

Shell colour variation in *Bullia digitalis*, a sand-dwelling, intertidal whelk (Gastropoda: Prosobranchia)

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Bullia digitalis is an intertidal whelk that lives on sandy beaches in South Africa. It is highly variable in shell colour, with individuals varying from white to dark brown. This paper describes shell colour variation of *B. digitalis* at seven sites, along a 230 km coastline east of the Cape Peninsula. Seven colour forms were found: striped, violet, banded violet, banded brown, orange, pale yellow and white. These forms are probably genetically determined morphs. The striped form is the most common at all sites, constituting 53–62% of each sample. The violet is the second most common morph. Its frequencies are remarkably stable at 15–17%. The striped form blends well into the sandy environment and may therefore be of considerable cryptic value in concealing *B. digitalis* from predators. The violet form is highly conspicuous. Its stable frequency throughout the study area may represent a genetic balance that is not relevant to any visual advantages of the violet colour.

KEY WORDS: – Colour – polymorphism – selection – *Bullia* – sand – intertidal – snail.

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INTRODUCTION

Bullia digitalis (Nassariidae) is a blind, intertidal whelk that lives on sandy beaches in South Africa (from Port Nolloth to Transkei, a range of 1800 km). It spends most of the tidal cycle buried in the sand, with only the top of the siphon protruding into the overlying water. If attracted by the odour of carrion on the beach it emerges from the sand, turns on its back and spreads its large thin foot so that it surfs up the beach with the wave swash of the incoming tide, anchoring itself in the sand as the wave recedes. When near the carrion, olfactory stimuli initiate rapid crawling in the direction of the food. These and many further aspects of the biology of *B. digitalis* have recently been reviewed by Branch & Griffiths (1988) and Brown, Stenton-Dozey & Trueman (1989).

Bullia digitalis is highly variable in shell colour, with individuals varying from white to dark brown. McGwynne (1980) investigated this variation near Port Elizabeth, where she recognized six colour forms: cream with brown rays; cream with purple rays, purple, orange, cream and grey. She found that the frequencies of these colour forms were very similar in two populations that differed in their population densities; and that there was no significant relationship between population density and the combined frequencies of conspicuous colour forms (purple, grey and cream-with-purple rays were considered conspicuous).

A further study of the shell patterns of *B. digitalis* was carried out by Webb (1985), who investigated several populations around the Cape Peninsula. As he found that the colour forms of McGwynne could occur in any combination on one shell, he suggested a new classification: stripes, coloured without stripes and cream. He found that there were no significant colour differences between male and female whelks, or between those infected by helminth parasites and uninfected ones.

Initial examination by the author of some populations around the Cape Peninsula revealed that shell patterns on the eastern coast, where conditions are temperate, differ considerably from those of the western coast, where the water temperatures are 7°C–9°C lower. This preliminary observation suggested that it might be beneficial to separate the study of these two areas and this paper describes variation in shell colour of *B. digitalis* at some sites that range to the east of the Cape Peninsula.

METHODS

Sites

Shell colour variation of *B. digitalis* was studied on seven beaches that extend from False Bay to Cape Agulhas, a coastline of 230 km. In this area the beaches are composed of clean sand more or less free from silt and organic matter. They are subject to considerable surf action and it is within the surf zone that *B. digitalis* are active as the most abundant whelk, though two other species (*B. pura* and *B. rhodostoma*) are also found. The seven populations, with the distances between them, are (from the west eastwards): Fishoek, 5 km to Muizenberg, 15 km to Mnandi, 42 km to Rooilesbay, 55 km to Hermanus, 35 km to Franskraal and 75 km to Struisbay (Cape Agulhas). These populations are separated from each other by unsuitable habitats such as rocky areas, and it can be assumed therefore that there is only limited exchange of genes between them (*B. digitalis* lays eggs from which miniature adults emerge, not pelagic larvae). The shores further east of Cape Agulhas were not included because in them the dominant intertidal *Bullia* was *B. rhodostoma*, and *B. digitalis* (which was found lower down the shore) was difficult to collect in sufficiently large samples.

Material

A total of 2053 live snails was collected from the seven beaches, during June and July 1989. Collecting took place at rising mid-tide, from the upper edge of the surf zone, by use of mussel bait: several mussels were squashed, and their body fluids left to ooze out into the sea. Those *Bullia* that emerged from the sand

in response to the bait were then hand collected. The rising tide usually set the time limit for collecting, as the snails could not be seen when covered by more than about 30 cm of the in-coming swash.

