Studies on the Ecology and Ecogenetics of the Helicid Land Snail *Theba pisana* (Müller).

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by Robert Hulin Cowie.

April 1982

Studies on the Ecology and Ecogenetics of the Helicid Land Snail *Theba pisana* (Müller).

R. H. Cowie - Ph.D. thesis - abstract

Theba pisana is a highly variable, widespread and locally abundant, coastal Mediterranean land snail which reaches the northern limit of its distribution at a number of localities in the southern and western British Isles. Most of my work has concentrated on the colony at Tenby, South Wales.

Its recorded distribution in Britain is reviewed, and, with a field survey of known localities, suggests that it was probably introduced to Britain as little as three centuries ago, and that its present distribution is restricted both by overall climate (probably low winter temperatures) and by local climate related to aspect.

Changes in population size-structure over four years, with estimates of growth rates and observations of reproductive maturity, show that *T. pisana* is biennial and semelparous at Tenby. Populations elsewhere in the species' range adopt both biennial and annual patterns, depending upon the length of the growing season. In a laboratory study, mean lifetime egg production per pair was about 700 (when those pairs producing less than 100 are ignored), with a maximum of 1,512 in 15 clutches. In comparison with *Cepaea nemoralis*, *T. pisana* appears more '*r* - selected', which agrees with theoretical predictions only if habitat characteristics are more important than climate in determining its strategy.

In the field at Tenby, adults and juveniles show different microhabitat or microclimate preferences. Their marked difference in shape may be related to this. They have different high temperature tolerances, consonant with their behaviour. Shadier and less exposed parts of their microhabitat are preferred by adults (at least), and laboratory experiments suggest that they can use direction of the sun and/or wind as cues to do this. There may be genetic differences in temperature tolerance between individuals from Spain and Tenby.

Estimates of dispersion, dispersal and density, with data on fecundity, allow the estimation of effective population size at Tenby. Minimum estimates indicate that drift cannot be discounted as a potential factor determining genetic diversity.

Laboratory breeding has broadly characterised genetically the variation in shell banding pattern at Tenby. Three loci are involved, but epistasy allows only four phenotypes to appear. Morph frequencies in the field at Tenby appeared fairly constant over five years. Banded snails appear to be at a selective advantage during at least the second year of life. Either unbandeds are at an advantage earlier in life, or gene frequency equilibrium has not yet been attained in these populations.

Variation in mantle collar colour at a wide range of British, northern French and Mediterranean colonies is described; it may be related to climate, but reasons for this remain obscure.

There is considerable intra-population variation in shell thickness, but little inter-population variation at a range of localities from Britain to Israel.

The findings of the thesis are compared with ecological and ecogenetic knowledge of other species in western Europe.

ACKNOWLEDGEMENTS

The work presented in this thesis was carried out on a part-time basis while working as Professor A. J. Cain's assistant. I am deeply indebted to him for giving me this opportunity. I am also grateful to him, as my supervisor, for encouragement, discussion and thorough criticism throughout the time I was working with him.

Professor Cain, Professor C. J. Duncan and Dr. R. G. Pearson, while each was Head of Department, allowed me the time and provided me with the facilities to undertake the work.

For hospitality in Spain I am grateful to Mr. and Mrs. R. V. Corsgreen and Miss P. A. Corsgreen; and in Sardinia, to Dr. and Mrs. C. Inglesfield.

The following provided me with valuable samples or assisted me with field work: Professor A. J. Cain, Drs. R. A. D. Cameron, M. A. Carter, I. Denholm, C. N. Goodman, J. Heller, C. Inglesfield, P. Karayiannis, G. Lewis, J. Osborne, C. R. C. Paul, J. Whitelaw, Mr. J. Cooper, Mrs. J. E. Hunter and Miss C. T. French.

I am grateful to the following for discussion, criticism, and for computational and statistical advice: Dr. M. E. Begon, Dr. A. R. Cossins, Professor J. D. Currey, Dr. J. J. D. Greenwood and Mr. S. M. Spelling. I especially wish to thank Dr. J. A. Barrett for going over drafts of parts of chapters 3, 5 and 6, and for cogently imparting some of his knowledge of statistics to me. Numerous others, either in writing or in person, have made valuable comments on various parts of my work.

Dr. A. R. Cossins allowed me to carry out the temperature tolerance experiments in his laboratory.

Mr. B. Lewis photographed the shells; Miss L. Begg typed the text efficiently; and Dr. D. J. Dutton assisted me with presentation.

Finally, I owe a debt of gratitude to my parents for their encouragement, confidence in me, and support during the difficult times.

Contents.

Tables and figures are placed together at the end of the relevant chapter, tables following figures.

Chapter 1

Introduction

1.1. Aims of the thesis.

Land snails provide excellent material for the study of ecology, variation and adaptation; they tend to be somewhat sedentary and thus easy to sample relatively accurately; the nature of much of the variation manifested by them is readily recorded by simple methods, and often, if shell variation is being characterised, a permanent record (the shell itself) is available. It is for these reasons that much enlightening work on natural selection has been carried out on the genus Cepaea Held. over the last thirty years (reviewed by Jones, Leith and Rawlings, 1977; Clarke, Arthur, Horsley and Parkin, 1978; Cain, in press b).

Theba pisana (Müller) (nomenclature discussed in appendix 1) is particularly interesting because of the profuse variation in shell pattern it exhibits. It also provides very tractable material because of its high population densities and the fact that it rarely burrows in the field, and the ease with which it can be maintained in the laboratory. It has achieved pest proportions in parts of its natural and introduced range (section 1.3.), yet little is known of its basic ecology and behaviour. In part, my aim has been to reduce this gap in our knowledge. To this end, I have investigated the life-history strategy (chapter 3), thermal and desiccation relations (chapter 4), and population size and structure (chapter 5). The main study populations (at Tenby, South Wales) have been set in their biogeographical context in chapter 2.

Biogeographical, ecological and behavioural information is essential before the results of studies of variation can be adequately understood. The genetic control of the variation must also be known. Breeding experiments were therefore set up to elucidate the genetics of shell pattern variation, and with these results as a basis, variation in the field was investigated (chapter 6). Chapters 7 and 8 describe variation in mantle collar colour and shell thickness respectively, but any genetic basis of these has not been investigated experimentally.

Of particular interest at all stages was the significance of both macro- and micro-climate, especially as Tenby is at the northern limit of the species' range. For comparison with the Tenby populations I have been able to analyse many samples from elsewhere in Britain, northern France, and the Mediterranean, collected both by myself and others. It has been possible to draw some inferences about strategies adopted under different climatic regimes.

The significance of the results of these studies is discussed at the end of each chapter; their more general biological significance is considered in the final discussion chapter (chapter 9).

Specific names of British snails follow Waldén (1976), and of plants, Clapham, Tutin and Warburg (1962).

1.2. Taxonomic position of T. pisana.

T. pisana belongs to the superfamily Helicacea of the stylommatophoran gastropod molluscs. The family Helicidae belongs to the Helicacea, and itself is divided into a number of sub-families, including the Helicinae, Helicigoninae and Helicellinae (Taylor and Sohl, 1962; but see Shileyko, 1978).

Some of these have from time to time been raised to family status (e.g. Pilsbry, 1939). T. pisana is a helicid, but posesses features of all these three sub-families (see Cain, in press a). The appearance of its shell is very helicelline, particularly in the banding patterns and in the absence of a definite apertural lip in the adult. However, shell characters may be very prone to convergence (e.g. Cain, 1977a), the internal structure of the animal less so. Indeed the accepted classification of the pulmonates rests heavily upon the structure of the reproductive system. The fact that the right ocular retractor muscle of T. pisana passes between the penis and vagina rather than to one side of them, prevents it being placed with the Helicellinae; although Shileyko (1978) has implied that even this may not be of great taxonomic significance. In its reproductive system, described in great detail by Noyce (1973), it posesses a combination of helicigonine characters (spermathecal duct and its diverticulum bound in close apposition to the oviduct by connective tissue; simple, unbranched, paired mucus glands) and helicine characters (particularly the four-bladed dart). The haploid chromosome number (30 - Perrot, 1939; Mallett, 1962; about 28 - Rainer, 1967) is higher than in most helicines and more similar to those of the few helicigonines which have been studied (Perrot, 1939; Mallett, 1962; Rainer, 1967). It is clearly not possible to place it with any confidence in either sub-family. The absence of a flagellum on the penis or epiphallus is uncharacteristic of most helicids, and indeed Perrot (1939) has placed it in a separate sub-family, the Euparyphinae. It is not possible to decide which of these various characters is the least prone to convergence and therefore of the most taxonomic value (Cain, in press a), but although Taylor (1912) acknowledged its distinctly helicigonine features, it is usually placed with the Helicinae (e.g. Taylor, 1912; Thiele, 1931; Zilch, 1959-1960; Backhuys, 1975; Kerney and Cameron, 1979) on the basis of its four-bladed rather than two-bladed dart.

1.3. World distribution and introductions.

Morocco has been suggested as the region of origin of T. pisana on various bases. Sacchi (1971) considered that its Atlantic habitat and climate would have been the optimum for T. pisana in the Pleistocene, when it is thought to have appeared, while Mediterranean areas would have been less suitable. It may exhibit a wider range of shell colour and pattern variation in Morocco than elsewhere in its range, and the other species in the genus Theba (= Euparypha) are present only in this part of North Africa (Sacchi, 1955, 1971). Until very recently when it was discovered in the Pleistocene of Menorca (C. R. C. Paul, personal communication) it had only been known as a fossil from the Pleistocene of the Casablanca area (Biberson and Jodot, 1965), and in deposits estimated as 30,000 ± 5,000 years old from the Canary and Salvage Islands (Backhuys, 1972). These various pieces of circumstantial evidence may be suggestive of Morocco as its region of origin, but since few other localities within its range have been investigated palaeontologically (except e.g. some in the Pleistocene of Israel, where Heller and Tchernov (1978) found no sign of it), they are insufficient to support a definite conclusion.

T. pisana is now found in coastal habitats around almost the whole of the Mediterranean, including southern Europe, part of Asia Minor, the Near East, and North Africa. It is also found on most of the Mediterranean islands. Its range extends southwards along the Atlantic coast of Morocco and as far as northern Mauritania, and northwards up the Iberian and French coasts, reaching its continental mainland limit on the Belgian coast, the northernmost colonies in Belgium being considered by Deblock and Hoestlandt (1967) to be the result of artificial introductions. There are colonies in the Channel Islands on Jersey and Guernsey (introduced from Jersey in 1860 - Barrett, 1972), in the south-west of England and Wales, and on the east coast of Ireland, this being its northernmost locality. The British distribution is described in detail and its probably artificial origin discussed further in chapter 2. It may have been present before man in the Canaries and Salvages (Backhuys, 1972), and the Madeiran archipelago (Cook, Jack and Pettitt, 1972), although Cockerell (1921) suggested that it might have been brought to the latter by the Moors. It is almost entirely restricted to coastal regions but does extend inland at some localities (Taylor, 1912; Deblock and Hoestlandt, 1967; Sacchi, 1965, 1971), and has become an agricultural pest in some areas (de Stefani, 1913 - referred to by Basinger, 1927; Harpaz and Oseri, 1961; Avidov and Harpaz, 1969).

Much of this Mediterranean and Atlantic distribution (summarised diagramatically by Sacchi, 1971) may well be the result of the activities of man in historic times in addition to the natural spread of the species, as suggested by Bullen (1910) and Heller and Tchernov (1978); but certainly, introductions further afield are due to man. A single shell has been found in Bermuda (Peile, 1926) but there is no record of an established colony. It is also recorded from Somaliland (Taylor, 1912; Spence, 1938) and Mozambique (van Bruggen, 1964), an extension of the South African distribution (see below), but the most important introductions have been to the United States, South Africa, and Australia.

T. pisana was first noticed in the U.S. in 1914 at La Jolla in southern California (Chase, 1915; Pilsbry, 1939), although large numbers had been imported from Sicily prior to this (de Stefani, 1913 - referred to by Mead, 1961). It also became established elsewhere in California and achieved pest proportions at some localities, finally being eradicated by the late 1940's (McLean, 1922 - quoted by Basinger, 1927; Basinger, 1927; Pilsbry, 1939; Gammon, 1943; Armitage, 1949). It has been accidentally introduced to various eastern U.S. ports, but has never become established (Dundee, 1974).

It was first recorded from South Africa in 1881, and rapidly became abundant in the western Cape Province (Swanton, 1902; Connolly, 1916; Hickson, 1972; McQuaid, Branch and Frost, 1979). Later it spread to most of the coastal regions of the east and west seaboards (Spence, 1938; Quick, 1952; van Bruggen, 1964; Noyce, 1973) and has become an agricultural pest (Dürr, 1946; Joubert and Walters, 1951).

It was probably introduced to Australia during the 1920's, and is now known from South Australia (Taylor, 1928; Pomeroy and Laws, 1967; Lim and Jenkins, 1972; Butler and Murphy, 1977), Western Australia (Spence, 1938; Johnson and Black, 1979;

Johnson, 1980), and Victoria (Quick, 1953).

No extensive eradication programmes have been initiated in South Africa or Australia, as in the U.S., and T. pisana is undoubtedly too well established in these countries, for such a programme to be successful. The ease and frequency with which T. pisana is transported, either deliberately or unintentionally, by man (Dundee, 1974), its high fecundity (chapter 3, section 3.3.), and its high potential for dispersal once introduced (Johnson and Black, 1979, and chapter 5, section 5.4.) mean that without strict control, its range may expand even further until it becomes a serious pest elsewhere.

