanding of selective pressures and the maintenance of variability. Among these, colour variations have been extensively considered in lepidopterans such as *Panaxia* (Sheppard and Cook 1962), *Biston* (Kettlewell 1955; Bishop 1972), and *Papilio* (Clarke and Sheppard 1963) and in molluscs such as *Cepaea* (Cain and Sheppard 1954; Cain and Currey 1963; Sheppard 1951; Arnold 1971), *Partula* (Clarke and Murray 1969), and *Acmaea* (Giesel 1970).

In the intertidal region, there are a number of gastropod species which show variation in shell colour, and as in *Cepaea*, have morph frequencies which differ markedly between localities. Barkman (1956), working with samples of a small prosobranch *Littorina obtusata* from Holland, Norway, Scotland, and Brittany, found that the common colour morphs, citrina, olivacea, and reticulata, varied significantly between shores, generally in an unpredictable manner. When Sacchi and Rastelli (1966) split *L. obtusata* into two sibling species, *L. obtusata* and *L. mariae*, they found that the morph

frequencies differed between the species. Many of the differences in frequencies observed by previous workers were in fact changes in the abundance of the two siblings.

With further work by Sacchi (1969) in Brittany, it was apparent that the highly variable morph frequencies in each species behaved in a predictable pattern on shores of different exposure. He found that in sheltered conditions, olivacea was the most common morph of *L. obtusata* while citrina was the most common in *L. mariae*; on exposed shores dark reticulata predominated in both species. Sacchi considered each of the morphs, except citrina, to be relatively well camouflaged against their algal background. To account for the occurrence of the bright yellow citrina and the variation in frequencies, he suggested that selection was acting on pleiotropic characters such as salinity tolerance and adhesion ability rather than on shell colour itself. Similar conclusions were also reached by Gratton (1969) with regard to the variation in *L. mariae* from southern Wales.

However, in a genus such as *Littorina* which has a number of visual predators (Pettitt 1975), shell colour itself should contribute to the fitness of the individual. The present study on *L. mariae* was undertaken to examine aspects of the life history which might lead to functional interpretations of the colour polymorphism. Its purpose was to document the extent of geographical variation in morph frequencies, the precise microdistribution of individuals against the algal background, and the influence of a visual predator on the polymorphism.

Breeding experiments with the two common morphs, citrina and dark reticulata, have shown that the colour polymorphism is genetically determined with no detectable environmental influence (Reimchen 1974). Although it was not possible to choose between a single or double loci system, dark reticulata generally behaves as a single allele dominant to citrina.

Methods

Collections of *L. mariae* were obtained from 91 localities on the coasts of Ireland, Wales, and southern England between 1970 and 1973 (Fig. 1). Sites were chosen so as to include samples from a wide range of shore exposures, from luxuriant algal cover in sheltered bays to near algal-free exposed headlands. On some of these shores where gradients of exposure were present, subsamples were taken from the most sheltered and most exposed areas. To obtain some indication of morph stability, 27 localities were resampled over a period of 3 years.

Procedures for collecting were to choose representative areas on the shore and collect all *L. mariae* from randomly chosen plants in the area. Each algal frond was vigorously rubbed against the underlying rock and collections made of individuals

which had fallen on the rock surface. The frond was also visually checked for remaining individuals. Additional plants, at least 3 m apart, were also sampled.

Exposure was estimated at each site using indicator species which vary predictably according to differing degrees of wave action (Ballantine 1961). A scale of 1 (sheltered) to 5 (exposed) was constructed using principally the presence and abundance of *Ascophyllum nodosum*, a surf-intolerant brown alga, and *Verrucaria maura*, a black lichen which thrives only in the splash zone above high water mark. Values of 1 and 5 in this exposure scale are equivalent to the "very sheltered" and "semi-exposed" categories of Lewis (1964).

Following the geographical survey, observations were made on the morphology and colour variation of *Fucus serratus*, the major substratum and food plant of *L. mariae*. Data were collected on the microdistributions of individual *L. mariae* during low tide from nine shores in Anglesey, all differing in the amount of exposure. For each snail, a record was made of the specific part of *F. serratus* on which the snail rested (stem or lamina), its age (juvenile or adult), and its colour phenotype (citrina or reticulata). To obtain a quantitative description of position, the total frond length, from the holdfast to the apex of the lamina, was measured along the axis of the frond; the position of each snail along this length was then scored. To determine the microdistribution on submerged plants, some general observations were made at high tide with SCUBA in two of the localities.

Samples were taken of six common species of intertidal fish for examination of stomach contents. The species and numbers collected were *Gobius paganellus* (18), *G. ruthensparri* (23), *Blennius pholis* (137), *Cottus bubalis* (24), *C. scorpius* (24), and *Onus mustellus* (16). They were captured from tidal pools and from under rocks at three localities in Anglesey (Porth Swtan, Sandy Bay, and North Stack). All *L. mariae* found in the stomachs were measured for length. One of the species, *B. pholis*, was collected for predation experiments and kept in glass holding tanks with circulating seawater at 10 to 15°C.

As many as 14 categories of shell colour have been delineated in previous studies of *L. obtusata* and *L. mariae* (Dautzenberg and Fisher 1914; Reimchen 1974). For the purpose of this study, I have followed Sacchi's distinctions of the morphs (Sacchi 1969) in recognizing four broad colour categories: citrina (yellow), olivacea (olive–green to olive–brown), light reticulata (brown reticulations on a yellow ground colour), and dark reticulata (dark reticulations on a brown ground colour). In the majority of populations, shells were easily scored into four principal phenotypes. Occasionally, however, colour discontinuities were less clearly expressed, and in these cases, the individuals were grouped according to their colour proximity to one of the four major phenotypic classes. Barkman (1956) reported that a small percentage of light-coloured juvenile shells became darker with new increments of shell growth; accordingly, for the geographical survey in this study, only adult shells have been scored.

Results

Aspects of the Life History of L. mariae

L. mariae, ranging from 6 to 14 mm in adult size, is commonly found on one species of lower intertidal fucoid, *Fucus serratus*. It is relatively sedentary and may graze on a single plant for up to 2 weeks before moving to an adjacent frond. Sexes are separate and breeding occurs from spring through to autumn. Under laboratory conditions,
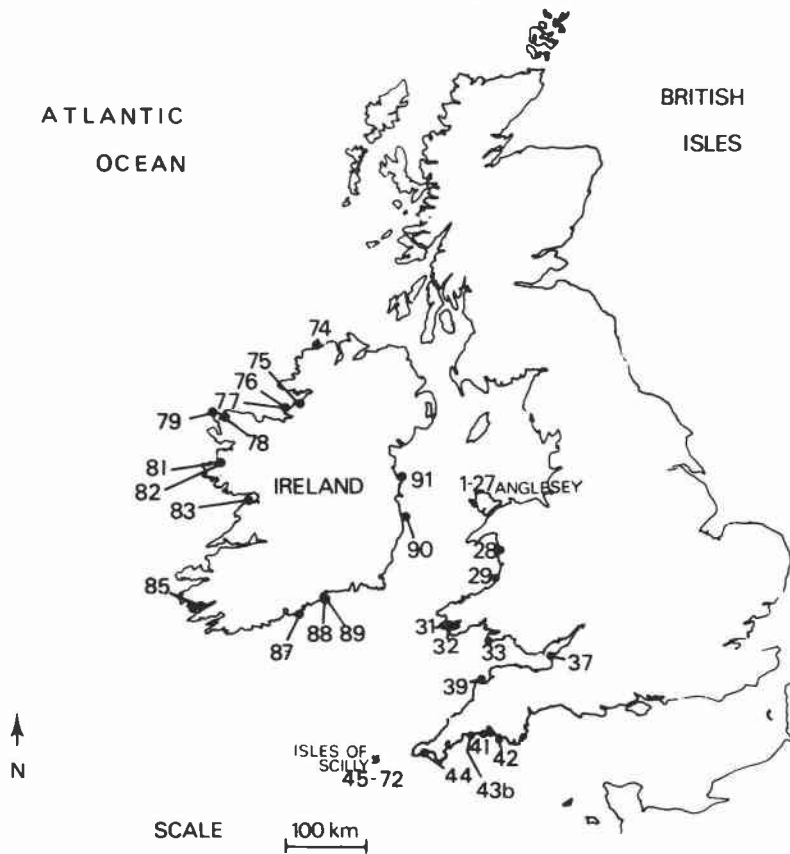
FIG. 1. Collection sites. See Table 2 for locality names.

