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ECOLOGY OF THE COMMON SNAIL *HELIX ASPERSA* MÜLLER IN A DISTURBED DUNE ENVIRONMENT

A thesis presented in partial fulfilment
of the requirements for the degree of
Master of Science in Zoology
at Massey University

Ian Robert Millar

1978

Helix aspersa Müller on lupin in study area 3

A B S T R A C T

A study was made of the population ecology of Helix aspersa Muller in coastal dunes at Santoft forest, near Bulls. The environment was being altered by afforestation processes.

The distribution of the animals is affected by the presence of tree lupin, Lupinus arboreus Sims, to which they are strongly attracted. Areas planted with lupin are capable of supporting a much greater density of snails than non-lupin areas, and this is thought to be due to the nutritive value of this species.

Snail population densities appear to increase rapidly after lupin seeding in the dunes and this results in widespread lupin die-back after as little as three years from seeding. After lupin die-back the snail population decreases again. Some suggestions are made as to the origin of H. aspersa in the dune country and on the eventual fate of the populations under the maturing forest.

Using shell characteristics, it was found that most juveniles in expanding populations reach maturity in little more than one year whereas those in high density, declining populations generally take two or three years. Individuals in expanding populations also attain a greater size on maturity than those in high density populations. The main factor affecting population density appears to be adult recruitment, which is considerably higher in expanding than in stable or decreasing populations.

H. aspersa is found to be socially gregarious and this is particularly marked over the winter period when adults and large juveniles aggregate for hibernation. Hibernation begins in May and reaches a peak in July. Many animals are active again in mid-August.

Predation by the song thrush Turdus philomelos was studied in one area. Predation occurs throughout winter and generally increases over late spring/early summer.

Snails affect nitrogen fixation levels in lupins before lupin death occurs and it is considered that this is due primarily to disruption of the phloem tissue of the stems during snail feeding.

It is suggested that this disruption of the translocation tissues is the ultimate cause of plant death. The possible economic significance of H. aspersa in dune forestry through its effects on lupin is discussed, and the need for further investigation indicated.

A C K N O W L E D G E M E N T S

I wish to thank Dr J.P. "Skip" Skipworth for his supervision and practical aid during the course of this study. Mr Ian Hunter, at that time the Forester at N.Z.F.S. Bulls District Office, suggested the topic, and he and Messrs Jock Sutton and Arnold Terpstra of Santoft Forest H.Q. showed a continuing interest in the study and gave much practical assistance.

Mr N. Withers, Dr W. Sutton (D.S.I.R.), Dr D Charlton (D.S.I.R.) and Mr C.W.S. van Kraayenoord (M.W.D.) discussed aspects of the study. Mr A.G. Robertson made equipment available for the acetylene reduction assay. Dr David Fountain gave much practical assistance in operating the gas chromatograph and showed considerable interest in this and other aspects of the study. Mr M. Greenwood (D.S.I.R.) kindly provided the Rhizobium culture used in setting up this experiment.

I would particularly like to thank John Innes who gave much invaluable aid in drawing diagrams and proof-reading much of the final text. Neville Henderson read and criticised part of the initial draft, and Isabelle Verry translated a paper from the French.

My parents gave much encouragement and put up with my erratic working hours during the final year of this study.

Mrs Val Swan typed the script and corrected many of my errors.

Finally, thanks to all of those people who abused, pleaded and threatened me into completing this work, including Alistair.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

SECTION I

INTRODUCTION

CHAPTER 1

SAND DUNE FORESTRY AND THE ROLE OF LUPIN

1.1 Background

One of the largest extents of actively prograding sandy shoreline in New Zealand lies on the west coast of the lower part of the North Island, where it stretches for approximately 190 km., from Paekakariki to Patea. Inland lies an extensive complex of dunes, sand plains and peaty swamps covering an area of about 85,000 hectares (Cowie, 1963). Here, the older dunelands have a well-developed soil profile and are relatively stable, but the youngest dunes, just inland from the coast, are unstable and prone to severe wind erosion. Incautious use of such areas in the past has accelerated erosion, causing sand to encroach on pasture land and coastal settlements.

Coastal dune areas have generally proven suitable for establishment of Pinus species, especially P. radiata D. Don. (Levy and St. John, 1964). Not only does afforestation enable the productive use of dune areas, but by reducing wind speed over the sand and inducing buildup of the soil profile, it also has an important protective role.

The history of sand dune use and reclamation on the Manawatu coast has been briefly reviewed by Hocking (1964), Whitehead (1964) and Ritchie (1968). Ritchie describes the process of forest ecosystem development for a typical coastal dune forest.

1.2 Initial dune stabilization

Before tree-planting can proceed, the sand must be sufficiently stable to allow seedling pines to take root and get established. This is especially important in areas exposed to severe wind-blow. Initial stabilization is achieved by planting the mobile sand with marram grass, Ammophila arenaria (L.) Link, and then seeding with tree lupin Lupinus arboreus Sims. (Whitehead, 1964; Ritchie, 1968; Gadgil, 1971a).

Both of these species are exotic and they were introduced specifically for the task of sand-soil stabilization (White, 1943; Slobodchikoff, 1977). Lupin is generally difficult to establish without some stabilization by the marram having occurred, and the young pine trees require the shelter provided by lupin and dense marram before they will establish (Gadgil, 1971 a).

Lupin is an especially suitable plant in this role as its extremely long tap root system makes it resistant to summer drought conditions, while its nitrogen-fixing capacity makes it independent of the soil for this important nutrient. The dense, spreading growth habit of lupin makes it an effective barrier to wind at the sand surface. Lush (1948) has studied the ecology and growth of L. arboreus on coastal dune in New Zealand, while Davidson and Barbour (1977) have made a similar study of the species in California.

1.3 Nutritional role of lupin

Lupin has always been primarily regarded as a sand stabilizer in New Zealand dune forestry and it is only recently that its possible significance in forest nitrogen nutrition has been studied (Gadgil, 1971 a, b, c.). Coastal sand dunes generally contain only low quantities of available nitrogen (Willis et al., 1959; Willis and Yem, 1961; Hassouna and Wareing, 1964; Willis, 1965; Gadgil, 1971 a), and biological nitrogen inputs are limited. Hassouna and Wareing noted that marram benefited from the nitrogen-fixing activities of soil-dwelling bacteria, notably Azotobacter. In the temporary ponds which form in dune slacks during the winter high water tables, nitrogen accumulation probably occurs due to the action of blue-green algae (J. Skipworth, pers. com.).

Will (1964) gave an estimate of the nitrogen requirement of a first crop P. radiata forest growing on pumice soil, and Gadgil (1971 c) has shown that a large proportion of this requirement (at least 50%) can be provided by L. arboreus after three years' growth from seeding. Gadgil considered that this was the optimal time for tree-planting, as there tended to be a net loss of nitrogen from the total plant biomass in subsequent years. In practice, tree-planting usually occurs four to five years after the seeding of lupin. Individual lupin plants normally live for about four to five years in New Zealand sand dunes

(Lush, 1948; Gadgil, 1971 c).

When the P. radiata is planted, the lupin is usually cut back, crushed, or sprayed to release the young pine seedlings from competition. The lupin soon resumes growth, and even after the first crop has died, lupin seedlings continue to grow under the rapidly growing pines. The trees are pruned and thinned for the first time at about six to seven years, and the lupin continues to flourish for some time after this, although some of it gets trampled during the pruning operations. At about nine to ten years the pine canopy becomes sufficiently dense that much of the undergrowth is inhibited through lack of light. A second, utilization thinning occurs at 11 to 12 years, and once again lupin seedlings appear, giving rise to taller, partly etiolated plants of spindly appearance. The important lupin growth, however, is that occurring prior to or during the first ten years of pine-tree growth. Will (1964) found that after this time, nitrogen requirements of the stand decrease, and the nitrogen demand is met by the release of this nutrient into the soil from pine-needle litter.

1.4 Invertebrate pests of dune-country lupin.

A number of invertebrate species attack lupin in the sand dunes. The most noticeable of these is the larva of the endemic kowhai moth, Uresiphitz polygonalis maorialis, which frequently occurs in heavy infestations during late summer (Lush, 1948; Gadgil, 1971 b). Lush also mentions another, unnamed caterpillar species which sometimes occurs in large numbers, and an unnamed species of longhorn beetle. A species of thrip also appears to be quite common but it does not seem to have any major detrimental effect.

In recent years the New Zealand Forest Service have noticed heavy infestations of the common garden snail, Helix aspersa in Santoft forest and they have linked these with large-scale lupin die-back. The aim of the present study is to investigate the population ecology of snails in the sand dune environment, and to examine the snail-lupin association.

CHAPTER 2

HELIX ASPERSA

2.1 Introduction

The common garden snail, Helix aspersa Müller (Pulmonata; Helicidae) was first named and described from Italy by O.F. Müller in 1774 (Taylor, 1907-14; Basinger, 1931). Descriptions of the animal, its general biology and habits are given by Taylor (1907-14; 1912), Ellis (1926) and Basinger (1931), and its anatomy has been described in detail by Taylor (1894-1900; 1907-14).

A substantial body of literature deals with many aspects of the biology of Helix aspersa and related species. Particularly emphasized are aspects of the physiology and general biology of the animal, while there is a relative paucity of ecological studies. General reviews of literature on Mollusca or Pulmonata containing information relevant to H. aspersa include Wilbur and Yonge (1964, 1966), Hyman (1967), Newell (1967), Florkin and Scheer (1972) and Fretter and Peake (1975).

Literature on H. aspersa with specific bearing on sections of this study will be reviewed in the relevant chapters. The remainder of this chapter is concerned with those aspects of the biology and ecology of H. aspersa which have a general bearing on the study. The aspects covered are the range and habitat of H. aspersa and the factors determining these, and the food, pest-status and natural enemies of the animal.

2.2 Range

Helix aspersa is endemic to southern and western Europe (Taylor, 1907-14). Its range also extends completely around the Meditteranean, but Taylor indicates that this is a more recent occurrence. There is some fossil evidence for the species being endemic to Britain also (Taylor, 1907-14; Ellis, 1951) but this has been disputed by Kerney (1966).

Through the activities of man, H. aspersa has been introduced to many parts of the world, including North and South America,

Australia and New Zealand (Taylor, 1907-14; Thomson, 1922; Ellis 1926; Basinger, 1931; Hanna. 1966; Potts, 1975). Introductions have frequently been intentional, usually because of the esteem in which the species is held as an article of food by migrants from some countries (Taylor, 1907-14; Basinger, 1931; Hanna, 1966; Ratanarat-Brockelman and Jackson, 1974). Accidental introductions with plants have also occurred and this is the probable explanation for the introduction of the animal to New Zealand (Thomson, 1922).

In New Zealand, H. aspersa was first recorded in numbers in the Nelson district in 1861 (Thomson, 1922). Thomson described it as being common in most coastal towns "where it is a significant garden pest", but "much more abundant in the north than at Christchurch or further south". There has been no more recent survey of the distribution of this species in New Zealand.

2.3 Terrestrial life and the restriction of range.

Many of the physical and behavioural adaptation of land gastropods are consequent upon the constraints placed upon soft-bodied animals by a terrestrial environment. Those species not living in the relatively constantly favourable conditions of a tropical rain-forest must be able to survive varying periods of dryness and/or cold. Generally, the partially or wholly shell-less slugs have avoided surface restraints by adopting a burrowing, soil-dwelling habit, whereas snails have the ability to wait out unfavourable periods by remaining inactive.

2.3.1 Water relations and estivation.

In the past it has generally been assumed that the extrusion of mucus onto the body surface of the active snail from glands in the body wall has a role in preventing water loss by evaporation (e.g. Ellis, 1926). However, Machin (1964 a, b; 1965) showed that the rate of evaporation of water from H. aspersa mucus was similar to that from a free water surface. He found that direct permeability of the skin to water was too low to prevent harmful desiccation of the skin when the body was extended from the shell. Mucus is therefore extruded to moisten the skin and prevent it from drying and consequently it is the main source of water-loss from the snail.

Helix aspersa, like many related species, is predominantly nocturnal in activity (Bailey, 1975) and this is probably partly due to the need to escape the drier conditions of daylight hours. During periods of prolonged dry weather, even most nocturnal activity ceases and the animals remain in a resting state, termed estivation, until more favourable conditions occur. The body is withdrawn some distance into the shell and the aperture is usually closed off with a fragile, semi-transparent membrane, the estivation epiphragm, formed of dried mucus secreted by the mantle collar. Animals that are estivating on trees, shrubs and walls attach themselves by this membrane.

Estivation allows snails to remain inactive for a considerable length of time. Cases have been cited of individuals of H. aspersa surviving in an inactive state, without food or water, for periods of up to 13 months (Ward, 1897; Machin, 1965).

The relationship of activity and inactivity to the state of hydration of the snail was studied in the closely related Helix pomatia (the Roman or edible snail) by Howes and Wells (1934) and Wells (1944). The weight of H. pomatia was found to undergo continual fluctuation, with day to day changes often of a considerable magnitude. The changes appeared to be present as an irregular rhythm. They were found to be primarily due to changes in water content of the snails, but their amplitude was greater in fed than fasting animals when both groups had water available (Howes and Wells, 1934). Wells (1944) considered that feeding stimulated the body metabolism, producing a more vigorous hydration and dehydration cycle.

There was found to be no correlation between weight fluctuations and environmental conditions as snails kept in the same container did not display co-ordinated fluctuations. Individual animals tended to be inactive or estivating when their weight was low, and to be active when it was high.

If no water was made available, snails would fail to recover from the first dehydration weight loss and they would remain inactive or estivating until more water was available. Once active again, new cycles of weight gain and loss would begin.

An inactive snail does not become active as a result of hydration, but rather is stimulated to activity as a result of which it eats and drinks and becomes hydrated (Wells, 1944). A degree of

control is therefore imposed on the mechanism of weight fluctuations by the selection of stimuli to which the animal will respond by becoming active. Bailey (1975) demonstrated that the nocturnal behaviour of H. aspersa is a response to the decrease in light intensity of the late afternoon/evening period. Mead (1961) had earlier suggested that this was the case also for the giant African snail, Achatina fulica, and Lewis (1969) reached the conclusion that light is the most important environmental factor controlling field activity in the slug Arion ater.

Other stimuli can also be significant. When a period of summer drought is ended by rainfall, the animals rapidly become active, even during the day. In this case, the falling of the raindrops, and probably some physical contact with the water as it finds its way into the shell, stimulates the animals to become active. Similarly, handling an estivating snail will eventually cause it to become active. Herzberg and Herzberg (1962) have also suggested that H. aspersa is able to detect the presence of moisture in the air while in an induced dormant state and therefore becoming active, but this process was found to take a number of days.

The rhythm of weight fluctuations is not, however, rigidly controlled by reaction to decreasing light intensity and other stimuli, and at any time in average weather conditions, some animals will be found to remain inactive overnight, and some to be active during the day (e.g. Cameron, 1970). This can be an important factor in the control of snail pests, as control measures usually involve movement of the animal towards a poisoned attractant (Mead, 1961; Basinger, 1931).

When a snail withdraws into its shell, the only part of the body surface left exposed is a part of the mantle known as the mantle collar. The mantle collar secretes the mucus which forms the estivation epiphragm. It has generally been assumed that the epiphragm is necessary to prevent dehydration of the inactive animal (e.g. Ellis, 1926) but Machin (1966) demonstrates that this is not necessarily so. In a series of experiments on H. aspersa (Machin, 1965, 1966) and Otala lactea (Machin, 1972) it was shown that the mantle epithelium has a considerable ability to resist water loss and desiccation. This ability was lost at the onset of epiphragm formation (when mucus is produced), when the inactive snail was artificially stimulated to produce mucus, or when the snail died. Normal inactive live mantle tissue has a permeability to water apparently almost as low as that of

insect cuticle, and this can be maintained for several weeks (Machin, 1972).

Histologically, mantle epithelium is very similar to body wall epithelium (Campion, 1961) and Machin was unable to determine the nature of the permeability barrier. Formation of the estivation epiphragm is a further aid to water conservation as it is also highly impermeable to water.

Species which normally inhabit drier areas tend to have a greater ability for prolonged inactivity. Increased shell and epiphragm thickness and reduced aperture size act to reduce water-loss and these are important factors in the successful colonization of arid environments by terrestrial snails (Machin, 1967). In this way, sealing of the aperture to a tree or bank during estivation is adaptive in that aperture size is effectively decreased. The configuration assumed by the aperture rim of H. aspersa and other species, just prior to the cessation of shell-growth when the snail becomes "adult", allows a closer fit of the rim to a flat surface, thereby enhancing this effect. "This structural modification of the aperture rim involves a substantial downward deflection in the angle of growth ....as the shell approaches completion, since the globose or nearly spherical form of the shell would not normally permit intimate contact with a flat surface." (Machin, 1967). Machin considered that it is structural differences such as these, rather than physiological differences, which make some species better adapted to arid environments than others. He found that these features were more pronounced in Otala lactea and Sphincterochila boissieri than in H. aspersa, and this is consistent with their inhabiting more arid environments. S. boissieri is a successful colonizer of desert habitats (Yom-Tov, 1971).

2.3.2 Hibernation

In cold weather H. aspersa hibernates, usually in crevices in rocks or walls or buried under litter or soil at the base of herbage. A much thicker epiphragm, the hibernating epiphragm, is produced by the mantle collar, and more than one may be produced as the animal retreats further into its shell during its confinement. Each successive epiphragm is generally thinner than the preceding one (Taylor, 1907-14; Lind, 1968). Those individuals hibernating buried in soil, if not

attached to another snail, are usually found with the aperture facing the soil surface, and the epiphragm slightly inset from the aperture rim. They are generally found about 5 cm below the surface, but may go deeper (Taylor, 1907-14).

Whereas estivation is a short-term phenomenon related to the state of hydration of the animal and to current weather conditions hibernation appears to be more akin to a diapause. Hibernation in the closely related Helix pomatia can be induced by exposure to low temperatures in autumn, but not in summer. Also, it has been found that even if snails are not exposed to cold they will still begin normal hibernation some time in autumn. It appears that hibernation is brought about by internally regulated physiological changes which take place in autumn. The factors which trigger this seasonal rhythm are unknown (Lind, 1968).

The hibernating behaviour of H. pomatia has been detailed by Lind (1968), while the physiological changes occurring during the hibernation of this species were briefly reviewed by Hyman (1967).

Small juvenile H. aspersa appear to be more resistant to cold weather than adults and larger juveniles. They enter hibernation later and reappear earlier (Taylor, 1907-14) and may frequently become active during milder weather. They invariably become active rapidly if disturbed.

Some adults will also emerge from hibernation briefly on milder days. This occurs more frequently in populations inhabiting warmer areas (Taylor, 1907-14). All hibernating H. aspersa will eventually become active after prolonged handling and disturbance.

2.3.3 Reproduction

Hermaphroditism is a common characteristic in the Mollusca. In H. aspersa and most other terrestrial gastropods fertilization is reciprocal; i.e., both partners are fertilized simultaneously (Herzberg and Herzberg, 1962). The advantages of this to an animal with limited mobility are obvious. Self -fertilization is said not to occur in Helices (Herzberg and Herzberg, 1962). The behavioural sequence of mating in the closely related Helix pomatia is described in detail by Lind (1976).

Eggs are laid in a cavity in the soil to a depth of 2.5 cm, giving them some protection from climate and predators. Soil conditions must be suitable before oviposition proceeds. Pollard (1975) found that H. pomatia would not lay eggs if the soil was not "thoroughly wet" to the depth of the cavity. Desiccation was a major cause of egg mortality. H. aspersa lays between 10 and 110 eggs in one batch (Taylor, 1907-14; Basinger, 1931; Herzberg and Herzberg, 1962).

H. aspersa and other species have the ability to retard egg development after copulation for a considerable length of time until conditions are suitable for oviposition (Mead, 1961; Herzberg and Herzberg, 1962). Viable eggs have been produced without further copulation after over 10 months of dormancy (Ward, 1879). This would be particularly useful to an animal with limited mobility, as copulation could occur whenever the chance arose, and oviposition withheld until conditions were suitable.

2.3.4 Restrictions on range.

Restrictions on the possible range of H. aspersa are applied by those extremes of climate under which either individuals could not survive, or suitable conditions are not sufficiently prolonged for the processes of population recruitment. Taylor (1907-14) considered that the absence of H. aspersa from the northern part of Scotland was due to the colder, harsher weather there, and he noted that considerably more time was spent in hibernation by this species in northern England than in the warmer southern areas. Pomeroy and Laws (1967) found that H. aspersa could only survive in South Australia in cultivated areas receiving summer watering. Potts (1975) found that one small population of H. aspersa in California became extinct when long drought periods prevented population recruitment during a time of heavy predation.

2.4 Habitat preferences

Although H. aspersa is known to occur in every county in England (Taylor, 1907-14; Ellis, 1951), it has been stated by Boycott (1929) that "the square miles of England from which it is absent are probably a good deal more numerous than those in which it is present". The habitat preferences of this animal are not easily defined, as it is generally found in a variety of quite different situations.

While generally dwelling in more open areas rather than woodlands (Taylor, 1907-14), H. aspersa is also found in some woodlands in England (Boycott, 1929, 1934). Kerney (1966) suggests that the habitation of these and other "natural" habitats is restricted to the coastal areas of Britain.

H. aspersa occurs widely in cultivation areas and wasteland, among the rocks and vegetation of chalky and limestone areas, and in many coastal situations, particularly coastal sand dunes. Within these areas it is often found on cliffs, banks and old walls, usually sheltered from direct sunlight. (Taylor, 1907-14 Ellis, 1926; Boycott, 1929, 1934; Herney, 1966; Potts, 1975). Habitation of, and even restriction to cultivated areas seems to be particularly marked in countries to which H. aspersa has been introduced (Hanna 1966; Kerney, 1966; Pomeroy and Laws, 1967; Potts, 1975). Generally, habitation of cultivated and "natural" areas is more pronounced in coastal districts, and in New Zealand coastal sand dunes and recently stabilized dune areas seem to be the preferred habitat (F. Climo, in lit.).

2.4.1 The significance of calcium

The types of habitat frequented by H. aspersa indicate a preference for at least some degree of aridity. However, the main factor affecting habitat suitability appears to be the presence of calcium in some form (Boycott, 1929, 1934; Crowell, 1973). A large number of land snail species are similarly limited to a greater or lesser extent (Boycott, 1929, 1934; Karlin, 1961; Mead, 1961; Owen, 1965; Pomeroy, 1967; Warborn, 1969, 1970). Many, including H. aspersa, can obtain calcium directly from sources such as limestone outcrops, shell fragments in dune sands, calcarcous soils, and from the shells of dead and sometimes living conspecifics (Mead, 1961; Owen, 1965; Wolda, 1972; Crowell, 1973). The usual source however is the mineral content of foodplants which in turn is regulated by soil mineral content.

Obligate calciphiles are not necessarily restricted to areas with high soil pH or with surface lime in some form. Strongly acid soils in Ceylon, particularly in the tea-growing areas, were found to support large populations of the giant African snail Achatina fulica (Mead, 1961). This was due to the ability of the plants to extract from the soil calcium which was bound up in silicates and combinations of

iron and aluminium, making it immune to leaching. A more detailed study of this phenomenon has been made for various snail/plant associations by Wäreborn (1969, 1970).

In addition to this, H. aspersa has been shown to have some ability to extract calcium directly from acid or neutral soils (Crowell, 1973).

2.5 Food and pest-status.

2.5.1 Food.

There appear to have been few studies made of the foods taken by H. aspersa. Those articles that do name food species are usually concerned with cultivated plants, the consumption of which has been noted by irate gardeners and nurserymen.

Taylor (1907-14) lists a number of foodplants, but the list is virtually restricted to live plant material. Boycott (1929, 1934) suggested that dead plant matter probably formed the major part of the diet for most herbivorous landsnails and more recent research on Cepaea nemoralis supports this (Wolda et al., 1971; Richardson, 1975b; Williamson and Cameron, 1976).

Taylor (1907-14) also mentions that H. aspersa has been observed to eat decaying shore-line seaweed, dead or dying earthworms, and birds eggs, which are said to be perforated by the snail in order "to get at their contents". Considering this animal's requirements for calcium it seems possible that in fact the eggs were attacked simply for the calcium in the shell.

2.5.2 Pest-status

In California, H. aspersa has been found to cause considerable damage to the flowers of some garden plants (Hanna, 1966; Basinger, 1931). Three plants mentioned by Basinger are begonia, dahlia and canna.

While generally well-known as a pest of vegetable gardens and also of flower gardens and nurseries, H. aspersa has undoubtedly achieved its greatest notoriety as a pest of citrus orchards in California and New South Wales (Basinger, 1931, 1940; Lewis and La Follette, 1941, 1942; Hely, 1946). The citrus orchards are in areas

of warm, dry climate and because they usually receive regular irrigation, conditions are excellent for H. aspersa. In the past, enormous populations have become established in citrus groves, causing considerable damage.

Leaves of the citrus trees are eaten, as well as the rind of the fruit. Damage to fruit varies from superficial, shallow penetration of the rind, to holes penetrating as far as the flesh. This damage can allow the entry of decay organisms, particularly in the damper conditions when the snails tend to be active. Even if decay does not occur, the appearance of the fruit is spoiled and this affects its market value (Basinger, 1931). Basinger also refers to claims that snails remove the bark from growing twigs of orange trees. He was unable to personally substantiate these claims but he did observe stripping of bark from dead twigs. Hely (1946) states that living wood and twigs are not damaged but dead branches are, as is the desiccated rind of dried oranges.

In California, the most severe infestations are generally found in coastal areas. At times, damage in citrus orchards has been as severe as that caused by insect pests (Lewis and Lafollette, 1941, 1942). Grapefruit and particularly oranges are the fruits most affected (Hely, 1946).

2.5.3 Control

Control of H. aspersa has usually involved the use of attractant baits mixed with a suitable molluscacide. Bran is the traditional attractant, but dried orange pulp has also proven effective in citrus orchards (Anon., 1940; Lewis and Lafollette, 1941). Calcium arsenate was widely used as a molluscacide in California citrus orchards, but later metaldehyde became the most popular, particularly with commercial production of baits (Basinger, 1931, 1940; Anon., 1940; Lewis and Lafollette, 1941, 1942; Persing, 1944). The action and effectiveness of the various attractants and poisons that have been used in snail control were reviewed by Mead (1961).

More recently, other poisons such as methiocarb have been found to be equally or more effective (Proude, 1970).

In some cases, control of H. aspersa in citrus orchards

has been achieved by allowing ducks to have access to the orchards (Hely, 1946).

2.6 Natural enemies.

Taylor (1907-14) lists amongst the vertebrate predators of H. aspersa rats, moles, hedgehogs, rabbits, ducks, geese, thrushes and blackbirds. Potts (1975) adds to this list several species of mouse including Mus musculus. The reference to predation by rabbits would appear strange considering the herbivorous nature of this animal. It is apparently based on observations of "gnawed and empty shells" about the entrances of rabbit burrows (Taylor, 1907-14). Both Morris (1954) and Potts (1975) mention rabbits as predators of snails, without giving any details or further references. Predation by rabbits could be of interest in the sand dunes as the dunes of the Manawatu coast typically have large rabbit populations.

Predation by the songthrush, Turdus philomelos Turton, is a well-known phenomenon, and this will be discussed in detail in chapter 8.

Morris (1954) considered that blackbirds could not break open snail shells in the same manner as thrushes and that they were therefore limited to preying on smaller juveniles with their thinner, more fragile shells. He observed also that blackbirds would "rob" thrushes of their snails once the shell had been broken.

The other predator of interest in the present study is the hedgehog Erinaceus europaeus. These animals are present in large numbers in Manawatu coastal dune areas where they are thought to be an important predator of snails (Brockie, 1957).

A number of Diptera and Coleoptera are known to prey on H. aspersa and other species. The common European glowworm, Lampyris noctiluca (Coleoptera) was stated by Clausen (1940) to have been introduced to New Zealand specifically to control H. aspersa. However, no reference to such an introduction exists in D.S.I.R. records, and it is likely that the introduction was unsuccessful, if it occurred at all (L. Hansen, in lit.).

A number of predaceous snail species exist which prey on other snails. Two such species, the European Helicella cellaria and the Australian Strangesta capillacea were found to prey on H. aspersa in gardens in Sydney, New South Wales (McLauchlan, 1949).

Boycott and Oldham (1938) discuss an apparently contagious disease of H. aspersa which affected shell deposition. In extreme cases animals apparently died without maturing. More usually, growth was slowed, with the recently deposited portions of the shell being "greyish" and "wrinkled". The degree of contagion of the disease appeared to be low.

A disease found in the giant African snail, Achatina fulica, was successfully transmitted to fifteen of one-hundred and six specimens of H. aspersa (Mead, 1961). This rate of infection was considerably lower than that of the host species (Mead, 1956, 1961). The symptoms displayed by infected H. aspersa were different to those of A. fulica. The nature of the disease organism was unknown.

CHAPTER 3

INTRODUCTION TO STUDY AREAS

3.1 Santoft forest.

Santoft forest is a coastal dune forest stretching about 25 km., north from the Rangitikei river mouth almost to the Turakina river mouth (Fig. 1). The total area of the forest is 5486 ha. but not all of this is yet planted with pines.

Apart from a few small areas of pines planted privately before the land was obtained by the New Zealand Forest Service, the first P. radiata were planted in 1955, four years after marram planting and lupin seeding. These trees are due for clear-felling in 1984.

The forest is divided into two portions by an area of unplanted land used as a bombing range by the nearby N.Z.R.A.F. base at Ohakea. Most of the infestations of H. aspersa noticed by Forest Service staff to date have occurred in the northern part of the forest, and this is where all of the study areas were situated.

3.2 Study areas.

Study sites were chosen in blocks 100, 101 and 129 (Fig. 2). Towards the end of the study, some sampling was also undertaken in blocks 122 and 83.

The main biological differences between the study sites were the age of the pine trees (where present), the condition of the lupin, and the density of the snail population. Of the remaining plant species, all areas were typically dominated by marram. Other species usually present included Leontodon spp., Sonchus spp., Calystegia soldonella, Senecio elegans, Erigeron canadensis, Oenothera biennis, Scirpus nodosus and several species of grasses. All of these species were irregularly distributed, and this distribution was frequently influenced by the uneven nature of the ground.

In all areas there occurred small and large patches of bare sand on which few or no plants were found to be growing. Pine seedlings in these patches were generally stunted in comparison to those in surrounding areas.

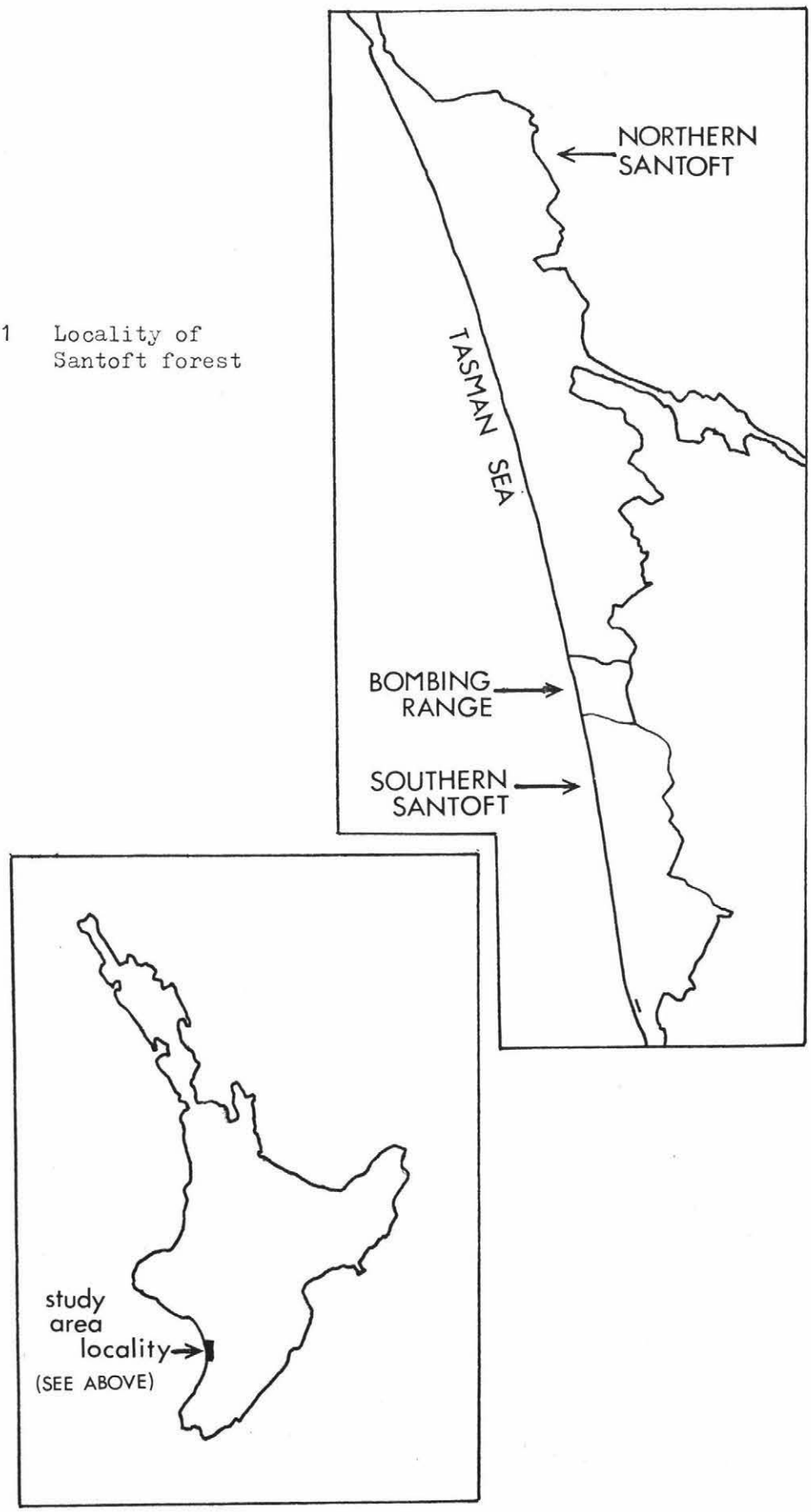


Fig. 1 Locality of Santoft forest

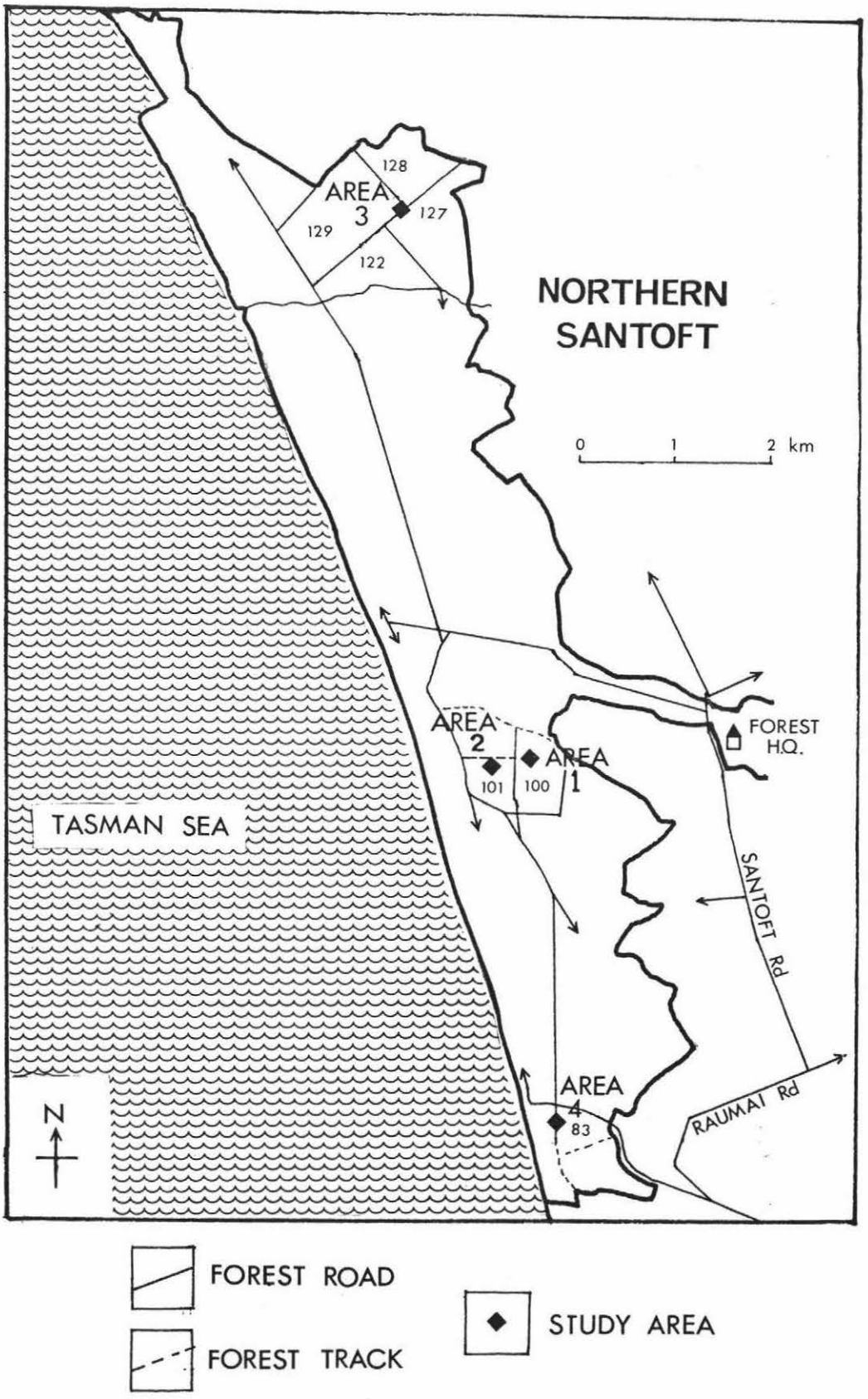


Fig. 2. Northern Santoft, showing study site locations.

