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ROCKY SHORE SNAILS AS MATERIAL FOR PROJECTS (WITH A KEY FOR THEIR IDENTIFICATION)

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Abstract

Rocky sea shores are amongst the best habitats in which to carry out biological field projects. In that habitat, marine snails (prosobranchs) offer the most opportunities for individual investigations, being easy to find, to identify, to count and to measure and beng sufficiently robust to survive the experience. A key is provided for the identification of the larger species and suggestions are made for investigations to exploit selected features of individual species.

Introduction

Rocky sea shores offer one of the best habitats for individual or group investigations. Not only is there *de facto* public access (once you have got there) but also the physical factors that dominate the environment - tides (inundation versus desiccation), waves, heat, cold, light, dark, salinity etc. - change significantly over a few metres in distance. As a bonus, most of the fauna and flora lives out on the open rock surface and patterns of distribution may be clearly visible to the naked eye. Finally, they are amongst the most 'natural' of habitats in the British Isles; unless there has been an oil spill, rocky sea shores are unlikely to have been greatly affected by covert human activity.

Some 270 species of marine snail (Phylum Mollusca, Class Gastropoda; Sub-Class Prosobranchia) live in the seas around the British Isles (Graham, 1988) and their empty shells may be found on many beaches. Most of these species are small (less than 3 mm long) or live beneath the tidemarks. The key, overleaf, refers only to those species that grow larger than 3 mm and are regularly found ***living*** on rocky shores, in some part of the British Isles. If a specimen does not key out easily, reference should be made to Graham (1988) or to Hayward & Ryland (1990, 1995).

Although a few species complete their life cycle within a year, others may live 15 - 20 years. As many of these continue to grow throughout their lives, individuals may be found at any size from one or two millimetres up to the maximum noted in the key. However, as very few individuals ever reach their potential, it is highly unlikely that your specimen will be as big as the figure given.

Shells are frequently very attractive objects and beautifully coloured. However, colour variation within some species is so great (greater than the variation between species) that this is rarely a useful character for identification, which is why the key relies on line drawings.

There is no shore in the British Isles where all the species included in this key can be found alive so, in practice, recognition of the species you are looking for is much easier than the key suggests. Readers who know that they are only going to work on the south coast of England may care to draw a line through all the species confined to northern Scotland, and *vice versa*.

KEY TO THE LARGER SPECIES OF MARINE SNAILS THAT *LIVE* ON ROCKY SHORES AROUND THE BRITISH ISLES

NOTE. The terminology of shell ornament (Fig 1)
Suture; the continuous line running round the spiral of the shell separating one whorl from another.
Costae; numerous, often regular, ridges across the outer surface of the shell, running parallel to the outer lip.
Spiral ridges; numerous, often regular, ridges across the outer surface of the shell, running at right angles to the outer lip.
Varices; occasional pronounced ridges running parallel to the outer lip, also called 'growth checks.' (not featured on this shell but see Fig. 62).
Body whorl; The whorl between the aperture and the 'first suture line' occupied by most of the animal's body.

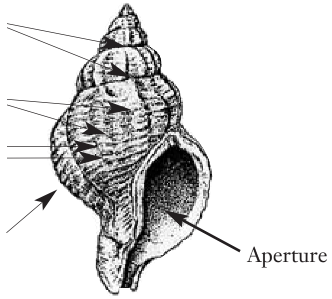

FIG. 1

1 The calcareous shell is all in one piece **2**

\- The shell is composed of two, eight, or ten calcareous plates or valves ..... not a snail
Molluscs with the shell in two pieces are bivalves; those with it in eight pieces are chitons (coat-of-mail shells). Barnacles, which are not molluscs but sessile crustaceans, have a shell comprising of a 'wall' of four or six plates and four moveable opercular plates in the middle - see Rainbow (1990).

2 (1) When alarmed, the snail withdraws *into* its shell .. **3**

\- When alarmed, the snail withdraws *under* its shell .**30**

FIG. 2

3 (2) On the top of its foot, the snail bears an operculum - a plate (Fig. 4) used to close off the shell aperture when the animal withdraws inside (often ear-shaped [Fig. 2] or circular [Fig. 3]) **4**

FIG. 3

\- The snail lacks an operculum **29**

4 (3) The operculum is calcareous - hard, white and shiny (Fig. 3) ..... **Pheasant shell**, ***Tricolia pullus***
Lower shore, western coasts. Up to 10 mm

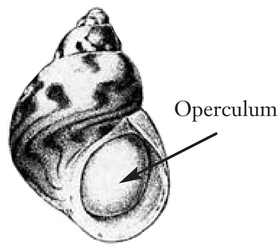

FIG. 4

\- The operculum is chitinous, and flexible; green, brown, orange or red in colour **5**

5 (4) At the front edge of the shell aperture (the lower end in these drawings; the opposite end from the apex of the spire) there is a notch, groove or tube through which the snail can extend a siphon (tube) to suck in water .... Whelk ... **6**

\- The front edge of the shell aperture is a continuous smooth curve (as in Fig. 4) **12**

6 (5) The long siphonal groove is, at least partially enclosed as a tube (Fig. 5). Shell, generally, heavily ornamented.

Sting winkle, ***Ocenebra erinacea***

Lower shore, southern coasts. Up to 50 mm

\- Siphonal notch or groove, not a tube **7**

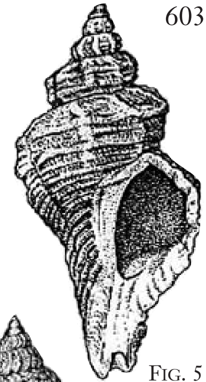

FIG. 5

7 (6) In the living snail, the outer surface of the shell (the periostracum) is furry to touch. The fur is rubbed off empty shells, when the curved nature of the costae becomes more apparent (Fig. 6). Siphonal notch rather than a groove

Buckie or **Common whelk**, ***Buccinum undatum***

Lower shore, all coasts. Up to 100 mm, but usually 15 - 40 mm on the shore.

\- Any periostracum is not brown and furry **8**

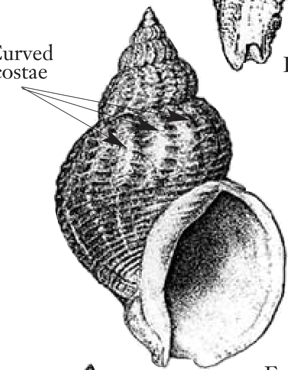

FIG. 6

8 (7) The shell may bear spiral ridges but not costae (Fig. 7), although one or two varices may be present ...... **Dog-whelk**, ***Nucella lapillus***

Middle and lower shore, all coasts. Up to 56 mm, but usually less than 30 mm on the shore.

\- The shell bears costae and spiral ridges **9**

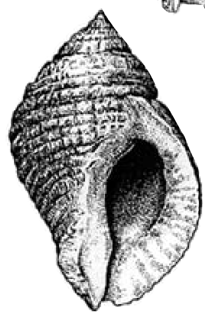

FIG. 7

9 (8) The siphonal groove projects so far forward (downwards in Figs 8 and 9) as to make the shell appear pointed at both ends **10**

- Siphonal groove short, or reduced to a notch (cf. Fig. 6) **11**

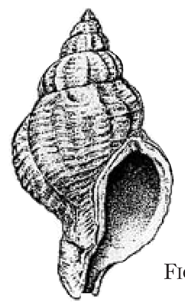

FIG. 8

10 (9) Yellowish-grey or dirty-grey shell with 16-19 fine spiral ridges on the body whorl (Fig. 8)

American oyster drill, ***Urosalpinx cinerea***

Lower shore, Kent and Essex only. Up to 40 mm,

\- Yellowish-white shell has 6-9 broad spiral ridges on the body whorl (Fig. 9)

a young **Sting winkle, Ocenebra erinacea**

Lower shore, southern coasts. Up to 40 mm

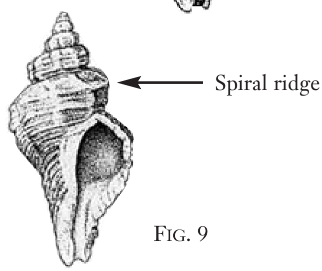

FIG. 9

11 (9) The costae and spiral ridges are equally prominent, forming a pattern of squares over the surface. Shell with a siphonal notch (Fig. 10). Shell lip only thickened in adult specimens - *i.e.* in animals larger than 15 mm
.... **Netted dog-whelk**, ***Hinia reticulata***
Lower shore, all coasts. Up to 40 mm

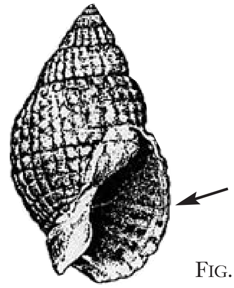

FIG. 10

\- Costae more prominent than the spiral ridges. Shell with a short siphonal groove. Shell lip notably thickened and white in colour. (Fig. 11)
...... **Thick-lipped dog-whelk**, ***Hinia incrassata***
Lower shore, all coasts. Up to 12 mm

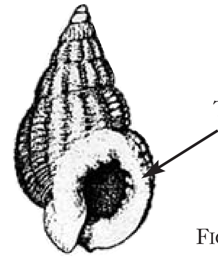

FIG. 11

12 (5) The animal has a circular operculum (Fig. 12) and the inside of the shell is nacreous (mother -of-pearl), white and shining .... Topshell ... **13**


FIG. 12

- The operculum is ear-shaped, or sub-oval (Fig. 13). The inside of the shell is dark in colour or is the same colour as the outside **20**


FIG. 13

13 (12) The shell has an umbilicus (Fig. 14). (In such shells, the whorls do not touch in the centre of the spiral, leaving an open space; the umbilicus is the lower opening to that space)
.... **14**

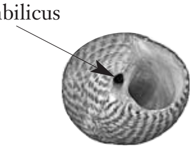

FIG. 14

\- The umbilicus is closed, but its position may be marked by an umbilical scar **18**

14 (13) There is a coloured layer on top of the nacreous layer of shell, more or less hiding it from view, except inside the aperture. NOTE that the coloured layer is frequently worn off the apex of the spire **15**

\- Shell white, shiny, faintly iridescent, lacking any superficial coloured layer (Fig. 15)
Pearly topshell, ***Margarites helicinus***
Lower shore, northern coasts. Up to 10 mm

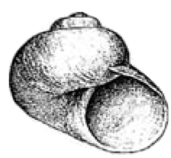
FIG. 15

15 (14) Shell looks as though the spire has been squashed down into the body whorl, so there is a definite 'shelf' below the suture (Fig. 16). On this shelf there are various tubercles (lumps and bumps). Colours include red and cream but not green or grey
.... **Turban topshell**, ***Gibbula magus***
Lower shore, south and west coasts. Up to 35 mm

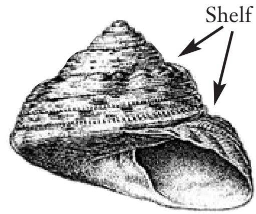

FIG. 16

\- No obvious shelf below the suture and there are no tubercles on the shell surface. Colours include greens and greys; rarely red or cream .. **16**

16 (15) The columella bears a white lump ('tooth') projecting into the aperture (Fig. 17). Decoration is essentially a pattern of fine dark lines zigzagging over a green or light brown background
.... **Common topshell**, ***Osilinus lineatus***
Upper middle shore, southwestern coasts, Up to 34 mm
NOTE. Very young common topshells have an open umbilicus but, in almost all British specimens, it has closed by the time they reach 7 mm. Only very occasionally, are adult specimens found with open umbilici. Further south (*e.g.* in Portugal) half the population may have an open umbilicus.