clutches of 50 to 100 eggs are laid soon after copulation. Within 4 to 8 weeks the eggs hatch and the young snails, about 0.5 mm in length, disperse on the plant feeding on settled matter and on the softer areas of the lamina. Although adult size is reached after 1 year, the actual life span is not known; in the laboratory, adult individuals were kept for a period of 2 years.

Mortality is high at the juvenile stage, and much of it appears to be due to *Blennius pholis*, a common species of fish that seldom exceeds 110 mm in length. In the stomach analysis of six species of intertidal fish, only *B. pholis* contained shells of *L. mariae*. The number of shells consumed per individual was variable; there were no *L. mariae* in 49% of the stomachs, 1 to 5 shells in 39%, 6 to 10 in 9%, and over 10 in 3%. Observations with SCUBA at high tide provided supplementary information on the predation rate. Within 60 min, a blenny approximately 70 mm in length consumed 14 out of 64 *L. mariae* from a single plant. In the laboratory, 30 individuals were consumed in the same period of time. The predation by this species was primarily on juveniles; mean shell size in the stomachs of

field-caught individuals was 2.4 mm, with a range of 0.5 to 8 mm (Fig. 2). The upper size limit in the shells appears to be due to the difficulty that blennies have, at least in the laboratory, in swallowing larger individuals.

There are a number of other possible predators, such as crabs (*Carcinus*, *Cancer*, and *Macropipus*), birds (*Larus* and *Haematopus*), and subtidal fish (*Pleuronectes* and *Gadus*). These species and others, many with well developed colour vision, have been tabulated by Pettitt (1975) in a review of the predators on *Littorina*. From the abundance of these species, as well as *B. pholis*, in the study area, the visual predators may be important selective agents in the life history of *L. mariae*.

General Distribution of the Morphs

Citrina and dark reticulata were the two most common morphs throughout the study area, occurring with mean frequencies of 47% and 36% respectively. Light reticulata was less common in most localities, having a mean frequency of 16%, while olivacea was rare, at a mean of 0.5% (Table 1). In four out of five of the geographical regions,
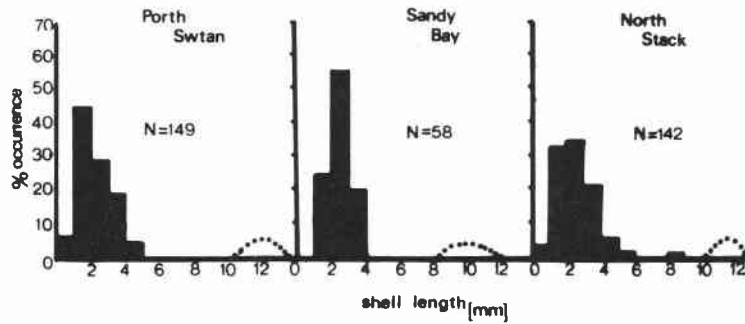
FIG. 2. Distribution of shell sizes in stomachs of *B. pholis*. Collections of 135 blennies made during April, July, and October. *N* = total number of shells. Dotted line shows adult size range for each locality.

TABLE 1. Distribution of morph frequencies between major collecting areas. Values shown as percentages

Area	Citrina			Olivacea			Reticulata			Dark reticulata			No. localities
	$\bar{x}$	s	Range	$\bar{x}$	s	Range	$\bar{x}$	s	Range	$\bar{x}$	s	Range	
Anglesey	44.6	36.5	1–100	0.2	1.2	0–6	19.1	22.3	0–70	36.1	25.4	0–98	36
Rest of Wales	66.0	29.7	50–100	0	0	0	10.2	7.9	0–15	23.8	29.2	0–67	5
South England*	26.0	35.1	0–100	1.4	7.0	0–11	1.4	4.1	0–10	72.6	36.8	0–100	6
Isles of Scilly	43.1	28.7	0–100	2.9	7.5	0–22	15.5	16.3	0–54	38.5	36.3	0–100	18
Ireland	44.1	35.4	0–100	0	0	0	11.3	16.6	0–56	44.6	33.8	0–100	15

*Includes Somerset, Devon, and Cornwall.

the two common morphs showed extensive variation in frequencies, ranging from near 0% in some localities to near 100% in others.

When the relative proportions of the morphs were considered in relation to exposure at each site, certain trends were evident. Citrina was most abundant in sheltered localities, often representing 100% of the sample, whereas dark reticulata predominated in exposed conditions. For example, in the sheltered Menai Straits at Anglesey, northern Wales (Fig. 3, sites 19–27), frequencies of citrina were greater than 95% in all localities. However, 5 km to the north at Fedwfawr (site 1), a very exposed shore, the frequency decreased to 1%, being replaced principally by dark reticulata. This trend was also evident in the other major collecting areas, mainland Wales and southern England, the Isles of Scilly, and Ireland. Weighted regression analyses indicate a significant relationship between exposure and morph frequency for each area (Figs. 4 and 5).

Steep clines in morph frequencies were occasionally evident over short distances along the shore. Between Sandy Bay (site 8*a*) and Sandy Point (site 8*b*) the frequency of citrina decreased from 53% to 4% over a distance of 25 m, while dark reticulata increased from 0% to 75% (Fig. 3). Between Rhosneigr Bay (site 16*a*) and Rhosneigr

Point (site 16*b*) over a distance of 50 m citrina decreased from 30% to 4% while dark reticulata increased from 5% to 96%. In both of these localities, there was a steep exposure gradient, with the highest frequencies of dark reticulata corresponding to the greatest exposure. Similar steep clines were also present on the Isles of Scilly (sites 46*a* and 46*b*; sites 57 and 58; Table 2).

There were exceptions to the above relationship between morph and exposure. At Weston-super-Mare in the Bristol Channel (site 37), a locality categorized as sheltered, citrina was absent and dark reticulata predominated. In three very exposed localities on the west coast of Ireland, Tiraun Point (site 79), Cloonagh (site 82), and Ballynagaul Point (site 89), dark reticulata was present at unusually low frequencies of 35%, 27%, and 25% respectively. In addition, at two of these localities, the 'dark' reticulata was lighter in colour in comparison with other samples.