Chapter 2

Distribution and Origin in the British Isles

2.1. Introduction.

The purpose of this chapter is firstly, to bring together and review in detail the literature on the distribution of *T. pisana* in Britain and Ireland (excluding the Channel Islands which are associated zoogeographically with France rather than Britain and Ireland); secondly, to present the results of a survey carried out during the summers of 1978 and 1979 of its present mainland British localities; and finally, to discuss possible reasons for the changes in distribution which have taken place since the species was first recorded in Britain, its status as a 'lusitanian' species, and its origin in the British Isles.

2.2. Historical review of the British distribution.

2.2.1. Introduction.

T. pisana was first recorded from Britain by Pennant (1777) under the name *Helix zonaria* L. but he did not give any locality for it.*

During the early part of the nineteenth century a number of valuable accounts of the British terrestrial Mollusca were published (Montagu, 1803; Maton and Rackett, 1807; Jeffreys, 1833a, b). These accounts were followed by the extensive manuals and monographs of Forbes and Hanley (1853), Jeffreys (1862) and Taylor (1894-1921) which drew together the available information

---

*Turton (1819) referred to the 1770 edition of Martin Lister's *Historiae Conchyliorum* (Huddesford, 1770; original edition published in 1678), but this was not necessarily a British record, since Lister also figured Continental species; and besides, the figure referred to by Turton is certainly not of *T. pisana* which has a much smaller umbilicus; neither does any other figure resemble *T. pisana*.

from the literature and from communications with other shell-collectors and naturalists, and added this to the authors' own observations. All these accounts indicated the presence of T. pisana in South Wales, Cornwall, the east coast of Ireland, and the Channel Islands. Taylor (1912), inparticular, gave more precise details of distribution and included records from other localities in Britain. In addition to these major works, a large number of popular handbooks were published which gave some details of the distributions of the species of British molluscs, but added little to the knowledge available on T. pisana (e.g. Turton, 1819, 1831; Gray, 1840, 1857; Leach, 1852; Tate, 1866; Rimmer, 1880; Adams, 1896; Ellis, 1926; Step, 1927). The information presented in these books was not always based on personal observation, and often largely derived from previous works.

Alder (1837) published the first critical check-list of species recognised as British, including T. pisana. Gray (1840) produced, in his re-written version of Turton's Manual (Turton, 1831), what Kerney (1967) considered to be the first census of British land and freshwater molluscs. Following these, the Conchological Society of Great Britain and Ireland started systematic censuses, the first being published in 1885 (Taylor and Roebuck, 1885). This has been followed by further censuses (Taylor and Roebuck, 1889, 1901; Adams, 1896; 1902; Roebuck, 1921; Ellis, 1951) and in 1976 by the Atlas of the non-marine Mollusca of the British Isles (Kerney, 1976). All these censuses indicated the presence of T. pisana in South Wales (Glamorgan and Pembrokeshire), Cornwall, the east coast of Ireland, and the Channel Islands.

The documented histories of the British colonies (excluding the Channel Islands) are now reviewed in greater detail.

2.2.2. Dyfed (formerly Pembrokeshire). - figs. 2.1., 2.2., 2.3.

The largest mainland British colony of *T. pisana* is at Tenby and all the general accounts mentioned above indicate its presence here. Montagu (1803) found *T. pisana* at Tenby in about 1791. He recorded it under his new name *Helix cingenda*. This appears to have been the first record of the Tenby colony. Jeffreys (1833a) found *T. pisana* 'in vast profusion' on the 'sandy plains near Tenby' and later, Tye (1877) considered that the species' distribution at and around Tenby had broadened considerably since Montagu's day when it was 'confined to a small spot'. Other nineteenth century records of *T. pisana* at Tenby are little more than notes indicating the discovery of a new variety at this locality, without giving any detail of precise distribution (Tye, 1874; Taylor, 1883, 1888, 1890; Cockerell, 1886), although Cundall (1889) did indicate that the type and var. *alba* Shuttleworth were particularly abundant 'on the Castle Hill and on the coarse grass bordering the Esplanade'.

During the nineteenth century *T. pisana* was also recorded from Manorbeer (*sic*), about 8 km west of Tenby along the coast (Jeffreys, 1862; Tye, 1877). Milnes (1889) found two shells on the 'downs above Giltar Point', just west of the Tenby Burrows, but these may well have been imported accidentally. Gosse's observation (Gosse, 1856) of 'hundreds of *Helix virgata*' on the isolated outcrop of rock just behind the sandhills (no doubt the 'Black Rock' of Stubbs, 1900) is quite possibly an incorrect identification, since Gosse was primarily a marine and littoral biologist. This comment may in fact refer to *T. pisana*.

Cernuella virgata (Da Costa) is present at this locality but not in the numbers Gosse's comment might suggest.

Pre-1900 records, then, do not give any clear indication of the extent of the distribution of T. pisana in and around Tenby, but simply record its presence in Tenby itself, on the Tenby Burrows, and at Manorbier. It was not until Stubbs (1900) published the results of his extensive and detailed survey of the land and freshwater molluscs of the Tenby area, that more information became available. He recorded the precise distribution of each species that he found, as well as incorporating notes on the varieties present. His work remains the most informative account of molluscan distributions in this area.

Stubbs' survey showed that T. pisana's range at Tenby extended from Castle Hill and St. Catherine's Rock, along the South Cliff and below the Esplanade, and thence, via the Jubilee Gardens and Wreck (sic) Field, to the railway banks and Burrows, where he said it was abundant. From the western end of the Burrows its range extended onto the cliff tops at Giltar, and along the cliffs almost to Lydstep. At the eastern end of the Tenby range, Stubbs found T. pisana 'from the bottom of the Norton to a distance of about a mile up the Narberth Road', this being its most inland locality. He also remarked on finding particularly globular shells on the Marsh Road'. (Pitchford (1973) also mentioned finding T. pisana at this locality in 1954).

Stubbs indicated that T. pisana occurred also at Manorbier, and that odd specimens had turned up at Saundersfoot (on the coast about 5 km north of Tenby), at Penally, and on the North Cliff at Tenby; he considered these odd specimens to have been 'obviously imported', although Taylor (1912) recorded a

Mr. C. Jefferys's observation of T. pisana found plentifully at Saundersfoot in 1883. Stubbs also found T. pisana to be 'fairly common' on the south side of Caldey Island.

Since Stubbs' survey, little has been added to the information presented regarding T. pisana in Pembrokeshire. Wintle (1925) remarked that the Tenby Burrows were noted for their molluscan fauna, including T. pisana in greater profusion and variety than at any other locality in Britain. He also gave the only details available for the actual distribution on Caldey Island (rather than simply a record of the presence of T. pisana there); he recorded it from the sand dunes and cliffs around Priory Bay and from the sloping sands behind Sandtop Bay. He considered that T. pisana may have been more widespread previously on Caldey Island, since he found dead shells elsewhere on the island in blown sand deposits, although these were of unknown age (see also Wintle, 1922). He did not mention finding it in abundance on the south side of the island as Stubbs had.

Deblock (1962) undertook a large-scale survey of the British distribution of T. pisana, and in Pembrokeshire, only found it at Saundersfoot, Manorbier, and Tenby. Unfortunately he gave no further details. Earlier, Oldham (1928) had discovered T. pisana on dunes at Stackpole Warren, about 9 km further west than Manorbier. (He did not find any specimens at Freshwater East, between Manorbier and Stackpole Warren). Although Deblock (1962) investigated a number of localities further west than Manorbier, it is possible that he overlooked the colony at Stackpole Warren, since this colony was again recorded as extant later than 1950 by Kerney (1976) in the Atlas of the non-marine Mollusca of the British Isles. This record was based on observations in 1969 by A. Norris and B. Colville (M. P. Kerney in litt. 23 VII 1979).

These observers did not find T. pisana further along the coast at St. Govan's Head (A. Norris in litt. 5 IX 1979).

The Atlas (Kerney, 1976), in bringing together and summarising the recorded distribution of T. pisana in the British Isles, did indicate post-1950 records in the 10 km grid squares including Tenby and Saundersfoot, and the Tenby Burrows and Caldey Island; but only pre-1950 records in the square including Manorbier. It is likely that Kerney may not have had access to the data of Deblock (1962) who had recorded T. pisana at Manorbier in 1961. (The broad basis of the records, and the use of the 10 km squares of the National Grid for the mapping of distributions are explained in the Atlas).

Published work, summarised and augmented by unpublished records by Kerney (1976), thus suggests that the distribution of T. pisana in Dyfed is centred around Tenby, where it is extremely abundant; and that it extends to Saundersfoot to the north-east, and to Manorbier and Stackpole Warren to the west. The distribution does appear, however, to be discontinuous.

2.2.3. Swansea (West Glamorgan)- fig. 2.4.

The presence of T. pisana at Swansea is almost certainly due to its introduction from Tenby by J. G. Jeffreys, although Jeffreys himself at first considered these introductions to have been unsuccessful (Jeffreys, 1862). Jeffreys released his snails at various places in the dunes close to the sea between Swansea and Mumbles. In 1874 it was found in large numbers on these sandhills (Rimmer, 1877). Tye (1978) commented on the unbanded variety of T. pisana found at Swansea, and Kew (1893) stated that the species was still living on the dunes in 1884. Taylor (1912) recorded observations by various collectors and naturalists including those of Jeffreys (1862) and Rimmer (1877). He also noted that in 1883 T. pisana had been found to be quite common, especially near the starting-place of the old tram line to Oystermouth. Since about this time it seems to have declined in this area. Taylor reported that by 1877 the species was considered far from common at this locality, and that by the time he was writing this section of his monograph (Taylor, 1912), Mr. H. Rowland Wakefield no longer included it among his list of species for Swansea, although he had picked up a few dead shells at Singleton.

However, T. pisana was recorded again at Swansea by Quick (1927) who found it in an 'area of a few square yards at Mumbles Road'. Boycott (1934) did not include Swansea in his list of localities for T. pisana, but Quick (1943) again recorded its presence, this time a very small colony on the seaward slope of the railway facing south-west at Mumbles Road station. Deblock (1962) searched the dunes near Black Pill but found no living specimens,only shell debris. He therefore concluded that T. pisana was extinct at Swansea. Kerney (1976) indicated a post-1950 record of T. pisana in the 10 km grid square covering the Swansea area. This was based on observations by Dr. P. Makings in 1969 (M. P. Kerney in litt. 23 VII 1979). Dr. Makings (in litt. 30 VIII 1979) and Dr. M. J. Isaac (in litt. 12 IX 1979) had observed this colony at Black Pill, near the railway line, for some time, but few snails were ever seen.

All the reports of T. pisana in the Swansea area since 1900 indicate small colonies at Black Pill near the railway line (which has now been dismantled, and the area landscaped). At no time since the turn of the century has it been numerous in this area. No doubt, reports of its absence have been simply the result of not finding the small, sparsely populated colony, or colonies, which have persisted. The various reports of T. pisana colonies may not necessarily refer to precisely the same one.

Kerney (1976 and in litt. 23 VII 1979) recorded T. pisana at Port Eynon on the Gower peninsula west of Swansea. This, however, appears to be the result of a misinterpretation of an observation by Quick (1927), who said, in reference to H. barbara (= Cochlicella acuta (Müller)) that:

> 'This species lives close to Swansea on a small area of a few square yards at Mumbles Road with H. pisana which is supposed to have been introduced by Gwyn Jeffreys ... and also at Port Eynon two and a half miles south-west, but not elsewhere on the Gower coast as far as I know'.

2.2.4. Porthcawl (Mid Glamorgan)- fig. 2.5.

Cooke (1916) was the first to record T. pisana at Porthcawl. He found many specimens on the sand hills to the east of the town, but the colony did not extend far along the dunes. He considered the species to have been introduced by man during the previous few years. Roebuck (1921) and Boycott (1934) included Porthcawl in their lists of localities for T. pisana, but these records may well have been based simply on Cooke's observation. Quick (1943) considered T. pisana to be 'abundant at Porthcawl on the dunes' but that it did 'not extend to Kenfig' which is just north of Porthcawl itself. It is not clear whether Quick (1943) was referring to the dunes east of the town mentioned by Cooke (1916), or solely to those north of the town. Deblock (1962), in his survey of the British localities of T. pisana, found it at Porthcawl but gave no details. Kerney (1976), in the Atlas, indicated post-1950 records of T. pisana near Porthcawl. These records were based on information from Mr. S. P. Dance who, in 1969, observed it north of Porthcawl in the 10 km grid square which includes Kenfig Pool; and from Mr. M. Goodchild who, in 1970, observed it east of Porthcawl in the area mentioned by Cooke (1916) (M. P. Kerney in litt. 23 VII 1979; M. Goodchild in litt. 24 VIII 1979).

Published accounts therefore suggest that T. pisana has at least a foothold both to the north and east of Porthcawl.

2.2.5. St. Ives (Cornwall). - fig. 2.6. (after Humphreys, 1976)

T. pisana was first recorded at St. Ives by Maton (1797) under the name Helix maculosa. All the general accounts mentioned at the start of this review indicate its presence here. Turk (1966) recorded the observations of some other nineteenth-century naturalists, who also indicated its presence at St. Ives. Taylor (1912) recorded the species as

> 'formerly and probably still in profusion at St. Ives, on the slopes of the hill descending into the town and chiefly about the promontory to the north'.

Boycott (1934), in listing localities for T. pisana considered it to be absent from St. Ives, although the basis of this contention was not made clear. Ellis (1951) included west Cornwall in his list of localities, but indicated that the species had not been recently reported from there. However, the presence of T. pisana at St. Ives was noticed in 1948 or 1949 by Mr. C. Thomas (Turk, 1966). The colony was at that time confined to St. Ives Island (St. Ives Head) at the north-western end of Porthgwidden Cove, as a result of the destruction of suitable habitat by building both on the Island and on the slopes of the hill descending into St. Ives (Turk, 1966). Humphreys (1976) described the colony of T. pisana on the Island in detail, and recorded the presence of a small 'secondary' colony, also on the Island. Humphreys' map is reproduced in fig. 2.6. Kerney (1976) recorded T. pisana as extant in the 10 km grid square in which St. Ives is situated, and Humphreys (1980) recorded its continued presence on St. Ives Head between 1975 and 1978.