3.2.1 Area 1.

Study area 1 was situated in block 100. The snail population in this area was sampled from April 1976 to January 1977.

Block 100 was planted with P. radiata in 1972. The trees are planted in rows, adjacent rows being 3.0 m apart. Consecutive trees in one row are planted 2.4 m apart. The density of young pines in any area is thus 1800/hectare.

In block 100, most of the trees were between 2 and 2.5 m in height. Many had grown to 4 m by the end of sampling.

Some large lupin bushes and groups of lupins were present in the block, but these were frequently widely scattered and large areas of block 100 had no lupins. According to Forest Service staff this area had a particularly dense snail population prior to the time of tree-planting, and there had been widespread lupin dieback.

At the time of the study, snail density in this area was low.

3.2.2 Area 2.

Study area 2 was situated in block 101, on the south side of the access track which ran through the middle of the block (see Fig. 2). Area 2 was about 300 - 400 m from area 1.

Block 101 was planted with pines in 1970. These trees had attained heights of 5 m or more at the time of sampling. Their lower branches were particularly long and densely foliated and in places where pine growth was vigorous, the undergrowth appeared to be showing the effects of the resultant shading. In such places much of the marram was dead and undergrowth generally was more sparse.

In one part of this area was a series of more open patches, with smaller trees. Lupin bushes were still to be found in these places, with considerable numbers of snails in evidence. Most of the lupins actually in the sampling area were dead by the beginning of sampling in April 1976, but others further in from the track were still densely foliated.

The snail population in this area was sampled only from April to June. The thrush predation study also took place here, mainly centred around the lupins.

The trees in block 101 north of the track had been pruned and thinned before sampling began in area 2. The southern portion, including the study area, underwent pruning and thinning operations in December 1976.

3.2.3 Area 3. (Plate 1)

Study area 3 consisted of the southeast corner of block 129 plus the adjacent portions of blocks 127 and 128 (Fig. 2).

Block 129 was planted with pines in 1975. Block 127 was planted in 1977 during the course of the study. Block 128 was unplanted.

This area had a dense snail population. (See frontispiece). There were large stands of live lupins through the area, but most of the lupin was dead. Much of the dead lupin was still standing. One part of area 3 also contained a number of large tree lucernes, Cytisus proliferus, which had grown from seed mixed with the lupin seed.

Area 3 was sampled from April 1977 to February 1978.

3.2.4 Blocks 122 and 83.

Block 122 was largely similar to block 129 to which it was adjacent. However, it contained a large area of densely foliated, apparently healthy lupin. Snail samples were taken from the lupin area.

Block 83 (area 4) contained no pines at the time of sampling. Marram planting and lupin seeding had occurred three or four years prior to sampling. At the time of sampling, the area had a very dense snail population and lupin dieback was occurring.

Plate 1. Area 3.

a. View of part of area 3, showing standing lupin that has died after snail attack.

b. H. aspersa estivating on lupin.

SECTION II

POPULATION DYNAMICS OF *H. ASPERSA*

This section of the study has been divided into four chapters. The first of these is primarily an introduction to the other three. It begins with a brief review of literature and a general statement on the aims of the population dynamics study. This is followed by a description of those methods and results which have a bearing on each of the three following chapters.

The second chapter deals with the dispersion of *H. aspersa* within the environment and the factors affecting this. The third looks at changes in population composition over the study period and attempts to analyse these in terms of biological and environmental variables. The fourth chapter attempts to interpret observed differences between populations in terms of longer term population processes affected by the establishment of lupin in the sand dunes.

CHAPTER 4

GENERAL INTRODUCTION TO POPULATION DYNAMICS STUDY

4.1 Introduction to topic

Population ecology studies of terrestrial snail species are relatively few in number. The most intensively studied species has been the polymorphic landsnail, Cepaea nemoralis. Interest in Cepaea has largely stemmed from the many genetical studies which have been undertaken in relation to the nature of selection on the frequency of its shell colour and banding morphs (e.g. Cain and Sheppard, 1950; Sheppard, 1951). Population ecology studies on C. nemoralis include those by Wolda (1963, 1972), Wolda and Kreulen (1973); Richardson (1975), Williamson (1976) and Williamson et. al. (1977).

It appears that the only quantitative population ecology study to have been undertaken on H. aspersa is that of Potts (1975) who worked on small populations in an abandoned garden in California. As irrigation and other cultural practices had ceased in the study area, the major feature of this environment was six to eight months annual drought, and Potts was particularly interested in the factors affecting population survival under these unfavourable conditions.

Individual marking studies showed that although local populations were only a few metres apart, and snails from the different populations mingled when feeding during the night, migration between populations was minimal due to strong "homing tendencies in the animals.

As a result of the long dry periods growth was intermittent so that juveniles in some populations were up to four years old on attaining adulthood. In one population, seepage water during dry weather allowed snails to reach adulthood in six to eight months, while under favourable laboratory conditions, this process took as little as two months.

In spite of the unfavourable conditions, the animals could survive by estivating during drought periods and Potts could find no evidence that prolonged drought was a direct cause of mortality. The major cause of mortality was predation by small mammals, and one

population became extinct as the unfavourable conditions prevented sufficient population recruitment from occurring during a period of heavy predation.

4.2 Aims of the study.

The major aim of this study was to obtain a picture of the population processes in the ecology of H. aspersa in the dune environment, and the effects on these of human activities. Data were derived primarily from sampling programs which were particularly aimed at demonstrating changes in age-composition within populations, and from comparing and contrasting different populations.

4.3 Sampling program methods

4.3.1 Sampling procedures

4.3.1.1 Areas 1 and 2

Population sampling was undertaken in areas 1 and 2 using a one square metre quadrat. To obtain sampling sites, a one-hundred metre baseline was staked out in the sampling area. A point along this baseline was chosen using a table of random numbers. From this point a distance of between zero and nine metres, also chosen randomly, was measured at right angles to the baseline and the quadrat placed. The quadrat was searched for all snails present and these were measured and recorded as adult or juvenile and then replaced in the quadrat. A further distance of between zero and nine metres was then measured in the same direction and the quadrat placed again. This was repeated another three times, so that five sampling sites were chosen from a single baseline point, after which a new point on the baseline was chosen and the process repeated. One sample consisted of approximately twenty quadrats chosen in this manner.

If the same baseline point was chosen twice, even on different sampling occasions, sampling would begin from the final quadrat site chosen from that point on the previous occasion. This avoided sampling of the same quadrat site twice, as sampling was partly destructive to vegetation.

In area 2, the baseline was placed along the side of the access track. Measurement of sample site distances in this area began five metres into the block from the track. Pine tree foliage in this area was too dense to conveniently place the baseline further into the block.

In area 1 a second method of sampling was adopted from September 1976, until the completion of sampling in that area in January 1977. About thirty metres north of the original baseline, an area of 32 m by 100 m was marked out with stakes (Fig. 3.). This area was subdivided into ten sections of 16 x 20 m. A sample consisted of two quadrats chosen randomly in each section.

The reason for this change in sampling site selection was to attempt to detect any gross snail distribution patterns arising from the distribution of vegetation in the area. Particularly in mind was a fairly large stand of lupin occupying the western side of sections 1 and 6 (see Fig. 3.). If in the course of sampling, no quadrats fell in this lupin patch, an extra quadrat was placed within it. Also, if a quadrat fell in an area of completely bare sand, this fact was noted and an alternative site chosen.

At all times a note was made of the vegetation within each quadrat.

Over the winter most adults and large juveniles hibernated, many of them buried in the soil. During this period the soil in each quadrat was sifted by hand to a depth of about five centimetres. This proved to be a suitable method for locating hibernating animals.

The small size of the younger juveniles and the denseness of the vegetation and litter in many areas meant that quadrat sampling was a very time-consuming process. Individual quadrats frequently took in excess of one hour for locating, measuring and releasing of all snails. For this reason, sampling in area 2 was carried out for only three months. This was considered sufficient to obtain age-structure data for comparison with area 1.

In both sampling areas, all pine trees which fell inside a quadrat were searched for snails to a height of one metre, after which searching was continued until the first layer of branches containing no animals was encountered. Young snails were frequently found estivating

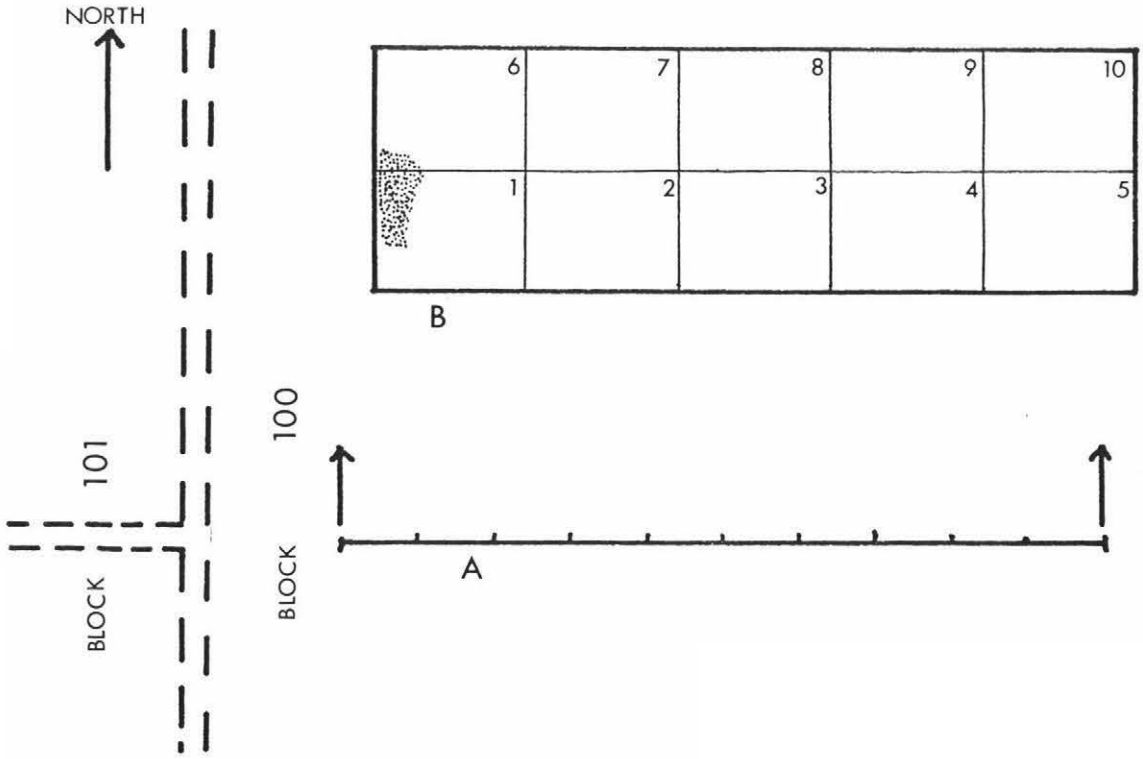


Fig. 3. Study sites in area 1

A 100 m baseline of initial sample area
B Second sample area (100m x 32 m)
Direction of sampling
Vehicle track
Lupin

at the base of needles out towards the end of a branch. The larger size of the pine trees made searching for snails particularly tedious and time-consuming in area 2.

Sampling was begun in areas 1 and 2 in April 1976 and ceased in June, 1976 in area 2, and in January 1977 in area 1. Sampling was carried out monthly, with the exception of November 1976 in area 1.

Work in area 3 began with a preliminary sampling of 20 quadrats in December 1976. Five stations were marked at twenty metre intervals along the side of a track. From each of these a distance of eighty metres was measured at right angles to the track and a quadrat placed at twenty metre intervals.

During 1977, monthly samples were taken from April to October, with the exception of May. Small areas, usually including lupins and all of the plants and litter beneath these, were thoroughly searched and all animals removed. Because of the much greater density of animals in this area, an adequate sample could in this way be removed from just a few square metres. When time permitted, a sample would consist of the results of searching three or four different places in the area rather than a single spot. In this area, the object was simply to gain an indication of population composition.

4.3.2 Shell measurements and characteristics.

4.3.2.1 Adults and juveniles.

The growth of H. aspersa is determinate, i.e. when a particular size is attained by an individual, growth ceases and the animal remains that size for the remainder of its life. In H. aspersa, as in other helicid species, when the final size is attained, the rim of the shell aperture grows outward to form a reflected lip of up to two millimetres in width. At the base of the final or body whorl, this lip extends over and closes off the umbilicus, the entrance to the hollow central axis, or columella, about which the spiral of the shell has developed (Taylor, 1894-1900). For convenience, individuals with this aperture lip and with the umbilicus sealed (imperforate) are regarded by most authors as adults or "mature", and those still growing as juveniles.

This division is, in fact, rather more complex in terms of the animal's sexual maturity. Williamson (1976) gave evidence to suggest that Cepaea nemoralis did not mature sexually until some months after attaining "adult" features, while growing H. aspersa "juveniles" have been found to be quite capable of copulating and producing viable offspring some time before attaining these features (e.g. Herzberg and Herzberg, 1962). In this study "adult" will be used in reference to those snails which have ceased growth and have developed an aperture lip, so that it must be remembered that the breeding population will therefore generally be greater than the "adult" population.

4.3.2.2 Shell size.

The division of snails into approximate age categories must rely on arbitrary divisions of shell size or growth characteristics. Traditionally, the standard measurements made of spiralled univalves are "height" and "breadth" which are defined as follows: "Height" is the distance from the apex of the spire to the base of the body-whorl (the final whorl ending with the shell aperture), and "breadth" is the maximum transverse diameter, one end of which is the most distal portion of the shell aperture (Ellis, 1926).

However, growth of the spiralled univalve shell is mathematically complex (Thompson, 1942; Williamson, 1976) and the rate of change of a single linear shell measurement is not arithmetically proportional to increase in body dry weight. Williamson (1976) found for Cepaea nemoralis that log shell diameter (= shell "breadth" of Ellis) was proportional to log dry weight of body or shell.

A major difficulty is also presented by the considerable variation in size attained at adulthood by individuals in a single population. In order to present more realistic data which would take into account individual size variations, Pomeroy (1969) used whorl number, estimated to the nearest tenth of a whorl, in his study on Helicella virgata. This assumes that all snails with the same number of whorls are at the same developmental "stage" regardless of inter-individual differences in actual size.

In this study, it was decided, for convenience, that a simple linear measurement would be used for collecting field growth data as such a measurement would be the most rapidly obtainable in the field. "Height as defined by Ellis (1926) was considered unacceptable as the

globose nature of the H. aspersa shell means that the spiral is offset considerably to one side and any slight pressure from closing the measuring calipers causes the shell to move around out of position.

Potts (1975) used "breadth" or maximum diameter to measure H. aspersa. As the most distal part of the aperture is one end of this measurement, it is complicated in adults by the development of the aperture lip. Potts measured adult diameters immediately behind the lip. It was felt, however, that when many such measurements are made in rapid succession, it would be very easy to hold the shell in an incorrect position, resulting in an inaccurate measurement. Once again this is largely due to the globose nature of the shell.

The measurement finally adopted was what could be described as the "true height" of the shell when placed on the ground with the aperture down. One part of the calipers is placed across the proximal part of the aperture, including over the umbilicus, and the other against the opposite side of the body whorl (Fig. 4.). Through the remainder of this study, this measurement will be referred to as "shell height".

Vernier calipers were used to obtain measurements to 0.1 mm.

Even this measurement has a drawback to the characteristics of snail growth. As the large juvenile shell nears completion the angle of growth of the aperture rim undergoes a "substantial downward deflection" (Kachin, 1967). This change particularly involves downward growth of the proximal portion of the aperture rim and this is emphasized by lip formation, particularly over the umbilicus. The result of these growth processes is an exaggeration of the height measurements in the adult snail, so that adult measurements are not directly comparable to those of juveniles. Fortunately, this is not important as adults as a group are immediately recognizable by their shell characteristics.

4.3.2.3 Estimating juvenile size at emergence.

In order to divide the range of juvenile sizes into arbitrary size-classes, it was necessary to obtain an estimate of the size-range of newly emerged juveniles.

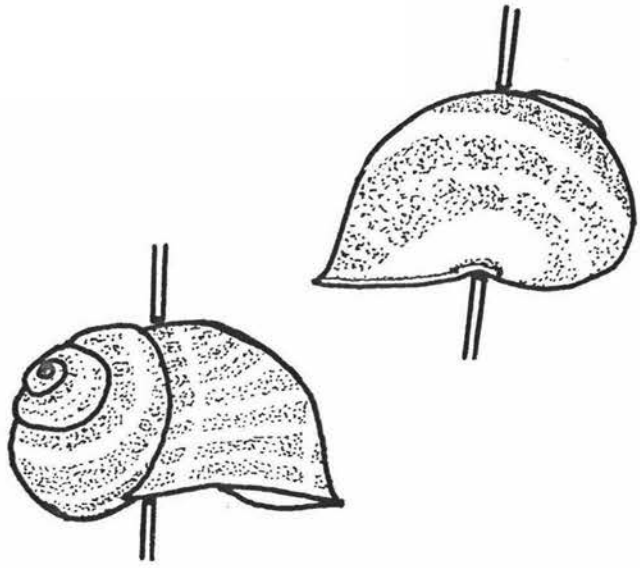


Fig. 4. Method of obtaining shell height measurement with vernier calipers

Pairs of snails found copulating in the field were captured and placed in quart "Agee" preserving jars filled with soil to a depth of approximately seven centimetres. The jars were kept in a constant temperature cabinet at 20°C and with a day length equal to that at the time of capture. The animals were fed with fresh cabbage leaves and filter paper and the soil in the jars was moistened each day.

In this way several pairs were induced to lay eggs. These were produced in roughly spherical egg masses in a cavity excavated in the soil two or three centimetres below the surface. On hatching, the young juveniles remained in the cavity for several days before coming to the surface. When they had emerged from the soil, they were measured with vernier calipers.

4.4 Division of juvenile snails into size groupings.

Division of the sample populations into size-classes posed a number of problems. First, adult snail sizes covered a considerable size range in each population, indicating considerable individual variation in body weight increase from emergence to adulthood. Second, in the two populations studied most intensively (areas 1 and 3) large juveniles in excess of a height of about 1.00 cm were relatively uncommon throughout the study. Splitting up the population into a large number of size-classes would tend to "dilute" any useful information on these animals by dividing them into too many groups. Finally, it was desirable to make the size range of newly emerged juveniles into a single size class.

As mentioned earlier, the height measurement of the adult snail is not directly comparable to that of the pre-adult juvenile because of the slight increases in height brought about by development of adult shell characteristics. In spite of this however, the range of adult sizes can be used to deduce the approximate size-range of those juveniles which are about to become adult.

The range of heights of adults found in area 1 was 1.37 - 1.86 cm. (Fig. 21). These data exclude adults taken in the December and January samples, in which adults were counted but not measured. Mean height was 1.56 cm and 85% of the animals were found to lie in the height range 1.41 - 1.70 cm; a range of 0.30 cm.

Table I gives the height distribution of all juveniles over 1.20 cm captured in area 1. Of thirty-nine animals in this category only one was recorded with a height in excess of 1.50 cm, while thirteen were in the range of 1.41 - 1.50 cm. The assumption is therefore made that the majority of juveniles in area 1 reach a height of not more than 1.50 cm before assuming adult characteristics, and further that a juvenile of approximately 1.50 cm height will become an adult of approximately 1.70 cm height once growth and thickening of the aperture rim and lip have ceased.

Assuming that the height-gain generated by this juvenile - adult transition is equal for all snails regardless of size, then the adult range of 1.41 - 1.70 cm is equated by a pre-adult range of approximately 1.21 - 1.50 cm. In fact it is probable that the height gain in transition will be less for smaller snails but the difference can be assumed to be insignificant.

Heights of the emergent juveniles from the egg batches laid in the laboratory ranged from 0.25 cm to 0.32 cm, with the mean at about 0.28 cm. In the field some juveniles were found with heights below this range, including one of 0.22 cm.

It is assumed, then, that juveniles in an approximate size-range at emergence of 0.25 - 0.32 cm give rise to "pre-adult" juveniles in a range of approximately 1.21 - 1.50 cm. The division of the sample populations into size-classes was therefore based on these ranges which, as approximations only, were not considered to be fixed.

After some trial and error a basis of division was found which did not substantially alter the estimated ranges. The range finally accepted for newly-hatched juveniles was 0.23 - 0.32 cm and that for "pre-adult" juveniles was 1.22 - 1.51 cm. The relationship between these and the intervening size-classes is shown in Fig. 5 where the horizontal line is proportional to the height increment between the lowest heights of each of the two estimated ranges, and the sloping line is proportional to the increment between the greatest heights of the two ranges. The angle between the two lines is θ, and the range of any size class is given by

$$x = \frac{x'}{\cos \theta},$$

where x' is the range of the previous size-class. This can be calculated mathematically after measuring θ, or graphically as in Fig. 5.

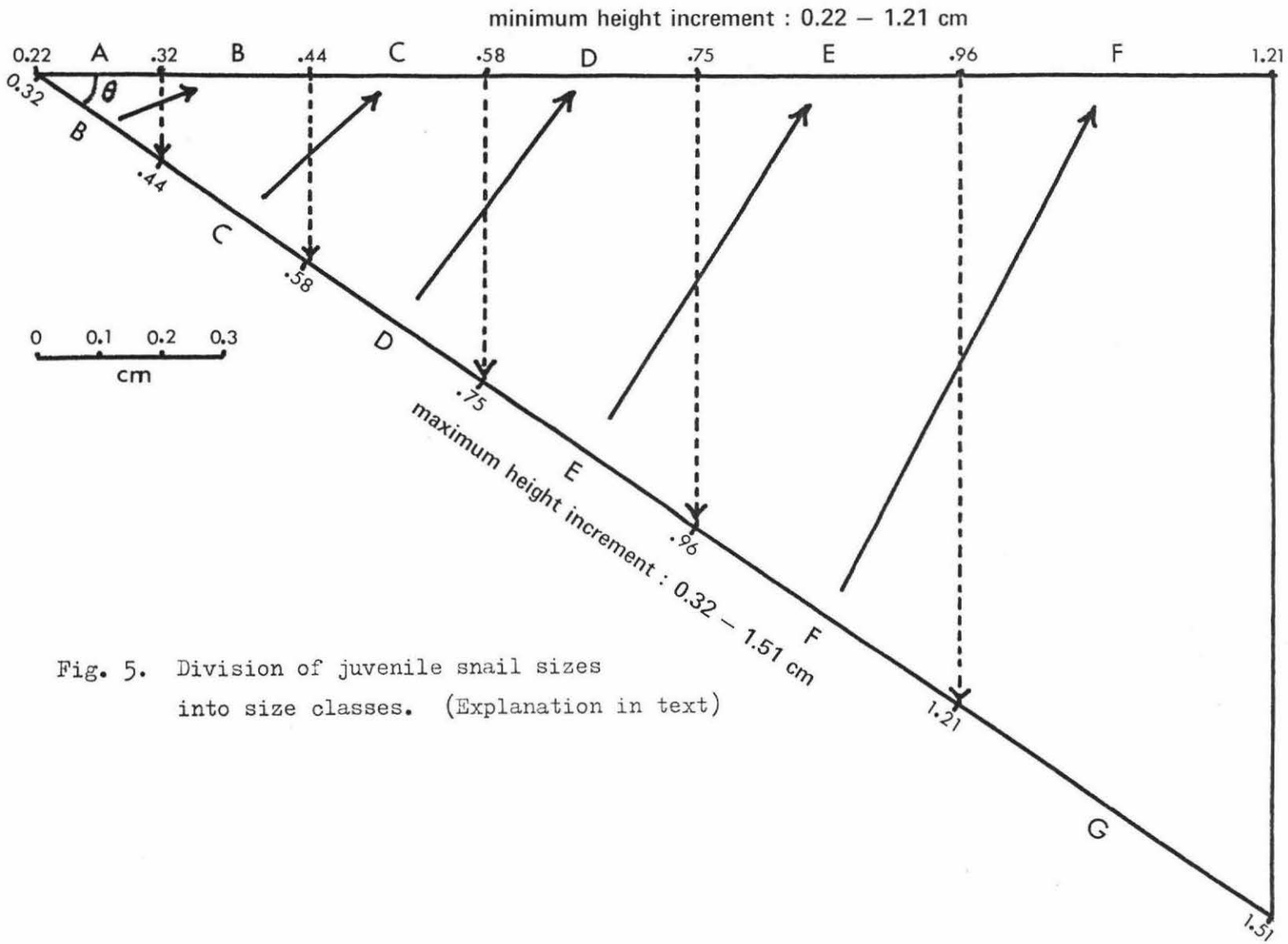


Fig. 5. Division of juvenile snail sizes into size classes. (Explanation in text)

Table I : Shell height distributions of all juveniles exceeding 1.20 cm captured in area 1.

Shell heights (cm)	1.21–1.30	1.31–1.40	1.41–1.50	1.51–1.60	1.61–1.70
Number of juveniles	12	13	13	1	0

The inverse of cos θ is found to be approximately 1.20. The range of each consecutive size class is therefore larger than the preceding one by a factor of 1.20.

The size classes are :

A = 0.23 - 0.32 cm
B = 0.33 - 0.44 cm
C = 0.45 - 0.58 cm
D = 0.59 - 0.75 cm
E = 0.76 - 0.96 cm
F = 0.97 - 1.21 cm
G = 1.22 - 1.51 cm

This series of size-classes essentially satisfied the main requirements of such a division as stated earlier; emergent juvenile sizes are represented in a single category, as are those of the majority of juveniles which have reached a size at which attainment of adulthood is imminent. The increasingly large range of each size-class effectively groups the less-well represented large juvenile data. However, care must be taken in analysing data grouped in this way, as it may cause some of the patterns of population development to be obscured.

Adult snail sizes were found to differ significantly between area 1 and areas 2 and 3 (see Chapter 7) and theoretically this should slightly alter the acceptable size-range for pre-adult juveniles from these areas, and therefore all of the other classes also, to a decreasing extent. However, as the division of these data is essentially arbitrary, it was not considered necessary to make these adjustments. As a result, the population size-divisions for area 1 are not entirely comparable, in terms of animal development, to those for areas 2 and 3, but this should not have any significant effect on the comparison of overall population trends.

CHAPTER 5

DISPERSION

5.1 Introduction

The dispersion, or distribution within the environment of a species may be the net effect of many factors. To begin with, the nature of the environment itself may be a major determinant of an observed distribution pattern. If an area is highly heterogeneous with respect to vegetation, physical aspect, etc., it is likely that this will result in a patchy distribution of any species as individuals seek out the microhabitats best suited to their particular needs. They will generally concentrate in those places with a sufficiency of food and shelter and be found only infrequently in those places lacking these primary requisites. In the case of, for instance, a herbivore which eats a variety of plant species, the distributions and relative palatabilities of the available species may well have a significant effect on the animal's distribution. These environmental effects are largely negated only in homogeneous environments, although even here an invertebrate species may, for instance, be found only on certain parts of a host plant.

In addition to this, various behavioural attributes of a species may predispose it to a particular distribution pattern, even within a relatively homogeneous environment. Dispersion of newly emerged young will depend on whether the adult lays eggs in batches or singly throughout the habitat, and on the availability and distribution of suitable oviposition sites. This dispersion pattern will change as the juveniles become increasingly mobile and move away from the emergence site.

Subsequent dispersion of individuals will depend on the behaviour patterns of the species. A dispersive phase in the life-cycle of the species may result in a random distribution of individuals, where the presence of one individual does not influence the chances of finding another in the same area. Intra-specific competition may result in a regular distribution, subject to territorial behaviour, while mutual attractiveness will tend to produce a contagious or aggregated distribution (Southwood, 1966). Each of these conditions

may well be prone to seasonal variation, so that at any one time, the pattern of dispersion may depend on such factors as the time of year and the age-composition of the population.

Dispersion studies on invertebrates, particularly insects, have shown that most populations exhibit a degree of contagion or aggregation. In such a case, where distinct clumps or aggregations occur, these clumps themselves may be distributed in a regular, random, or contagious manner.

As the present study progressed it soon became obvious that the distribution of H. aspersa tended towards the contagious or aggregated, and an attempt was made to elucidate some of the factors involved. Of particular interest was the attractiveness of lupin to H. aspersa and the nature of any behavioural factors which might lead to aggregation.

5.2 Methods.

5.2.1 The distribution of H. aspersa in the environment.

The quadrat sampling methods used in areas 1 and 2 and for the preliminary sampling in area 3 give information on the overall distribution of H. aspersa in the environment, and its relationship to environmental factors such as the presence of lupin. Information could also be gained on the effects of some behavioural phenomena such as egglaying and hibernation.

5.2.2 Aggregation for estivation.

In addition, sampling was undertaken to test for aggregation on a smaller scale, such as would result entirely from behavioural phenomena. Quadrat sampling results and general observations indicated a strong tendency to aggregate during estivation and this tendency was investigated more closely.

As sampling was, of necessity, performed during daylight hours, on most non-winter days a significant proportion of the population would be estivating or at least relatively immobile. As estivating animals were likely to assume a different dispersion pattern to active ones, it was desirable to sample at a time when virtually all animals would be

estivating. For this reason, sampling was undertaken during prolonged dry periods. An initial sample was taken during a dry spell in area 3 in April 1977 and this was followed up by samples from area 4 in November 1977.

As it was necessary to avoid as much as possible any effects of environmental heterogeneity on the observed dispersion, a small quadrat sampling of ground-cover was ruled out. Instead, use was made of the fact that large numbers of snails frequently estivate along the stems of lupin bushes, with many of the smaller juveniles being found around and on the foliage at the ends of stems. The larger woody stems were chosen as sample sites.

The most effective sample unit size for the measurement of aggregation is one that is relevant to the approximate size of the aggregations or clumps formed. A sample unit smaller than this will tend to give a false picture of the degree and size of aggregations, while too large a unit may include more than one clump of animals and therefore obscure the pattern and probably under-estimate the degree of aggregation.

Observations showed that the animals frequently estivated in small clumps which would be spread along perhaps six or eight centimetres of stem, depending on how distant an individual has to be before its presence can be considered not to be due to the presence of others. Such a clump could include ten or more animals as several can fit around the circumference of a larger stem. Some apparent aggregations were more widely spaced than others. The size of unit chosen for the initial sampling in area 3 was 15 cm (length) of stem. The size of unit eventually chosen for the main sampling in area 4 was 10 cm of stem.

In area 3 the two end bushes of each of two long lupin patches beside the track were selected. On each plant, the branch nearest to the track and the branch most nearly opposite it were chosen for sampling. Only the larger branches were chosen and the thicker, lower portions of each were sampled. The number of snails in each consecutive 15 cm of stem was counted, beginning at the base. The number of sample units taken for each stem depended on the length of that part of the stem not significantly reduced in size by branching.

When such a point was reached, sampling ceased. This resulted in five or six counts being taken for each stem.

In area 4, two bushes over 100 m apart were chosen for their convenient growth form, each having several major stems beginning at or near ground level, and each stem retaining a large diameter for some distance before branching into smaller stems. Each bush was seen to contain a reasonable number of snails. Five woody stems (the thickest) were chosen from each bush. Stems varied in diameter between about 1.5 and 2.5 cm at their bases and 1.2 to 1.6 cm diameter at the highest point sampled. It was considered that this change in diameter over the length of the stem would not affect results in spite of the consequent reduction in stem surface per unit as there was no indication that an aggregation of snails was more widely spread along a thinner stem. Aggregations of different sizes were found to occur at a variety of stem thicknesses.

Sampling was performed as in area 3, but on this occasion the same number of sample units were counted on each stem of one bush. Ten 10 cm counts were taken per stem on bush 1 and 11 per stem on bush 2, which had longer stems.

Several of the stems sampled had one or two smaller stems branching from them along the sampled length, and when an aggregation of snails occurred at or near such a branch point, some of the animals would be found attached to the side branch rather than the main stem. Therefore, if a branch point was reached along the length of a 10 cm sampling unit which contained one or more animals, a distance along the side stem equal to the remaining distance of the unit was measured. Any animals along this length of side branch that were also within 10 cm of any animal in that same unit on the main branch were included in the catch. Any animals on side-branches arising from sample units containing no other animals were discounted. Generally, this situation was not often encountered due to the choice of bushes.

5.2.3 Measurement of dispersion

A number of methods of measuring and describing dispersion exist (see Southwood, 1966 and Patil et al., 1971). Many of these require that rigid sampling conditions and procedures be adhered to in order for them to be applied. The high environmental heterogeneity encountered in the present study precludes the use of many of these

methods.

The measure of dispersion used in this study is one known variously as the "index of dispersion", "coefficient of dispersion" or mean:variance ratio method. This index is based on the fact that in a completely random dispersion (Poisson distribution) the variance (σ^2) and mean (m) are equal whereas the variance is lower than the mean in a regular distribution and greater in an aggregated distribution. Therefore $\frac{\sigma^2}{m}$ will not differ significantly from unity in a population which is essentially randomly distributed, but will be significantly greater than unity for an aggregated distribution.

Clapham (1936) was apparently the first to use this ratio, which he called "relative variance", in an ecological context. He used it to assess dispersion in a large number of plant species. As an unbiased estimate of $\frac{\sigma^2}{m}$ he used :

$$\frac{\Sigma(x - \bar{x})^2}{\bar{x}\,(n - 1)} ,$$

where $\Sigma (x-\bar{x})^2 = s^2 (n - 1)$, and therefore the formula simplifies to $\frac{s^2}{\bar{x}}$. (s^2 = sample variance, $\bar{x}$ = sample mean; n = number of sample units).

Blackman (1942) estimated that the hypothesis of a random distribution could be rejected if $\frac{\Sigma(x - \bar{x})^2}{(n-1)\,\bar{x}}$, which he termed the coefficient of dispersion, differed from unity by more than 2 $\frac{2n}{(n - 1)^2}$ The index is used in this form by Salt and Hollick (1946) in their study on wireworms, by Milne (1963) for chafer larvae, and by Baker (1963) for the landsnail Helicella caperata in sand dunes.

However, $\frac{\Sigma (x - \bar{x})}{\bar{x}}$ $(= \frac{s^2 (n - 1)}{\bar{x}})$ has an approximate χ^2 distribution, with n - 1 degrees of freedom. (Greig-Smith, 1964; Southwood, 1966; Stiteler and Patil, 1971). If the distribution of the species under study is Poisson, the χ^2 value, estimated as

$$\chi^2 = \frac{s^2 (n-1)}{\bar{x}} ,$$

will not lie outside the limits (normally 0.95 and 0.05) of χ^2 for n - 1 degrees of freedom. If χ^2 is within these limits, it will be found that the index of dispersion,

$$I = \frac{\chi^2}{n-1} ,$$

will approximate to unity. (Southwood, 1966).

It must be noted that the term "index of dispersion" has in

cases been used to refer to the actual χ^2 value (e.g. Naylor, 1959), but more usually refers to $\frac{\chi^2}{(n-1)}$. The latter value is used in this study.

5.3 Results.

5.3.1 Environmental heterogeneity.

As an example of the type of variation encountered between quadrats in the course of a sample, results are given in Table II of the preliminary sample (20 quadrats) of area 3 in December 1976. Brief descriptions of the vegetation, and the number of snails in each quadrat, are given. Of the 167 animals comprising the sample, 137 are adults and there are no newly emerged juveniles so that aggregation arising from batch-laying of eggs is not present.

Table II : Sample results from area 3, December 1976

Number of quadrats	Vegetation	Number of snails per quadrat
1	Bare sand with single pine tree seedling.	0
1	Bare sand with several small marram clumps.	0
1	Pingao (Desmochoenus spiralis). Some bare sand.	0
5	Predominantly dense marram, with some other plant species.	0, 1, 2, 3, 14
6	Predominantly marram, but less dense. Other small plant species and some patches of bare sand also present.	0, 0, 0, 2, 4, 8
1	Large marram clump in bare sand.	0
1	Few Oenothera, sparse marram, bare sand.	0
1	Sparse marram, Erigeron, 50% bare sand.	0
1	Several Oenothera, little marram.	23
2	Portions of live lupin bushes; one with considerable marram, the other with little marram and some bare sand.	52, 58
20		167 (137 adults)

Of particular note in this sample is that 110 (66%) of the animals captured were distributed between the two quadrats containing live lupin. Further evidence of the effects of lupin on snail

distribution is given in Table III. The results presented in this table are from the September to January samples from area 1, when one quadrat of each sample was placed in a lupin patch. The table gives the proportion of the total catch found in the single lupin quadrat. Newly emerged juveniles are excluded from the December and January results.

Table III : Snail dispersion in relation to lupin in area 1.

Sample	Number of quadrats	Catch		Lupin quadrat catch		Percentage of catch in lupin quadrat	
		Adult	Total	Adult	Total	Adult	Total
September	20	19	93	10	35	52.6	37.6
October	20	25	83	14	50	56.0	60.2
November*	21	13	32	6	17	46.2	53.1
December*	21	8	12	2	10	25.0	83.3

* Newly emerged juveniles discounted.

Table IV gives the total catch per quadrat for each of the areas 1 and 2 samples, excluding results for quadrats placed in live lupin, in order to remove this large source of variance. Even with this modification, it is still obvious that several samples display considerable degrees of aggregation. In order to attempt to analyse their causes, these dispersion patterns were quantified.

