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COMMON TOPSHELLS: AN INTRODUCTION TO THE BIOLOGY OF *OSILINUS LINEATUS* WITH NOTES ON OTHER SPECIES IN THE GENUS

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Abstract

This review concentrates on those features of common topshell biology that are amenable to field study – distribution, abundance, population structure, response to environmental stimuli etc. It was written to help students plan simple but interesting projects by providing the essential background information. As the title suggests, it is concerned primarily with the northern species but includes sufficient information on the others to stimulate interest during Mediterranean and Macaronesian holidays.

Introduction

Many students of Biology are required to carry out some form of individual project as an integral part of their course. Despite reminders that assessment is usually directed at the manner in which the work was planned and executed (and not on the scientific interest of the result), the more able candidates often insist on choosing an 'interesting' topic - in an 'interesting place'. For many of us, that 'interesting place' means a rocky sea shore. In that habitat, marine snails offer the widest range of possibilities for projects.

A 'Good Project Species*' must (a) be easy to find, (b) be easy to identify, (c) show striking differences in some measurable feature (*e.g.*, abundance, size, age, shape) that can be related to a measurable environmental factor and (d) have an adequate background literature, sufficient to allow the student both to predict patterns and also to interpret any results derived from the investigation.

Osilinus Philippi, 1847 is a genus of herbivorous gastropod molluscs (snails) of rocky sea shores in the North-East Atlantic. At least five, and perhaps seven, species occur in and between the Mediterranean Sea and the Macaronesian Archipelago (Madeira, Canaries, Selvagens etc.); one of which, *O. lineatus* (da Costa, 1778), extends northwards to southern and western Britain. This species grows throughout its life, which may reach at least fifteen years, and, at least near the northern / eastern limits of its range, individuals can be aged in the field; two features which offer a range of projects within and between populations.

This paper was written to demonstrate the case for *Osilinus* as a genus of 'Good Project Species'. It attempts to summarise those features of *Osilinus* biology relevant to field studies, but information about these animals is patchy and it is quite likely, even probable, that some student projects will ask questions to which there is, as yet, no established answer. It is assumed that most readers of this paper will be working in southwestern Britain and with *O. lineatus* and the text is biased accordingly. But many British people visit the Channel Islands and the west coast of France each summer and most of the text will be relevant there as well. Notes about the southern species is appended for people visiting Mediterranean or Canary Island resorts where this genus is especially common.

* In the 1960s, Charles Sinker urged FSC staff to look for 'Good Teaching Plants' that could be used to highlight relevant biological principles. The concept of a 'Good Project Species' is a direct development of that advice.

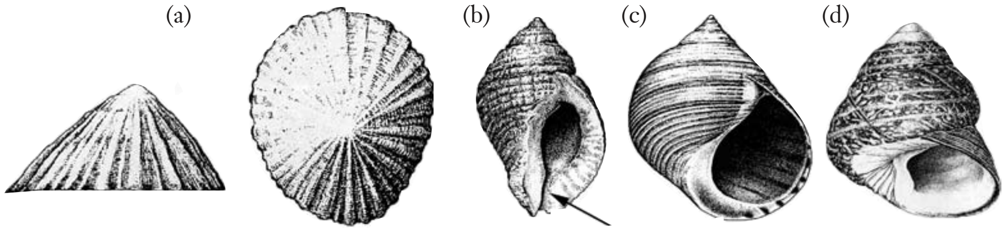

FIG.1. Shells of the four major groups of snails found on British rocky shores
(a) the simple conical shell of a limpet, (b) the spirally-coiled shell of a whelk, showing the siphonal groove (arrowed), (c) that of a winkle with an ear-shaped aperture and (d) that of a topshell with a nacreous inner layer to the shell visible externally at the apex where the outer surface has worn away.
From Graham (1988)

IDENTIFICATION

Snails are one of the few unmistakable groups of animals. There are four major groups amongst the larger species on British rocky shores (Fig. 1). Limpets and whelks are easily recognised as such but some people initially confuse winkles with topshells. Diagnostic features are given in Table 1 and Fig. 2.

In South and West Ireland, South and West Wales and Southwest England there are four species of topshell regularly found on rocky shores (Fig. 3) which may be separated on colour and the presence or absence of an umbilicus (Fig. 2b). Identification is not as easy further south. Complications begin in the Channel Islands, where there is a second species of purple topshell, *Gibbula pennanti* (Philippi, 1836) that lacks an umbilicus. In Spain and Portugal, additional species of *Gibbula* and *Osilinus* appear; some species of *Gibbula* lack an umbilicus and an increasing number of *O. lineatus* retain one into adulthood.

TABLE 1 Some characters that serve to distinguish topshells from winkles see Fig.2

Topshells	**Winkles**
Have a circular operculum (the horny plate which seals off the aperture when the snail retracts into its shell).	Have an ear-shaped or sub-oval operculum.
Have a nacreous (mother-of-pearl) layer on the inside of the shell - most obvious on the inside of the outer lip - which may become visible on the outside of older shells as the coloured layer is eroded away.	Lack a nacreous layer on the inside of the shell. The inside of the outer lip is dark or the same colour as the outer surface.
Have shells marked with a complicated pattern composed of blotches and/or zigzag lines. There is a pure white form of one species, but none has a pattern of simple stripes.	Have shells which are uniformly coloured or which bear broad or narrow bands that run round the spiral at right angles to the lip.
Usually have an umbilicus.	Never have an umbilicus.

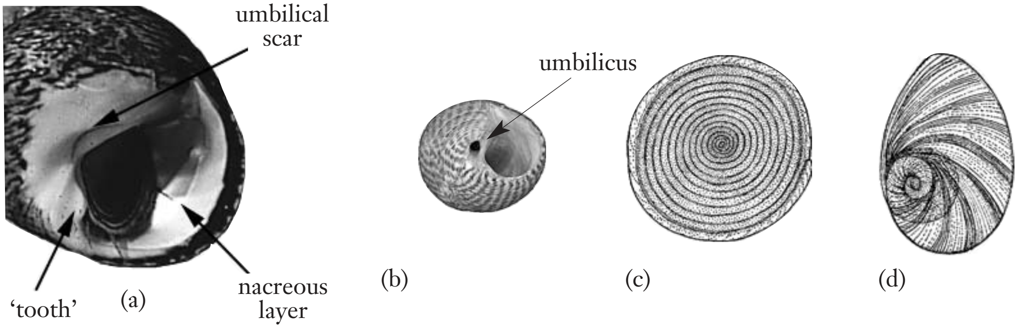

FIG. 2. Some characters used to separate topshells from winkles.
(a) *Osilinus lineatus* to show the nacreous, or mother-of-pearl, layer that forms the inner surface of a topshell shell. Note the 'tooth' on the columella and the umbilical scar. (b) The umbilicus of a purple topshell. It is seen when the whorls of the shell do not touch in the centre of the spiral, leaving a space up the middle. A much smaller hole is also visible in the apex of the shell. On British shores, an umbilicus is usually visible in all individuals of *Gibbula* but, in *Osilinus lineatus*, it usually has closed by the time the snail reaches 5mm, leaving an umbilical scar. (c) The circular operculum of a topshell, also visible in (a) and (d) the ear-shaped or sub-oval operculum of a winkle.

Drawings based on illustrations in Fretter & Graham (1994)

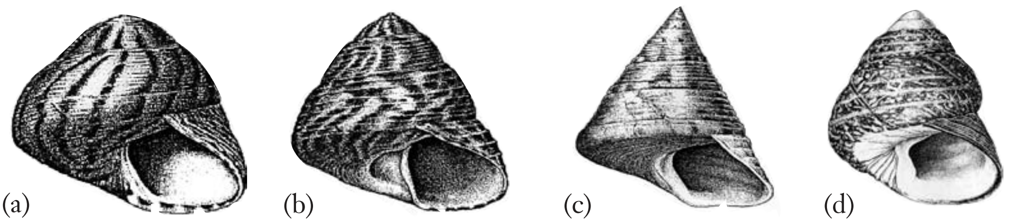

FIG. 3. Shells of the four species of topshell most commonly found on British rocky shores.
(a) A purple topshell, *Gibbula umbilicalis* (da Costa 1778). (b) The grey topshell or silver tommy, *Gibbula cineraria* (Linnaeus, 1758). (c) The painted topshell, *Calliostoma zizyphinum* (Linnaeus, 1758). (d) The common topshell, *Osilinus lineatus* (da Costa 1778). The two species of *Gibbula* both have umbilici and the other two usually do not, once larger than 3mm, although the position is marked in *O. lineatus* by an umbilical scar. *G. umbilicalis* reaches 16 mm in height and is green with a pattern of purple bands whilst *G. cineraria* only reaches 12 mm and is pale grey with a finer pattern of darker grey lines. Shells of *C. zizyphinum* may reach 34 mm, always have a sharply pointed apex and are usually brightly coloured in purple and gold - or are white. British *O. lineatus* may reach 35mm and usually have a complicated pattern of dark brown lines on a paler brown background but some are green rather than brown. There is a more or less rounded white tooth on the columella - see Fig. 2(a). *C. zizyphinum* lacks the tooth on the columella and does not show an umbilical scar.

From Graham (1988)

NOMENCLATURE

Unfortunately for the student collecting references to these animals in a library, there has been considerable dispute about the correct names. The present author uses 'common topshell' as the colloquial name of the British species, but others favour 'thick topshell' or 'toothed topshell'. The scientific name currently accepted by the International Commission for Zoological Nomenclature is *Osilinus lineatus* but most references will be found to *Monodonta lineata* and a few to *Trochocochlea lineata*, *Turbo lineatus* and *Trochus crassus*. Those interested may read more on p. 150.

ANATOMY

(See Fretter & Graham (1962; 1994) where no other reference is given)

Soft Parts

The body is dark ash-colour with a greenish tint (Jeffreys, 1865) but so successful is the shell in protecting it that the layout and organisation of the soft parts are unknown to most biologists (Figs 4 and 5). The details concern only the specialist malacologist but, as a species' performance (*i.e.*, its behaviour, ecology, etc.) is essentially a function of its anatomy, the principles are important.

The simplest way to view the layout of the body, should you want to, is to kill the topshell by dropping it into boiling water for a few minutes and, then, to pull the animal out of its shell using a stout pin. The body will appear as that drawn in Fig. 4, with those organs which always remain within the shell enclosed in a bag, called the mantle, which terminates in a flexible collar, labelled 'mantle edge' in Fig. 4. The mantle edge bears various sense organs and the cells responsible for secreting the outer layers of new shell. The inner, nacreous, layer of shell is secreted by the whole outer surface of the mantle. The mantle edge must obviously be extended forward to the shell lip when new shell is being secreted whilst the clearly-defined edge of the nacreous layer inside the lip (see Fig. 2a) marks the usual position of the mantle edge when crawling.

The powerful columella muscle, labelled in the lower drawing of Fig. 4, attaches the animal to its shell and, on contraction, draws the body safely inside. Some of the fibres of this muscle run into the head so that, as the muscle retracts, the top of the head is withdrawn first, followed by the snout, the front end of the foot and finally the operculum which acts as a trap door to seal off the aperture. The operculum protects the vulnerable head of the snail from predators such as prawns, crabs and fish etc. but this arrangement means that sense organs on the head are poorly placed for the snail to detect when it is safe to re-emerge. It is a matter of surprise, to some people, that there is room to accommodate the head and foot within the shell. In practice, they are withdrawn into the mantle cavity - a large space behind the head - expelling much of the water that normally fills it in the process.

The most important organ permanently within the mantle cavity is the gill (ctenidium) which occupies most of the upper left-hand side. Cilia on the gill create a water current that draws fresh sea water into the upper left side of the mantle cavity, through the gill lamellae, and then over the urinogenital apertures and the anus on the way out. De-oxygenated blood is passed to the gill along the afferent vessel (not visible in Fig. 5) along the upper surface of the mantle cavity, and passed through capillaries in the afferent branchial membrane (labelled afferent membrane in Fig. 5) which attaches the gill to the roof of the cavity. The oxygenated blood is collected in capillaries of the efferent membrane of the gill, which fixes it to the wall of the cavity, and passed to the heart via the efferent vessel.

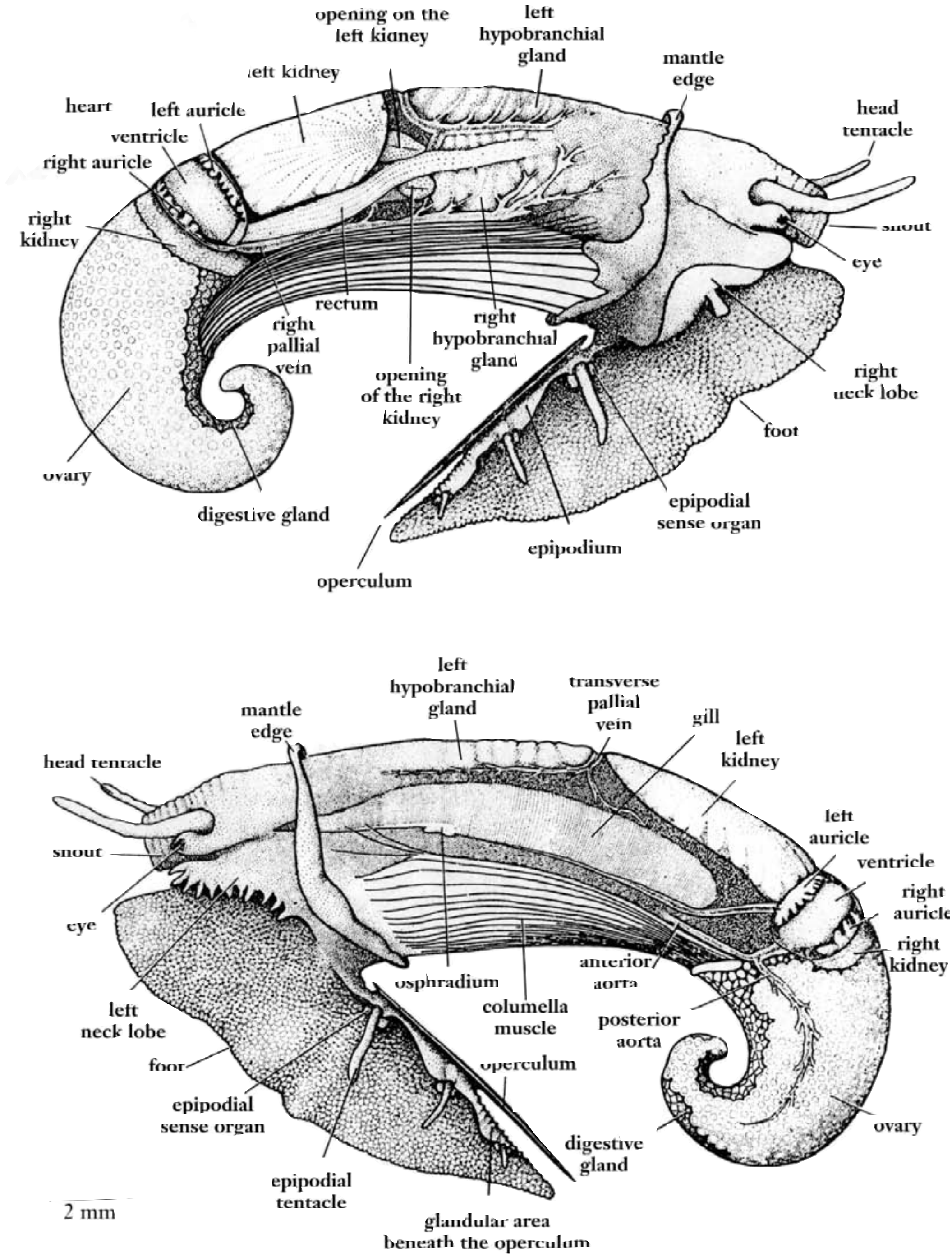

FIG. 4. A female *Osilinus lineatus* removed from its shell to reveal those of the soft parts that are visible through the mantle. Based on Fig. 324 in Fretter & Graham (1994)

