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THE COMPARATIVE ECOLOGY OF THE FLAT PERIWINKLES,

Littorina obtusata (L.) and *L. mariae* Sacchi et Rastelli

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ABSTRACT

The flat periwinkles, *Littorina obtusata* and *L. mariae* are abundant and conspicuous members of the rocky intertidal community, living on fucoid algae. As such, they are ideal subjects for many field projects and class studies. Despite this, their potential is not fully realised due to taxonomic confusion and identification problems. This paper seeks to redress the problem and describes each species' ecology. The two are very different, ecologically, and variation between them can be used to great advantage in comparative studies. Of particular interest will be the relationship between the winkles and their food plants, and between the winkles and their predators. Whether used for manipulative field/laboratory-based experiments or simple mensurative surveys of distributions, *L. obtusata* and *L. mariae* will be a useful teaching medium for many ecological theories.

INTRODUCTION

FLAT PERIWINKLES are abundant on North Atlantic temperate rocky shores. Unlike other littorinids (winkles), they belong to the epiphytic (that is living on plants) community and are further distinguished by the very low spire to their shells. Unfortunately, many people still treat them as a single species, often termed "*L. littoralis*". This classification is now 25 years out of date (see Raffaelli, 1982, for review) and yet, due to the extreme conservatism of many biologists, the longevity of identification books, and the inadequacy of many recent keys, it is still in use today. This paper hopes to redress a gap in people's understanding and to encourage workers to investigate the two flat winkle species in their own right, as they are very different animals.

Flat periwinkles were formally recognised as belonging to two distinct species by Sacchi et Rastelli (1966): *L. obtusata* (L.) and *L. mariae* Sacchi et Rastelli. Separation was based on physical characteristics as the two species were then considered to be extremely similar ecologically. They appeared to inhabit the same niche; both spending their entire life histories on similar algal species, and often on the same shores. Niche theory dictates that two species cannot live in the same niche without competing with one another for one or more of the available resources (see Begon, *et al.*, 1986). It was therefore assumed that the two had diverged from a common ancestor and that competition was the driving force for this divergence. Competition would select for niche partitioning (division of resources) between the two forms, enabling them to coexist on the same shore.

This paper is one result of an investigation into the ecological differences between flat winkles, and an attempt to find evidence for the selective force responsible for the evolution of the two species.

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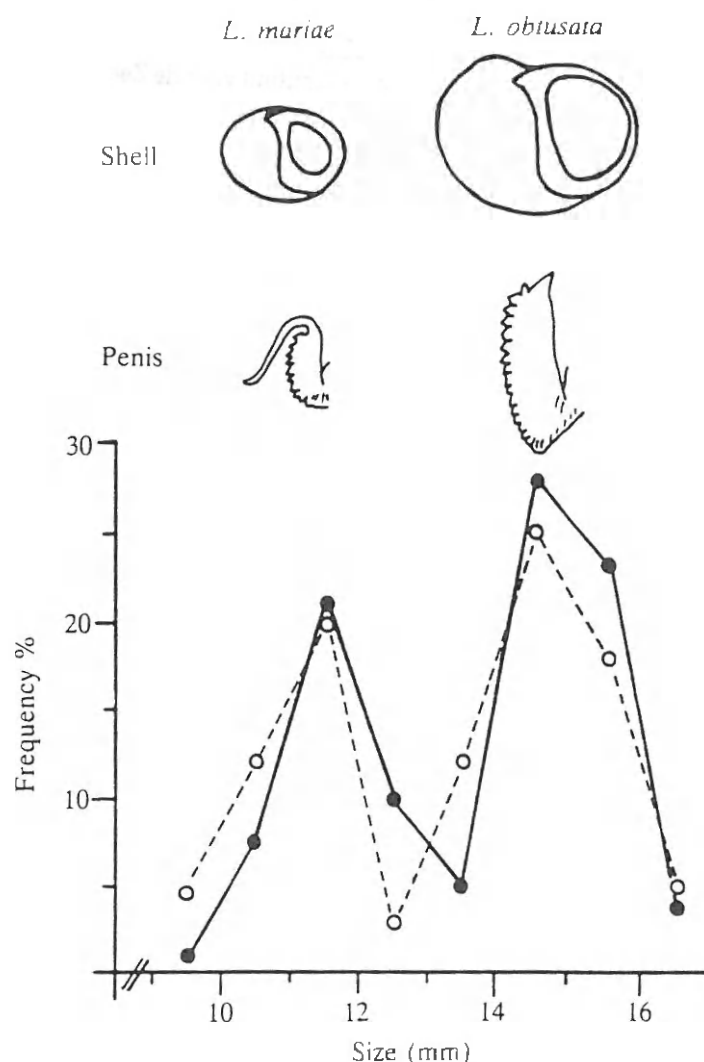
FIG. 1.

Original description of the size difference between "dwarf" (*L. mariae*) and "normal" (*L. obtusata*) flat periwinkles (after Sacchi et Rastelli, 1966). Broken lines and open circles represent male animals and unbroken lines and closed circles represent females. The top diagrams show typical penis and shell morphology of the two species.