The light reticulata phenotype did not show any consistent pattern in relation to exposure. In Anglesey and the Isles of Scilly, the highest frequencies were observed on both sheltered and semiexposed shores, while in Ireland it was common on exposed localities (Fig. 6).

Olivacea was rare or absent from localities in Wales and Ireland but was commonly observed in
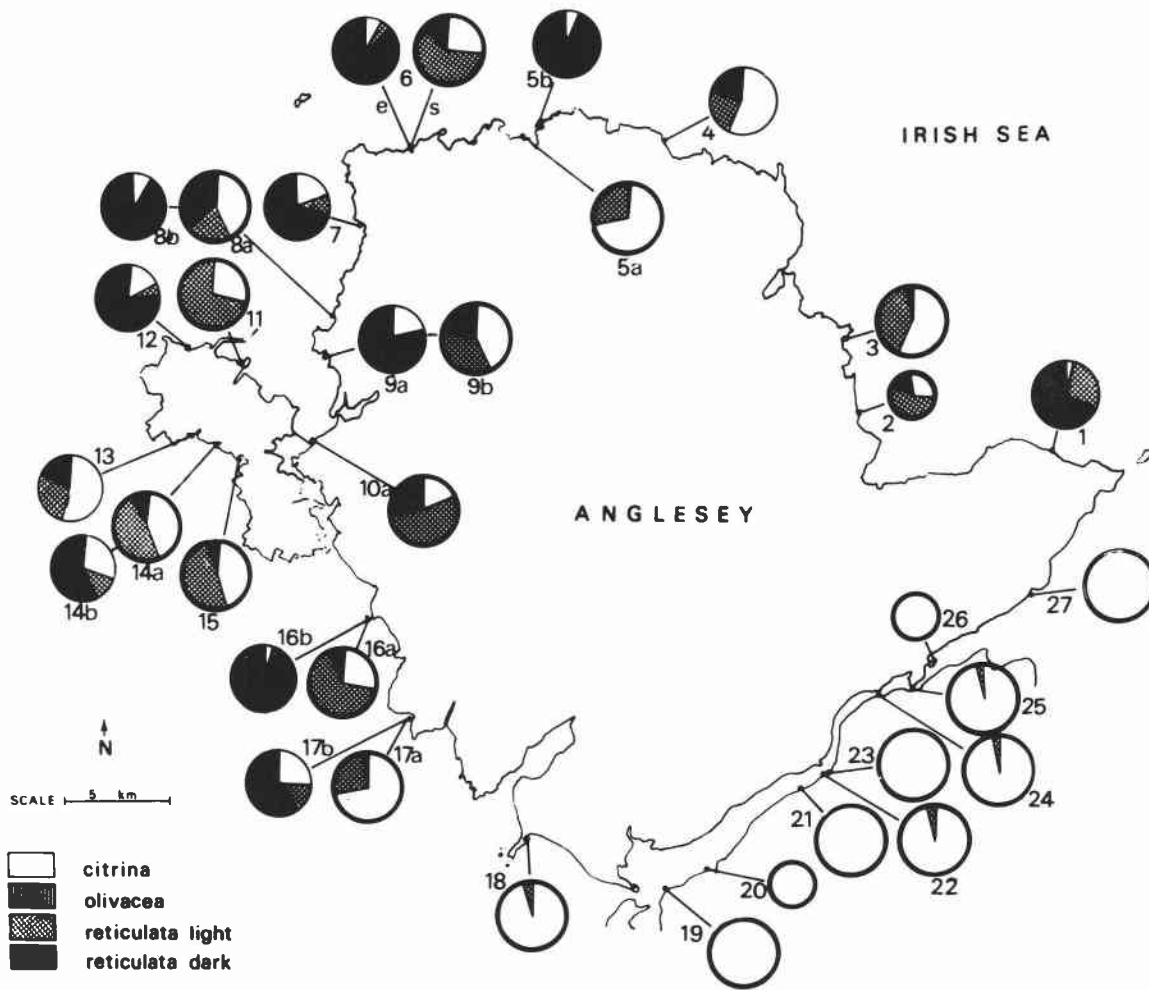
FIG. 3. Colour-morph frequencies in Anglesey, North Wales. Small circles, less than 10 individuals in sample. One locality shows subsample from exposed (*e*) and sheltered (*s*) conditions. 1% = 3.6 degrees of arc.

southern England and the Isles of Scilly. When present, it was usually associated with sheltered conditions where citrina was common.

Some data are available on the stability of morph frequencies from Anglesey and the Isles of Scilly (Table 2). The most comprehensive collections were made at Sandy Bay (site 8*a*), where over a period of 2 years citrina fluctuated between a low of 31% and a high of 53%. Differences of this order of magnitude were seen on the Isles of Scilly as at Old Quay (site 63). Dark reticulata, absent from the sample taken in 1971, constituted 64% of the individuals in 1972. The majority of localities, however, showed relatively small fluctuations in morph ratios.