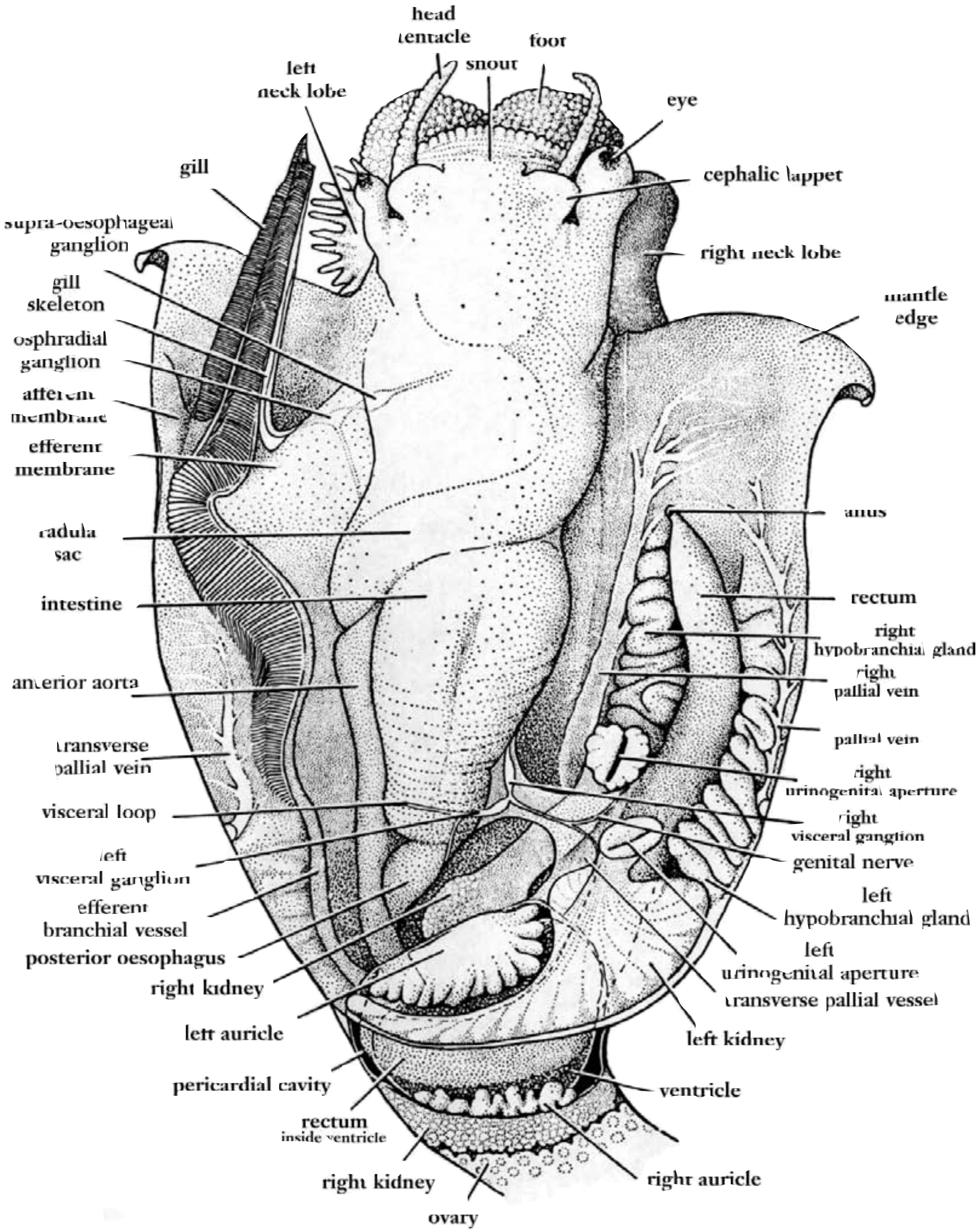

FIG. 5. A female *Osilinus lineatus* dissected to display the contents of the mantle cavity. Based on Fig. 53 in Fretter & Graham (1994)

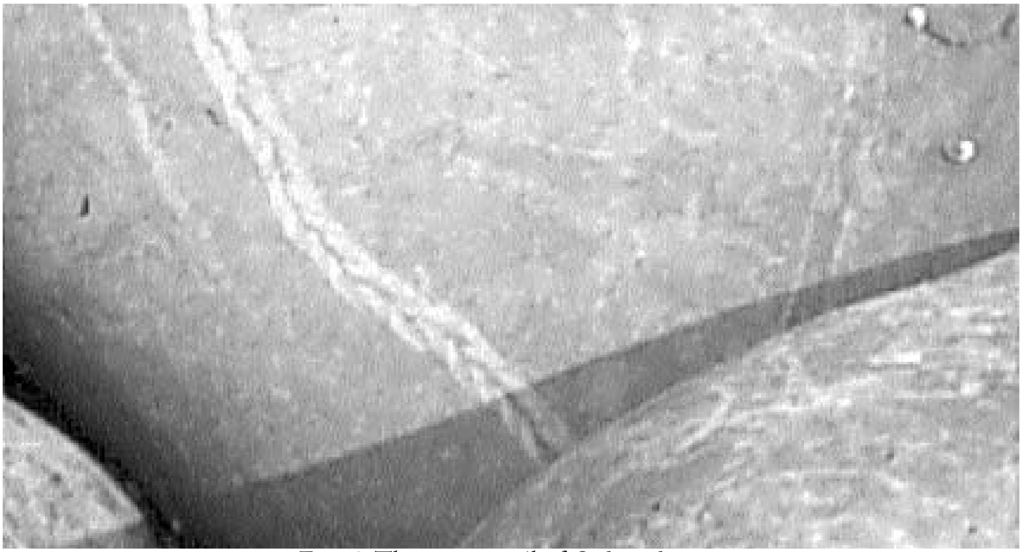

FIG. 6. The mucus trail of *Osilinus lineatus*
showing that the left and right sides of the foot are discrete and that the snail moves forward in 'steps'.

A feature characteristic of topshells, and not seen in winkles or whelks, is the pronounced asymmetry of the neck lobes; the left lobe being greatly expanded and equipped with sense organs. As the inhalant current of water entering the mantle cavity, en route to the gill, passes over the left neck lobe, it is a reasonable assumption that this structure has evolved to 'smell' the incoming water. Waste products are discharged from the right side of the mantle cavity, so there is no matching sensory structure on that side.

Topshells of the genus *Osilinus* are amongst the most active snails on rocky sea shores and, when crawling, they make much use of their sensory tentacles - one pair on the head and three epipodials (*epi*- outside, *pod* foot) along each side of the foot. They are shown retracted in Fig. 4 and are greatly extended when the animal is active. Note also their associated sense organs. Surprisingly, because they seem to be so useful to a topshell, epipodial tentacles are considered to be a 'primitive' feature which have been 'lost' in more 'advanced' groups of snails such as winkles and whelks.

Another feature to be noted in the crawling snail is a tendency to rock slightly, from side to side, unlike a winkle which usually glides steadily along. Like most of the larger snails, topshells progress forwards as waves of muscle contractions pass backwards along the sole of the foot, lubricated by copious quantities of mucus to facilitate passage over the rough rock surface. The resulting mucus trails are highly visible on dry rocks and offer possibilities for projects comparing the level of activity in different areas. The explanation for the rocking is revealed from an examination of the mucus trail left by a topshell. Unlike the continuous broad trail of a winkle, the distinctive topshell trail is divided down the midline and each side is broken up into a series of steps (Fig. 6)

Osilinus lineatus is dioecious (*i.e.* the sexes are separate) but it is not possible to distinguish them in the field. Males lack a penis and, even when the animal is removed from its shell, the only reliable character for telling them apart is the appearance of the urinogenital aperture: the lips of which are said to be yellow and swollen in the female but unpigmented and smaller in the male (Randles, 1905; Williams, 1965; Desai, 1966).

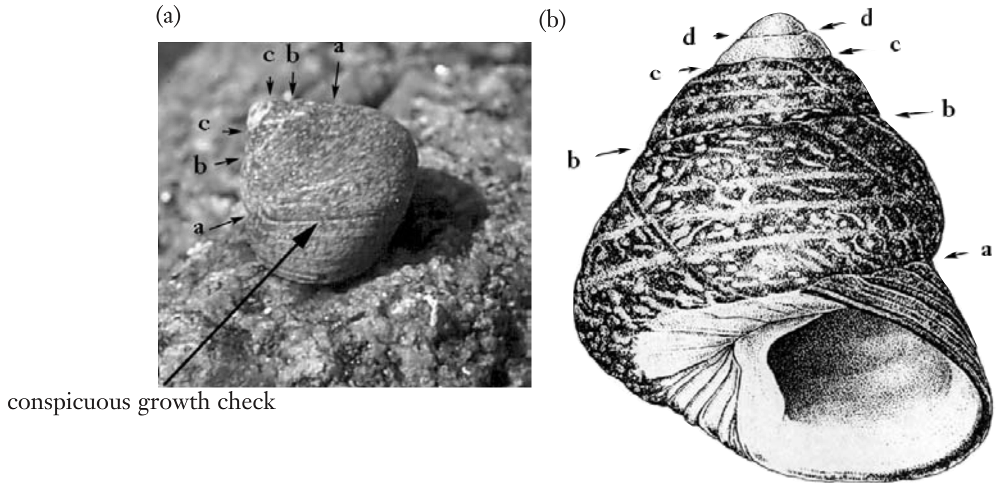

FIG. 7 The shell of *Osilinus lineatus*.to distinguish suture lines from growth checks. Suture lines, which run around the shell from 'a' to 'a', 'b' to 'b', etc., separate the whorls. Growth checks, which run across the whorls parallel with the shell lip indicate where the shell lip was when growth was interrupted. 'Conspicuous' growth checks indicate extended periods without growth and, in the British Isles, represent winters. (b) From Graham (1988)

However, in a female ready to breed, the greyish-green ovary, packed with mature oocytes, completely envelopes the digestive gland and viscera, whilst the testis of a ripe male is cream (Desai, 1966).

The shell

Like other snails, *Osilinus lineatus* secretes a shell around its body to protect it from the biotic and abiotic hazards of its environment. The shell is impervious to gasses and liquids and surprisingly resistant to crushing, so there are no special precautions to be taken for handling it although the animal inside may be harmed by shock if the shell is thrown away!

The young topshell first forms a shell whilst a free-swimming larva and it continues to add new material to the shell lip throughout its life, whenever conditions are favourable; so the apex is the oldest part of the shell and the lip the youngest. A young small snail naturally produces thinner shell than an old large one so that, if this secretion from the edge of the mantle were the only process involved, the end result would have a thin delicate apex and a massive, thick aperture. To ensure that this does not happen, the inner, nacreous, layer of the shell is secreted by the whole outer surface of the mantle. Thus, the apex comes to have a thin outer layer and thick inner whilst, at the lip, the outer layer predominates. Sand and other abrasive materials wear away the thin outer layers near the apex and, in most large specimens (*e.g.* Fig. 7b) the nacreous layer is exposed at the surface.

Nacre is the strongest form of microstructure found in mollusc shells (Vermeij, 1993) and, consequently, it is comparatively rare to find damaged shells on living animals (but see Fig. 8). According to Vermeij (pages 50-51), the disadvantages of nacre include the fact that, if it does break, it tends to shatter and so is difficult to repair but, more importantly, it is an energy-demanding substance. Not only is it heavy to move around but it also requires regular maintenance; empty shells rapidly lose their strength.

Growth lines run across the shell, parallel to the shell lip, and indicate (former) positions of the lip when growth was temporarily interrupted (Fig. 7). For, although growth continues throughout life, it is not continuous; any of a number of environmental shocks from bad weather to disturbance or attempts at predation may cause a slight check and the outer surface of the shell usually bears innumerable discontinuities - see, for example, the shell in Fig. 7a below the large black arrow. (Notice, also, the distinction between suture lines and growth checks. Actually, the suture is a single groove, separating the whorls, that runs from the apex around the shell to terminate at the inner end of the shell lip. However, unless you examine the shell in apical view, it appears as a series of lines across the shell.)

Superimposed on these minor fluctuations, British populations of *O. lineatus* also show 'conspicuous*' growth checks which indicate the snails' size during previous winters for most adults do not grow at all between November and May/June (Williamson & Kendall, 1981). The snail illustrated in Fig. 7a shows one annual growth check, arrowed; that illustrated in Fig. 7b has least eleven whilst Fig. 15 illustrates one of the oldest common topsdhells I have seen. Much of the research reported later in this paper depends on snail ages determined by the counting of annual growth checks and it is important to realise the limitations of this technique, which include:-

• Some individuals commence growth much earlier in the year than others so, when sampling in April, May, June or even July, it is advisable to assume that all individuals have a growth check (representing the winter just passed) at or close to the shell lip, even if you can only see it in some individuals.

• The growth check marking an individual's first winter may be difficult to see the following summer and will completely disappear in old snails as the outer layer of the shell is abraded. Little *et al.* (1986) simply assumed that this first growth check must have been there and included it in their count even when they could not see it.

• In mild winters, growth may not be checked in all individuals for the whole six month period and some shells may be found with a cluster of growth checks close together where others have a single line. It is best to treat the cluster as a single winter.

• Damage to individuals surviving a storm or crab attack can induce growth checks. If the incident occurred in summer, the check will be additional to the annual checks, but not if it occurred in winter. The decision whether, or not, to count growth checks associated with shell damage in the annual count is clearly subjective. Physical damage is usually recognisable, but temporary starvation induced by being washed away from the food supply would leave no other indication on the shell.

Behaviour

Food and Feeding

On British rocky sea shores, topshells, winkles and limpets form a guild of microphagous herbivores (= eaters of microscopic plants) and they can all be found together, grazing on the open rock. According to Gause's Competitive Exclusion Principle (Gause, 1934) you should not find similar species living in the same place and feeding on the same food because, if they did, they would be in competition and, over time, one would exclude the others. Although it is not easy to prove this principle, it is impossible to disprove it and the

* 'conspicuous' is a technical term! Some individuals, such as that used to illustrate Williamson & Kendall (1981), Little *et al.* (1986) and Crothers (1994) show them very clearly but, in others, they are more difficult to determine with any precision, especially those of the juvenile snail.

FIG. 8 Growth checks may be induced by damage.
The right-hand common topshell recovered from serious damage to its shell at least two winters ago

principle has become widely accepted (Begon *et al.*, 1986 page 260). Hence, it is probable that these various snail species do not feed in exactly the same place, at the same time or in the same manner on exactly the same food.

Some spatial separation exists due to zonation patterns. If the four topshells illustrated in Fig. 3 are present on the same shore, *Calliostoma zizyphinum* and *Gibbula cineraria* are found low down, *G. umbilicalis* in the middle and *Osilinus lineatus* high up; any two species, but not more, may overlap, at least in summer. Nevertheless, it is still commonplace to find limpet, *Patella vulgata*, edible winkles, *Littorina littorea*, purple topshells, *Gibbula umbilicalis* and common topshells, *O. lineatus* living side by side on the same rock.