THE SPECIES

Division of flat winkles into two species was prompted by size differences. Prior to 1966, flat winkle populations were regarded as comprising normal-sized animals and dwarf (Sacchi, 1966) or "*minima*" forms (Dautzenberg et Fischer, 1914). On investigation, dwarf and normal forms were found to vary consistently in gross size and (males) in penis morphology (see Fig. 1). Subsequently, a number of additional characters have been suggested as being diagnostic between the two species. Goodwin and Fish (1977) proposed colour of the ovipositor (a fold of skin on the side of the female's head that aids formation of the egg masses), considering it to be pigmented in *L. obtusata* and unpigmented in *L. mariae*. This character seems useful on some shores but is unreliable in general (Nielsen, 1980) as female *L. mariae* sometimes have pigmented ovipositors and female *L. obtusata* often don't (Reid, 1989; Williams, 1990). Reimchen (1974) showed differences in the number and sequence of ridges and grooves of the periostracum (a protein outer-covering of the shell). This character, too, is reliable on some shores but confusing on others where both species appear to have similar patterns. Shells of adults are often fouled or eroded, and

this removes the periostracum. Reid (1989) noted a difference in the relative lengths of the bursa copulatrix (a sac in the female reproductive tract that stores sperm from the male) which enables females to be distinguished on dissection.

Most of these characters are of little help in the field! Identification of living specimens may be difficult (especially on more exposed shores, see later) but is not, however, impossible. Using visual characteristics (such as shore level, shell colour, and so on) backed by confirmatory dissection of a few specimens in the laboratory, it is relatively easy to distinguish between adults. On some shores, judgement can be made by shell colour alone (Williams, 1987).

Both species exhibit sexual dimorphism (there is a size difference between the sexes), which is more pronounced in *L. mariae* than in *L. obtusata*. Females are larger than males (Sacchi, 1969). The shell lip is thin and sharp in juvenile winkles, becoming thickened once the animal reaches sexual maturity (see Fig. 1).

In general, *L. obtusata* is the more highly spired with the less thickened aperture. Adults range from 15–17 mm on British shores. The shell is usually green, yellow or brown/black. On sheltered shores the dominant colour morph is green (*olivacea*); on more exposed shores it is brown with black markings (*reticulata*). The periostracum is smooth in the adult.

Shells of *L. mariae* are smaller and much thicker than those of *L. obtusata*. The adult size ranges from 9–12 mm. The shell is very rarely green and tends to be yellow or brown/black, with yellow (*citrina*) the dominant colour morph on sheltered shores and *reticulata* on more exposed ones. Often, the shell of old individuals becomes covered in microalgae, giving it a green appearance. Scratching the surface with a thumbnail removes this coating and reveals the true colour of the shell. The outer covering of the shell often appears slightly rough (slight ridges in the periostracum) in adults as well as juveniles, although the same is true for juvenile *L. obtusata*.

It is most easy to distinguish between the two species by looking at large mid shore flat winkles (*L. obtusata*) and small, low shore animals (*L. mariae*) as, when directly compared, the two are quite easily separated.

FOOD AND FEEDING

There has been confusion regarding the way in which flat winkles feed, and this is still a subject for debate. Both species are herbivores, and both are found on the fronds of macroalgae, yet they feed in different ways and usually on different plants.

L. obtusata actively selects brown algae over the greens and reds, and within the brown algae, *Ascophyllum nodosum* (the egg wrack) is the preferred food plant, where available. *L. obtusata* is one of the few grazers capable of eating this plant which produces noxious chemicals to repel grazers. Most winkle species avoid encountering it (Watson and Norton, 1987, see Norton, *et al.*, 1990 for review) but *L. obtusata* is actively attracted to the alga and responds positively to the alga's exudates. *L. mariae* has a similar attraction for *Fucus serratus* (saw wrack) and will choose this alga over others in choice experiments.

On British shores, *L. obtusata* is a macroalgal grazer, actively excavating into the thallus tissue and often leaving visible gouge marks in the frond. There is no evidence that winkle grazing is harmful to the plant's success. *L. mariae*, on the other hand, browses on epiphytes (organisms living on plants). The fronds of *F. serratus*, a low shore alga, usually support a rich variety of microalgae and sessile invertebrates (bryozoans, serpulids, barnacles and hydroids). The browsing of *L. mariae* may be beneficial to *F. serratus* as a heavy loading of epiphytes can decrease the plant's fitness (Williams, 1990).

Comparatively few epiphytes grow on *A. nodosum* (and the red alga *Polysiphonia lanosa* appears not to be favoured) and therefore this food source is unavailable to *L. obtusata*. In the U.S.A., however, *A. nodosum* is seasonally loaded down by dense epiphytes and, there, *L. obtusata* is regarded as instrumental in cleaning the plant of potentially harmful growths (Menge, 1975).

DISTRIBUTION

The distribution of flat periwinkles is closely related to that of their food plants. On coasts where macroalgae are absent flat winkles will also be scarce or absent. Consequently, factors that affect algal distribution will also affect winkle distribution.

Geographical distribution

Littorina obtusata is found from the Western Mediterranean to Northern Norway. In North America it extends from Canada to New Jersey (Fretter and Graham, 1980). Size and shape of the shell vary greatly across the range. So much so that there were a number of forms given taxonomic status until Colman (1932) showed them to represent stages in a geographical cline of morphology (that is a continuous change in shape along a long length of coastline). A very high-spired flat-winkle is found in Iceland, but there is doubt as to whether this is a form of *L. obtusata* or a separate species.