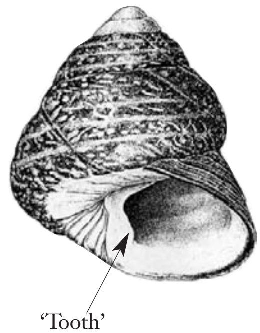

FIG. 17

\- No tooth on the columella. Decoration composed of bands rather than lines **17**

17 (16) Shell taller than broad (Fig. 18). Decoration a pattern of narrow dark grey or black zigzag bands on a pale grey background
Grey topshell or **Silver tommy**, ***Gibbula cineraria***
Lower shore, all coasts, Up to 18 mm

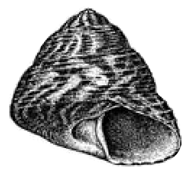
FIG. 18

\- Shell broader than tall (Fig. 19). Decoration a pattern of broad purple zigzag bands on a green background
.... **Purple topshell**, ***Gibbula umbilicalis***
Middle shore, south and west coasts, Up to 22 mm

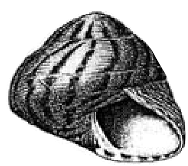
FIG. 19

18 (13) Shell is an almost perfect cone (Fig. 20), with a very shallow suture. Either pure white or brightly coloured, purple, red, yellow or cream
.... **Painted topshell**, ***Calliostoma zizyphinum***
Lower shore, all coasts, Up to 30 mm


FIG. 20

\- Outline of the cone interrupted by the suture .. **19**

19 (18) The columella bears a white lump ('tooth') projecting into the aperture (Fig. 21). Decoration is essentially a pattern of fine dark lines zigzagging over a green or light brown background
.... **Common topshell**, ***Osilinus lineatus***
Upper middle shore, southwestern coasts, Up to 34 mm

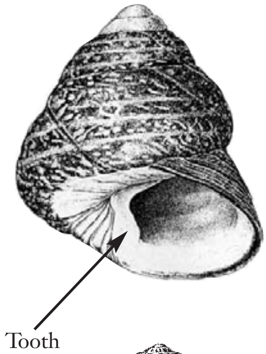

FIG. 21

\- No tooth on the columella. Decoration is essentially a pattern of red or purple zigzag bands on a greyish green background (Fig. 22). .... ***Gibbula pennanti***
Middle shore, Channel Islands, Up to 18 mm
NOTE: Very similar to *Gibbula umbilicalis* but without an umbilicus. May be recognised from that species, without great difficulty, on shores where both occur.

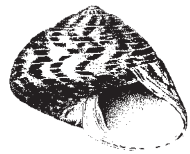
FIG. 22

20 (12) The buff-coloured horny outer layer of the shell (the periostracum) is heavily ridged and conspicuous. Suture very prominent (Fig. 23)
.... **Thick chink shell**, ***Lacuna crassior***
Lower shore, most coasts, rare. Up to 14 mm

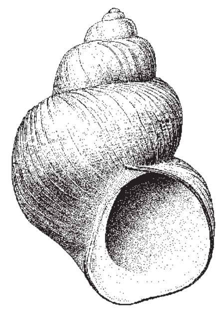
FIG. 23

\- Periostracum inconspicuous or absent **21**

21 (20) The shell has an umbilicus (Fig. 24), or chink. (In such shells, the whorls do not touch in the centre of the spiral, leaving an open space; the umbilicus is the lower opening to that space)
....Chink shell ... **22**

\- There is no umbilicus. The inner margins of the whorls are in contact and form a solid rod up the centre of the shell (the columella) ....Winkle ... **24**

22 (21) The shell has a high spire (Fig. 24) and is buff-coloured with 3 or 4 orange bands running round the whorl at right angles to the shell lip ....**Banded chink shell**, ***Lacuna vincta***
Lower shore, all coasts, on red seaweeds. Up to 10 mm

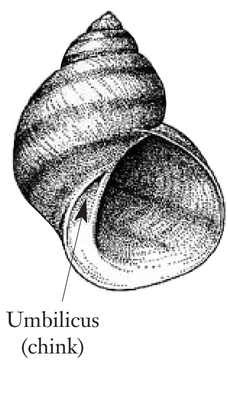

FIG. 24

\- Shell has a low spire and is not banded **23**

23 (22) Aperture enormous; appears to be larger than the rest of the shell which has such a low spire as to be virtually non-existent (Fig. 25). Pale green in colour.
...................**Pallid chink shell**, ***Lacuna pallidula***
Lower shore, all coasts, on *Fucus serratus*. Males up to 6 mm, females up to 12 mm

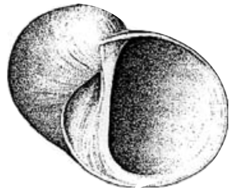

FIG. 25

\- The aperture does not appear to be larger than the rest of the shell which has a distinct spire (Fig. 26). Buff coloured.
........................**Small chink shell**, ***Lacuna parva***
Lower shore, all coasts, on red seaweeds. Up to 4 mm.

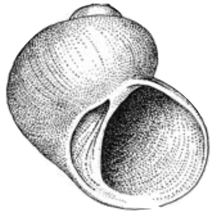

FIG. 26

24 (20) The periostracum extends beyond the lip of the calcified layers and appears as colourless flexible rim to the shell lip. Shell long and pointed with a shallow suture (Fig. 27); the colour of the bloom on purple grapes.
.................**Small winkle**, ***Melarhaphe neritoides***
Splash zone, all coasts except southeast England. Up to 9 mm.

\- Shell lip without a colourless flexible rim
.... **25**

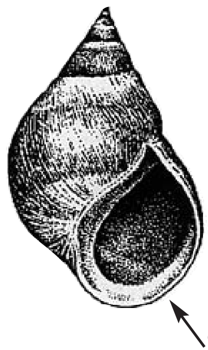

FIG. 27

colourless, flexible rim to shell lip

25 (24) The shell has a distinct spire **26**

\- Shell low- or very low-spired (Fig. 28)
....Flat winkle... **28**

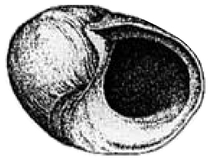

FIG. 28

26 (25) The shell is more than 26 mm long **OR** there are a series of dark lines crossing the shell outer lip at right angles (Fig. 29). Suture shallow (arrowed in Fig. 30). Outer lip of the shell meets the body whorl at an acute angle (Fig. 30). Black markings run across the head tentacles (Fig. 31)
.... **Edible winkle, *Littorina littorea***
Middle and lower shore, all coasts. Up to 56 mm

\- Shell 26 mm or smaller. Black lines cross the shell lip *only* if the shell has a black line in each spiral groove. Suture deep (arrowed in Fig. 31). Outer lip of the shell meets body whorl at an obtuse angle (Fig. 32). A black line runs along each side of the head tentacles (Fig. 33)
.... Rough winkle ... **27**

27 (26) The spiral ridges of the shell ornament have rounded tops and are wider than the grooves between them .... ***Littorina compressa***
Middle shore, north and west coasts. Up to 26 mm. Often the grooves are black, contrasting with the yellow or greenish ridges (Fig. 34).

\- Shell smooth (Fig. 35) or, if ridged, with sharp crested ridges narrower than the grooves between them
.... ***Littorina saxatilis***
Upper middle shore to splash zone, all coasts. < 26 mm.
or .... ***Littorina arcana***
Upper middle shore to splash zone, all coasts except southeast England. < 17 mm

NOTE: The essential difference between these two species is that whilst female *L. arcana* lay their eggs in masses of jelly attached to the rock, those of *L. saxatilis* retain them within their shell and appear to give birth to live young. Whilst, on any particular shore, it is usually possible to separate the two species (where both occur) there are no reliable characters applicable nationally as both display similar ranges of variation. *L. saxatilis* is the more widely distributed and much the commoner in sheltered sites. See Reid (1996).

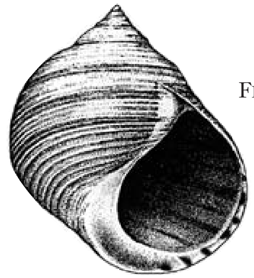
FIG. 29

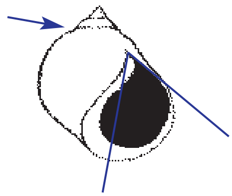
FIG. 30

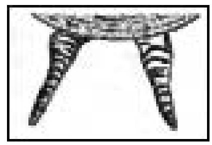
FIG. 31

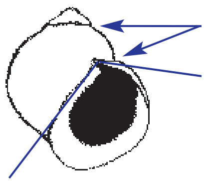
FIG. 32

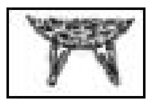
FIG. 33

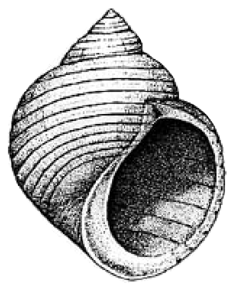
FIG. 34

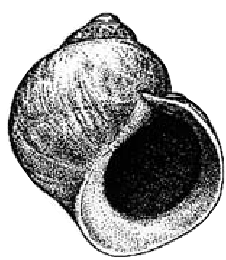
FIG. 35

28 (25) Found on or near bladder wrack (*Fucus vesiculosus*) or egg wrack (*Ascophyllum nodosum*). The population contains animals of at least two markedly different sizes (separate generations). The shell has a detectable spire (Fig. 36). If it is smaller than 12 mm it probably has a thin sharp lip.
.... **Common flat winkle**, ***Littorina obtusata***
Middle shore, all coasts. Up to 20 mm.