All these snails feed by rasping the rock surface using their horny tongue (radula) but these are of such different patterns (Fig. 9) that it is easy to believe they feed in different ways. The multi-fine-toothed rhipidoglossan radula of a topshell (Fig. 9b), the less complex taenioglossan radula of a winkle (not illustrated) and the simple docoglossan radula of patellid limpets (Fig. 9a) were likened to 'brooms', 'rakes' and 'shovels' by Steneck & Watling (1982). Hawkins, *et al.* (1989) confirmed a brushing action in *Gibbula umbilicalis* (which has a radula similar to that illustrated in Fig. 9b) and found it consistent with the ten-page description of '*Monodonta*' radula action in Fretter & Graham (1962, 1994) and earlier descriptions of grazing by the Mediterranean *Osilinus turbinatus.*

The radula teeth also differ in hardness; on Moh's Scale, where human hair rates 2.0 and human teeth 5.0, winkle and topshell teeth fall between 2.0 and 2.5 whilst those of patellid limpets attain 4.5-5.0 (Hawkins *et al.*, 1989). Limpet grazing tracks (Fig. 10) are, therefore, much more conspicuous than those of topshells and winkles (Fig. 11). Quite apart from the depth of the scratches, limpet tracks have a formality of pattern that catches the eye more easily than does the more erratic brushwork of the topshell. It is probable that topshell tracks only show up when the snails are feeding on rocks covered by a fine deposit for Hawkins *et al*. (1989) were unable to produce clear radula traces from *O. lineatus* in the lab. although they quote an observation by Imrie of 'paired bite-like marks' (recognisable in Fig. 11). Torunski (1979) wrote that *O. turbinatus*, in the Northern Adriatic, did not leave

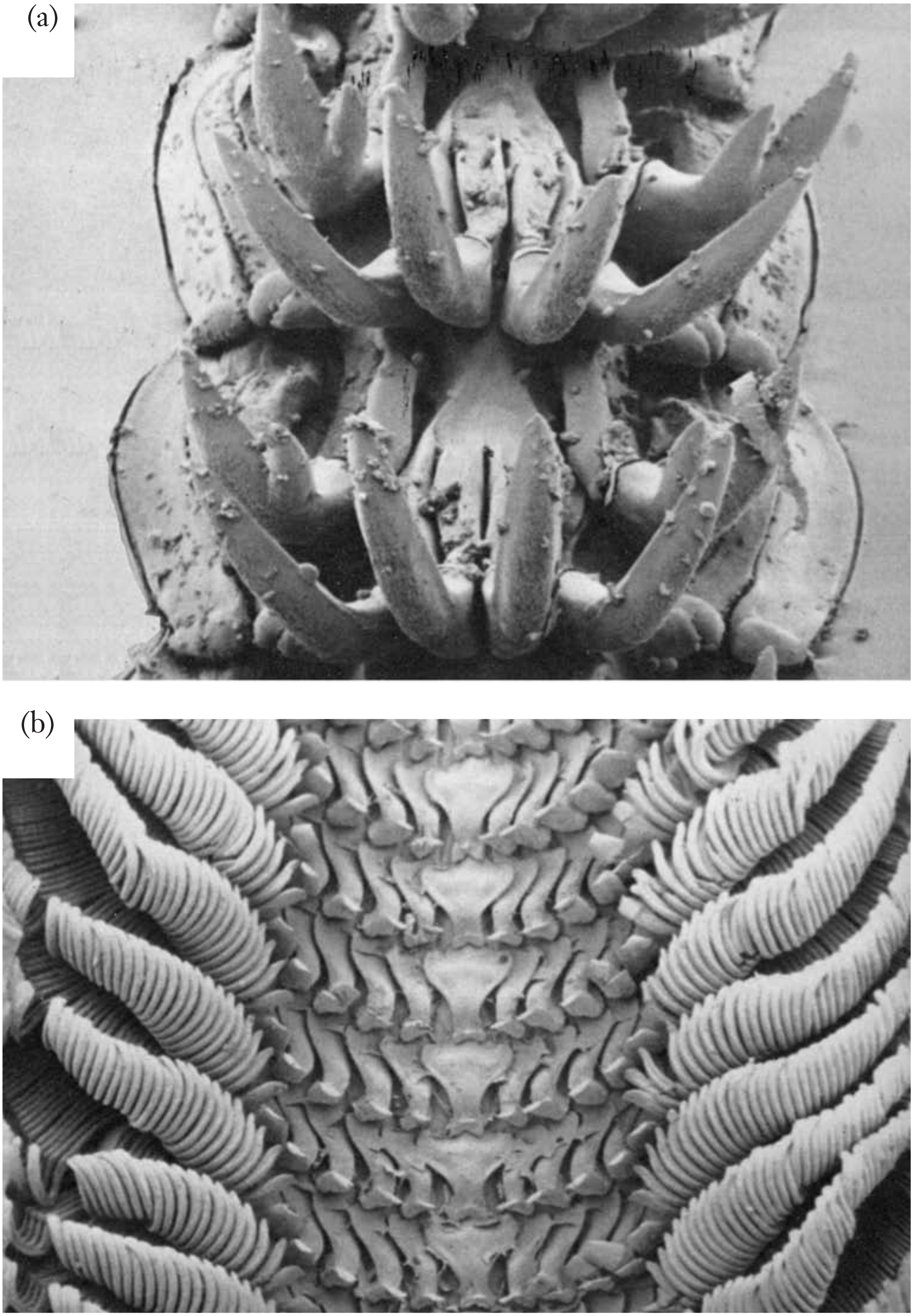

FIG. 9. Radulae. Scanning electron micrographs of
(a) the common limpet *Patella vulgata* and (b) the common topshell *Osilinus lineatus*,
each of about 20mm in length taken from the shore at Dale, Pembrokeshire.
photo: the late Dr T. E. Thompson

FIG. 10 Grazing track of a common limpet, *Patella vulgata* L., at Watchet, Somerset. The track is composed of parallel-sided radula scratches ('tongue licks') where the limpet has removed the algal 'felt' and revealed the underlying rock. When grazing, the snail crawls slowly forward, swinging its head from side to side so this one entered the frame at top right and departed centre left.

grazing trails. Their faecal pellets contained undigested algae and general microdetritus - bits of sea urchin spines, shells of ostracods, mussels, winkles and chips of the boring sponge *Cliona* - but little sediment.

Table 2 shows that slight differences did exist between the gut contents of the four species of microphagous grazers of the upper middle shore at Woolacombe in November 1986. Hawkins *et al.* (1989) described these as a preliminary analysis of ten guts for each species and commented that the differences found were not as large as they had expected. Although there is considerable evidence that this microbial food resource may be limiting, these authors consider that there are so many fluctuating environmental conditions operating on a rocky shore that the equilibrium conditions necessary for Gaussian competitive exclusion are unlikely to occur often or persist for long. In other words, although it may be possible to demonstrate differences in the microdistribution of the four snails listed in Table 2, it is unlikely that those differences are due, primarily, to competition for food.

Table 2 suggests that common topshells do not graze on macroscopic algae, but it is probable that this was through preference or lack of opportunity rather than incompetence. Visiting Ireland in July 1994, I made several collections to establish the population structure. Unfortunately, I did not have time to age and measure all the specimens on the shore and some were taken back to our 'chalet' on Annaváan Island and subsequently released on the local shore (Fig. 12). The shores of this island are very sheltered and the

FIG. 11. Grazing tracks of common topshells, *Osilinus lineatus*, on Gore Point, Somerset Limpets are scarce in this habitat, where a freshwater stream flows across the beach, and almost all the tracks are made by common topshells and edible winkles. The rather haphazard pattern of radula scratches is more difficult to see than the systematic alga-clearance of a limpet.

TABLE 2. Gut contents of common limpets, *Patella vulgata*, common topshells, *Osilinus lineatus*, purple topshells, *Gibbula umbilicalis* and edible winkles, *Littorina littorea*, from Woolacombe, North Devon. The diatoms indicated by + signs together totalled about 6%. From Hawkins *et al.* (1989)

	P. vulgata	*O. lineatus*	*G. umbilicalis*	*L. littorea*
Diatoms				
Acnanthes	14%	21%	15%	7%
Navicula	40%	24%	31%	43%
Raphoneis	+	-	+	+
Coscinodiscus	-	-	+	-
Podosira	+	+	+	+
Actinocyclus	-	-	+	+
Cocconeis	+	+	+	+
Grammatophora	-	-	-	+
Pinnularia	+	-	-	+
Biddulphia	-	-	-	+
unidentified	41%	49%	47%	44%
Foraminifera	+	-	-	+
foliose red algae	-	-	+	-
foliose green algae	-	-	+	-
crustose calcareous algae	+	+	-	-
bivalve fragments	+	+	-	-

(a)

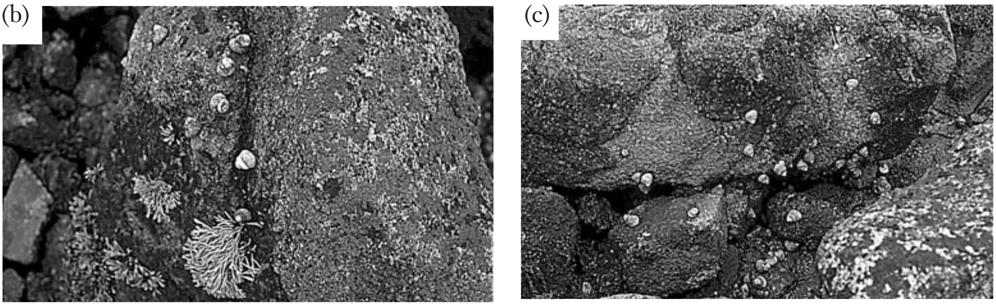

FIG. 12 The Southwest shore of Annaváan Island, Lettermullen Island in the background. In July 1994, common topshells collected from other parts of Western Ireland were released onto the upper shore (*Pelvetia* zone) in the foreground of (a). (b) The rock surface and some *O. lineatus* one day after release and (c) four days after release. The paler areas reveal where the topshells have grazed off the algal felt .

middle shore rocks were swathed in egg wrack, *Ascophyllum nodosum*. *O. lineatus* appeared to be absent, as were limpets and edible winkles. The released snails were placed on the upper shore algal felt, amongst scattered *Pelvetia canaliculata* above the *Ascophyllum*. After their first night on this beach, there were suggestions of grazing trails in the algal felt; after four nights paler grazed areas were visible where the underlying rock had been exposed.

Most snails on rocky sea shores do not move about very much at low tide by day, at least not in bright sun or in pouring rain, and the assumption is made that they usually feed at high tide or at night. Unpublished hourly observations on edible winkles, limpets and the two upper shore topshells were made in Castlebeach Bay by students attending a course at Dale Fort Field Centre in July 1966. As soon as the shore was dry enough, students marked individual shells with enamel paint, making the same mark beside them on the rock. The marked sites were visited on foot at low tide and, by swimming or from a boat (using a glass-bottomed box) at high tide by day. No activity was detected at low tide by day, and very

FIG. 13. Snails that have moved since the tide went out.
Common topshells and edible winkles crawl out of the water where a freshwater stream flows across the shore on Gore Point, Somerset. March 1976.

little at high tide by day - in bright sunny conditions. At low tide by night, however, most of the snails were crawling about. Sampling at high tide by night was considered inappropriate for a student field course, even in the mid 1960s!

On British shores, few species are active when awash* (Little, 1989) (although the Mediterranean species of *Osilinus* are awash most of the time and *have* to be active in these circumstances) and I have not observed any response from *O. lineatus* to submergence as the tide comes in. As the tide ebbs, however, many individuals are to be seen climbing out of any remaining water and thereby avoiding unfavourable conditions of salinity or oxygen concentration in a few hours time (Fig. 13). At least three species of *Osilinus*, *O. articulatus (*Houlihan & Innes, 1982), *O. lineatus* and *O. turbinatus (*Micalleff & Bannister, 1967) have a well vascularised mantle cavity which they use for respiration, along with their gill, and may breathe more effectively in air than under water.

Dr Colin Little (*e.g.*, Little, 1989, Little & Kitching, 1996, page 89, Little *et al.*, 1990, 1991) has studied the foraging patterns of limpets for many years, especially in Lough Hyne, southwest Ireland, where the tidal range is so small and the water so clear and calm that cameras and other delicate equipment can be left on the shore over high tide. Initially it was thought that all limpets fed at night, with some additional activity at high tide by day in June, when nights were short. Later work showed differences between limpets with homes on verticals and those on horizontals. Dr Richard Thompson, from the University of Plymouth has written (personal communication.) "my view is that the time of activity varies considerably between locations. Some populations are mostly active at high water by day, others at low water by night. Low water by day is not a 'popular' time but the population examined here (in Plymouth) were active during this period on shaded verticals

* Awash - when the waves are actually washing over them

and seemed to prefer this time to high water by day."

Osilinus may show a similar range of variability, for salinity tolerance behaviour experiments have shown it to be much more active than *Patella*, *Littorina* or *Gibbula*. Stanbury (1975) noted marked topshells that had moved across the shore 20 feet (over 6m) in two days, Underwood (1973) recorded movement of 11m between monthly visits to his site and two of the 2274 snails marked on 2 June 1996 by Mr J. A. Bayley and a group of Open University students on Gore Point were found 200m from their release site in the spring of 1998. This level of activity presents problems for scientists monitoring long-term effects of oil pollution or other disruption (Little, 1983). Moreover, *O. lineatus* is sensitive to weather conditions. Large individuals are to be seen 'sunning themselves' on the open rock surface in dry, warm weather but they hide in crevices on cold or wet days. Little, *et al.*(1986) observed *O. lineatus* "to respond within minutes or hours to changes in weather conditions as they occurred." Some may crawl towards shelter when a human starts sampling in their vicinity, apparently recognising a large dark shadow as potentially dangerous.

For all these reasons, simply counting common topshells in quadrats or along a transect line is an extremely inaccurate method of assessing their abundance. This may be one of the few species of animals amenable to the mark-release-recapture technique, so beloved of the writers of ecology textbooks. The technique involves marking a large number of individuals, releasing them back into their habitat again and, on a subsequent visit to the site, making another collection and noting the proportion of marked to unmarked individuals in the catch. Assuming that the marked ones had mixed at random with other members of the population, the proportion of marked to unmarked in the second catch is taken to indicate their proportion in the whole population. Since the total number of marked is known, the size of the total population may be calculated. In order for this technique to work, it must be possible to mark the animals without affecting their behaviour or chances of survival, and without making them more visible. A blob of paint on the underside of the shell is effective. As this active species shows no territorial behaviour and appears to show no mating behaviour, there is a possibility of individuals mixing 'at random' during the interval between samples.

On 2 June 1996, a 20m x 20m square was marked on the shore of Gore Point and twenty-five people collected, marked and released 2274 common topshells within that square. About 800 others were released unmarked because the tide would have covered them before the paint had had time to dry. The following day, a second collection was made. The 2493 common topshells collected in the 20m x 20m included 1230 marked individuals. These figures estimate the population to be 4,609 or 12 m^{-2}, which is of the right order of magnitude. However, at least 25 marked animals had already left the marked area. This second collection was released back into the marked area.

A week after the original release of marked animals, a third collection was made. This time, the 2539 common topshells collected included only 579 recaptures, figures which estimate the population to have risen to 9,972 or 25 m^{-2}. These estimates must have been distorted by the rate of emigration from the marked square as the size of the collections shows that there were actually about the same number present on all three occasions. The recommendation must be that recaptures should be made no more than 24 hours after release of the marked animals.

REPRODUCTION

(See Fretter & Graham (1962; 1977; 1994) where no other reference is given)

Spawning

Both sexes liberate their gametes into the sea and fertilisation occurs in the water. Desai (1966) observed spawning. The males emitted white clouds of spermatozoa which showed little movement at first but became very active after 2 or 3 minutes. Females released oocytes separately, a few at each spasm. This is unusual amongst marine snails, most of which lay eggs in capsules of one kind or another. External fertilisation, generally regarded as a 'primitive' trait in snails, is obviously a high risk strategy and unlikely to be successful unless the species is locally common. Scattered individuals cannot form a self-sustaining breeding population.

In the early 1960s, Williams investigated a population of common topshells on a rocky shore in mid Wales, beneath the 66m headland Craig-yr-Wylfa, south of Borth (Williams, 1965). At monthly intervals from May 1961 to January 1963, he collected all the individuals present in each of eleven $1m^2$ stations along a transect spanning the vertical range of the species on that shore - an average of 208 per visit. Preliminary investigations revealed that individual *O. lineatus* less than 11mm in basal diameter* were all immature. From the samples collected between January 1962 and January 1963, all individuals larger than 11 mm were removed from their shells, examined in water under a binocular microscope, sexed and assigned to one of 8 breeding stages: five developmental and three spawning (Table 3). Both sexes showed much the same pattern: gonadial development started at the end of October but it was not until the following August that the first animals were considered capable of spawning (*i.e.* had reached Spawning Category 3).

In these 'broadcast spawners', synchronisation of gametogenesis within the population followed by simultaneous release of gametes by males and females clearly enhances the likelihood of fertilisation (Lasiak, 1987). But, surprisingly, not all species do synchronise. In habitats subject to unpredictable fluctuations in the physical environment, a sudden temperature change coinciding with breeding could eliminate a whole cohort. In these circumstances, 'dribble spawning' over a prolonged period would be more successful.

In west Wales, *Osilinus lineatus* shows a combination of simultaneous and dribble spawning. Garwood & Kendall (1985), working with animals from Aberaeron and using a much more objective technique, reaffirmed the general pattern described at Craig-yr-Wylfa some twenty years earlier. They noted that the qualitative methods used by earlier workers (Williams, 1965; Desai, 1966; Underwood, 1973) tended to smooth out the reproductive cycle, obscuring the major spawning peak, because they failed to distinguish between potential and effective spawning periods. Effective spawning seems to require an environmental trigger (perhaps a sharp change in temperature or pressure), causing many individuals to release gametes at the same time and initiate a chain reaction. The result is a highly synchronised breeding event superimposed on low-level dribble breeding, perhaps by a minority of individuals that mature out of synchrony with the rest of the population (my interpretation).