The distribution of *L. mariae* is not as well documented but is apparently more restricted. The European distribution is similar but it has not been found in the U.S.A. (R.H. Seeley, personal communication). *L. mariae* also exhibits geographical variation in shell size and shape. The taxonomy and relative status of these differing forms are currently under review.

Horizontal distribution

Horizontal distribution patterns refer to gradients in the exposure of the winkles' habitat to wave action or salinity, such as the difference between exposed and sheltered shores or between sequential shores along an estuary. Both species of flat winkle are extremely abundant on sheltered shores dominated by large beds of fucoid algae. As conditions become more exposed, so algal cover decreases and this is mirrored by a decrease in winkle numbers. On very exposed shores, flat winkles can be found only if algae are present, and even then populations tend to be sparse. Such winkles tend to have larger apertures (G. A. Williams and C. Little, unpublished data), a feature associated with their ability to "hang on" to the alga (Grahame and Mill, 1986) and one seen in other gastropods—e.g. dog-whelks (Crothers, 1985). In general *L. obtusata* and *L. mariae* are found on shores of moderate exposure to sheltered shores, as defined on Ballantine's (1961) scale. The size of *L. obtusata* increases with shelter, exposed forms being relatively small. The converse is true of *L. mariae*: as shores become more exposed so the size of *L. mariae* increases (Goodwin and Fish, 1977; Reimchen, 1982). There is, therefore, a great difference between the sizes of the two species on sheltered shores (see Fig. 2) and a marked similarity on exposed shores. Unfortunately, a similar pattern is found with colour morphs. On sheltered shores *L. obtusata* tends to be green and *L. mariae* yellow; on exposed shores both species tend to be reticulated. This makes identification most difficult on more exposed shores, where there may be a size difference of only 1 or 2 mm between them. In general *L. mariae* is more common in this habitat, than *L. obtusata*, and has even been referred to as "surf loving" (Sacchi, 1969).
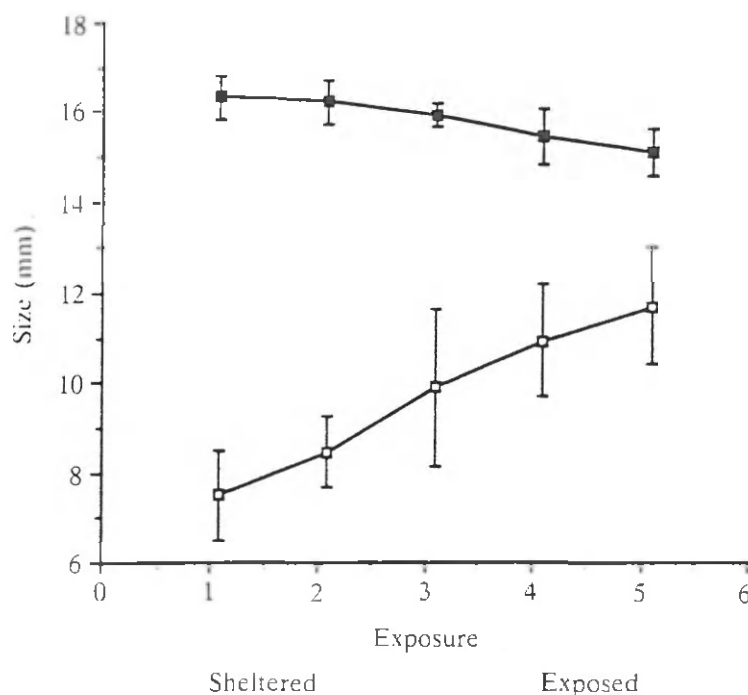
FIG. 2.

Variation in adult shell length with exposure. Closed boxes represent *L. mariae*, open boxes *L. obtusata*, values are means + S.D. (after Reimchen, 1982). Reimchen's exposure scale runs from 1 (sheltered 8 on Ballantines scale) to 5 (moderately exposed 4 on Ballantines scale).

The distribution of the two species also varies along the estuarine gradient. *L. obtusata* extends further along the Severn Estuary than *L. mariae* (Williams, 1987; 1990). However, small forms of *L. mariae* have been recorded in brackish water lagoons in Denmark (Nielsen, 1980), showing the species to be tolerant of less saline conditions. This difference in distribution along the Severn Estuary is not a reflection of the distribution of the algal food species as *F. serratus* is found much further up the estuary than is *L. mariae*. Colour morphs also change along estuaries (Gratton, 1969 for *L. mariae*) but whether this is to do with the salinity gradient, exposure gradient or some other factor is unclear.

Vertical Distribution

On sheltered shores, there is a clear separation of the zones occupied by the two species. Large, green *L. obtusata* are found all over the shore, but principally at mid shore on *Ascophyllum nodosum* (the egg wrack). Small, and usually yellow, *L. mariae* are almost exclusively found at low shore on *Fucus serratus* (the serrated wrack) (see Fig. 3) (Williams, 1987; Watson and Norton, 1987). This zonation pattern is less clear on more exposed shores, where algal distribution patterns are more ragged. On these shores, the zones of the two species overlap (see Fig. 3), as do their colour morphs and size ranges and both can be found living on *F. serratus* or *F. vesiculosus* (even the bladderless forms) (Reimchen, 1974; Williams, 1987; Little and Williams, 1989). The greater similarity in shell form and behaviour shown by the two species on moderately exposed shores suggests that, here, they are experiencing the same selection pressures. The much wider range of habitats available to the winkles on sheltered shores result in clear niche partitioning of the two species.