The snails were examined for shell colour immediately upon returning to the laboratory. Sorting of the morphs was carried out in a shallow white enamel tray filled with water (to ensure that the full colour is seen), in a well-lit room. To ensure an unprejudiced sorting, the colour classifications of McGwynne (1980) and of Webb (1985) were put aside until after my own classifying was completed. The colour nomenclature adapted here is that of the Methuen Handbook of Colour (Kornerup & Wanscher, 1983). After colour scoring, the shell height of all snails was measured to the nearest 1 mm with vernier callipers. To test for the consistency of the colour classification, in each sample the snails were then mixed again and the animals extracted from their shells. After one month the now empty shells were reclassified for colour. The results of the two colour classifications were almost always identical but some differences did occur, and these are mentioned in the text. In the Fishoek sample a few shells were discarded, because they were worn or covered by green algae to such an extent that they could not be colour-classified.

DESCRIPTION OF COLOUR FORMS

(Fig. 1)

The shells of the study area resemble those of Port Elizabeth, about 600 km further east, more than do those of the western coast, just a few km further west.

Seven major colour forms were found: striped, violet, banded violet, banded brown, orange, pale yellow and white. One rare colour form was also found: pink. There almost always appeared to be a definite discontinuity between these colour forms and all but three of the 2053 shells collected in this study could be classified without difficulty into one of them. Within each of the colour forms there may, however, be considerable variation. In some shells the intensity of colour alters with growth, suggesting that pigment deposition is more intense when growth is slow (as in bivalves, Smith, 1971).

Striped

The overall colour of the shell is greyish yellow to beige. In each whorl, the upper half is usually yellowish white to pale yellow. The lower half is usually grey, greyish yellow or yellowish grey. On this lower half (of each whorl) there is a series of light brown, more-or-less regularly spaced axial stripes. In each of these stripes the uppermost part (around the mid of the whorl) is usually of a more intense and saturated brown. Further down the stripe (towards the suture with the underlying whorl) the brown pales, as if fading away. In some shells a continuous brown band is present on the inner side of the shell, just beneath the overlying suture. It shows through the shells as a light brown to violet grey band that runs along the upper part of the whorl, just beneath the suture.

In shells larger than 15–20 mm, the well-defined distinction between the upper and lower halves is most noticeable in the spire. In the body whorl the lower half becomes gradually an ill-defined grey, yellowish white or pale yellow,

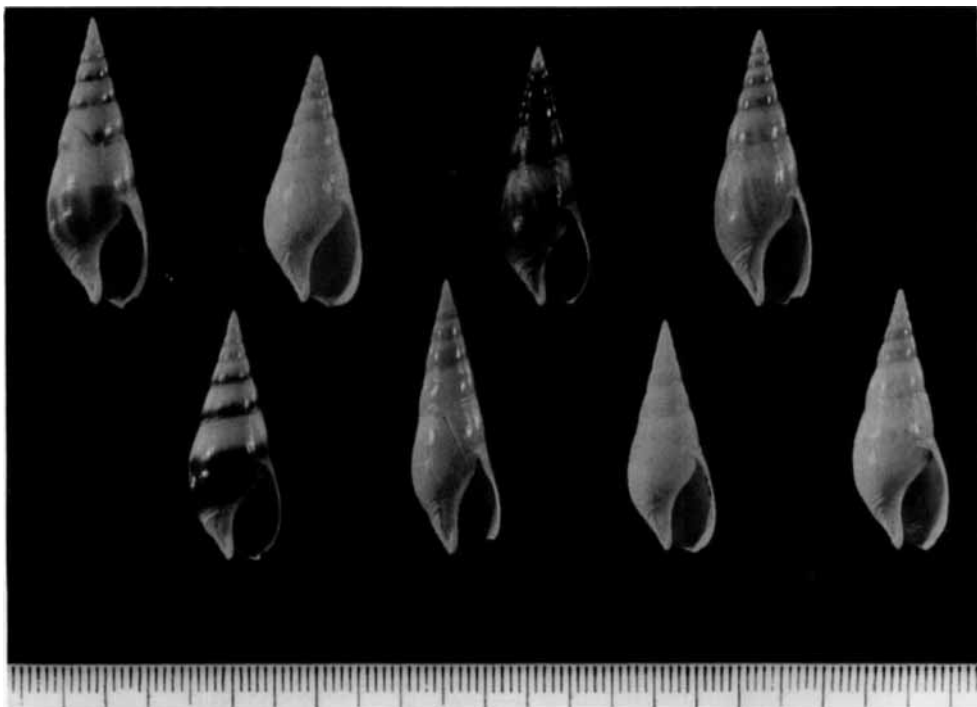


Figure 1. Morphs of *Bullia digitalis*. Upper row, left to right: banded brown; pale yellow; violet; striped. Lower row, left to right: banded violet; orange; white; striped pale.

not clearly separated from the upper half; and the brown axial stripes become less regular, faint, ill-defined and may even be absent.