Northern geographical limits of rocky-shore molluscs are set primarily by re-

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* Measurement of size. Many people have used basal diameter as their measurement of size, others use shell length - the maximum dimension of the shell including the apex. I favour the latter as it is less subjective but it does not make much difference. Many populations average 1.0 for height/ basal diameter but young snails tend to be broader than tall and large ones taller than broad.

TABLE 3. The breeding cycle of *O. lineatus* at Craig-yr-Wylfa in 1962, based on individuals larger than 11 mm basal diameter (simplified from Williams, 1965). The number of animals in each stage is expressed as a percentage. Developmental stages: 1, Inactive; 2, Beginning of maturation; 3 and 4, Progressive increase in gonadial tissue; 5, Fully mature. Spawning stages: 1, Spawning; 2, Partially spent, 3, Completely spent.

Date	Females								Males							
	Breeding					Spawning			Breeding					Spawning		
	1	2	3	4	5	1	2	3	1	2	3	4	5	1	2	3
9 Jan.	2	62							4	31						
8 Feb.	3	58							3	37						
7 Mar		66							13	21						
6 Apr		50							5	45						
4 May	2	7	26	17					2	9	23	13				
4 Jun.			2	19	42							5	30		2	
1 Jul.					24	29								47		
2 Aug.						6	15	27						13	31	8
30 Aug.						4	4	41								52
2 Oct.	52								48							
30 Oct.	32	16							34	18						
27 Nov	19	23	6						13	19	21					
27 Dec.	4	38	5						9	9	35					
28 Jan. 63		39	16						3	13	13	13				

population failure and northern populations are characterised by short, mid-summer, breeding periods. Further south, breeding periods lengthen, extending in some cases throughout much of the year but with least or no activity in mid summer (Lewis, 1986). Sicilian *O. turbinatus* appear to spawn in spring and autumn (Schifano, 1983).

The dispersal phase

The eggs are extruded singly and, initially, measure between 165 - 195µ but, on contact with seawater, the external coat of jelly outside the egg rapidly swells, making it buoyant (Fig. 14a). Within 20 minutes (at 15-17°C), the jelly layer dissociates and the egg sinks. The first cleavage appears 1hr after fertilisation and the larva hatches, about 29 hours later, as a free-swimming veliger (Desai, 1966). Four days after fertilisation, the veliger begins to make repeated attempts to crawl over the substratum rather than swim and the velum (larval swimming organ: Latin for sail) gradually becomes reduced. At six days of age, the creeping habit is fully developed; the young *O. lineatus* is a snail.

I have never (knowingly) seen an *Osilinus* veliger, nor have I found any published illustration, other than that reproduced in Fig. 14. All the veligers taken in August plankton hauls on the Somerset coast between 1970 and 1990 were thought to be *Littorina littorea* (Boyden *et al.*, 1977, and subsequent observations). Fretter & Graham's (1962; 1994) Table 13, compiled from Lebour (1947), and listing the occurrence of veligers taken from the inshore plankton off Plymouth between 1940 and 1945 does not include *O. lineatus*. There are (at least) two explanations: either, the breeding is so synchronised that the larvae are only available for three days a year and nobody has yet sampled on one of those days; or,

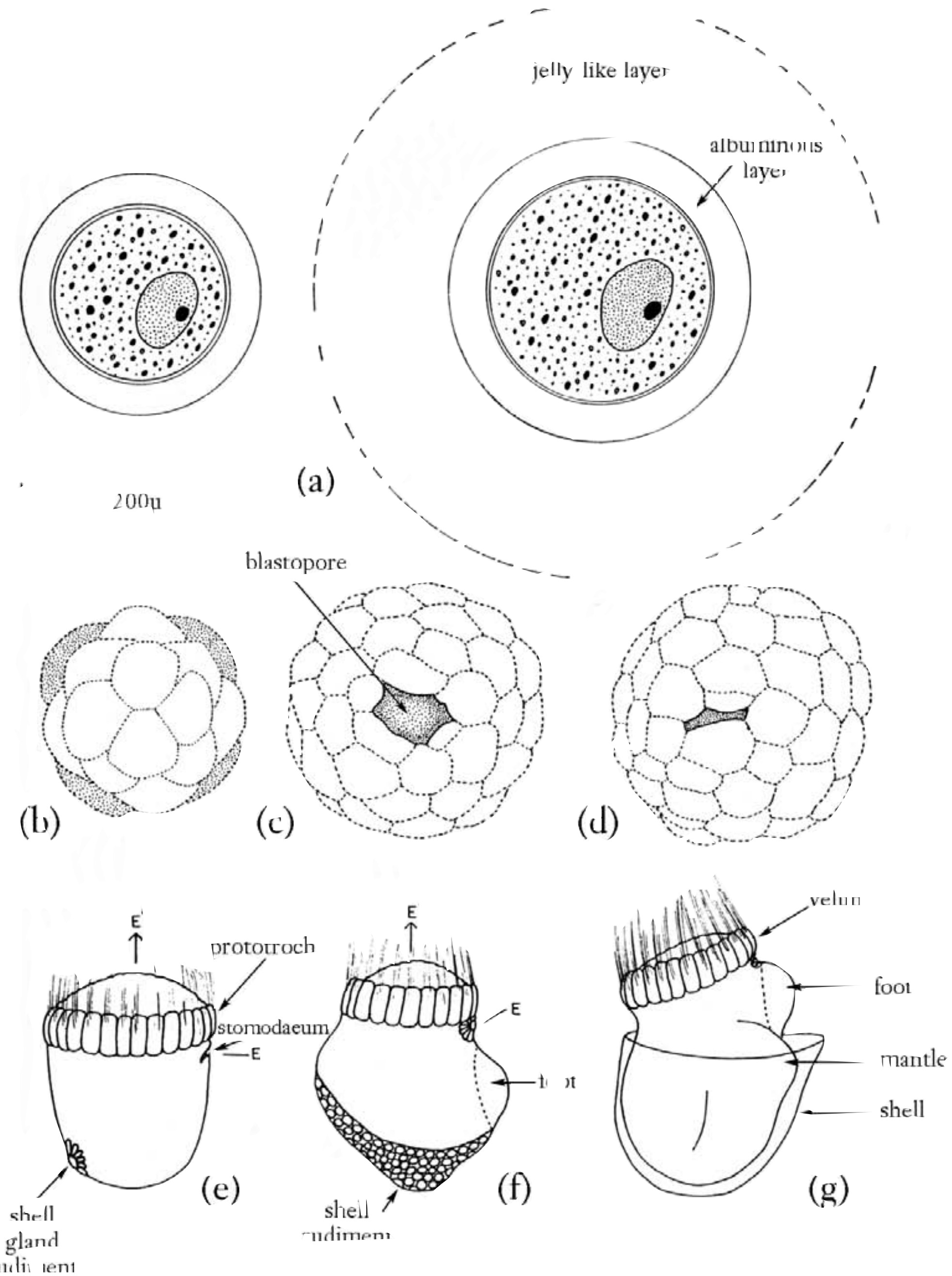

FIG. 14. Diagrams illustrating the development of *Osilinus lineatus*

(A) Egg - [left] appearance in the ovary [right] after swelling in seawater. (B) 16-cell stage with the fourth quartet shaded [6hr]. (C) Early gastrula, looking into the open blastopore [10hr]. (D) Late gastrula with blastopore almost closed [14hr]. (E) Early trochophore [18hr] E-E[l] is the embryonic axis. (F) Late trochophore and (g) early veliger, just before hatching [30hr]. After Desai (1966).

FIG. 15. An elderly *O. lineatus*, with fifteen conspicuous growth checks on the shore at Kilronan on Inishmore, Aran Islands, Ireland.

the larvae stay close to the bottom and are not taken in plankton hauls.

At settlement, the shell measures a little over 1mm across. Williams (1965) found the first members of the 1961 cohort on 11 August, but he did not find any of the 1962 cohort on the 30th August. On the Somerset coast, I have only twice found members of the new cohort in August and most settlement occurs in early September; by the end of that month, the largest are 4mm in height and will have reached 6mm by November.

DISTRIBUTION

Geographical distribution

O. lineatus extends much further north than any other species of *Osilinus* (see p. 155) but, from a British point of view, it is a characteristic 'southern' species (McMillan, 1944) at the northern edge of its geographical range. The heavy black line, in Fig. 16, indicates the stretch of coastline along which one may expect to find common topshells, where suitable habitats (see below) are available. Like its predecessor in Lewis (1964), it is inaccurate in detail but true in general, for this species has a distinctly patchy distribution, being absent from some apparently suitable sites even within the area of the heavy black line.

Several authors have speculated about the factors affecting northern and eastern limits - including Crisp & Knight-Jones (1955), Crisp & Southward (1958), Crothers (1998), Garwood & Kendall (1985), Hawthorne (1965), Kendall (1987); Lewis (1986), Lewis *et al.* (1982), McMillan (1944), Preece (1993), Southward & Crisp (1954) and Williams (1965) - and most conclude that they are related to temperature. It is usually suggested that the length of time temperatures remain below some critical value (*e.g.* winters too cold for too long or summers not warm enough for long enough) may be more significant than maxima or minima *per se*. However, the exceptionally cold winter of 1962-1963 demonstrated that winter cold can be limiting (Crisp, 1964) and can affect distribution patterns for a surprisingly long time (see below). No comparable effect relating to summer temperatures has been published to date and Fig. 16 would support the contention that winter temperatures are the controlling factor. Crisp and Knight-Jones (1955) noted that the limital populations in North Wales were in south-facing sites or otherwise protected from easterly winds.

As mentioned above, external fertilisation is unlikely to occur unless the parental population is reasonably dense (I cannot quantify that) and, from a mass of sometimes conflicting reports, there emerges the picture of a core distribution beyond which new enclaves may become established and flourish in benign periods only to be eliminated by

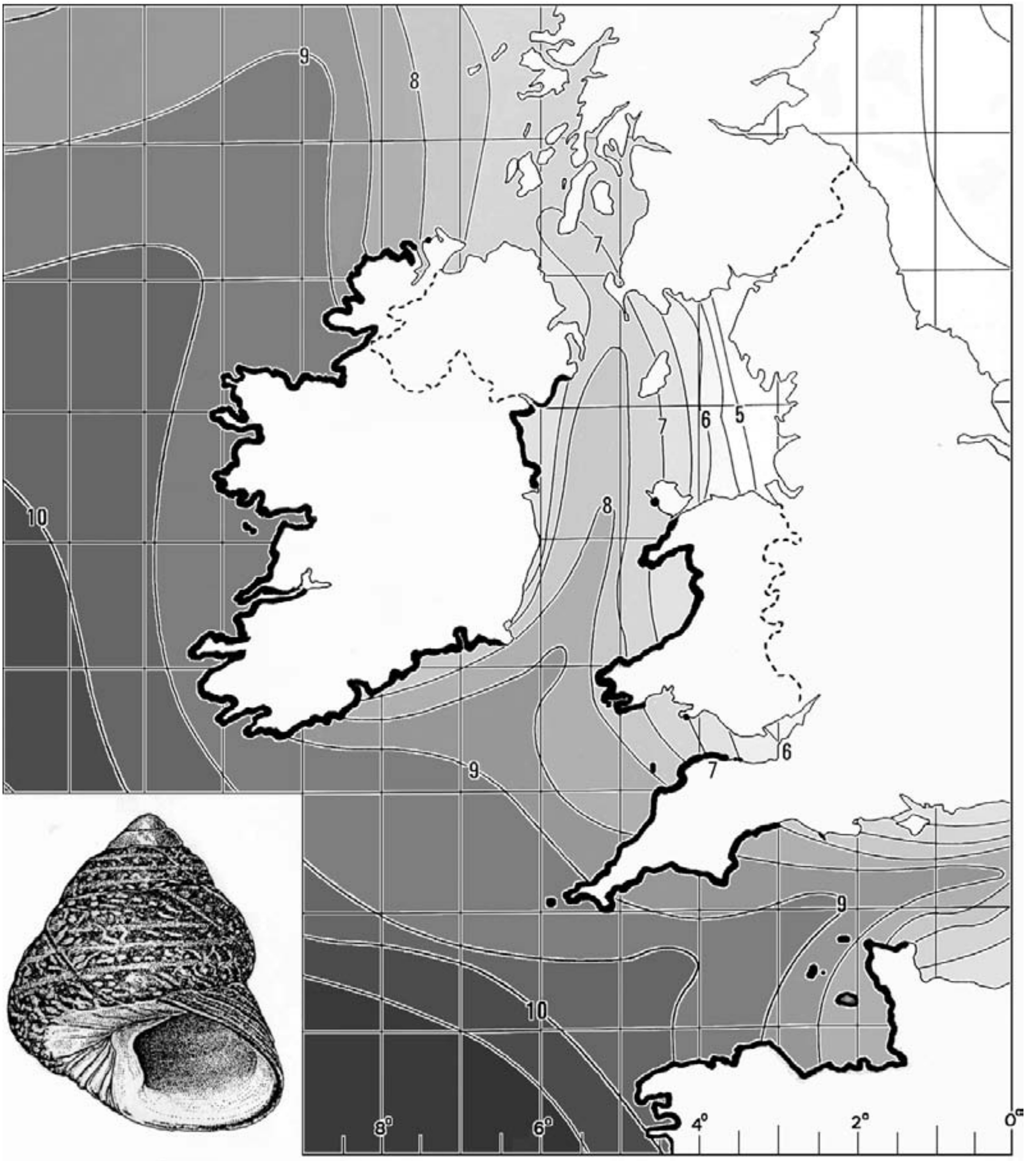

FIG. 16. The distribution of *Osilinus lineatus* in relation to winter temperature.
The common topshell may be found, in suitable habitats, along those sections of coast marked by a heavy black line but it has a notably patchy distribution and not all apparently suitable habitats, even within this area, support populations.

Modified from a map in Lewis (1964)

severe ones. In other words, there may be satellite groups of topshells in the general vicinity of a breeding population; too small to reproduce themselves but reinforced by occasional recruitment. For example, *O. lineatus* is much rarer on Lundy than it is on the adjacent coast of mainland Devon (Hawkins & Hiscock, 1983). Dr S. J. Hawkins only found 2 in a week of fieldwork and, although Boyden (1971) seemed to have found more, the authors doubted whether their density was high enough for them to form a breeding population on the island. The population in South Haven, Skokholm, studied by Stanbury (1975) from 1959 until 1974 clearly depended on recruitment from elsewhere. From 1959 to 1962 the total population rose steadily from 110 to 364. Mortality following the cold weather in early 1963 was just over 40%, higher than for most shores on the nearby Dale Peninsula. Even so, the 256 survivors outnumbered the 110 present in 1959 and 225 in 1960, yet the numbers continued to fall and were down to about 100 by 1974.

Edible winkles, *Littorina littorea*, which also have planktonic eggs and larvae in their life cycle, show the same pattern in North Devon (Hawkins & Hiscock, 1983), presumably for the same reason. However, whilst *L. littorea* is also notably rare on Alderney and the Isles of Scilly, *O. lineatus* is abundant on suitable shores. Crisp & Southward (1958) put this difference down to residual drift and the length of the larval stage. Sea water does not simply move up and down with the tide, it also moves slowly along the coast; at the mouth of the English Channel the general movement of water is easterly. Juvenile edible winkles spend five or six days in a free-floating egg capsule and then four to seven weeks as a planktonic veliger larva (Fretter & Graham, 1980), during which time the said residual drift will have moved most Scillonian offspring away from the Isles (and brought in no replacements). Common topshells, on the other hand, spend 20 minutes as a buoyant egg and some three days as a veliger (see above); residual drift does not take them very far in that time.