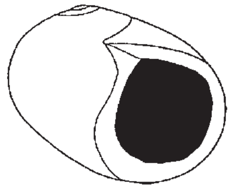
FIG. 36

\- Found on or near saw wrack (*Fucus serratus*). All members of the population belong to the same generation (but there is some sexual dimorphism). The shell has no detectable spire (Fig. 37). Shells between 9 and 12 mm usually have a thick lip.
.... **Annual flat winkle**, ***Littorina fabalis***
Lower shore, all coasts. Up to 12 mm

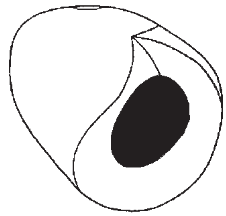
FIG. 37

NOTE: The two species of flat winkle are not easy to separate. Where they occur together, *L. obtusata* grows to a larger size. Both show the same range of colour variation, but winkles with olive green shells are most likely to be *L. obtusata*

29 (3) The shell aperture is a long narrow slit (Fig. 38) .... **Cowrie**, ***Trivia monacha***
Lower shore, all coasts. Up to 12 mm.

\- The aperture occupies the whole under surface of the shell **30**

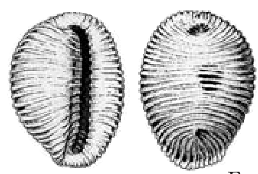
FIG. 38

30 (2, 29) The shell has perforations (a slit, hole or holes) in its surface in addition to the aperture (Figs 39-41) **31**

\- The aperture is the only opening in the shell .. **33**

31 (30) The perforation is a slit (Fig. 39).
.... **Slit limpet**, ***Emarginula fissura***
Lower shore, all coasts except SE England. < 10 mm.

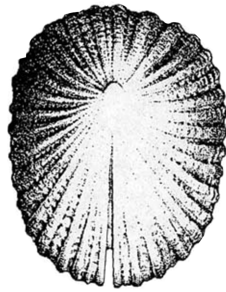

FIG. 39

\- The perforation is a hole or holes **32**

32 (31) A line of holes mark exit siphons from the mantle cavity (Fig. 40).
.... **Ormer**, ***Haliotis tuberculata***
Lower shore, Channel Islands. Up to 90 mm.
NOTE: As the animal grows, and the mantle cavity moves forward, redundant holes are sealed from inside.

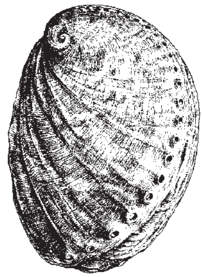

FIG. 40

\- There is a single hole at the apex of the shell (Fig. 41). .... **Key-hole limpet**, ***Diodora graeca***
Lower shore, all coasts except North Sea. Up to 25 mm.

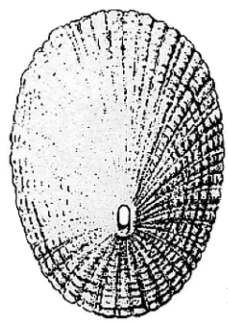

FIG. 41

33 (30) The shell is a cone with strong ribs radiating out from the axis (Fig. 42) **34**

\- Shell without strong *radiating* ribs **36**

NOTE: To see the sole of the foot, it is necessary to take the limpet off the rock - which will almost certainly injure or kill it. Hence, unless it is essential to determine the species, concentrate on the other characters. It is possible to see the pallial tentacles (Fig. 43) on limpets crawling in rock pools. The apex is over the head, so the head is to the right in Fig. 42. Figs 43-50 are drawn with the head downward.

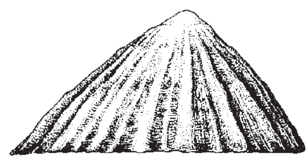

FIG. 42

34 (33) Posterior margin of the shell is smoothly rounded (Fig. 44). Pallial tentacles colourless. Sole of the foot dusky grey in colour.
.... **Common limpet**, ***Patella vulgata***
Whole shore above lowest levels, all coasts. < 60 mm.

\- Posterior margin of the shell is angulated. Pallial tentacles white or cream **35**

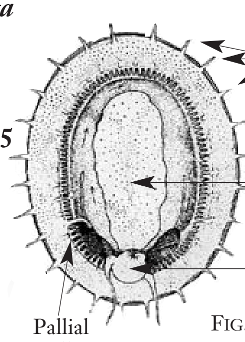

FIG. 43

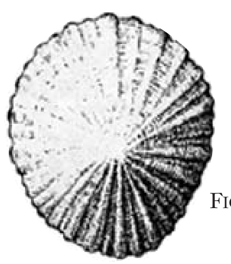

FIG. 44

35 (34) Sole of the foot apricot in colour. Shell a very low cone decorated with a large number of rather fine radiating ribs (Fig. 45) .... **China limpet**, ***Patella ulyssiponensis***
Lower shore (and rock pools), all coasts except E England. Up to 50 mm.

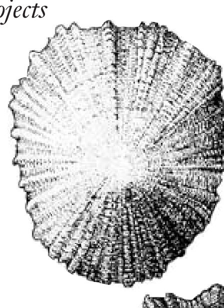
FIG. 45

\- Sole of the foot black. Shell usually a low cone decorated with heavy radiating ribs (Fig. 46). ...**Black-footed limpet**, ***Patella depressa***
Middle shore, south and west coasts. Up to 30 mm.

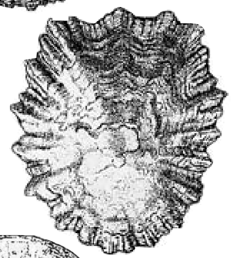
FIG. 46

36 (35) Shell a nearly symmetrical cone bearing an ornament of concentric ridges - each parallel to the shell margin (Fig. 47) ... **Chinaman's hat limpet**, ***Calyptraea chinensis***
Lower shore, SW coasts. Up to 15 mm.


FIG. 47

\- Shell not a symmetrical cone (the apex is nearer the front end). Shell surface smooth, with a pattern of radiating lines. No concentric ridges **37**

37 (36) A lower shore limpet living on kelp (*Laminaria*) or saw wrack (*Fucus serratus*). The brown shell bears radiating flashes of irridescent blue (Fig. 48). The animal has pallial gills (secondary gills lying in the pallial groove, around the foot, cf Fig. 39) .... **Blue-rayed limpet**, ***Patella pellucida***
Lower shore, Atlantic coasts. Up to 18 mm.

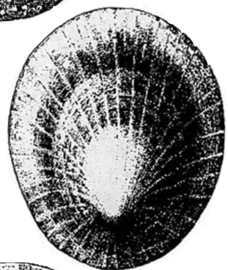
FIG. 48

\- A lower shore limpet living on the rock surface. The shell lacks blue flashes and the animal has no pallial gills **38**


FIG. 49

38 (37) Shell basically cream or greenish marked by chocolate brown splodges (Fig. 49) .... **Tortoiseshell limpet**, ***Tectura tessulata***
Lower shore, Northern and Western coasts. < 20 mm.

\- Shell basically white or yellowish marked by pink lines, often broken into splodges (Fig. 50) .. **White tortoiseshell limpet**, ***Tectura virginea***
Lower shore, most coasts. Up to 10 mm.

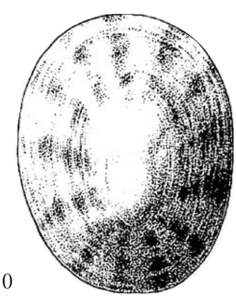
FIG. 50

BOX 1
NAME CHANGES

Revision of the taxonomy in many groups of rocky shore snails has resulted in a significant number of name changes in recent years. Natural history books are notably conservative in their usage of names, so Box 1 is provided to help people to match the specimens identified from this key to information to be found in the literature.

Name used in the Key	Name that may be found in the Literature	Name used in the Key	Name that may be found in the Literature
Emarginula fissura	*Emarginula reticulata*	***Osilinus lineatus***	*Monodonta lineata*
Hinia incrassata	*Nassarius incrassatus*		*Trochocochlea lineata*
H. reticulata	*Nassarius reticulatus*	***Patella depressa***	*Patella intermedia*
Littorina arcana	*L. saxatilis* (in part)	***P. pellucida***	*Helcion pellucida*
L. compressa	*L. nigrolineata*		*Patina laevis*
	L. saxatilis (in part)		*Patina pellucida*
L. fabalis	*L. mariae*	***P. ulyssiponensis***	*Patella aspera*
	L. littoralis (in part)	***Tectura tessulata***	*Acmaea tessulata*
L. obtusata	*L. littoralis* (in part)		*Acmaea testudinalis*
L. saxatilis	*L. neglecta*		*Collisella tessulata*
	L. rudis	***T. virginea***	*Acmaea virginea*
Melarhaphe neritoides	*Littorina neritoides*	***Tricolia pullus***	*Phasianella pulla*
Nucella lapillus	*Purpura lapillus*	***Trivia monacha***	*Cypraea monacha*
	Thais lapillus		

Name that may be found in the Literature	Name used in the Key	Name that may be found in the Literature	Name used in the Key
Acmaea tessulata	*Tectura tessulata*	***Littorina saxatilis***	*L. saxatilis* and
A. testudinalis	*T. tessulata*		*L. arcana*
A. virginea	*T. virginea*		*L. compressa*
Collisella tessulata	*T. tessulata*	***Monodonta lineata***	*Osilinus lineatus*
Cypraea monacha	*Trivia monacha*	***Nassarius incrassatus***	*Hinia incrassata*
Emarginula reticulata	*Emarginula fissura*	***N. reticulatus***	*H. reticulata*
Helcion pellucida	*Patella pellucida*	***Patella aspera***	*P. ulyssiponensis*
Littorina littoralis	*L. obtusata* and	***P. intermedia***	*Patella depressa*
	L. fabalis	***Patina laevis***	*Patella pellucida*
L. mariae	*L. fabalis*	***P. pellucida***	*Patella pellucida*
L. neglecta	*L. saxatilis*	***Phasianella pulla***	*Tricolia pullus*
L. neritoides	*Melarhaphe neritoides*	***Purpura lapillus***	*Nucella lapillus*
L. nigrolineata	*L. compressa*	***Thais lapillus***	*Nucella lapillus*
L. obtusata	*L. obtusata* and	***Trochocochlea lineata***	*Osilinus lineatus*
	L. fabalis		
L. rudis	*L. saxatilis*		

Some Suggestions for Projects using Snails on Rocky Sea Shores

1. Synecological Investigations

Species diversity

Biodiversity (= diversity of life) remains a 'buzzword' and, whilst it is almost impossible to establish the full diversity of all life in any habitat, some of the basic principles of the concept may be demonstrated using rocky shore snails. Moreover, the fieldwork is simple because all you have to do is to count the number of individuals of each species present within a given area.

It is necessary to distinguish between 'species diversity' and 'species richness.' The latter is simply the number of species present within the given area; species diversity incorporates a measure of the number of individuals of each species. Imagine two communities, each of 100 snails, members of 10 different species. A community made up of 10 individuals from each of the 10 species would be regarded as much more diverse than one in which one species was represented by 91 individuals and the others by just one each.

Obtaining a single measure of species diversity of the snail fauna is not of any great value; the interest lies in the differences between different shores, or between different parts of the same shore. Theoretically, we should expect species diversity to be lower in more stressful habitats and higher in more benign ones.