This morph varies considerably. In some shells the ground colour of the lower half of the whorl is dark whereas in others it is pale, and the overall appearance is a very pale yellow or light grey. Also, in some shells the axial stripes are strong and prominent whereas in others they are reduced to small brown blotches along the mid of the whorl. Further, in many shells the continuous band of the upper whorl is faint, reduced or absent. All these differences form part of a continuous, rather than discrete variation.

The striped morph was further subdivided into 'striped standard' and 'striped pale'. To examine whether this subdivision is consistent, in the Muizenberg and Fishoek samples all the striped were remixed, and then reclassified after two weeks. At Fishoek the results were precisely the same; at Muizenberg two shells were reclassified differently.

The striped form corresponds broadly to the "cream-with-brown rays" variant of McGwynne (1980) and is included in the "stripes" variant of Webb (1985).

Violet

The overall appearance is violet. Closer examination reveals that the apex is white (this includes the first 2 mm of the shell), the spire whorls are frequently violet brown and the body whorl is greyish violet. The columella is usually grey rose. A good colour photograph of this morph is given by Branch & Branch (1981: pl. 116-w).

The violet form corresponds to the "purple" variant of McGwynne (1980) and is included in the 'colour-without-stripes' variant of Webb (1985).

Banded violet

In each whorl the upper half is yellow, off-white or white. The lower half is covered by a continuous, intensive violet band. Axial stripes are absent, or very faint. In some shells the violet band is very faint.

The banded violet form is included in the "cream-with-purple rays" variant of McGwynne (1980) and in the "stripes" variant of Webb (1985).

Banded brown

In each whorl the upper half is yellow, off-white or white. The lower half is covered by a more-or-less continuous violet brown band. Dark axial stripes are found within the band, protruding slightly above it and into the upper half of the whorl.

The banded violet and banded brown forms are very similar and the distinction between them is often not easy. In the rescoring of the shells and reclassifying them into banded violet and banded brown, four out of 101 shells were rescored differently from the original scoring. Further, three shells at Struisbay and one each at Hermanus, Rooilesbay and Fishoek respectively were intermediate between banded brown and striped. These intermediates amount to 0.6% of the striped and 6% of the banded brown shells found in this study. To conclude, the banded brown form, though usually recognizable as a separate form, is not always distinguished from either the banded violet or the striped forms by a clear-cut, well-defined boundary.

The banded morph is included in the "cream-with-purple rays" variant of McGwynne (1980) and in the "stripes" variant of Webb (1985).

Orange

The overall appearance is orange. Closer examination reveals orange, light orange or greyish orange. In some large shells, the last whorl is a pale orange. In most shells, the upper half of each whorl is paler than the lower half. This morph is variable. In some of the shells the orange is very pale, in others it is darker. In two shells only the upper part was orange, whereas the lower part was brown. In one shell the orange pattern was overlaid by stripes, like those of the striped form.

The orange morph corresponds broadly to the "orange" variant of McGwynne (1980) and is included in the "coloured-without-stripes" of Webb (1985).

White

The shell is usually plain white, apparently produced by the absence of pigments. In some shells the upper whorls, of the spire, are grey. White shells are not mentioned by McGwynne (1980; she does mention grey shells) and are included in the "cream" variant of Webb (1985).

Pale yellow

The overall appearance is pale yellow (cream). The pale yellow form is included in the cream variant of Webb (1985).

Pink

The general appearance of the shell resembles the white form. The spire is white or grey and the body whorl may be reddish grey or dull red. The inside of the mouth is pinkish to white.

The striped, violet, banded (brown and violet) and orange colours of *B. digitalis* bleach to pale yellow when exposed to very high temperatures (as discovered accidentally, when drying some of the shells in my kitchen oven). At boiling temperature the colours are stable, suggesting that this bleaching does not bear much biological significance to the living snail.