5.3.2 Changes in dispersion with time.

Table V gives the mean, variance, χ^2 and I for the total population for each quadrat sample from areas 1, 2 and 3, excluding the lupin quadrats. The index of dispersion is plotted against time in Fig. 6 for the area 1 population.

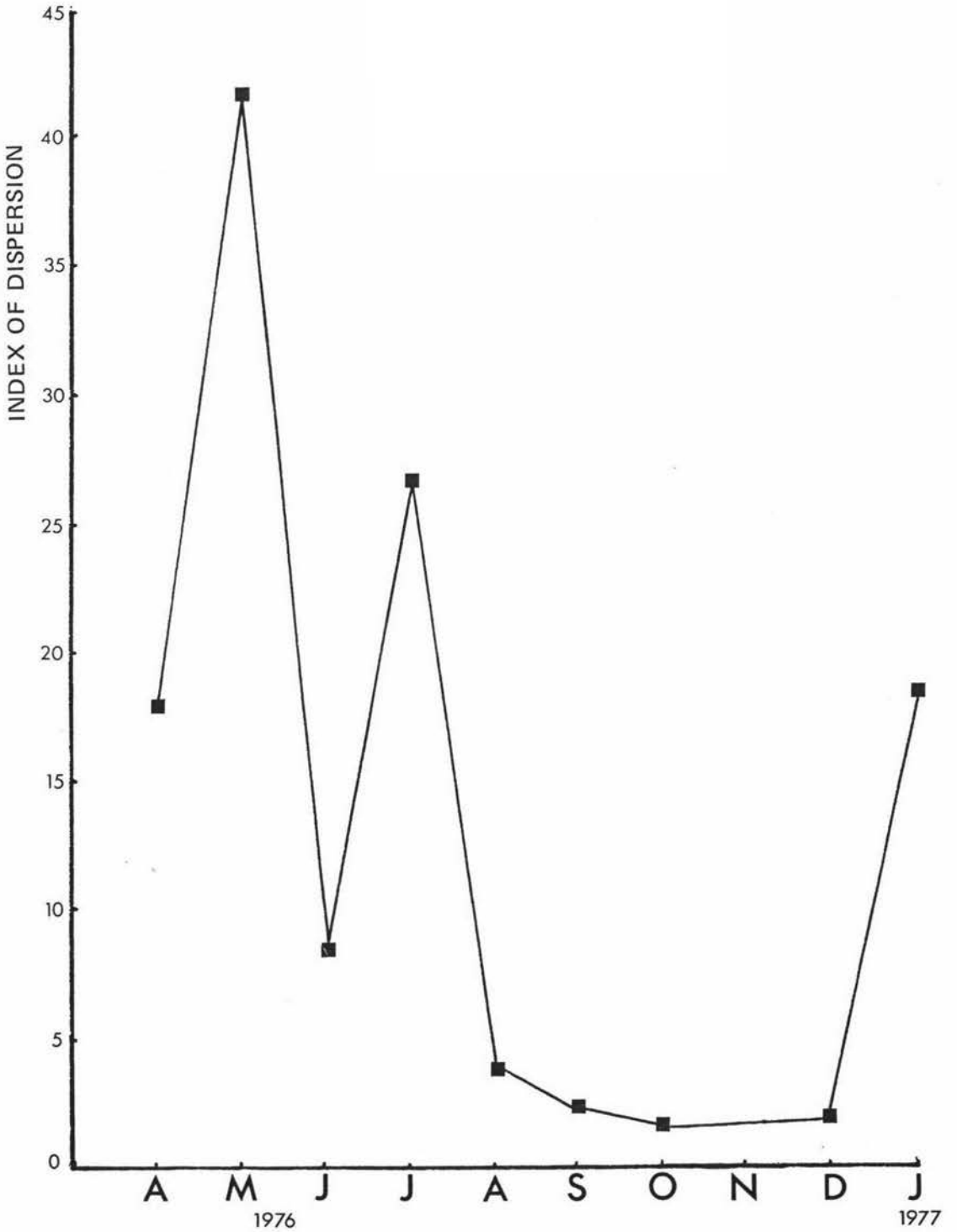


Fig. 6. Dispersion of the total population of area 1 over the study period (Index of dispersion, $I = s^2/\bar{x}$)

Table IV : Sampling results from areas 1 and 2. (lupin quadrats excluded).

Sample	Number of quadrats	Frequency of zero counts	Number of animals in other quadrats
Area 1			
April	21	5	1,1,1,2,2,5,5,6,7,11,12,13,15,20,31,51
May	24	5	1,1,1,1,1,2,3,3,4,4,4,6,8,14,14,18,20,41,96
June	20	5	1,1,1,3,4,4,4,5,7,7,13,15,15,19,25
July	21	9	1,1,1,3,3,3,4,6,9,9,39,47
August	19	7	1,1,1,1,1,2,2,4,4,5,8,9
September	19	3	1,1,1,2,2,2,2,3,3,3,4,5,5,6,9,9
October	19	6	1,1,1,1,2,2,2,3,3,3,4,5,5
December	20	12	1,1,1,1,2,2,3,4
January	20	12	1,1,1,1,1,1,2,25
Area 2			
April	17	4	1,1,1,2,2,2,3,4,5,6,6,10,29
May	23	8	1,2,2,2,2,2,3,4,4,5,7,12,14,25,27
June	21	6	1,1,1,1,2,3,3,4,7,7,11,13,15,17,26

As it can be expected that the dispersion pattern displayed by newly emerged juveniles will differ from that of larger juveniles and adults, it is more instructive to follow changes in pattern of a single cohort rather than the whole population. Identification of the cohort is based on the sampling results from areas 1 and 2 which are presented in Chapter 6, (Figs 10 and 11.). From these results, the cohort of summer, 1975-76 was considered to consist of juveniles in classes A, B, C for April, May and June; A, B, C, D for July; B, C, D, E for August, September and October; and D, E, F, G for December.

Indices of dispersion are given for the 1975-76 cohorts of areas 1 and 2 in Table VI and I is plotted against time for the area 1 results in Fig. 7.

Results are also presented in Table VII for adults only from all quadrat samplings; for adults and large juveniles (classes F and G) combined; and for hibernating adults and large juveniles over the relevant period. Plots of I against time for each of these groups are

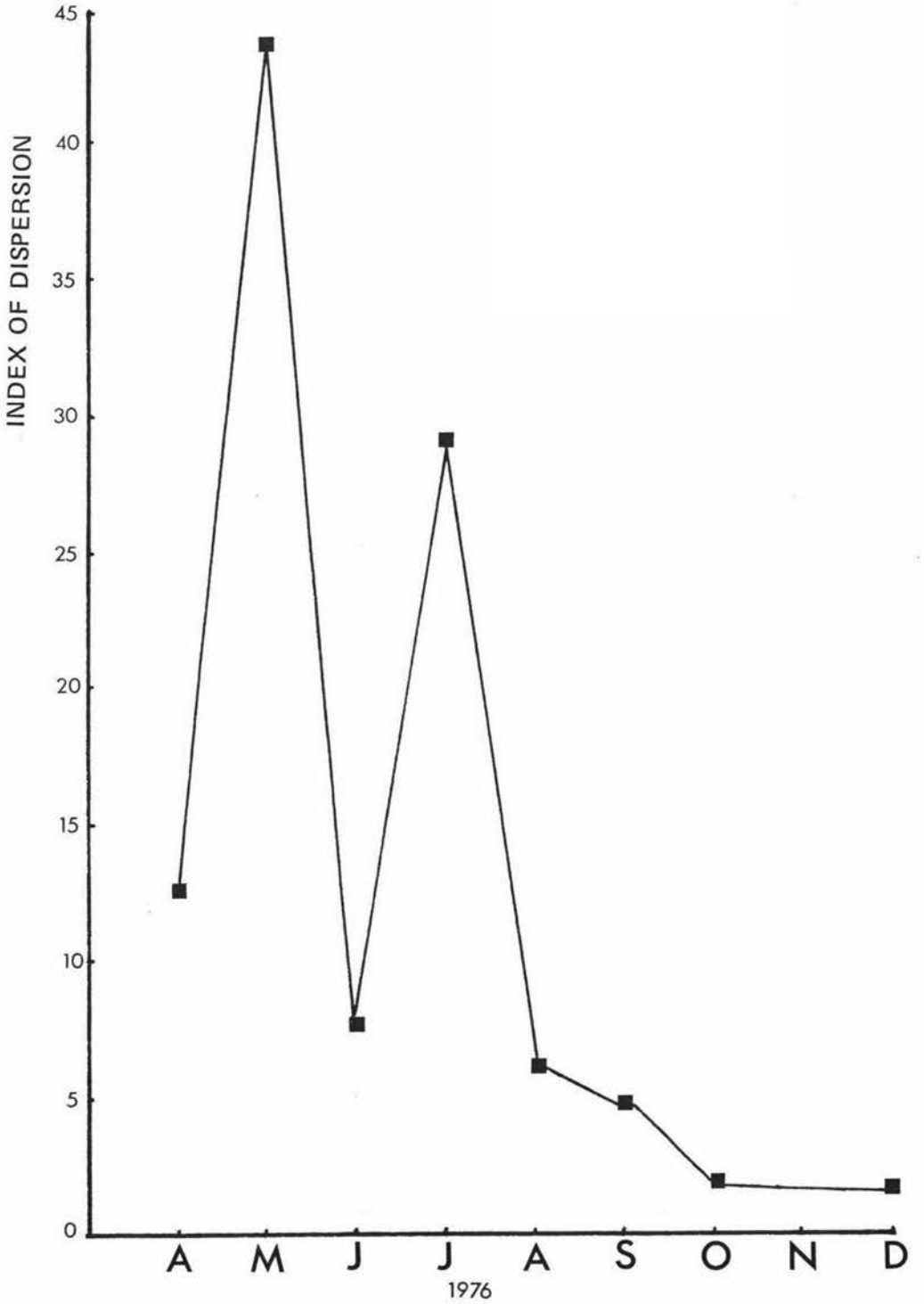


Fig. 7. Dispersion of the 1975-76 juvenile cohort (area 1) over the study period.

presented in Fig. 8 for the area 1 data.

Table V : Indices of dispersion (I) for total population results from areas 1, 2 and 3 (excluding lupin quadrats).

Sample	Mean ($\bar{x}$)	Variance (s^2)	χ^2	Degrees of Freedom	P	I
Area 1						
April	8.71	158.61	364.0	20	< 0.001	18.2
May	10.17	424.57	960.5	23	< 0.001	41.8
June	6.20	53.64	164.4	19	< 0.001	8.7
July	6.00	160.90	536.3	20	< 0.001	26.8
August	2.05	7.50	65.7	18	< 0.001	3.7
September	3.05	7.39	43.6	18	< 0.001	2.4
October	1.74	2.87	29.8	18	< 0.05	1.7
December	0.75	1.36	34.3	19	< 0.05	1.8
January	1.65	30.55	351.8	19	< 0.001	18.5
Area 2						
April	4.23	48.32	182.5	16	< 0.001	11.4
May	4.87	58.39	263.8	22	< 0.001	12.0
June	5.33	51.13	191.8	20	< 0.001	9.6
Area 3						
December	3.17	37.79	202.9	17	0.001	11.9

The distribution pattern differs significantly from random (Poisson) when $P < 0.05$, and the population is therefore clumped or aggregated.

5.3.3 Dispersion of estivating snails on lupin stems.

Table VIII gives the size-composition of the sample populations involved for each of the bushes sampled in area 4 and for the combined area 3 samples. No attempt was made with these samples to separate the different size-classes for the presentation of data, even though animals of different ages may aggregate to different extents. It was felt that arbitrary divisions of these data based on animal size were unlikely to be satisfactory as inter-individual attractiveness

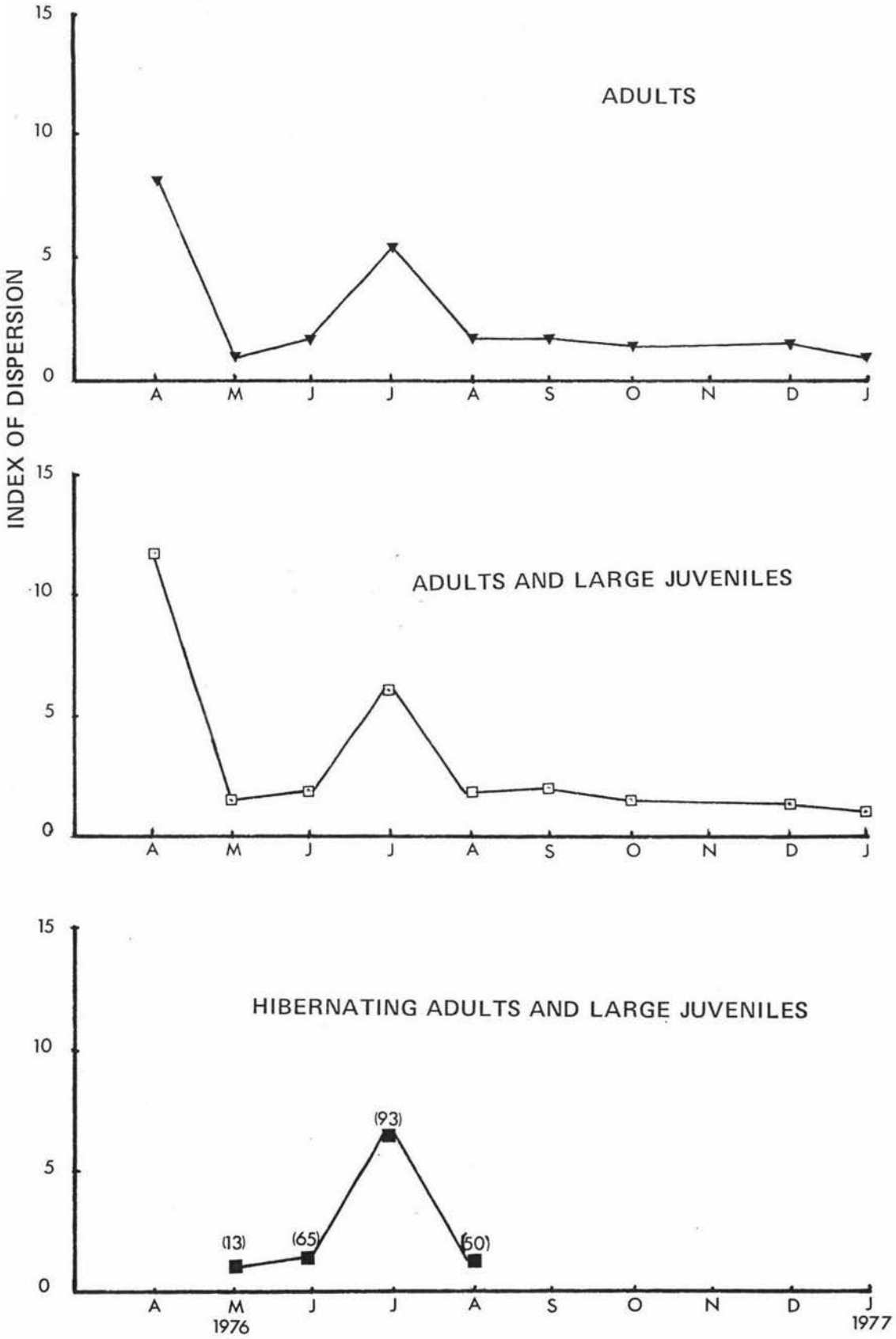


Fig. 8. Dispersion of area 1 adults; adults and large juveniles; and hibernating adults and large juveniles.

Number in brackets is the percentage of adults and large juveniles found hibernating.

involving animals differing greatly in size is probably complex. For instance, whereas the presence of a small juvenile estivating in a particular place may not affect the "decision" of an adult to settle for estivation there also, it is possible that in a reverse situation an estivating adult may exert some attraction to the small juvenile.

Table VI : Indices of dispersion (I) for the 1975-76 cohort, areas 1 and 2 (lupin quadrats excluded).

Sample	Mean ($\bar{x}$)	Variance (s^2)	χ^2	P	I
Area 1					
April	6.7	83.8	251.5	<0.001	12.6
May	9.3	402.2	1000.1	<0.001	43.5
June	5.1	37.8	140.7	<0.001	7.4
July	5.3	151.6	568.6	<0.001	28.4
August	1.5	6.3	112.7	<0.001	6.3
September	1.8	4.8	87.2	<0.001	4.8
October	0.9	1.7	33.3	<0.05	1.9
December	0.4	0.7	32.0	<0.05	1.7
Area 2					
April	1.5	33.8	367.4	<0.001	23.0
May	2.0	27.4	308.1	<0.001	14.0
June	2.3	13.0	113.9	<0.001	5.7

The index of dispersion was used to analyse the lupin stem samples. Results are presented in Table IX, and I is plotted against the sample mean, $\bar{x}$, in Fig. 9.

The data were not sufficiently extensive to detect differences in aggregation response resulting from the different age-class compositions of the samples.

Table VII : Indices of dispersion for adults; adults and large juveniles, (classes F and G); and hibernating adults and large juveniles. Data from areas 1 and 2, excluding lupin quadrats.

Sample	Adults			Adults and large juveniles			Hibernating adults and large juveniles		
	$\bar{x}$	P of χ^2	I	$\bar{x}$	P of χ^2	I	$\bar{x}$	P of χ^2	I
Area 1									
April	1.3	<0.001	7.9	1.7	<0.001	11.8			
May	0.3	>0.05	1.0	0.6	<0.05	1.6	0.2	>0.05	0.9
June	0.6	<0.05	1.8	0.9	<0.05	1.8	0.7	>0.05	1.5
July	0.6	<0.001	5.5	0.7	<0.001	5.9	0.6	<0.001	6.4
August	0.4	>0.05	1.3	0.5	>0.05	1.3	0.3	>0.05	1.2
September	0.5	<0.05	1.7	1.3	<0.05	2.0			
October	0.6	>0.05	1.4	0.8	>0.05	1.3			
December	0.4	>0.05	1.3	0.5	>0.05	1.2			
January	0.3	>0.05	1.1	0.4	>0.05	1.0			
Area 2									
April	1.4	<0.05	2.1	2.3	<0.001	2.8			
May	1.8	<0.001	5.8	2.8	<0.001	11.1	2.0	<0.001	11.7
June	1.5	<0.001	4.6	2.7	<0.001	6.8	2.2	<0.001	6.2
Area 3									
December	2.3	<0.001	8.7						

Table VIII : Age/size compositions of lupin-stem sample populations.

Sample	Adults	Juveniles	
		Height > 1.00 cm	Height < 1.00 cm
Area 3 (April, 1977)			
Combined samples	53	4	17
Area 4 (November, 1977)			
Bush A	28	14	28
Bush B	9	61	15

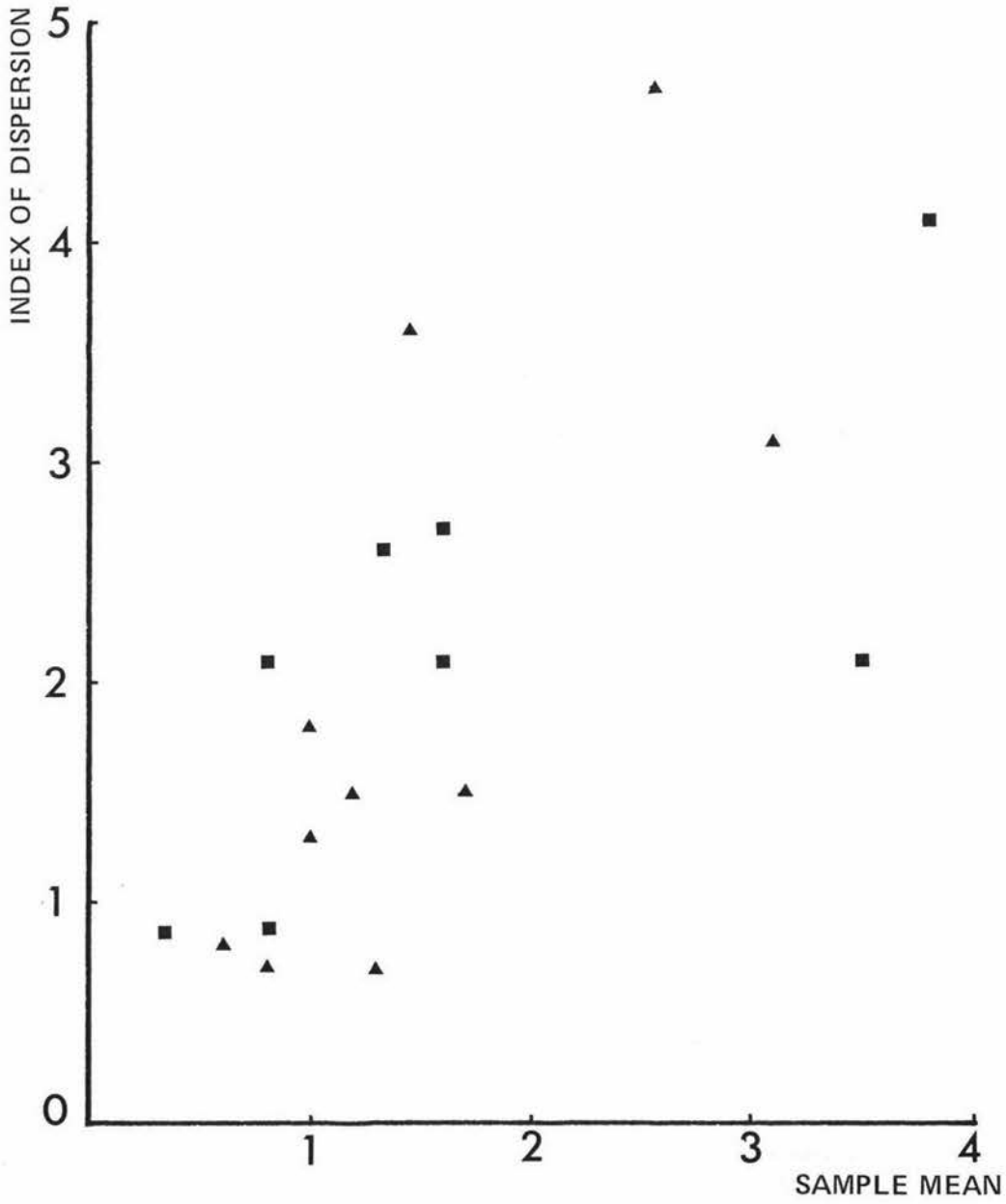


Fig. 9. Index of dispersion (I) plotted against sample mean ($\bar{x}$) for the lupin-stem samples

■ Area 3

▲ Area 4

Table IX : Indices of dispersion (I) for lupin-stem samples.

Sample	Mean ($\bar{x}$)	Variance (s^2)	χ^2	Degrees of freedom (n - 1)	P	I
Area 3						
1.	1.33	3.47	13.00	5	<0.05	2.6
2.	3.50	7.50	10.71	5	>0.05	2.1
3.	0.80	1.70	8.50	4	>0.05	2.1
4.	0.33	0.27	4.00	5	>0.05	0.8
5.	1.60	4.30	10.75	4	< 0.05	2.7
6.	3.80	15.70	16.53	4	< 0.05	4.1
7.	1.60	3.30	8.25	4	> 0.05	2.1
8.	0.80	0.70	3.50	4	> 0.05	0.9
Area 4						
A 1.	3.10	9.66	28.03	9	< 0.001	3.1
A 2.	1.00	1.33	12.00	9	> 0.05	1.3
A 3.	1.00	1.78	16.00	9	> 0.05	1.8
A 4.	0.60	0.49	7.33	9	> 0.05	0.8
A 5.	1.30	0.90	6.23	9	> 0.05	0.7
B 1.	2.55	11.87	46.64	10	< 0.001	4.7
B 2.	1.18	1.76	14.92	10	> 0.05	1.5
B 3.	1.45	5.27	36.25	10	< 0.001	3.6
B 4.	0.82	0.56	6.89	10	> 0.05	0.7
B 5.	1.73	2.62	15.16	10	> 0.05	1.5

5.4 Discussion

5.4.1 Environmental heterogeneity.

The heterogeneous nature of the environment is amply demonstrated by the results presented in Table II. In spite of the variation of vegetation encountered in this sample, all of these vegetation/ground-cover types have been found to be occupied by H. aspersa at some time during the study. Snails have been found to be estivating on pine tree seedlings in otherwise bare sand, and to be inhabiting marram clumps surrounded by bare sand. Snails were actually noticed in several marram clumps near to those sampled while

sampling was in progress. Apart from the first quadrat mentioned in Table II, all other quadrats had signs of snail activity in the form of faeces.

Obviously the main requisite of a site of habitation during daylight hours is its suitability for estivation. However, when prolonged dry periods in summer are broken by rain showers, virtually the entire snail population will become active, moving through all types of habitats, including completely bare sand. At such a time, it is likely that dispersion is close to random, although naturally, attraction to food plants will result in aggregations about these plants.

Snails found estivating on small pine seedlings or attached to two or three isolated stems of marram in otherwise bare sand have probably had to resort to such refuges as a result of being caught out on drying sand after rain has ceased and the sky has cleared during the day, or as a result of a hot clear day following a dewy night. For those animals not caught out in this way, it is likely that the species of vegetation resorted to for estivating is unimportant, provided that the desired degree of shelter is available.

The effect of the presence of lupin on snail distribution is obvious in Tables II and III. Snails fed on the lupin when they were active and many of them estivated on it during the day, attaching themselves by the estivation epiphragm. This strong attraction to lupin suggests the significance that this plant may have to snail ecology in the dune environment.

The fact that live lupin was very patchily distributed in those areas under study would tend to increase the overall patchiness of snail distribution.

5.4.2 Population dispersion

5.4.2.1 Dispersion of the 1975-76 cohort.

Adult snails lay eggs in batches of between approximately ten and 100 (Taylor, 1907-14; Basinger, 1931; Herzberg and Herzberg, 1962a). This means that emergent snails will tend to be highly aggregated in distribution. The pattern of this distribution will presumably be affected also by the pattern of vegetation and physical aspect in any area as it is likely that these features will affect site selection for oviposition. Distribution will tend to become less aggregated as young

juveniles disperse from their emergence sites. The speed of this dispersal will depend on the mobility of the juveniles and possibly the degree to which movement is favoured by weather conditions. In the populations studied, juvenile production occurs largely over the summer, when drought periods may make conditions unfavourable for activity for reasonable lengths of time. It is worth noting also that the apparent speed with which dispersal from the emergence site is effected, as measured by a quadrat sampling method, will depend on the size of the quadrat in relation to juvenile size and mobility.

Comparison of Figs. 6 and 7 shows that the high initial aggregation of large numbers of juveniles in area 1 accounts for the high total population aggregation observed over the first four months of the study. This high aggregation appears to have decreased rapidly in area 1 around August and to have remained low thereafter. Total population dispersion increased again markedly over the December–January period, as a new cohort of juveniles was produced.

The χ^2 of the 1975–76 cohort remains just significant at the 0.05 level from August to December but is considerably lower than for the previous four months. It is tempting to ascribe this observation entirely to the increased dispersal of juveniles, and undoubtedly this is a factor. However, it may also be due in part to other factors. Over this period, the mean density of these animals has also decreased. Taylor (1961) showed that the mean and variance of a population vary together such that a log–log plot of s^2 on $\bar{x}$ for any species yields a linear relationship between the two. The more aggregated the population, the steeper the line, such that the increase in s^2 is disproportionately great with increase in $\bar{x}$. This means that at low $\bar{x}$, s^2 is also very low, and dispersion tends to randomness. In this respect it is worth noting that whereas χ^2 for adults in area 1, December, ($\bar{x}$ = 0.35 adults/m^2) indicated that dispersion was not significantly different from the Poisson, the results for adults in area 3 in the same month ($\bar{x}$ = 2.28 adults/m^2) show a highly significant deviation from the Poisson ($P < 0.001$). (This is excluding lupin quadrats.)

Furthermore it is a weakness of the index of dispersion itself that it is affected by this relationship between $\bar{x}$ and s^2. That is, as the mean, and therefore variance, decrease in an aggregatively dispersed population, I tends to decrease also, regardless of the

fact that the actual dispersion pattern may remain the same.

5.4.2.2 Dispersion of adults and large juveniles.

The dispersion of adults over the period of the study displays rather different trends to those of the '75 - '76 cohort. Divergence from random is particularly marked in April and July, whereas P lies close to 0.05 for the other months.

Although the April results have a higher mean than those of other months, the high I for April may also be explained by a strong aggregating response during a dry period with much time spent in estivation. In one quadrat alone, 14 adults and several large juveniles were found, the majority of them estivating close together in a single aggregation.

The large I obtained for July can be explained by comparing the adult results with those for hibernating adults and large juveniles (Fig. 8). There is a strong tendency to social hibernation in this species, with large numbers of animals found close together and frequently attached to each other by the hibernating epiphragm (Taylor, 1907-14; Wynne-Edwards, 1962). A similar trend is seen in the area 2 results. Frequently a group of hibernating animals, numbering up to ten or more, would all be found in an area of only one-fifth or so of the total quadrat, despite the fact that the remainder of the quadrat seemed in every respect to be identical to that portion frequented.

During the June 1977 sampling in area 3 a group of hibernating adults and large juveniles was found in a natural depression of the soil surface under a thick layer of dead vegetation and litter. Over 90 animals were counted, the total being estimated at between 150 and 200. The animals were all sealed to each other's shells by their hibernating epiphragms, so that clumps of up to 20 snails could be picked up by lifting one animal. The area occupied by all of these animals was approximately 20 x 20 cm, so that they were present in a density far in excess of the mean for the area. Although it is possible that site-suitability was involved here, it seems likely that some type of inter-individual behaviour is also involved. Site-suitability alone cannot explain how a large number of animals with

limited mobility, presumably dispersed over a reasonable area, all managed to locate a single small hibernating place without some type of directional cues, such as spatial memory or some type of behavioural interaction with other individuals.

There are no obvious differences displayed between dispersion results for the bulked adult and large juvenile data, and those for adult data alone.

5.4.3 The importance of dispersion to the accuracy of population data

It can be seen, then, that the observed dispersion of snails in quadrat sampling is the result of a combination of factors. This dispersion, which tends to a high degree of aggregation for much of the year is of direct relevance to the collection of accurate population data. The frequently high sample variance means that accurate estimates of population density in any area could only be made if sampling was to occur on a logistically prohibitive scale. This was particularly the case with area 1 where this problem was compounded by a low adult population so that captures were relatively few in number. In area 3 the main problem would be the very patchy distribution of live lupin, which would have to be taken into account.

A possible way around these problems in an area such as area 3 with a dense population would be to sample only within a region, as large as could be found, that was relatively uniform in character, such as one of the larger patches of lupin. However, a region or a particular vegetation type that is suitable for one aspect of an animal's requirements is not necessarily suitable for others. A good feeding site may be shunned for hibernation or oviposition. If there was a tendency for animals to migrate into or away from the study area at some stage during the study, then some population processes would be obscured.

Without accurate density data, overall population trends are more difficult to analyse (see Chapter 6), and the processes involved tend to be obscured. For instance, by presenting data on a particular juvenile size-class as a percentage of the total catch, a change in this percentage over two consecutive months can only indicate a change in numbers relative to the other size classes. It cannot indicate

whether an absolute change in numbers in that size class has occurred. These difficulties of data analysis are compounded for those size-classes which at all times constitute a relatively small proportion of the total population.

5.4.4 Lupin-stem aggregations.

Aggregations of estivating snails on lupin stems were frequently observed in the field in areas of heavy infestation. Within an aggregation there was frequently a degree of physical contact between individuals, with many being attached to the shells of others, rather than to the stem, (e.g. see frontispiece). The measurements of lupin-stem dispersion were simply an attempt to quantify this observed tendency to aggregate.

Aggregation was found to occur in several cases (Table IX) particularly on stems with higher mean densities of snails (Fig. 9). The relationship of mean to aggregation and to the index of dispersion has already been discussed.

Ideally, a measure of aggregation that is more sensitive to inter-individual attraction than the index of dispersion is required for the type of dispersion displayed by estivating and hibernating H. aspersa. Lloyd (1967) developed the concept of mean crowding, measured as "the mean number per individual of other individuals in the same quadrat". This measure is only interested in those quadrats which contain animals and not those with zero counts. The aim is to measure the degree of inter-individual interaction in the population, and therefore the quadrat size is chosen so as to approximate to the ambit of an average individual. Division of the mean crowding ($\overset{*}{m}$) by the mean density (m) gives an index of the species' dispersion which Lloyd called patchiness. It can be seen that if mean crowding is reduced for an aggregative species due to a decrease in mean density, this is taken into account by the measure of patchiness. Patchiness is smaller than, equal to, or larger than unity in uniform, random or clumped distributions, respectively, (Lloyd, 1967; Iwao and Kuno, 1971).

Possibly some type of nearest-neighbour method, where the distance between two individuals is of primary importance, would be even more suitable in the present context. (See Southwood, 1966).

With the variance : mean ratio method the fact that two snails were present in a 10 cm sampling unit does not indicate whether they were 9 cm apart or whether one was attached to the other, as was often the case. This information is the basis of the nearest-neighbour method. Unfortunately, use of either of these alternative methods, and particularly that of Lloyd, are restricted by requirements for habitats that are larger and more suitable for sampling than short lengths of lupin stem, and considerably more homogeneous than the sand dune environment.

5.4.5 Possible behavioural bases for aggregation.

The types of behaviour which lead to aggregation in snails for hibernation and estivation may well be related to those which allow many species of gastropod to "home", i.e. to return to a particular spot on many consecutive occasions in order to enter a resting phase such as estivation or hibernation. Indeed, Potts (1975) showed that H. aspersa itself has this homing ability. He found that individuals invariably returned to the same area to estivate, so that different "populations" of estivating snails could be distinguished on the basis of the area chosen. Individuals from different populations mingled during feeding and other activities at night, but always returned to their particular area. Within the estivation area, individuals did not show a homing response to one particular position. Taylor (1907-14), on the other hand, cites cases where this has occurred.

The same type of homing response is found in a number of species of aquatic gastropods, notably limpets. In these species it is considered to be largely due to the ability of individuals to sense and follow the slime trails they deposit in moving to and from their resting point, although spatial memory is considered to be important in some species (Cook et al, 1969; Cook, 1969; Wells and Buckley 1972).

Wells and Buckley have shown that the freshwater pulmonate, Physa acuta also follows trails which it has previously laid down as it journeys to the water surface to replenish its air supply. Snails would also follow trails of conspecifics, and if they happened upon such a trail within about 30 minutes of it having been laid, they would

usually follow it in the direction taken by the animal laying the trail. Apparently some type of temporary polarisation was to be found in the freshly-laid trail. Physa was found not to follow the trails of other pulmonate species. Similar responses, including those indicating the occurrence of temporary trail-polarization, were found in another freshwater pulmonate, Biomphalaria glabrata by Townsend (1974).

Pollard (1975) found that individuals of Helix pomatia from some populations showed a tendency to move to a particular area for hibernation during winter, returning to more favourable feeding areas in the summer. He found also that individuals moved from a particular feeding site showed a tendency to return to that site, but this ability was lost for distances in excess of about 20 m. Edelstam and Palmer (1950) also studied the homing response in Helix pomatia and concluded that some accuracy in homing was demonstrated over distances of 40 m or more. They felt that this response owed much to a well-developed spatial memory aided by directional cues provided by familiar odours from the "home" area. Certainly, in some of the evidence provided by these two studies, trail-following would be insufficient to explain observed phenomena.

The possibility remains, however, that individuals of terrestrial snail species may follow the slime trails laid down by themselves and other conspecifics. Slime trails appear to be reasonably persistent in terrestrial environments, drying out in warm weather but becoming slimy to the touch again when wet. In the case of H. aspersa evidence that the information necessary for trail-following may exist in the trail is given by McLauchlan (1949) who found that two carnivorous snail species, the European Hellicella virgata and the Australian Strangesta capillacea follow newly laid trails of H. aspersa in order to capture and eat them. These observations were unfortunately not quantified and the experiments were carried out in fairly confined conditions so that the possibility that other senses also played a part in detection of the prey cannot be discounted.

Initial laboratory tests on trail-following in H. aspersa appear to indicate a significant tendency for individuals to follow their own trails in a choice situation (Dr D.W. Fountain, pers.com.).

Homing ability is a rather more difficult phenomenon to explain in terms of trail-following than aggregation. The ability to home accurately without being misled by the trails of other animals suggests either that individuals can detect their own trails amongst others, or that some type of spatial memory is in fact the major factor. Furthermore, homing for estivation may be synonymous to some extent with aggregation if a number of individuals all home to the same place.

Homing ability is presumably adaptive to animals with limited mobility as it imparts a degree of familiarization with the habitat, allowing more direct movement to a specific site, with a minimum of trial-and-error.

A common feature of aggregations of H. aspersa which has already been mentioned and is worthy of further consideration is the tendency for individuals to attach themselves to the shells of others in order to hibernate or estivate. This indicates a tactile response to other individuals which may be part of the aggregating behaviour, or which may simply be an adaptive response in that the shell of another individual probably provides the best fit of any object in the environment to the shell aperture, thus providing a very effective seal.

Testing experimentally for trail-following ability in H. aspersa is beset by a number of problems. H. aspersa characteristically reacts to disturbances such as handling, particularly when in a resting state, by becoming very active. In such a state it is possible that a snail will not respond to stimuli, such as a slime trail, to which it normally would respond in some manner. Furthermore, response to such a stimulus may only occur in particular circumstances anyway. Response to trails laid by other individuals may only occur when an animal is responding to a physiological need to estivate, hibernate, or reproduce. It is possible that trail-following phenomena would best be studied in individuals that had been isolated from others for some time.