It is clear from the published accounts that the St. Ives colony (or colonies) of T. pisana was much more widespread in the nineteenth century and in the early part of the twentieth century, than it is now. The remaining colony is now confined to two small areas on the Island, and even this colony has fluctuated considerably in size and numbers over the greater part of this century. As emphasized by Turk (1972), the prospects for its continued existence are not good.

2.2.6. Other mainland British records.

Taylor (1912) listed a number of localities from which T. pisana had been recorded. These included Falmouth, Whitesand Bay (a locality often quoted by nineteenth century authors, but on what basis was not made clear), and Crantock near Newquay in Cornwall; on sandhills at Woolacombe and at Braunton Burrows in north Devon; in Dorset on the coast between Lulworth and Weymouth, and on Muston Down, Winterborne (a record based on two shells - Ellis, 1969); at Bath; at Oxford (a single specimen); and on the Durham and Northumberland coast. Shells labelled 'Sussex' and 'Scarbro' were also mentioned. Taylor did indicate that he himself had verified records from West Cornwall, Dorset, Glamorgan and Pembrokeshire, but he gave no more precise details.

However, most of these records, particularly those from inland and northern localities, were no doubt based on the observation of one or two shells accidentally introduced (cf. the supposed short-lived introduction of Cochlicella acuta to Aldbourne, Wiltshire, by children after an excursion to the sea - Heginbothom, 1946). Dr. M. P. Kerney (in litt. 27 III 1980) recently received two fresh shells of T. pisana from a locality in north Lincolnshire. Such introductions would presumably not have survived for any great length of time. T. pisana has been deliberately introduced to a number of other British localities, including Scotland (Baillie, 1887, 1889), Lancashire and in particular the Southport sandhills (Kew, 1893), and Derbyshire (Taylor, 1912), but it is presumed that these attempts were all eventually unsuccessful.

McMillan (1968) retained Dorset in her list of localities for T. pisana, and Ellis (1969) considered the St. Ives colony to be the only remaining one in Cornwall, although the basis for these statements was not made clear. Kerney (1976) included the majority of the above records mentioned by Taylor (1912) in his Atlas as either 'before 1950 only' or 'casual'. It seems safe to assume that the records mentioned in this section were not based on the observation of established colonies, or if they were, that these colonies have since perished.

A previously unreported colony has recently been discovered at Treyarnon Bay, on the north Cornish coast, 6 km west of Padstow (Turk and Turk, 1981).

2.2.7. Ireland.

Taylor (1912) stated that T. pisana was first recorded from Ireland in 1818 in Pennant's British Zoology. This record was based on shells collected in County Meath, on the east coast just north of Dublin. Since then T. pisana has been recorded from the sandhills near the sea in Counties Louth, Meath and Dublin (Jeffreys, 1833b; Cockerell, 1885; Scharff, 1892; Welch, 1904; Stelfox, 1911). Most of the early, general accounts mentioned in the introduction to this review, indicate the presence of T. pisana on this part of the coast. All the Conchological Society censuses, including the Atlas (Kerney, 1976) also do, but none gives any further details. However, Kerney (1976) indicated post-1950 records only for County Dublin, his other records being pre-1950. No doubt, he did not have access to the data given by Deblock (1962). Deblock (1962) indicated the almost uninterrupted presence of T. pisana on this section of the coast from Malahide (Co. Dublin) in the south, to Clogher Head (Co. Louth) in the north. (He did not find it at his site between Skerries and Laytown). He also extended his survey both north and south of this part of the coast but found no specimens of T. pisana.

T. pisana has also been recorded in Ireland from Kildare, Queen's County, Galway and Kerry, but both Stelfox (1911) and Taylor (1912) were doubtful of the validity of these records, as none could be adequately confirmed. Stelfox (1911) also mentioned shells in the Dublin museum from Drumcondra, a suburb of Dublin, and suggested that this might indicate that T. pisana occurred further inland than previously thought. However, this record was probably as inadequate as Stelfox considered the others to be; that is, the result of an accidental and short-lived introduction. Stelfox (1911) recorded the introduction of T. pisana to Belfast with bananas, but he did not indicate whether this had resulted in the establishment of a colony. Presumably it has not, as no further mention has been made in the literature of T. pisana this far north.

2.3. The Survey.

2.3.1. Introduction.

A survey of the distribution of T. pisana on the British mainland was undertaken during the summers of 1978 and 1979. All the localities at which T. pisana had been recorded by Taylor (1912) and Kerney (1976) were investigated, except those obviously based on dubious or 'casual' (Kerney, 1976) records, or on records of one or two shells accidentally introduced (see Roebuck, 1921; Ellis, 1969). Thus, the Dorset, Cornwall, Devon, Glamorgan (except Port Eynon) and Pembrokeshire localities were visited; the Somerset, Sussex, Oxford, Gloucester, Yorkshire, Northumberland and Durham ones were not. Special attention was given to the detailed recording of the distribution of T. pisana in and around Tenby, and to making an accurate comparison with the information presented by Stubbs (1900). T. pisana was only found in Cornwall at St. Ives, in Glamorgan at Porthcawl, and in Dyfed (Pembrokeshire) at Tenby, Saundersfoot, Stackpole Warren, and on Caldey Island.

2.3.2. Dyfed.

The whole coastline from Manorbier Bay (National Grid reference SN055977) to Wiseman's Bridge (SN147063) was searched, with the exception of the short section fenced off by the Ministry of

Defence at Old Castle Head (SN073969 to SN082974). No live specimens or dead shells of T. pisana were found at Manorbier, despite a thorough search of likely sites. Manorbier Bay is a very popular beach during the summer; a large area behind the beach itself is used as a car-park, although this is not tar-macadamed; the dunes around the Bay are heavily used by people. No live specimens were found between Manorbier and the Tenby Burrows, nor were any found at Penally. Only a single empty, worn shell was found - at Giltar Point in July, 1981. The cliff-tops between Manorbier and the Tenby Burrows are heavily trampled by people walking along them, and animals graze right to the edges along some sections. The vegetation is mostly short, and typical of cliff-tops, or else it consists of bracken and grass. This type of habitat is probably not suitable for T. pisana. Also at Penally, which is further inland, there appeared to be little suitable habitat, except for a few areas of rough, roadside vegetation including some alexanders (Smyrnium olusatrum L.) and sea radish (Raphanus maritimus Sm.). T. pisana was present on parts of the Tenby Burrows and at a number of localities within Tenby itself; these colonies are described in greater detail below.

On Caldey Island T. pisana was present in abundance on the dunes behind Priory Bay, but only very few specimens were seen on the sloping sands behind Sandtop Bay, and none on the south side of the island. People arriving from Tenby for a day on Caldey Island disembark from the boats at the jetty at the western end of Priory Bay. The dunes of Priory Bay are thence within easy access. Those behind Sandtop Bay are much more difficult to get to, and there are no well-worn paths for public use leading to this part of the island. This area is thus much less subject to human interference. The vegetation on the south side of the island was largely short turf, unsuitable for T. pisana.

On the coast north of Tenby, at Saundersfoot, two very small colonies of T. pisana were found in patches of vegetation of only a few square metres at the very edge of the beach. One of these (grid reference SN138051) was situated in a small area at the top of the stony upper beach, beside the garden wall of the recently built flats (fig. 2.9.). The other (SN140055) was situated between the beach and the coast path, with a large, unmetalled car park adjacent (figs. 2.10. and 2.11.). Both small colonies are thus subject to intense human interference.

No sign of T. pisana was found at Freshwater East, nor at St. Govan's Head, despite the presence of apparently suitable vegetation, particularly at Freshwater East. However, a rather sparse but widespread colony was found on the dunes at Stackpole Warren (fig. 2.12.), on the edge of Broad Haven (approximate grid reference SR978943). The vegetation here was mostly bracken and brambles but some alexanders and sea radish were present, and it was with these rather than the former that T. pisana was associated. All the localities mentioned in this section are indicated on the maps (figs. 2.1. and 2.2.).

At Tenby all the localities mentioned by Stubbs (1900) were visited and thoroughly investigated. Fig. 2.3. indicates where T. pisana was found. No specimens were found on the North Cliff, nor on the north and east facing sides of Castle Hill. Stubbs (1900) did not find T. pisana on this part of Castle Hill, and the few specimens he found on the North Cliff, he considered to have been imported. The North Cliff has now been developed, with the building of an extensive promenade and paths leading up and down the cliff; this has left virtually no suitable habitat for T. pisana.

Although no specimens were found on the north and east facing sides of Castle Hill, the species was present in large numbers on the south facing side in the areas of rough vegetation beneath the mowed area, delineated by a path and wall, which covers the top of the hill (fig. 2.13.). It was often associated with alexanders, as it is elsewhere at Tenby. Similarly, it was present only on the south-west side of St. Catherine's Rock. Here, the greatest numbers were seen close to the Fort (built between 1868 and 1870) although scattered individuals were seen elsewhere. The presence of T. pisana on only these south and south-west slopes, combined with the apparent suitability of parts of the north and east slopes suggested that its distribution here was restricted largely by aspect. In order to ascertain whether this was indeed the case, and that variation in vegetation could not have accounted for its absence from the north and east facing slopes, a survey of the vegetation of Castle Hill (though not of St. Catherine's Rock) was carried out. Presence or absence of plants with which T. pisana has been found to be associated at Tenby was recorded both above and below the path round the Hill from 40 points spaced approximately 10 m apart along this path, giving 40 transects from top to bottom of the Hill, starting with transect 1 at the lifeboat station on the north facing side and ending with transect 40 near the arches over the path on the south facing side. The results of this survey are presented in table 2.1. The whole of the top of the Hill is regularly mowed and is therefore not suitable for T. pisana. It is also clear that some parts of the slopes below this mowed area may be unsuitable: the vegetation between transects 12 and 24 may be too short, and also in this area, alexanders, if present, was not very abundant; from transect 37 to 40, trees overhang the slope, and the vegetation here is rather different from that on the greater part of the Hill. However, most of the remainder appeared to be suitable, yet T. pisana was only present in the area between transects 36 and 28, this area having a southern aspect. As the aspect of the slope became more south-eastern, between transects 27 and 25, it was no longer found, although the vegetation appeared suitable. Further, on the north facing part of the Hill, it was absent from the area between transects 1 and 11, despite the apparent suitability of the vegetation.

There was little suitable habitat for T. pisana along the South Cliff, where the gardens of the houses on the cliff top extend right to the edge. However, a few specimens and one or two small colonies were found, particularly in the rough vegetation between the well kept public gardens just beneath the Esplanade, and the edge of the cliff. The most extensive area inhabited by T. pisana in Tenby, and the area where its population density appeared highest, was centered around the western end of the Esplanade and the sloping, tar-macadamed path leading from it down to the beach. This included the areas Stubbs (1900) had indicated as the 'Jubilee Gardens' and the 'Wreck Field' ('Wreck' was presumably a mis-spelling of 'Rec', short for 'Rectory' - the Rectory Field is now a metalled car park which retains this name). The largest single part of this area which is inhabited by T. pisana is the bank between the Rectory

Field car park and the sloping path to the beach, an area of about 30 m x 8 m (fig. 2.14.). For a fuller description of the vegetation of this area see appendix 2. T. pisana was also found in large numbers in patches alongside the path down to the beach, associated with similar vegetation. From this centre its distribution extended inland around the edges of the Rectory Field car park, along Battery Road, and down the road to the now demolished 'Fundrome' (fig. 2.15.). Most of this area is now well tended and the vegetation is largely short turf. The paths and roads are metalled, and some of the paths have railings along their seaward sides. T. pisana was often found stuck to these railings, or in the uncut vegetation at their bases. Elsewhere, it was found in the few areas of rough vegetation remaining, particularly in the area behind the small amusement arcade/cafeteria towards the bottom of the cliff, near the beach. The building of the car park and 'Fundrome' have obviously taken place since Stubbs' survey, as probably has the metalling of the paths and roads. The available habitat for T. pisana therefore must have been decreased since this time.

Inland further still, a small colony was found on the seaward side of the railway bank at the bottom of the track leading from the inland end of Queen's Parade down to the golf clubhouse and Burrows (fig. 2.16.). The vegetation here was uncut, and T. pisana seemed to be associated with fennel (Foeniculum vulgare Mill.) up to 2 m tall.

The half of the Burrows nearer to Tenby is covered by sea buckthorn (Hippophaë rhamnoides L.) and little other vegetation grows here. This area was devoid of T. pisana. A few individuals were found by the large rocky outcrop beside the railway about half-way along the Burrows (this, no doubt, is the 'Black

Rock' of Stubbs, 1900). A few specimens were also found near the track which passes over the railway line, alongside this outcrop, and onto the Burrows. From here, T. pisana was found in a number of areas scattered over the remaining south-western part of the Burrows. This part of the Burrows does not carry sea buckthorn, the dominant plant being marram (Ammophila arenaria (L.) Link). Where T. pisana was found, it was often associated with sea radish. However, nowhere was a large area of the Burrows covered with vast numbers of T. pisana.

Both sides of the Narberth Road were searched from where it joins the Norton (a road running parallel to the North Cliff - grid reference SN132010) to beyond the boundary of Tenby (SN128025). Old empty shells were found in the earth of the roadside bank as far inland as the point where this road joins the main road leading out of Tenby (about 1 km inland). However, living specimens were only found on a 20 m length of the northern (i.e. south facing) bank of the road, opposite The Glebe (fig. 2.17.). No more than seven specimens were seen at any one time. The banks alongside this road are largely overhung by trees and appear quite damp; as such they do not seem to provide the kind of habitat T. pisana is usually found in, that is, an unshaded, more exposed habitat.