Substratum Heterogeneity and Shell Colour

There is a great deal of colour heterogeneity

within a frond of *F. serratus*. The holdfast, stem, and base of the lamina are dark brown to black; medially the colour becomes progressively lighter to an olive–brown, and finally to an olive–yellow at the apex of the lamina. There are differences in plant morphology both between and within shores. In sheltered conditions, the plants often exceeded 1 m in length and were composed of broad laminae with short thin stems. In exposed localities, the fronds were short (approximately 0.5 m) with narrow laminae and large thick stems (Fig. 7). Within shores, these same differences occurred where sharp gradients in exposure were present. In addition, younger plants were composed predominantly of broad laminae, while in older individuals, laminae were reduced in breadth often with only the midrib remaining. These differences in the morphology between plants change the relative
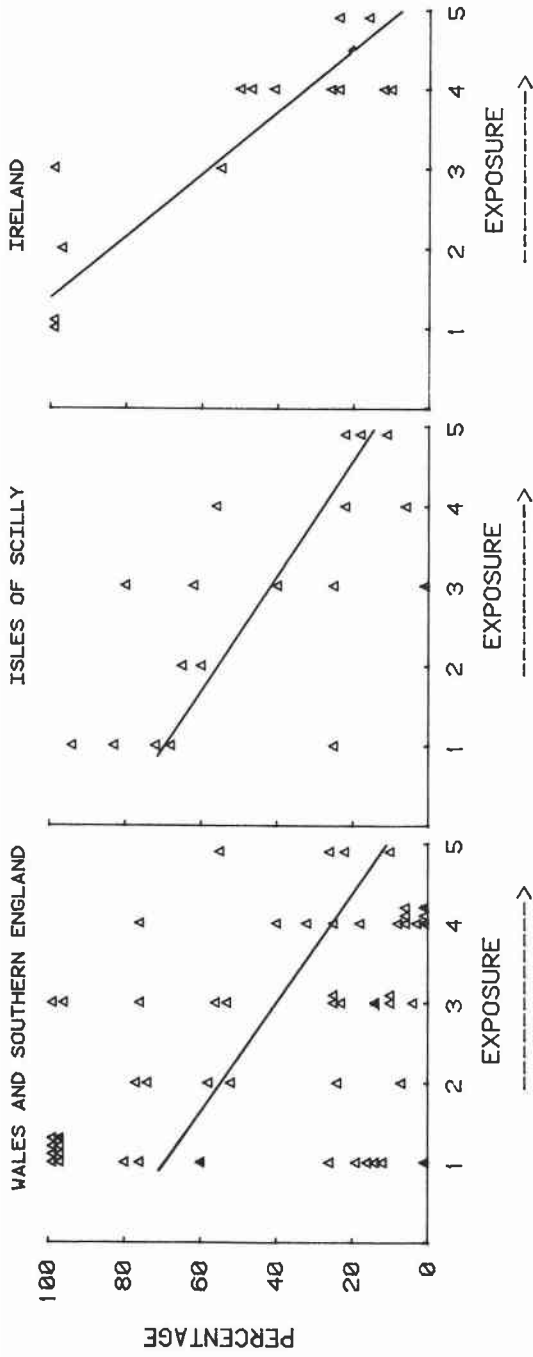
FIG. 4. Relationship between citrina and exposure with weighted regression analysis. Localities weighted in proportion to sample size. Wales and southern England, $y = 84.6 - 14.6x$, $t = 4.60$, $P < 0.001$; Isles of Scilly, $y = 82.6 - 13.3x$, $t = 3.58$, $P < 0.01$; Ireland, $y = 133.5 - 24.4x$, $t = 7.03$, $P < 0.001$. ▲ localities from southern England.
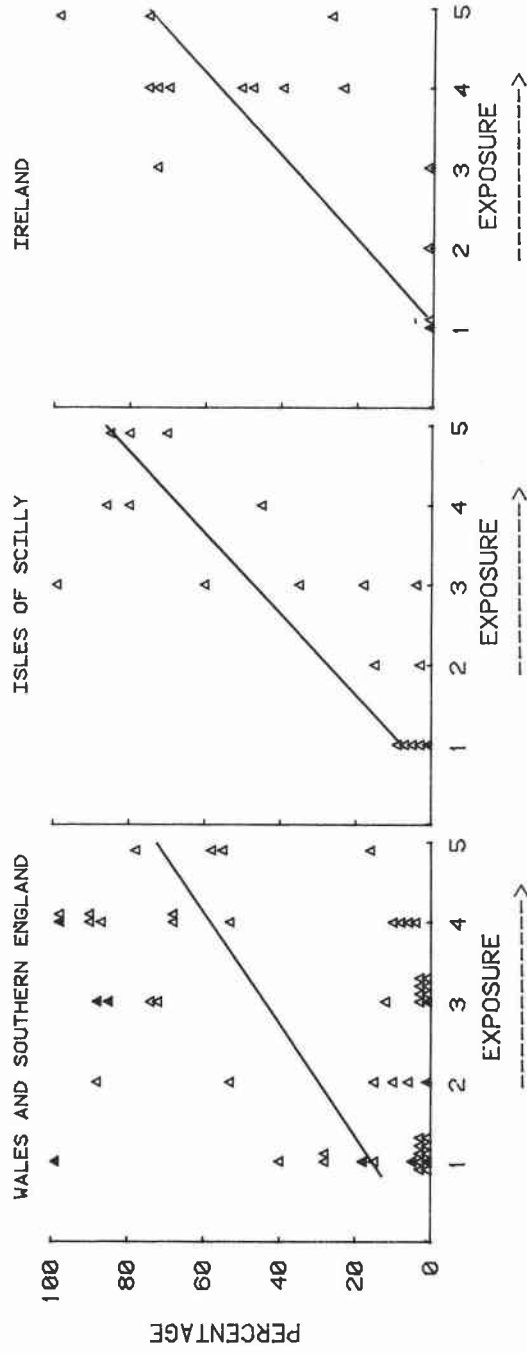

FIG. 5. Relationship between dark reticulata and exposure with weighted regression analysis. Wales and southern England, $y = 1.7 + 12.0x$, $t = 3.57$, $P < 0.001$; Isles of Scilly, $y = -15.5 + 19.6x$, $t = 5.08$, $P < 0.001$; Ireland, $y = -20.7 + 18.6x$, $t = 3.65$, $P < 0.01$. ▲ localities from southern England.

TABLE 2.* Morph distributions for localities with repeated sampling

No. Locality		Exp	Date, month/year	Phenotype				Total
				cit	lr	dr	ol	
Anglesey, North Wales								
1	Fedwfawr	4	11/70	1	20	55	0	76
		4	6/71	0	3	14	0	17
4	Bull Bay	2	2/71	44	16	13	0	73
		2	5/72	15	4	1	0	20
5a	Cemaes Bay	2	3/71	12	4	0	0	16
		2	3/73	45	18	0	0	63
7	Porth Swtan	4	2/71	25	13	90	0	128
		4	6/71	24	13	130	0	167
		4	4/72	4	1	26	0	31
		4	11/72	4	0	35	0	39
		4	3/73	6	0	31	0	37
8a	Sandy Bay	3	11/71	36	10	40	0	86
		3	1/72	29	3	44	0	76
		3	5/72	56	18	31	0	105
		3	8/72	8	2	12	0	22
		3	11/72	12	4	16	0	32
		3	2/73	49	22	54	0	125
		3	5/73	77	26	101	0	204
		3	8/73	64	17	103	0	204
8b	Sandy Point	4	5/72	3	0	75	0	78
		4	3/73	1	0	49	0	50
9b	Penrhyn-mawr	1	3/71	38	42	6	0	86
		1	4/73	34	34	18	0	86
11	Holyhead Bay	1	4/71	1	7	0	0	8
		1	6/72	13	30	0	0	43
12	North Stack	5	5/71	22	8	101	0	139
		5	9/71	9	3	52	0	64
		5	4/72	5	3	49	0	57
		5	4/73	11	10	53	0	74
15	Trearddur Bay	3	5/71	49	53	4	0	106
		3	6/72	8	23	0	0	31
16a	Rhosneigr Bay	2	5/71	41	101	9	0	151
		2	4/73	22	49	5	0	76
17a	Cywfan Bay	2	5/71	74	29	1	0	104
		2	4/73	20	15	0	0	35
18	Llanddwyn	3	5/71	120	2	0	0	122
		3	9/72	41	1	0	0	42
19	Ysgubor Isaf	1	5/71	10	0	0	0	10
		1	6/72	16	0	0	0	16
24	Train Bridge	1	5/71	108	2	0	0	110
		1	5/72	177	3	0	0	180
		1	4/73	66	0	0	0	66
25	Menai Bridge	1	5/71	107	3	0	0	110
		1	4/72	124	7	0	0	131
Cornwall								
44	Penzance	1	4/71	5	0	3	0	8
		1	5/72	24	0	0	0	24
Isles of Scilly								
46a	Heathy Point	5	4/71	10	1	41	0	52
		5	5/72	6	0	21	0	27
59	Top Rock Point	3	4/71	32	0	44	0	76
		3	5/72	5	0	30	0	35
60	Top Rock Bay	2	4/71	104	32	19	0	155
		2	5/72	7	0	2	0	9
61	Bull's Porth	5	4/71	37	8	107	1	153
		5	5/72	6	1	21	0	28
63	Old Quay	3	4/71	8	16	0	0	24
		3	5/72	4	4	14	0	22

TABLE 2.* (*Concluded*)

No. Locality		Exp	Date, month/year	Phenotype				Total
				cit	lr	dr	ol	
64	Lawrence Bay	1	4/71	4	6	2	3	15
		1	5/72	4	5	0	2	11
66	Toll's Island	4	4/71	2	0	8	0	10
		4	5/72	1	1	10	0	12
68	Porthloo	2	4/71	6	2	0	2	10
		2	5/72	14	10	3	2	29

NOTE: Exposure scale (Exp) from 1 (very sheltered) to 5 (very exposed). cit, citrina; lr, light reticulata; dr, dark reticulata; ol, olivacea.