POPULATION DYNAMICS

The population dynamics of *L. obtusata* are well understood and have been investigated at a number of different locations by various workers (Goodwin, 1978; Hollingworth,
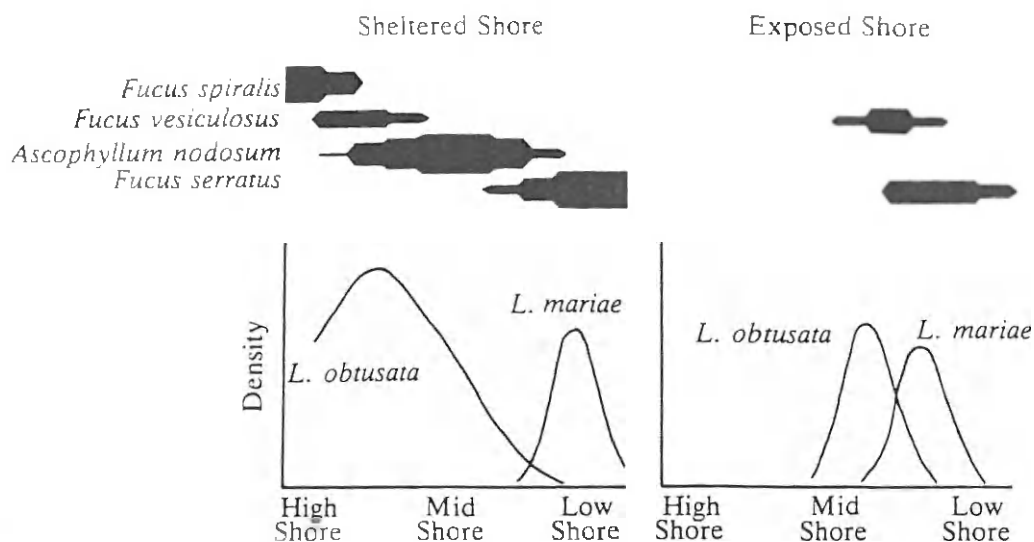
FIG. 3.

Vertical zonation of *L. obtusata, L. mariae* and associated macroalgae (after Reimchen, 1974; Goodwin, 1975; Watson, 1983 and Williams, 1987). This figure is based on data from these sources and is intended to show the general trend between vertical zonation and exposure on "typical" shores.

1981; Williams, 1987). Those of *L. mariae* have only been investigated at one very sheltered site at Sawdern Point in Angle Bay, West Wales (Williams, 1987). Data for the two species, displayed as size frequency curves, are summarised in Fig. 4. It can be seen that they are very different.

L. obtusata may live for 3–4 years. Throughout the year, the population has a stable adult component composed of sexually mature individuals (all greater than 1 year old and usually above 14 mm). Following copulation, females lay egg capsules, usually on the alga, which contain a number of eggs in a jelly-like covering. These are laid in spring with a peak of laying in May–June. Hatchlings subsequently emerge, producing a peak of very small winkles (July in Fig. 4). At the same time, individuals from the previous year's hatching (at 10–12 mm) are approaching adult size and join the adult population in the following weeks. Briefly, the population is made up of three components; adults, immatures and juveniles. The juveniles grow throughout the year (growth rates are decreased in winter) and reach sexual maturity by July of their second year. When the winkles reach sexual maturity they thicken their shells and this is a diagnostic character of adulthood (Reimchen, 1974). Throughout the year, the adult population fluctuates very little. In the early summer, there is the influx of immatures recruiting from the previous year's offspring and in the winter there is some mortality. Recruitment in *L. obtusata* can be termed "trickle recruitment" as it maintains a stable adult population, balancing mortality effects.