FREQUENCY OF COLOUR FORMS IN DIFFERENT POPULATIONS

The geographic variation of the colour forms is shown in Table 1 and in Fig. 2. *Striped* is the most common colour form at all seven sites, constituting 53–62% of each sample (mean 58.1%). The striped morph was further subdivided into striped standard and striped pale. Table 2 shows that striped pale constitute 14–32% in each sample. *Violet* is the second most common morph at all seven sites. Its frequencies are remarkably stable, 15–17%, which is about one sixth (16.35%) of each sample. *Banded brown* varies from 1 to 9% (mean 4%). *Banded violet* varies from 4 to 6% (mean 4.7%), but for the Mnandi population this is only 2%. *Orange* varies from 1 to 8%. *White* varies from 4 to 10% (mean 6.7%). *Cream* is 3–4%, but for Fishhoek where it is missing. *Pink* is rare, 1% at Fishhoek and Hermanus and absent elsewhere.

Morph distributions are not random, and in some samples a certain morph appears other than the expected ($\chi^2_{36} = 69.72$, $P = 0.0006$, chi-square test for heterogeneity or independence). This is due to the uncommon morphs, found at frequencies of less than 10%: banded brown at Franskraal, Muizenberg and Hermanus, and banded violet and white at Mnandi, for all of which differences between observed and expected were high. When all the uncommon morphs are pooled together, so that we are left with just three categories (striped, violet and uncommon morphs), then there is no significant difference between the expected (if the frequency of the morphs was random between the populations) and the observed distributions ($\chi^2_{12} = 8.233$, $P > 0.05$); that is, there is no significant difference between the morph frequencies of the two major morphs, striped and violet, in any of the seven samples.

When all samples were pooled together and considered as representing one

TABLE 1. Morph frequencies (%) of *Bullia digitalis* at seven sites between Cape Point and Cape Agulhas, South Africa

	Fishhoek	Muizenberg	Mnandi	Rooilesbay	Hermanus	Franskraal	Struisbay
Striped	53	60	58	62	61	54	59
Violet	17	17	17	15	16	16	16
Banded brown	7	1	7	3	3	9	5
Banded violet	5	5	2	5	6	4	6
Orange	8	7	4	1	5	7	7
White	6	5	10	8	6	8	4
Cream	—	3	3	4	4	3	4
Others	5	—	—	2	—	—	—
<i>N</i>	88	255	384	125	544	303	354

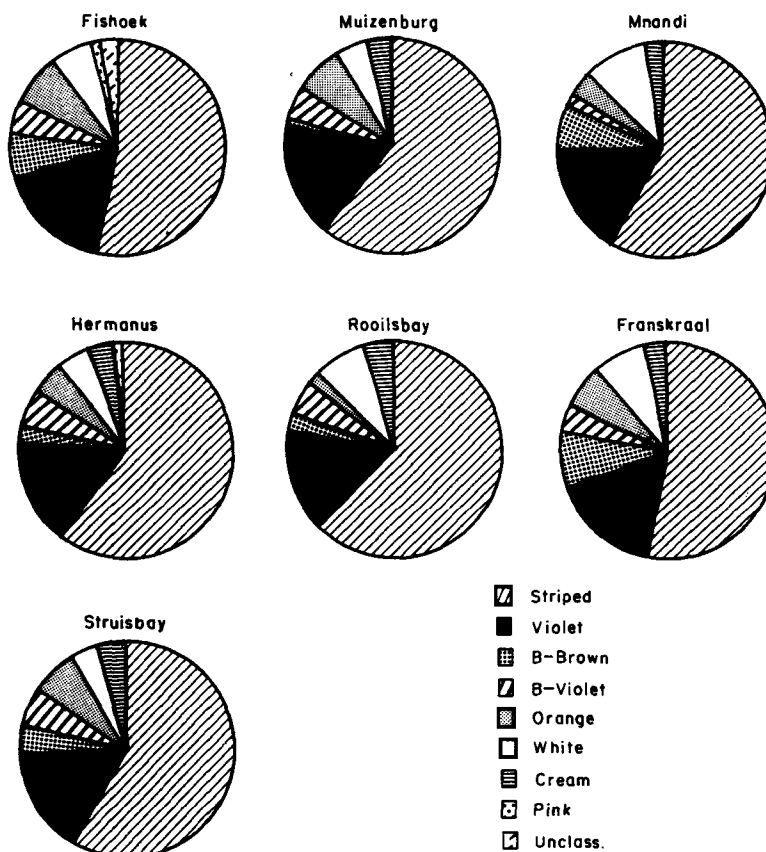


Figure 2. Morph frequencies (%) of *Bullia digitalis* at seven sites between Cape Point and Cape Agulhas, South Africa.

single population, the pooled frequencies were: striped 58.7%, violet 16.3%, banded brown 4.6%, banded violet 4.5%, orange 5.4%, white 6.6%, cream 3.5% and others 0.4%.