A further colony was found alongside the south side of the Marsh Road, for a distance of about 500 m more or less opposite the County Secondary School (fig. 2.18.). T. pisana was found in the low vegetation (up to about 50 cm) which extends beyond a low wooden railing set back about 2 m from the road, the area between the road and this fence being short grass. T. pisana was not particularly abundant at this locality.

The Tenby colony of T. pisana appeared, then, to comprise:

1. a fairly abundant population on Castle Hill,
2. a large, dense population around the western end of the Esplanade,
3. a series of scattered groups, possible constituting one large, diffuse population, on the half of the Burrows distant from Tenby itself,
4. a very small population on the Narberth Road,
5. the Marsh Road population,
6. odd specimens or small groups found between these various populations.

The three main populations of T. pisana (Castle Hill, western end of the Esplanade, Burrows) may be separate from each other but the Narberth Road and Marsh Road populations are the only ones which can definitely be assumed to be isolated.

2.3.3. Glamorgan.

Swansea: The whole area of dunes and embankment adjacent to the sea from Swansea, past the University, to Black Pill, Oystermouth and The Mumbles has been searched and no specimens of T. pisana, either live animals or empty shells, have been found. The dunes are covered more by shrubs than by the alexanders and sea radish that T. pisana appears to prefer (at Tenby). These dunes are also widely used for human recreation. The landscaped embankment is well-maintained with few areas of rough vegetation suitable for T. pisana.

Porthcawl: North of Porthcawl itself T. pisana was found to be widespread, but not particularly abundant, up to about 100 km inland on the dunes south west of Kenfig Pool (approximate grid reference SS787807). This area is a large expanse of dunes, apparently little used by man. East of the town, only a very few individuals were found, on the dunes near Black Rocks, Newton, (fig. 2.19.), at the extreme western end of Merthyr-mawr Warren (grid reference SS839771). This is the exact locality indicated by M. Goodchild (in litt. 24 VIII 1979) and on which the record of Kerney (1976) was partly based (M. P. Kerney in litt. 23 VII 1979). This area of dunes is close to the town and caravan sites, and is well used for recreation. The snails were found alongside a rough track used by cars for access to the dunes.

2.3.4. Cornwall.

The only locality in Cornwall at which T. pisana was found was at St. Ives, on St. Ives Head, or the 'Island'. It was not found at Falmouth, Crantock near Newquay, or Whitesand Bay on the west coast north of Sennen. The colony at Treyarnon Bay (Turk and Turk, 1981) had not been reported at the time of the survey, and this site was not visited.

The latest detailed record of the colony at St. Ives was given by Humphreys (1976) with a map showing the exact extent of the colony, and indicating a small 'secondary' colony. The colony was visited in August 1979 during the present survey and appeared to be very slightly reduced in extent since Humphreys' record. T. pisana was found in a small area at the eastern end only of the strip of rocks and vegetation mentioned by Humphreys adjacent to the car park, and along which his principal colony had extended. The remaining larger part of the principal colony was as Humphreys had described it and T. pisana was plentiful in this small area. The secondary colony was also as he had described it. His map is reproduced as fig. 2.6 and the slight change in the extent of the principal colony is indicated. Humphreys himself (<u>in litt</u>. 21 III 1980) has also noticed this change.

The area occupied by the principal colony at the north-western end of Porthgwidden Cove is a steep bank with mixed herbage up to about 50 cm high. At the top of this bank, where the ground flattens out, is a well used path and beyond this the vegetation is short turf which is mowed from time to time. The tar-macadamed car park is edged with large stones and it was on the uncut vegetation between and surrounding these stones that <u>T. pisana</u> was found. The secondary colony, on the north-west side of the Island, was also at the top of a bank of uncut vegetation at the cliff top. A footpath runs along here.

2.4. Discussion.

2.4.1. Present distribution in the British Isles, and recent changes in it.

2.4.1.1. General considerations.

<u>T. pisana</u> is at the very northern limit of its range in the British Isles, where it appears to be confined to some of those areas with the highest average winter temperature. The 7°C isotherm for mean January temperature in Western Europe is shown in fig. 2.7. The Porthcawl and eastern Irish colonies are in slightly colder areas, but then there is no reason to suppose that it is precisely the 7°C isotherm for January that defines the distribution of <u>T. pisana</u>. (The colonies on the French and Belgian Channel coasts (see Germain, 1930; Adam, 1947; Deblock, 1962; Deblock and Hoestlandt, 1967) are also in colder areas).

Populations at the limits of the range of a species must be highly susceptible to minor climatic fluctuations, and require very precise combinations of climatic conditions which may be different for different stages of the life-cycle. Exact correlation of a distribution with one particular climatic variable would not be expected. T. pisana may be confined to its present low number of British localities because few places have the necessary complex of climatic factors. This could explain its absence from the warm but very damp south-west of Ireland (see fig. 2.8.). (The Irish distribution is discussed more fully below). Further, subtle differences (see Geiger, 1965) important to the snails may not be obvious to the human observer.

The contention that small differences in local climate are important in determining the distribution of a species such as T. pisana at the edge of its range is supported in particular by its distribution on the Castle Hill at Tenby, where it is present only on the south facing side. Its absence from apparently suitable areas of Castle Hill, particularly from the area between transects 25 and 27 which has a south-eastern aspect, and from that between transects 1 and 11 on the north facing side (see the results of the vegetation survey, section 2.3.2. and table 2.1.), strongly suggests that at the periphery of its range T. pisana may be restricted in local distribution not only by availability of suitable vegetation but also by the aspect of an area, only those slopes receiving the most sun being suitable. Smith (1980) has discussed the importance of aspect in determining local distributions (e.g. Watson, 1960), particularly of species of plant near their northern limits in the British Isles, where they are absent from north facing slopes (e.g. Pigott, 1968).

Since the post glacial 'climatic optimum', the warmest period since the glaciations, which is usually considered to have extended from about 8000 B.P. to about 5000 B.P. (Lamb, 1970), mean temperatures in the British Isles have fallen despite a number of partial recoveries (Manley, 1952; Lamb, 1965, 1966, 1970). The effects of this on the molluscan fauna have been discussed by Kerney (1968), Evans (1972) and South (1974). Lamb (1970) indicated how important small changes in climate could be; for instance, an increase of 1°C in the mean summer temperature of Britain would give southern Britain the type of climate now experienced in the Loire Valley. However, such long-term changes are less important than the shorter-term flucuations within the general trend, for influencing the distribution of T. pisana from the time it was first recorded in the British Isles (1777). Manley (1952) and Lamb (1965) gave details of the changes in Britain's post-glacial climate, and in particular of the short-term changes which have taken place since reliable records have been kept. South (1974) discussed the effects of such changes on the terrestrial mollusc fauna.

Small, isolated populations at the climatic limits of a species' range would be very susceptible to short-term fluctuations such as these. Even a single particularly cold winter could result in the extinction of small colonies such as those of T. pisana seen at Stackpole Warren, Saundersfoot, Porthcawl (Newton), St. Ives, and some of the more isolated colonies at Tenby (e.g. Narberth Road). This may well be the reason for the apparent extinction of T. pisana at Manorbier, from where it was last recorded in 1961 (Deblock, 1962). Some helicid species (e.g. Cepaea) are well known to burrow during the winter months in order to escape extremes of cold, but personal observation suggests that T. pisana rarely exhibits this behaviour, although some individuals may retire to crevices in walls, or to the bases of plants (chapter 3, section 3.2.1.2.). These habits may, in part, be the cause of T. pisana's apparent sensitivity to winter cold (cf. Cochlicella acuta which has a southern and western distribution in Britain, and also is not known to burrow (Lewis, 1968)).

While climatic fluctuations, either long- or short-term, will certainly play a part in limiting and altering the distribution in Britain of a species such as T. pisana, the activities of man may well be more important. Kerney (1966), Evans (1972) and South (1974) have reviewed the ways in which man has affected the snail fauna of the British Isles since the climatic optimum, discussing particularly the effects of deforestation and development of agriculture. South (1974) also briefly discussed the more recent effects, in particular the pressures of increased urbanization and public recreation. T. pisana is restricted over the whole of its range to maritime habitats. As such, at its British localities, it is highly susceptible to this sort of pressure, resulting particularly from the demands of the dramatically increased tourist industry (Crowley, 1961; Turk, 1966, 1972; Pitchford, 1973; Humphreys, 1976). Humphreys (1976), however, did note how tolerant the species appeared to be of protracted human disturbance resulting from increased tourism and development. It seemed capable of surviving in the remaining small patches of suitable habitat, close to areas of intense human activity.

2.4.1.2. Changes in the distribution.

The most striking change to have taken place in the distribution of T. pisana in mainland Britain since previous accounts, is the reduction in abundance on the Tenby Burrows, and the complete absence of the species from the cliff tops from Giltar to Lydstep. (cf. Stubbs (1900) and Wintle (1925) who both indicated T. pisana in profusion on the Burrows, although whether it was particularly abundant on the cliff tops was not said). This reduction in range has probably been to a large extent the result of man's activities. The complete absence of T. pisana from the half of the Burrows nearer to Tenby itself is certainly the result of the planting of sea buckthorn in about 1940 (Stratton, 1970). This part of the Burrows is now densely covered by this shrub, and little other vegetation is present. It therefore no longer provides a suitable habitat for T. pisana. The development and increased use of the golf links, which Stubbs (1900) implied were part of the same system (with respect to T. pisana) as the Burrows and railway banks, has undoubtedly contributed to the demise of T. pisana in this area. Barrett (1972) indicated how trampling of areas of marram grass and cutting of the vegetation excluded T. pisana from otherwise apparently suitable areas in Guernsey.

There appeared to be little suitable habitat for T. pisana on the cliff tops from Giltar to Lydstep. The cliff tops have become extremely trampled as a result of human recreational activity, and both sheep and cattle graze right to the edges of the cliffs along parts of this section of coast. Chappell, Ainsworth, Cameron and Redfern (1971) have indicated how trampling can change a habitat and hence the associated snail fauna; and Morris (1968) indicated similar changes resulting from grazing. These authors did not deal with *T. pisana* but showed that species belonging to the xerophile group of Boycott (1934) were favoured by trampling and grazing. Although *T. pisana* is included in this group, it is not favoured by these factors, in as much as short turf is not a suitable habitat for it, as it is for other species in the group (see also Barrett (1972), mentioned above). Humphreys (1976) did say that the area inhabited by *T. pisana* at St. Ives had the appearance of a 'short, dense grass sward', but the same area, observed during the present survey was covered by mixed vegetation up to about 50 cm high, a relatively normal habitat for *T. pisana*, if not as high as the alexanders and sea radish it is often associated with at Tenby. It does seem probably, then, that increased trampling and grazing may well partially account for the extinction of *T. pisana* along the cliff tops from Giltar towards Lydstep, although it may never have been particularly abundant here.

However, climatic factors may also have played a part. The slight warming of the climate of the British Isles between 1890 and the 1930's (Lamb, 1965, 1966) could have resulted in an increase in abundance and a widening of the distribution of *T. pisana* around Tenby. An increase in abundance since the beginning of the nineteenth century was indicated by Tye (1877), although it had probably occurred in the early part of the century, since Jeffreys (1833a) had previously found *T. pisana* 'in vast profusion' near Tenby. The present reduction in abundance and range may be the result of the reversal of this climatic trend, indicated by Lamb (1965). It is difficult to estimate how rapidly a species would respond to an improvement of climate by widening its range, but certainly its response to a worsening climate would be faster (Lamb, 1970). It seems quite possible that T. pisana could have colonised a large area such as the Tenby Burrows in less than a century. This would require an advance of only about 15 m per year over a continuous habitat, and this is well within its capabilities (chapter 5, section 5.4.).

In Tenby itself the present survey has shown that the overall extent of the distribution of T. pisana has remained much as indicated by Stubbs (1900), but the colony has undoubtedly been fragmented by the development of housing, roads, car parks, public gardens, etc. During the course of the survey a part of the colony was destroyed when the 'Fundrome' was demolished (fig. 2.15.), and presumably part was also destroyed during its construction. During the summer months the Esplanade and paths down to the beach, around which T. pisana lives, are in constant use by large numbers of people. In order to keep the area looking tidy and to allow unhindered views, the alexanders (Smyrnium olusatrum L.) with which T. pisana is largely associated in this area, is cut down each year in about July. At this time of year the alexanders is dying, but at places where it is not cut down, the stems remain standing and provide positions for T. pisana to sit above the ground. Many specimens are found doing this (chapter 4, section 4.3.). Despite these apparent pressures, T. pisana has remained abundant in this area. The drastic reduction of the Narberth Road population and the restriction of the Marsh Road population seem likely to be due to the destruction of habitat resulting from the metalling, and presumably, widening of the roads, and the increased traffic, and also the building of houses alongside parts of the road.

The colonies on Caldey Island must be subject to considerable human interference during the summer months when large numbers of people come to the island by boat from Tenby. The effects of this are impossible to estimate since few accurate details of T. pisana at this locality have been published (Stubbs, 1900; Wintle, 1925). The Priory Bay colony appeared to be thriving; but perversely, since it is much less subject to the depredations of the day-trippers, the Sandtop Bay colony was extremely sparse and may well be unlikely to survive.

The two tiny colonies at Saundersfoot are in an extremely precarious position, being at the edge of a very popular beach, and in small, isolated patches of vegetation. The rather larger colony at Stackpole Warren is probably less subject to human interference, despite being in close proximity to a popular beach (Broad Haven), and may not be in any imminent danger from this source. However, as mentioned above, such small isolated colonies are highly susceptible to extinction by sudden climatic effects like a particularly harsh winter.