*An expanded table including sites with single collections is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2.

proportions of background colours and presumably, therefore, the fitness of the colour morphs depending upon their positions on the plant.

The dark reticulata phenotype, although relatively cryptic on the lamina, is remarkably cryptic on the stem and holdfast. The colour is so well matched that very close inspection is required to locate the shells, especially those of the juveniles because of their size. The crypsis is further enhanced by the orientation of the shell, which is usually towards the base of the plant. The dark lines of the reticulate pattern create a disruptive effect to the outline of the shell when it is orientated along the longitudinal axis of the stem.

The discrete appearance of the bright yellow citrina appeared, at first sight, to have no corresponding background colour on *F. serratus*, suggesting that apostatic selection could be operating. However, during underwater field work, additional background colours were discernible when viewed from the hunting positions of one of the predators. In their natural habitat, *B. pholis* spent much of their time under and within the fronds of *F. serratus* searching for *Littorina* on the laminae above them. When a snail was seen they would swim upwards, pluck it from the frond and swallow it. From my vantage point on the side of the plant, the reticulata morphs appeared well camouflaged while citrina appeared conspicuous. But when I moved to the base of the plant and was now viewing the snails from the same position as the blenny, that is from below the fronds, the significance of the bright yellow colouration in citrina became evident. The lamina, instead of appearing olive–brown from reflected light, which is the common situation from the human standpoint, appeared brilliant yellow when viewed with transmitted light through the fronds. When seen against this background, citrina was extremely well camouflaged, while dark reticulata became very conspicuous (Figs. 8, 9, and 10). In fact, if citrina was even slightly duller in

appearance, the very exact crypsis would have been lost.

Transmitted light influences the apparent colour of *F. serratus* in further ways. The blennies were occasionally seen within the algal clump preying on snails resting on the laminae beneath them. This would seem to favour one of the darker morphs as perception of the lamina was now with reflected light. However, citrina was again well camouflaged as the interior fronds were illuminated in yellow from light transmitted through the outer fronds. Plants with broad thin laminae provided the greatest transmission of yellow light, these being the most prevalent on sheltered shores.

The lamina is not of uniform thickness throughout its length and consequently will show differences in the amount of transmitted light and therefore background colour. Near its origin adjoining the stem (which is completely opaque), there is a small thickened area through which only a limited amount of light passes. When placed against this background, both citrina and dark reticulata were equally conspicuous, but a third morph, light reticulata, was very cryptic.

From the observations on the role of reflected and transmitted light, there appeared to be four principal background colours: a dark brown on the stem and holdfast, a light brown near the base of the lamina, a bright yellow on the lamina with transmitted light, and an olive–green on the outer lamina perceived with reflected light. The four morphs, dark reticulata, light reticulata, citrina, and olivacea, correspond very well to these colours.

Laboratory experiments were set up to determine whether the blenny would demonstrate a preference for a certain phenotype depending upon the position of the prey and the manner of illumination. A *F. serratus* plant was placed in each of three glass tanks illuminated from above by a white fluorescent light with two 60-W tubes. One blenny was then placed in each tank and allowed 1 day for
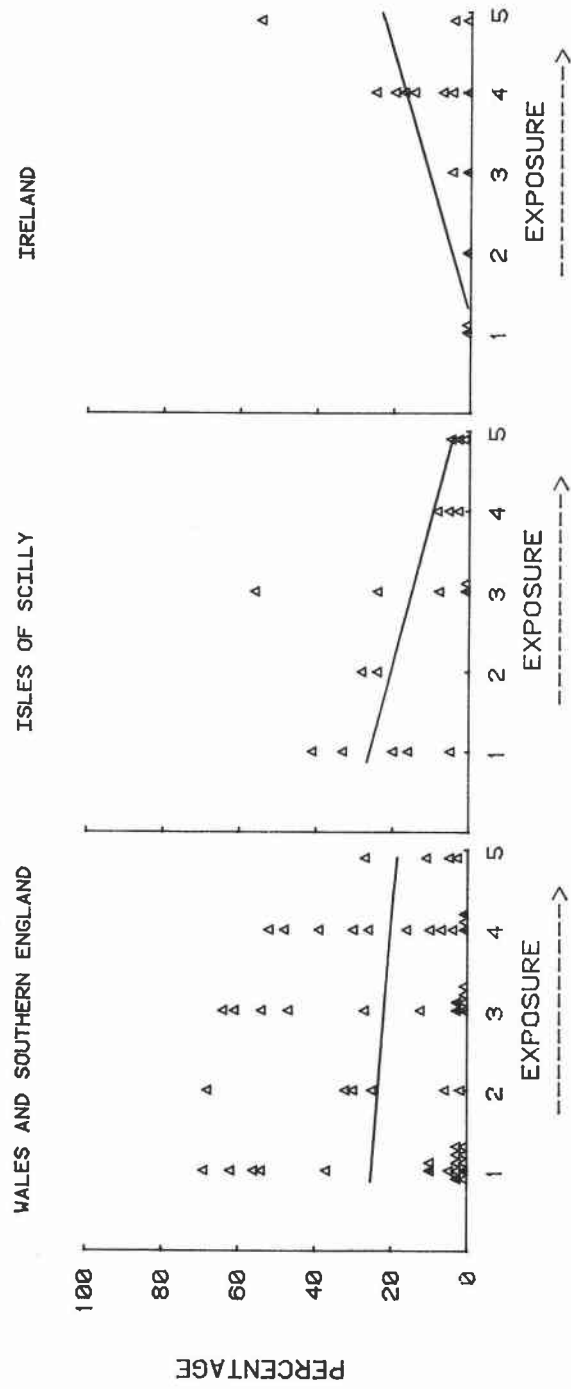
FIG. 6. Relationship between light reticulata and exposure with weighted regression analysis. Wales and southern England, $y = 26.5 - 2.0x$, $t = 0.96$, not significant (NS); Isles of Scilly, $y = 31.7 - 6.0x$, $t = 2.63$, $P < 0.02$; Ireland, $y = -7.1 + 4.7x$, $t = 1.71$, NS. ▲, localities from southern England.
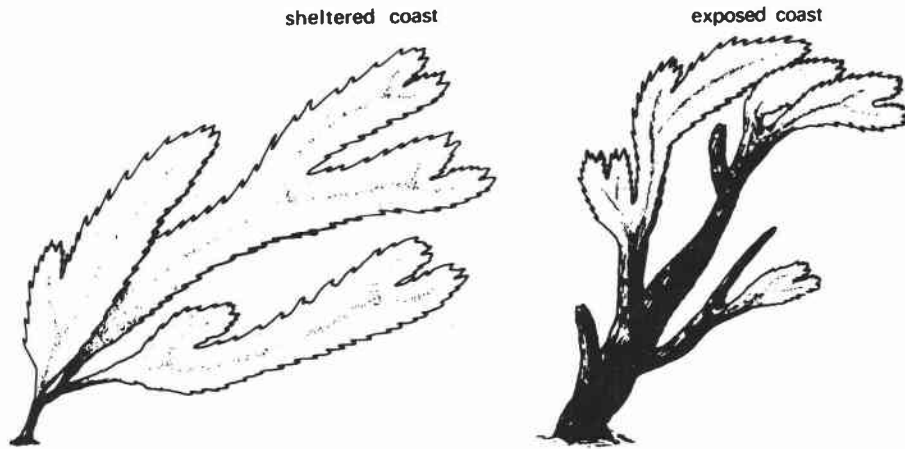
FIG. 7. Generalized sketch of *F. serratus* from sheltered and exposed shores.