To investigate whether the frequency of violet varied with age, each sample was divided into young and old specimens. One natural value by which to divide the shells into young and old ones is 23 mm, which is about the size at which sperm production commonly starts (Webb, 1985). Percentages of both young (< 23 mm) and old (> 23 mm) shells are shown in Table 3 (Mnandi is not included because it was not measured, and Rooilesbay is not included because it contained only two young shells). For the striped form, χ^2 tests show that at Franskraal, Hermanus, Struisbay and Muizenberg there were no differences in

TABLE 2. Morph frequencies (%) of *B. digitalis* at seven sites: subdivision of the striped morph into striped normal and striped pale

Colour	Fishoek	Muizenberg	Mnandi	Rooilesbay	Hermanus	Franskraal	Struisbay
Striped normal	77	69	79	76	86	68	70
Striped pale	23	31	21	24	14	32	30
<i>N</i>	47	154	221	78	330	165	210

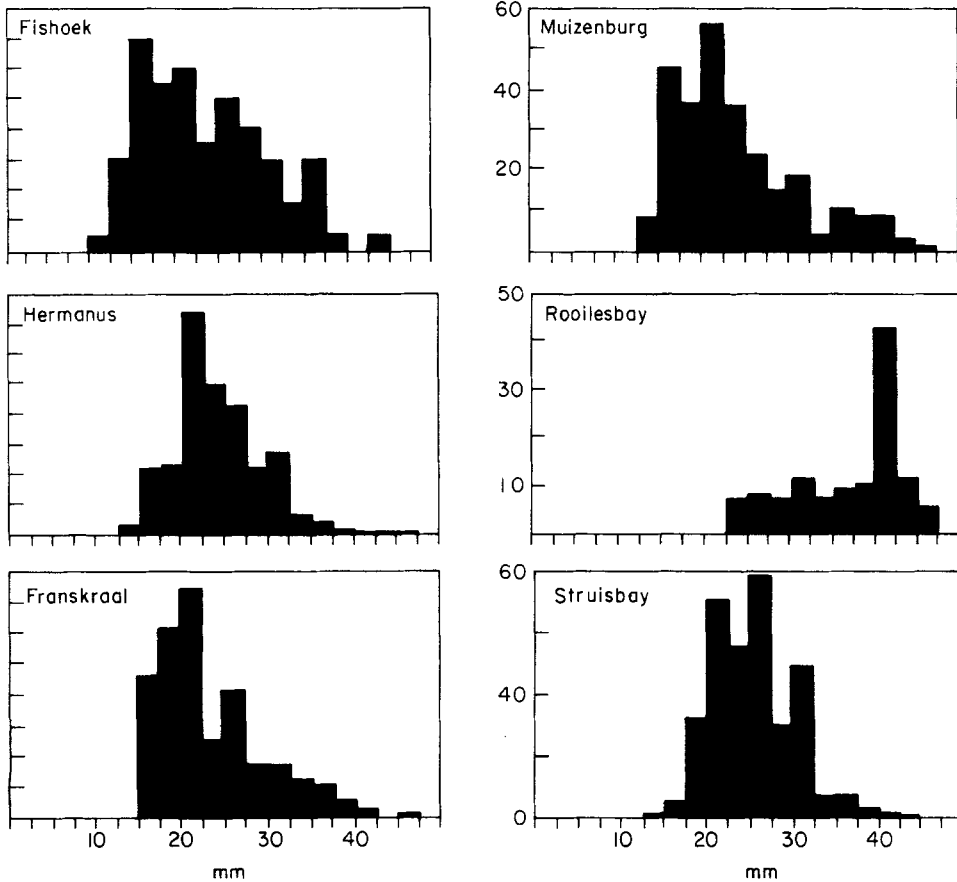


Figure 3. Size frequencies of *Bullia digitalis* at six sites between Cape Point and Cape Agulhas, South Africa.

morph distribution between young and old animals, but at Fishhoek there was a significant increase. For the violet form, χ^2 tests show that at Franskraal, Hermanus and Fishhoek there were no differences in morph distribution between young and old animals, but at Struisbay and Muizenberg there was a significant decrease.