The latest record (in 1969) of T. pisana at Swansea (Kerney, 1976, and in litt. 23 VII 1979) was based on a small, sparse colony at Black Pill (P. Makings in litt. 30 VIII 1979), and M. J. Isaac in litt. 12 IX 1979). It is possible that if T. pisana is very scarce at this locality, it has been overlooked in the present survey, despite an extensive search. However, since the record of 1969, the old railway line has been dismantled and the whole area landscaped. It thus seems highly likely that the Swansea colony of T. pisana, originally introduced by Jeffreys in the nineteenth century, is now extinct. This view is held by

Dr. Makings and Dr. Isaac.

The only remaining locality for T. pisana in Glamorgan is therefore Porthcawl. At Newton, just east of Porthcawl itself, the dune system on which a few individuals were found, is used extensively for recreation, although signs are displayed indicating its scientific importance (fig. 2.19.). This colony appears to be retaining a very tenuous hold indeed. The population on the Kenfig dunes, just north of Porthcawl is much more free from human interference and may not be in any imminent danger of extinction or reduction from this cause.

At St. Ives, development had already drastically reduced the size of the colony (Turk, 1966) and the present survey has shown that since 1974 and 1975 (Humphreys, 1976) the colony has been further very slightly reduced, undoubtedly as a result of increased human demands.

The Treyarnon Bay colony (Turk and Turk, 1981) may be long established but only recently recorded, or a new introduction.

2.4.2. T. pisana as a 'lusitanian' species.

The British fauna and flora have been divided into various elements by different authors (e.g. Forbes, 1846; Matthews, 1937; Beirne, 1952). Most have distinguished a southern or 'lusitanian' element. This has been defined in a number of ways, classically, those species confined to the north-west of Portugal and the south-west of Ireland, but it is more generally considered to include those western European and Mediterranean species that have their centres of distribution in the Iberian region, and reach the northern limits of their ranges in the south-western parts of the British Isles, that is, those areas with the highest average winter temperatures (Beirne, 1952) (see fig. 2.7.).

Gloyne (1878) considered T. pisana to be a maritime species, uncharacteristic of any particular geographical range. He apparently failed to recognise the significance of its very limited British distribution, and the fact that these southern British localities are at the very northern edge of the species' range. Taylor (1900), whose views were unusual, considered the present British molluscan fauna to be the result of an invasion from the continent of advanced forms (the Eastern, or Teutonic, element), driving in front of them the more ancient, less highly developed species which were once spread over the whole of the British Isles (the Western, or Celtic, element). He did recognise a group of species, persisting in the south-west of Ireland, although he did not include T. pisana within it. However, this group was simply thought to be the oldest part of the Celtic element, and to have been already pushed to this remote part of the British Isles by the pressure from the advancing Teutonic forms. Taylor did not consider the lusitanian group (although he did not actually call it by this name) to belong to a third, southern element. Forbes (1846) considered T. pisana to be associated with his 'Gallican' element of the British flora, those species found in south-west England and south-east Ireland, and intimately related to the flora of the Channel Islands and the neighbouring part of France. He did not associate T. pisana with the group of plants found only in the west and south-west of Ireland, the nearest points in Europe where these plants are native being in the north of Spain. This latter group simply comprises those species which show the extreme form of lusitanian distribution, and with the Gallican element, can probably be combined to form a southern element, as Forbes did, although he also included a further element containing species distributed more generally over southern Europe.

The broad Mediterranean distribution of T. pisana argues against its being included in a true Gallican element, and its presence on the east coast of Ireland combined with its absence from the south-west are not the marks of a classic lusitanian species. It is probably more accurate to consider it as a Mediterranean species whose range extends northwards.

When considered as such, its apparently anomalous Irish distribution can be explained. The south-west of Ireland is noted for its extremely damp climate (higher annual rainfall, and a higher number of days with rain per year than anywhere else in the European range of T. pisana - see Lamb, 1964; Thran and Broekhuizen, 1965; Steinhauser, 1970; and fig. 2.8.), and as such may be too damp for an essentially Mediterranean species. The work of Heller and Volokita (1981 a, b, and reported by Jones, 1980), on the Israeli snail Xeropicta vestalis Pfeiffer has shown that during the early stages of the life-cycle, when growth is taking place, the shells are dark in order to absorb as much energy as possible from the sun, rather than pale to reflect too intense radiation. It is therefore reasonable that Helicella itala (L.) at the north of its range (Scotland) is generally darker than elsewhere (Cain, Cameron and Parkin, 1969; Cain, 1977b) and that darker and more coloured species such as Cepaea nemoralis (L.), C. Hortensis (Müller) and Arianta arbustorum (L.) occur on dunes only in northern parts of Europe (Cain, 1981a). In south

Wales the shells of T. pisana are generally not as white as those from the Mediterranean (chapter 6, section 6.5.) suggesting that at these northern localities it is responding to the reduced amount of sunshine. As a Mediterranean species it may require a drier and more sunny climate than obtains in the south-west of Ireland. (The possibility still remains that the south-west of Ireland is indeed suitable for T. pisana but that it simply has not migrated or been introduced there yet).

Deevey (1949) and Godwin (1975) gave maps showing examples of lusitanian distributions indicating the variation encompassed within the broad lusitanian concept. The Gallican and south-western Irish distributions can certainly be included within such a concept, as can the distribution of T. pisana. 'Lusitanian' has thus acquired a rather general meaning describing a number of types of distribution of southern species included in the British fauna and flora; T. pisana has usually been included within this lusitanian grouping (e.g. Kennard and Woodward, 1901; Scharff, 1905; Charlesworth, 1930; Praeger, 1950; Beirne, 1952; Kerney, 1966).

Within the British terrestrial Mollusca an extreme form of lusitanian distribution is shown by Geomalacus maculosus Allman which is restricted to south-west Ireland and coastal areas of northern Spain and Portugal (Kerney and Cameron, 1979) with two rather dubious records from Brittany (see Germain, 1930). Ponentina subvirescens (Bellamy), although absent from south-west Ireland, is present in Britain only in the extreme south-west (Kerney, 1976). It can certainly be considered a lusitanian species since its only other localities are in western France, Portugal and Spain (Germain, 1930; Nobre, 1930; Kerney and Cameron, 1979). Pomatias elegans (Müller) is essentially a southern and western species, but is not usually considered in a lusitanian group, since its range extends right accross France, with isolated colonies further to the north-east (Kerney, 1968). Helix aspersa Müller has a similar distribution but spreads further north in Britain (Kerney, 1968, 1976). These four species thus provide examples of southern and western European distributions, although only two of them are usually considered lusitanian (G. maculosus and P. subvirescens), the other two being more continental as well (P. elegans and H. aspersa). These two types form the extremes within a continuum of distributions. An example within this is Cochlicella acuta which is restricted to western coastal habitats (mainly duneland) in Britain (Kerney, 1976) where it is at the northern limit of its range, but is less restricted in Ireland and on the continent, particularly in the Mediterranean (Germain, 1930; Nobre, 1930; Alzona, 1971; Kerney and Cameron, 1979). T. pisana shows a distribution similar to C. acuta but not extending so far north, and even more restricted to maritime habitats.

It is clear, then, that all the species mentioned above are essentially southern and western, although only some would usually be considered lusitanian. Each species has precise requirements at the edges of its range, these therefore defining the edges and restricting the species to more limited habitats than in the centres of their ranges. For example, at their northern limits P. elegans is more restricted to calcium rich areas than it is in the centre (Kerney, 1968), and C. acuta and T. pisana are more restricted to coastal habitats (usually duneland). To generalise, these southern and western species are those which, to a greater or lesser extent, require an oceanic climate, and cannot tolerate the extremes of a continental climate. *T. pisana* is one of the least tolerant.

2.4.3. Origin in the British Isles.

The history of the lusitanian element of the British fauna and flora has been the subject of much discussion; did it survive through the Pleistocene glaciations (the 'Ice Age'); was it partially or wholly exterminated and subsequently reintroduced; or is it an entirely new post-glacial element? Such questions, and also the following arguments concerning the lusitanian fauna and flora, can equally be applied to other species not usually considered lusitanian, but also having broadly southern and western distributions. As discussed above, the lusitanian species simply show extremes within a continuum of such distributions. Forbes (1846), considering the whole of the fauna and flora, and Kennard and Woodward (1901), considering the molluscan fauna, implied that at least some of the species included in the lusitanian element were relics of a pre-glacial fauna and flora. Praeger (1939, 1950), concerned largely with the Irish biota, considered that the marked discontinuity of the distributions of the lusitanian species indicated their pre-glacial origin; that they were once more widely distributed; and that they are now fighting a losing battle in isolated colonies against more recent arrivals and possibly against a deteriorating climate.

The present confinement of the lusitanian species to the very warmest parts of the British Isles, combined with the intolerance of many of them to low temperatures, does suggest however that it is extremely unlikely that they could have survived *in situ* in close proximity to the ice-sheet (Corbet, 1961).

Some authors (e.g. Beirne, 1952; Mitchell and Watts, 1970) have proposed refuges on the now submerged areas to the south-west of Cornwall and Ireland. The possibility of per-glacial survival in such refuges cannot be ruled out, particularly for some of the south-western Irish species. Some of these have been discovered in interglacial deposits (Praeger, 1950; Mitchell and Watts, 1970), although this does not necessarily imply their persistence through the later glaciations, since extinction and recolonisation is also a possible explanation. Deevey (1949) argued that increasing evidence, particularly from pollen stratigraphy, indicated that the Pleistocene ice-sheets were bordered by broad belts in which peri-glacial climates prevailed, and that these climates were as effective barriers to the spread (or the persistence) of warm temperate species as were the ice-sheets themselves. This may be true in general, but, as Manley (1952 pp. 266-270) suggested, maritime areas in the south-west of the British Isles, subject to Gulf Stream influence, may have had a much milder climate than their proximity to the tundra covering the rest of southern Britain would suggest. However, Deevey (1949) did indicate the difficulty encountered in proving that a given locality could act as a glacial refuge, and for economy of hypothesis, suggested that all distributions of species should be considered to have resulted from post-glacial colonisation, unless it could be proved otherwise. This view had been succinctly expressed previously by Jackson (1925) who said that

> 'Unless we can be certain of the presence of suitable sanctuaries ... the glacial survival of any pre-existing species cannot be maintained, and we are obliged to fall back upon the theory of migration after the glacial period had partially, or wholly, passed away'.

The post-glacial origin of at least most of the lusitanian element of the British fauna and flora had also been considered more likely than per-glacial survival by Reid (1899), Stapf (1917), Matthews (1937, 1955) and Beaufort (1951). Beirne (1952), although considering a pre-glacial origin more likely for the lusitanian element, acknowledged the possibility that at least part of it could date from the 'climatic optimum'.

Britain and Ireland were connected to the Continent by a land-bridge during the glaciations. The main arguments against post-glacial migration into Britain and Ireland have been centred around the evidence for the persistence into the Flandrian (the post-glacial period) of these connections between the Continent, Britain and Ireland, and whether the length of time between the retreat of the ice and the severance of these land-bridges was sufficient for immigration of the lusitanian species, which are intolerant of low temperatures. Only hardy species would have been able to colonise regions recently freed of ice, and therefore with tundra-like conditions (Corbet, 1961; Berry, 1979). Since the Irish Sea is considerably deeper than the North Sea and English Channel, it is clear that Ireland was separated from Britain earlier than Britain was separated from the Continent. The precise timing of these events has been subject to much discussion. Deevey (1949) considered that the geological data available suggested that Ireland was separated from the rest of Britain very soon after the retreat of the ice, and that Ireland was therefore an island through the whole of the Boreal period. This supposition, combined with arguments for the existence of refugia, and the presence of lusitanian species in Ireland as pre-glacial fossils, can be used to support per-glacial survival of lusitanian species in Ireland. Such arguments are not needed to explain the distribution of the lusitanian species in mainland Britain, since the land-bridge to the continent was not severed until much later. Immigration can therefore explain their presence (Deevey, 1949; Godwin, 1975). Godwin (1975) indicated the increasing but unpublished evidence that the post-glacial rise in temperatures in the British Isles had occurred earlier than had previously been considered, and therefore if this were so, and sea level remained low, that migration over land could explain the presence of the lusitanian species not only in Britain but also in Ireland. Immigration by this land route from the Continent however, might be expected to have left fossil remains of T. pisana in south-east England, and such fossils have not yet been discovered. Praeger (1939) and Deevey (1949) have argued that land-bridges are a necessity for the post-glacial immigration of some species (including T. pisana and the Kerry slug, (Geomalcus maculosus) to Britain and Ireland, dispersal across the sea being considered highly unlikely for them. However, Deevey (1949) also emphasized the potential ability of species to spread rapidly, and cited the example of the almost complete recolonisation of Krakatau in the fifty years since its fauna and flora were destroyed by volcanic explosion. He argued that many postulated land-bridges were, in fact, unnecessary for the explanations of animal and plant distributions. Simpson (1952) also considered the probability of dispersal over a water barrier to be often underestimated, if the length of geological time available were taken into account. It is conceivable that T. pisana could have immigrated to the British Isles without the help of land-bridges.