The population dynamics of *L. mariae* are very different. As can be seen in Fig. 4, very few individuals are found at the end of the winter and most of those are adults. The peak of egg mass production is in April–May (Goodwin, 1975, for West Wales populations). The eggs start hatching shortly afterwards, and there is a huge influx of juvenile winkles, which grow rapidly. The juveniles suffer heavy mortality and most do not reach maturity, as there is an exponential decrease in their numbers during the summer and autumn. The survivors reach sexual maturity (at 8–10 mm) by the end of the year. These adults reproduce in the following spring and do not appear to live past the summer of their second year. It should be emphasised that this pattern has, as yet, been described on only one shore (Williams, 1987 and R.G. Crump, *personal communication*), and the situation may be different elsewhere. Further studies would be rewarding.
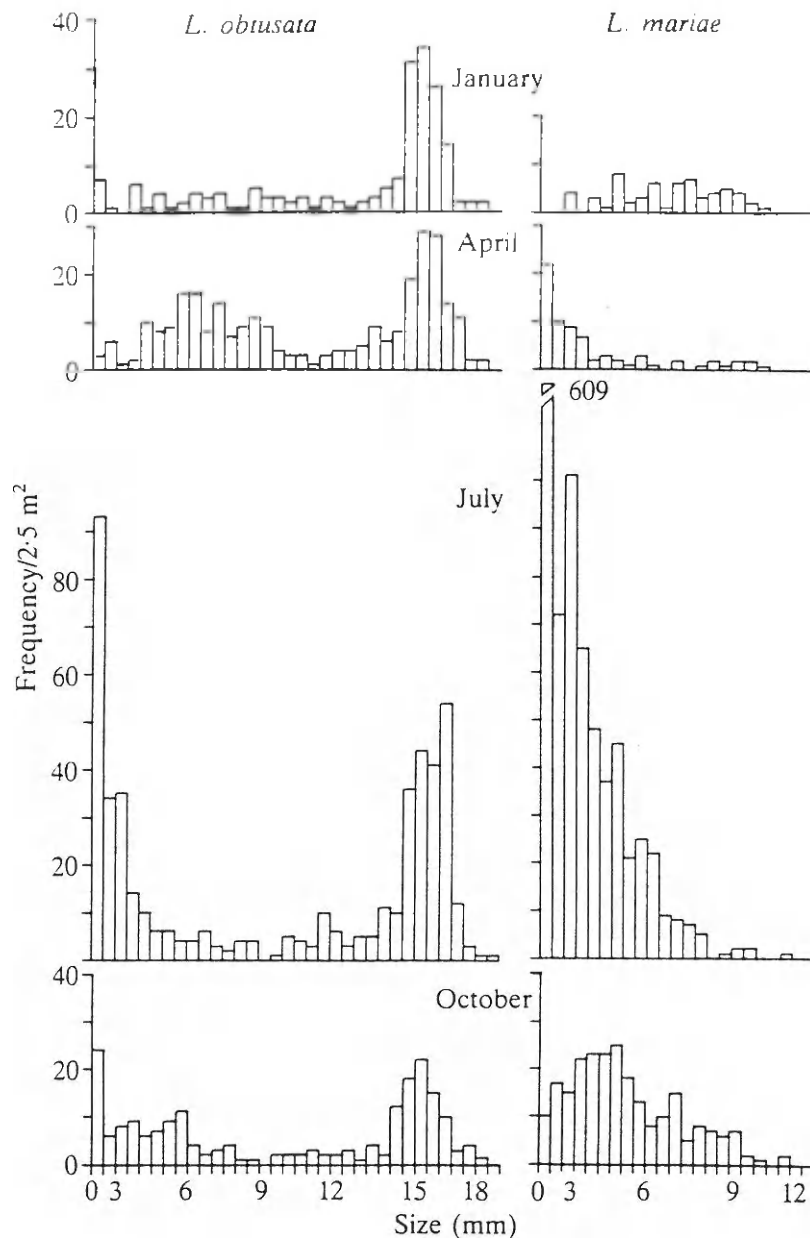
FIG. 4.
Seasonal variation in population size frequencies of *L. obtusata* and *L. mariae* (after Williams, 1987 and 1990).

At least in Angle Bay, the life histories of the two species are very different. *L. obtusata* is a comparatively long-lived animal. Few juveniles reach adulthood, when compared to the number that hatch, but they are sufficient to maintain a stable adult population. That stability is enhanced by the life style of *Ascophyllum nodosum*, a perennial alga that lives for decades if not centuries (Baardseth, 1971; Cousens, 1981). As a food source and habitat it is very reliable for *L. obtusata*. At no time of the year did the cover of *A. nodosum* fall below 80% (Williams, *in preparation*).

L. mariae exhibits an annual life history, individuals hatching in the early spring and growing to maturity within the year. Very few reach maturity as there is a high juvenile mortality. The population dynamics of *L. mariae* are linked to those of its food plant. Most *Fucus* plants live for about three years, and exhibit seasonal variation in cover, losing frond tissue in the autumn and winter due to storm damage and frond shedding of post-reproductive tissue. As a result the cover of *F. serratus* varies from over 95% in the summer

to as low as 40% in the winter. This decrease in the algae cover is mirrored by the decrease in *L. mariae* numbers in the autumn.

The life history of a chink shell, *Lacuna pallidula* is very similar to that of *L. mariae*. It also lives it's entire life span on *F. serratus* (Grahame, 1985). It appears that the life history of these two species are particularly well suited to *F. serratus* as they both accommodate the seasonal nature of the algal resource.

FACTORS CONTROLLING ACTIVITY AND DISTRIBUTION

Behaviour

Field and laboratory experiments have investigated the behaviour of the two species. *L. obtusata* is negatively phototactic (moves away from light) and negatively geotactic (moves away from the pull of gravity) in the laboratory (Guiterman, 1970) whereas *L. mariae* has been shown to be less inhibited by light. This explains the different behaviours of the winkles on the shore. When *L. obtusata* is uncovered by the tide, it crawls into the algal mass and remains dormant—unless conditions are very damp. *L. mariae*, however, remains active and crawls around feeding during its brief period of emersion (except on the brightest of days). In laboratory experiments, *L. obtusata* was found to be far more tolerant of temperature and desiccation extremes than *L. mariae* (Sacchi, 1972 *a* and *b*). This probably reflects the different shore levels that the two species inhabit. The low shore *L. mariae* has a much narrower range of physical extremes to combat than the mid shore *L. obtusata*. *L.mariae* is only uncovered for between 2 and 4 hours of the 24 hour cycle. Even on the hottest days this does not represent too much physical discomfort to the species. For *L. obtusata*, conditions are far more variable, as the mid shore is uncovered for 12 of the 24 hours. This winkle thus spends half its life under terrestrial conditions (hot sunshine and dry conditions in summer; cold (often freezing) and wet in the winter) and half under the buffering influence of the sea (cool in summer, relatively warm in the winter). From the brief experiments on the physical tolerances and the behavioural adaptations of the two species it appears that *L. obtusata* is far better able to cope with these extremes than *L. mariae*.