TABLE 3. Results of predation experiments

Substrate	Tank	First taken		$\chi^2_{(1)}$	P
		Citrina	Dark reticulata		
F. serratus lamina with reflected light	1	13	7	1.8	0.10–0.25
	2	15	5	5.0	0.03–0.05
	3	12	8	0.8	0.25–0.50
Total		40	20		
Summed				$\chi^2_{(3)} = 7.6$	0.05–0.10
Pooled				$\chi^2_{(1)} = 6.8$	<0.01
Heterogeneity				$\chi^2_{(2)} = 0.8$	0.25–0.50
F. serratus lamina with transmitted light	1	3	17	9.8	<0.005
	2	8	12	0.8	0.25–0.50
	3	4	16	7.2	0.01–0.03
Total		15	45		
Summed				$\chi^2_{(3)} = 17.8$	<0.005
Pooled				$\chi^2_{(1)} = 15.0$	<0.005
Heterogeneity				$\chi^2_{(2)} = 2.8$	0.05–0.10
F. serratus stem at bottom of tank	1	14	6	3.2	0.05–0.10
	2	18	2	12.8	<0.005
	3	17	3	9.8	<0.005
Total		49	11		
Summed				$\chi^2_{(3)} = 25.8$	<0.005
Pooled				$\chi^2_{(1)} = 24.2$	<0.005
Heterogeneity				$\chi^2_{(2)} = 1.6$	0.25–0.50
F. serratus stem at water surface	1	14	6	3.2	0.05–0.10
	2	15	5	5.0	0.03–0.05
	3	11	9	0.2	0.50–0.90
Total		40	20		
Summed				$\chi^2_{(3)} = 8.4$	0.005
Pooled				$\chi^2_{(1)} = 6.7$	0.01–0.05
Heterogeneity				$\chi^2_{(2)} = 1.7$	0.25–0.50
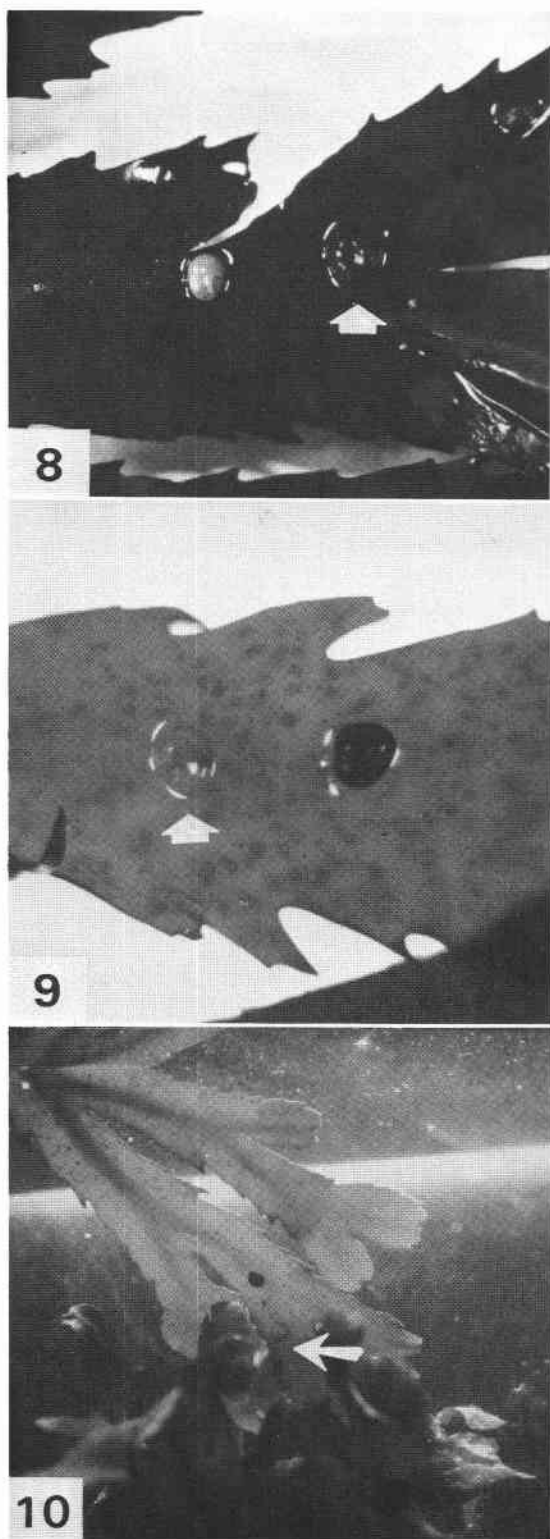
habituation to the artificial conditions. Individuals of citrina and dark reticulata of the same size were presented in pairs to the blennies in the following ways: (1) On the surface of the lamina placed at the bottom of the tank necessitating the blenny's approach from above. Visual perception by reflected light. (2) On the underside of a lamina which was held near the water surface allowing an approach from below. Illumination by transmitted light. (3) On the upper side of a stem at the bottom of the tank. (4) On the underside of a stem held near the surface.

Usually within 30 s, the blenny approached the frond and took one or both of the phenotypes (Fig. 10). In each case the first snail taken was recorded. The four substrata were presented in alternating sequences with a 15-min interval between each trial. The experiment was carried out for 20 days in succession with a total of 80 trials for each fish.

The results suggest very strongly that the fitness of the two common morphs is in part a function of both position and light regime (Table 3). Citrina was eaten preferentially on the lamina perceived with reflected light and on the stem in both light regimes; with transmitted light through the lamina, dark reticulata was preferred.

These experiments and the observations on background colour provide a functional explanation for the visual appearance of the four different colour phenotypes. It is necessary to consider, therefore, whether each morph is nonrandomly distributed with respect to specific substratum and whether differences in morph frequencies between localities are reflected in differences in the proportions of backgrounds.