Considering the foregoing arguments regarding the origin of the lusitanian element of the fauna of the British Isles, and the inclusion of T. pisana within this element, it is reasonable to conclude that T. pisana is of pre- or inter- glacial origin, neither in Britain, nor probably in Ireland. This contention is supported, as Kobelt (1897) considered, by the fact that it has never been found in any pre-glacial deposits. Scharff (1905) agreed emphatically with Kobelt's suggestion. Furthermore it has not been discovered as a post-glacial (Holocene) fossil (Kennard and Woodward, 1901; Kennard, 1923), which suggests an even later and probably artificial introduction. Wintle (1922, 1925) did find T. pisana in blown sand deposits, but these were probably of very recent origin. Rimmer (1880) argued that the presence of T. pisana far inland in France and Spain (records based, no doubt, on casual, short-lived introductions) and its presence only at maritime localities in the British Isles, suggested artificial introduction, perhaps in ships' ballast. Lindroth (1957) indicated the use of soil or sand as ballast, and emphasized the ease with which species of animal and plant could be introduced with it, particularly to the environs of ports and harbours. Rimmer's suggestion was repeated by Kew (1893) and Step (1927), and Kerney (1966) also suggested its accidental introduction, perhaps with unloaded ballast. Turk (1966) mentioned the finding of Breton pottery on an area once used as the town dump at St. Ives, indicating a link between that town and the continent, and therefore a means of introduction. Evans (1972) suggested its introduction since the Bronze Age, but was not more specific. However, Turk (1966) suggested that there was insufficient negative evidence from post-glacial deposits to disprove its native status. Turk (1966) also suggested that its presence in Holocene (Flandrian) deposits, which have been relatively little studied (Kennard, 1923), may yet be detected. This is, of course, a possibility because the most commonly investigated types of Holocene deposits, listed by Kennard (1923), seem unlikely to yield T. pisana, which tends to inhabit sandy areas near the sea. Later, Turk (1972) did accept that T. pisana had probably only been in this country (England) for a few centuries, and was perhaps introduced as food by travellers from the continent (presumably traders or fishermen using the harbours of the southern British Isles). The species is well-known as food in the Mediterranean area (Companyo, 1863; Lovell, 1884; Adams, 1896; Bullen, 1905a; Backhuys, 1975; Sacchi, 1977; and information gathered personally in Spain). Humphreys (in litt. to Professor A. J. Cain, 13 V 1980) considers this extremely likely for the St. Ives colony, and Stelfox and McMillan (1966) suggested it as the explanation of its presence near Dublin on the east coast of Ireland. (Salisbury (1952) indicated the introduction of T. pisana to Tenby from Natal, but this is extremely unlikely, the introduction to Natal from Europe being eminently more plausible).

It seems, then, that T. pisana is almost certainly post-glacial in origin in the British Isles. Whether it has arrived by natural or artificial means is still open to question, although the latter view is more usually accepted.

Fig. 2.1. Map of the Dyfed localities, excluding Stackpole Warren.

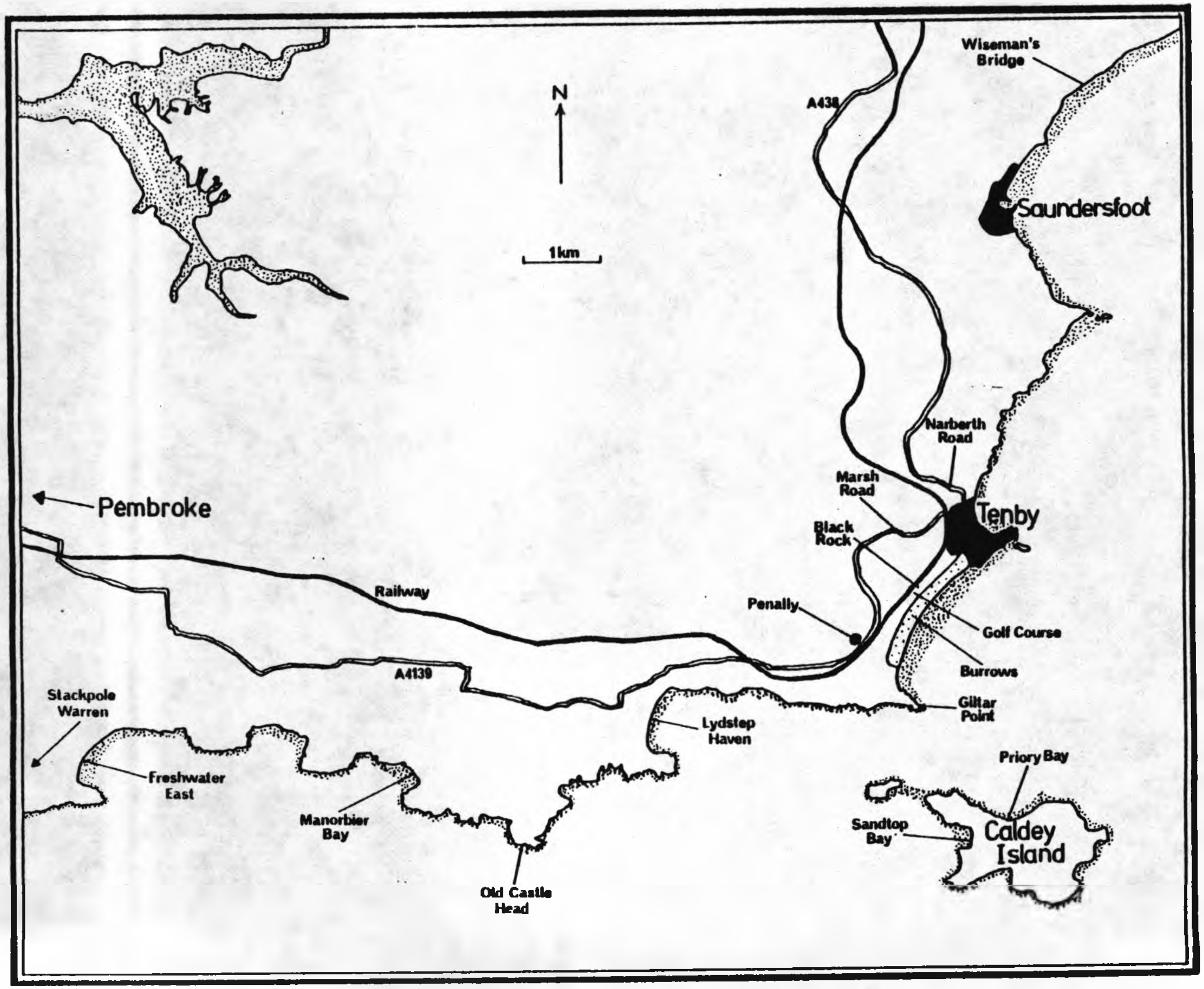

N
1km
Wiseman's Bridge
A438
Saundersfoot
Narberth Road
Marsh Road
Black Rock
Tenby
Pembroke
Railway
Penally
Golf Course
Burrows
A4139
Stackpole Warren
Lydstep Haven
Giltar Point
Freshwater East
Manorbier Bay
Priory Bay
Sandtop Bay
Caldey Island
Old Castle Head

Fig. 2.2. Map of Stackpole Warren indicating the area inhabited by _T. pisana_ at present.

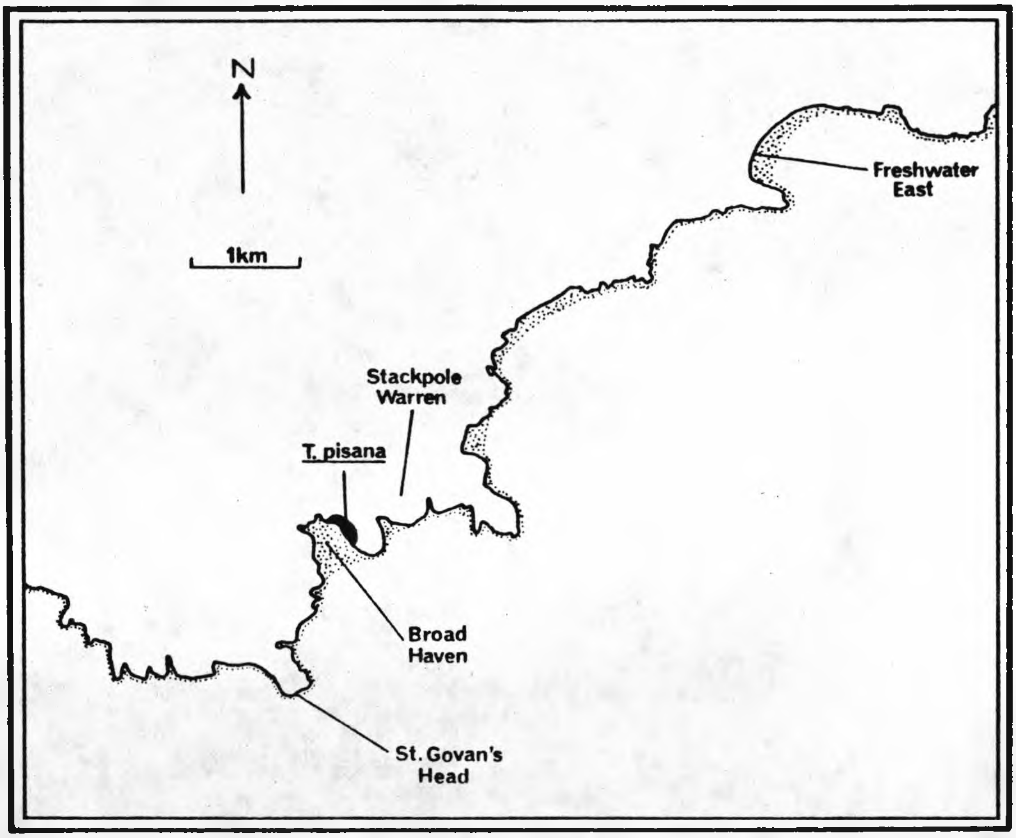


Fig. 2.3. Detailed map of Tenby indicating the present distribution of _T. pisana_.

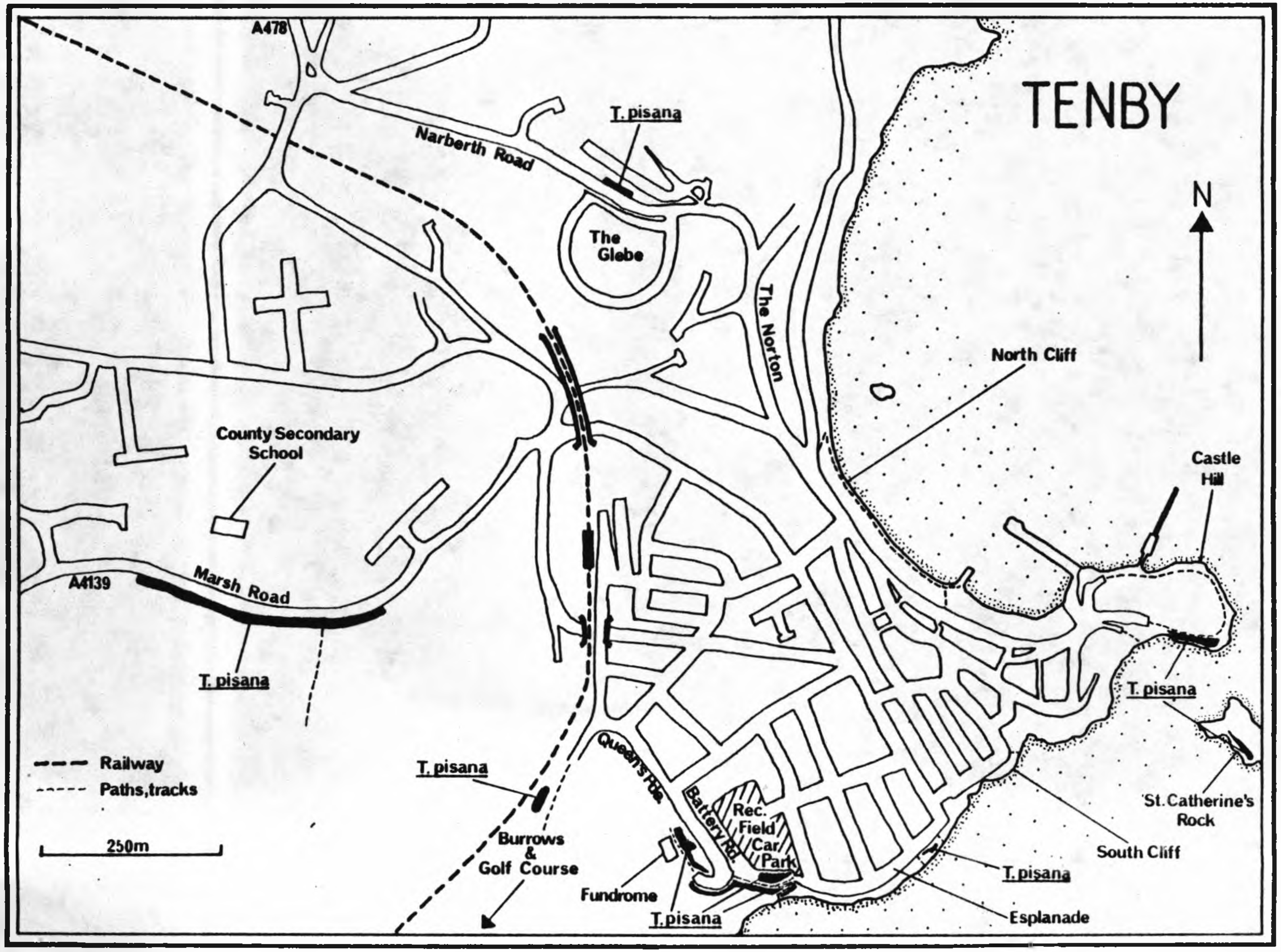

TENBY
N
A478
T. pisana
Narberth Road
The Glebe
The Norton
North Cliff
County Secondary School
Castle Hill
A4139
Marsh Road
T. pisana
T. pisana
Railway
Paths,tracks
250m
T. pisana
Burrows & Golf Course
Queen's Pde.
Battery Rd.
Rec. Field Car Park
Fundrome
T. pisana
T. pisana
Esplanade
South Cliff
St. Catherine's Rock

Fig. 2.4. Map of the coastline from Swansea to The Mumbles.