Movement of both species is random at their own shore levels (Williams, in preparation). When either is transplanted to the shore level of the other (i.e. *L. obtusata* to low shore and *L. mariae* to mid shore) both show a homing response, moving towards their home zone. Individuals returning to their own shore level move faster that those at their normal level. This is interpreted as a behavioural mechanism to maintain the species at their correct tidal level, enabling animals that are washed out of their normal zone to regain it. The mechanism for this homing is thought to be a combination of taxes (behaviourally induced movements) to environmental cues, such as gravity, light, temperature and the presence of the winkles' preferred food plant (see Underwood, 1979 for review). Both species (and most other intertidal snails Ed.) exhibit negative geotaxis when dislodged (they move upshore, away from gravity) which may be overridden by the attraction of their food plant (Underwood, 1972). Therefore *L. obtusata*, transplanted downshore, will move up until it finds *Ascophyllum nodosum*. The movement of *L. mariae* downshore, is suggested to be the result of physical intolerances driving the winkle to reach its home zone (Williams, *in preparation*).

Limiting factors

It is often easier to ask what limits the distribution of a species than attempt to establish the conditions it prefers. On sheltered shores, zonation patterns of *L. obtusata* and *L.*

mariae are clearly partitioned, and are behaviourally maintained. But what inhibits *L. obtusata* from living lower on the shore and *L. mariae* higher? Individuals of both species were kept in cages, at the tidal height preferred by the other, during the summer and autumn months (Williams, 1987 and *in preparation*). *L. mariae* did not grow as well at mid shore, as it did at low shore, and the mortality rate was much higher at this level. This was in direct contrast to *L. obtusata*, which grew faster at low shore as compared to mid shore. A number of inferences can be made. Firstly *L. mariae* is only successful at low shore. This may be due to a change in alga, as *A. nodosum* (a very tough and inedible alga) supports very few epiphytes, or it may be due to the relatively more extreme physical environment. In formal terms, low shore appears to be both the realized and potential niche of *L. mariae*.

Low shore is, however, clearly within the potential niche of *L. obtusata*. This animal actually grows faster at low shore. This is probably due to the increased time spent underwater and therefore greater time spent feeding. The winkle gouges huge holes from the fronds of *F. serratus* and greatly affects the alga. Cages which contained *L. obtusata* suffered very high losses of algal material as compared to cages with just *L. mariae*, further confirming the different feeding methods of the two species. If they were competing for this resource (*F. serratus*), *L. obtusata* would deplete it rapidly, presumably reducing the success of *L. mariae*. Whether this would lead to competitive exclusion, or whether *L. obtusata* would be limited by density dependent factors is an area for further research. The interesting question is; "As *L. obtusata* does so well at low shore, why doesn't it always live there?"

The cages used in these experiments effectively removed other species from influencing the growth and performance of the winkles. In the wild, those other species compete with or prey upon the winkles and it is the interaction of flatwinkles with their biological counterparts to which we now turn.

Predation & parasitism

Winkles fall prey to many species of predator (see Pettitt, 1975, for detailed review). Both species of flat winkle may become prey items for birds, fish (especially blennies), crustacea (especially the common shore crab) and dog-whelks. They are also intermediate hosts to a number of digenean parasites which infect birds or fish as their definitive hosts.

The effect of parasitism on the flat winkles is of great importance (Williams and Brailsford, 1990). Parasitised individuals are unable to breed due to a stunting of the gonads. In some areas of Britain up to 10% of the population is affected, and in some Russian populations of *L. obtusata* up to 50% (Sergievsky, 1985; A. Granovitsch, *personal communication*). *L. obtusata*, because of its longer life span, is exposed for longer to these infections and so carries a greater parasite load than the annual *L. mariae*.

The effects of predators are many and varied. Visual predation by blennies has been proposed as selecting for the different colour morphs exhibited by *L. mariae* (Reimchen, 1979). The yellow morph appears cryptic (hidden) on a frond of *F. serratus* when viewed against the light from underneath (the attacking position of the blenny). The reticulated morph is cryptic when on the top of the frond and seen from above (the position normally seen by a bird). The relative activity of these predators will determine the selective advantage of the different colour morphs to the populations of the two species.

The effect of predation by crabs is perhaps the most significant interaction between the flat winkles and predators. Numerous authors have suggested that crab predation accounts for the variation in gastropod shell thickening (e.g., Crothers, 1985; Kitching *et al.*, 1966; Vermeij, 1972) and may affect the size ranges of species on shores of varying exposures

(exposed shores will experience a lower predation pressure than sheltered shores as crab. prefer the latter).