All the snails mentioned in this paper are of marine origin; their ancestors lived below the tide marks and they have colonised the shore from below. It would seem likely, therefore, that life out of water (at low tide) is more stressful than life under water (at high tide) for the environment is altogether more extreme out of water. Not only does the rock surface dry out; it may become much hotter by day and/or colder by night and experience the full salinity range from fresh water to crystalline salt. It might be supposed that diversity would increase with the period of time the area of rock is submerged under water - a value that is difficult to measure directly but, is closely correlated with height up the shore.

Complicating any pattern relating to these abiotic environmental factors, however, are the biotic factors of predation and availability of food. At low tide, rocky shore snails may be eaten by birds whilst at high tide they are vulnerable to predators, including fish, octopuses, crabs, lobsters and prawns. So, whilst it may be expected that diversity would increase from the upper down to the middle shore, it may not always escalate lower down.

Comparison of snail faunas from different areas at the same level on a shore will avoid this complication. For example, comparing the fauna where a freshwater stream flows across the shore with that of an adjacent community unaffected by the stream. It could be hypothesised that the additional salinity stress of the freshwater at low tide would decrease species diversity (Table 2). Note that these are not field data; their purpose is to provide a worked example of the calculation.

Practicalities

A number of different indices have been devised to quantify species diversity. Some examination specifications stipulate use of a particular index; with other awarding bodies you are free to choose. That used in Table 2 was recommended by the Open University Ecology Course Team and has the advantage that the highest possible value is very close to one and the lowest is zero.

As usual in scientific data collection, the two samples should differ only because of the factor under investigation. Thus, the samples should come from the same sized areas of

BOX 2

The species diversity of marine snails where a freshwater stream runs across the shore as compared with a site at the same height up the shore but away from the stream. The procedure is to write down the number of individuals of each species found in equivalent areas at each site and to determine the proportion of the total fauna represented by each species. These proportions are then squared, summed and the result subtracted from one. Imaginary data.

Species	In the area of the stream	away from the stream
Patella vulgata	4	8
Littorina littorea	41	25
Littorina saxatilis	32	45
Littorina obtusata	0	4
Gibbula umbilicalis	0	36
Osilinus lineatus	54	38
Total	131	156

Species	Proportion P_1	Proportion² P_1^2	Proportion P_2	Proportion² P_2^2
Patella vulgata	0.03	0.0009	0.05	0.0026
Littorina littorea	0.31	0.0979	0.16	0.0257
Littorina saxatilis	0.24	0.0597	0.29	0.0832
Littorina obtusata	0	0	0.03	0.0006
Gibbula umbilicalis	0	0	0.23	0.0532
Osilinus lineatus	0.41	0.1699	0.24	0.0593
Total (Σ)	1.00	0.3285	1.00	0.2248
Diversity index	$D = 1 - \Sigma P_1^2 = \mathbf{0.67}$		$D = 1 - \Sigma P_2^2 = \mathbf{0.77}$	

shore; if one has pools in it, so must the other; if a search is made under stones in the one site, so it must in the other. The sample area, which may be of any convenient size and shape, is known as a quadrat. It is often helpful to define the area by using a quadrat frame of some kind. On flat rock surfaces, it easy to form a $1m^2$ quadrat by laying down four metre rules to form a square. This is less meaningful on uneven surfaces, or on boulder shores, because the actual rock surface area, so enclosed, is often much greater than $1m^2$. In these circumstances, it may be appropriate to kneel down (on the smoothest available surface!), count the number of limpets and collect all the other snails that can be reached without moving the knees. Once all the snails have been captured, they can be sorted into species and counted.

Note that it is not necessary to name the species in order to work out diversity, provided that they can be recognised as separate entities.

2. AUTECOLOGICAL INVESTIGATIONS

Species diversity looks at the whole fauna but for most other projects, it is advisable to concentrate on one or two easily recognisable species. Choice of species depends on availability, the type of project envisaged and personal preference. There follow just a few suggestions for the use of limpets, topshells, winkles and dog-whelks, but there are very many other possibilities.

FIG. 51
A limpet resting by day on a rocky shore, with grazing tracks radiating out across the rocks as evidence of its night-time activity.

FIG. 52
At higher magnification, the track is seen to be composed of discrete radula scratches (limpet-tongue-licks)

LIMPETS.

The common limpet, *Patella vulgata*, is one of the most ubiquitous animals on British rocky shores; it is also one of the most important because it controls the growth of seaweeds. But it has failed to make much of an impression on the Great British Public, being night-active in wet conditions whilst humans prefer to visit sea shores by day when it is dry and sunny. Very few limpets 'do anything' at low tide by day and so they never attract the attention given to crabs, for example. If anything, their value as project material is enhanced by the lack of attention shown by people in general because 'human interference' is unlikely to be a complicating factor in most investigations. Limpets are 'Good Project Animals' because of the ease with which they can be counted, measured, and marked and because of the tracks they leave on the rock.

Grazing tracks

At low tide by day, most limpets are inactive, but they are often surrounded by grazing tracks which record their night-time activity. The tracks (Fig. 51) show where the snail has scraped a pale-coloured algal film off the dark grey rock. Close up (Fig. 52), a track is seen to be made up of discrete, parallel-sided marks (radula scratches) formed as the grazing limpet crawls slowly forward, swinging its head from side to side.The most recent tracks

FIG. 53
The track of a limpet grazing over barnacles

FIG. 54
Even when individual tracks are not visible, the home range of limpets may be measured.

will be the most clearly defined; older tracks become blurred as the algae grow back - in something of the same way that mower stripes fade away on lawns.

It is likely that a limpet makes only one trail a night. So the animal illustrated in Fig. 51 appears to have had a 'home' to which it returned each day. Tracks are only visible because most of the algae were not harvested; where limpets are very numerous (or when algal growth is slow) no tracks may be visible. But in those times and places when tracks are clearly seen, they can be used to investigate;-

• the distance crawled when feeding. Is this related to the size of the limpet, to the availability of food, to the weather or to height up the shore?

• the direction usually crawled. Does it usually set off uphill, downhill, in the direction in which it is facing, or towards the rising moon?

• the substrate usually selected. Is it easier to graze a smooth rock surface than mountaineer over barnacles (Fig. 53)? for instance.

It may be possible to investigate patterns of limpet grazing even when individual tracks are not visible. Fig. 54 illustrates limpet home ranges on a newly re-faced concrete wall. The dark areas are green seaweeds and the pale concrete shows through where limpets have cleared the algae away.

FIG. 55
Two limpets 'at home' on a comparatively soft rock surface. To the right, a limpet scar made by a limpet which formerly had a home there.

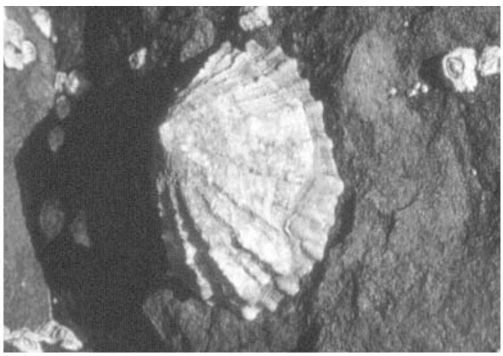

FIG. 56
A limpet 'at home' on quartzite. The shell now fits the rock here but, formerly, it matched a different location

Homing behaviour

Homing behaviour is a characteristic feature in limpets of the genus *Patella*. It is generally observed that a limpet's shell fits the rock surface of its home very closely - far too closely for this to have occurred by chance. On soft surfaces, the snails grind their shells into the rock to make it fit their shape, forming 'scars' (Fig. 55). On hard igneous or metamorphic rocks, a limpet could spend a lifetime grinding without affecting the rock very much. On such surfaces they grow their shells to conform to the rock. (Fig. 56) Why? The answer probably is to conserve water, enabling them to breathe using gills on the dry rock surface close to their feeding site.

In *Patella* limpets, the gills lie in the pallial groove between the mantle and the foot. (Fig. 57). Thanks to the close fit between shell and rock, the limpet 'at home' is able to hold water in this groove before the rock dries out and, after very slightly relaxing its hold on the rock, can establish an air-water interface around the margin of the shell through which oxygen may diffuse in and carbon dioxide out during the low tide period.

Major disruption of limpet populations is usually followed by recolonisation of 'damaged' sites by adult limpets (e.g. Crump *et al.*, 2003) and the individual illustrated in Fig. 56 had colonised its new home following an oil pollution experiment (which eliminated the existing limpets), rapidly producing more shell to conform to the rock surface. But, in an undisturbed location, homing was generally assumed, for this is such a beautiful example of the co-evolution of behaviour and morphology.

However, this is not the case. Pupils from Selwood Middle School carried out a 5-day investigation, one June, that involved marking limpets (as in Fig. 58), using a different

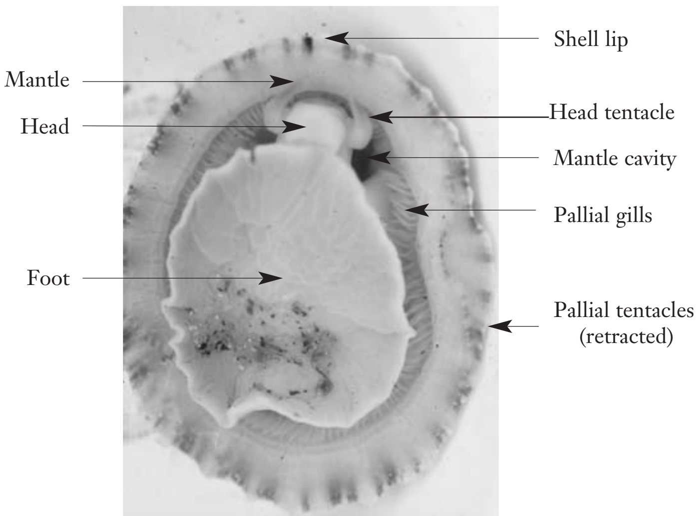

FIG. 57

Patella vulgata removed from the rock and photographed upside down in seawater.

At the front end, the head bears two tentacles, each with a simple eye near the base. When the limpet clamps down to the rock surface, the head retracts into the mantle cavity. Feathery pallial gills lie in the pallial groove between the mantle and the foot (they are shown semi-diagrammatically in Fig. 43). Cells on the outer surface of the mantle secrete new shell. Those along the mantle edge form the outer, coloured, layers (some of these cells have been accumulating pigment to mark the stripes) whist the inner layers are secreted by the outer surface. The pallial tentacles, shown extended in Fig. 43 are used by the limpet to recognise the outline of its home and manoeuvre into position.