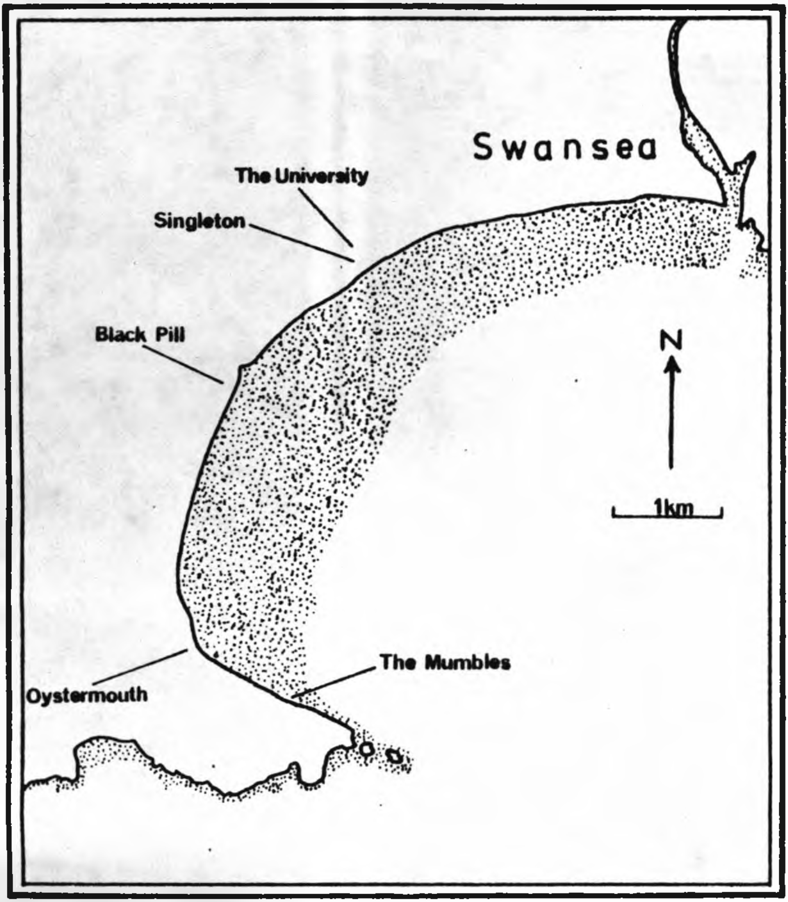


Fig. 2.5. Map of the Porthcawl area, indicating where T. pisana was found in this survey.

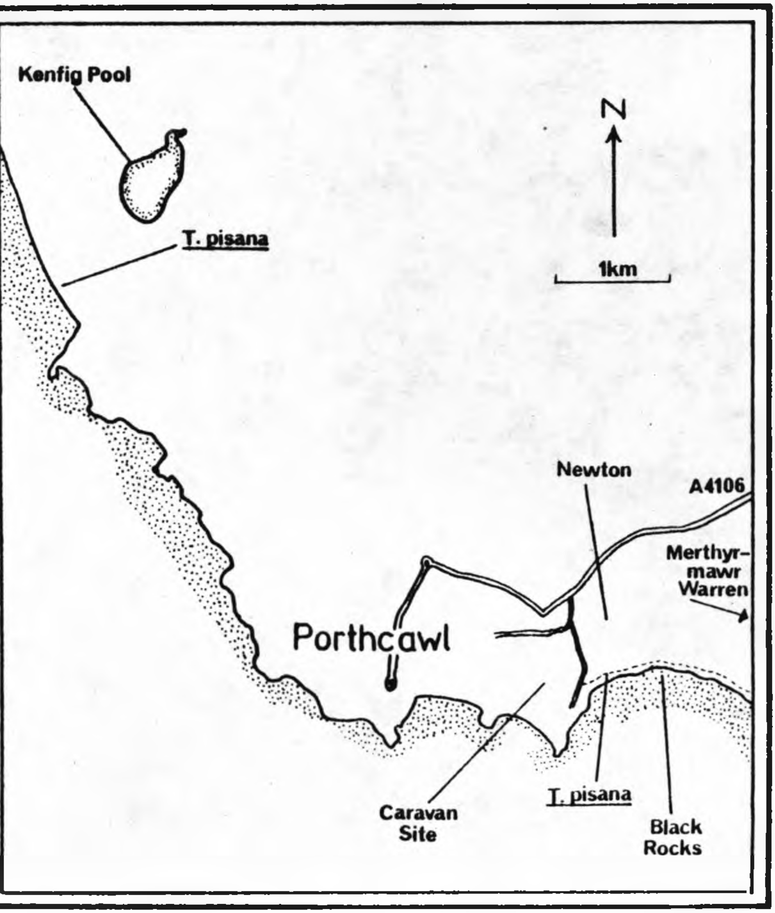


Fig. 2.6. Map of the St. Ives colonies of T. pisana (altered from the map of Humphreys (1976, with his permission).

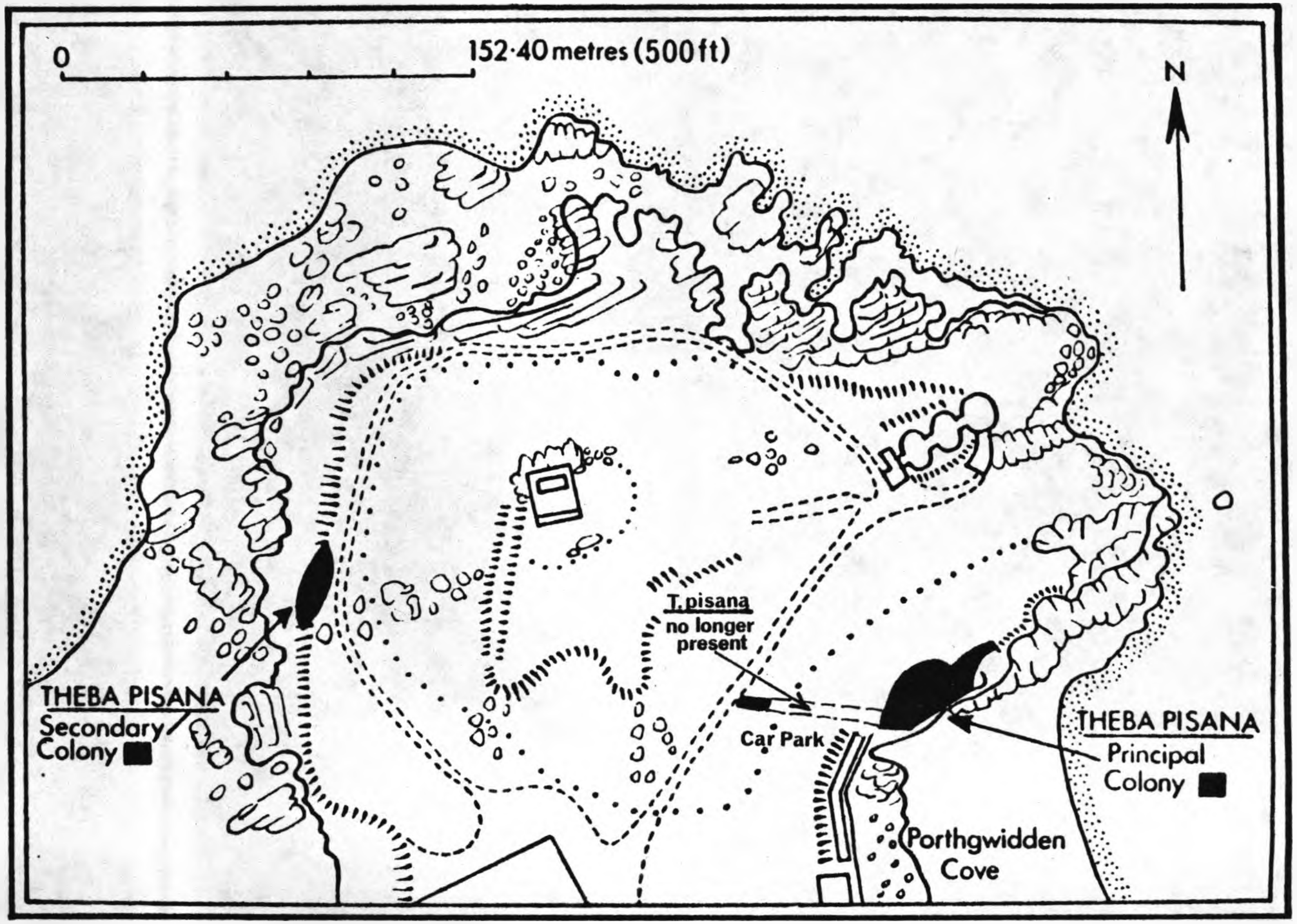
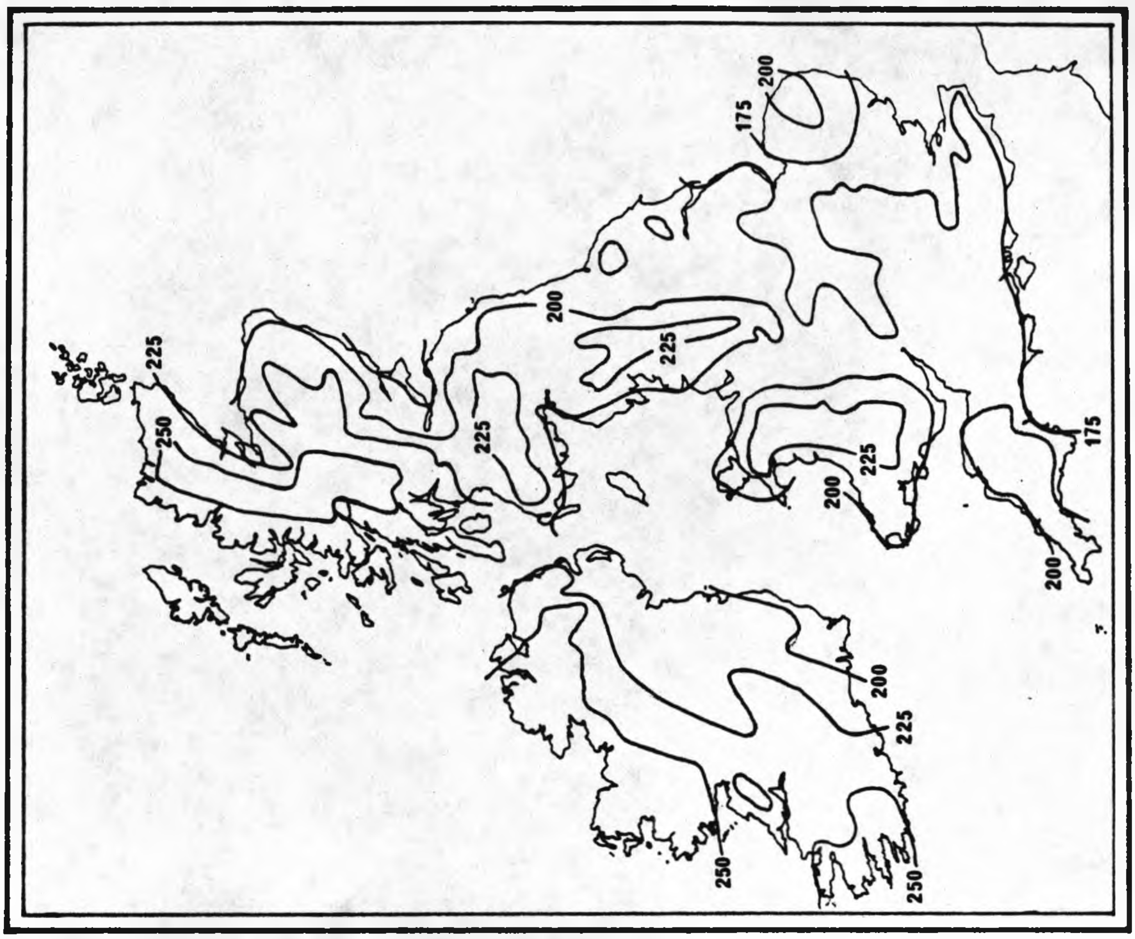


Fig. 2.7. Map of western Europe showing the 5°, 7° and $10^{\circ}C$ isotherms of mean January temperature at station level (after Wallén, 1970).

Fig. 2.8. Map of the British Isles showing the average number of days a year between 1901 and 1930 with over 0.25 mm of rain (after H.M.S.O.,1952; Lamb, 1964).