Many workers have investigated the effect of crab predation on winkles in the laboratory. It has been shown that juvenile *L. obtusata* are more susceptible to predation than adult *L. obtusata*, or adult *L. mariae* (Reimchen, 1982). This may have a profound effect on the ecologies of the two species. *L. mariae*, living at low shore, will be susceptible to greater predation pressure than *L. obtusata* at mid shore. This is due to the large numbers of marine predators which have longer foraging times at low shore as compared to mid shore, because of the tidal cycle. Consequently *L. mariae* needs to be better protected than *L. obtusata*. In a series of tethering experiments, carried out in the summer, adult *L. mariae*, together with adult and juvenile *L. obtusata* were tethered to clumps of algae at low shore. After 74 days, all replicates had suffered heavy mortality, suggesting that even the adults of both species were vulnerable to crab attack at low shore (Williams, *in preparation*). This predation pressure was quite intense and would seriously affect the population dynamics of both species. In the case of *L. obtusata* both adults and juveniles were taken. This suggests that *L. obtusata* would be unable to maintain a viable population at low shore as the species requires a year in which to reach maturity. It would also explain why the species is not found in great numbers at this level on sheltered shores. *L. obtusata* has a spatial escape from this pressure. Living at mid shore it reduces contact with the largest crabs, which can attack adults, and only the juveniles are significantly vulnerable at this level. Pressure is not severe, and sufficient juveniles reach maturity to maintain adult populations.

This does not explain how *L. mariae* lives at low water under such intense predation pressure. The life history of *L. mariae*, however, does provide an explanation as the species escapes in time as opposed to space. The main predator, the common shore crab *Carcinus maenas*, has three components to its population (Crothers, 1967, 1968 and 1970). The first is made up of small crabs that remain onshore (these are the main predators at mid shore), the second are larger crabs that migrate with the tide; foraging when the shore is under water (these are the main predators of the winkles at low shore) and the third are the crabs that permanently remain offshore (most of the largest individuals). During the winter months crabs in the first two components of the population migrate offshore and become relatively inactive, reducing their foraging and providing *L. mariae* with a temporal escape from predation. The life history of *L. mariae* is such that this period of reduced predation pressure coincides with the breeding period of the winkle when the maximum number of adults are present. Prior to this seasonal escape *L. mariae* reduces the effect of crab predation by being too small for the large crabs to handle and too thick for the small crabs to crack. The life history and morphology of the winkle allow it to inhabit the low shore despite the high predation pressure.

As predation has such a large impact on the two winkle species, limiting the distribution of *L. obtusata* and affecting the life history of *L. mariae*, it is appropriate to ask whether this is the factor which may have driven the evolution of the two species.

EVOLUTION

The evolution of body size and life histories are closely linked. Large species tend to live for a number of years, reproducing a number of times, whereas smaller species usually have a shorter life span and reproduce only once (Calder, 1984). Flatwinkles seem to fit this basic pattern; *L. obtusata*, the larger of the two, lives for 3–4 years and breeds more than once, whereas *L. mariae* is much smaller (on sheltered shores) and lives for one year and breeds once.

L. *obtusata* 1871   L. *obtusata* 1982   L. *obtusata* (GB)

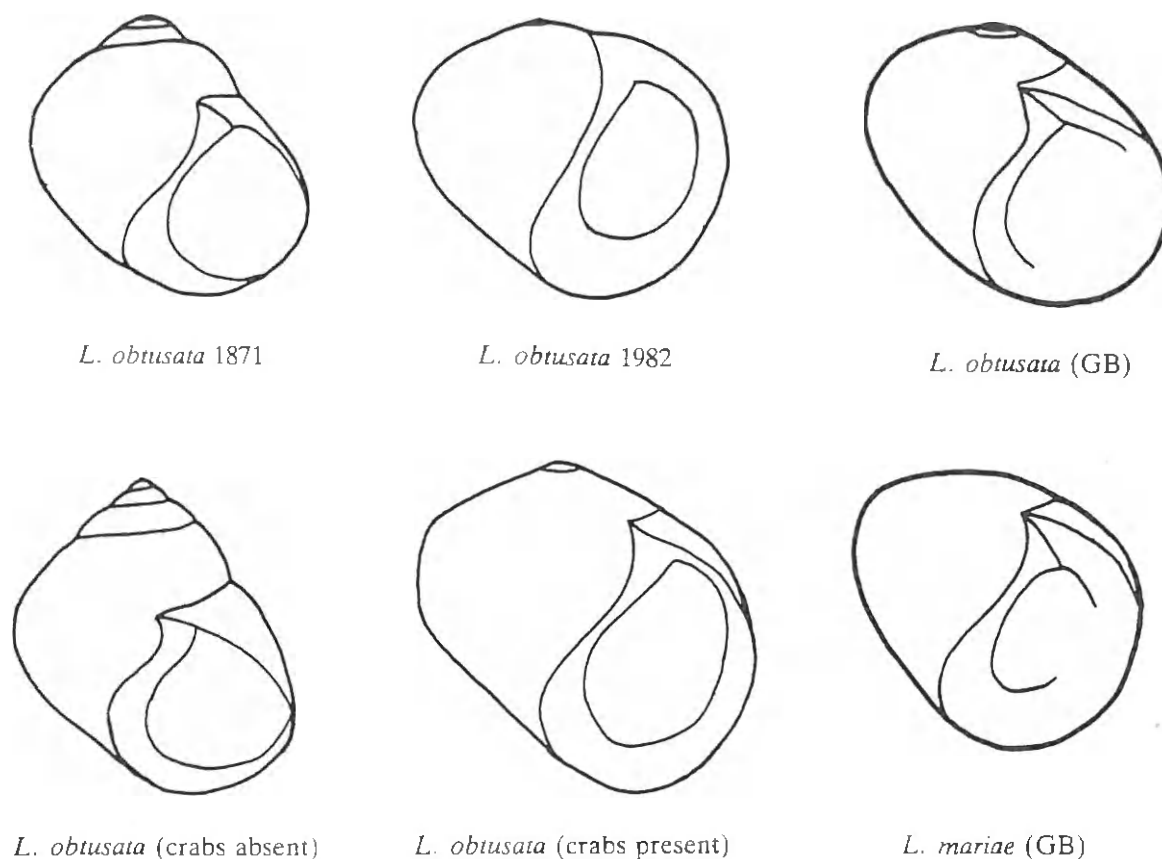L. *obtusata* (crabs absent)   L. *obtusata* (crabs present)   L. *mariae* (GB)