FIG. 58
A limpet on the shore at Watchet, marked by a pupil from Selwood Middle School as part of an investigation into limpet homing

FIG. 59
Ridges running around a limpet shell, parallel with the shell lip represent growth checks.

colour of paint on successive days, found that only 60% of the animals were in the same home every morning. Some had two homes. Is homing behaviour more important on the upper shore than on the middle or lower shore? Is it more important on rough surfaces than on smooth; on steep slopes than on horizontal surfaces?

The oldest part of a limpet shell is the apex and the newest part is the margin (lip); the limpet increases the size of its shell by adding material to the margin. In Fig. 59, the shell secreted during the snail's first year is still recognisable atop the adult shell. Growth continues throughout life but not at a steady rate. When growth is checked for any reason, the edge of the shell becomes abraded and, when growth eventually recommences, the former shell lip remains visible as a growth check running around the shell parallel to the lip. If the growth check is not parallel to the lip, as on the shell in Fig. 56, the limpet has moved home.

Where the upper shore is a cliff, or a wall, the limpet homes are often clustered (Fig. 60). It has been hypothesised that this behaviour may help the limpets to retain moisture at low tide by day. Experiments, using empty limpet shells filled with wet blotting paper, could be devised to test this suggestion. Is the clustering habit associated with height up the shore (= length of time out of seawater) or with the steepness of the rock?

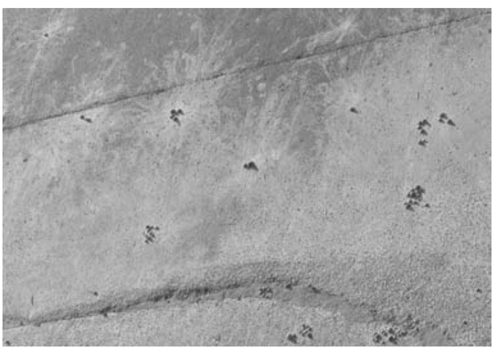

FIG. 60
High on the outer face of a harbour wall, limpet homes are clustered together.

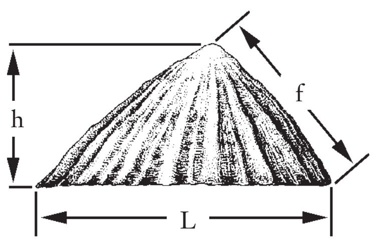

FIG. 61
The measurements taken on a limpet shell; height (h), length (L) and frontal length (f).

Orientation of limpets in their homes is another source of investigation; sometimes local topography is the most important factor but, on other occasions, almost all individuals will be found facing in the same direction. Are most of them head downward in their homes? (the head is under the apex of a *Patella* shell; *i.e.* to the right in Fig. 61). Is the pattern related to the steepness of the rock? or height up the shore ?Do they face into the waves?

Biometrics

A wide range of projects can be devised to investigate the variation in size and shape of limpets in different parts of the shore. Baby limpets arrive on the shore less than 1 mm long and have the potential of reaching 60mm and/or 16 or more years.

When measuring limpets, do not remove them from the rock, as injury is almost inevitable. Lengths and breadths of limpet shells are most easily measured using a pair of dividers and a ruler for, except on the flattest of surfaces, callipers are awkward to use. Shell height (h in Fig. 61) is more difficult to measure directly, but a simple ratio of frontal length (f) to overall length (L) may be calculated; higher values indicate more conical shells (Fig. 62). The relationship between this ratio and h may be established from measurements on empty shells.

There is usually an inverse relationship between limpet size and abundance, which is what one would expect if food is limiting; a fixed amount of food will support more small individuals than large ones. Generally speaking, exposed, barnacle-dominated shores support high densities of small limpets whilst sheltered seaweed-covered shores tend towards low densities of large ones. The big brown seaweeds exclude most of the light from the rock surface, shading out the diatoms and other components of the algal felt upon which limpets graze. Moreover, by the whiplash effect of their fronds on the rock (Fig. 63) they abrade any remaining small algae (and limpet spat) from their area of influence. The limpets found under seaweeds were either living there before the seaweed arrived or settled somewhere else and migrated under the canopy once they had reached a size able to withstand the whiplash. Both Boaventura *et al.* (2003) and Crump *et al.* (2003) demonstrated that that it is shortage of food that keeps exposed shore limpets small; not wave action. If density is reduced, and the food supply improved, the survivors grow rapidly.

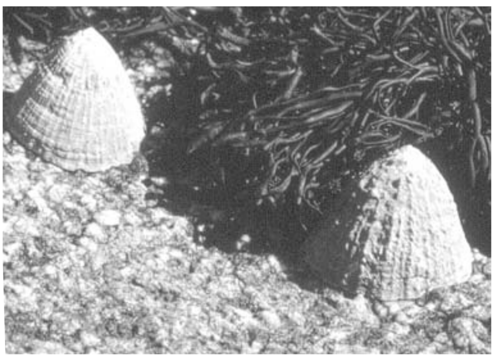

FIG. 62
Limpets with homes high on the shore are often found to have shells of a highly conical shape

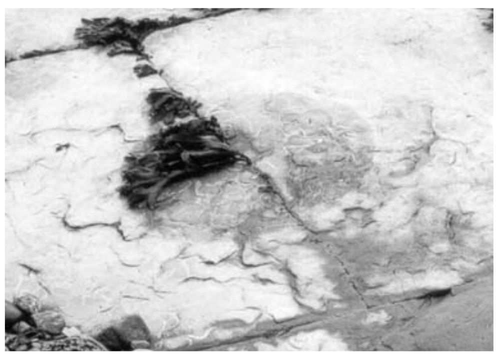

FIG. 63
The dark rock showing through the paler algal felt where it has been swept clean by the whiplash effect of the brown seaweeds.,

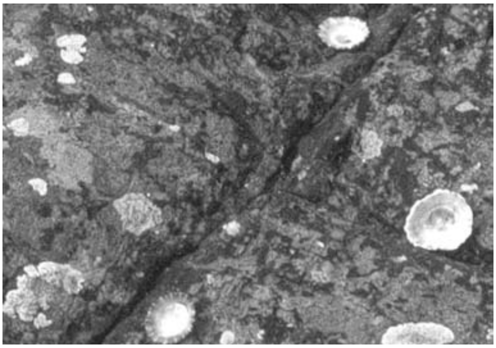

FIG. 64
Limpet shells, knocked off their homes by gulls and carried above high water mark where their owners were eaten

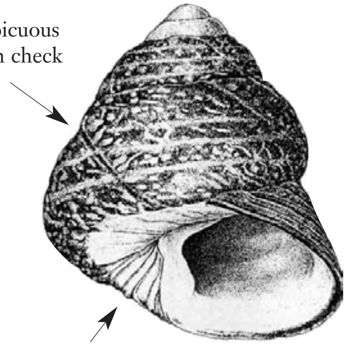

FIG. 65
Conspicuous growth checks, running across the shell parallel to the outer lip, record winters past on common topshell shells

Often it is observed that the mean size of the limpets varies as you move up or down the shore - but the maximum size hardly change. The variation in the mean depends largely in the numbers of small individuals present. It seems likely that there are nursery levels for, whilst limpet spat are broadcast across the entire shore, survival of baby snails is much more restricted. Shortage of food due to overcrowding, after a successful spatfall, will encourage the youngster to move away as soon as they can tolerate conditions away from the nursery.

Upper shore limpets often have more highly conical shells (Fig. 63) than those on the middle shore. Traditionally (Orton, 1929), this has been explained as the effect on growth of the inward pull of the shell muscle to keep the shell close to the substratum for the long periods of low tide. However, limpets do not spend the low tide period clamped hard down, but relax in order to breathe. Boaventura *et al.*, (2003) found that limpets living at low densities, with a good food supply, grew rapidly and developed rather flat shells. Does that suggest that the high conical shells indicate slow growth? perhaps due to shortage of food.

Bird predation

Gulls, *Larus* sp., and oystercatchers, *Haematopus ostralegus*, are able to knock limpets off their homes when they are relaxed in order to breathe. The bird then wedges the shell in a crevice before pecking out the meat. Gulls often fly up above high water mark to do this (Fig. 64), but oyster-catchers usually feed where the prey was found. If several clean, inverted, limpet shells are found on the top of rocks, birds have been feeding since the tide has gone out.

If the birds were taking prey items at random, the size frequency of the predated shells should be the same as that of the surviving population. This is rarely the case because the birds select within a preferred size range. Do they favour the largest available prey? or, perhaps, the commonest size?

These are but a few suggestions for investigations that can be carried out with these interesting animals. The best sources of information on basic limpet biology are Fretter & Graham (1962, 1972, 1994). The only drawback to limpets as the perfect project animal is that they cannot be aged; size being related more to the amount of food they have eaten than the length of time over which they have been in feeding.

FIG. 66
Growth checks may also be caused by severe damage to the shell which must be repaired before growth can continue.

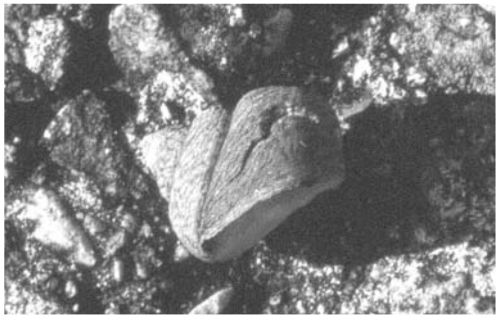

FIG 67
Damage probably caused by a crab chipping away at the outer shell lip

COMMON TOPSHELLS

Population studies

The common topshell, *Osilinus lineatus*, is at the northeastern limits of its geographical range in southwest Britain (see Crothers, 2001, for a review of this species' biology). At least close to those limits, growth is usually suspended for several months each winter and a 'conspicuous growth check' (Fig. 65) is subsequently seen on the outer surface of the shell. Counts of these growth checks give an estimate of the number of winters the snail has survived. It is often possible to distinguish the various age classes within the population and determine their rate of growth.

Breeding is largely confined to a short period in mid-summer, so the population is made up of discrete age classes. The young snails appear on the shore in August or September each year. Juveniles grow rapidly to reach adulthood; adults continue much more slowly for the rest of their lives which may total more than 15 years.

The annual growth checks cross the outer surface of the shell, parallel to the outer lip and are most clearly defined where they cross the white area underneath (arrowed in Fig. 63). In old individuals, the recent checks may be quite close together in contrast to others now higher up the spire which were formed when the young snail was growing rapidly, as in Fig. 63. In such individuals, the outer, coloured layer of shell is abraded from the apex, removing all trace of any growth check relating to the animal's first winter - so it is best to assume its presence on all shells even if it cannot be seen.

However, 'conspicuous growth check' is a technical term and they are not always that obvious - especially after a mild winter when growth was not totally suppressed; in such circumstances, many shells show a band of 'barely-discernable growth checks'. The most difficult season to age these snails is May-July for young snails commence growing long before older ones and so appear to have additional check.