Microdistribution

Comparisons were made of the microdistributions of citrina and dark reticulata within each of six sites in Anglesey. There were no statistically significant differences between the morphs with respect to the two major substrata, stem and

FIG. 8. Influence of reflected light on the colour of *F. serratus* in relation to crypsis of citrina and dark reticulata, the latter shown with an arrow. Light source from above with a single 6 W fluorescent tube. FIG. 9. Influence of transmitted light on the colour of *F. serratus* showing citrina (arrow) and dark reticulata. Major light source from below shining through lamina. FIG. 10. *Blennius pholis* in common hunting position. Dark reticulata and citrina on lamina viewed against transmitted light (citrina near mouth of *B. pholis*). Figures 8–10 are available in colour, at a nominal charge, from the Depository of Unpublished Data, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2, or with reprints if requested.

TABLE 4. Microdistribution of citrina and dark reticulata on the stem and the lamina

Locality	Shell size	Phenotype	Position on F. serratus stem	Position on F. serratus lamina	χ^2	$P*$
Rhosneigr	Adult	Citrina	1	41	—	0.65*
		Dk. ret.	4	64		
Sandy Bay	Juvenile	Citrina	6	22	1.49	0.10–0.50
		Ret.	24	41		
	Intermediate	Citrina	4	37	—	0.18*
		Dk. ret.	11	64		
	Adult	Citrina	6	125	0.06	0.50–0.90
		Dk. ret.	15	192		
Hen Borth	Adult	Citrina	1	19	—	0.65*
		Dk. ret.	12	95		
Porth Swtan	Juvenile	Citrina	7	9	0.32	0.50–0.90
		Dk. ret.	21	16		
	Adult	Citrina	20	204	0.71	0.25–0.50
		Dk. ret.	84	666		
Cemaes Hd.	Juvenile	Citrina	3	5	—	0.05*
		Dk. ret.	77	31		
	Intermediate	Citrina	6	9	0.97	0.25–0.50
		Dk. ret.	42	36		
	Adult	Citrina	1	9	—	0.40*
		Dk. ret.	10	76		
Sandy Point	Juvenile	Citrina	12	6	—	0.16*
		Dk. ret.	70	23		
	Intermediate	Citrina	12	4	—	0.19*
		Dk. ret.	39	7		
	Adult	Citrina	2	14	—	0.34*
		Dk. ret.	18	52		

NOTE: Ret., light reticulata and dark reticulata not distinguishable; Dk. ret., dark reticulata; *, where expected value is less than 5, P is given as exact probability.

lamina (Table 4). However, in each of the 13 comparisons, the morphs were slightly more common on their expected substratum, dark reticulata on the stem and citrina on the lamina. These small differences could be due either to microhabitat preferences or to selective elimination by predators. It is improbable that the trend is an artifact of collecting, for this would tend to show relatively fewer numbers of dark reticulata on the stem due to their excellent crypsis, especially in juvenile shells.

There were major differences between the distributions of juvenile and adults on *F. serratus*. One method of comparison was to record the percentage of snails at various positions between the holdfast and the apex of the lamina (Fig. 11A). In the most sheltered locality, Menai Bridge, both juveniles and adults were found principally near the apex of the lamina. In localities with increased exposure, the adults occupied the same position near the apex, but the juveniles became progressively more common near the base of the plant. On the very exposed shore, Sandy Point, the majority of

juveniles were found near the base while the adults remained near the apex.

A second method of comparing distributions was to consider the proportions found on the stem and on the lamina (Fig. 11B). This takes into account the variation in the amount of stem within and between shores (Fig. 7). At Menai Bridge 96% of the juveniles and 95% of the adults were located on the lamina. On a more exposed shore such as Porth Swtan, the lamina contained only 50% of the juveniles but 92% of the adults. At Sandy Point, the most exposed of the localities, the proportion of juveniles was reduced to 25% while the proportion of adults decreased slightly to 75%. Underwater observations with SCUBA at this exposed locality revealed that microdistributions were similar during low and high water.

These differences in juvenile distributions indicate major differences in background colour between shores. In exposed localities, the majority of juveniles were found on the dark brown substratum of the stem and the holdfast on which dark re-
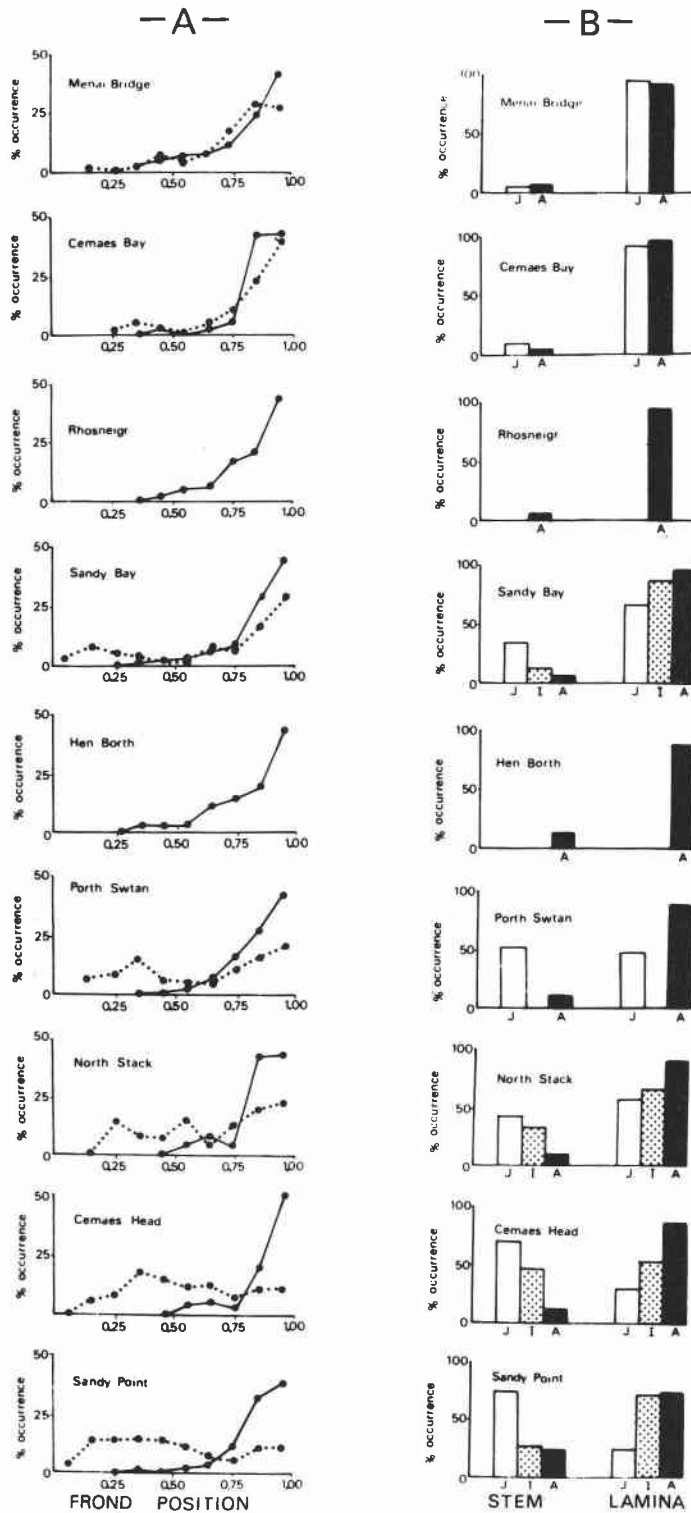
FIG. 11. Distributions of juvenile and adult *L. mariae* on *F. serratus* on shores differing in exposure. Localities arranged from most sheltered (top) to most exposed (bottom). (A) Proportions of juveniles (dotted line) and adults (solid line) along length of frond, values near 0 representing the holdfast and base of the stem, values of 1 indicating apex of lamina. (B) Proportions of juveniles (plain), adults (solid), and in some graphs, intermediate size classes (dotted) on the stem and the lamina. For sample sizes, see Table 3.
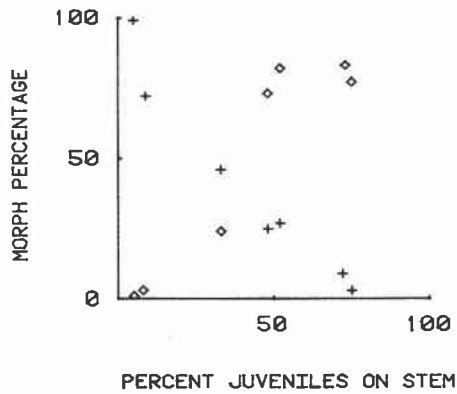
FIG. 12. Frequencies of juveniles on stem in relation to population morph frequencies from seven localities in Anglesey. +, citrina; ◇, dark reticulata.