The age structure of the populations varied considerably (Fig. 3), with

TABLE 3. Morph frequencies (%) of *Bullia digitalis* in juveniles and adults at five sites between Cape Point and Cape Agulhas

	Fishhoek		Muizenberg		Hermanus		Franskraal		Struisbay	
	juv.	adult	juv.	adult	juv.	adult	juv.	adult	juv.	adult
Striped	61	47	60	60	59	63	52	58	59	60
Violet	17	17	21	11	17	15	16	16	22	12
Banded brown	12	2	1	2	3	2	11	4	3	5
Banded violet	2	6	5	6	6	5	5	2	5	7
Orange	2	13	4	11	5	5	8	5	5	8
White	5	6	5	5	7	5	7	8	5	3
Cream	—	—	3	3	3	5	1	7	2	5
Others	—	9	1	1	—	—	—	—	—	—
N	88		255		544		303		354	

Rooilesbay differing from the other samples in that it contained only two shells that were less than 23 mm. A likely explanation for the small numbers of young snails at Rooilesbay is the lack of reproductive success. This could perhaps be because of heavy parasite infection (which in some *B. digitalis* populations may reach up to 46%, Webb, 1985).

DISCUSSION

The morph classification of this study, which limits itself to the eastern coast, differs from that of Webb (1985) which combines east and west coast populations. On the west coast, where other colour categories seem to prevail, my preliminary observations suggest that this morph classification is probably not relevant.

With its wide range of striped, violet, banded (brown and violet), orange, cream and white shells, *B. digitalis* belongs to Type 1 ("highly coloured and variable") on Cain's scale of shell colour variation (Cain, 1988a). One central issue in any discussion of these shell colours is the extent to which they are genetically inherited, as in the East African bivalve *Donax faba* (Smith, 1975) and European bivalve *Macoma balthica* (Cain, 1988b), or induced by environmental factors, as in the Australian gastropod *Austrocochlea constricta* (Creese & Underwood, 1976; Underwood & Creese, 1976). In this context it should be remembered that *B. digitalis* is a scavenger that feeds mainly upon carrion—an extremely erratic and apparently seasonal input of food (McGwynne, 1980). Further, in addition to eating carrion *B. digitalis* may also turn predator upon crustaceans, molluscs, amphipods and isopods, may harvest an algal garden growing on its shell (in this study algal gardens were found only at Fishoek), and may absorb dissolved organic matter from sea water (Brown *et al.*, 1989). If the shell colours of *B. digitalis* are due to environmental sources then, bearing in mind this extreme variety of feeding methods and diets, we might expect shell colours to vary inconsistently with shell growth, to merge into one another and to vary, in their frequencies, from one site to another. However, the shell colours form discrete categories that do not vary inconsistently nor merge into one another (except for a very few intermediate shells). This suggests that the shell colours of *B. digitalis* are genetically determined morphs, rather than environmentally induced colours.

A further issue is whether these colours are of any adaptive value in concealing *B. digitalis* from predators. The diversely coloured shells of *B. digitalis* are all the more bewildering because, for a snail that reaches a height of 45 mm, sand is as uniform a natural habitat that one can think of (for minute shells and for newly hatched spat, sand may of course present a rather diversified habitat, as pointed out by Smith, 1975). Predators of *B. digitalis* mentioned by Brown *et al.* (1989) include the swimming crab *Ovalipes punctatus*, the elasmobranchs *Rhinobatis* spp. and *Myliobatus aquila*, and the teleosts *Lithognathus lithognathus*, *L. mormyrus*, *Pomadasys commersoni*, *Coracinus capensis* and *Rhabdosargus holubi* (these authors note that *Bullia* appears not to be attacked by birds). Many fish have an acute visual sense, and may be expected to exert considerable selection in favour of cryptic shells. When surfing and actively seeking for food, its very large, whitish foot makes *B. digitalis* very conspicuous (to the human eye), regardless of shell colour. But when inactive, shallowly buried beneath the surface and uncovered by the

occasional movement of sand, a shell with a concealing colour may offer some selective advantage.

The striped form (the most common morph in all the samples of this study) blends well into the sand coloured environment (as seen by the human eye) and may therefore be of considerable cryptic value. The stripes tend to break up the shape of the shell, thereby adding to the cryptic effect. Also pale yellow resembles the colour of sand. The white form is very conspicuous on wet sand but it approximates foam when covered by the swash of the incoming tide, so that it too may be considered as cryptic. Combining these three colour forms together, it seems that the great majority of shells in each sample (64–81%) is cryptic, to the human eye, in the natural environment of *B. digitalis*.

The violet form (the second most common form in all of the seven samples) is definitely not cryptic. Its hue, saturation and shade do not come anywhere near to those of the background against which *B. digitalis* would normally be seen, and it is highly conspicuous. It could perhaps be suggested that violet resembles empty mussel shells—these are sometimes found, strewn here and there, along the beach. However, these empty mussels are far too uncommon to be regarded as a background against which whelks are seen, in any of the seven sites. Also the possibility that violet whelks resemble mussels because of some sort of Batesian mimicry should not be embraced, until evidence is offered that mussels are poisonous to at least some of their natural predators.