In the Bristol Channel, residual drift is eastward along the English coast but westward along the Welsh coast. This fact, combined with the extensive tidal range and concomitant tidal ebb and flow, makes it easy for larvae to settle eastward of established populations along the southern shore but difficult on the northern one; which is an explanation why Welsh common topshell populations, in 2000, had yet to recolonise all the sites lost in 1963

It is not, at present, possible to provide a similar map to cover the southern limit of *O. lineatus* although Macedo *et al.* (1999) gave a thumb-nail-sized map that suggests that it spreads all the way down the coast of Portugal and southwest Spain to the Straits of Gibraltar, and then down the Atlantic coast of Morocco, without entering the Mediterranean. Their map is inaccurate at the northern end of the range but that does not necessarily cast doubt on the remainder. As these authors note, whilst the typical form is found in northern Portugal, towards the Algarve *O. lineatus* becomes increasingly difficult to identify; not only is there greater variability in colour but many retain an open operculum into adult life. There is also at least one additional species present, probably *O. sauciatus* (Dr Serge Gofas, personal communication, 1998) but see p. 156.

Local distribution

Ballantine (1961) used *O. lineatus* as an indicator of sheltered shores. On his exposure scale that runs from 1 (extremely exposed) to 8 (extremely sheltered) he considered this snail to be common or abundant on shores of exposure 6 and 7. They were absent from shores of exposure 1-4, rare on shores of exposure 8 and unpredictable on shores of exposure 5. He used the Crisp & Southward (1958) abundance scales so, for a topshell, 'abundant' meant more than 10 m^{-2} generally and 'common', 1-10 m^{-2}, locally sometimes more.

The initial survey of Milford Haven confirmed this impression (Fig. 17). Common topshells were absent from the exposed shores in the mouth of the Haven and common throughout the sheltered reaches inside until the mud and rapid tides of the estuary made life difficult for them. However, Moyse & Nelson-Smith (1963) and Nelson-Smith (1967) disagreed with Ballantine about their inevitable absence from shores of exposure 4 (Fig. 18).

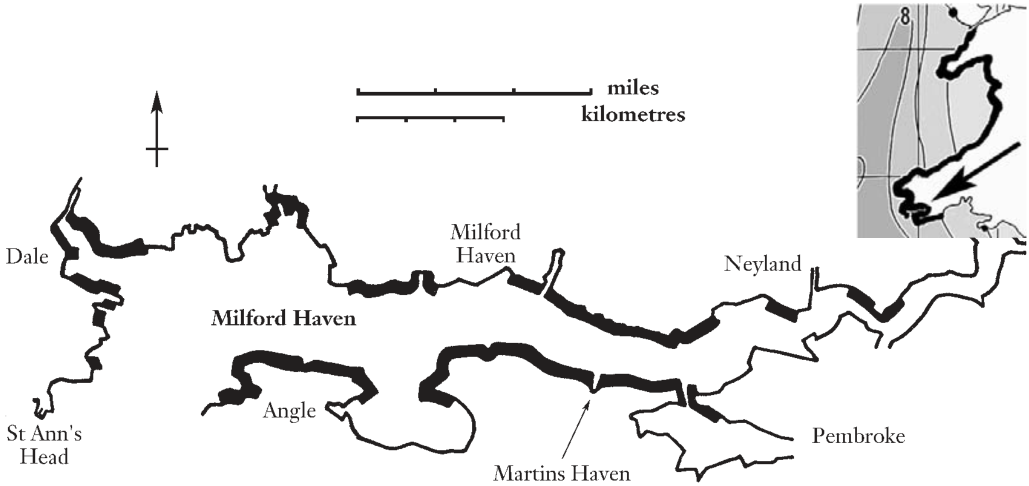

FIG. 17. The distribution of *Osilinus lineatus* in Milford Haven before the 1962/63 cold winter. from Nelson-Smith (1967) with (*inset*) the relevant part of Fig. 16 for location purposes.

In an equivalent survey of rocky shores in West Somerset (Figs 19 and 21), I assessed the exposure of Yellow Rock as between exposures 3 and 4, Gore Point as exposure 4 and Blue Anchor as exposure 6 (Crothers, 1976). It is difficult to apply Ballantine's scale to Somerset shores for many of the indicator species reach their eastern limit in this area and the upper zones are usually more exposed than the lower ones on the same shore, but I now regard the sites in the left hand part of Fig. 21 as between exposure 4 and 5 and those in the right hand side as between exposure 5 and 6.

The common topshell reaches its eastern limit along this stretch of coast, and suffered severe mortality in the winter of 1962-1963. Crisp & Southward (1964) noted "None observed in north Devon east of Woolacombe though previously common at Ilfracombe and Lynmouth" in April/ May 1963. With hindsight, it seems likely that, at time of my

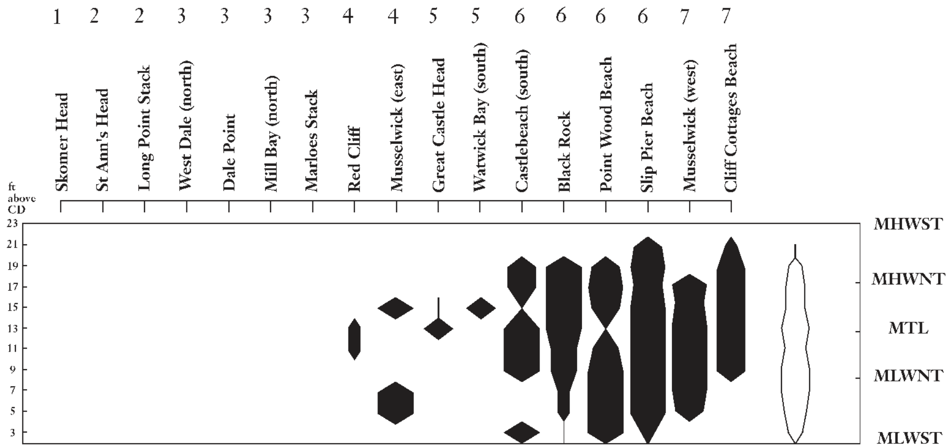

FIG. 18. The zonation of *Osilinus lineatus* on rocky shores around Dale, Pembrokeshire, before the cold winter of 1962 - 1963, according to Moyse & Nelson-Smith (1963). The numbers across the top are their assessment of the Ballantine exposure grades.

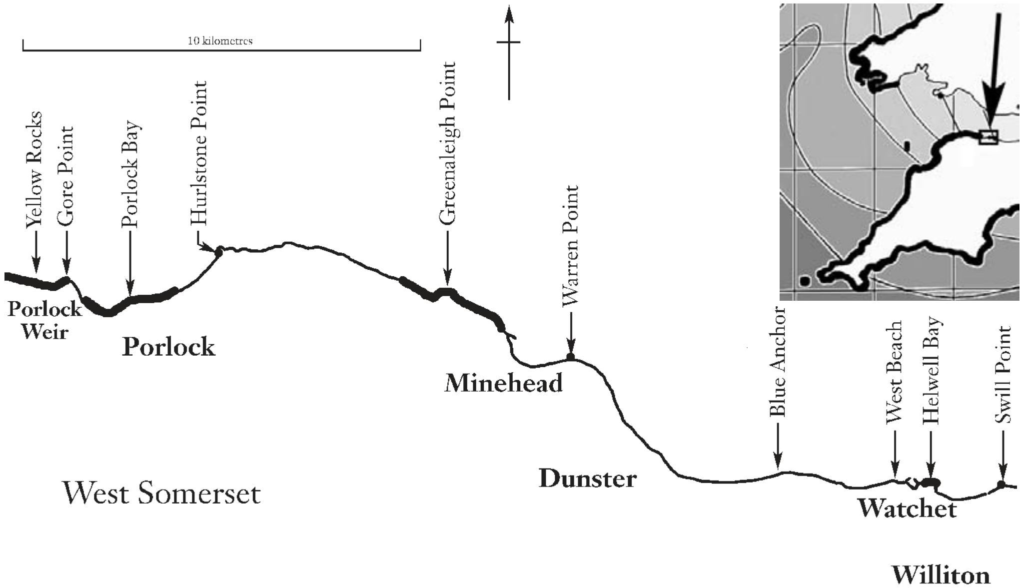

FIG. 19. The coast of West Somerset
showing the location of the transect sites used by Crothers (1976) and (the heavy black line) the known distribution of *O. lineatus* in 2000. *Inset*, part of Fig. 16 for location purposes

survey in autumn 1974, *O. lineatus* was still recovering ground. It was notably less abundant than the purple topshell, *Gibbula umbilicalis* (which was not the case throughout the 1990s), and did not spread east of Porlock Bay - except for a single record from Blue Anchor (Crothers, 1976). By 1977, however, a small enclave had been found on Greenaleigh Point (Boyden *et al.*, 1977) and individuals had been found at Watchet, Helwell Bay; by 1995, student groups had little difficulty in collecting 150 to measure and age.

The enclaves on Warren Point (Minehead) and Swill Point (Doniford) were discovered in August 1990 whilst I was collecting samples for a survey of edible winkles (Crothers, 1992). The existence of the eastern enclaves is somewhat precarious; those at Swill Point and Helwell Bay were eliminated in the winter of 1995-1996 (Crothers, 1998) but re-established subsequently.

The 1962-1963 cold winter had severe effects in Pembrokeshire (Moyse & Nelson-Smith, 1964; Stanbury, 1975), in mid and North Wales (Crisp, 1964). Presumably the previous really cold winter, 1947, had had a similar effect but note (in Fig. 20) that the species had not recolonised all the sites lost in 1947 by 1963.

Zonation

Common topshells are animals of broken rocky shores, avoiding verticals and mobile shingle. In Pembrokeshire (Fig. 18), Moyse & Nelson-Smith (1963) found them to occupy most of the shore, perhaps being commonest at Mean Low Water level of Neap Tides, in July 1961. Nelson-Smith (1967) gave a similar figure for other sites in Milford Haven whilst in Somerset (Fig. 21) they are commonest around High Water level of Neap Tides.

In general, *O. lineatus* is found grazing in the upper half of the intertidal zone (Desai, 1966). But, at least on some shores, zonation may change with the season. Fretter & Graham (1962; 1994) noted that common topshells move away from the upper surfaces of

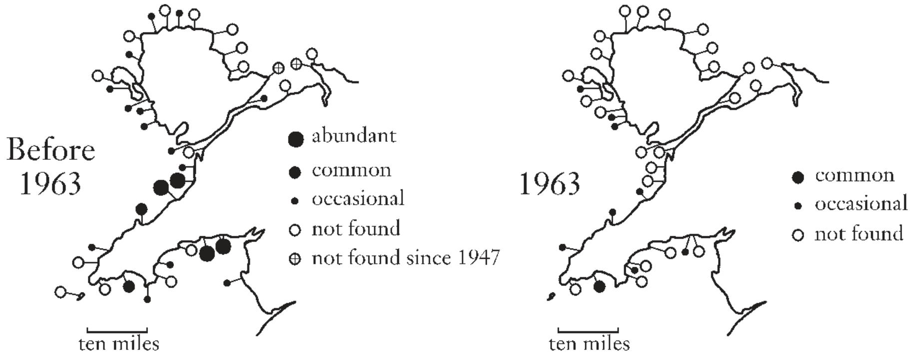

FIG. 20. The effect of the 1962-1963 cold winter on common topshell distribution in North Wales. Based on a figure in Crisp (1964). The 'before' figure also appeared in Crisp & Knight-Jones (1955)

boulders in winter and both Desai (1966) and Williams (1965) provide figures showing a seasonal migration upshore in summer and downshore in winter (Fig. 22). Desai noted that migration was most evident in the larger size groups and that the first winter animals (those of 5 mm or less in length) showed no evidence of migration remaining buried in sand or gravel beside and beneath boulders.

Little (1983) could find no evidence for a migration of this kind in Milford Haven but Little *et al.* (1986) found that the population at Martins Haven (labelled in Fig. 17) had a nursery area low on the shore from which the older age-class migrated upshore. As far as I can tell, neither type of migration occurs in Somerset; the enclaves under long-term study (see below) are always sampled in the same area of shore and have never been found lower down at many of the sites.

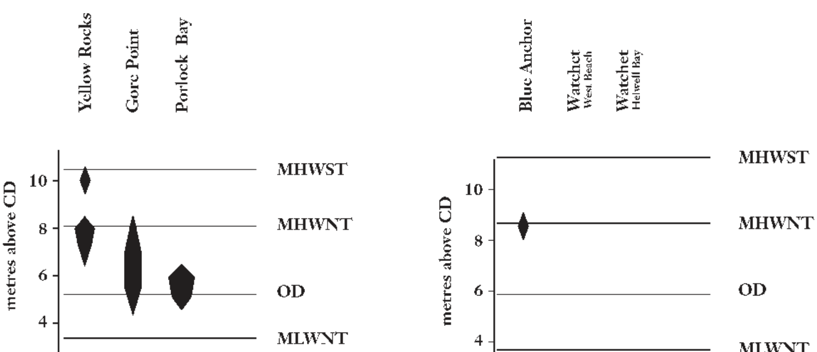

FIG. 21. The zonation of *Osilinus lineatus* on rocky shores in West Somerset.
Sites are listed from west to east and some others, on which no common topshells were found, have been omitted (from Crothers, 1976). Fieldwork was carried out in the autumn of 1974. None have been seen on the shore at Blue Anchor in recent years, but they have been present at Watchet (Helwell Bay), although rarely in sufficient numbers to appear in student transects.

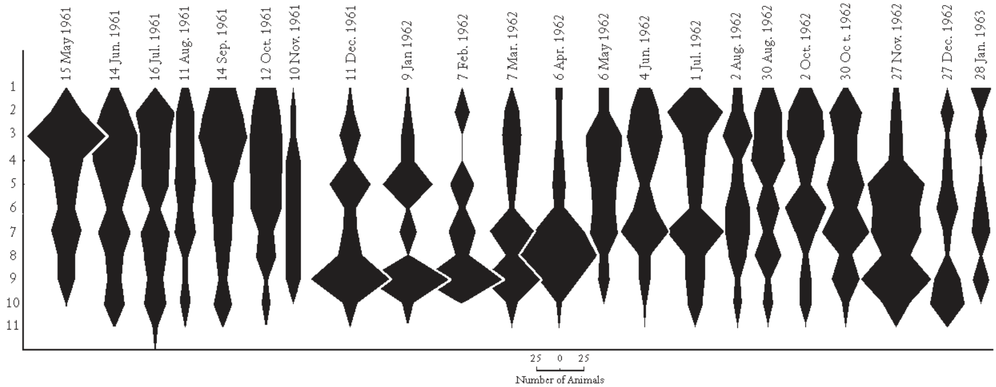

FIG. 22. Seasonal movement of *Osilinus lineatus* at Craig-yr-Wylfa

Data were counts from eleven 1 m^2 quadrats along a transect line (Williams, 1965). The sampling sites were arranged sequentially down the shore but not at regular intervals. All were below Mean Tide Level; stations 1-6 were all above Mean Low Water mark of Neap Tides and station 11 was at Mean Low Water Springs. Due to the broken nature of the shore, stations 1-6 are all at much the same height.

POPULATION STRUCTURE

Terminology

Two terms are, here, used in a technical sense: 'age-class' and 'cohort'. Both are familiar concepts to people who have worked their way up a school. Pupils/ students in a school are generally taught in age classes - year 1, year 2, year 3 etc. (5 year olds, 6 year olds, 7 year olds etc.) - whilst particular groups of individuals (cohorts) steadily progress through the system, moving from one age-class to the next each September. So -

Age-class : The group of individuals currently of a particular age. Those less than one year old are designated 0+; those between 1 and 2 years old, 1+; those between 2 and 3, 2+; and so on.

Cohort: The group of individuals born in a particular year.

[Some authors use 'year-class' in place of 'cohort' which can lead to confusion.]

Thus, if the population modelled in Fig. 23 had been sampled in the spring of 1997, the 1996 cohort would be the 0+ age-class, the 1995 cohort the 1+ age class, the 1994 cohort the 2+ age-class. In 2001, those cohorts would have progressed to be 4+, 5+ and 6+ respectively. Note that each cohort is predicted to show a normal distribution with respect to size.

The model assumes a stable population in which recruitment and mortality are constant, year on year; a situation unlikely to occur on British sea shores, although Stanbury (1975) recorded very even rates of adult mortality, apart from the blip caused by 1963 (Fig. 24), and I deduced similar trends on Gore Point (Crothers, 1994).