5.4.6 Adaptiveness of aggregation.

Perhaps the most obvious adaptive function of aggregative behaviour prior to estivation or hibernation is the facilitation of reproduction. Animals are brought together at the beginning of an unfavourable period, so that mates are immediately available when activity resumes in favourable conditions. This could be particularly important for animals with limited mobility when population density in an area is low. This possible function is not negated by the fact that hibernation ceases up to four months prior to the first appearance of emergent young, as many species, including H. aspersa, have the ability to retard egg development after copulation for a considerable period of time, until conditions are suitable for oviposition (Ward, 1879; Mead, 1961; Herzberg and Herzberg, 1962a).

The implications of aggregation may go beyond simply the facilitation of reproduction. Wynne-Edwards (1962) suggests that it may have an epideictic function. The occurrence of aggregations at particular times of the year may allow regulation and adjustment of the population through density-dependent feedback processes involving inter-individual behaviour. Involved in this could be the synchronization of population processes through behavioural interactions. Wynne-Edwards suggests further that if such a function is involved in aggregation, that it has probably become secondarily associated with the independent phenomena of winter hibernation and summer estivation.

CHAPTER 6

POPULATION PROCESSES OVER THE SAMPLING PERIOD.

6.1 Introduction

The main aim of the sampling program described in Chapter 3 was to observe and interpret population changes over the course of a year.

Sampling began in area 1 in April 1976 and was discontinued in January 1977. Over this time, population density appeared to have decreased somewhat, and sampling was abandoned when it became obvious that insufficient information was being obtained for the amount of time involved.

Interest was shifted to area 3 which had previously been pointed out by Forest Service staff as an area of heavy snail infestation. Access to this area in winter and spring of 1976 was restricted to four-wheel-drive vehicles due to the remarkably high water tables in the dunes that year. An initial sampling of the area was therefore not made until December 1976. After this quadrat sampling was abandoned due to the excessive time required and because sampling error was extremely high from the effects of the patchily distributed live lupin on snail distribution. At this stage, information was sought mainly on the fate of large juveniles and it was considered that the alternate sampling method employed would yield this information.

To add to the information obtained from sampling, ageing of some snails was attempted on the basis of shell characteristics. Also, an experiment was performed aimed at determining the possible hazardous effects of the physical nature of the sand substrate.

6.2 Methods

6.2.1 Sampling

Details of sampling methods used in areas 1, 2 and 3 were given in Chapter 4, section 4,3,1,1. Shell heights of animals were measured using vernier calipers. For some samples adult animals were counted but their shell heights not measured.

In areas 1 and 2, a record was kept during the winter months of all snails found hibernating (i.e. complete with hibernating epiphragm), and of the situations in which these individuals were found.

Monthly weather data for the study period were obtained from records produced by the meteorological office of the R.N.Z.A.F. base at Ohakea, about 16 km southeast of the northern Santoft area.

6.2.2 Ageing methods using shell characteristics.

6.2.2.1 Juvenile ages

Over the course of a year juvenile snails cease growth for varying periods due to adverse climatic conditions, namely summer droughts and winter cold. It seems reasonable to expect that such growth checks, which would be associated with cessation of shell growth, might result in some visible mark or break in the growing shell. Discontinuities in shell deposition, usually associated with a break or change in the shell's colour pattern, have long been known to occur in many helicid species, including H. aspersa (Taylor, 1894-1900, 1907-14). It has usually been assumed that they occur only as a result of the prolonged winter growth break. Furthermore, they give only a minimum estimate of the number of winters undergone as a juvenile as they do not always occur (Potts, 1975).

Pollard et al. (1977) made a close study of this phenomenon in Helix pomatia and found that the number of separate periods of shell growth indicated by the pattern of growth checks in the shells of adults corresponded with a previously estimated two to five year age at maturity in their study area. They therefore concluded that growth breaks did not occur as a result of periods of prolonged summer estivation.

In view of these findings, an attempt was made to use shell growth-checks to more accurately assess juvenile age at maturity.

The September 1977 snail catch from area 3 was used to obtain growth-check data. The animals were submerged in hot water for a few seconds and the bodies removed from the shells with a needle. Shells were then dried and examined under a binocular dissecting microscope for any apparent growth checks.

6.2.2 Adult ages.

Many landsnail species, including H. aspersa, continue to thicken the shell internally after ceasing growth on attaining adulthood. As with juvenile shell growth this process ceases over the hibernation period. Pollard (1973, 1975) and Pollard et al. (1977) found in H. pomatia that this resulted in the appearance of distinct separate layers of shell deposition on the rim of the aperture lip, each of which could be interpreted as a single growing season. In fact it was found with animals that had been captured, marked and released previously that the older the snail was, the more likely that the number of ridges on the aperture lip would tend to underestimate the number of years spent as an adult. Adults with as many as eight aperture lip ridges were found.

The adult animals of the September 1977 sample from area 3 were examined under a binocular dissecting microscope for traces of aperture lip ridges.

Relative indications of the age of an animal can sometimes be obtained by assessing the degree of "wear and tear" suffered by some hard permanent body feature, characteristic of the species, from contact with the environment (Southwood, 1966). The shells of many adult snails showed various signs of "wear and tear" such as irregularities where breakages had obviously occurred. Breakages are repaired by the snail which can, if necessary, mobilize calcium from other parts of the shell (Wagge, 1952).

However, the most notable sign of shell-wearing was the progressive removal of the very thin periostracum, the pigmented, organic outer layer of the shell. The removal of this layer gives the shell a bleached appearance, with a more or less white to light grey ground colour with darker grey to brownish banding. The beginnings of this condition were often in evidence on large and even some medium juveniles, and very few adults were entirely free of it.

While wearing of the periostracum did not add directly to knowledge of individual ages, it was a useful aid when used in conjunction with the growth-check analyses.

6.2.3 Desiccation and heat mortality on bare sand.

An important characteristic of the sand dune environment to the snail population is the physical nature of the substrate itself. Because of the particular method of locomotion utilized by snails dry sand represents a virtually insurmountable barrier. Mucus produced by glands on the foot is laid out in a trail over which the animal moves. On dry sand the sand particles adhere to and are lifted up in the mucus, which remains on the animal's foot. An animal caught in such a situation can usually only withdraw into its shell and wait for rain or dew to moisten the sand so that movement can be resumed. The moisture coating the wet sand particles causes them to stick together, presenting a more solid substrate than dry sand.

During late summer, drought periods of considerable duration cause virtually the entire snail population to enter estivation. The occurrence of summer rain showers after a week or more of drought with little evening dewfall has the effect of stimulating to activity almost the entire population, regardless of whether it is day or night. At such times large numbers of snails may be seen swarming over vegetation and wet, bare sand alike. At this time of year a heavy shower may end soon after it began and if this occurs, especially during the day, consequent wind and/or clearing of the sky can cause the sand to dry out again rapidly. Snails caught in this way are vulnerable to both desiccation and the intense heating of the sand which occurs on clear days.

In area 3, a 30 m stretch of bare sand vehicle track was cleared of all snails and shells during a dry period in early March 1977. The cleared area was approximately 2.5 m wide. Along one side was dense marram and a large stand of live lupin, while the other side had isolated patches of dense marram and other species, with some lupin further back, as well as a considerable portion of bare sand which was continuous with the track.

Light rain showers were beginning to fall as the track-clearing neared completion in the late afternoon. Intermittent light showers with a cloud cover continued until dusk. The following day was fine and very hot, and the sand had dried out completely. Stranded snails were collected off the cleared section of track at about midday. The animals were measured for shell size.

6.3 Results.

6.3.1 Population sampling.

The population sampling results for areas 1, 2 and 3 are presented in Figs. 10, 11 and 12. The animals are divided into adults and the various juvenile size-classes, and each group is presented as a percentage of the total catch. Large juveniles showing the beginnings of adult lip formation were sometimes captured, and these were counted as adults. However, where shell size data was collected for adults, the sizes of these individuals were not included.

From the area 1 data, mean density is plotted against time for adults, for the juveniles of the 1975-76 cohort, and for large juveniles (classes F and G). (Fig. 13).

Hibernation data from areas 1 and 2 are presented in Fig. 14 for adults alone, and for adults and large juveniles combined.

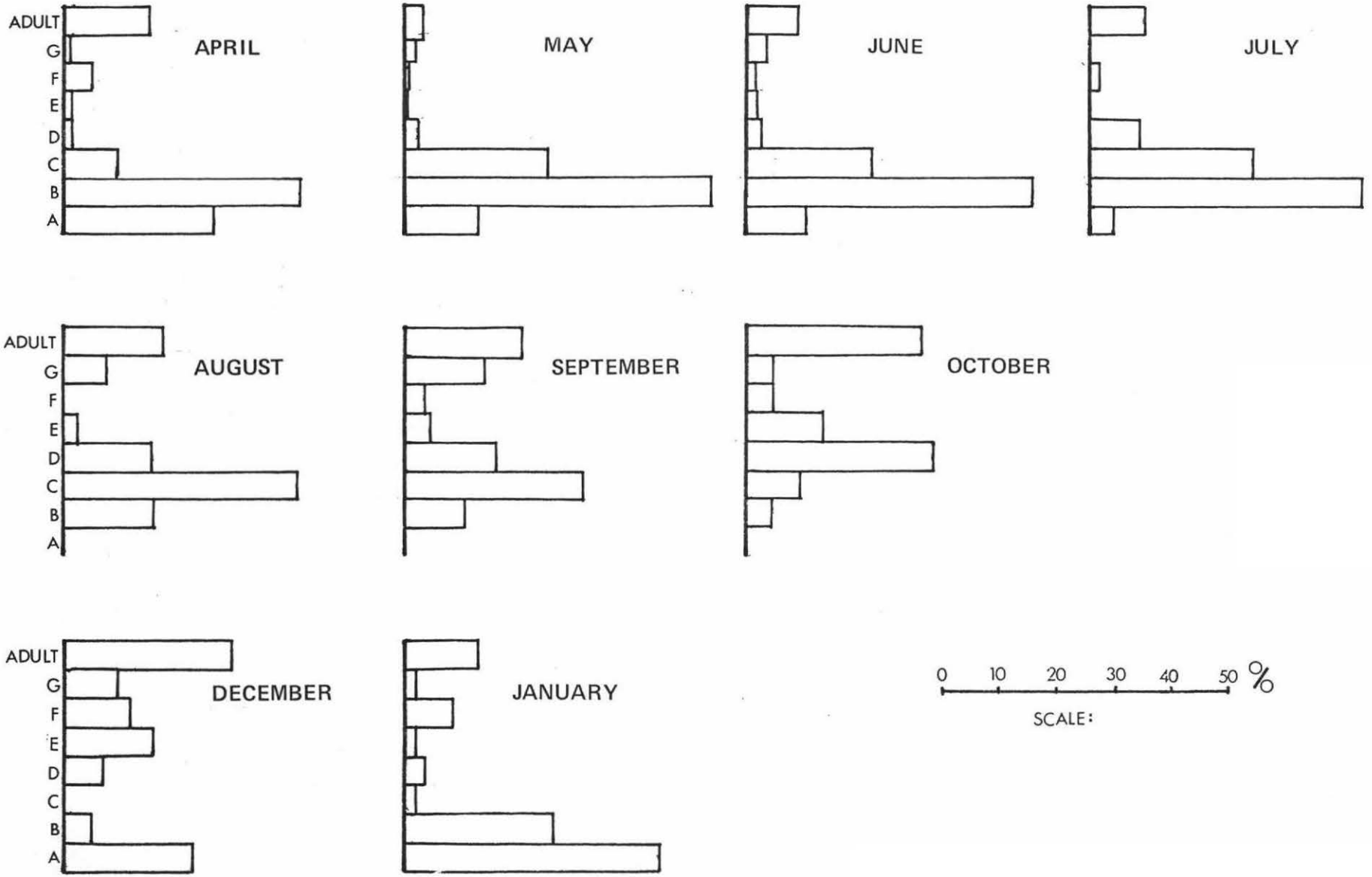
Weather data are plotted against time in Fig. 15. The data recorded are rainfall (total monthly rainfall; number of days on which rain fell) and temperature (mean daily maxima and minima for each month; absolute monthly minimum temperature).

6.3.2 Individual ages from shell characteristics.

6.3.2.1 Juvenile growth-checks.

In order to count the number of juvenile growth-checks on a shell it was found to be necessary to make a decision on just what constituted a winter growth-check. Pollard et al. (1977) studied growth-checks under the microscope and found that where a cessation of shell growth had occurred, subsequent shell deposition resumed from underneath the old shell. This resulted in a distinct discontinuity in shell deposition. Each discontinuity found on a shell was therefore considered to be a single growth-check. Potts (1975) does not indicate whether the growth-checks he refers to in his study of H. aspersa are the actual shell deposition discontinuities or the break in shell colour pattern that usually accompanies the growth-check.

In the present study it was frequently found that an apparent growth-check, visible as a break in colour pattern, proved on microscopic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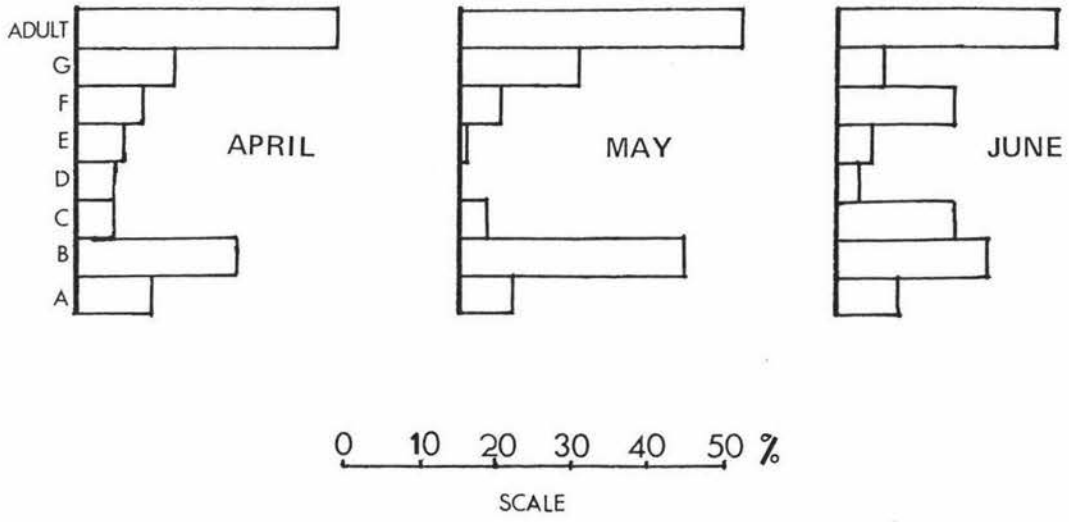
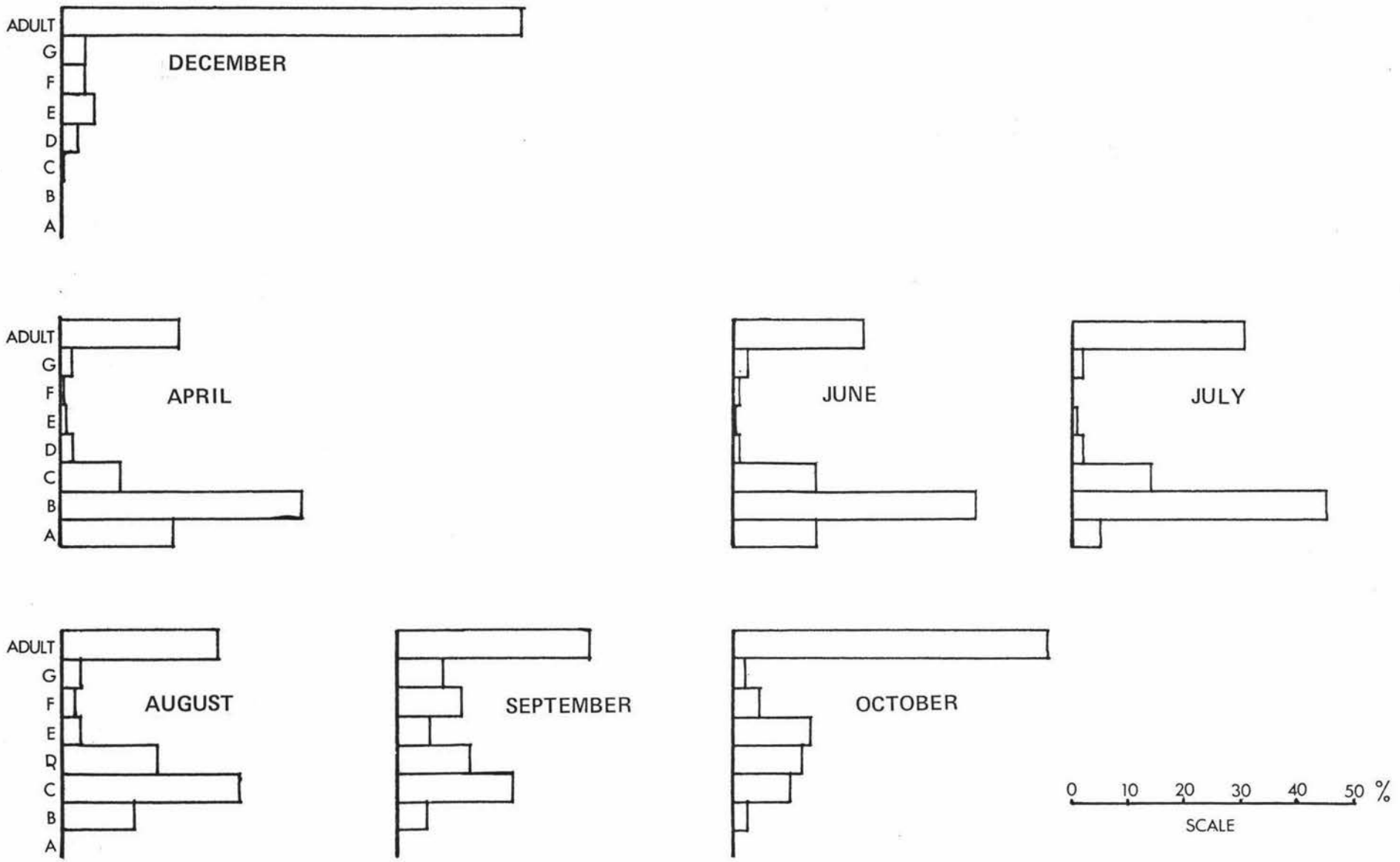


Fig. 11. Population sampling results, area 2
(see fig. 10 for juvenile size classes)


ADULT
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SCALE

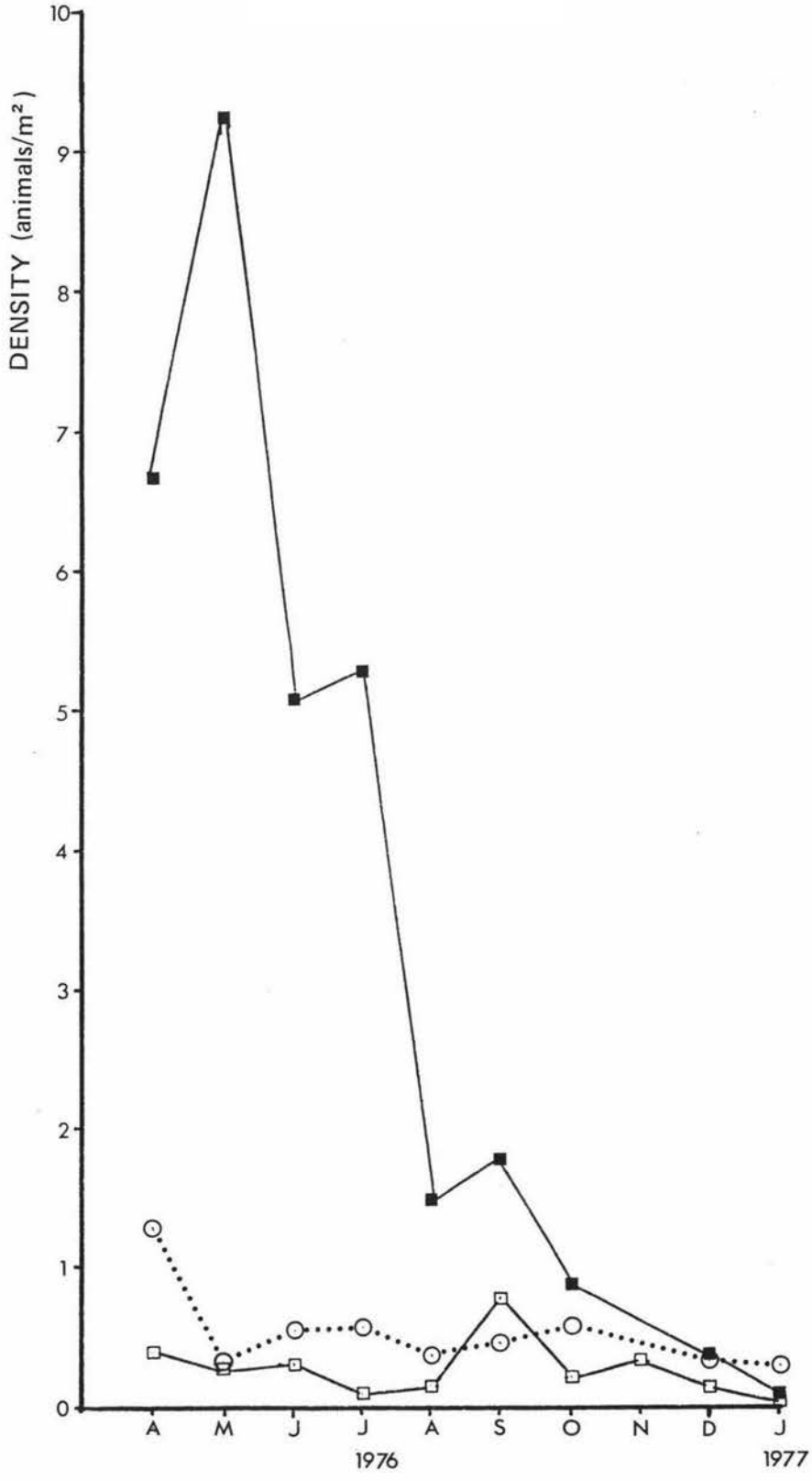
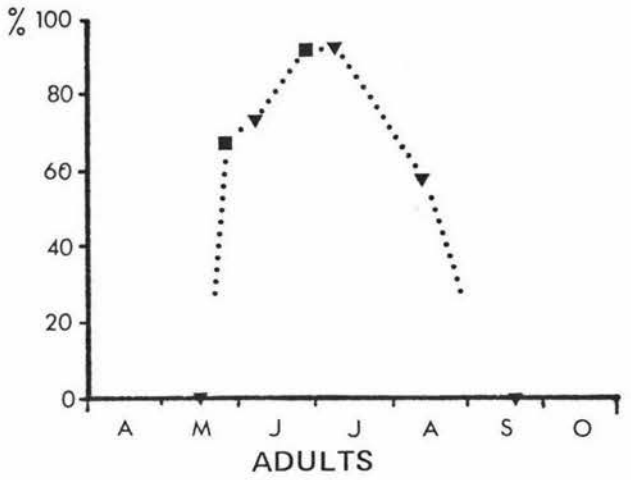


Fig. 13. Population densities in area 1 over the sampling period

■ 1975-76 cohort
□ large juveniles
○ adult



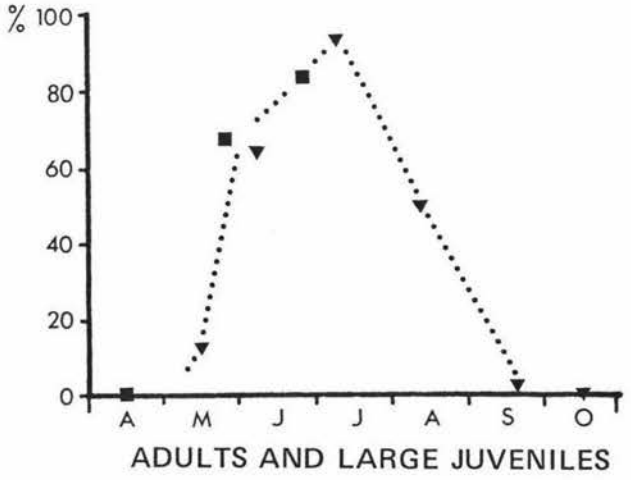
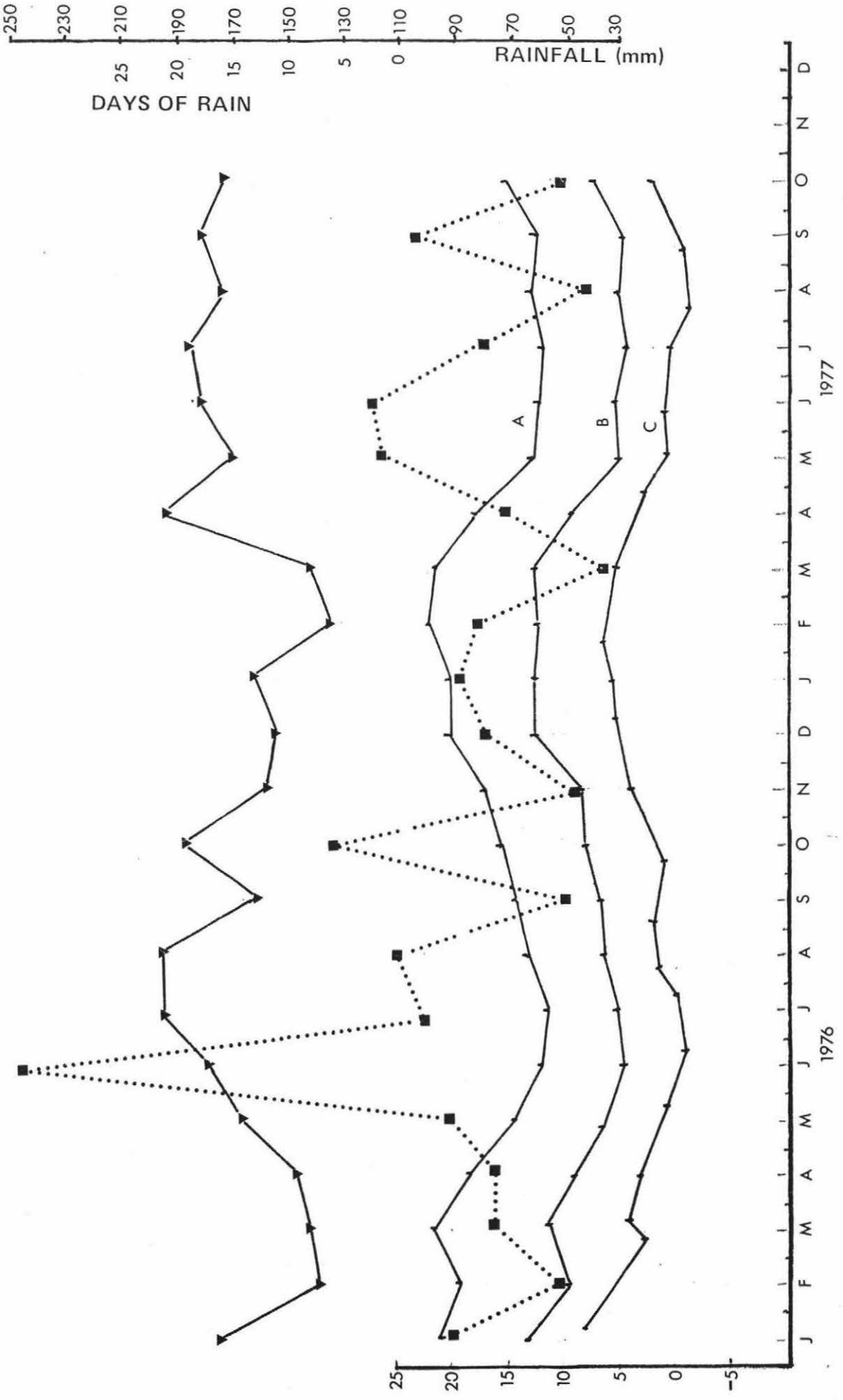


Fig. 14. Hibernation data: Percentage of adults, and of adults and large juveniles hibernating

▼ Area 1

■ Area 2


250
230
210
190
170
150
130
110
90
70
50
30
RAINFALL (mm)
25
20
15
10
5
0
DAYS OF RAIN
A
B
C
25
20
15
10
5
0
-5
J F M A M J J A S O N D J F M A M J J A S O N D
1976
1977

examination to be associated with up to four deposition discontinuities, all situated very close together. Sometimes a series of discontinuities would be found to occur without any obvious break in the colour pattern. It was assumed that where such a group of discontinuities existed, they represented a single break between two consecutive growing seasons. The alternative was to assume that almost no growth had occurred over each of two or three consecutive growing seasons (see Plate 2).

Where two or more discontinuities were more widely separated, each was assumed to be a separate growth-check. In a number of cases it was difficult to decide whether two consecutive discontinuities were separated by a season in which only a little growth had occured or whether the two should be considered together as the end of a single growth season. In these cases the decision was made following examination for associated changes in colour and banding pattern and in shell wear, especially the removal, by abrasion, of the thin, pigmented periostracum.

Some shells were found to have features which could not positively be identified as growth-checks. These may conceivably have been old shell-damage repairs or abnormalities in the shell deposition, and were discounted.

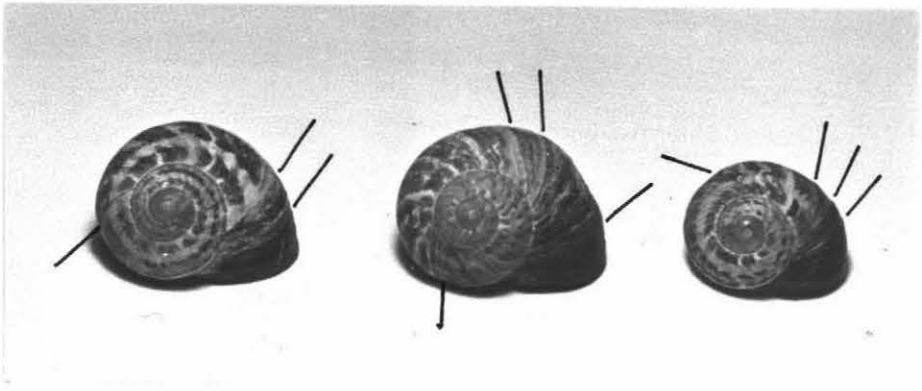
Table X : Numbers of juvenile growth-checks on the shells of adult and sub-adult animals (September sample area 3). Sub-adults are those juveniles beginning to develop adult shell characteristics.

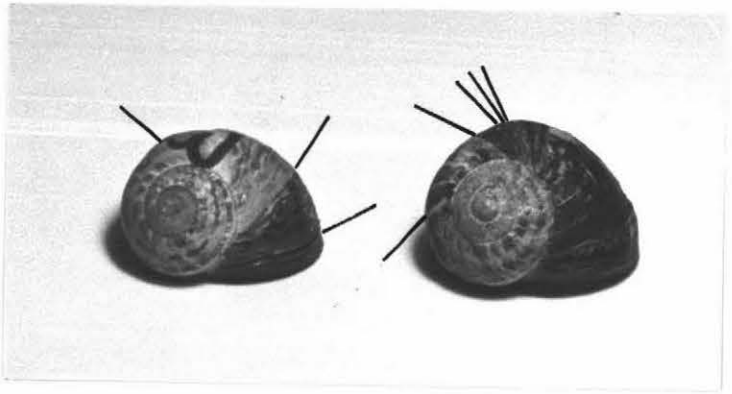
Number of growth-checks	Adults	Sub-adults
0	8	0
1	36	5
2	45	6
3	18	5
4	3	1
	110	17

Plate 2. Growth-checks on adult and large juvenile snails from area 3.

Positions of shell deposition discontinuities are indicated on the photographs. Note the progressive wearing of the darker periostracum from the older portion of shells

The animal on the lower right had three discontinuities close together at the top of the shell. These were assumed to be from a single growth-check.





The shells were divided into adults, juveniles whose features suggested the onset of adult shell characteristics (sub-adults), and juveniles. Juvenile shells below a height of 0.60 cm were not examined, as the majority of these were too fragile to attempt body extraction without breaking them. The majority of small juvenile shells do not appear to have any obvious growth-checks.

Tables X and XI give the results of the juvenile growth-check analysis for these groups.

Table XI : Numbers of juvenile growth-checks on the shells of juveniles (September sample, area 3.)

Number of growth-checks	Shell height (cm)								
	0.60-0.69	0.70-0.79	0.80-0.89	0.90-0.99	1.00-1.09	1.10-1.19	1.20-1.29	1.30-1.39	1.40-1.49
0	5	3	3	2	5	7	1	-	-
1	1	6	4	8	6	5	2	1	-
2	-	-	-	-	1	4	4	2	-
3	-	-	-	-	-	1	3	2	1
4	-	-	-	-	-	-	-	-	-

Total = 77 animals

6.3.2.2 Adult growth layers.

While there was evidence supporting the existence of a layering effect on the aperture lip of adult H. aspersa, in the majority of cases ridges were not sufficiently distinct for shells to be scored with a reasonable degree of accuracy. This could be due to the abrasive action of sand on the shell. Where individual shells did have more distinct layering at least one was found to have as many as four ridges, and there were several with two or three.

Many adults had the periostracum almost completely worn away, and there was a tendency for shells with no apparent ridging of the aperture lip to show less wear of this shell layer.

6.3.3 Sand-stranding mortality.

A total of 1,186 animals were collected off the section of track that had been previously cleared. The size distribution of these animals is shown in Table XII. Of nine adults, five were still alive, as was the single size G juvenile, although this one showed signs of a considerable degree of desiccation along the posterior portion of the foot. The desiccated parts of the animal were apparently insensitive to stimuli as prodding them with a sharp stick brought no response from the animal. Prodding the non-desiccated parts of the animal, further in the shell, brought some response but the animal was obviously no longer able to withdraw its body into the shell. These observations are similar to those of Richardson (1974) who studied the same phenomenon in dune populations of Cepaea nemoralis.

Table XII : Age/size distribution of 1,186 snails stranded on a 30 m section of bare sand tracks which had been previously cleared of all shells.

Age/size class	A	B	C	D	E	F	G	Adult
Number	528	472	149	20	4	3	1	9
%	44.5	39.8	12.6	1.7	0.3	0.3	0.1	0.8

Of the remaining juveniles, fewer than 50 individuals showed signs of life between collection in the field and sorting in the laboratory. Many of them were found sealed to small fragments of vegetation lying on the track or to the shells of other individuals by their estivation epiphragms.

6.4 Discussion

6.4.1 Juvenile growth and density.

From the areas 1 and 3 sampling results (Figs. 10 and 12) it appears that juvenile emergence reaches a peak around late January and that minimal growth and development occurs from then until July. This may be due largely to the effects of climate over this period (Fig. 15).

The rising temperatures of the December-February period coincide with a general decline in rainfall which reaches its lowest point in February or March, giving rise to drought periods of two weeks or more. At such times the majority of snails either estivate or maintain a very low level of activity in the most sheltered places during the day. Some nocturnal activity will occur if there is sufficient dew.

April is probably quite favourable to growth as rainfall increases again, but temperatures soon begin to decline and by the end of May the majority of adults and large juveniles are found to be hibernating (Fig. 14). This continues through to August, and one individual in area 1 was found hibernating in September.

Many small juveniles were found to be hibernating during the winter months, with their shell apertures closed by a hibernating epiphragm, but more frequently they were found to be withdrawn into the shell with no epiphragm in evidence. All small juveniles usually became active soon after disturbance (e.g. being handled) and it is likely that some may become active briefly during the milder winter days. It is possible then that low levels of growth may continue even over this period.

Assuming then that the majority of juveniles emerge in January, in their first six months they have only about two-and-a-half to three months of conditions optimal for growth.

Because they are less affected by cold weather than the large animals, the small juveniles become active sooner and by the middle of August, when many of the larger animals are still hibernating, significant growth has already taken place. Growth appears to be maximal in the period between August and January.

Over the course of this first year of development, a high mortality reduces the numbers of this cohort to a very small proportion of their original number. This mortality appears from the area 1 data (Fig. 13) to be particularly high over the May-August period. The result of this reduction in numbers is that these approximately one year old juveniles represent only a small proportion of the total population, with relatively few captures, and their fate after this time is unclear.

It is likely that a number of these juveniles become adult before their second winter, probably around April. It is more clear that a substantial number, perhaps the majority, spend at least one more winter as juveniles before becoming adult. This is particularly suggested by the results from area 2.

The question of the age attained by juveniles before becoming adult is found to be considerably more complex when the results for ageing using juvenile growth-checks are considered (Tables X and XI).

Of 32 juvenile shells between 0.60 and 1.00 cm in height, 13 had no apparent growth-checks while 19 had one each. All of these animals had just been through a winter and therefore a period of little or no growth. As the sample was taken in September, it is unlikely that those with no visible growth-checks had not begun the second season's growth. The reduced need to undergo a long hibernation period displayed by small juveniles may explain the lack of visible shell-deposition discontinuities in the shell. It is apparent, then, that shell ages estimated in this way are minimal.

It is clear from the growth-check data that a substantial number of individuals in area 3 have undergone a minimum of two or three winters as juveniles before becoming adult, by which time they were up to three or four years of age. This trend was found to be continuing in juveniles captured in the September sample.