Damage to the shell usually causes a growth check as well (Fig. 66); storm damage is, perhaps, more likely in winter, but chips out of the lip resulting from crab attack probably occurred in summer (Fig. 67) when large crabs are more active on the shore. It would be possible to estimate the comparative importance of (unsucessful) crab attack on different shores by comparing the proportions of living snails which bore such injuries. Successful attacks could be estimated from the number of empty shells with large chips missing from the shell lip. For information about shore crabs, see Crothers (1967, 1968).

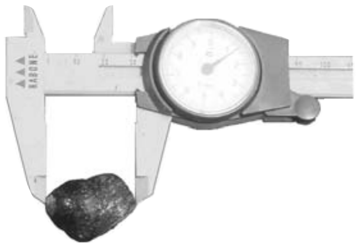

FIG. 68
Shell length - the maximum distance from the apex to the outer shell lip

FIG. 69
Common topshells and edible winkles crawl out of the water, at low tide, where a freshwater stream runs across the shore.

Growth rates may be established by calculating the mean size of each year class. It is probably most objective to measure shell height (Fig. 68) but some people have used basal diameter; they are very similar figures in this species. There are often quite large differences in growth rates, longevity and population structure between different shores and even between different areas of the same shore.

There is a tendency to find with this species, as with limpets, that where the animal is comparatively rare their shells have grown rapidly to a large size but not to any great age; where they are really common, they grow slowly, perhaps taking an extra year to reach maturity, but live to a ripe old age. It seems likely that size and rate of growth are limited by the food supply whilst abundance is controlled by the successful settlement of spat and subsequent evasion of predators (see Williamson & Kendall, 1981; Little *et al.*, 1986, Crothers, 2001). As nobody has discovered any major difference in the food preferences of *Osilinus lineatus*, *Gibbula umbilicalis*, *Littorina littorea* and *L. saxatilis*, it is probably the combined density of these rock-scraping snails that matters. Slow growth may be associated with long life and vice versa.

Behaviour

Limpets may be inactive at low tide by day, but the same is not true for common topshells. This can be a serious concern to scientists involved in monitoring surveys where the inhabitants of permanent quadrats are counted at regular intervals; counts of this species vary with the weather. Little *et al.*, (1986) observed them to respond within minutes to changes in weather conditions, moving out into the open when the sun shone whilst hiding from rain or cold winds.

As with limpets, there appear to be nursery areas in that small juveniles are much commoner in certain parts of the shore but there appears to be no uniform pattern; sometimes the chosen site is low down, sometimes higher up. Perhaps it is related to particle size of the substrate, perhaps to the availability of pools of an appropriate size.

Certainly on some shores, large individuals may migrate upshore in summer and retreat downshore in winter

Mention was made earlier, p. 614, of a site where a small freshwater stream runs across the beach. Although *Osilinus lineatus* is no more tolerant of freshwater than the other grazing snails, it is the only one to be more abundant in the area of the stream (Box 2).

Marked animals (see below) moved into the stream area; snails in the stream grow larger and live longer. Why?

Estimation of Population Size

BOX 3

THE ESTIMATION OF POPULATION SIZE BY MARK RELEASE RECAPTURE

A sample of animals (S_1) is collected and the individuals marked in such a way as to render them recognisable on recapture. The sample is released back into its habitat and given time to mingle at random with other members of the population. A second sample (S_2) is then taken, at random, and divided into marked (R) and unmarked individuals. The estimate of population size (N) is based on the presumption that the ratio of recaptures to the whole of the second sample ($R:S_2$) is the same as the ratio of all the marked individuals to the total population ($S_1:N$). So,

$$N = (S_1 \times S_2) \div R.$$

The 95% confidence limits of the estimation (within which lies the true value of N) are given by

$$N \pm (2N \sqrt{(1 \div R) - (1 \div S)}$$

The estimation of population size by use of the Lincoln Index following a procedure of mark, release and recapture (Box 3) is much favoured by the writers of text books (Chalmers & Parker, 1989) but, in practice, there are few animal species on which it can be applied. Common topshells are an exception.

It is an elegant idea and the mathematics present no problems. It presumes, however, that the individuals can be sampled, handled and marked without harm; that the environment is not damaged by the sampling process; that individuals mix at random within the population; that that population remains in the same location between the release and recapture; that there are no births or deaths, immigrations or emigrations during that period; and that marked individuals are neither more nor less likely to be taken in the second sample.

The technique is obviously inappropriate for territorial animals, such as limpets, or those forever on the move, such as shore crabs, and presupposes that it is possible to mark them in a manner that does not affect their behaviour. But the real problem is the requirement for marked individuals to mingle at random within the unmarked population. It is hard to imagine that adult males and females are ever distributed at random within a population, let alone after the shock of capture and release.

Osilinus lineatus is a suitable subject for this technique because:

- It is easy to collect the initial sample without disturbing the habitat - the snails sit on the top of the rocks.
- They are easy to mark - with a small dab of paint on the underside of the shell.
- They can be left in full sun while the paint dries.
- They are active mobile animals which move about readily.
- Males and females do not copulate (the male does not have a penis); both sexes release their gametes into the sea and fertilisation occurs in the water. No courtship behaviour has been described so individuals of this species may really mingle at random.
- It is difficult to obtain an accurate estimate of abundance by direct count, because

individuals move in and out of cover according to the weather

In an earlier paper (Crothers, 2001), I reported the result of such an experiment on the shore of Gore Point, Somerset. Resampling after 24 hours suggested a density of 12 m^{-2}, which appeared to be of the right order of magnitude. The second sample was released again and a third sample taken 6 days later. The estimate had risen to 25 m^{-2}, distorted by the rate of immigration and emigration in and out of the marked square as the size of the collections shows that there were actually about the same number present on all three occasions.

This example highlights the problem of deciding when to recapture; too soon, and the marked individuals do not have time to mingle with unmarked members of the population; too long, and immigration/ emigration seriously distorts the result. For this species, in summer, it seems as though the following day (allowing two tides to cover the site) is optimal.

Post-mortem Studies

The nacreous shell laid down by a topshell requires regular maintenance, by the snail, to maintain its strength and it deteriorates quite rapidly after the death of its owner. One would expect, therefore, to find that empty shells of topshells were proportionally less abundant, as compared to those of winkles, on a shell beach than the living snails are on the adjacent rocky shore.

For the same reason, hermit crabs should select shells of winkles and whelks more often than those of topshells. Do they? or is hermit occupancy of snail shells proportional to the number of shells available? See Lancaster (1988) for information on hermit crabs.

FLAT WINKLES

Food preference

Limpets and topshells are generalist grazers, scraping the algal felt off the rock surface in a wholly unselective way. By contrast, flat winkles show strong preferences for particular species of brown algae. Williams (1990) showed that one species favoured the middle shore bladder wrack, *Fucus vesiculosus*, and egg wrack, *Ascophyllum nodosum*, whilst the other grazed the epiphytes off the lower shore saw wrack, *Fucus serratus*.

Virtually all shores which support *Ascophyllum nodosum* will support at least one species of flat winkle in reasonable numbers. The degree of association between a winkle and its putative food plant can be determined by calculating χ^2 from a 2 x 2 contingency table or by use of Cole's coefficient of interspecific association (Box 4). In both cases, it is a matter of scoring presence or absence of one species of snail and one of algae in a large number of quadrats.

Especially on dull days, flat winkles are active when the tide has just left them, before the rocks dry out. Experiments could be devised to investigate whether individuals were attracted to or repelled from particular species of alga - but allowance should be made for the possibility that they are merely seeking to get under cover. It may be that the winkles are attracted to their preferred food plant by chemical cues. Dr Trevor Norton showed that they respond positively to a current of seawater in which their preferred alga had been stored for 24 hours. It would be easy to keep seaweeds overnight in plastic watering cans filled with seawater, and then to dribble the water across the rock or investigate whether the winkles could discriminate between pieces of absorbent paper soaked in the water.

2 x 2 Contingency Tables BOX 4

		Species A present	Species A absent	
Species B	present	a	b	a+b
	absent	c	d	c+d
		a+c	b+d	a+b+c+d = n

$$\chi^2 = \frac{n\,([ad-bc] - (n \div 2))^2}{(a+c)\,(b+d)\,(a+b)\,(c+d)}$$

where [ad-bc] signifies placing the term in the positive form

Cole's Coefficient of interspecific Association

This coefficient is a number varying from +1 (complete positive association) through 0 (no association) to -1 (complete negative association). It, and its standard deviation, can be calculated by using one of the following formulae.

When ad ≥ bc:

$$C_{AB} = \frac{ad-bc}{(a+b)\,(b+d)} \pm \sqrt{\frac{(a+c)\,(c+d)}{n\,(a+b)\,(b+d)}}$$

When bc > ad and d ≥ a:

$$C_{AB} = \frac{ad-bc}{(a+b)\,(a+c)} \pm \sqrt{\frac{(b+d)\,(c+d)}{n\,(a+b)\,(a+c)}}$$

When bc > ad and a > d:

$$C_{AB} = \frac{ad-bc}{(b+d)\,(c+d)} \pm \sqrt{\frac{(a+b)\,(a+d)}{n\,(b+d)\,(c+d)}}$$

Colour variation

"Although some other species of *Littorina* may be able to match the wide range of shell colour and pattern shown by *L. obtusata* and *L. fabalis*, none of the others displays such a consistently high density of colour polymorphism within local populations." (Reid, 1996). Both species show essentially the same range of variation, although the olive green morph (olivacea) is much commoner in *L. obtusata* and the yellow (citrina) in *L. fabalis*.

The polymorphism is under genetic control but the disproportional abundance of particular morphs is presumed to be due to natural selection. Some authors, reviewed by Reid (1996), have linked various morphs to environmental variables including salinity and temperature (height up the shore) but British workers have generally concentrated on predation as the selective instrument.

Smith (1976) linked morphs of *Littorina obtusata* to the algae on which they were found, citing crypsis as the cause and assuming that the predators (gulls, ducks, waders, intertidal fish and crabs) take most of the more conspicuous individuals. He found the yellow form (citrina) to be most abundant on flat wrack, *Fucus spiralis*, which has globular yellow receptacles at the end of the fronds in spring. The olive-green morph (olivacea) which has a shell the size, shape and colour of the bladders on bladder wrack, *Fucus vesiculosus*, (Fig.

FIG. 70
The shells of olive green *L. obtusata* are much the same size, shape and colour as the bladders on bladder wrack, *Fucus vesiculosus*

FIG. 71
Flat winkles of the same size. Left. Adult *Littorina fabalis*, with a thickened lip: Right, juvenile *L. obtusata* with a thin lip

70) was most abundant on that species and *Ascophyllum nodosum*. Saw wrack, *Fucus serratus*, has neither bladders nor rounded receptacles and the winkle resembles the plant only in colour. The weed is dark brown during the summer but a good deal of black stipe is visible in winter. Smith found the dark morph with reticulate black markings (reticulata) commonest here. In that paper, he did not investigate whether the different colour morphs actively selected the appropriate alga but assumed that observed distribution was the result of selective predation.