It could perhaps be suggested that violet is favoured because variation *per se* is adaptive, due to apostatic selection—selection which overlooks the morphs of different appearance from the common ones. This mode of selection has been reviewed and discussed in detail by Cain (1983) as concerning terrestrial snails and marine bivalves (Cain, 1988b). It has been offered as an explanation for two other variably coloured sand dwelling molluscs, the East African bivalve *Donax faba* (where apostatic selection may play a key role, Smith, 1975) and the British bivalve *Macoma balthica*, (where shell colour polymorphism may be maintained by apostatic selection but other factors may be acting as well, Cain, 1988b). Beyond the sandy habitat it has been offered as an explanation also for the rock dwelling, highly variably coloured winkle *Littorina rudis* (Atkinson & Warwick, 1983; but see Byers, 1990).

For the *B. digitalis* samples here studied, I doubt whether the frequency of violet should be explained in apostatic terms. It should be emphasized that in all our samples violet had remarkably similar frequencies of 14–18% and any selective explanation must take this consistency into account. Apostatic selection stems from a very delicate interaction between predator and prey, and it is highly sensitive to prey density (Greenwood, 1969; Allen, 1972). Though I do not have data on population densities, it would be odd to suggest that the seven *B. digitalis* populations, differing so much in their population structures, would all have the same density and the same predator pressure. Moreover, near Port Elizabeth, some 600 km of coastline east of Cape Agulhas, McGwynne (1980) found remarkably similar frequencies of the violet morph in two populations that differed considerably in their population densities (17% at Maitlands, with 22 snails/25 m²; and 14% at King's Beach, with 9 snails/25 m²). To conclude, an apostatic selection argument cannot explain the consistency of the violet frequencies in all the samples.

To a certain extent, the consistency of the violet frequencies over a large

region resembles the "area effects" of the European terrestrial snail *Cepaea nemoralis*—large areas (as compared with the panmictic unit) characterized by a uniformity of morph frequencies, in spite of visual predation and variation in habitat (Cain, 1983 and references therein). In *Cepaea nemoralis*, these area effects may be the result of intense grazing that took place at the end of the last century and the beginning of this one, causing extreme reduction and subsequent spread of populations (Cain, 1983 and references therein). Area effects have also recently been described in the Caribbean landsnail *Cerion* (Gould & Woodruff, 1990).

In *B. digitalis*, however, the situation concerns the uniform frequency of a conspicuous morph, in a very uniform habitat (rather than in a varied one). Also, in *B. digitalis* as an intertidal species, the distribution is linear rather than areal. Hence, the corresponding situation concerns at least one-tenth of the entire range of the species, much more than the area effects in *Cepaea nemoralis*. Also, the situation concerns the uniform frequency of a conspicuous morph in a very uniform habitat, not of a somewhat cryptic morph in a varied one. Further, no event that could have caused extreme reduction and subsequent spread of *B. digitalis* populations is known to have taken place in the last 400 years (namely since the European colonization of South Africa).

At our present state of knowledge, the uniform frequency of violet throughout the study area could perhaps best be explained as representing a genetic balance that is not relevant to any visual advantages of the violet colour. It is noteworthy that the subtidal *B. callosa* is also variable in its shell colouration, and the frequencies of its dark brown shells at three sites off the Eastern Cape were recently found to be very similar (30%, 33% and 36%, see Muller, 1989).

Banded violet is also conspicuous to the human eye, though to a somewhat lesser extent than violet. The banded brown shells are less conspicuous than the banded violet.

The orange form was listed by McGwynne (1980) as among the inconspicuous colour forms, but to me it seems very conspicuous in its natural environment. Owing to this disagreement, the orange morph is best left out of the present discussion.

It may be of interest, as a final note, to compare the sandy, intertidal sandy and terrestrial habitats. The latter has a highly variable vegetation cover, creating a wide variety of colour backgrounds. Accordingly, many polymorphic gastropods of terrestrial sands vary in their morph frequencies from one vegetation cover to another. Thus, in *Cochlicella acuta* of western Europe, the sand-coloured morph predominates on backgrounds of exposed sand, whereas the dark morph predominates on dark-coloured substrates (Lewis, 1977). In *Theba pisana* of Israel, dark shells are associated with the presence of rodents in heavily vegetated areas, whereas white shells predominate in exposed, rodent-absent areas (Heller, 1981; Heller & Gadot, 1984). Intertidal sands lack vegetation, creating a background that is far less variable. On this monotonous background, the rich colour variation of *Bullia digitalis* is all the more impressive.