That these large juvenile development trends are not apparent in the population sampling data is due in part to the shortcomings of using a simple linear measurement to measure shell size, and the method of division of the total juvenile size range, which bulked data for the larger juveniles. For example, an animal whose shell height increases from 1.25 to 1.45 cm over one growing season remains in one size-class (G) in spite of a large increase in volume; a much larger volume increase than that for a smaller animal increasing its height by the same amount. The smaller animal would also undoubtedly change from one size-class to another in the course of such an increase.

This means that an animal attaining size-class F or G in one season will not necessarily become adult the following season, but may in fact take another two or so years to do so. It is likely that such a development pattern would remain obscured no matter how the size data were divided up, as the numbers of large adults taken were always

only a small proportion of the total catch. The only way to get this information accurately from a field study under these circumstances would be to initiate a large mark-recapture program, and relocating marked animals in the type of vegetation encountered in this study would involve extensive searching.

No comparable growth-check data were collected from area 1 animals, so conclusions must be restricted to the area 3 population. In the next chapter, evidence is given which suggests that development times may have actually been more rapid in area 1.

Finally, it must be noted that growth-rates over consecutive growing seasons as indicated by the distances between consecutive growth-checks display considerable variation both between individuals and between consecutive seasons on a single shell (Plate 2.).

The density data for large juveniles in area 1 show a rather curious anomaly in the September sample (Fig. 13). There is a sharp increase in density of these animals during this month and this is associated with an increase in the proportion of these animals in the total population for this month (Fig. 10). In the October sample, the density has fallen to its former level.

The possibility that this change is due to recruitment from the 1975-76 cohort is not supported by the population size-composition results, and the October decrease in density of large juveniles is not correlated with an increase in density of the adult population.

The most significant change to occur between the August and September samples which may have a bearing on this anomaly was the shifting of the area 1 sampling area about 30 m north from where it was previously located. Significant changes in the size-composition of a population have been found to occur over relatively small distances (see Chapter 7), and this could explain the abruptness of the change.

Furthermore, plotting the positions in which these animals were captured shows that they tended to be concentrated at the eastern end of the new study area (Fig. 16). This degree of clumping is suggestive of hibernation and it was found that one of three large juveniles found in a single quadrat with three adults was, in fact, hibernating. In the August sample of area 1, two of only three large

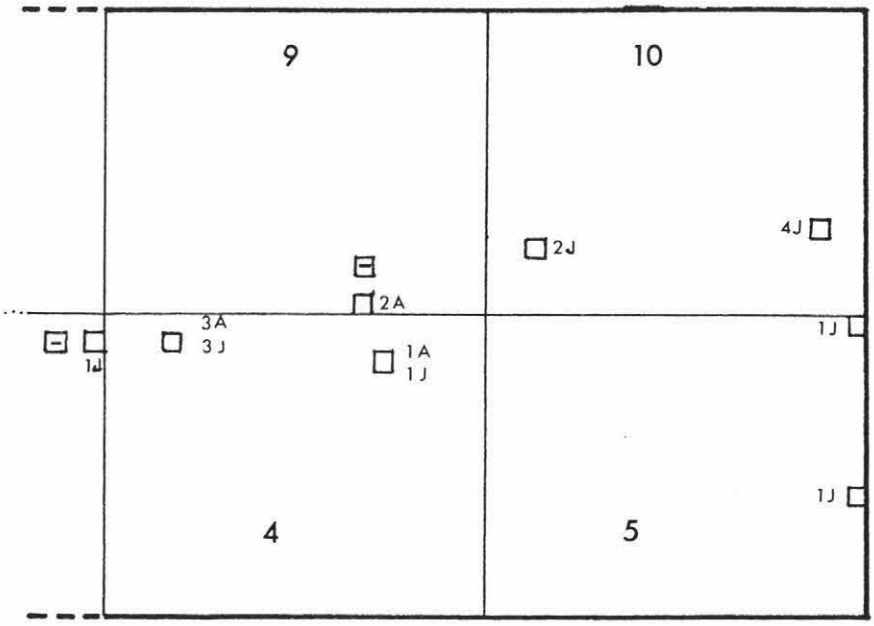


Fig. 16. Distribution of adults and large juveniles captured in the September sample from area 1

A Adults

J Large juveniles

⊟ No snails captured

(c.f. Fig. 3)

juveniles captured were hibernating as were two of seven adults.

It is suggested then that these animals had aggregated in this particular area for hibernation and had become active again not long before the September sampling. The reduction in density found in the October sample suggests a dispersal of these animals back to a more normal non-hibernation distribution, which would undoubtedly take a number of them out of the sampling area.

These results along with the hibernation data (Fig. 14) suggest the possibility that large juveniles may hibernate for a longer period than adults.

An increase in the proportion of large juveniles in the total population is also found to occur in the September sample results from area 3, with a subsequent decrease in the October sample (Fig. 12). Unfortunately no density data are available for this population, so that whether this increase in proportion is due to an increase in density of these animals cannot be determined. However, it is felt that these observations can be adequately explained in this case by a number of circumstances.

First, it was found later in the course of the study that population size-composition can vary considerably over a small distance within a single sample area, and the sampling procedure used in area 3 would be particularly prone to this type of variation (see Chapter 7). This in itself could explain the changes in proportion of large juveniles between the August and September samples and between the September and October samples.

An increase in proportion of one group in a population can also be due to a decrease in density of the other groups comprising the population and this occurred to some extent in the populations of both of the main study areas. In area 1, a large decline in density of the animals of the 1975-76 cohort occurred and this resulted in an increase in the relative proportions of adults and large juveniles that is visible in the August sample. It is believed that a similar high mortality of small juveniles occurred in area 3. Furthermore, there appeared to be a marked decrease in adult numbers in area 3 over the late winter/early spring period, and this coincides with observations made in this area at this time.

Large numbers of dead adults were found over the August-September period, generally lying on the ground at the base of vegetation but not buried under litter or soil. They generally consisted of the shell bearing no signs of predation, containing a semi-liquid mass of decomposed snail tissue. In some cases the contents had largely dried out, but in all cases it appeared that death had only recently occurred. As the majority of adults had emerged from hibernation at this time it could be assumed that these dead individuals had become active, if only to a limited extent, before death. There were no signs of hibernating epiphragms in the majority of cases.

Apart from the possibility of disease, the most likely explanation for these deaths would be the frosts which occur over this period. Frosts were particularly severe in August and September of 1977, and temperatures over this period generally remained much cooler than usual (Fig. 15). Wolda (1972) suggested that frosts were a likely cause of death in adult Cepaea nemoralis which died leaving an intact shell, and he pointed out that those individuals which become active on the milder winter days, leaving hibernation temporarily, would be particularly prone to subsequent frosts.

If frosts are a significant mortality factor at this time, it does not explain why adults should be affected more than large pre-adult juveniles. Possibly the older, more senescent adults are the most affected by frosts and cold weather generally, and these would therefore contribute most to adult mortality at this time. Also, if the suggestion made earlier that large juveniles may hibernate longer than adults is correct, this would make large juveniles less vulnerable to frost.

A similar adult mortality was observed to have occurred during the August sampling in area 1 but the incidence of dead individuals was much smaller, and no significant decreases in adult density occurred.

6.4.2 Adult longevity.

In area 3, the population composition histograms for December 1976 and October 1977 (Fig. 12), together with the long maturation times suggested by growth-check data, indicate that adult recruitment for each of those years was very low. This means that many of the adults

encountered in sampling must have reached adulthood two years or more previously, and this figure would be even higher if low recruitment rates had always been the norm in this population.

Comfort (1957) gives three records of maximum longevity for Helix aspersa in captivity, as observed by three different authors. These are five to six years, five-and-a-half years and eight to ten years. Presumably these are total ages, from hatching to death, and there is no indication of juvenile development times. All of these observations were made in captive conditions.

The attempt to age adults by counting aperture lip ridges at least indicates that some snails in area 3 in September had lived for up to three or four years after attaining maximum size. It is possible that absolute longevity depends on the amount of time spent in such resting phases as estivation and hibernation.

Even though no density data are available from area 3, observations over the period of study gave the strong impression that a significant reduction in adult numbers had occurred, particularly after the winter/spring mortality. The low adult recruitment over this year failed to make up for this mortality. In view of this it seems probable that adult recruitment has been greater in this population in the past and that the low recruitment over the study period represents a particular phase in population growth. In this respect it is of interest that juvenile production per adult appears to have been greater in area 1 than area 3.

The question of long-term population changes is considered again in section 6.4.5. and in detail in Chapter 7.

6.4.3 Mortality from environmental hazards.

The density data for the 1975-76 juvenile cohort of area 1 indicate a high mortality in this group over the May-August period. The large decrease in numbers between the July and August samples was particularly evident in the field. The source of this mortality is unknown, but given the tendency for small juveniles to become active sooner after cold weather, it is possible that early spring frosts may have had a significant effect. It is also possible that at this time

juvenile snails may be one of the few sources of food available to predators. However, the possible significance of frost as a mortality factor in dune populations of H. aspersa cannot be discounted.

The other obvious time of year for mortalities due to environmental hazards to occur is the late summer period, when areas of bare sand can dry out rapidly, stranding snails attempting to cross them. On hot sunny days the surface temperature of the sand can reach very high levels, and Richardson (1974) found that individuals of Cepaea nemoralis were killed by this heat. Pomeroy (1968) found that Hellicella virgata in Australia climbed poles to heights in excess of two metres to estivate in order to avoid the considerably higher temperatures at and near ground level.

The results of the experiment on the bare sand track indicate that stranding on dry sand and subsequent heat-deaths may be a significant source of mortality to young juveniles over the summer period. Extrapolating from the population data for the area, the main juvenile classes appear to be present in approximately the ratios they would have formed in the population at that time. Adults, and possibly large juveniles, appear to be less prone to this type of stranding, although there are always considerable numbers of these found lying on tracks in the area. Possibly these larger animals are more rapidly able to seek shelter as the sand begins to dry.

The results of this experiment are rather surprising in one respect in that area 1 sampling results indicated that small juveniles tended to remain relatively aggregated in distribution for some time after emergence, whereas newly emerged juveniles are the most highly represented size-class of those animals found stranded. Many of these animals would have had to have travelled a considerable distance from their emergence sites to be caught on the track. The reason may well be that juveniles which have emerged in an area of dense vegetation may be able to move a considerable distance over a lupin stem or marram plant without actually achieving much horizontal distance from the emergence site. The large sample unit used would not detect this movement.

The larger animals appear to be more resistant to heat than the smaller ones. This is likely to be due entirely to their greater volume and thicker shells.

Although the bare sand track may represent a particularly severe trap in dry conditions, especially with its wheel ruts at either side (although the contours of these are little more than gentle slopes in dry weather), large and small bare sand patches are nonetheless a significant feature of the dune habitat. Bare sand areas at Santoft almost always contain large numbers of bleached, unbroken snail shells which are likely to be the remains of previous dry-sand strandings.

The hazards of bare sand areas are further enhanced by the activity of rabbits which dig small holes in the sand up to 10 or 12 cm deep, apparently in search of plant roots. Rabbits were numerous in all study areas and their scratchings were frequently observed to act as pitfall traps for snails. The holes are generally steep-sided and only stable enough for a large snail to exit under very moist conditions. The ultimate fate of many of the snails caught in this way as the sand dried was to be buried when the sides of the holes collapsed.

6.4.4 Hibernation.

During winter sampling in areas 1 and 2 at no time were all of the adults found to be hibernating, although those not hibernating during the coldest periods were usually found to be in a resting state; withdrawn into the shell and in a sheltered position. The hibernation trends of the F and G juveniles appeared to be largely the same as those of the adults, although the possibility that they might hibernate for a longer period has been mentioned. Information on the E juveniles was limited by the fact that they are poorly represented in the population at that time of year. Of nine E juveniles found in either area during May and June, three were found to be hibernating.

Of the A,B,C and D juveniles, the majority of individuals during the June-July period were found secreted under litter or dense vegetation in a relatively inactive state. A number were found to have hibernating epiphragms, but the majority did not. In a number of instances however, individuals or small groups were found buried under about one centimetre of soil, with or without epiphragms.

There appeared to be a distinct tendency for juveniles to aggregate to a greater extent during the peak hibernation period of July in area 1. The large increase in the index of dispersion from June to July for the 1975-76 cohort (Fig. 7, Chapter 5) is independent of the mean which remained stable (Fig. 13; Table VI, Chapter 5). The effect of hibernation on adult dispersion and the possible significance of this was discussed in Chapter 5.

Positions favoured for hibernation by adults and large juveniles were at the base of dense vegetation such as marram, beneath dead vegetation and litter, or buried in the soil. Those not buried in the soil were frequently attached to the vegetation or litter under which they were secreted, or to another snail. A number were found unattached beneath litter in slight depressions in the soil, usually with the aperture facing up. Over half of those buried in the soil were found with the aperture facing up towards the surface.

Hibernation is a useful method for long-lived poikilotherms to survive periods of low temperature which would either kill them or reduce their metabolism to a point where effective functioning was impossible. Hibernation sites obviously serve the double purpose of insulation against low temperatures and protection from easy detection by predators.

6.4.5 Comparisons of populations from areas 1 and 3.

In the course of studying the short-term population dynamics and processes in areas 1 and 3, some obvious differences between the two populations have come to light.

Area 1 is an area of relatively low adult snail density, apparently the remnant of a once dense population which existed when the lupin originally planted in the area was flourishing. Area 3 is an area with a comparatively high adult density, the population appearing to be "top-heavy". This population appears to have a lower rate of juvenile production per adult snail than that in area 1, and both appear to have only limited adult recruitment.

Obviously a significant factor in the ecology of these populations has been the role of lupin. In each case, a large infestation of snails has apparently been coincident with a dense, mature lupin crop. In area 1, this crop has since undergone a

considerable die-back, apparently as a result of the snail infestation and only a few isolated patches of lupins, which would have been seeded by the original crop, remain. Presumably, lupin dieback is correlated with snail population decrease, explaining the low snail density presently found in area 1. The remaining lupin patches probably still exert some influence on local snail populations. In area 3, the population is, perhaps, in the process of decreasing at present, with lupin dieback now complete over a large area. However, it must be noted that the portion of area 3 in which most of the sampling took place still retains appreciable quantities of live lupin.

In view of this apparent importance of lupin to H. aspersa ecology, it is necessary to consider the possible beneficial effects to the snails of the introduction of lupin to the dune environment.

The most obvious role of lupin is as a food-source. Snails are strongly attracted to lupin, probably by smell, and they find it highly palatable (see Chapter 9). Other factors which may also be significant here are the nutritional value and assimilability of the lupin.

The physical effect of lupin on the snails' environment is also quite considerable, and may enhance snail survival. At its peak, three to four years after seeding, the lupin crop is a single continuous cover of dense foliage, giving a considerable degree of shelter from such elements as wind, sunlight, frosts and possibly even some predators. For example, snails climbing and feeding or estivating on lupin at night will be safer from hedgehogs and other ground-dwelling predators than those in non-lupin areas which cannot climb substantially above ground level. Also, during the spring a phase of rapid growth of the lupin occurs during which many fast growing and heavily foliated shoots appear off the older branches (Lush, 1948). At this time, the lupin may present a barrier to the songthrush (Turdus philomelos) which preys on H. aspersa. Lupin bushes growing in areas of otherwise bare sand may reduce the hazards of these areas to snails by shading the sand from direct sunlight and depositing a substantial layer of litter over the sand surface. Also, with much contact occurring between the shoots and branches of adjacent bushes, animals could theoretically move considerable distances without having to return to the ground.

The presence of lupin in an area effectively increases the amount of space available to animals per unit of habitat, by making the existing habitat more 3-dimensional. This would reduce the degree of crowding of the animals.

While the increase in food supply is likely to be the most significant factor influencing snail population increase, it is apparent that the physical effects of lupin in enhancing snail mobility and survival cannot be discounted.

Whatever the reasons, it is obvious that the occurrence of heavy snail infestations in lupin areas within about three to four years of the seeding of the lupin means that juvenile survival and/or juvenile production must be considerably greater at the population build-up stage than that found in either of the main study areas.

It appears that the eventual dieback of lupin, resulting from the activities of the snails (see Chapter 9), brings about a decrease in the snail population also. However, the evidence available from area 3 suggests that snail population decrease may occur in advance of lupin dieback to some extent.

These longer term population processes are studied more fully in the following chapter.

6.4.6 Area 2.

The snail population in area 2 differs in some respects from each of the other two populations. The sample area included an area of lupin which had a heavy snail infestation about four months prior to sampling. This lupin was virtually all dead by the beginning of sampling, and the snail population appeared to have dissipated to some extent, but large numbers of animals were still to be found in the dense marram of the lupin patch. This lupin patch was mainly limited to a more open area of forest where the five to six year old pines had not grown as tall or as bushy as the surrounding trees. In most other parts of the sample area, dense pine tree growth appeared to be in the process of modifying the forest floor vegetation.

It appears then, that the area 2 population was the remnant of a heavy snail infestation at a time when the lupin was more widespread in the area. This whole region (block 101) contained signs of

a large snail population in the past in the form of old empty shells and the remains of long-abandoned thrush "anvil" sites.

Adult density in area 2 ranged from 1.4 to 1.8 animals/m^2 over the three samples. This density is considerably higher than that in area 1 but not as high as that of area 3. Presumably, density had decreased with the die-back of virtually all of the lupin in the area. Also, thrush predation may have been a significant factor here. (See Chapter 8).

One anomalous feature of the area 2 results was the large proportion of large juvenile animals in the population. These gave the impression of high adult recruitment in this area, yet at the same time, young juvenile production appeared to be much lower per adult than in areas 1 and 3. Why this should have been so is not certain.

CHAPTER 7

LONG-TERM POPULATION PROCESSES

7.1 Introduction

As the study in area 3 progressed, it became obvious that a more complete picture of the long-term population ecology of *Helix aspersa* in the disturbed dune ecosystem would only be obtained by studying areas in other stages of infestation, especially those in which the species was increasing in density in response to the availability of lupin. This would, in turn, raise the question of the source of snail infestations: do snails move into a block with dense lupin from another area of infestation, or have they always been there in small numbers, increasing in density in response to lupin growth? Furthermore, what is the eventual fate of all snail populations under the rapidly growing pine forest, with its associated modification of the environment?

At the beginning of November, 1977, Forest Service staff pointed out an area of lupin in block 83, not planted with trees at that stage, which had been noticed for the first time to have an exceptionally dense snail infestation. This area (area 4) was briefly described in Chapter 3, (Section 3.2.4). It was visited and sampled on November 8th and again on the 29th of that month.

A second area of interest was also found near area 3. About 400 m southeast of area 3, alongside the approach track, was a large area of live lupin, stretching a considerable distance back into block 122 (Fig. 17). Although this lupin had always been observed to have snails on it, they were not noticed in as large numbers as in area 3. Also, in spite of a heavy infestation of Kowhai moth larvae on the lupin in this area during the summer of 1976-77, the bushes remained in reasonable condition and did not appear to have suffered greatly from the presence of the snails. Towards the end of the study, the snail density appeared to have increased considerably.

In early December samples were taken from area 3, from the lupin patch in block 122, and from lupins about the same distance north of area 3. A second sampling was undertaken in early February, 1978,

with samples being taken from a series of lupin bushes and patches at intervals from area 3 to the lupin area in block 122.

The aim of sampling the new areas was to learn about the snail population composition of these areas and to compare their compositions and densities with those of the other study areas.

7.2 Methods

7.2.1 Sampling and sample sites

7.2.1.1 Area 4.

Area 4 was first visited during showery weather in early November just after a short dry spell, and the snail population was rapidly becoming active. Large numbers of snails were feeding on live lupins alongside the vehicle track. A large branch was removed from one lupin bush to assess the amount of snail damage, and all of the animals on it were removed and taken as a sample (Sample 1).

The area was visited again near the end of November when most of the population was estivating during a period of dry weather. On this occasion the lupin-stem sample for snail dispersion was taken, the details of which are in Chapter 5 (Section 5.2.2). The snails collected in the process of this sample were also used as the population composition sample (Sample 2).

All animals from both samples were scored as adult or juvenile and measured for shell height.

7.2.1.2 Area 3 and adjacent areas

Samples in these areas were taken in the same manner as those during the main area 3 study. All animals were removed from one or more lupin bushes and from the ground and vegetation beneath those bushes. In this case, sampling was mainly restricted to single lupins or groups of lupins rather than being spread over several sites.

On the first occasion (8.12.77) samples were taken from: a portion of a small lupin patch in area 3 (Sample A1);

a single lupin in the block 122 lupin area, isolated from surrounding bushes by bare sand (Sample A2);

three lupins several metres apart in block 128 near the northern boundary of the forest, and adjacent to farmland (Sample A3). The state of the lupin in this area was similar to that in area 3.

The positions of these three sites are shown in Fig. 17.

On the second occasion (2.2.78), samples were taken from three different locations in area 3, from two bushes about 15 cm apart in the block 122 lupin area (one of these was the bush sampled previously from this area), and from two locations between area 3 and the block 122 lupins. Each of these samples (B1 - B7) involved a single lupin bush or a portion of a small group of lupins. These locations are also shown in Fig. 17.

All animals were scored as adult or juvenile and shell heights were measured. In addition, the shells of the adult snails from samples B1 - B7 were examined under a stereo dissecting microscope and the number of juvenile growth-checks on each shell counted.

7.2.2 Data analysis

The juvenile shell height data from each sample population was divided into the juvenile size-classes so that population compositions of the different samples could be compared with each other and with size-compositions of the populations of the main study areas. The growth-check data was used to compare maturation times in the different sample areas.

In addition to this, the results of the earlier studies indicated that adult size, as measured by shell height, varied between different areas. Mean heights of adults were determined for areas 1, 2 and 3 using the data collected during the studies in these areas. These were then compared with each other and with the mean heights of adults in the samples described above.

7.3 Results

The sampling results from area 4 are presented in Fig. 18. The number of animals in each size-division are expressed as a percentage of the total catch. As the second sample in this area consisted of two subsamples from two lupin bushes about 150 m apart, the results are presented both combined and separately for each bush.

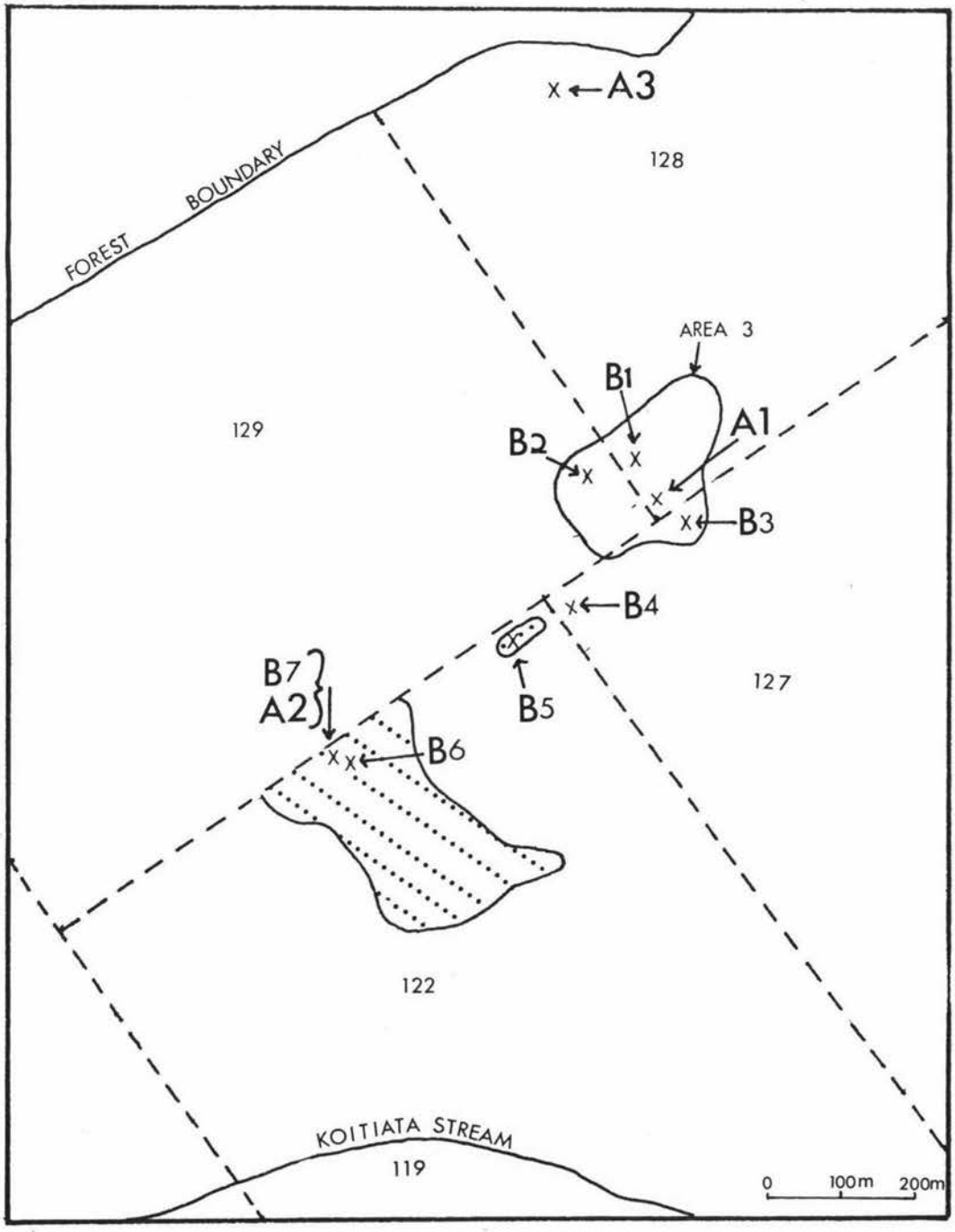


Fig. 17. Area 3 and surrounding areas, showing sites of samples A1 - A3 and B1 - B7

129 Forest block number

Lupin

Vehicle track

Of interest in area 4 was that the lupin bush from which the first sample was taken and a number of surrounding bushes, all of which appeared to be well foliated and healthy at that time, were dead two-and-a-half weeks later when the second sample was taken. This appeared to be due to the heavy snail infestations found on them.

The population compositions of samples A1 - A3 are presented in Fig. 19, and those of samples B1 - B7 are presented in Fig. 20.

Growth-check results for the adult shells from areas B1 - B7 are presented in Table XIII. The results for samples B2 and B3 are combined as the shells involved were inadvertently mixed in the laboratory.

Table XIII : Growth-check numbers on the shells of adult snails in samples B1 - B7. (2.2.78)

Number of Growth-checks	Sample					
	B1	B2 and B3	B4	B5	B6	B7
0	-	6	5	3	4	22
1	14	45	13	24	1	4
2	11	33	1	3	-	-
3	4	15	2	-	-	-
4	-	3	-	-	-	-
Total animals	29	102	21	30	5	26

Adult shell-height data from areas 1, 2 and 3, collected over the course of the study, are presented in histogram form in Fig. 21. Adult heights from samples A1 and B1 - B3 were included in the area 3 data.

Means and standard deviations for adult shell heights are given in Table XIV for areas 1, 2 and 3; for samples 1 and 2 of area 4, combined and separately; and for samples A1 - A3 and B1 - B7, with the data from B6 and B7 combined as only five adults were found in sample B6. Also, mean and standard deviation results are given for the combined data of all samples taken from the block 122 lupin area (A2, B6, B7).

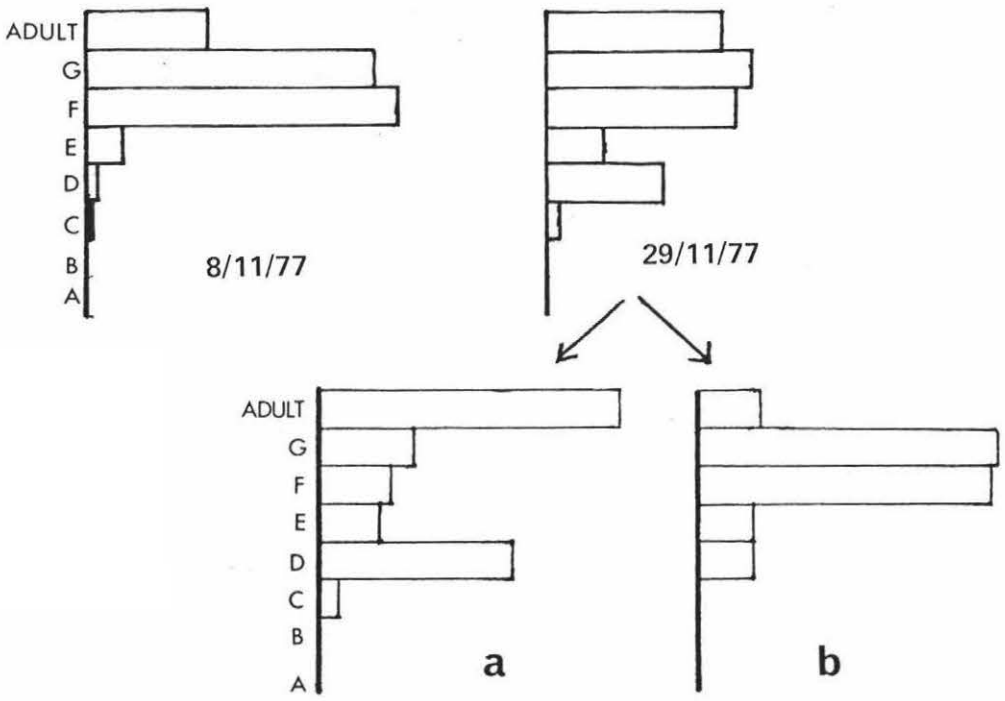


Fig. 18 Area 4 sampling results.
subsamples of 29/11/77

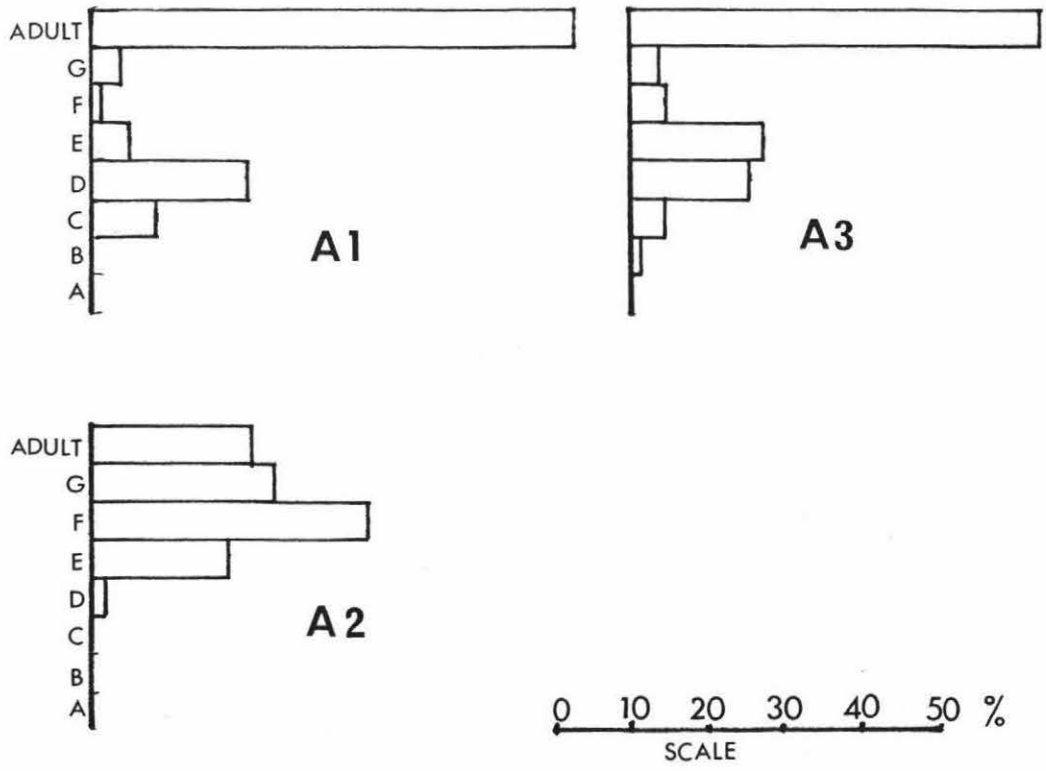


Fig. 19 Population compositions of single-site samples,
A1 – A3

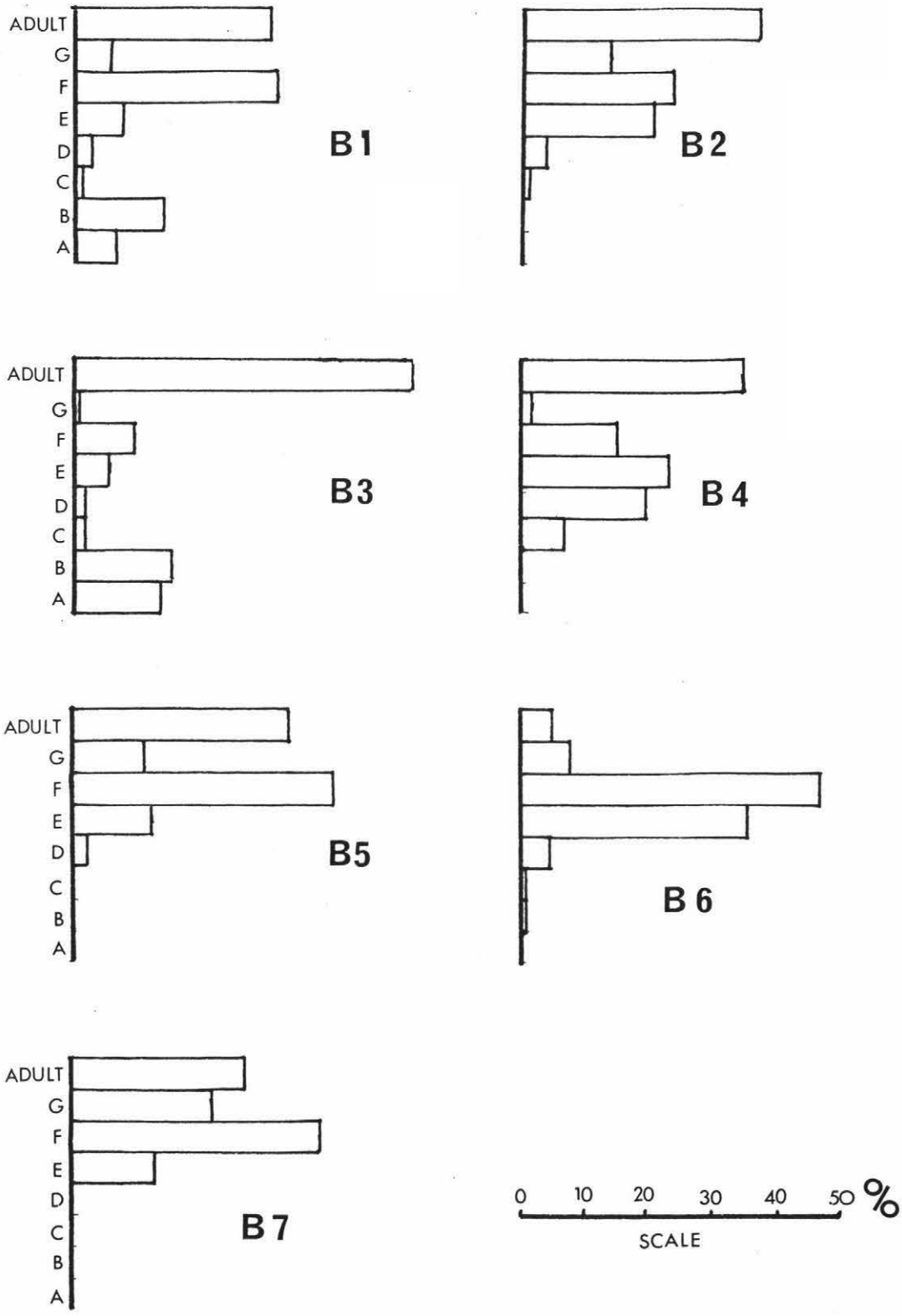


Fig. 20. Population compositions of single-site samples, B1 - B7

Fig. 21. Adult height distributions, areas 1,2 and 3

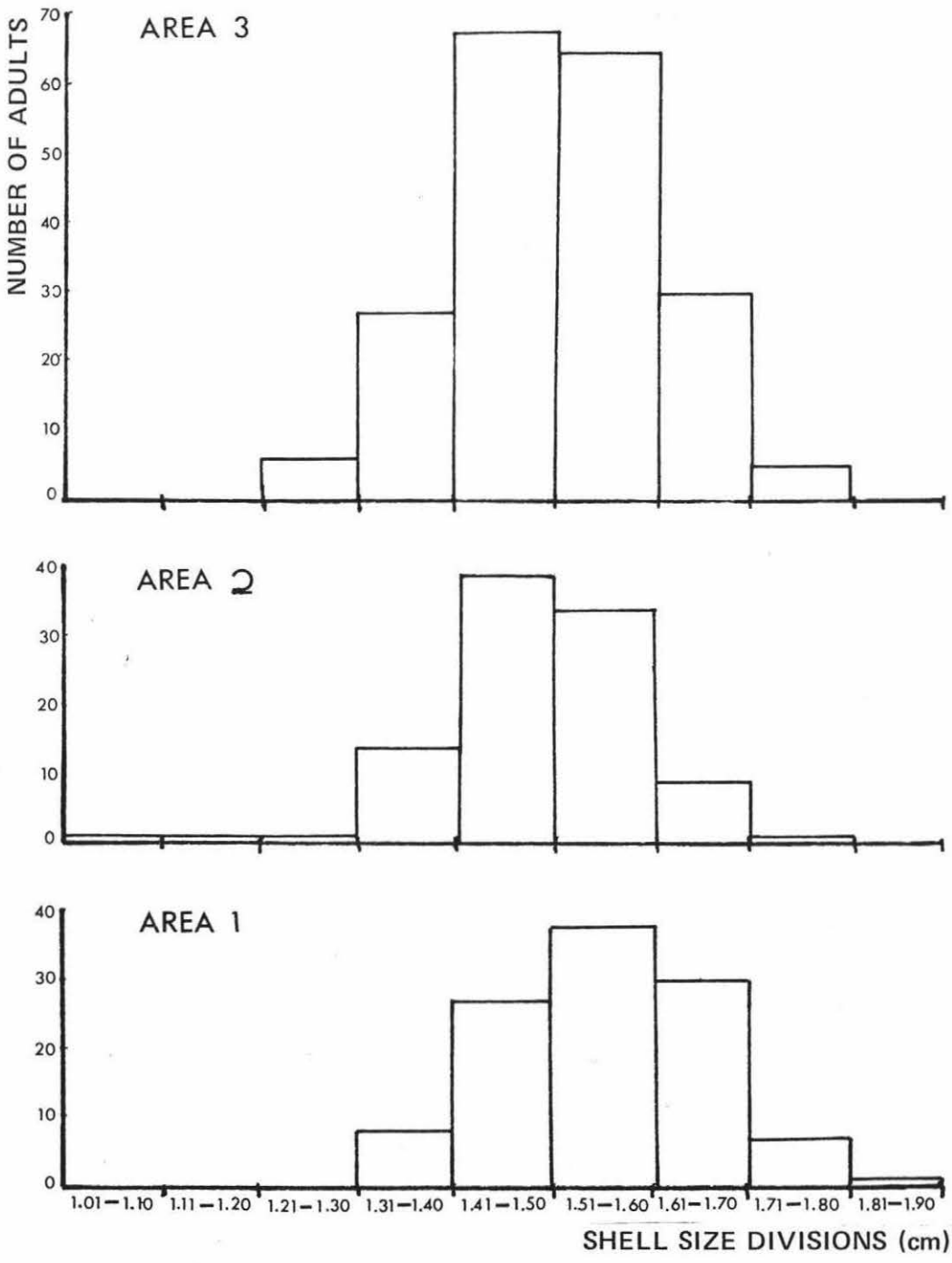


Table XIV : Mean adult shell heights.