Samples from real populations (*e.g.* Table 4) almost never show the high 0+ peak, but it must be present because there are always plenty of 3+ animals - and their presence cannot be explained by the spontaneous creation of animals aged 3! As Desai (1966) reported in North Wales, 0+ animals on Gore Point spend much of the low tide period in gravel-bottomed pools under or near stones and boulders. Only in warm sunny weather do they

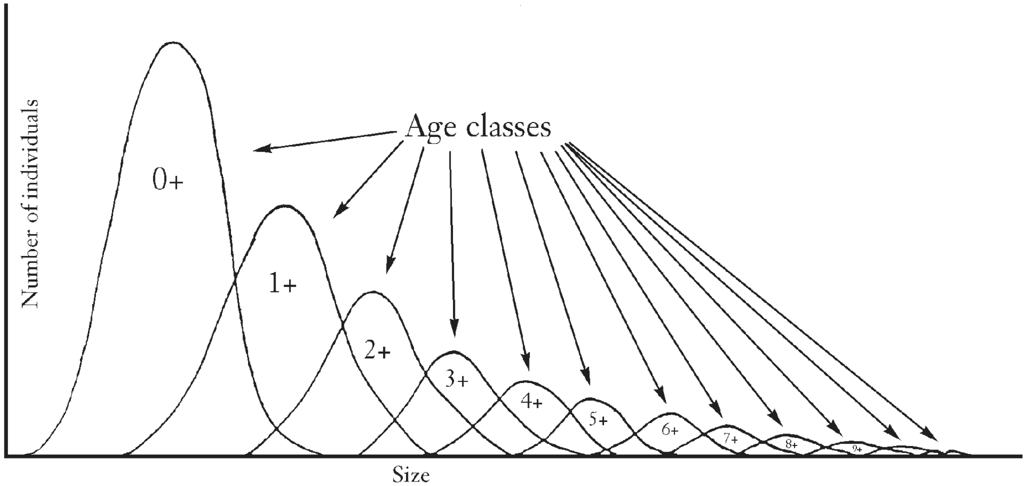

FIG. 23. Theoretical model of the structure of a stable population of animals that have a short breeding season every year and continue to grow throughout their lives. In practice, most animals grow much faster whilst juveniles than they do after reaching sexual maturity but that fact was ignored when drawing this figure, in the interests of clarity.

crawl about, and then usually under water. The older age-classes are generally out of the water, often rather conspicuous on the surface of boulders.

The 1999 cohort settled on Gore Point in September. They either settled at a shell length of 3mm or grew to this size extremely quickly. A month later their mean length was 4.9mm (Table 4). The 1998 cohort averaged 11.6mm, a 137% increase in size. The 1997 cohort, averaging 15.7mm, had grown by 35%and the 1996 cohort by a further 12%. In contrast, all the older cohorts had grown by 5% or less.

In an earlier paper (Crothers, 1994), I averaged the 1988 data collected by students attending field courses at Nettlecombe Court by season. The result reinforced the impression that the young snails grew very rapidly during their first year, less so in their second and, thereafter, grew about a millimetre a year.

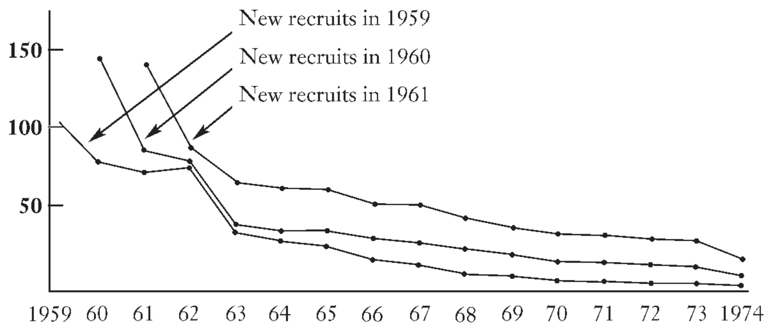

FIG. 24. Survival curves for common topshells recruited in 1959, 1960 and 1961 to the population in South Haven, Skokholm. Deduced by annual marking, release, recapture, remarking, rerelease etc of the entire population. From Stanbury (1975)

TABLE 4. The population structure of common topshells on Gore Point, Somerset, as measured in October 1999. Combined totals of data collected by students from Felsted School, The Holt School and Queen's College, London

	Age-classes											
	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	
Shell length (mm)												Total
1												0
2	1											1
3	7											7
4	10											10
5	**10**											10
6	10											10
7	3	2										5
8	2	13										15
9		23										23
10		75										75
11		94										94
12		**123**	3									126
13		63	4	1								68
14		38	28	1								67
15		15	84	15	24	2	1					141
16		3	**98**	63	54	20	27	1		1		267
17			32	**93**	98	48	31	10				312
18			13	90	**123**	91	65	31	3	6	1	423
19			5	36	102	**117**	77	71	17	12	4	441
20				19	59	110	**80**	**73**	35	7	8	391
21				10	18	28	50	47	**36**	**15**	5	209
22				5	3	3	21	9	17	8	1	67
23				1	1		8	2	1	3		16
24							1		1			2
25												0
26												0
Totals	43	449	267	334	482	419	361	244	110	52	19	2780
Presumed Year of settlement	1999	1998	1997	1996	1995	1994	1993	1992	1991	1990	1989	
Mean shell length (mm)	4.9	11.6	15.7	17.6	18.0	19.0	19.3	19.6	20.5	20.2	20.1	

Figures 25-28 present size/ age data on a monthly basis from January 1994 to March 2001, with an unfortunate gap from August to December 1998, mostly collected by A-level or undergraduate students attending field courses at Nettlecombe Court. Samples frequently exceeded 1,000 shells measured and the figures entered are means when two or more samples were obtained in the same month. Some much smaller samples (*ca* 100 shells measured) were taken by the author alone when no students were available, for example the data for January 1994, January 1999, most Augusts and almost all months after March 2000.

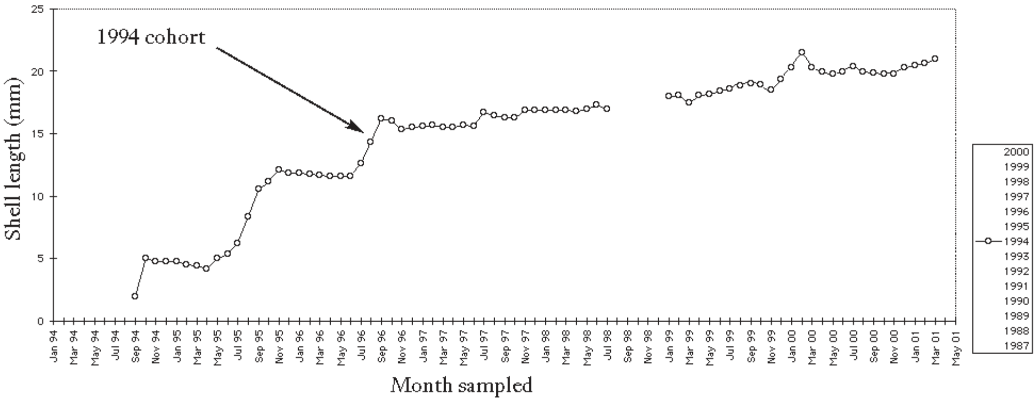

FIG. 25. The relationship between size and age in the Gore Point population [1].

Only the 1994 cohort is shown on this graph. Members of this cohort were first recorded in early September of that year at a mean shell length of 2.0 mm. They grew quickly to reach a mean length of 5.0 mm in October. Growth then ceased for the winter and the mean size declined to 4.2 mm by April 1995. Then followed the maximum period of growth, the snails passing a mean of 10.5 mm by their first birthday to reach 12.1 by November. The cohort's second winter cessation of growth lasted until June and the mean size again declined (to 11.6 mm) in April and May. A second burst of growth took the mean up to 16.2 mm for their second birthday. The third winter passed at a mean size of around 15.5 and it was not until July 1996 that the figure passed 16 again. Growth slowed right down so that on their third birthday (September 1997) the cohort averaged 16.3 mm and by September 2000 was around 20 mm in length.

Because of the much smaller sample size, some age classes may be represented by a single individual and give anomalous results - as for the 1994 cohort in February 2000 (Fig. 25). Where no sample was taken for a winter month, an average has been inserted in the table.

The sheer volume of information may make the graph (Fig. 27), initially, somewhat confusing. However, if the progress of the 1994 cohort is appreciated on its own (Fig. 25) and together with the next two (Fig. 26) the final result (Fig. 27) is readily understood.

Each September, a new cohort settles on Gore Point and grows to around 5 mm shell length before winter cold slows metabolism down. After a winter hiatus, growth continues rapidly through the first summer and second autumn before slowing for the second winter. Each cohort displays a discrete trace for about three years before disappearing into the general melée of the adult population.

In some winters, the averages decline. This is not due to shell abrasion by winter storms and suggests differential mortality. In the case of the 0+ age class, the spring decline in mean size usually indicates the presence of shells of 3mm or 4mm along with the 5mm and 6mm ones. At the time of writing, it is not clear whether these settled in September, but did not grow, or are new arrivals. More southerly populations are known to breed in both spring and autumn (Fretter & Graham, 1977).

These graphs show that the growth pattern of this species in this place is remarkably consistent year by year (and the data for 1987-1991 are very similar, Crothers, 1998) but do not facilitate comparison of one population with another. In order to attempt such a comparison, monthly averages were calculated from the data used to compile Fig. 27. From this plot, (Fig. 28) it is evident that, on Gore Point, the 0+ age class overwinters at 5mm shell length, the 1+ at about 12mm and the 2+ at about 15mm. Thereafter they enter the

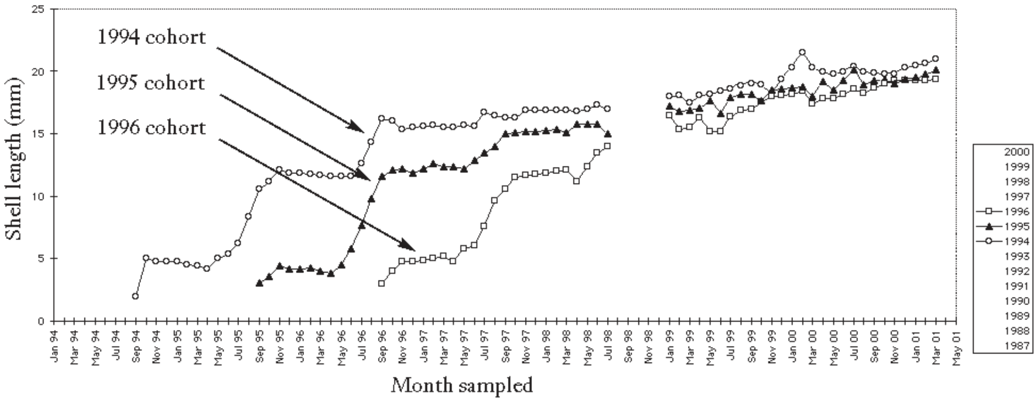

FIG. 26. The relationship between size and age in the Gore Point population [2].
The 1994 cohort, from Fig. 25, is shown with the two following cohorts. Clearly distinct on the left hand side of the graph, they have merged into the adult population in the autumn of 1999.

adult population and probably breed for the first time the following summer. They would then be at the same size as the Aberaeron population studied by Garwood & Kendall (1985) - but one year older.

Observation of the enclave at Swill Point, Doniford (labelled in Fig. 19), between 1994 and 1996 showed that *O. lineatus* grew much faster there (Crothers, 1998). Unfortunately these snails all died early in 1997 but, by October 1999, the enclave was re-established and measurements have been made in most months. Growth patterns appear similar to the earlier enclave which, on 26th August 1996 showed the 1995 cohort to have reached a mean length of 16.1mm; the 1994 cohort, 18.6mm; and the 1993 cohort, 19.5 mm (Crothers, 1998).

The provisional plot for this site (Fig. 29) suggests that these common topshells reach 15mm in shell height in their 1+ age class and breed for the first time as they approach the age of 2 years. Mean sizes of the 0+ and 1+ age classes in July were comparable to those shown in Garwood & Kendall's Fig. 8. Williams (1965) was clearly seeing the same pattern

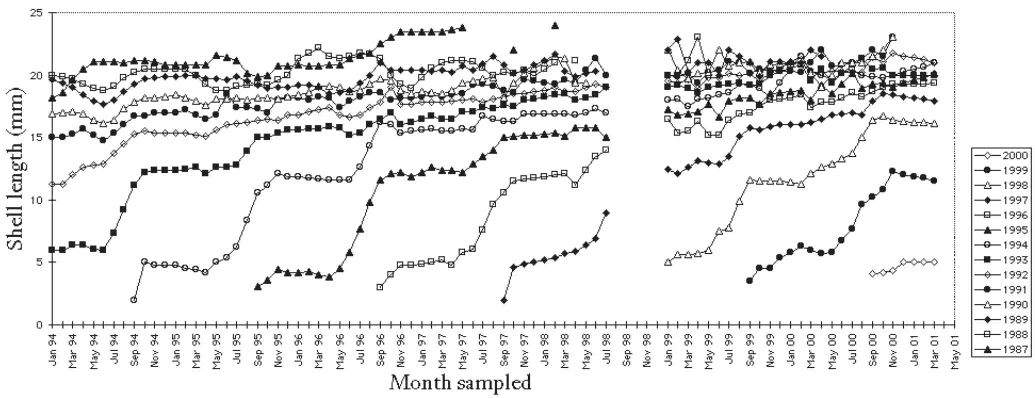

FIG. 27. The relationship between size and age in the Gore Point population [3].
The complete plot from January 1994 to March 2001; unfortunately, no data were collected between August and December 1998. The adult age classes are more distinct to the left of the plot, where most data points display means of large samples, than those to the right which are from small samples.

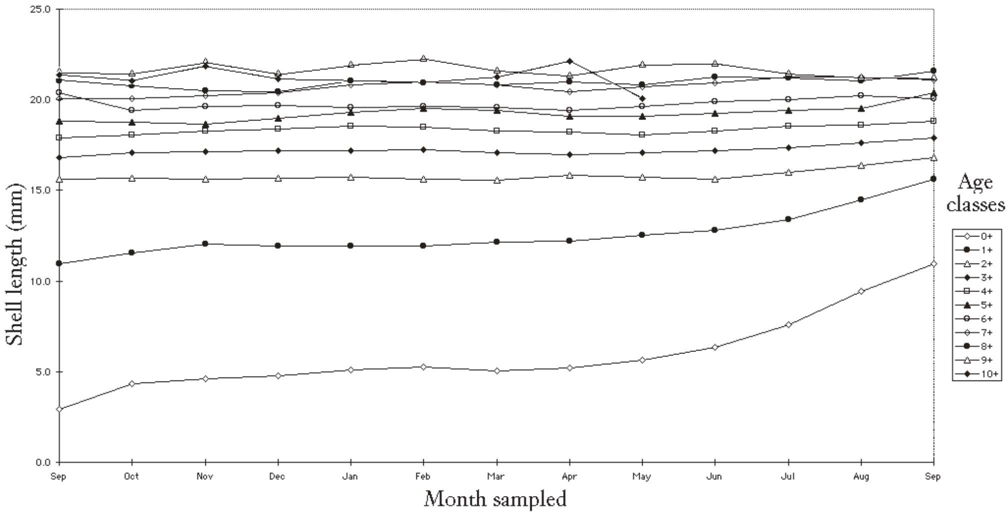

FIG. 28. The relationship between size and age in the Gore Point population [4].
Mean monthly sizes for the different age-classes, derived from the data used to plot Fig. 27. Note that the September value at the end of one age class is repeated as the beginning value for the next.

at Craig-yr-Wylfa, although he did not know about the ageing technique. Gametogenesis takes about a year in virgin animals (Garwood & Kendall, 1985). It seems likely that individuals at Gore Point have not reached a large enough size to initiate this process at the age of one year.