As mentioned above, the yellow morph (citrina) is often the most abundant form in the annual flat winkle, *Littorina fabalis.* Reimchen (1979), quoted by Little & Kitching (1996) and by Reid (1996), investigated selective predation on two morphs of this snail by a rockpool fish, the shanny *Lipophrys pholis*, in aquaria. He found that the dark reticulata morph was more cryptic near the base of the alga, and when seen by reflected light but the paler citrina morph was almost invisible seen by transmitted light. If, as seems likely, the fish swim under the algal fronds looking upwards to seek their prey, this would explain the abundance of yellow *L. fabalis.*

As *L. obtusata* lives higher up the shore than *L. fabalis*, it is reasonable to suppose that bird predation is the controlling factor in the former species and fish (or some other aquatic animal) in the latter.

In both species, females lay their eggs in blobs of jelly attached to their favoured food plant. Juvenile snails complete the (normally free-swimming) veliger phase of their life cycle within the jelly capsule and hatch onto the food plant as tiny snails. Natural selection on earlier generations is likely to have influenced the genetic balance in the current population.

Practical Points

Rapidly-growing winkles have a thin outer lip to their shell, which becomes thicker on reaching maturity. *Littorina fabalis* matures at a much smaller size than *L. obtusata* (Fig. 71).

There is variation within each colour morph but, with a little experience it should be possible to categorise most individuals without difficulty. There should be two different sizes of *L. obtusata* in all collections, but only one of *L. fabalis.* Beware of the chink shell *Lacuna pallidula* (Fig. 25, p. 606) which also lives on fucoid algae and is superficially somewhat like a flat winkle. However, the much more fragile shell is pale green in colour and has an umbilicus (the chink).

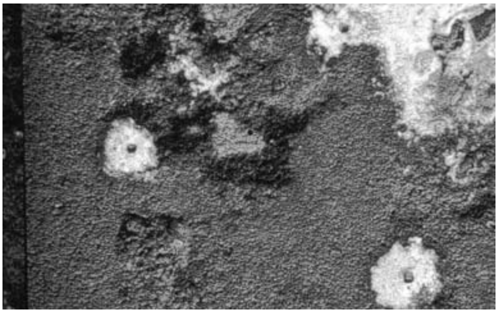

FIG. 72
Rough winkles, *Littorina saxatilis*, occupying small holes in the concrete of Minehead harbour wall, surrounded by their grazing area.

FIG. 73
Rough winkles clustered in a splash zone cranny on Hurlstone Point.

If the abundance of yellow *Littorina fabalis* is indeed due to its crypsis in transmitted light one might suspect it to be most abundant in clear water, and least so in the muddy water at the mouth of an estuary.

ROUGH WINKLES

The taxonomy of rough winkles was a minefield from the early 1960s until Reid (1996), and field biologists generally lumped them all together. Now that the dust has settled, there is no reason to ignore the potential of these near ubiquitous snails for projects.

There are three species (p. 608). *Littorina compressa* is easily identified by its ridged shell, usually yellowish green in colour with black lines in the grooves that separate the round-topped ridges. [It was called *L. nigrolineata* for several years but, alas, that name is not available; it having been used for a black-lined variety of *L. saxatilis* in Spain.]. The other two show much the same range of variation, nationally, but can usually be separated without difficulty on those shores where both occur together. For example, on Hurlstone Point, *L. saxatilis* has a ridged shell whilst that of *L. arcana* is smooth and with a notably wider aperture; a few miles along the Somerset coast, at Watchet, *L. saxatilis* is smooth shelled. To decide which was which, it was necessary to sacrifice a few of each (dropped into boiling water and the body pulled out of its shellt with a pin) when female *L. saxatilis* are instantly recognised by the masses of purple embryos in their mantle cavity.

L. compressa is essentially a middle shore species but the other two extend into the splash zone, above the upper barnacles and limpets. They surmount the same desiccation problems as do limpets, often clustering together in crevices (Figs. 72 and 73). They do not make homes, like limpets, but fill the space between their shell and the rock with mucus as the rock dries. This not only holds them in place but also hardens into a semipermeable membrane through which the snail can breathe but water cannot evaporate.

They may not make homes but may show homing behaviour. Those in Fig. 72 appear to graze in a well defined home range around a particular cranny. The white concrete is, elsewhere, invisible under a ‘felt’ of algae. The pattern is rarely as obvious as this, but particular crevices and crannies always seem to have winkles in residence at low tide by day. Are they the same winkles each day? Marking the shells (and the ‘home’ crevice) in a distinctive way and returning on subsequent days would answer the question.

FIG. 74
Common dog-whelks, *Nucella lapillus*, feeding on barnacles.

FIG. 75
Common dog-whelks feeding on mussels, *Mytilus edulis*.

Females of *L. compressa* and *L. arcana* lay their eggs in blobs of jelly, stuck to the rock in crevices, from which the young emerge as crawling snails. Females of *L. saxatilis* retain their eggs in a brood pouch and appear to give birth to crawling snails. Thus, in all three species, the spread of genes is limited by the crawling of snails. In some localities, shells of a distinctive colour are locally abundant, whilst a short distance away a different colour stands out. It would be interesting to find out if these 'areas of genetic dominance' are of similar sizes and/or whether their boundaries coincide with some physical boundary.

DOG-WHELKS

The common dog-whelk, *Nucella lapillus*, is an excellent subject for projects. These snails are conspicuous, of a convenient size (usually between 20 and 35 mm in shell length), comparatively long-lived, harmless to man, of no commercial importance, widely distributed and common (except along parts of the south coast of England). The shell is usually robust and individuals are easily marked – you can write on the shell with a pencil, paint numbers on it or saw grooves into the aperture. As with flat winkles, the equivalent of larval stages are completed within an egg capsule so that the young emerge at the crawling stage when they are easily visible to the naked eye. They grow for two or three years but do not increase the size of their shell as adults.

At all ages, dog-whelks feed on discrete, easily identifiable, macroscopic sedentary or slow-moving prey (upon which they remain for many hours or days) which renders predator/prey investigations possible in the field. Above all, they lend themselves to a study of variation and the morphological response of a species to environmental selection processes.

Feeding

For all but the smallest prey, *Nucella* must penetrate the victim's shell before paralysing it by injecting a narcotic. The dog-whelk then inserts its proboscis into the body of its prey, secretes digestive enzymes and later resorbs a rich 'soup'. On most shores, *Nucella lapillus* is a predator of barnacles (Fig. 74) and /or mussels (Fig. 75). A large dog-whelk can inject the narcotic between the opercular plates of a small barnacle, which relaxes the opercular muscles and the snail does not have to bore a hole in the shell in order to insert its proboscis. Small dog-whelks feeding on large barnacles do bore holes (Fig. 76) and all dog-

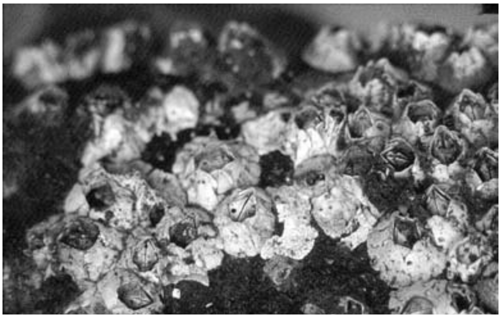

FIG. 76
Shells of the lower shore barnacle, *Balanus crenatus*, bored by juvenile dog-whelks in an aquarium tank

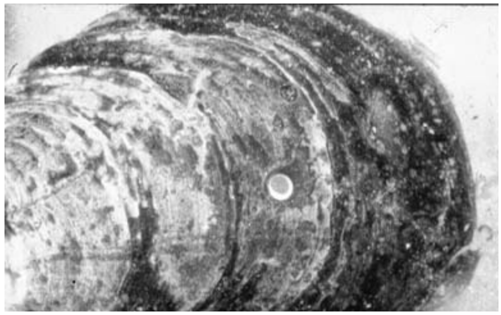

FIG. 77
Shell of a mussel, *Mytilus edulis*, bored by an adult dog-whelk

whelks have to bore all but the smallest mussels (Fig. 77). See Crothers (1985) for further information.

I read that the proboscis is roughly the length of its owner's shell. If a good supply of bored shells is available, it could be interesting to investigate where, on the prey shell surface, the predator chose to bore the hole. A mussel shell is thinnest at the margins and thickest at the umbo (the oldest part). It is easiest to bore through near the margin but the main organs of the body may then be beyond the reach of the proboscis.

Do many shells have more than one bore hole?

Prey selection

Most books claim that *Nucella lapillus* favours barnacles over mussels. This often appears to be the case, especially in northern Britain, but the situation is not usually as simple as that.

The null hypothesis must be that the dog-whelks do not select their prey but take every prey item they come across, in the order in which they encounter it. Very few animals actually do this. Theoretically, natural selection should have favoured those dog-whelks which fed most efficiently; that is they chose prey which gave them the most calories for the least effort expended whilst feeding. Carefoot (1977) [quoted by Crothers, 1985] showed that, in aquaria, Pacific *Nucella lamellosa* gained an average of 23 calories per hour from feeding on barnacles (*Balanus glandula*) but only 15 calories per hour from feeding on mussels (*Mytilus edulis*).

We might hypothesise that the dog-whelks would show apostatic selection, feeding disproportionally on the most abundant prey species available. Having enjoyed a meal on an individual of species A, the predator looks for another individual of A rather than risk disappointment from attacking an individual of species B. In the absence of choice, and feeling hungry, the snail is likely to switch to an individual of the most abundant species. Over time, all members of the population should end up searching for what was, originally, the most abundant prey species.

In addition to mussels, *Mytilus edulis*, dog-whelks may have up to four species of barnacles on the middle shore available as potential prey, plus two more on the lower shore. *Semibalanus balanoides* (Fig. 78) is probably the most widely distributed of the mid-shore species and may be the only species present in the north and eas of Britain. It becomes increasingly rare in the far southwest and may be absent from south-facing shores.

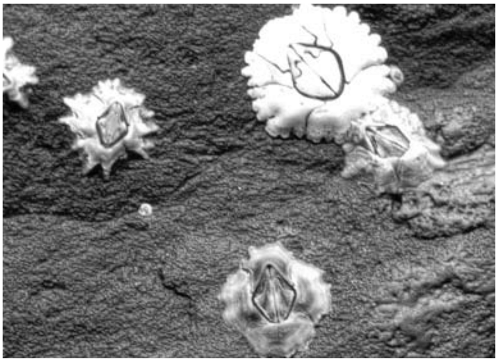

FIG. 78
The mid-shore barnacles. *Semibalanus balanoides* (top right) and *Elminius modestus* (below). *S. balanoides* shells have six plates in the 'wall' surrounding the diamond shaped aperture; *E. modestus* shells have four. *S. balanoides* is notably white-shelled.