Area/Sample	$\bar{x}$ (cm)	s	Number of adults
Area 1	1.564	0.103	109
Area 2	1.496	0.104	100
Area 3 : Total	1.490	0.098	635
Sample A1	1.511	0.082	55
Sample B1	1.460	0.117	28
Sample B2	1.482	0.090	36
Sample B3	1.464	0.090	59
Sample B4	1.486	0.082	19
Sample B5	1.501	0.107	31
Sample A3	1.520	0.079	46
Block 122 Lupin patch : Total	1.566	0.097	53
Sample A2	1.601	0.079	30
Samples B6 and B7	1.521	0.101	23
Area 4 : Total	1.568	0.089	55
Sample 1	1.578	0.097	21
Sample 2	1.561	0.086	34

7.4 Discussion

7.4.1 Population density increase.

The population size-compositions of area 4 and the lupin area in block 122 stand out immediately from those previously found for areas 1 and 3 by the high proportions of large juveniles in comparison to adults. Assuming that many of these animals will survive to maturity, this will mean a considerable increase in the adult populations of both areas. Adult recruitment in these populations is obviously well in excess of the other areas studied.

Not only are the populations in these areas increasing but they are doing so at a much greater rate than would be expected from the juvenile growth-check data obtained from the September sample of area 3. The growth-check results from adult shells obtained from block 122 (Samples B6 and B7) indicate that juveniles are maturing at a

considerably younger age in this area than those of nearby area 3. Possible reasons for this are discussed later.

These results demonstrate that major increases in population density of H. aspersa can take place within a few years, and that these occur in the dunes in response to lupin establishment. This suggests that non-lupin areas restrict adult-recruitment processes, presumably as a result of factors related to diet. This could operate at several levels in the recruitment process, such as egg production or juvenile development and survival.

7.4.2 The origin of snail infestations.

Area 3 is reported by Forest Service staff to have had a high snail population density for a number of years, whereas the lupin area in block 122 has only recently acquired a comparable density. In view of the fact that lupin seeding took place at about the same time in each of these areas, an explanation is required as to why snail population growth was delayed in block 122.

The most probable explanation is that there were no snails in the block 122 area prior to lupin seeding and that establishment of a snail population by individuals dispersing from surrounding areas was a slow process. Before the planting of marram and lupin occurred, bare sand areas and other habitats unsuitable to snails were more widespread than at present, and the distribution of snails would have been correspondingly patchier. Probably, quite large areas would have been entirely free of snails. A combination of limited mobility and a homing tendency (Potts, 1975) would ensure that movement into an area that had since become more favourable would occur slowly.

Establishment of lupin in these areas occurred not more than six years prior to the beginning of sampling in area 3. It is therefore likely that small numbers of H. aspersa occupied area 3 before Forest Service operations began, and that their numbers increased in response to the growth of lupin.

The patchy distribution of snails and their uneven population build-up over an area was demonstrated by the pattern of lupin die-back observed in area 4. Areas of almost completely dead lupin, 20 to 50 m in diameter, were found to be more or less surrounded by live lupin.

Large numbers of snails were found on both the dead and live plants. It is likely that this die-back pattern is due to a local population increasing to a high density and gradually dispersing into surrounding areas.

The strong homing tendencies of H. aspersa observed by Potts (1975) would have an important effect in slowing dispersal into new areas, and maintaining initially patchy distributions. In this respect it is of interest to note the population size-composition differences which can exist between lupin bushes which are only a few metres apart. Examples are the two sample sites comprising Sample 2 of area 4; samples B1 - B3 taken from sites within area 3; and samples B6 and B7 from two lupin bushes in block 122. These sites differed from each other with respect to the relative proportions of adults and juveniles, and the distribution of juveniles in the various size-classes. However the overall population trends are still visible in each site of a particular area. It is possible that the populations of the different sites function independently of each other to a certain extent as a result of limited mobility and homing tendencies. In Potts' (1975) study strong homing behaviour was the single factor causing marked delineation of populations of H. aspersa which mingled at night during feeding and other activities. This phenomenon was not investigated in the present study.

Whatever the causes, variations in population size-composition between sites in one area will affect sampling programs such as the one adopted in area 3, in which only one or two sites were sampled on most occasions. This is the most likely explanation for the anomalies which sometimes occurred between results of consecutive monthly samples.

7.4.3 The origin of snails in the sand dunes.

It appeared to be the general belief amongst the Forest Service staff at Santoft that their activities in the dunes had resulted in the introduction of H. aspersa. Pine tree seedlings, marram grass, and a number of other plant species being tested for stabilization of the foredune, are all grown in Forst Service nurseries before being transplanted into the dunes. It was believed that snails or their eggs

were introduced with these plants and thereby became established in the dunes, especially in lupin areas.

While it is quite possible that snails have been, and still are, introduced into the dunes in this way, there is evidence to suggest that snails were present in at least some regions prior to Forest Service activity. Mr C.W.S. van Kraayenoord (pers. com.) found that snails were present in dune areas south of the Turakina river mouth, and about 2 - 3 km northwest of area 3, during the late 1950's. Large numbers of bleached snail shells were in evidence, scattered over areas of bare sand. The Ministry of Works were experimenting with Lotus spp. in this area, and heavy snail infestations were occurring in trial plots two years after their establishment.

Snails have also been found in dune country in the Himatangi area about 5 km south of the Rangitikei river mouth, some distance from the nearest Forest Service activity.

There is no doubt that lupin strongly attracts snails and that snails disperse into lupin areas from surrounding regions. However, this occurs on a scale rather smaller than that involving whole forest blocks of up to 100 hectares. The speed of snail population density build-up over large areas in response to lupin growth, and within only two or three years of lupin seeding, suggests that low density snail populations inhabited these areas prior to Forest Service activity. Areas such as the block 122 lupin area were probably devoid of snails initially, so that infestation was delayed considerably compared to the surrounding areas. On the other hand, block 128 , a portion of which was included in areas 3, as well as the eastern portion of block 129 all display the same level of lupin dieback, suggesting that all of these areas were infested at much the same time. This is supported also by the results of sample A3 which has a similar population composition to the area 3 samples.

The initial introduction of snails to dune areas is therefore open to speculation. It is possible that it may have occurred during early use of these areas by farmers, before the Waitarere dune-building phase (Cowie, 1963) began.

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7.4.4 Density effects in snail populations.

The comparison of mean adult heights from the different study areas show that adults in areas 2 and 3 are smaller on average than those of areas 1 and 4 and the lupin area of block 122 ($P < 0.001$). It would appear, therefore, that animals in populations that have exhibited a high degree of adult density for some time do not grow as large as animals in populations with low density or which are in the process of attaining high densities. This suggests the existence of some type of density-dependent factor having an inhibitory effect on growth.

Even more striking are the results of growth-check analysis of the adult animals taken during the sample of 2.2.78 in the area 3 - block 122 region. Samples B1 and B3, all within area 3, gave similar growth-check analysis results to the September sampling of this area. The majority had one or two growth-checks, with a substantial number having three, and only a few having zero or four. On the other hand, the combined results of samples B6 and B7 from block 122 show that 2 of 31 animals had no growth-checks, the remaining five having one each. Samples from the areas in between these (B4 and B5) are also intermediate in respect of growth-check number.

It would appear that juvenile snails in areas with increasing adult population density grow much faster than those in areas with high adult density. The former reach adulthood as much as two years before the latter. This interpretation is supported by the fact that all but one of the B6 and B7 adults displayed very little wearing of the periostracum, whereas at least half of the area 3 adults would have had 40% or more of this layer worn off. An intact periostracum was also characteristic of snails from area 4. Once again, some type of density-dependent inhibition in high density populations is suggested.

Herzberg (1965) found that crowding under experimental conditions adversely affected growth and reproduction in H. aspersa. Even when the animals were not crowded, the containers housing them had to be cleaned out thoroughly at regular intervals to prevent them being similarly affected. Both crowding and failure to clean containers housing uncrowded animals resulted in the animals being less active, reproducing less frequently, and growing irregularly, with some ceasing growth entirely. Under optimal conditions (no crowding and regular

cleaning of containers) growth and reproduction results were relatively consistent. Herzberg considered that excretory products were implicated in the observed inhibition.

Effects of crowding on growth have also been observed in natural populations of Cepaea nemoralis. Williamson et al. (1976) found that denser populations had a smaller average adult shell size; shell diameter decreasing by 6 - 9% as adult density increased from 0.5 to 5.5/m^2. This diameter decrease correlated with body weight decreases of as much as 24% (Williamson, 1976). It was found that preferred food species were present all year round and that calcium reserves were adequate, and it was therefore concluded that snail-snail interactions (chemical or behavioural) were responsible, through their effects on juvenile growth. Initial laboratory studies indicated that the presence of mucus trails of other snails inhibited snail activity (Williamson et al., 1976).

A notable anomaly in the adult shell height data in Table XIV is the large decrease in mean height between the two samples, A2 and B6, B7, taken two months apart from the lupin area in block 122. Williamson (1976) found that there was a reduction in size of adult Cepaea nemoralis maturing later in the season, and he assumed that this was due to the increasing density of large animals over the season. This explanation may hold in the present case also. Most of the adults of the first sample would have reached maturity either the previous year or before that and they would therefore have grown at a time of relatively low snail density. The second sample undoubtedly included animals which had matured in the intervening two months and these animals would have been exposed to density effects not only from the adults but from other members of their own cohort. The greater range of adult sizes produced by this situation is reflected in the larger standard deviation and variance of the second sample.

Wolda and Kreulen (1973) observed that in a rapidly expanding population of C. nemoralis, 25% of the juveniles which survived to adulthood did so in their first year. In another study, on a declining population (Wolda, 1963), there was no evidence of such fast-growing juveniles.

While density-dependent processes may explain differences in maturation times and adult size between populations, there still remains the question of juvenile survival (adult recruitment). The low juvenile survival in area 1 has been suggested to be related in some way to the paucity of lupin in this area. However, rates of juvenile survival in area 3 appeared to be even lower in spite of the fact that considerable quantities of live lupin still remained in parts of the area and most of the samples were taken from these.

Wolda and Kreulen (1973) compared the results of studies on a declining population Cepaea nemoralis (Wolda, 1963) and an expanding one (Wolda and Kreulen, 1973). They found that egg production per snail in the expanding population was more than twice that in the declining one. Egg survival was also 25% higher, so that juvenile production per adult was about three times higher in the expanding population. However, the main difference between the two was in the survival of young juveniles. In the expanding population, 46% of the juveniles hatched were still alive after one year, compared with 2.3% in the declining population. Wolda and Kreulen (1973) suggested that the major factors affecting juvenile survival were probably drought and predation and that the declining population happened to be affected by these to a far greater extent at the time of study than the expanding population when it was studied. However they were uncertain on this point as in the great majority of cases the causes of juvenile death could not be established. They considered that while some density governing processes were probably acting, their influence on population size was negligible.

Williamson et al. (1977) made a six-year study of a natural population of C. nemoralis in grassland and found that the most successful year for juveniles was produced when adult population density was relatively low, while the least successful years occurred when adult densities were high. They considered that the study provided circumstantial evidence for some type of density-dependent control of Cepaea populations affecting juvenile survival. They agreed with Wolda and Kreulen (1973) that adult recruitment from juveniles was the most important factor determining adult population size.

In the present study there is some evidence for a considerably lower rate of juvenile production per adult in area 3 than in area 1.

This may be a direct result of the lower mean adult size in area 3. Adult size has been found to affect egg production in Cepaea nemoralis, smaller adults being found to produce smaller egg clutches than larger adults (Wolda, 1963, 1967; Wolda and Kreulen, 1973). However, the data provided for Cepaea would be insufficient to explain the differences observed in this study.

While there is no data available on egg production and juvenile survival in area 4 and the block 122 lupin area, the population compositions of these areas at the time of sampling suggest that the major factor affecting adult density in dune populations of H. aspersa is also juvenile survival to adulthood. No study of juvenile mortality was made in the course of this work, so that factors which might be responsible for the differences in juvenile survival displayed by different populations are unknown. However, the effects of drought and other environmental hazards can presumably be ruled out as these will be similar in all areas. Also, the availability of lupin as a food source was not a limiting factor in area 3, which showed very low juvenile survival rates.

The remaining obvious possibility is predation, and this is an unknown factor. If differences in rates of predation are significant, this would mean a considerable change in predation rates over the distance of 400 m separating area 3 and the block 122 lupins.

While the possible effects of predation on young juveniles cannot be overlooked, it is suggested that circumstantial evidence, at least, indicates that some type of direct density-dependent control of juvenile survival may be implicated in H. aspersa populations.

Obviously, this point will only be settled by further intensive population studies, particularly into the sources of mortality of young juveniles in natural populations. Some of the difficulties inherent in such a study were briefly mentioned by Williamson et al. (1977). They include the need for careful handling of very small juveniles and the impossibility of marking them to make them individually recognisable. Also, an intensive sampling program, particularly in the dune environment, would be impossible without widespread destructive sampling of the vegetation for animals.

Lack (1954) pointed out that fecundity falls and larval mortality rises with increased density in laboratory insect populations, but that these occurrences are directly related to food shortage. In these circumstances in natural populations adults would tend to move elsewhere to lay their eggs. He suggests that the main density-dependent effect in nature is probably movement. In a terrestrial snail species, however, the amount of movement may be limited by both the animals' mobility and the type of terrain over which movement may have to occur. In this case it is possible that direct density-dependent control of recruitment, in the form of reduced fecundity and juvenile survival, etc. may be a necessary alternative.

7.4.5 The patterns of snail population growth and decline in the dunes.

It appears that H. aspersa has been introduced into the sand dune country in the past as a result of human activity. Its initial distribution was probably limited by the large extents of bare sand which existed at that time. The introduction of marram and lupin into this environment has resulted in rapid population density increases, presumably as a result of the lupin being a highly nutritious food plant. Increases in adult population density eventually appear to cease due to a significant decrease in adult recruitment. This appears to be correlated partly with decreased production of young juveniles but to a greater extent with increased juvenile mortality. It is possible that both of these phenomena are affected by adult density. More certainly, adult density has an effect on both the maturation times of juveniles, and the size they attain at adulthood, the former increasing and the latter decreasing in more dense populations.

When the population reaches this stage, recruitment appears unable to balance adult mortality and density decreases. It is probable that this allows some increase in juvenile production and adult recruitment, and this appears to be occurring in some of the sites sampled in and around area 3 on 2.2.78. Presumably, the population eventually decreases to a much lower density when lupin die-back, which has been progressing rapidly up to this point, is completed.

Areas of marram with little or no remaining lupin, such as area 1, appear unable to support large snail populations. Adult recruitment again appears to be the critical factor, but this time it is presumably influenced more by factors such as available food or food quality rather than adult densities. At this stage, animals are attaining a larger size at adulthood again. Development rates, as determined by shell growth checks, were not obtained for the area 1 population.

The population of area 2, in terms of stage of growth, probably lies between areas 3 and 1. It has reached and passed its peak of adult density and is well into the decline period. However, the situation here may be somewhat complicated by the greater age of the pines in this area than in area 1. At the time of the study in this area, the shading caused by the densely foliated young pines already appeared to be having a significant effect on the undergrowth over large areas.

The area 2 adults, many of which showed signs of being rather old (aperture-lip ridges, wear and tear), remained of a small average size. The relatively large numbers of large juveniles found may be associated with the decreased densities. Surprisingly few small juveniles were found, and these mainly from only one or two quadrats in each sample. This may have been due in part to the recent die-back of most of the remaining live lupin, which could have meant that the adult population was too dense for the available food. It may also have been a result of the effects of pine growth on the undergrowth, and therefore the other food items of the animals in some areas. However, no entirely satisfactory explanation could be found for these observations.

The ultimate fate of snail populations in the dune-forest ecosystem is probably an eventual demise under the rapidly growing Pinus. As the trees grow, the undergrowth species gradually die back until there are few, if any, left. In one area of 14-year-old pines, a search for live snails failed to reveal any traces, in spite of the fact that large numbers of spindly, etiolated lupin bushes had grown under the trees. There was virtually no nother undergrowth. There had apparently been a snail population in the area at one time, as

large numbers of highly weathered snail shells were found under the pine-needle litter and in the soil.

SECTION III

PREDATION BY THE SONG THRUSH

CHAPTER 8

PREDATION ON H. ASPERSA BY THE SONG THRUSH (TURDUS PHILOMELOS) IN AREA 2

8.1 Introduction

Predation on snails by song thrushes, Turdus philomelos Br., and their use of hard-surfaced "anvils" on which to break the shells open is a well-known phenomenon (Taylor, 1907-14). The various types of behaviour involved, and the typical damage caused to the shell have been described by Morris (1954). Seasonal changes in the snail predation activities of thrushes have been studied in different areas by Goodhart (1958), Davies and Snow (1965) and Cameron (1969). Other useful observations on this subject have been made as a result of many studies of the effects of predation on the frequencies of the genetically based colour and banding-pattern morphs of the landsnail Cepaea nemoralis (e.g. Cain and Sheppard, 1950; Sheppard, 1951; Richardson, 1974).

Thrush predation in the study areas appeared to be irregular in occurrence from one area to another. Frequently there was ample evidence of previous activity in the form of many old, weathered shells strewn about anvil sites, but with little or no current activity apparent. This was the case especially in areas 1 and 3.

Area 2 (Block 101), however, appeared to have reasonably high levels of current predation, judging from the numbers of unweathered shells encountered on anvil sites during sampling. Objects chosen for anvils included the bases of pine trees, fallen pine cones or branches, and the hard woody parts of fallen lupin stems. In other places, use was frequently made of stones and rocks along the edges of Forest Service tracks.

The part of area 2 around which thrush activity appeared to be particularly concentrated was a more or less continuous series of patches of live and standing, dead lupin, mainly in dense marram, where the pine trees tended to be smaller in size than those nearby. These areas were

more open to sunlight than the surrounding forest. It was on this lupin that heavy snail infestations were noted in December 1975. Most of the lupins which at that time had been alive and heavily infested with snails were dead in March, and the snail population was no longer as evident as it had been. It appeared that the snail density had decreased to some extent.

In May 1975, the Forest Service commenced some pruning operations in block 101. These were mainly confined to a swampy area where tree growth was more rapid than on the higher ground. The operations extended as far as, and included most of, the lupin area described. Many of the unpruned trees were not thinned out at this time. In spite of this disturbance, thrush predation continued to occur judging from the shells building up around anvils under the unpruned trees east of the lupins.

At this stage it was understood that further operations would not be taking place in this area until some time into the following year, and the thrush predation study was therefore commenced. Unfortunately full pruning and thinning operations recommenced in early December. Many of the anvil sites were covered by fallen branches and trees and as the disturbance and the radical alteration of the habitat would have had a major effect on the birds, the study was abandoned at this stage.

A note on nomenclature : Although many authors still refer to the song thrush as Turdus ericetorum (Turton), in this study the more recent tendency to use the name T. philomelos is followed.

8.2 Methods

8.2.1 The thrush anvil study.

8.2.1.1 Anvil site locations.

An initial assessment of thrush predation on snails was begun during March 1976 when a rock was placed near the base of a pine tree where damaged snail shells had been appearing. The site was cleared of all shells, and further shells were collected from around the rock at regular intervals. Further study did not get under way until June, when

sampling in area 2 ceased, making more time available.

The area of unpruned trees along the eastern side of the lupin areas was searched and over a period of about one month, eight natural anvil sites were located. In each case all existing shells were cleared from the site and a large rock placed beside the existing anvil. It was hoped that the birds might concentrate smashing open of shells from that locality on the rock provided, rather than using several natural anvil sites which was likely to have been occurring (Morris, 1954). The rock also served to mark the site location as visibility amongst the young, unpruned trees was very restricted in most places and there were few readily identifiable landmarks. Relocating a natural anvil site which had not been used since the previous removal of shells could have proven rather difficult. A painted stick was placed a few yards away from most of the anvils as a further aid to relocation.

In each case, the birds used the rocks provided in preference to the original anvil. This was probably due to the hardness and rigidity of the rocks in relation to the available natural anvils. It could not be established with certainty whether or not other natural anvils in the locality were also being used.

8.2.1.2 Shell collection and analysis.

All shells were collected from each anvil at approximately two-week intervals. As thrushes sometimes carry empty shells to anvils (Morris, 1954) and as old broken shells are sometimes unearthed by wind or rabbit activity, unbroken shells and any shells displaying weathering or dulling of the inner, shiny nacreous layer were rejected. Some shells tended to be broken up more completely than the others, and in order not to count the same shell twice, only fragments which included over half of the aperture lip were counted.

Aperture lip characteristics were used to divide shells into adults and juveniles. Juvenile shell heights were measured when this was possible. When the damage sustained by the shell made measurement impossible, an estimate of height was made based on other dimensions such as aperture size. Not all juvenile shells could successfully be estimated for height.

During the winter months, the number of shells with remains of

hibernating epiphragms were noted.

8.2.1.3 Predation mortality in relation to snail density.

It was desirable to attempt to relate the observed predation mortality of snails to their density in the environment. Morris (1954) found from marking studies that released snails always reappeared as broken shells in the same general 20' x 20' (6 m x 6m) area in which they were released. In this case however, a series of concrete paths provided almost unlimited anvil sites so that it was unnecessary for birds to move very far between capture and consumption of snails. Sheppard (1951) similarly released marked snails in woodland localities and found that anvils 30 yards outside the area in which the snails were released never had marked individuals broken on them. Further evidence showed that thrushes in that study area were never carrying snails more than 20 yards and usually less than this.

It was found during the study that natural anvils tended to be located in patches of bare sand or at least in places where vegetation was either sparse or dead and flattened. No anvil sites were found, for example, in dense, long marram. Presumably avoidance of anvil sites enclosed by dense vegetation makes the birds less vulnerable to predators while using the anvils. Suitable sites were common in area 2, especially where pine tree growth was advanced and dense, as much of the undergrowth, where there was any, consisted of species with a low or sparse growth habit. There seemed to be no shortage of suitable sticks and other objects for anvils, quite apart from the tree trunks. It was therefore considered that the distance moved by a thrush from the place of capture of a snail to a suitable anvil site would tend to be minimal.

In view of this, approximate "areas of activity" of thrushes around each anvil were calculated assuming maximum activity radii of 10 m and 20 m. Where this meant that activity areas around different anvils overlapped, the combined area was calculated and considered as a single unit of thrush activity.

The relative positions of the anvils within the study area were established using tapemeasure and compass. The low unhindered visibility under the young pines and the generally uneven nature of the ground mean that there is a degree of inaccuracy in the resulting map.

8.2.2 Predation on juvenile snails

As collection of shells from the anvils proceeded it became obvious that no juvenile shells below a certain size were appearing. This could be due to, 1. a lack of small juveniles in the population; 2. only large animals being taken; 3. shells of small juveniles being sufficiently fragile that the animals were consumed complete with shell or the shells were removed at the place of capture and the animals then consumed.

Although sampling data revealed that small juveniles were considerably less common than in other sampling areas it was felt that they were present in sufficient numbers that the thrushes would be preying on them if they took them at all. An attempt was therefore made to see whether this was actually occuring.

Lobb and Wood (1971) used 5% KOH to break down starling faeces in order to collect the resistant chitinized parts of the birds' food species, which could then be identified. As the radula and mandible of snails are also chitinized, it was decided to use a similar technique to break down thrush faeces.

The standard method for preparation of snail radulae involves boiling the head of the animal in a 10% KOH solution for a few minutes (Mahoney, 1973). In view of this, this treatment was given to the thrush faeces to ensure as complete a breakdown of extraneous matter as possible.

8.2.2.1 Collection of faeces and extraction of radulae.

Bird faeces were frequently found on the ground or on tree branches near to anvils. These were assumed to be thrush faeces, and they were collected whenever found from July onward. The amounts of faeces found in this way were rather small, so that they were all bulked for analysis. This material was insufficient and too irregularly available for a realistic monthly analysis for snail radulae. The faeces were collected in unstoppered bottles and allowed to dry out. They were stored in the laboratory to await analysis.

For radulae extraction, the faeces were placed in an aqueous solution of 10% KOH and boiled for five to ten minutes. The solution was then allowed to cool and the excess KOH decanted. The remainder

of the solution, containing all of the resistant solids, was diluted with water and then sieved through a standard kitchen sieve, diameter 12.5 cm, with a mesh size slightly in excess of 1 mm. This was simply to divide the solids into large and small particle sizes to facilitate searching. Both fractions were searched under a binocular dissecting microscope for radula fragments, which were collected into 70% ethanol.

8.2.2.2 Preparation of standard radulae for comparison.

Radulae from juveniles of known size were prepared for comparison by excising the heads of the extended snails and boiling them in 10% KOH. The individual radulae, with mandible attached, were removed with forceps and placed in 70% ethanol.

8.2.2.3 Staining and mounting of radulae.

Staining and mounting of the radulae was performed using the second method described by Mahoney (1973). Radulae were stained in a concentrated solution of chlorazol black E in 70% ethanol for 10 - 15 minutes, differentiated in terpineol for 20 minutes, then dehydrated in absolute alcohol for a further 20 minutes.

The curved nature of the radulae, especially the standards, made them difficult to mount whole, so that they were cut with a scalpel into three or four fragments before being mounted in euparal.

8.2.2.4 Description and measurement of the radulae.

The radula of H. aspersa is described in detail by Taylor (1894 - 1900; 1907 - 14). It consists of a series of transverse rows of teeth attached to a basal membrane. The median tooth of each row is symmetrical, with a large central cusp or cutting edge (mesocone) and a small lateral cusp (ectocone) at each side. The median tooth is attached to the basal membrane by a basal plate. The lateral teeth, on either side of the median tooth, are assymetrical, with the lateral cusp nearest the median tooth (endocone) being considerably smaller than the outer lateral cusp or ectocone. Similarly, the basal plate of the lateral tooth is assymetrical (see Plate 3).

In adult and large juvenile H. aspersa, there are 20 lateral teeth on either side of the median tooth in a single transverse row.

Plate 3. Snail radulae prepared from thrush faeces.

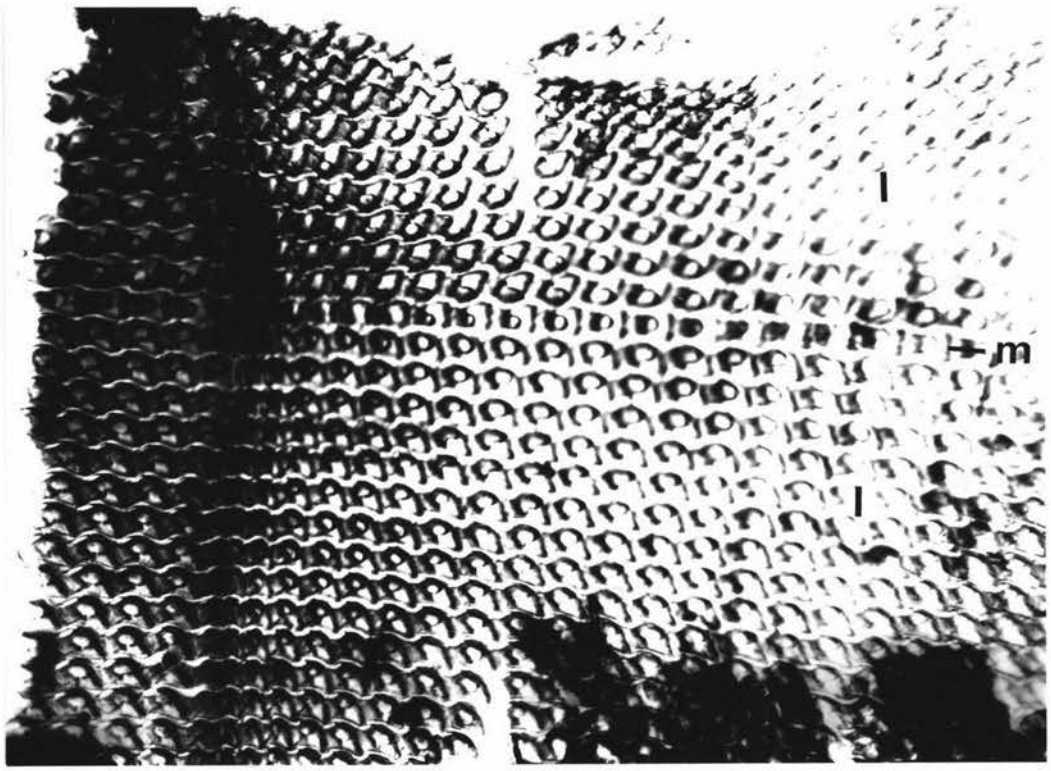
a. adult or large juvenile

b. small juvenile

m median teeth

l lateral teeth

u uncini



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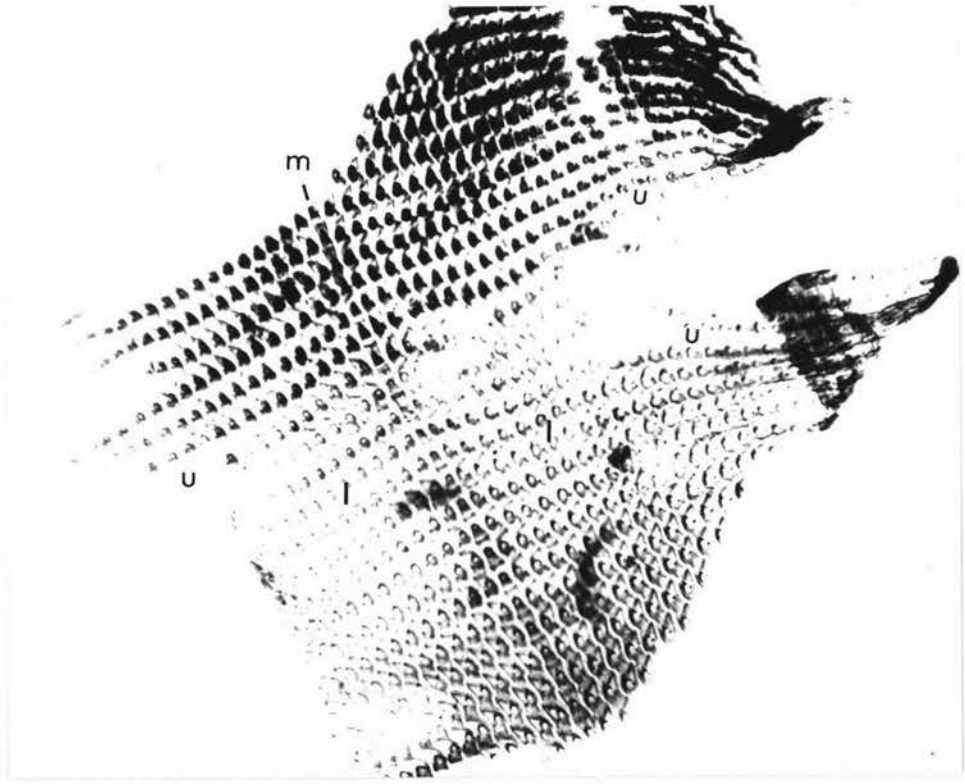


The laterals become increasingly assymetrical the further they are from the median tooth. The ectocone is completely lost, the endocone becomes quite large and prominent, and the mesocone of the outer laterals begin to bifurcate.

Beyond the lateral teeth of each row are the marginal teeth or uncini, occupying the longitudinal outer areas of the radular membrane. On these the mesocone is increasing bifid and the endocone also becomes strongly bifid. The uncini vary in number but there may be in excess of 20 on each side of each transverse row. They become progressively smaller towards the outside of the row.

In smaller juveniles the lateral teeth and uncini are both fewer in number in each row than in the large juveniles and adults. Also, the individual teeth are smaller in size. Estimates of snail size from radulae could therefore be based either on tooth size or on the numbers of lateral teeth in each row. In practice, distinguishing the endmost lateral teeth from the first of the marginals was often difficult as it was necessary to obtain a clear view of the cusps on each tooth. These tended to be obscured by the basal plates which appeared to stain more readily. It was therefore decided to use size as the criterion, basing the measurement on the basal plates.

The measurements chosen were: 1, the width across the central tooth and the two adjacent laterals, measuring from the outermost point of the anterior portion of the basal plate of each lateral, and 2, the total length of the basal plates of three consecutive median teeth (see Fig. 22).

Measurements were made under a binocular microscope with 40x objective and 10x oculars, using a micrometer eyepiece (100 divisions). The measurements were taken from the flatter central and posterior portions of the radulae rather than the strongly curved anterior part. Where possible three separate length and width measurements were taken from each radula and the results averaged.