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REFERENCES

- ALLEN, J. A., 1972. Evidence for stabilizing and apostatic selection by wild blackbirds. *Nature, London*, 237: 348–349.
- ATKINSON, W. D. & WARWICK, T., 1983. The role of selection in the colour polymorphism of *Littorina rudis* Maton and *Littorina arcana* Hannaford-Ellis (Prosobranchia: Littorinidae). *Biological Journal of the Linnean Society*, 20: 137–151.
- BRANCH, G. M. & BRANCH, M. I., 1981. *The Living Shores of Southern Africa*. Struik: Cape Town.
- BRANCH, G. M. & GRIFFITHS, C. L., 1988. The Benguela ecosystem. Part 5. The coastal zone. *Oceanographic and Marine Biological Annual Review*, 26: 395–486.
- BROWN, A. C., STENTON-DOZEY, J. M. C. & TRUEMAN, E. R., 1989. Sandy-beach bivalves and gastropods: a comparison between *Donax serra* and *Bullia digitalis*. *Advances in Marine Biology*, 25.
- BYERS, B. A., 1990. Shell colour polymorphism associated with substrate colour in the intertidal snail *Littorina saxatilis* Olivi (Prosobranchia: Littorinidae). *Biological Journal of the Linnean Society*, 40: 3–10.
- CAIN, A. J., 1983. Ecology and ecogenetics of terrestrial molluscan populations. In K. M. WILBUR (Ed-in-chief), *The Mollusca 6, Ecology* (W. D. RUSSEL-HUNTER Ed.): 597–647. New York: Academic Press.
- CAIN, A. J., 1988a. The scoring of polymorphic colour and pattern variation and its genetic basis in molluscan shells. *Malacologia*, 28: 1–15.
- CAIN, A. J., 1988b. The colours of marine bivalve shells with special reference to *Macoma balthica*. *Malacologia*, 28: 289–318.
- GREENWOOD, J. J. D., 1969. Apostatic selection and population density. *Heredity*, 24: 157–161.
- CREESE, R. G. & UNDERWOOD, A. J., 1976. Observations on the biology of the trochid gastropod *Austrocochlea constricta* (Lamarck) (Prosobranchia). 1. Factors affecting the shell-banding pattern. *Journal of Experimental Marine Biology and Ecology*, 23: 211–228.
- GOULD, S. J. & WOODRUFF, D. S., 1990. History as a cause of area effects: an illustration from *Cerion* on Great Inagua, Bahamas. *Biological Journal of the Linnean Society*, 40: 67–98.
- GREENWOOD, J. J., 1969. Apostatic selection and population density. *Heredity*, 24: 157–161.
- HELLER, J., 1981. Visual versus climatic selection of shell banding in the landsnail *Theba pisana* in Israel. *Journal of Zoology, London*, 194: 85–101.
- HELLER, J. & GADOT, M., 1984. Shell polymorphism of *Theba pisana*—the effects of rodent distribution. *Malacologia*, 25: 349–354.
- KORNERUP, A. & WANSCHER, J. H., 1983. *Methuen Handbook of Colour*. Methuen: London.
- LEWIS, G., 1977. Polymorphism and selection in *Cochlicella acuta*. *Philosophical Transactions of the Royal Society of London, Series B*, 276: 399–451.
- MCGWYNNE, L., 1980. *A comparative ecophysiological study of three sandy beach gastropods in the eastern Cape*. Unpublished M.Sc thesis, University of Port Elizabeth.
- MULLER, S., 1989. Polychromes in two closely related South African subtidal whelks. *South African Journal of Science*, 85: 12–13.
- SMITH, D. A. S., 1971. Polymorphism and population density in *Donax rugosus* (Lamellibranchiata: Donacidae). *Journal of Zoology, London*, 164: 429–441.
- SMITH, D. A. S., 1975. Polymorphism and selective predation in *Donax faba* Gmelin (Bivalvia: Tellinacea). *Journal of Experimental Marine Biology and Ecology*, 17: 205–219.
- UNDERWOOD, A. J. & CREESE, R. G., 1976. Observations on the biology of the trochid gastropod *Austrocochlea constricta* (Lamarck) (Prosobranchia). 2. The effects of available food on shell-banding pattern. *Journal of Experimental Marine Biology and Ecology*, 23: 229–240.
- WEBB, S., 1985. *A survey of helminth parasites in surfing whelks on the western Cape coast of South Africa*. Unpublished M.Sc thesis, University of Cape Town.