Monthly sampling on Warren Point, Minehead, was begun at Easter 2000 and Fig. 30 presents the result of the first year's work in a comparable form. As on Swill Point, and

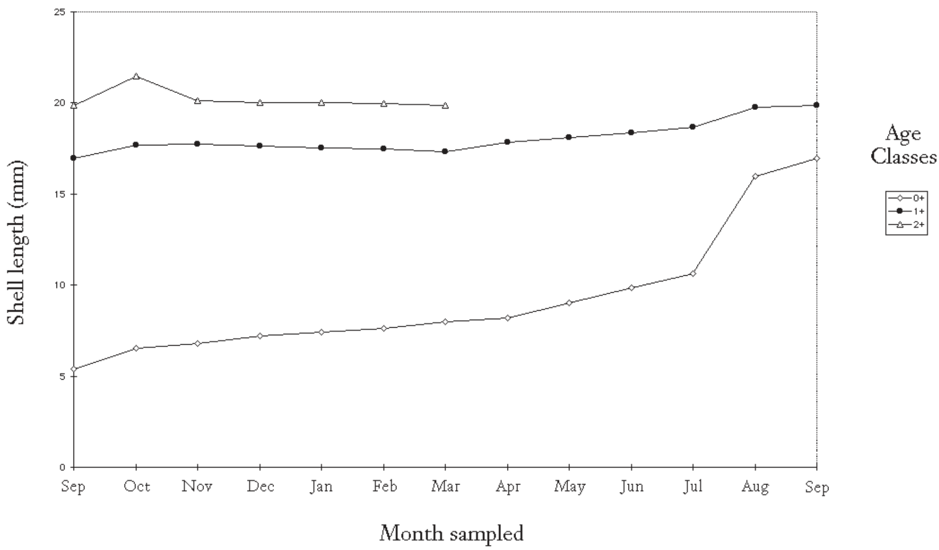

FIG. 29 The relationship between size and age in the Swill Point enclave.
Provisional pattern based on data collected between October 1999 and March 2001. At that time, the enclave was recovering from annihilation in the winter of 1996-1997. The data suggest that these snails reach adulthood a year sooner than do members of the Gore point population.

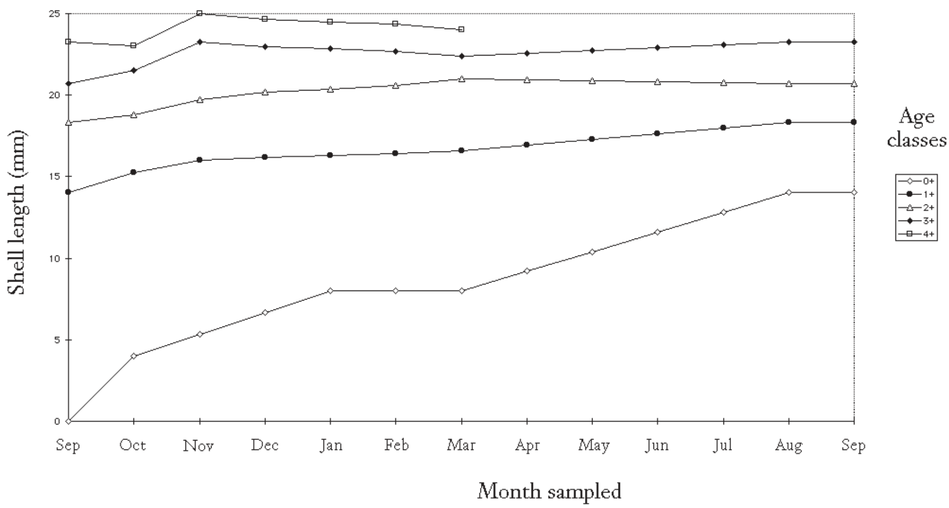

FIG. 30. The relationship between size and age in the Warren Point enclave. Provisional pattern based on data collected between April 2000 and March 2001. The data resemble those from Swill Point, Doniford, more than they do the Gore point population.

unlike on Gore Point, the common topshells reached adult size in one year and grew more slowly thereafter.

According to Kendal (1987), the pattern of growth after the second growth check is remarkably similar in most populations so that, by the end of their third winter, most snails have reached between 65% and 75% of their site's maximum size. At Gore Point, Swill Point and Warren Point, respectively, the 2+ age class averages 15.8 mm, 19.9 mm and 20.9 mm in April; suggesting maximum site sizes between 21.6 and 24.3 mm, 26.5 and 30.6 mm, and 27.9 and 32.1 mm. These figures appear reasonable; snails measuring 29 and 30 mm were recorded at Watchet (Helwell Bay) in October and November 1995. On Gore Point, where tens of thousands of measurements have been recorded, very few individuals over 24 mm have been found.

THE GORE POINT POPULATION

The Gore Point population may be the most extensively-studied in Britain, but it is clearly far from typical. As well as taking an extra year to reach maturity, few individuals reach 25 mm in length or 10 years of life. This situation has not arisen because of the Bristol Channel's extraordinary tidal range or because Gore Point is close to the edge of the species' geographical range. At other Somerset sites, even closer to the edge, shells up to 29mm have been recorded and snails with shells bearing more than 10 growth checks have been found on many occasions.

Larger and older shells are also found further from the geographical limit. The largest common topshell I have measured was 34 mm (Skomer, North Haven, 30th June 1996) and the oldest, from the Aran Islands, was 17 years old (Fig. 15). Of 1195 snails measured around the Isles of Scilly in June 1994, the largest were 32 mm in length and 13 years of age (25. 2%, were over 30mm and/or over 11 years of age).

On Gore Point this animal is truly common: I can usually collect between 30 and 70

TABLE 5.
Differences in the marine snail community where a stream flows across the beach, west of Gore Pt.

	Away from the stream	In the area affected by freshwater
Marine snails		
Species diversity	higher; >70	lower; >60
Species richness	higher; >7	lower; >4
Common topshells		
abundance	lower	higher
size	3 - 22 mm	15 - 25 mm
age classes	0+ to 5+	1+ to 9+
juveniles	present	absent

without moving my knees; the time to make a collection is governed by the speed at which they can be picked up. At Warren Point and Swill Point it is rarely possible to see more than five at the same time and the time taken to make a collection is governed by the distance walked.

It is evident that individuals grow faster, mature more rapidly and have the potential to achieve a larger size in sites where the species is less abundant*; which makes it difficult to define what is meant by 'a good habitat'! Edible winkles *Littorina littorea* (see Crothers, 1992) and purple topshells *Gibbula umbilicalis* also reach much larger sizes at Watchet but are commoner on Gore Point.

I suggest that conditions are suitable for reproduction on Gore Point so that settlement is successful in almost all years, and winter conditions have not been too severe since the site was recolonised after 1963. This is an established permanent population. However, the density of grazing snails is so high that food is limiting, especially in winter, and therefore growth is slow and growth-checks are well-marked. I further suggest that outlying enclaves at Swill Point, Helwell Bay, Blue Anchor and Warren Point depend on the arrival of larvae from elsewhere for recruitment and are at risk in winter cold snaps but, as there is plenty of food for the survivors, they grow fast, mature sooner and achieve a larger size.

There is another interesting feature of snail distribution on Gore Point. There are some seven species to be found on the upper middle shore. Two of these are often represented by one or two individuals, and another is often very common but, overall, Simpson's index of species diversity (Begon *et al.*, 1986, p.595) usually works out between 55 and 70. Common topshells are numerous but are not the most abundant species.

About 200 m to the west of the Point, a freshwater stream runs across the beach (see Wilson *et al.*, 1983). It is unusual to find more than four species of snail present and diversity is usually between 45 and 60. Generally, snails are commoner and the community is more diverse away from the stream. This is in accordance with ecological theory, the more benign habitat should support the more diverse community (Begon *et al.*, 1986). But common topshells are more abundant, achieve a greater size and age in the area affected by freshwater (Table 5).

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* Kendal (1987) reported an inverse relationship between size and density in common topshell populations but found no suggestion that early growth rate of juveniles was related to the density of adults, or that age and density were related.

TABLE 6. The average rate at which *O. lineatus* crawled (cm. min^{-1}) across a Perspex plate at different temperatures. From Desai (1966)

	0°C	3°C	5°C	7°C	9°C	13°C	14.5°C	16.5°C	18.5°C
Size (mm)									
>5				0.3	0.3	0.3	0.5	0.5	0.5
5-10				0.5	0.5	1.0	1.0	1.5	1.5
10-15			2.1	4.2	4.6	5.7	7.6	9.3	9.3
15-19			2.3	5.3	5.3	6.2	6.8	7.2	10.3
19-22			4.3	4.3	5.5	6.1	11.8	12.0	12.4
22-25			4.0	4.0	5.4	6.2	10.7	11.1	12.5
25>			2.9	3.2	5.1	6.1	9.3	10.2	12.8

Probably as a direct result of fewer snails living in the area of the stream, green algae are more abundant on the stones and it is reasonable to assume that the common topshells are commoner and larger because of the better food supply. It follows that they must enjoy some competitive advantage over the limpets, winkles and purple topshells that enables them to exploit the better food supply.

The first hypothesis was that *O. lineatus* was more tolerant of brackish/ fresh water than the other species. Salinity-tolerance behaviour experiments (see Wilson *et al.*, 1983) failed to support this idea. All sorts of extraneous factors may affect the results but, usually, all intertidal snails showed much the same dislike of hypo (and hyper) saline water and are most active in normal seawater. Common topshells differ from the other species only in their level of activity, being much more active than the others and more likely to crawl out of the water.

O. lineatus is thus able to feed in the stream bed during the period of high tide and has time to escape lowering salinities, on the ebb, by crawling out (Fig. 13) and their ability to breathe gaseous oxygen (Micalleff & Bannister, 1967) allows them to survive on the tops of rocks in full sun. Freed from interspecific competition, individuals grow faster and live longer.

Juvenile *O. lineatus*, on the other hand, do not crawl fast enough (Table 6) to escape from the stream (or, perhaps, are less able to withstand desiccation). In addition, the gravel-in-pools habitat that they favour is not available on that part of the shore. It is known, from the mark-release-recapture experiment described earlier, that individual topshells have moved into the area of the stream from the other site.

A GOOD PROJECT ANIMAL ?

On moderately sheltered, broken rocky shores in western Ireland, southwest Britain, the Channel Islands and western France, *Osilinus lineatus*, the common topshell, meets all the requirements for a Good Project Animal. They are conspicuous, reasonably large snails that are easy to identify and measure. With a little practice, they can also be aged. Living high on the shore, they are accessible on all tides and for most of the tidal cycle. In the Mediterranean, Algarve and the Canaries, species of *Osilinus* are the most conspicuous and abundant snails on rocky sea shores. Many of the suggestions that follow would also apply on there - if a warmer location appeals.

Some suggestions for projects

When selecting a topic to investigate, students should remember that most of the marks are given for the manner in which the investigation was carried out and not for the result itself. Keep It Simple Students (KISS) is good advice; many of the simplest projects concentrate on a single species. Essentially, all that is required is the ability to show that the group of individuals at site A differs from the group at site B due to the effect of a critical environmental factor C. Sites A and B can be on different shores or different places on the same shore.

In the example given on page 147/8, variable salinity was the critical factor. The group of individuals in the area of the stream was composed of larger (or older) individuals than the group away from the stream. Rather than look at the population structure as a whole, the investigator might compare the proportion of the group that was, say, more than 20 mm long (or showing more than, say, 3 growth checks).

In other situations, the critical factor might be exposure to wave action - there may be differences in the groups of topshells living either side of a large rock. It might be exposure to strong sunlight - compare those under boulders with those on the top. It might be exposure to the air at low tide - there are likely to be differences up or down the shore and in or out of pools. It might be the availability of fine gravel in pools, the habitat seemingly favoured by the 0+ age class. It might be competition from other grazing snails - the higher the density of competitors the more stunted the common topshell population [remember that whelks are carnivores and so are not competitors]. The permutations are endless.

Other suggestions include:-

• As nacreous shells require regular maintenance to maintain their strength and deteriorate quite rapidly after the death of their owner, hermit crabs should select shells of winkles and whelks more often than of topshells. Do they? This investigation would only be worthwhile at a site where hermits were common, but there are possibilities for behaviour experiments - which shells do hermits select? and field surveys - is hermit occupancy of snail shells proportional to the number of shells available? or are topshells rejected disproportionately? See Lancaster (1988) for information on hermit crabs.

• According to Gause's Competitive Exclusion Principle (see Begon *et al.*, 1986 page 260), the rock-grazing herbivorous snails (topshells, limpets and winkles) should be avoiding competition by feeding at different times, and/or in different places, using different techniques or choosing different algal species. It is comparatively easy to demonstrate differences in the microdistribution of the different species up or down the shore, in and out of pools, near a freshwater stream etc.

• Attempted predation. On moderately sheltered shores in southern Cornwall, the Isles of Scilly and the Channel Islands, barnacles and mussels are often in short supply. As these are usually the primary prey species for dog-whelks, those predators have to find alternatives amongst the grazing snails. In these sites, I have frequently found dog-whelks attacking limpets, flat winkles and purple topshells but never, as I recall, common topshells. 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.

When planning a project, it is important to remember Safety - of the investigator as well as any bystanders. An individual project does not require the student to work alone and it is usually much more efficient, as well as safer, to take an assistant. Consideration should be given to conservation. In practice, this means seeking to reduce any human impact to a minimum by not taking more samples than is necessary, returning any animals to the spot at which they were found and replacing any boulders that have been moved. Planning anything on sea shores requires knowledge of the times of high and low water but it is surprisingly easy to misread tide tables and it is advisable, before starting work, to confirm the state of the tide, to ensure that the escape route is clear and that there is no possibility of being cut off.

APPENDIX 1: SCIENTIFIC NAMES

Common, conspicuous, edible or harmful species of animals and plants have acquired at least one colloquial name in every relevant language and dialect around the globe. Some species have literally dozens of names, most of which do not translate into other languages or dialects with any ease. The same name may refer to different species in different countries. The potential for confusion is obvious (and dangerous with some 'edible' fungi).

Scientific names provide, by International Agreement, an independent standardised nomenclatural system to aid co-operation and communication between biologists of differing disciplines and nationalities. The name is formed of two latinised words - a generic noun (written with an initial capital letter) and the specific epithet, an adjective. The name is printed in italic script, or underlined in manuscript or typescript. For example, the common octopus was given the scientific name of *Octopus vulgaris* ['vulgaris' = 'common' in Latin, our word 'vulgar'). Now this, or any other, name is not of much use by itself. We need a description of the organism as well. So the full scientific name incorporates its author's name and the date when (s)he designated a type specimen and described it. The common octopus is really *Octopus vulgaris* Cuvier, 1797.

It is, of course, quite possible that different people in different countries used different scientific names for the same species, or the same name for different species. The International Code of Zoological Nomenclature takes care of that by ruling that the earliest proper description of a species, unequivocally tying the name to a designated type specimen, shall have priority. However, to prevent pedants from scouring ancient manuscripts in search of the earliest known name, the system (for animals) starts with Linnaeus, 1758 *Systema Naturae* 10th Edition and there are clauses that enable the Commission to ignore its own rules and retain a well-known name. Note, however, that, although the generic name is unique (amongst animals), no such bar is placed on the specific name. For instance, 'vulgaris' is used in 12 different genera (Howson & Picton, 1997) but such frequent use of the same adjective is discouraged as confusion can occur. Amongst topshells, da Costa (1778) unfortunately used 'lineatus' (= lined) twice; *Turbo lineatus* for the common topshell and *Trochus lineatus* for the grey topshell!

Nothing in this system implies that scientific names are immutable. A name is best regarded as a hypothesis. The user thinks that the group of individuals, to which (s)he is applying the name, form a genuine species and, moreover, that that species is most closely related to others in a particular genus. Thus, when I (as author of this paper) use the name *Osilinus lineatus* (da Costa, 1778) for a common topshell I have found at Porlock Weir, I am saying that I believe this individual to belong to the species *lineatus*, as defined by da Costa in 1778, which I currently regard as a member of the genus *Osilinus* Philippi, 1847.

The Genus

Bassindale (1943) also called this animal *O. lineatus* but Winckworth (1932) used *Monodonta lineata* (da Costa, 1778) in his definitive list of Mollusca found within the 100 fathom line around the British Isles and, from the late 1930s until the late 1990s (Howson & Picton, 1997), virtually all British authors followed suit. *Monodonta* seemed an appropriate name for the genus: 'one tooth' describing a diagnostic feature of the shell. But Lamarck, when coining this name, first used it for an Indo-Pacific species, *Monodonta labio* Lamarck, 1799. Is it likely that topshells in Britain and the Indo-Pacific belong to the same genus? Many people (including Cesari, 1986, Gofas & Jabaud, 1997, Herbert, 1994, Hickman & McLean, 1990; Howson & Picton, 1997; Nordsieck, 1974) doubt it in this case.