8.3 Results

8.3.1 Anvil study.

A map of the study area with anvil locations and other relevant features noted is given in Fig. 23. The first of the rock anvils to be

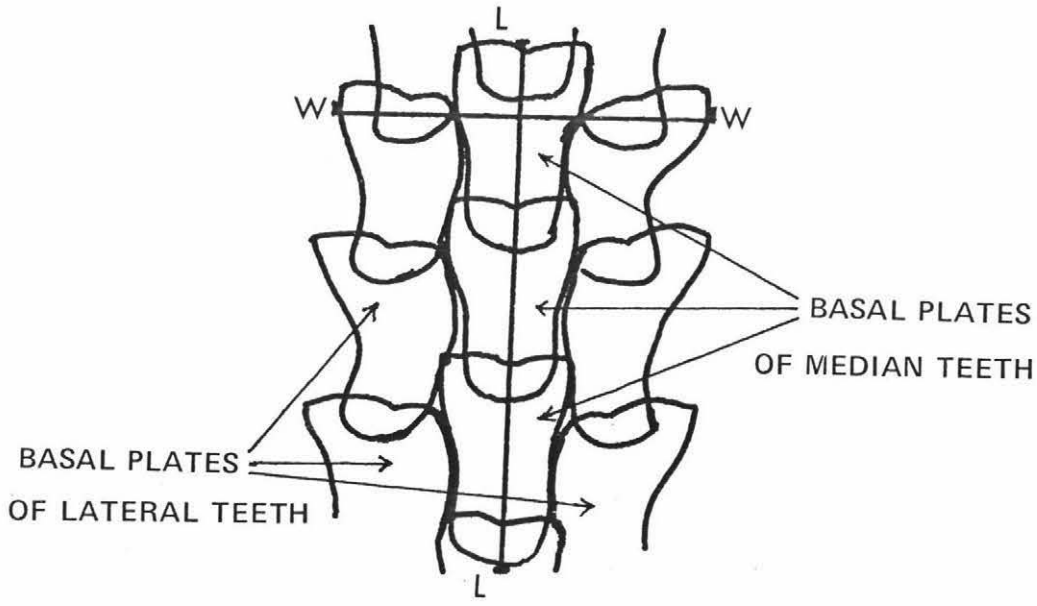


Fig. 22. Method of obtaining snail radula measurements
L–L Length of 3 consecutive median teeth.
W–W Width of median tooth and adjacent laterals

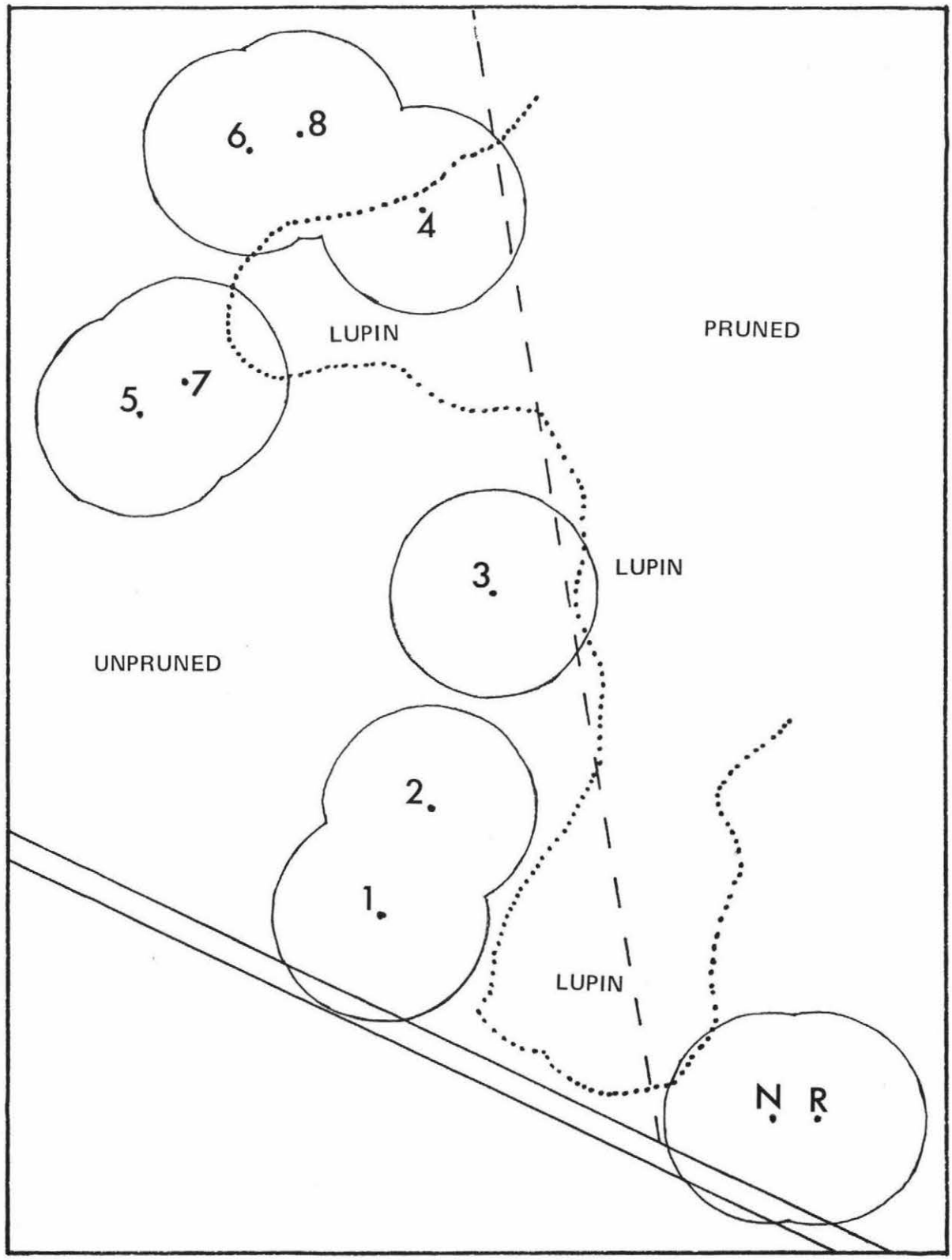


Fig. 23. Plant of anvil study area, with 10 m radius of activity around each anvil.

═══ Vehicle track
– – – – Extent of tree-pruning
····· Approximate boundary of lupin patches

placed is referred to as anvil "R". (This was the one placed in March). The eight anvil rocks which were placed during July are numbered one to eight in order of their times of placing.

Towards the end of the study, shells began to appear around a natural anvil site (a short pine branch from the initial pruning) only eight metres from anvil R. The site was cleared of shells and regular collections of shells were begun in October (anvil "N"). No further shells were found around anvil R after the collection on November 17th. This appeared to be due to rapid growth of Melilotus indica and other plant species on the site. By the time of the December collection, the anvil was virtually overgrown. Anvil N continued to be used.

All of the other anvils were in continual use for the duration of the study, with the exception of anvil 7 which accumulated no shells between 24th of August and 8th of September.

The numbers of juvenile and adult shells taken from each anvil over the course of the study are given in Table XV.

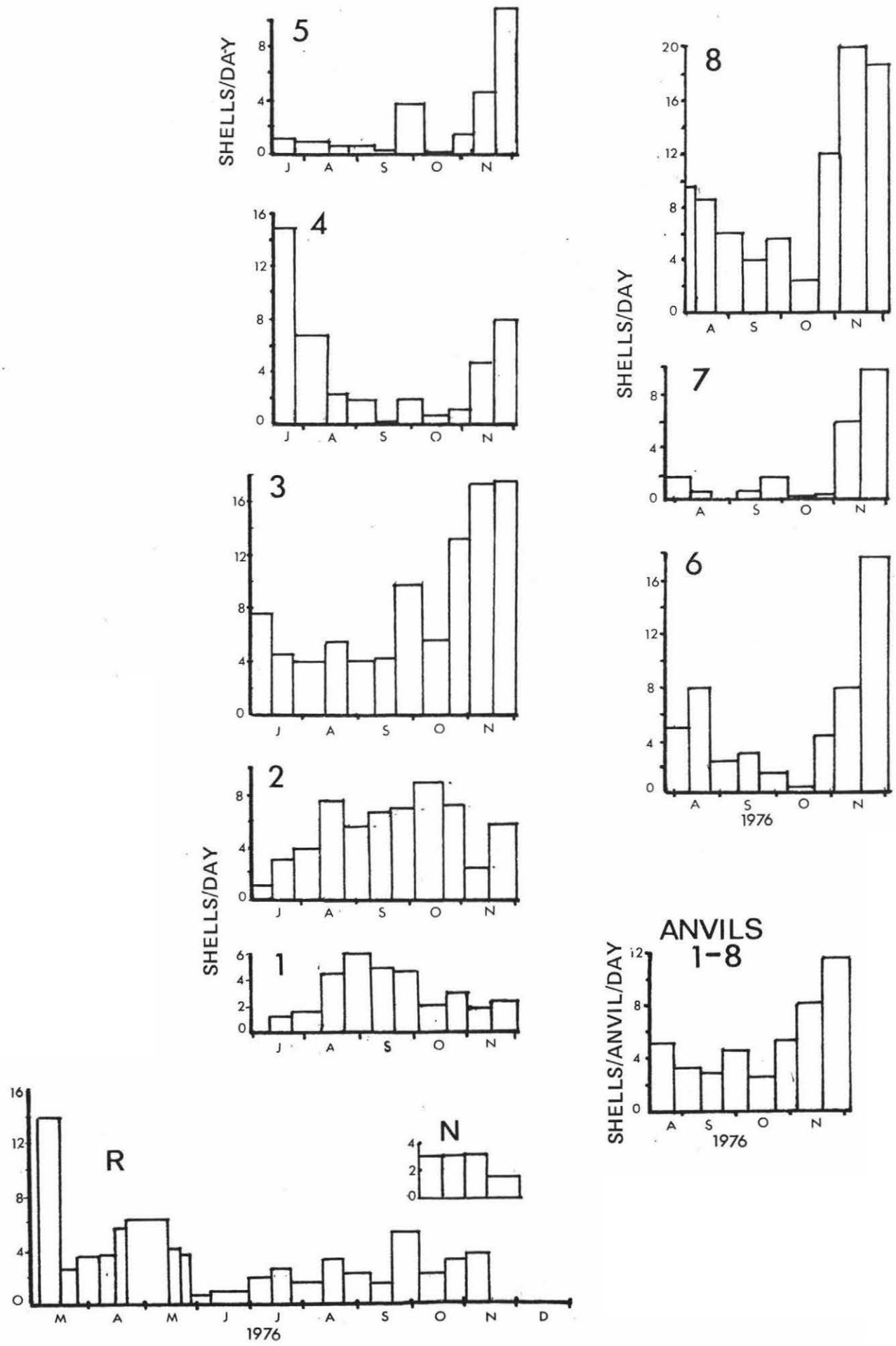
The total catch per day for the intervals between consecutive clearings of the anvil sites are presented in histogram form for each anvil, and bulked for anvils 1 - 8 for the time over which they were all operating (Fig. 24).

Allowing for a 10 m radius of thrush activity around each anvil in use, overlap of "activity areas" places the anvils into several groups; anvils 1 and 2; anvil 3; anvils 4, 6 and 8; and anvils 5 and 7 (Fig. 23).

Anvil R also represents one such group over the period preceding shell collection from anvil N. After this the two jointly form a group.

Allowing for a 20 m radius of activity placed anvils 1 - 8 in a single group (Fig. 25).

The size of the areas of activity associated with each group of anvils was calculated mathematically where possible, and by a combination of mathematical and graphical methods where more than two circles intersected in one place.


SHELLS/DAY
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M A M J J A S O N D
1976

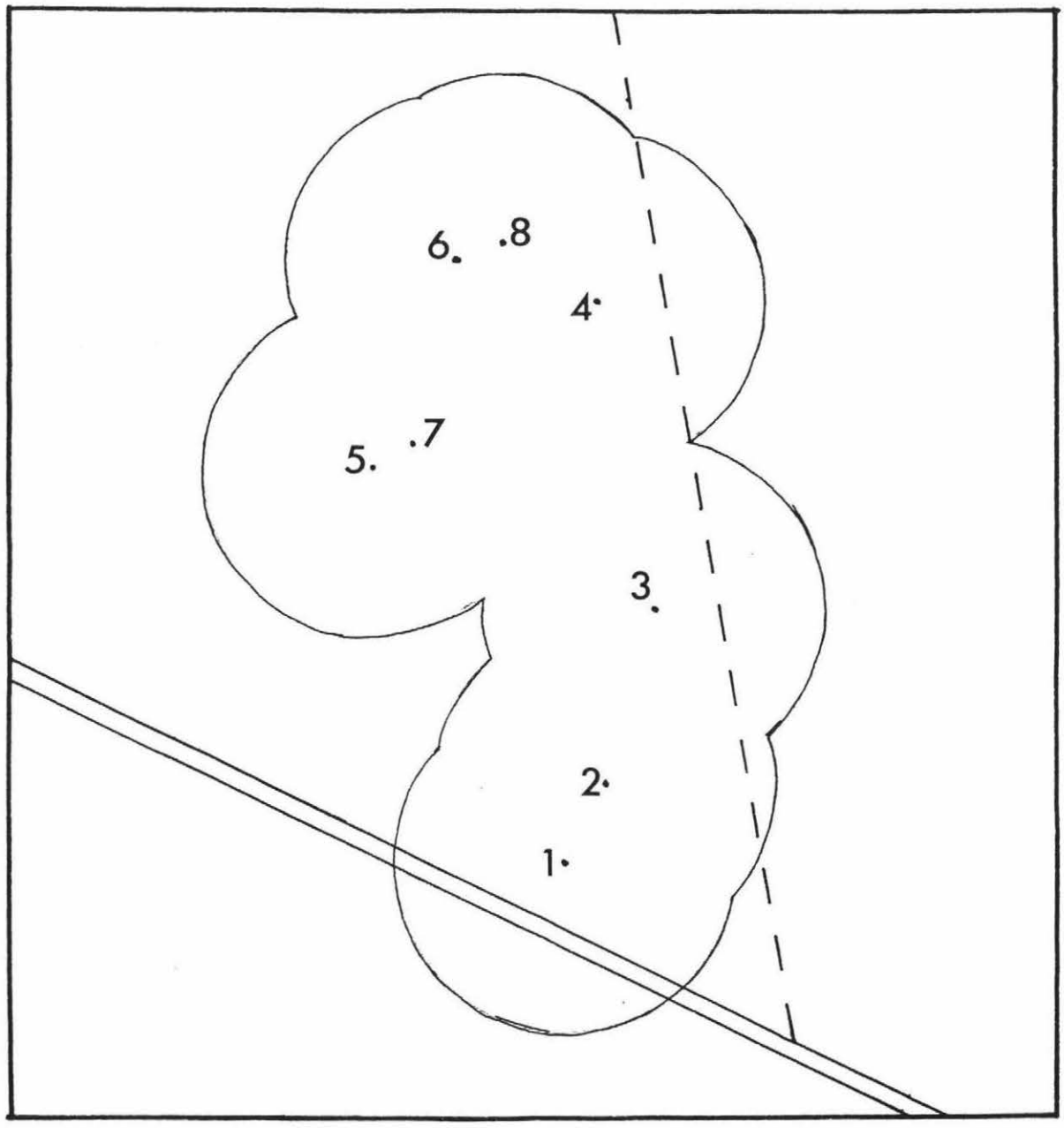


Fig. 25. Plan of anvil study area, with 20 m radius of activity around each anvil

Vehicle track

Extent of tree-pruning

Table XV : Catch per anvil over the study period.
Date of Final collection : 2/12.

Anvil	Date from which collection began	Days of operation	Catch			Total/ day
			Juvenile	Adult	Total	
R	4/3	261	36	879	915	3.51
N	6/10	57	16	147	163	2.86
1	1/7	154	49	384	433	2.81
2	1/7	154	116	722	838	5.44
3	1/7	154	118	1,193	1,311	8.51
4	12/7	143	40	593	633	4.43
5	12/7	143	28	315	343	2.40
6	26/7	129	76	645	721	5.59
7	27/7	128	22	271	293	2.29
8	5/8	119	128	1,004	1,132	9.51
Totals :		1,442	629	6,153	6,782	4.70*

*Number of snails per anvil per day.

Table XVI : Anvil catches as a function of a 10 m radius of thrush activity around each anvil.

Anvil Group	Area of activity (m^2)	Operation period	Days	Catch		Catch/m^2	
				Adults	Total	Adults	Total
1 and 2	530	1/7 - 2/12	154	1,106	1,271	2.09	2.40
3	314	1/7 - 2/12	154	1,193	1,311	3.80	4.18
4,6 and 8	678	12/8 - 2/12	112	1,806	2,010	2.66	2.96
5 and 7	417	26/7 - 2/12	129	570	620	1.37	1.49
R	314	4/3 - 6/10	216	770	796	2.45	2.54
R and N	395	6/10- 2/12	57	256	282	0.65	0.71

The "activity area" of each anvil group based on a 10 m radius of activity is given in Table XVI, along with the total number of shells taken and the total per unit area. The number of days for which shells were collected from each area is also stated. Table XVII gives these data for the groups involving anvils 1 - 8 for the

period from 12th August to 2nd December (112 days) during which all of these anvils were operating.

Table XVII : Anvil catches as a function of a 10 m activity radius around each anvil for the period 12/8 - 2/12 (112 days).

Anvil Group	Area (m^2)	Catch		Catch/m^2	
		Adult	Total	Adult	Total
1 and 2	530	964	1,112	1.82	2.10
3	314	988	1,093	3.15	3.48
4,6 and 8	678	1,806	2,010	2.66	2.96
5 and 7	417	531	578	1.27	1.39
Total	1,939	4,289	4,793	2.21	2.47

Table XVIII : Catch as a function of a 20 m activity radius around each anvil for the period 12/8 - 2/12 (Anvils 1 - 8)

Days of Operation	Approx. area of activity (m^2)	Catch		Catch/m^2	
		Adult	Total	Adult	Total
112	5,500	4,289	4,793	0.78	0.87

Table XVIII presents data for the period from 12th August to 2nd December based on a 20 m activity radius, which includes anvils 1 - 8 as a single group.

The proportion of the total adult catch bearing signs of a thick epiphragm for the period 15th April to 8th September is given in Table XIX.

Table XX gives the proportion of juveniles in the total catch over the period of study. The only figures given for the period during which anvil R was the only one operating are those for which the total catch is in excess of 100 shells, as the proportion of

juveniles was generally low and they were not represented in the smaller catches.

Table XXI gives the height distributions of the juvenile shells.

8.3.2 Thrush faeces analysis.

Juvenile height is plotted against each of the two radula measurements in Fig. 26. The two measurements are also plotted against each other in Fig. 27.

The measurements of all radulae found in the thrush faeces are given in Table XXII. This includes some estimates of numbers of lateral teeth on one side of a transverse row, as the last two radulae examined were stained for too long and basal plate measurements were impossible.

Table XIX : Percentage of total adult catch bearing the remains of a thick (hibernation type) epiphragm for each collection from 15/4 to 8/9.

Time period	Anvils	Total adults	Adults with epiphragm	%age with epiphragm
15/4 - 21/4	R	35	3	8.6
- 14/5	R	145	5	3.4
- 20/5	R	25	2	8.0
- 27/5	R	27	16	59.3
- 9/6	R	10	4	40.0
- 1/7	R	18	14	77.8
- 12/7	R, 1 - 3	113	61	54.0
- 26/7	R, 1 - 5	366	233	63.7
- 12/8	R, 1 - 8	445	81	18.2
- 24/8	R, 1 - 8	415	4	1.0
- 8/9	R, 1 - 8	392	4	1.0

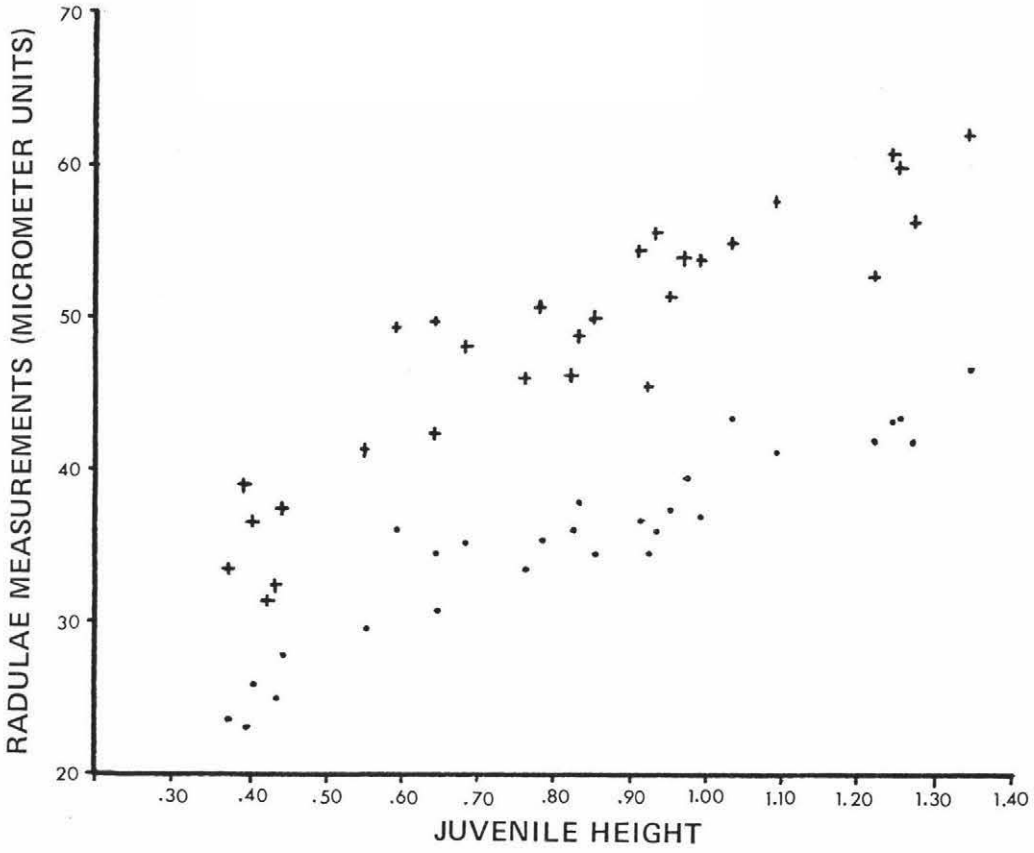


Fig. 26. Juvenile radulae measurements plotted against shell height

+ length

• width

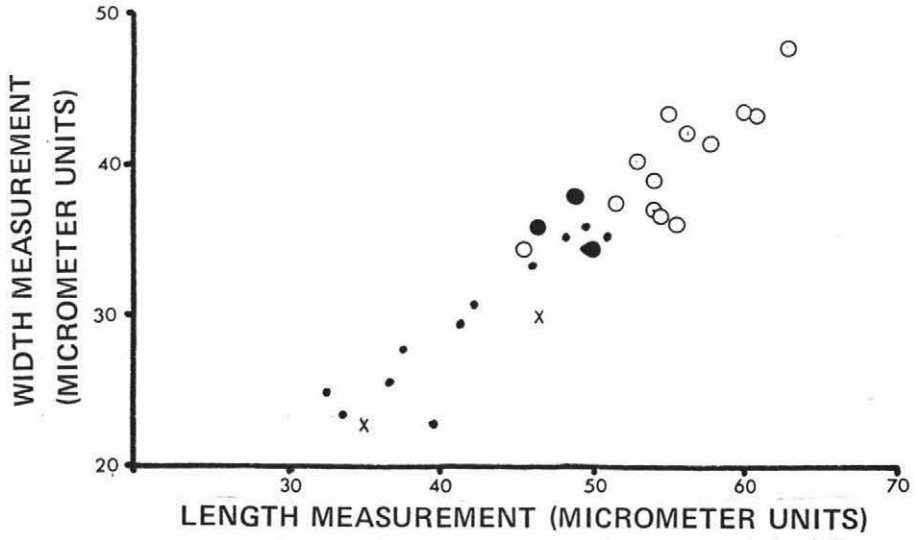


Fig. 27. Radula width measurement plotted against length measurement

O Juveniles with shells exceeding 0.89 cm height

● Juveniles with shell heights of 0.80 - 0.89 cm

• Juveniles with shells less than 0.80 cm height

X Smallest radulae from faeces

Table XX : Proportion of juveniles in anvil catches.

Time period	Anvils Operating	Total catch	Juveniles	%age juveniles in Total
4/3 - 16/3	R	172	6	3.5
21/4 - 14/5	R	152	7	4.6
1/7 - 12/7	R, 1 - 3	120	7	5.8
- 26/7	R, 1 - 5	384	18	4.7
- 12/8	R, 1 - 8	494	49	9.9
- 24/8	R, 1 - 8	486	71	14.6
- 8/9	R, 1 - 8	430	38	8.8
- 22/9	R, 1 - 8	344	49	14.2
- 6/10	R, 1 - 8	579	67	11.6
- 21/10	R, 1 - 8, N	379	49	12.9
- 3/11	R, 1 - 8, N	626	64	10.2
- 17/11	R, 1 - 8, N	1,007	95	9.4
- 2/12	R, 1 - 8, N	1,389	104	7.5
Total catch from all anvils over the study period.		6,782	629	9.2%

Table XXI : Height distributions of juvenile shells from anvils. Shells too damaged for height estimation are omitted.

Heights (cm)	0.71 -0.80	0.81 -0.90	0.91 -1.00	1.01 -1.10	1.11 -1.20	1.20	Total
Number of shells	0	8	32	72	108	400	620
%	0	1.3	5.2	11.6	17.4	64.5	

Table XXII : Measurements of radulae from thrush faeces.

Length of 3 median tooth basal plates. (micrometer units)	Width of basal plates of the median tooth and the 2 adjacent laterals (micrometer units)	Approximate number of lateral teeth on one side of a transverse row (Not estimated in all cases).
50.0	35.0	-
56.0	36.0	-
59.0	41.0	-
58.0	41.0	-
55.0	38.0	-
65.0	42.0	-
58.0	38.5	-
68.5	42.5	-
61.0	42.5	-
61.0	42.0	-
60.0	-	-
58.0	37.5	20
59.0	38.0	20
54.0	40.5	20
56.0	44.5	20
55.0	40.0	20
60.0	42.0	20
55.0	39.5	20
58.0	37.0	20
46.5	30.0	13
50.0	36.0	17
64.0	42.5	20
63.0	41.5	20
52.0	35.5	18
49.0	36.0	20
35.0	23.0	11
49.0	33.5	17
46.0	31.0	-
-	-	16
-	-	14

8.4 Discussion

8.4.1 Accumulation of shells on anvils.

The patterns of shell accumulation at each anvil display considerable varation. While certain trends in accumulation are common to several anvils, there is no single pattern common to all of them. Many factors may have a bearing on the variations in the rates of shell accumulation.

Davies and Snow (1965) found that thrushes became increasingly territorial during winter in preparation for the breeding season. However territories were not occupied regularly or consistently at this time, with individuals moving over considerable distances in search of food. Territorial behaviour were found to be in abeyance over spring and autumn.

It appears, then, that territorial behaviour would have been increasingly prevalent over the course of this study. It is unknown whether all or any part of the study area was in the territory of any bird or birds, however it is likely that this would have been so as the dense forest presented ideal nesting conditions. The number of birds feeding in the area, and the possibility that any one bird would feed only in a particular part of the area, could affect shell accumulation at the different anvils.

For example, if a single bird was preying on snails in a particular area, it is possible that predation might be concentrated in a particular part of that area with a high prey density and accessibility and then shift to another part as prey numbers in the first declined. Such a situation would mean a shift in predation peaks from one anvil to another with time.

Other aspects of thrush behaviour and biology may also be important. Morris (1954) found that a thrush would not take snails from within the immediate vicinity of its nest, even though they were abundant there. Capture and breaking open of snails did not usually occur within a radius of 10 m around the nest. On the other hand it is likely that predation in areas beyond the immediate vicinity of the nest would increase with the production of nestlings.

Richardson (1975 a) found that predation on a dune population of snails by thrushes was confined to winter. He considered that the absence of summer predation was due to the study area being a considerable distance from suitable nesting sites. This would suggest an increase in predation within the general vicinity of the nesting sites (excluding areas within 10 m of nests).

The relative palatability of H. aspersa to T. philemelos may also be significant. Goodhart (1958) and Davies and Snow (1965) considered that predation on various snail species by thrushes reached a peak only at those times when more palatable foods were scarce.

The ease of location and capture of prey will presumably affect the numbers taken. Hibernating snails are more difficult to locate than estivating or active snails, and this will presumably affect winter predation rates. Furthermore, snail density in the area around a particular anvil will affect the absolute number of shells accumulating around it. Density has already been shown to vary considerably over a short distance.

The combined shell accumulation data for anvils 1 - 8 show that predation on snails in this area increased rapidly from October onwards. This is probably due to the production of nestlings which would both increase the requirements for food and, according to Richardson (1975 a), limit the distance travelled by the birds to obtain food.

Goodhart (1958), Davies and Snow (1965) and Cameron (1969) all found winter and summer peaks in predation of snails by thrushes. In the former two studies it was suggested that these were the times of year when alternative food sources were largely unavailable. The results of the present study suggest that there may have been a small winter peak, but unfortunately data for the June and early July period are limited. Anvils 3 - 8 all displayed considerable increases in shell accumulation over the October-December period, which were presumably building up to a summer peak. Several of the anvils also showed a small isolated peak at the end of September/beginning of October.

It is felt that the results from anvil R over the period from March to August are inadequate on their own to show general trends in snail shell accumulation as the August to December results are quite different to those of the other anvils. This anvil was situated near to some lupins in which heavy predation had already taken place before the study began, judging from the large numbers of broken shells beneath them. It is possible that snail density in this area may have decreased considerably before the main anvil study began, and this would affect the numbers of further shells accumulating.

8.4.2 Catch as a function of area.

No accurate estimate is available of snail density in the area of live and dead lupins where the main thrush activity is presumed to have occurred. The portion of this area that lay within sampling area 2 was only a small part of the latter, and few quadrats were taken in it. It is considered from observations made after sampling in area 2 had ceased that the lupin area had a higher density of snails than area 2 overall. Adult densities in area 2 from the three samples ranged from 1.4 to 1.8 animals/m^2.

For the 112 days during which anvils 1 - 8 were all in operation, the number of adults taken averaged 2.21/m^2 for a 10 m radius of thrush activity and 0.78/m^2 for a 20 m radius of activity. The first estimate exceeds the area 2 adult density, while the second is equal to half of it. The period over which this catch was taken was less than one-third of the year (12/8 - 2/12), although how important this is depends on predation levels during the periods when the shell accumulation was not being measured.

From this it would seem that thrush predation may have been a highly significant mortality factor in the adult snail population in this area. A search in this area after the cessation of the anvil study disclosed very few snails and it was obvious that a drastic reduction in snail density had occurred. There appeared to be fewer adults in this region than in area 1. It is unknown what other factors may have been involved in this decrease in density but it appears that thrush predation may have played a major part.

Wolda (1972) found that thrush predation was the most important source of adult mortality in an experimental population of Cepaea nemoralis.

As juvenile snail production the previous summer appeared to be very low in area 2 generally, it is likely that the high mortality of large animals due to thrush predation would have a major effect on the population in this area.

This possibly useful effect of thrush predation appears to be a rather isolated circumstance. Observations in other areas of high snail density (notably area 3), show that thrush predation does not always occur to a significant extent in such areas. Although newly broken shells near natural anvils were occasionally found in area 3, predation was irregular in occurrence and insignificant in relation to snail density. This difference between areas 2 and 3 may be related to the age and size of the pine trees in the former area, making it considerably more suitable for nesting sites. It must be remembered also that the major lupin dieback had already taken place in area 2.

Forest Service operations occurring in such an area in early summer as was the case in area 2, are likely to have had a major effect on the thrush population and would probably have caused a high egg or nestling mortality.

8.4.3 Predation on hibernating snails.

Davies and Snow (1965) claim that thrushes, unlike blackbirds, do not sift through leaf litter to search for prey and therefore do not find hibernating animals buried in litter or soil. However, Richardson (1974) found that predation by thrushes on one sand dune population of Cepaea nemoralis only occurred in winter on buried, hibernating animals. In the present study, a large proportion of animals taken over the winter had the remains of hibernating epiphragms attached to their shell apertures.

It was found during snail population sampling that most snails hibernating at or above the soil surface attached themselves to vegetation or litter by the outer hibernating epiphragm. In these animals this epiphragm is usually formed at the aperture rim. In unattached animals buried in the soil, the epiphragm is usually formed a little distance in from the aperture rim. A number of the shells collected during winter had epiphragms inset in this way, with a single hole in them where the thrush had thrust in its mandible in order to

pick the shell up. From this it would seem that some snails buried in the soil were taken by thrushes. Virtually all hibernating animals taken would have been buried to some extent under litter at least.

On two occasions pairs of shells were collected from anvils in which one shell was firmly sealed to the other by a hibernation epiphragm. In each case, both shells had been broken open and the contents removed without the shells coming apart.

Shells with thick epiphragms found in April and early May were probably not those of hibernating animals. Estivation epiphragms were frequently found to vary in thickness from extremely thin transparent membrances to quite substantial structures. A tendency for snails to produce thicker epiphragms for estivation as the cold weather approached was observed.

8.4.4 Predation on juveniles.

8.4.4.1 Large juveniles.

Population sampling in area 2 produced 63 juveniles in size-classes F and G compared with 98 adult snails, a ratio of approximately 2 : 3. Of the shells collected on anvils during the entire study, only approximately 600 F and G juveniles were found, compared with 6,782 adults, a ratio of less than 1 : 10. Juvenile shells are considerably thinner and more fragile than those of adults and a larger proportion of them would tend to be broken up completely during the process of smashing on the anvil. This would not, however, explain such a large difference in the proportion of juvenile shells found.

The possibility that the large juveniles found in the population sampling all matured rapidly soon after sampling is rejected on the grounds that the majority of them were hibernating when sampling ceased so that large proportions of juveniles : adults should be present in the anvil shells at least up until August or September, and this is not seen to occur.

It is possible that a behavioural difference between adults and large juveniles may result in the former being more prone to predation than the latter. Lomnicki (1969) noted individual differences in behaviour amongst adults in a population of Helix pomatia, which caused some of these animals to become more prone to predation. Sub-

sequently, Pollard (1975) found that these individuals were actually the older adults in the population and he suggested that the behaviour might have a genetical basis which is only expressed in older animals. Wolda (1972) stated that a similar phenomenon appeared to occur in Cepaea nemoralis.

The most likely explanation, however, would appear to be that the population composition of snails in the lupin area was different to that for area 2 in general. The large juveniles found in sampling would have mainly hatched at least one-and-a-half years before sampling. At this stage the lupins in the lupin area would have all been alive, and this area would probably have had a very high snail density. The other parts of area 2, however, appear to have had no live lupins for some time, and it is possible that population densities in these areas would have been lower. Under these conditions, from the apparent effects of high snail density on juvenile production and survival (Chapter 7), it is possible that large juvenile production may have been considerably lower in the lupin area than the surrounding areas.

8.4.4.2 Small juveniles

The height distribution of juvenile shells taken from the anvils (Table XXI) displays a rapid drop-off in numbers of shells below a height of about 1.00 cm, with none smaller than 0.80 cm. It was hoped that the analysis of thrush faeces would show whether or not significant predation on smaller juveniles occurred.

From the results of the faecal analysis, it can be safely assumed that the faeces collected were those from thrushes. The radulae found were sometimes not whole but in most cases a major portion was present. Two small fragments found and measured may have been parts of the same radula, and/or they may have broken from some of the larger fragments measured. Generally, radulae appeared to survive passage through the bird's alimentary canal rather well.

Of the 30 radulae and fragments from faeces found and measured, only one definitely comes from a juvenile below the size range of shells on thrush anvils. The size of this individual appears to have been around 0.30 to 0.50 cm height. Several other radulae would have come from snails in the vicinity of 0.80 cm.

It would appear, then, that small juveniles may be eaten by thrushes. It is unknown whether the apparently low occurrence of small snails in the diet of thrushes in this case was due to selection by the thrush or whether it reflects the availability or density of small snails in the environment. More extensive faecal analyses from an area with a known population composition would be necessary to elucidate this point.

SECTION IV

FEEDING STUDIES

CHAPTER 9

THE FOOD OF DUNE POPULATIONS OF H. ASPERSA AND THE EFFECTS OF FEEDING ON LUPINUS ARBOREUS

9.1 Introduction

In Chapters 6 and 7 it was assumed that the main significance of lupin to H. aspersa is as a food source. Furthermore, observations of large-scale lupin dieback were linked with greatly increased snail densities. To substantiate these assumptions it was desired to show that lupin is, in fact, a major diet constituent in areas in which it is present, and to elucidate the possible causes of plant death. In view of the possible significance of lupin as a source of nitrogen in dune forestry, it was also desirable to test for any effects of snail attack on nitrogen fixation in living plants.

As snails are also found to inhabit non-lupin areas, although at a considerably lower density, it was of interest to obtain an indication of the plant species taken as food in these areas. A number of feeding studies have been undertaken on the banded landsnail, Cepaea nemoralis (Grime et al., 1970; Wolda et al., 1971; Richardson, 1975 b; Williamson and Cameron, 1976) and these have generally shown that this species prefers senescent or dead foliage to fresh green foliage of most food species.

A combination of field observations and laboratory experiments was used to investigate some of the foods taken by H. aspersa, and the effects on lupin of snail feeding. It was not intended that a complete feeding study be undertaken, as this could be a major project in itself.

9.2 Methods

Field observations of snails feeding were made during wet weather, particularly over the spring and summer periods, when snails were active during the day. It was necessary to ensure that feeding was actually taking place during observation, as snails are frequently found

on plants which form little or no part of their diet in the field (Grime, et al., 1970; Wolda et al., 1971). A note was made of all foods being eaten.

9.2.1 Cuticle analysis

A large amount of the plant material in the faeces of H. aspersa collected in the field was found to consist of quite large, distinct pieces of vegetation. Identification of this material was attempted using the cuticle analysis method.

The thin, non-living cuticle covering the epidermal layer of plant leaves and stems is composed of a waxy substance which has a high resistance to certain chemicals. Acidic digestion of the living tissues leaves the cuticle intact and bearing the shapes and impressions of the epidermal cells and hairs which it coated. Cuticles prepared from the stems and leaves of known plant species can be compared to cuticles similarly prepared from the plant material in the animals' faeces. Certain features, such as the number and arrangement of stomata in relation to the epidermal cells, and the shapes of stem and leaf hairs, are particularly useful in identification.

Snail faeces were collected in the course of population samplings. They were allowed to dry at room temperature and were then broken up by light grinding with a mortar and pestle. The faeces were then transferred to a watchglass and a solution consisting of a 50/50 mixture of 2N Nitric acid and concentrated chromic acid (a saturated solution of chromium trioxide in water) was added. Digestion of the dead plant tissue was allowed to proceed for 30 - 40 minutes, with occasional stirring with a needle to ensure that material which floated to the top did not escape the process. The contents of the watchglass were then washed into a glass filter funnel with an excess of water to prevent the acid from attacking and breaking down the filter paper. The filtrate, consisting of cuticles and other resistant material was washed to remove traces of the acid and then transferred to a stoppered bottle containing F.A.A. solution (70% ethanol : 90 parts; Formalin, 5 parts; Glacial acetic acid, 5 parts).

Cuticles of known plants were prepared by cutting up the leaves and stems into fragments, generally of about 3 x 3 mm in size. Size varied depending on the size and shape of the particular leaf or stem. The outer margins of leaves were cut away so that the upper and

lower cuticles would not be attached to each other. Stems were slit along their length at least once, depending on their size, so that flat pieces of cuticle could be obtained. The pieces of leaf or stem were placed in watch-glasses and the chromic acid/nitric acid mixture added. When digestion of the tissues was complete, cuticles were picked out with a needle or forceps and placed in a bottle of F.A.A. Digestion times were usually 20 - 30 minutes, but varied from species to species. Some, such as the woodier lupin stems, took considerably longer than this, and the hairy inner surface of the curled marram leaf had to be left for about 16 hours for preparation of a suitable cuticle.

Cuticles were examined under a compound microscope with 10 x oculars and generally using the 10 x objective. Cuticles from the faeces were compared with the standards. Some photo-micrographs were made of standard cuticles to facilitate this process.