ticulata is cryptic. Conversely, on sheltered shores, the juveniles were found on the lamina, on which citrina is cryptic. In these localities, adult morph frequencies varied from 97% citrina and 0% dark reticulata at Menai Bridge to 30% citrina and 70% dark reticulata at Sandy Point. These frequencies principally reflect the dominant colour backgrounds on which the juveniles were found (Fig. 12).

Discussion and Conclusions

Throughout the study area, in Ireland, Wales and southern England, and the Isles of Scilly, there was a general correlation between shelter and high frequencies of citrina and between exposure and high frequencies of dark reticulata. These relationships are in complete agreement with those observed by Sacchi (1966, 1969, 1974) in Brittany and by Gratton (1969) in southern Wales. These authors have interpreted the existence of the brightly coloured citrina and the variation in morph frequencies in terms of selection acting on characters other than shell colour itself.

However, a number of points have emerged in the present study on *L. mariae* which suggest a more functional interpretation of shell colour. The substratum of *F. serratus*, when viewed from the hunting positions of *B. pholis*, offers different backgrounds which correspond very closely to the colours of the major phenotypes. For the background of citrina, an important consideration was the influence of transmitted light through the lamina which provided a bright yellow substratum. In *L. obtusata*, a sibling of *L. mariae*, citrina becomes common when it is found in association with *Fucus spiralis* as opposed to the other common food plants of this species, *Ascophyllum nodosum* and *F. vesiculosus* (Reimchen 1974). Of these three species, *F. spiralis* is morphologically most similar

to *F. serratus* inasmuch as it possesses a very thin lamina through which yellow light is transmitted. Smith (1976), also documenting the relative abundance of citrina on *F. spiralis*, noted the similarity between this morph and the yellow receptacles of the algae. In the *L. saxatilis* complex, principally rock-dwelling littorines, Heller has suggested (personal communication) that the influence of transmitted light observed in the present study could also account for the presence of a yellow phenotype on *Fucus*-rich shores. The substrata underlying the plants are bathed in a yellow hue from light transmitted through the fronds.

Differences in morph frequencies between localities appear to be causally related to the distributions of juveniles who shift from the apex of the lamina in sheltered shores to the stem in exposed shores. This shift may be the result of differences in wave action; during rising and ebbing tides, the lamina are subject to a 'whiplash effect' from the movement of the surf and are often flung against the underlying rocks. The stem and holdfast are more rigid and remain relatively immobile. It is possible that the juveniles gain some protection from dislodgement in these areas. Their association with specific parts of the plant could explain the steep clines in morph frequencies within shores. In each case where a cline was observed, there was a corresponding sharp gradient in wave action.

Examination of apparent exceptions to the relationship between morph frequencies and exposure provide additional support for the importance of crypsis in this species. At Weston-super-Mare, in southern England, citrina should have predominated in the sheltered conditions, but was instead replaced by dark reticulata. However, the algal fronds at this locality were covered with a thick layer of sediment, characteristic of many parts of the Bristol Channel. This sediment created an opaqueness to the laminae upon which citrina was no longer camouflaged. At Ballynagual Point, on the south coast of Ireland, citrina reached a frequency of 50% despite the exposed conditions. Many plants at this locality were immature and appeared to be recent colonizers. The fronds of these individuals were predominantly laminae, in contrast to the reduced lamina and expanded stem of other exposed localities. In this situation, juvenile microdistributions, even if restricted to the base of the frond, would include the laminae substratum, thus providing an advantage to the citrina phenotype. There was a great deal of unpredictable variation in frequencies of light reticulata throughout the study area. At Cloonagh, a very exposed shore on the west coast of Ireland, light reticulata reached a frequency of 50%. Examination of the

field notes on *F. serratus* at this locality indicated that the laminae were leathery in texture and orange in appearance when viewed with reflected light. The colour in itself may provide an explanation for the abundance of the light reticulata as the phenotype was well camouflaged on the surface of the fronds. A contributing factor to the background colour is the influence of transmitted light. Fronds of similar thickness examined in Anglesey showed a reduced light transmittance throughout the length of the lamina. A major proportion of the substratum would therefore appear intermediate in colour between the yellow of a thin lamina and the dark brown of a stem.

The strong relationship observed between morph frequencies and dominant background colour in *L. mariae* suggest a polymorphism mediated by visual predators. Additional mechanisms are necessary to account for the maintenance of frequencies within localities. Two common explanations which have been discussed with reference to work on *Cepaea nemoralis* and *Partula taeniata* are heterozygote advantage and apostatic selection (Ford 1964; Murray 1972). In *L. mariae* no data are available to distinguish between these two modes of maintenance and therefore they remain as possible explanations. Direct observations of the hunting techniques of *B. pholis* suggested a different, although very basic mechanism for the maintenance of frequencies and the occurrence of steep clines, with characteristics similar to the multiniche models developed by Levene (1953), Levins and MacArthur (1966), and Maynard Smith (1970). In the field the blenny concentrated its hunting efforts on areas of *F. serratus* where the density of snails was high, a strategy shown by many predators (Tinbergen 1960; Clarke 1962). Consider a situation in which the juveniles distribute themselves at random with respect to the various substrata. If the blenny preys preferentially on conspicuous shells, as was the case in the laboratory, and secondarily in microhabitats where the density of snails is higher, a stable equilibrium will be reached. The fitness of the morphs will approach equality when the densities in the microhabitats become equal. Regardless of the initial proportion of the morphs on the plant, the result of this form of density-dependent predation will be to shift the morph frequencies to those which correspond to the proportions of backgrounds. This model appears attractive as it will account for the extremely local differentiation, such as in the steep clines, without introducing hidden components to fitness, historical phenomena, or gene flow.

The data presented in this paper have provided a partial understanding of colour variation in some intertidal gastropods. The differences that were obtained in the juvenile distributions between shores and the importance of the hunting positions of the predator in relation to reflected and transmitted light are suggestive in approach for further studies on colour polymorphisms.

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