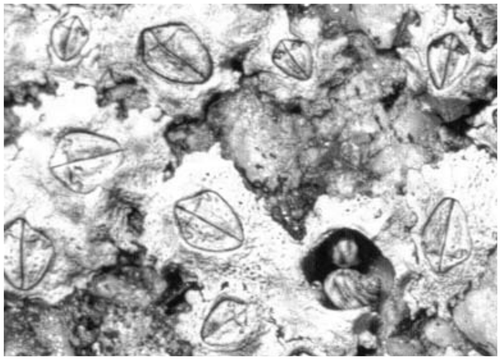

FIG. 79
Exposed-shore barnacles of the genus *Chthamalus*. Members of this genus also have six plates in their shell wall, but they rapidly become indistinguishable. The opening is kite shaped (*C. montagui*) or oval (*C. stellatus*)

Introduced from Australasia during the Second World War, *Elminius modestus* (Fig. 78) continues to spread, and seems to thrive best on sheltered shores and in estuaries. Species of *Chthamalus* (Fig. 79) are found on more exposed shores in the south and west of Britain, with *C. stellatus* favouring the most oceanic sites. For information about barnacles, see Rainbow (1984).

In the far southwest of England, and maybe elsewhere, *N. lapillus* also attacks limpets, flat winkles and purple topshells. Cannibalism has been observed. I have yet to see them attack the edible winkle, *Littorina littorea*, in Britain (although I have in Canada) and I have never seen a common topshell attacked. When that animal is far more common than winkles or the other topshells, as it is on Alderney, this situation requires an explanation. I suspect that *Osilinus* is too active for *Nucella* to handle.

Snails are often attacked through the aperture, so the fact that empty empty shells lack boreholes is not positive evidence that they were not victims of dog-whelk predation.

Whilst it is comparatively easy to see if a dog-whelk is feeding on a mussel or a limpet (Figs 80, 81) it is not easy to be sure which barnacle is under attack. Under optimal

FIG. 80
Dog-whelks selecting mussels over *Chthamalus* barnacles and limpets. Garretstown Strand, Ireland

FIG. 81
Dog-whelk attacking a limpet, *Patella vulgata* St Agnes, Isles of Scilly

FIG. 82
Nucella lapillus attacking a flat winkle, *Littorina obtusata*, through the aperture, amongst the fronds of egg wrack, *Ascophyllum nodosum*.

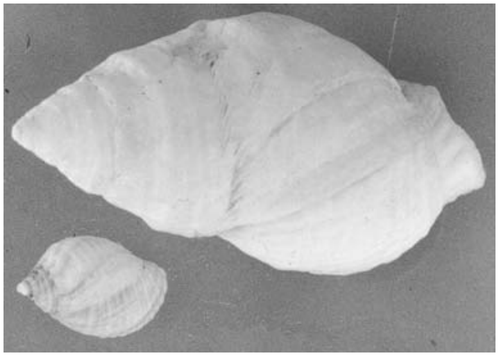

FIG. 83
There is enormous variation in adult shell size within *Nucella lapillus*

conditions, the predators consume an average of one barnacle per day so direct observations/ experiments will occupy several days. A helpful approach is to establish a number of permanent quadrats across the shore. I have done this, for a different purpose (Crothers, 1983), using a 0.1 m^2 (internal measurement) quadrat cut from a sheet of galvanised iron, leaving a wide border. Brass screws were used as locating pegs, fixed with 'Araldite' into holes drilled into the rock using a masonry bit. Holes drilled in the wide border of the quadrat were used to relocate it on each visit. The same frame was used on each of the permanent quadrats; I wrote the date and quadrat number, in chalk, on the border before taking a photograph of life inside.

With such a set-up in place, it would be straightforward to set up choice experiments for groups or individual *N. lapillus.* All the empty barnacle shells should be removed before starting. One could merely observe what happened over time or, by sacrificing selected barnacles, weight the choice experimentally.

It should be remembered that the predator may have an optimal size of prey item, as well as an optimal species, and that this size will probably relate to the size of the predator.

Variation in shell size, shape and colour

There is a great deal of visible variation in shells of the common dog-whelk. Size must be influenced by the supply of food available to the juvenile snail (Gibbs, 1993, found individuals reared on shores where no dog-whelks had fed for several years grew larger than individuals in the parental population) but that cannot account for the discrepancy in Fig. 83 which must involve a genetic component. The larger shell, from Porlock Weir in Somerset, is 56 mm in length; the smaller one is from a sample collected at Hartland Quay in North Devon which had a mean adult length of 17.1 ± 1.4 mm. The average mean size is 27.5 mm.

Very large individuals are usually extreme lower shore or sublittoral. The increased size and thickness may confer some protection from large crabs and lobsters.

Shell colour and banding patterns are under genetic control and not obviously related to any environmental factors (Crothers, 1985). In areas where distinctively coloured or banded individuals are common, such as north Cornwall, 'areas of genetic dominance' could be investigated in the manner suggested for rough winkles on p. 628.

Shell shape, however is usually related to wave action and the intensity of crab

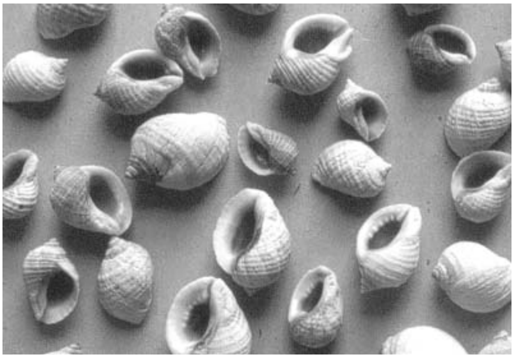

FIG. 84
Dog-whelks from exposed shores have squat globula shells with a wide aperture. Shells from Geassholm, Pembrokeshire.

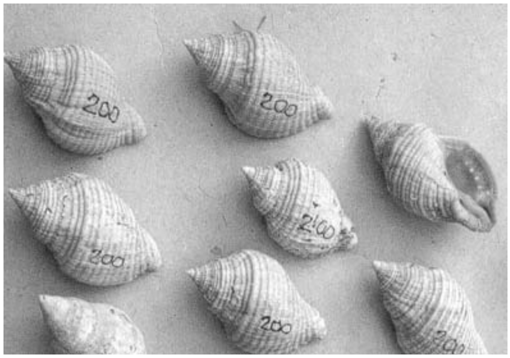

FIG. 85
Dog-whelks from sheltered shores have long pointed shells with an elongated aperture. Shells from the Salcombe Estuary, Devon

predation. The most exposed shores are inhabited by dog-whelks with short squat shells with a wide aperture (Fig. 84); the most sheltered shores support snails with a long spire and an elongated narrow aperture (Fig. 85) whilst shores of intermediate exposure produce shells of intermediate shape. Short squat shells fit into crevices (Fig. 86) and the wide mouth is required to accommodate the large foot which helps the snail cling to the rocks. Such a shape is, however, susceptible to crab predation but British crabs avoid surf. The elongated aperture of dog-whelks on crab-infested shores (Fig. 87) may prevent crabs claws from obtaining a purchase on the shell lip. This shape is able to hold more water inside the shell; sheltered shores are drier than wave-washed headlands

The ratio length / aperture length (L/Ap, Fig. 87) is a convenient measure of shell shape, although other people favour apical angle, and a sample of 30 adults, collected without conscious bias, adequate to determine the mean (Crothers, 1985). In most parts of Britain there is a strong correlation between mean L/Ap and the exposure grade, determined on Ballantine's (1961) scale. Changes in exposure round a headland are reflected in the mean shell shape of the dog-whelks.

There is a genetic component to shell shape, reinforced by selection on each new cohort of snails. It may be possible to demonstrate that selection has occurred if juveniles are more variable than adults. Berry & Crothers (1968) demonstrated selection for the exposed-shore shape but were unable to do the same for the sheltered shore one. An investigation of this kind would be best carried out in autumn when the current year's juveniles are easily distinguished from the previous year's cohort and the adults. Gibbs (1993) showed that the progeny of exposed coast animals could develop sheltered shore shape when reared in appropriate conditions.

However, dog-whelk populations differ genetically around Britain. The short squat form is apparently absent from south east England and the Bristol Channel supports a highly distinctive, very elongate, form of the species; between Minehead and Porthcawl, mean L/Ap is usually 1.6 or higher. There is little variation with exposure; Berry & Crothers (1970) found little evidence of selection because there was so little variation between individuals.

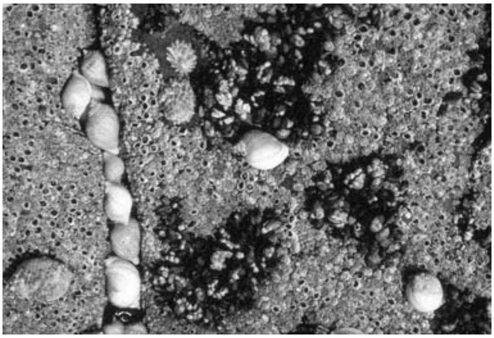

FIG. 86
The exposed-shore morph of the dog-whelk is well adapted to fit into crevices and so avoid the excesses of wave action

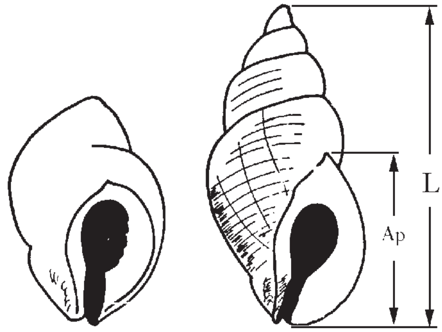

FIG. 87
Length divided by aperture length (L/Ap) is a convenient measure of shell shape. The left shell measures 1.30, the right is 1.86

CONCLUDING REMARKS

Rocky sea shores offer a wide range of habitats, in close proximity, populated by several species of snail which, with a little experience, can be identified reliably. Some species lend themselves to behavioural studies, others to biometrics. Many of the suggestions for investigations in this paper arose from fieldwork carried out from Dale Fort, Nettlecombe Court and Orielton Field Centres and the species chosen are amongst those common in those locations. There is no reason to suppose that other species may not be equally or more suitable elsewhere.

Many of the most successful projects were devised by younger students; some of the most disappointing, by undergraduates. Remember the first Duke of Wellington's adage "Time spent on reconnaissance is seldom wasted." Success or failure is closely related to the amount of time and effort devoted to planning - including, if at all possible, the collection of a practice set of data. Failures have resulted from an inability to find or identify the chosen species, an inability to sample in the planned manner at the chosen site and, most often, a gross underestimation of the time required.

The motto is KISS; Keep It Simple Students. Good luck.

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