FIG. 5.

Shells of flat winkles from the U.S.A. and Great Britain. The top left pair represent *L. obtusata* from Maine U.S.A. in 1871 and 1982, showing the change in morphology during this interval. The bottom left pair represent *L. obtusata* from different sites in the U.S.A., one of which has a large *Carcinus maenas* population and the other does not. The right hand pair are *L. obtusata* and *L. mariae* from Great Britain. The left hand pair are drawn from Seeley, 1986 and the right hand pair are taken from Goodwin and Fish, 1977 to avoid bias).

The two species fall on either side of the "r–K" continuum. "r" selected species (selected for their rate of increase) live for a short period of time, reproduce and then die. These are usually annual, opportunist, species. "K" selected species (selected for the carrying capacity of their populations) live for longer and reproduce a number of times. *L. obtusata* is a "K" selected species and *L. mariae* a "r" selected species (see Crump and Emson, 1983 for a similar example in the case of *Asterina* species).

On sheltered shores it is possible that crab predation is the evolutionary selective force that has driven the two species to these extremes. On more exposed shores predation pressure is not as extreme (fewer crabs) and other factors (such as the ability to remain attached) are probably more important in an evolutionary sense. As these factors will be similar for both species (due to their closely overlapping zones) divergence between the two species will not be as great (hence the similar body sizes and colour morphs). Whether this affects the life histories of the two species on these shores has yet to be investigated.

Predation pressure has been suggested as an important selective force on the evolution of life histories (Miller, 1979). It has been suggested that unpredictable predation pressure selects for early maturation and increased reproductive efficiency by favouring the offspring of those individuals which reproduce early in their lives, before predation is effective (Vermeij, 1972). This results in the species following the life style of a typical "r" selected species. *L. obtusata*, at mid shore, escapes the predation of large crabs and only

the thin lipped juveniles are susceptible. This may account for the trickle recruitment of juveniles to the adult population of *L. obtusata*. It seems therefore that the "Ghost of predation past" is more likely to be invoked as causing the divergence of *L. obtusata* and *L. mariae* than competition (Connell, 1980). There is some circumstantial evidence to support this hypothesis. In an elegant piece of work conducted on the eastern coast of the U.S.A., Seeley (1986) investigated the morphologies of *L. obtusata* before, and after, the introduction of *Carcinus maenas* to the States (*C. maenas* has only been present in that part of the U.S.A. for about 100 years—and there is no comparable native species). By comparing museum specimens with winkles now living on the same shores, Seeley showed a striking change in the morphology of *L. obtusata* at sites now inhabited by *C. maenas*. No comparable change was observed on shores where crabs were absent (see Fig. 5). Seeley conducted a number of predation experiments which showed that winkle shells from sites not exposed to crabs were more susceptible to damage than those from sites where *C. maenas* was now common. The interesting point is that *L. mariae* is absent from the U.S.A., and shells of *L. obtusata* from crab-occupied sites very closely resemble the shell form of *L. mariae* on sheltered British shores (Fig. 5). This supports the hypothesis that the two British species diverged as a result of predation pressure. It is possible that the recent arrival of *Carcinus maenas* in the U.S.A., has resulted in the opening of an escape niche that the "*L. mariae*" form fits. In species lacking a planktonic distribution phase in their life cycle (and therefore with very little outbreeding) such selection can be manifest within centuries or even decades (Seeley, 1986).

CONCLUSION

L. obtusata and *L. mariae* are taxonomically similar, but ecologically very different species. Their ecologies on sheltered rocky shores has been investigated but are less well understood on more exposed shores. This is an area worthy of further study.

Flat winkles provide excellent animals to work on for projects or class exercises. They are easy to maintain in the laboratory, and their behaviour is simple to investigate; whether it be their reaction to algae (whole; exudates; fronds; receptacles) or to light and gravity (winkles will crawl upwards until they come into contact with algae) or the effect of predation by different sized crabs. They are abundant on the shore making them well suited to class surveys; population frequency work; size range estimates and colour morph variation (be careful with colour morph experiments—they can be misleading). It is hoped that this paper will stimulate school children, students and staff to look more closely at these two species of winkle which should provide valuable investigations for rocky shore field courses.

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