9.2.2 Palatability trials

Palatability trials were performed in the laboratory as another method of testing for the suitability of various species as food items. In these trials interest was mainly on the palatabilities of fresh green foliage. The tests were not quantitative as only an indication of palatability was required. The procedure was based on that of Grime et al., (1970).

Adult animals that were being maintained in the laboratory were placed singly into 1 pint Agee preserving jars with a little water but no food for 24 hours preceeding the experiment. A piece of clear plastic held in place by a rubber band prevented escape from each jar. Over this period and during the experiment, the jars were kept in a constant temperature cabinet maintained at 20°C and with an artificial day-length approximately equal to that at the time of the experiment.

After the 24 hour fast, a piece of plant material from the species being tested was introduced into each jar. Pieces of leaf from large-leaved herbs were presented as leaf discs, with a diameter of 1.5 cm. Smaller leaves were presented whole, and leaves or stems of grasses and sedges were cut into lengths of about 3.0 cm. Flower petals which were too delicate for disc-cutting were presented whole. All plant material was collected in the field and stored in a refrigerator for not more than 24 hours before use.

A disc of filter paper (1.5 cm diameter) was also placed in each jar. Paper is readily consumed by snails and filter paper appears to be particularly palatable. This acted as a control in the experiments. If both filter paper and plant material were untouched at the end of the experiment the animal had not fed. If only the filter paper had been consumed, the plant material could be assumed to be unpalatable.

In the initial experiments, ten replicates were set up for each test material. Later only six replicates were used as usually not more than one or two in every ten replicates lacked all signs of feeding activity at the conclusion of the experiment.

After introduction of the filter paper and test material a little water was sprinkled into the jars and they were replaced in the constant temperature cabinet and left overnight. They were removed 16 hours after the beginning of the experiment, and the amount of food eaten was assessed.

Under the same conditions, individual animals were found to consume three or four filter paper discs, so that the food available during each experiment could be assumed to be less than that which the animal was capable of eating.

9.2.3 Structural damage to lupin caused by snail feeding.

It became obvious early in the study that feeding on lupins by snails was directed at the stems rather than the leaves of the plants. A branch from a lupin plant in area 4 that was heavily infested with snails was removed and examined in the laboratory. Damaged stems were sectioned and examined under the microscope to investigate the extent of the damage to the tissues.

9.2.4 The effects of feeding by snails on nitrogen fixation in lupins.

The amount of nitrogen fixation occurring in the root nodules of leguminous plants has been shown to be greatly affected by the supply of photosynthetic products to the nodules from the leaves of the plant. Energy for the fixation process is supplied to the nodule bacteroids in the form of sugars, mainly sucrose, which have been manufactured during photosynthesis (Evans and Barber, 1977).

Alterations in this supply will alter the rate of nitrogen fixation. The supply of sugars may be altered by any changes in the environment of the plant which affect the rate of photosynthesis (including defoliation by a herbivore), or by diversion of the sugars for use in other energy-consuming processes in the plant, such as seed formation (Sinclair, 1973; Lawn and Brun, 1974).

As snail attack on lupin appears to be confined mainly to the stems, rather than the leaves of the plant, it was of interest to determine whether this had an effect on nitrogen fixation rates.

9.2.4.1 Experimental procedure

About 30 lupins were grown from seed in early spring, 1976. The test of each seed was chipped with pliers to ensure even germination and the seeds were then planted in sand that had been heat-sterilized to kill any plant-parasitic organisms that may have been present. Once most of the seedlings had appeared, the ten largest were each transferred to individual five inch (12.7 cm) pots, also containing sterile sand. A culture of Rhizobium lupini, provided by Mr. M. Greenwood, was suspended in water, and a portion of the suspension was added to the soil in each pot.

The seedlings were fed a nitrogen-free nutrient solution (see Appendix) once a week and watered whenever necessary. They were kept in the greenhouse for about three months, and then they were placed on the ground out in the open. It was necessary to take particular care over water requirements during summer dry periods, as the sand could dry out rapidly.

The plants were ready for experimental use during November and December of the following year. By this time the older, thicker stems were becoming quite woody. After some preliminary trials, four plants were chosen for the experimental analyses, mainly because of their generally healthy appearance and their apparently high rates of nitrogen fixation. Two of these plants were used as controls and two as experimental plants. The rate of nitrogen-fixation was measured for each plant prior to experimentation using the acetylene reduction method. (See section 9.2.4.2).

For the experiment, a wire frame measuring 1.2 x 1.2 m and standing 0.6 m high was covered with wire netting of half-inch(1.2 cm)

mesh. Another piece of netting divided this cage into two separate enclosures of 1.2 x 0.6 x 0.6 m. The experimental plants were placed into one of these enclosures and the controls in the other. Eighty adult snails were introduced into the experimental enclosure. Extra pots filled with sand were placed in each enclosure to brace the pots containing the plants against being blown over. In the experimental enclosure these pots also served to provide extra estivation sites for the snails.

The plants were watered each evening to ensure that some snail activity took place. After three weeks, the rates of nitrogen fixation were re-measured.

9.2.4.2 Measurement of nitrogen fixation

The acetylene reduction technique for the measurement of nitrogen fixation has been used in isolated legume nodules for some time, and it has also been adapted for use with living, potted plants (Sinclair, 1973). The technique involves incubating the plant in an atmosphere containing acetylene gas. The acetylene competes with atmospheric nitrogen for binding sites on the enzymes which catalyse the reduction of nitrogen to ammonia. The acetylene is reduced to ethylene and comparison of the amounts of acetylene and ethylene in the atmosphere at the end of a given period of incubation gives an assessment of enzyme activity.

It was mentioned previously that environmental factors which altered rates of photosynthesis would thereby alter nitrogen fixation rates also. For this reason it is necessary to control the environments of the plants as completely as possible prior to and during the incubation period if reproducible results are to be obtained. In the present study, the plants were placed in a constant temperature room held at 15°C for two days prior to incubation. Even lighting was provided by a rack of fluorescent lights immediately above the plants. The room had a constant day-length period, approximately equal to the actual length of daylight at the time. Incubation with acetylene took place in the constant temperature room on the third day.

After addition of the acetylene to the atmosphere around the plants, infiltration of the nitrogen-fixing system of the nodules by the gas takes a little time. Over this period, the rate of production

of ethylene increases until the acetylene attains access to all sites of enzyme activity, after which the conversion of acetylene to ethylene takes place at a steady rate. The time required to reach this equilibrium is estimated by removing gas samples at regular intervals for analysis and plotting the proportion of ethylene to acetylene against time. When the points fall in a straight line, equilibrium has been reached.

Analysis of nitrogen fixation should be based on assays made after this equilibrium phase has been attained and subsequent analyses must involve exactly the same period of incubation, in order to achieve reproducible results. In the present study, equilibrium was achieved after little more than an hour of incubation and the experimental incubation period was set at two hours.

Nitrogen fixation also fluctuates with the plants' diurnal rhythm, so that incubation for the assay must occur at the same time of day on each occasion.

For incubation, each plant was placed in a glass cabinet measuring 20 x 20 x 35 cm (see Plate 4), and with a volume of 14 l. A flat glass lid was placed on top of the container and made air-tight by smearing petroleum jelly between the lid and the container.

A rubber injection port in the side or lid of the incubation chamber allowed the removal of 50 cm^3 of air with a syringe, and injection of 50 cm^3 of acetylene. A hand-operated metal propeller was rotated for a few seconds to promote diffusion of the gas. The insertion point of this propeller was also made air-tight with petroleum jelly. After incubation for two hours, the propeller was again rotated briefly before gas samples were removed for analysis. Three samples of approximately 1 cm^3 were taken from each chamber for analysis.

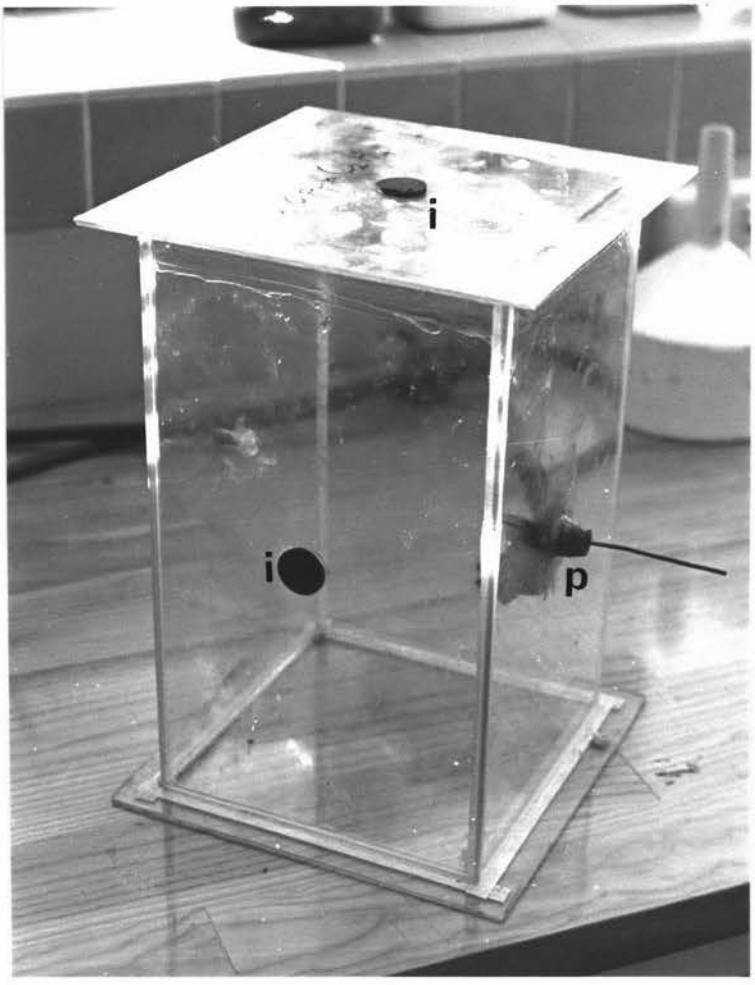
Analysis of the gas samples was performed using a Pye series 104, model 64 gas chromatograph. The glass column, slightly in excess of 60 cm in length and with a diameter of 3.2 mm, was filled with Poropak T, 80 - 100 mesh. The column temperature was 100°C. The flow rate of the carrier gas (N_2) was 45 cm^3/ minute. A Servoscribe chart recorder was fitted to the machine.

Gas samples of up to 1.0 cm^3 were injected for analysis. Once two samples from a plant had been successfully analysed samples from another plant were analysed.

Plate 4. Incubation chamber for acetylene reduction assay.

p propeller

i injection port


i
i
p

To obtain a direct measure of the full nitrogen fixation potential of a plant, its roots must be incubated in an atmosphere of 10 - 20% acetylene (Dr W. Sutton, pers. com.). In the present instance this would have required very large amounts of acetylene, due to the size of the incubation chambers. However, even at low concentrations acetylene is a powerful competitive inhibitor of nitrogen fixation and the results of acetylene reduction would give a sufficiently reliable indication of the rate of nitrogen fixation that changes in this rate could be detected.

9.3 Results

9.3.1 Cuticle analysis

Faeces collected from snails in lupin areas were predominantly green in colour, indicating that mainly live, green plant matter had been consumed. Faeces from snails in non-lupin areas tended to be brown in colour, indicating a greater proportion of senescent or dead plant material in the diet.

Cuticle analysis showed that lupin was by far the most predominant food consumed in areas in which it was present. The cuticles obtained were of lupin stems rather than leaves. Lupin leaf cuticles were in fact found to be very difficult to obtain from fresh leaves. They appeared to be rather fragile and tended to crumple and break so as to be unrecognizable, and this may happen to lupin leaf cuticles in the faeces. However observations in the field indicated that lupin stems were strongly favoured. Even the older woody stems of lupins were attacked.

Cuticle preparations generally contained a reasonable amount of extraneous matter, some of which may have been woody in nature. This type of matter was more noticeable in preparations from faeces collected in non-lupin areas. All preparations contained reasonable quantities of sand.

Cuticles identified in faeces from non-lupin areas included marram, Oenothera biennis, Hypochaeris radicata and Erigeron canadensis. None of these were strikingly common in occurrence. A number of cuticles could not be identified, including some that were apparently

from monocot plants! Marram was not present in the quantities that would have been expected if plant selection was entirely random. It was noticeable also that the smooth outer cuticle of the curled marram leaf was considerably more common in occurrence than the densely hairy inner cuticle.

Cuticles of a number of species were, like that of the lupin leaf, difficult to obtain. These included cuticles of Leontodon taraxacoides, Sonchus oleraceus and S. asper.

Cuticles in faeces collected on and around tree lucernes, Cytisus proliferus, showed that feeding on this species was as extensive as that on lupin. Once again, stems appeared to be the most extensively eaten part of the plant, but a reasonable proportion of leaves were also consumed. Cytisus leaf cuticles were easily obtained.

9.3.2 Palatability trials

Green leaf material tested in the laboratory for palatability was scored as palatable or non-palatable. Non-palatable species remained virtually untouched in all replicates, while palatable species were largely or wholly consumed. Table XXIII gives the results for those species tested.

Table XXIII : Palatabilities of green leaf material from different plant species.

Palatable	Unpalatable
Erigeron canadensis	Oenothera biennis
Cenecio elegans	Calystegia soldanella
Sonchus oleraceus	Leptocarpus simplex
Sonchus asper	Scirpus nodosus
Cytisus proliferus	Ammophila arenaria
Melilotus indica	

Of those species listed as palatable, Melilotus indica appeared to be less palatable than the others.

Also tested for palatability were mature lupin seed pods, rabbit faeces and flower petals of Oenothera biennis. All of these had been observed to be taken in the field, and they were all highly palatable.

Field observations showed that Oenothera petals were taken in fresh condition by snails climbing up the flower stalks, and as fallen, discoloured flowers on the ground. Flower petals of Leontodon taraxacoides and Cenecio elegans also appeared to have been taken.

Rabbit droppings were readily consumed and in wet weather, active animals could usually be induced to feed by placing rabbit faeces in their path as they moved along the ground. Cattle faeces, which were also found in some areas, did not elicit this response.

Snails were frequently found to be feeding on lupin seed pods, particularly when these had matured and were about to dehisce or had already done so. Feeding was confined to the black, hairy, fibrous material comprising the outer layer of the pod, while the smoother fawn inner layer did not appear to be touched. There was no evidence that this feeding particularly impaired dehiscence.

Finally, on one occasion a snail was observed to be eating the remains of another snail. The dead animal had apparently just been killed by being squashed, either by a vehicle or through being trodden on. If cannibalism is restricted to freshly-killed, non-decomposing animals, it would be a rare phenomenon in natural populations.

9.3.3 Structural damage to lupin stems caused by the feeding activities of snails.

Feeding on lupin stems resulted in removal of the outer stem tissues, usually as far in as the xylem. Usually most or all of the phloem would be removed where damage occurred. Feeding occurred as the animals moved along the stems, so that long strips of material tended to be removed. Frequently, small to medium diameter stems were found to have the phloem and outer tissues removed around their entire circumference, while small stems were occasionally eaten through. Even the older thick, woody stems were attacked, with removal of tissues again extending to the xylem.

Sections through damaged stems are shown in Plates 5 and 6.

9.3.4 Effects on nitrogen fixation.

The nitrogen fixation capacity of a plant is measured as the ratio of ethylene to acetylene at the end of the incubation period. This ratio is directly proportional to that of the peak heights for the two gases as recorded by the gas chromatograph.

In the present study, only a small proportion of the incubation atmosphere was occupied by acetylene so that the results provided an indication of the nitrogen-fixing activity rather than an absolute measure. Because of this, and the fact that interest is on changes in this activity rather than the quantification of the activity, results are presented simply as the ratios of the peak heights recorded for the gases. As acetylene is present in a concentration far in excess of the ethylene, the recording device had to be set at different attenuations (sensitivities) to record the two peaks. The peak heights had therefore to be set to the same scale to obtain the ratio.

The light intensity in the constant temperature room was considerably lower than normal daylight. As L. arboreus prefers a high light-intensity situation, it was found that nitrogen fixation levels in the plants continued to decline slowly in the constant temperature room even after a period of three days. These conditions were therefore not ideal for this experiment, but no more suitable set-up was available.

It was found also that the return to normal nitrogen-fixation levels after the plants were returned to the enclosures took up to two weeks. Until this was realized, it was a source of considerable difficulty in conducting the experiment, as assays for reproducible results were being attempted only one week apart. Eventually only two experimental assays were performed; one before and one after the introduction of the snails on to the experimental plants. Time did not permit further assays.

The results of the assays are presented in Table XXIV.

Plate 5 Snail damage to lupin stems.

a. Portion of damaged woody stem.

b. Section through part of stem.
Stem diameter: 1.1 cm

p Phloem tissue

x Xylem

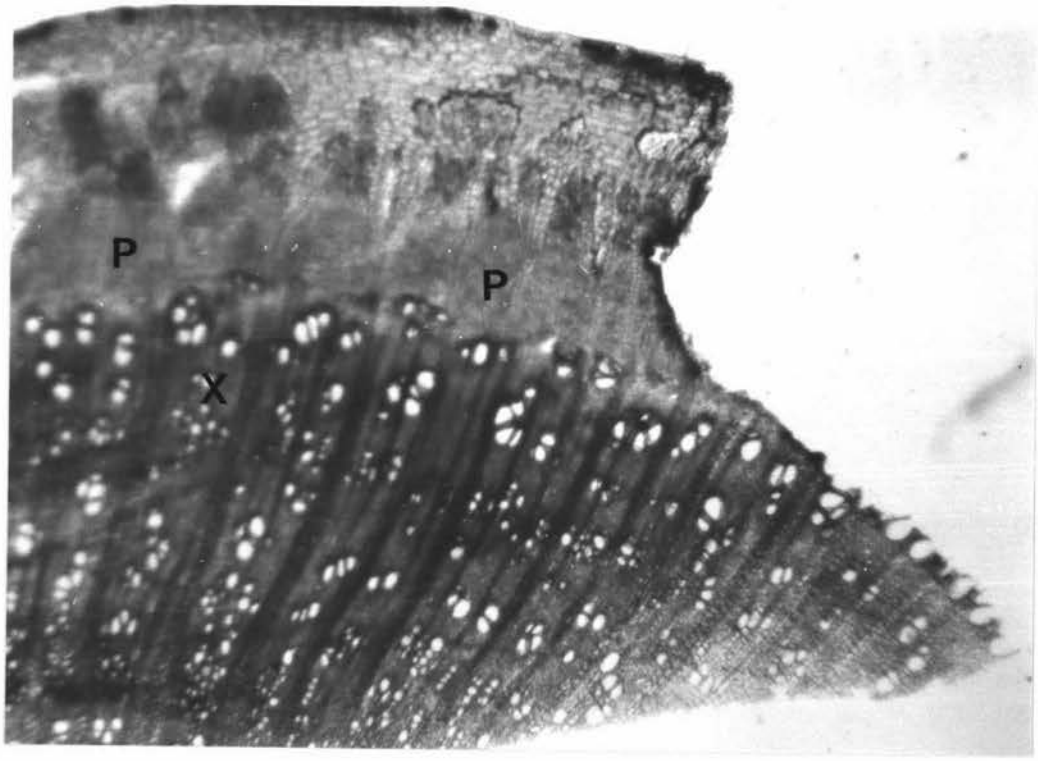

P
P
X

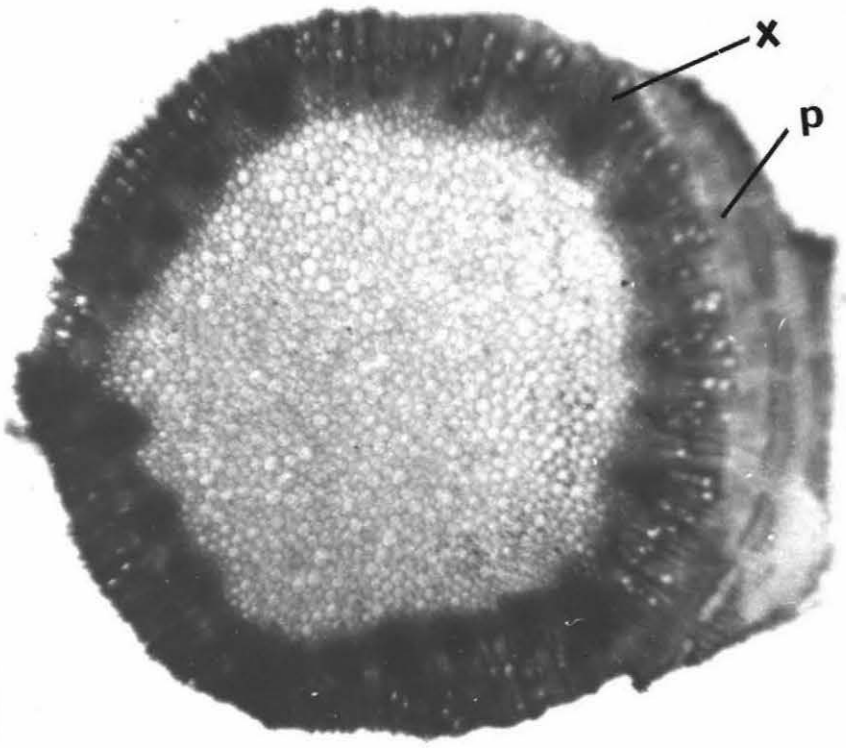
Plate 6. Snail-damaged lupin stems.

Stem diameters: a. 0.5 cm

b. 0.2 cm

p phloem

x xylem


x
p

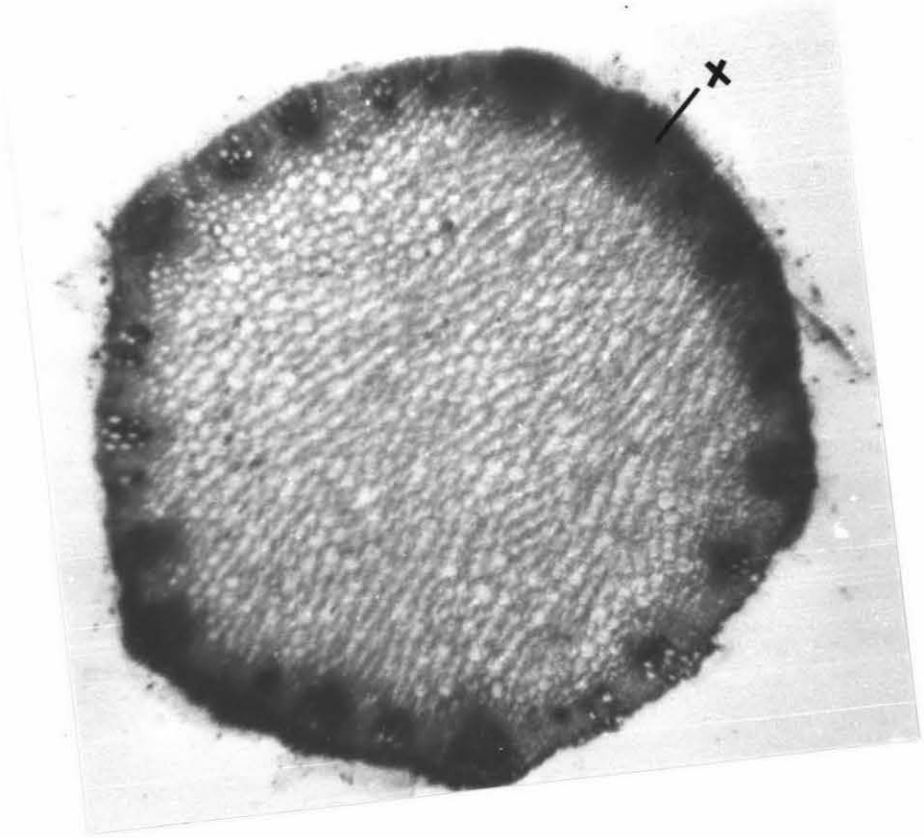

x

Table XXIV .: Ethylene/Acetylene peak-height ratios.

Plant	Assay 1 (11.11.77)	Assay 2 (12.12.77)	Assay 2/Assay 1
A	4.02×10^{-3}	3.49×10^{-3}	0.87
B	7.87×10^{-3}	7.29×10^{-3}	0.93
C	10.26×10^{-3}	3.45×10^{-3}	0.34
D	6.02×10^{-3}	2.81×10^{-3}	0.47

A and B are the controls; C and D are the experimentals.
The snails were introduced into the enclosure on 18.11.77.

It is obvious from these results that a considerable drop in the nitrogen-fixing activity of the experimental plants has occurred.

Snail feeding activities on the experimental plants caused a certain amount of leaf-fall. Leaves and leaflets were broken off directly by snails moving over them, and also by snails eating through leaf stalks while feeding on stems. Although leaf-fall explains some of the observed decrease in nitrogen fixation, it was not sufficiently heavy to explain the full decrease. It must be noted also that leaf-fall was heaviest on those stems most severely attacked by the snails. It is believed that the major portion of the nitrogen-fixation decrease displayed by the experimental plants was due to the disruption of phloem tissues by feeding snails, which thereby disrupted the supply of photosynthetic nutrients to the roots.

9.4 Discussion

9.4.1 Food of H. aspersa

While the consumption of large amounts of lupin and tree lucerne in the areas where they occur is indicative of the palatability of these plants to snails, it probably also indicates high nutritive value in comparison to other readily available food species. If this is so it would explain the large snail population increases which occur in lupin areas. Mead (1961) found that leguminous crops were particularly favoured by the giant African snail, Achatina fulica.

The brown colour of most of the snail faeces collected from non-lupin areas indicated that mainly senescent or dead plant foods were being taken. The results of the palatability trials suggest that the Oenothera and marram cuticles found in faeces would not have come from green foliage.

Palatability tests show that a number of plants appear to be palatable in green and fresh condition, but this does not indicate that they are more palatable this way than when they are senescent. Not all of the plants found to be palatable would be available with green foliage throughout those times of the year when snails are active. In particular, Melilotus indica has only a very short growing season over late spring and early summer, before seeding and dying. Also, many of these species are erratically distributed in the dunes and not available in sufficient quantities to be a major part of the food supply. Perhaps the only species tested to which neither of these limitations particularly apply is Erigeron canadensis.

There are some pitfalls inherent in the interpretation of palatability data. Grime et al. found that palatability of some plants to Cepaea nemoralis depended more on the nature of the leaf surface of the plant than on taste. Some particularly hairy species were not taken by the animals but extracts from them, soaked into filter paper discs, were palatable. Also, leaf discs are an unnatural form in which to present food, and some of the natural defences of a plant against feeding by snails may be circumvented by removing pieces of leaf in this way.

Furthermore, palatability trials have in some cases yielded results which were entirely opposite to those of related field studies. Wolda et al. (1971) found that one plant species which appeared to be actively avoided in the field and which was ascertained to be very rarely eaten, gave the highest results for palatability in laboratory tests which included species favoured in the field. This anomaly could not be explained by the authors.

Rabbit faeces are present in large quantities throughout the year in the dunes, and they may be a significant food source in non-lupin areas. The fact that rabbits are sometimes known to practice coprophagy with their own droppings suggests that there must be significant amounts of nutrient retained in them. On a practical level,

eating of rabbit faeces by snails may be a source of error in cuticle analysis of snail faeces.

The ability of snails to derive nutrient from dead plant materials, rabbit faeces, paper and the outer layer of mature lupin pods is undoubtedly greatly enhanced by the animals' possession of large numbers of carbohydroses, including celluloses, in the gastro-intestinal tract (Holden et al. 1950; Holden and Tracey, 1950; Myers and Northcote, 1958). The celluloses are produced by the animals themselves, rather than by symbiotic micro-organisms (Strasdine and Whitaker, 1963).

Sand appeared to be present in the faeces of H. aspersa in greater quantities than could readily be explained by particles adhering to the moist faeces when they were initially deposited. This suggested that some ingestion of sand had occurred. Williamson and Cameron (1976) found that soil and humus were ingested in significant quantities by Cepaea nemoralis, particularly small juveniles, and in some cases the faeces were occupied wholly by this material. They suggested that ingestion of soil could supply nutrient in the form of microbes or that it could be a source of minerals. Crowell (1973) showed that H. aspersa obtained calcium from the ingestion of soil. Storey (1970) showed that mineral particles were necessary in the diet of the aquatic snail Limnaea pereger for the breaking up of ingested foods for efficient assimilation.

Richardson (1975 b) could find no evidence to suggest that Cepaea nemoralis selected certain foods and avoided others in his study of a dune population of these snails. He found that the dead parts of the commoner plants, such as marram, were eaten most frequently. However, Grime et al. (1970), Wolda et al. (1971) and Williamson and Cameron (1976) found that natural populations of this species displayed considerable choice in selection of food species. Certain species were sought out while others appeared to be actively avoided. The results of the present study indicate that this is true also of H. aspersa. Lupin and tree lucerne are particularly favoured as food species at Santoft, while even in non-lupin areas, marram cuticles were not present in faeces to the extent that would be expected if plant species were eaten at random.

9.4.2 Effects on lupin of snail feeding

It appears that the major damage to lupins from the feeding activities of snails is the stripping of the outer tissues from the stems of the plants. Considerable damage to the phloem occurs and this would disrupt the movement of photosynthetic products and other substances around the plant. A degree of defoliation also occurs, but this is probably largely incidental, with many leaves being broken off rather than ingested.

This combination of defoliation and damage to the phloem has a significant effect on nitrogen fixation in lupin as was seen in the acetylene-reduction analyses.

The potted plants used in this experiment were probably growing under greater physiological stress than those growing in the dunes. For instance, the plants ideally required re-potting into larger pots to give more room to their root-systems but this could not be done as larger pots would not have fitted into the incubation chambers. However, in spite of these draw-backs in technique, it is felt that the results remain valid. The amount of damage caused to the experimental plants by the snails over the three week period has been seen to occur within a few days in areas of heavy infestation at Bantoft. Heavy damage may be sustained by lupins for several months at a time.

The period of heaviest snail attack appears to be spring and early summer. This is the main reproductive period and activity after this time is more restricted by the longer dry spells. Over this period the water tables in the dunes are dropping and plants are likely to be under increased water stress. The ultimate death of the plants could be the result of a combination of these factors.

Lupin death is probably not due directly to the decrease in nitrogen fixation as there are usually no signs of leaf yellowing in the plants prior to death. However the general disruption of translocation in the plants that occurs with damage to the phloem tissues is likely to be important. Decrease in nitrogen fixation is symptomatic of this disruption.

CHAPTER 10

CONCLUDING DISCUSSION AND COMMENTS

10.1 Issues for further investigation

10.1.1 Population ecology

Williamson and Cameron (1976) suggested that nettle (Urtica dioica) appears to be able to support greater populations of the snail C. nemoralis than do other food species. Similarly, tree lupin (Lupinus arboreus) can support unusually dense populations of H. aspersa. The factors which may be responsible for this remain open to investigation and include the relative assimilability of lupin, and its nutrient value and mineral content in relation to other food species. It seems significant that another legume, Cytisus proliferus appears to have the same effect.

In areas where populations of H. aspersa have attained high densities in response to lupin growth, there is strong evidence that density-dependent inhibition of juvenile growth occurs, producing a decrease in the growth rates of juveniles and the size that they attain at maturity. It is suggested also that this same factor may be the cause of the high juvenile mortality observed in these areas. The observations of Herzberg (1965) and Williamson et al. (1976) suggest that the inhibition is effected by the build-up of slime trails in the environment. Further investigation of this phenomenon is obviously required. The cause of the high mortality of small juveniles in these areas is of particular interest, whether it is density-related or not, as this may be the key to possible biological control methods for this species. The difficulties of attempting to research juvenile mortality and its causes have already been mentioned. A rather more experimental approach to this subject seems desirable.

Juvenile growth-check data were unfortunately not collected for the area 1 adults. It would have been of interest to compare juvenile development rates in this population with those of the block 122 lupin area to see whether the positive effect of lupin on juvenile survival and population growth was paralleled by a positive effect on

individual growth rates. Thomas and Benjamin (1974) and Thomas et al. (1974) found that increasing the population density of the freshwater pulmonate Biomphalaria glabrata from a low level initially had an enhancing effect on natality and growth rates. This was believed to be due to the positive effects of both the release of certain chemicals into the medium from plants injured by snail feeding, and snail-snail interactions of a chemical nature.

For animals living in low density populations, the ability to find a mate for reproduction is a primary concern, especially when the animals' mobility is limited. Many insects have been shown to rely on air-borne pheromones to overcome this problem. The possibility that H. aspersa and other terrestrial snail species may have the ability to follow the trails of conspecifics requires much closer investigation. That some species of aquatic snails do possess such an ability is well established (Wells and Buckley, 1972; Townsend, 1974). Of special interest in these cases is that the trails exhibit some degree of temporary polarisation, allowing animals to follow the trail in the direction taken by the individual that laid it. The chemical basis for this polarisation appears to be unknown as yet.

Possibly related to trail-following is the marked tendency for adult and large juvenile H. aspersa to aggregate for hibernation. Suggestions were made in Chapter 5 as to the possible adaptiveness of this phenomenon to the animal, but once again the need for further research is indicated.

10.1.2 Economic significance: friend or foe?

In most areas of snail population build-up at Santoft, lupin dieback is largely complete by the time of tree-planting. Although Gadgil (1971 a) states that it is "impossible to establish young (pine) trees" without the shelter of lupins, tree establishment in these areas at Santoft appears to take place without difficulty. It is likely that the generally dense marram, which has probably benefited from the nitrogen inputs from lupins, provides sufficient shelter.

Soon after tree-planting the lupins are normally sprayed with a herbicide to release the young pines from competition. This process has apparently been unnecessary in newly planted areas at Santoft for

the past four or five years, due to the activities of the snails (H.G.J. Sutton, pers. com.), and this means a saving on the cost of the herbicide and its application. On the other hand, however, the lupins in some of these areas do not survive through their fourth year from seeding, when nitrogen accumulation in the biomass reaches its peak (Gadgil, 1971 c) and therefore considerable potential for nitrogen fixation is lost. Whether or not H. aspersa is to be regarded as a pest depends on how necessary this extra production of nitrogen is to tree growth.

On most sites it is likely that the soil contains sufficient nitrogen to meet the requirements of the pine tree crop. However, Gadgil (1971 a) mentions that on some sites there is a rapid decline in tree growth rate from age 10 to 12 onwards, and that this is associated with symptoms suggesting a deficiency of nitrogen. This condition was found to be relieved by heavy thinning which not only reduced inter-tree competition, but also stimulated rapid lupin growth under the trees. It is in this type of situation that premature die-back of the initial crop of lupin, caused by snail attack, may aggravate the problem. In such an area, rapid lupin regrowth after the first tree-thinning (at five or six years) may be especially important, and at this stage, as some snails are still present, another snail population increase would probably also occur. It would be of interest to know whether this remnant of the snail population had a significant effect in preventing lupin regrowth by consuming seedlings. Some preliminary trials indeed suggested that lupin seedlings were eaten.

At Santoft, the occurrence of sites on which tree growth is sub-optimal appears to be frequently related to a coarser texture of the sand on these sites in comparison to surrounding sites. It is noticeable that on many of these sites initial establishment of marram and lupin has also met with little success. In these cases the tree-growth problems bear no relation to snail attack on lupins.

It would appear, then, that the question of whether or not H. aspersa can be considered a pest of economic importance in coastal dune forestry must await further assessment of all the factors affecting tree growth at particular sites.

Control of H. aspersa in these conditions using the methods available could not be guaranteed to be successful. Control methods usually involve attraction of active snails to a poisonous bait which is then consumed. If the animals are, however, in the position of being surrounded by a highly palatable food species (lupin) the attractiveness of the bait as an alternative food source will be diminished. Also, the logistics and cost of spreading bait preparations over tracts of land the size of a forestry block may well be prohibitive. The need for investigation into alternative control methods is indicated.

10.2 Comments on the study

Studies of the population ecology of terrestrial snail species are few in number, and very little work of this sort has been undertaken on H. aspersa. For this reason, considerable difficulty was experienced in finding suitable methods of approach to the present study. The difficulties were two fold : Those posed by the heterogeneous nature of the dune-country terrain and vegetation, which greatly affected sampling methods; and those posed by the biological characteristics of the animal itself. The highly advanced analytical techniques of the insect ecologist are of little use in studying an invertebrate which has a total life span frequently in excess of five years, which lacks any clearly defined developmental stages apart from the distinction between adult and juvenile, and whose juvenile growth rate can vary markedly within and between populations.

In the event the initial aims of the study, to provide an insight into the ecology of H. aspersa in the dune environment with particular interest in the role of lupin, were achieved, and possible lines of further research have been pointed out. It is likely, however, that further progress will require an approach that is less descriptive and considerably more analytical and experimental than that followed in this study.

A P P E N D I X

Formula for nitrogen-free liquid plant nutrient

Chemical	Stock solution		Amount of stock added to 4 l of water to make nutrient solution
	molarity	gm/l	
$MgSO_4.7H_2O$	1.0 M	246.4	2 (cm^3)
$Ca(H_2PO_4)_2.H_2O$	0.01 M	2.52	200
K_2SO_4	0.5 M	87.2	80
$CaSO_4.2H_2O$	0.01 M	1.72	800
Minor elements			4
$Na_2FeEDTA$			4

Minor elements	Amounts added to 1 l water for stock solution
$MnCl_2.4H_2O$	1.81 g
H_3BO_3	2.86 g
$ZnSO_4.7H_2O$	0.22 g
$CaSO_4.5H_2O$	0.08 g
$H_2MoO_4.H_2O$	0.09 g

$Na_2FeEDTA$ 1.643 g/50 ml for stock solution.

pH of the final solution adjusted to 5.0 - 6.0 with 0.1N HCl or 0.1 N KOH.

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