Cesari (1986) argued that *Monodonta* (in the wide sense in which it was used during the second half of the twentieth century) was better regarded as the sub-family Monodontinae Cossmann, 1916, composed of four genera: *Monodonta* (sensu stricto) Lamarck, 1799, from Papua New Guinea and Australia; *Diloma* Philippi, 1845, from South Africa, Japan and New Zealand; *Austrocochlea* Fischer, 1855, from Australia; and *Osilinus* Philippi 1847 in the Eastern Atlantic and Mediterranean. Most European authors, including Howson & Picton (1997), belatedly, followed this lead.

Unfortunately, the name *Osilinus* was actually the senior substantive synonym of the Australian *Austrocochlea (*Gofas & Jabaud, 1997). *Trochocochlea* Mörch, 1852 was the next available name for the species discussed in this paper. The confusion likely to follow from transferring the name *Osilinus* from the Atlantic/Mediterranean species to Australian species was so great that a proposal (no 3055) was made to the International Commission to retain *Osilinus* for the European species (and *Austrocochlea* for the southern ones) by designating *Trochus turbinatus* Born 1778 as the type species of *Osilinus* (Gofas & Herbert, 1998 or see Smith, 1998). Whilst the Commission pondered, the name *Trochocochlea* made a temporary appearance in the literature. The Commission duly ruled in favour of Gofas & Herbert's proposal in Opinion 1930, September 1999, and *Trochocochlea* was relegated to the official list of rejected and invalid names in Zoology.

Which is why references will be found to the British common topshell as *Monodonta lineata*, *Osilinus lineatus*, *Trochocochlea lineata* and *Turbo lineatus* as well as *Trochus crassus* (Pulteney, 1799).

Appendix 2: Species of *Osilinus*

Osilinus is a genus of high inter-tidal rocky shore topshells in the Eastern Atlantic Ocean and Mediterranean Sea. At the time of writing, there appear to be five or six species but there is considerable confusion in the literature. For example, all six have been recorded in Portugal but I could only find two. A programme of morphological and morphometric analysis complemented by DNA sequencing is currently in progress at Southampton University (Preston, 2001) and should clarify the situation. In the meanwhile, I offer a tentative summary.

In the British Isles and France, only *O. lineatus* present but, elsewhere, there is often an exposed shore species and a sheltered shore species. Thus *O. turbinatus* and *O. articulatus* are found in the Mediterranean, *O. sauciatus* and *O. lineatus* in Portugal and *O. edulis* and *O. atrata* around the Canaries. *O. sauciatus* may be a variety or sub-species of *O. edulis* but is treated as a separate entity in the section that follows.

Osilinus articulatus (Lamarck, 1822)

Geographical distribution. Common throughout most of the Mediterranean, but apparently absent from Africa between Libya and Egypt. Probably, does not extend far

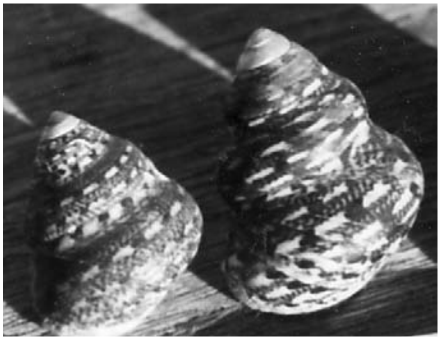

FIG. 31. *O. articulatus* in the collections of the Natural History Museum, London.

beyond the Straits of Gibraltar. Records from Portugal (*e.g.* Nobre, 1932; 1936; Macedo *et al.*, 1999) were doubted by Dr Serge Gofas (personal communication).
HABITAT. Intertidal on rocky shores. Favours broken shores with loose boulders, often in pools under stones. On Malta and Gozo, this is the sheltered shore species; where *O. turbinatus* was also present, *O. articulatus* was most abundant lower down the shore.
ADULT SIZE. Poppe & Goto (1991) give a range between 15 and 28 mm but "large shells reach 35 mm in height". The largest shell in the British Museum (Natural History) collection is 34 mm.
DESCRIPTION. Shell conical, longer than broad (*i.e.* maximum shell length measured from the apex shell usually exceeds maximum basal diameter) with an attractive but complicated colour pattern of dark lines on a cream background, over which is superimposed a series of bands running across it at right angles to the lip. Each band bears a pattern of alternating purple and white splotches; the thickest one on the inside of the whorl (Fig. 31). The operculum is brown, appearing uniform in colour when the animal is alive. On Malta and Gozo, large shells often bear conspicuous growth checks - perhaps indicating summers
SYNONYMS (Scientific names currently out of favour). *Monodonta* or *Trochocochlea articulata* Lamarck, 1822; *M., O., or T. draparnaudi* Payraudeau 1826; *blainvillei* (Pallary, 1902; *turbiformis* von Salis, 1793; *Trochus tesselatus* A. Adams
REFERENCES. Barash & Danin (1992); Cachia *et al.* (1991; 1993); Giannuzzi-Savelli *et al.* (1994), D'Angelo & Gargiullo (1978); Gofas & Jabaud (1997); Poppe & Goto (1991); personal observations on Malta and Gozo, 1994, 1996.

Variety *lineolata* Bucquoy, Dautzenberg & Dollfus, 1884. Found on Italian shores, *e.g.* at Palermo, may be a variety of another species, or a separate species in its own right.

Osilinus turbinatus (Born, 1780)
GEOGRAPHICAL DISTRIBUTION. Abundant throughout the Mediterranean. Probably, does not extend far beyond the Straits of Gibraltar. Records from Portugal (*e.g.* Nobre, 1932; 1936) were doubted by Dr Serge Gofas (pers. comm.); they probably refer to *O. sauciatus.*
HABITAT. Found on all but the most sheltered Maltese shores, seemingly able to obtain sufficient protection from minor weathering hollows in the limestone. Such sites are dominated by small individuals. This is the exposed shore species and, on shores where *O. articulatus* also occurs, is usually found higher up.
ADULT SIZE. Poppe & Goto (1991) give the normal adult size as between 15 and 38 mm in

FIG. 32. *O. turbinatus*. Mistra Bay, Malta

diameter. Shells as high as 43 mm exist. The largest shell in the British Museum (Natural History) collection is 41 mm.

DESCRIPTION. The shell is not as conical as it is in *O. articulatus*, (length and basal diameter are about equal). The pattern of decoration is best described as a series of black, olive green or almost purple blotches on a creamy background; the blotches being arranged in a series of interrupted bands running around the shell at right angles to the lip (Fig. 32). Individuals vary greatly in the intensity of pigmentation. The operculum is pale enough to be transparent, showing, in life, a yellow mark on the columella side where it is attached to the foot.

SYNONYMS (Scientific names currently out of favour). *Monodonta turbinata* (Born, 1780), *Trochocochlea turbinatus* (Born, 1780)*; M.*, *O.*, or *T. fragaroides* Lamarck, 1822; *Trochus tesselatus* Born, 1778; *O. olivieri* Payraudeau, 1826.

REFERENCES. Barash & Danin (1992); Cachia *et al.* (1991; 1993), Giannuzzi-Savelli *et al.* (1994), D'Angelo & Gargiullo (1978); Poppe & Goto (1991); Schifano (1983; 1984); Schifano & Censi (1983); Torunski (1979); personal observations on Malta and Gozo, 1994, 1996.

Osilinus atratus (Wood, 1828)

GEOGRAPHICAL DISTRIBUTION. Recorded from the Canaries, Madeira, Selvagens. Probably also along the West African coast and possibly Portugal, although Dr Serge Gofas doubts the latter (personal communication) and I haven't found any there yet.

HABITAT. Intertidal on rocky shores. On Gran Canaria, the species was commonest on (? confined to) flat shores, especially those with many loose stones on the southern coast of the island - where the chart indicated that the 5 m depth contour was a little way offshore. These shores probably receive least wave action. More widespread on Lanzarote, but still commonest in shelter.

ADULT SIZE. 10 to 18 mm in diameter. Up to 23 mm high (Poppe & Goto, 1991). 18 mm in height is a good average size but I have recorded them up to 32.2 mm (basal diameter

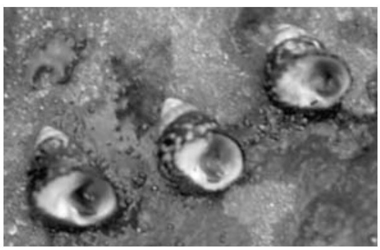

FIG. 33. *O. atratus* Maspalomas, Gran Canaria.

22.4 mm) on the Arrecife de Orzola, Lanzarote. On Gran Canaria, my largest specimen was 19 mm in height.

DESCRIPTION. The shell is almost always taller than it is broad and, apart from populations on the Selvagens, is predominantly black or dark brown, often with a pattern of fine white zigzag lines or dots. Like most topshells, the outer, coloured, layers of the shell are abraded from the apex, revealing the mother-of-pearl layer inside - and making this small dark snail surprisingly conspicuous (Fig. 33).

SYNONYMS (Scientific names currently out of favour). *Monodonta* or *Trochocochlea atrata*

REFERENCES. Poppe & Goto, (1991); personal observations on Gran Canaria, March 1997, and Lanzarote, January 1999. The shells illustrated under this name by Macedo *et al.* (1999) are of *O. edulis*

Osilinus edulis (Lowe, 1842)

GEOGRAPHICAL DISTRIBUTION. Canaries, Madeira, possibly the Atlantic coasts of north Africa. Possibly mainland Portugal but, at least for the time being, those populations are referred to *O. sauciatus*.

HABITAT. Found, and usually abundant, on all but the most sheltered Canarian shores, occupying the niche filled by *O. turbinatus* in the Mediterranean. This is the widespread, exposed shore species in comparison with *O. atratus*.

ADULT SIZE. My largest specimen measured 28.2 mm in length (Fig. 34). Poppe & Goto (1991) give the normal adult size as between 20 to 30 mm in diameter. Lanzarotian populations apparently contain more large individuals than those on Gran Canaria, where the islanders collect them for food and large individuals are rare near villages.

DESCRIPTION. Very similar to *O. turbinatus*, but the blotches are more often purple than green. Perhaps thinner shelled. Populations in the Canaries have a slightly glossy shell; a feature not found in the other species with a closed umbilicus that live in this region. Young shells, and sometimes adults, may have a subsutural spiral band with alternating white spots.

SYNONYMS (Scientific names currently out of favour). *O. colubrinus* (Gould, l849); *O. sagittiferus* (Lamarck, 1822). *O. sauciatus* (Koch, 1845) may prove to be a form of *O. edulis*.

REFERENCES. Poppe & Goto (1991); personal observations on Gran Canaria, March 1997, Lanzarote, January 1999.

FIG. 34 *O. edulis.* Gran Canaria

FIG. 35. *O. lineatus* Garrettstown Strand, Ireland.

Osilinus lineatus (da Costa, 1778)

GEOGRAPHICAL DISTRIBUTION An Atlantic species, living from the British Isles (Donegal /Anglesey /Dorset, Fig. 16) south to Morocco. Despite Sir Walter Calverley Trevelyan's record from Hyères, it probably does not extend into the Mediterranean. It is the only *Osilinus* on the coasts of France and in the British Isles. Type locality; Pwllheli (W. Wales).

HABITAT. Found on fairly sheltered broken rocky shores. Often abundant and conspicuous (sits on the top of boulders) but patchy in distribution, being absent from apparently suitable shores within its geographical range. In Portugal, where it occurs with *O. sauciatus*, it dominates in the more sheltered sites and is more likely to be found (by day) in pools than on the surrounding rock.

ADULT SIZE. Individuals have been known to reach 34 mm in shell height (Skomer and Scilly) and 15 years of age (Stanbury, 1975) but these are exceptional figures.

DESCRIPTION. The pattern of alternating fine dark and light brown streaks distinguishes *O. lineatus* from all other topshells and, throughout most of its range, this is an easily identified species. However, in southern populations (*e.g.*, in the Algarve), there is much more variation. In addition to 'typical' individuals, there are many in which the umbilicus remains open into adulthood and the pattern becomes less distinct on the body whorl. Many become an almost uniform sandy brown or reddish brown (well illustrated by Macedo *et al.*, 1999). This is sometimes attributed to abrasion by sand etc - but abrasion never seems to produce this effect in Britain.

SYNONYMS (Scientific names currently out of favour). *Monodonta* or *Trochocochlea lineata* (da Costa, 1778); *Turbo lineatus* da Costa, 1778; *Osilinus colubrinus* (Gould, l849); *Trochus crassus* (Pulteney, 1799).

REFERENCES. Bode *et al.* (1986); Crothers, (1994, 1998); Cundall (1887); Desai (1966); Fretter & Graham (1962, 1977, 1994); Gardiner (1923); Graham (1988); Kendall, (1987); Kendal *et al.* 1987); Little *et al.* (1986); Macedo *et al.* (1999); Poppe & Goto, (1991): Williams, (1965); Williamson, & Kendall, (1981); personal observations, England, Wales, Ireland, Channel Islands, France, Spain, Portugal.

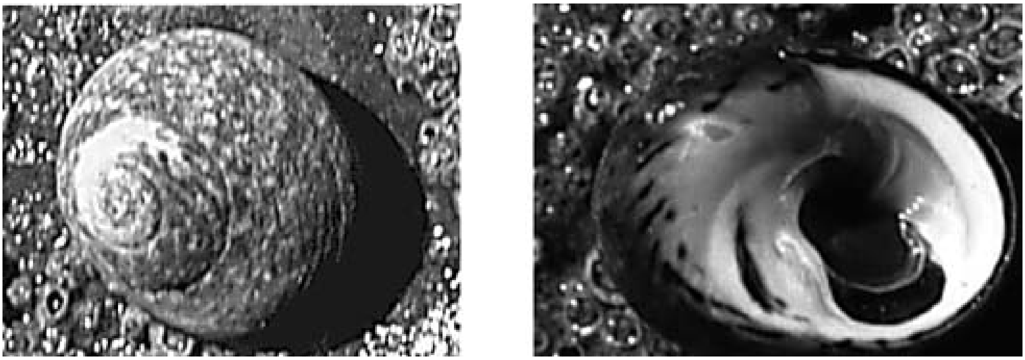

FIG. 36. *O. sauciatus* South of Silves, Portugal.
Two photographs of the same individual.

Osilinus sauciatus (Koch, 1845)
GEOGRAPHICAL DISTRIBUTION. Widespread and abundant on Portuguese coasts, extending north at least to Catalonia. Probably, does not extend into the Mediterranean (Dr Serge Gofas, personal communication).
HABITAT. Intertidal on rocky shores. Favours more exposed situations than *O. lineatus*, with which it is often found.
DESCRIPTION. Umbilicus closed. Tooth and umbilical scar indistinct, but often with a conspicuous dark purple mark in the umbilical area (Fig. 36) and the coloured layer of the shell is visible inside the aperture (Fig. 37). This is a duller, European Mainland edition of *O. edulis* (Lowe, 1842). If the two are eventually found to be the same species, *sauciatus* will become a variety of *edulis*.
SYNONYMS (Scientific names currently out of favour). *Monodonta/ Osilinus/ Trochocochlea edulis* (Lowe, 1842). Macedo *et al.* (1999) use *Monodonta/ Trochocochlea colubrina* (Gould, 1849) for this species but Fretter & Graham (1977) considered that name to be a synonym of *O. lineatus*.
REFERENCES. Macedo *et al.*(1999 as *Monodonta colubrina*), Mosquera *et al.* (1988); Dr Serge Gofas (personal communication); personal observations, Algarve; April 1998.

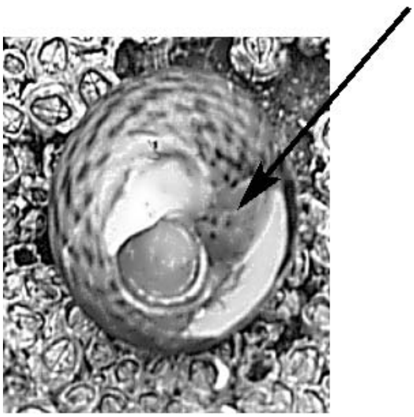

FIG. 37. *O. sauciatus* Sagres, Algarve, Portugal
to show that the nacreous layer does not completely obscure the coloured layer in the aperture

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