250
225
250
225
200
225
225
200
225
200
175
175
200
200
200
225
250
250

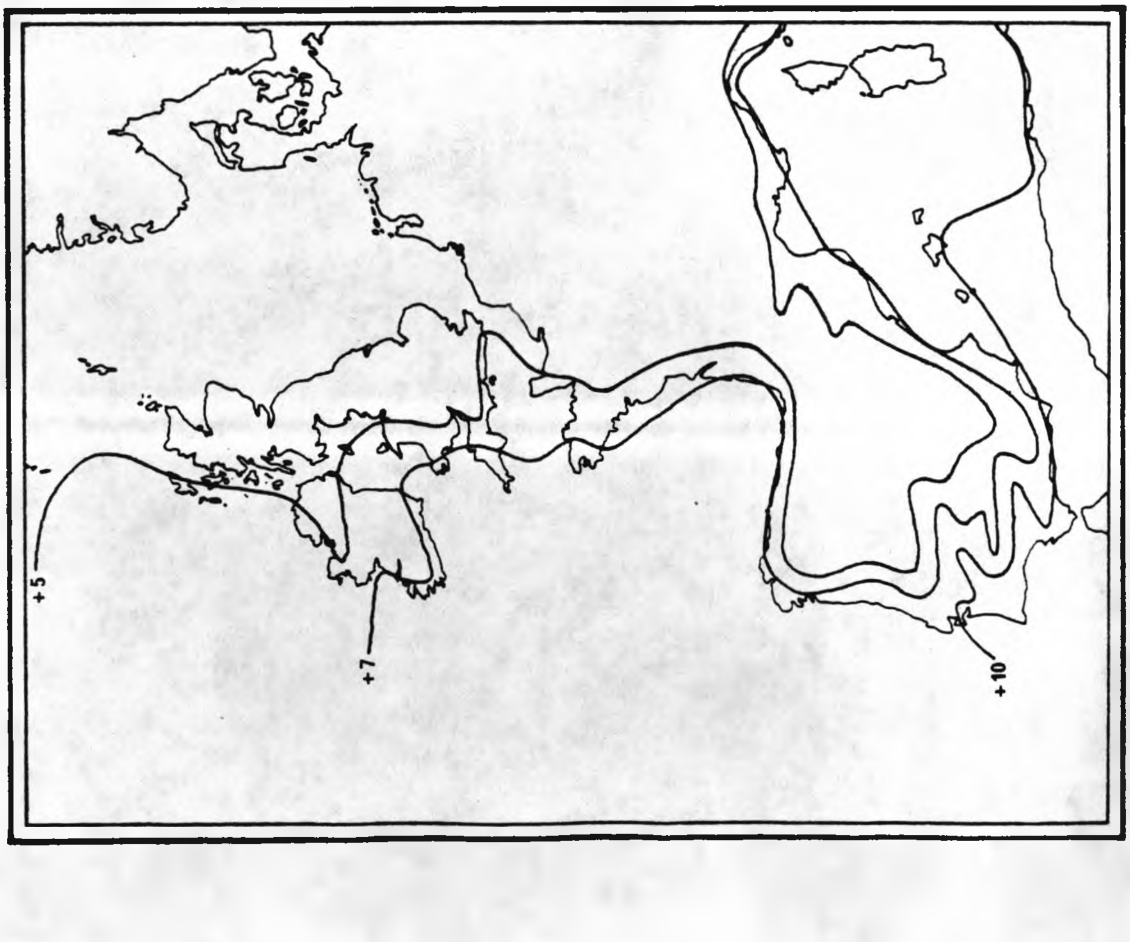

+5
+7
+10

Fig. 2.9. Saundersfoot site 1. The colony was found just to the left of the sloping path from the beach to the block of flats.

Fig. 2.10. Saundersfoot site 2. The colony was found at the back of the beach, roughly in the centre of the picture.

Fig. 2.11. Saundersfoot site 2. The photograph covers the whole extent of the colony.

Fig. 2.12. The dunes of Stackpole Warren. The photograph roughly includes the whole colony. The beach of Broad Haven is in the foreground.

Fig. 2.13. The south and south-west sides of Castle Hill, viewed from St. Catherine's Island.

Fig. 2.14. The bank between the Rectory Field car park (right) and the sloping path to the beach (left). The roof of the 'Fundrome' can be seen in the background.

Fig. 2.15. Demolition of the 'Fundrome'.

Fig. 2.16. The track from Queen's Parade to the golf clubhouse. The photograph includes the whole area in which T. pisana was present.

Fig. 2.17. Part of the area on Narberth Road in which _T. pisana_ was found.

Fig. 2.18. Part of the Marsh Road colony.

Fig. 2.19. Dunes at Newton, Porthcawl.

Table 2.1.

Vegetation survey of Castle Hill.

+ denotes presence of species

transect	Smyrnium olusatrum Alexanders	Plantago lanceolata Ribwort plantain	Crithmum maritimum Rock samphire	Beta maritima Sea beet	Rubus sp. Bramble	Brassica oleracea Wild cabbage	Centranthus ruber Red valerian	Lotus corniculatus Bird's foot trefoil	Cheiranthus cheiri Wallflower	Convolvulus arvensis Field bindweed	grass	Theba pisana
1	+	+				+	+					
2	+	+				+						
3	+	+									+	
4	+	+				+						
5		+									+	
6		+									+	
7	+				+						+	
8	+	+			+	+					+	
9	+				+	+					+	
10	+	+			+	+		+			+	
11	+	+			+	+					+	
12	+	+				+					+	
13	+	+									+	
14	+	+									+	
15	+	+									+	
16	+	+									+	
17	+	+						+			+	
18	+	+									+	
19	+	+			+	+					+	
20	+	+				+					+	
21	+	+		+							+	
22		+									+	
23		+									+	
24		+		+							+	
25		+	+	+		+					+	
26		+									+	
27		+		+							+	
28		+									+	+
29	+	+		+				+			+	+
30	+	+						+			+	+
31	+	+									+	+
32	+	+				+					+	+
33	+	+				+					+	+
34	+	+				+			+		+	+
35		+			+	+			+		+	+
36	+				+	+						+
37		+								+		
38		+								+		
39		+								+		
40		+								+		

Chapter 3

The Life-history Strategy

3.1. Introduction.

Since the first serious theoretical study of the ecological and evolutionary significance of life-history strategies (Cole, 1954), numerous biologists have attempted to deduce the optimal strategy that animals in populations subject to particular sets of conditions would be expected to show. These studies gave rise to either deterministic models, in particular the well-known theory of r- and K- selection (MacArthur and Wilson, 1967; Pianka, 1970, 1972), or stochastic models (e.g. Murphy, 1968; Schaffer, 1974). These two approaches lead to different predictions under certain conditions, but in essence arrive at the same conclusions (Horn, 1978; Begon and Mortimer, 1981).

Undoubtedly, this theoretical work (reviewed by Stearns, 1976), and in particular the development of the r/K concept, has been of great value in concentrating thought on this important aspect of an organism's ecology. However, the inadequacies of taking too simple a view have been hinted at by Wilbur, Tinkle and Collins (1974) and Lassen (1979); and Stearns (1977) in drawing together much of the published work on individual species' life-histories, found that only about half agreed with the theoretical predictions. Both Bronson (1979) and Hart and Begon (1982) have stressed the limited applicability of the theory, arguing that a particular organism's environment is too complex to be classified simply, as the theory demands. Southwood (1977) proposed a habitat classification on two axes, time and space, and suggested that the ecological strategies of a species are evolved in response to this 'habitat templet'. Although this is undoubtedly more realistic than a unidimensional classification, he accepted that it would not 'encapsulate without exception all the complexity of nature'.

Futher work to evolve a complicated mathematical theory of life-history strategies, which may not be of very general use, is perhaps of less value at present than attempts to understand in detail the strategy of particular species or populations, as Peake (1978), in reviewing the literature on life-histories of stylommatophoran molluscs, has said. He also called for detailed studies, not only of the many common and widespread molluscs about which so little is known, but also of those species rapidly disappearing in the wake of human disturbance.

This chapter describes an investigation of some aspects of the strategy of T. pisana. The work is divided into two sections: firstly, a detailed study, based on analysis of size-frequency distributions, of the life-cycle of T. pisana at Tenby over a four year period, and with this as a basis, a comparison of the life-cycles at different localities, as far as can be revealed from single samples, in an attempt to relate these to prevailing environmental conditions; secondly, a laboratory study of egg production to gain knowledge of reproductive potential. The information obtained is then discussed in relation to the overall strategy of the species.

3.2. Life-cycle.

3.2.1. Detailed study at Tenby.

3.2.1.1. Methods.

(i) Sampling procedures.

The first trip to Tenby (21 January, 1977), although at a time of year when T. pisana is not so easily found, did give a rough indication of the extent of the main colony, and of areas within this colony where T. pisana was relatively abundant. On the following trip (1 June, 1977) three of these areas were selected for intensive sampling (sites 1, 2 and 6, fig. 3.1.), two samples being taken from site 1, two from site 2, and one from site 6. On all subsequent sampling occasions (10 July 1977 until 2 July 1981) except one (11 July 1980, when no samples were taken from sites 2 and 6), a total of ten samples was taken, five as on 1 June 1977 and also a further five, from site 2 (one further sample), site 3 (one sample), site 4 (two samples) and site 5 (one sample). The location of these further sites is also shown in fig. 3.1. The precise situations of each of these sites are shown in the detailed sketch-maps and photographs (figs. 3.2., 3.3., and 3.4.). Further details of the sampling sites are given in appendix 2.

From 10 July 1977 until 22 June 1978 samples were taken at seven-week intervals. Between 22 June 1978 and 15 November 1979 sampling occasions were less evenly spaced because of the demands of other field work in the summers, and of weather and petrol shortages during the winter. However, when possible, samples were taken at times indicated by the previous year's work as being the most useful, either between the times of two of that year's samples, or at just the same time as a particular previous sample. This type of approach was used for the remainder of the study.

With two and a half years' sampling completed by 15 November 1979, visits thereafter were at intervals of from 12 to 25 weeks, so as simply to monitor the changes taking place, and to detect whether the same trends were being followed as in previous years.

Each of the ten samples taken on each sampling occasion was a collection of all the snails which could be found in an area of ground 0.5 x 0.5 m, including both those on the ground surface and those in the vegetation growing in the area. An imaginary wall was erected surrounding the sample area, and only snails on vegetation enclosed within this volume were collected. Thus, snails on parts of vegetation overhanging the area, although rooted outside it were collected; but snails on parts of vegetation extending beyond it, even if rooted within the area, were not.

On two occasions (17 January 1979 and 17 March 1979), after collection of the normal samples, the vegetation from two sample areas was clipped off down to ground level, taken to the laboratory and sorted through by hand. The earth to a depth of 15 cm was also dug up from the areas of these samples, taken to the laboratory and hand-sorted. The purpose of this was to attempt to shed some light on the apparent disappearance of half-grown individuals from the regular samples during the winter (see results section), either because they were missed while searching the vegetation, or because they had buried themselves in the soil.

The snails appeared to have a very contagious (clumped) distribution at most of the sites (chapter 5, section 5.2.), and so sampling positions were chosen at the beginning of the study in places where sufficient snails were present for a 0.5 x 0.5 m area to give adequate numbers. These positions were adhered to as closely as possible during the whole course of the study, except on a few occasions when the vegetation became so sparse that the original positions were abandoned and new ones containing vegetation and snails were selected as near as possible to them (within 2 or 3 m). The main disadvantage of such a non-random sampling technique lies in the very poor estimate (almost certainly an over-estimate) of overall population density which it permits (chapter 5, section 5.3.). However, it was felt that the very much larger and more consistent samples obtained, which were therefore more useful for the study of the life-cycle (as opposed to the population density), justified the adoption of this procedure.

On each sampling occasion , field notes were taken of the weather conditions and the state of the vegetation and soil at each of the sampling sites. Notes were also taken of the condition and activity of the snails, including their positions in the vegetation, occurrence of copulation and oviposition, and of any other observations which appeared relevant.

(ii) Measurements and laboratory observations.

The snails collected on each occasion were taken to the laboratory and kept dry in the cardboard collecting boxes until such time as they were dealt with. All measurements and observations were completed within two weeks of collection. Since the snails were kept dry and therefore inactive during this period, it has been assumed that no growth took place between collection and processing, and changes in reproductive condition, if any, were negligible.

The height (h) parallel to the columella, and maximum diameter (d) perpendicular to the columella (fig. 8.1., chapter 8) were measured for every shell to the nearest 0.1 mm using a dial caliper.

From the sampling occasion of 4 & 5 May 1978 onwards, the method of Bett (1960), since used by Mordan (1978), was employed to give an indication of reproductive maturity. A snail was considered mature if the hermaphrodite duct contained spermatozoa. It was first killed by immersion in boiling water for about 20 s and the animal removed from the shell using a small hook. The hermaphrodite duct was then removed and squashed on a microscope slide in a drop of water under a cover-slip. Presence or absence of spermatozoa could then be observed by viewing this preparation with a microscope. In addition, the appearance of the hermaphrodite duct was recorded; whether it was opaque, white and convoluted, or translucent, thin and straight. Intermediate conditions sometimes occurred but were always scored as either of these two. A minimum of two out of the ten samples was analysed in this way; usually one from site 1 and one from site 2. On some occasions, if none of the five samples from sites 1 and 2 contained many snails, or if none showed a broad distribution of shell sizes, then a different sample, or samples, was chosen. On others, particularly when sample sizes were small, more than two were used.

Observations were also made of the condition of the albumen gland and the presence or absence of a thickened peristome. (*T. pisana* does not form a definite lip as do adult *Cepaea* for example). It was hoped that this would give some idea of how these correlated with maturity as determined by the condition of the hermaphrodite duct.

(iii) Analysis

Rather than use a simple measure of shell size (e.g. height or diameter alone) as most authors have, it was decided to adopt height plus diameter (h+d) since it is the simplest measure of shell size which takes some account of variation in shell shape (cf. Gould, 1969).

For every shell collected, h+d was found, and a histogram showing the distribution of numbers of shells within each 2 mm category of h+d was drawn for each of the ten samples from each sampling occasion. From these histograms it was clear that there was a great deal of between-sample heterogeneity in the size distributions. Despite this heterogeneity it was also clear that the trends shown by the sequences of individual samples over the course of the study were all broadly similar to each other (see results section). The lumping together of the results from all ten samples from each sampling occasion was therefore used as a means of showing the more general trends in size distribution within the whole Tenby colony. On two sampling occasions fewer than ten samples were taken (1 June 1977 - 5 samples, 11 July 1980 - 6 samples). In these two cases the total number of snails in each 2 mm category of h+d was multiplied by either 10/5 (1 June 1977) or 10/6 (11 July 1980) so that the numbers of individuals represented in the overall size-frequency distributions for these two occasions would be comparable with those for the majority of occasions.

A method of analysing polymodal frequency distributions such as those obtained here has been described by Harding (1949), Lewis and Taylor (1967) and Southwood (1978), and applied in a study of snails by Williamson (1979). By plots on probability graph paper, it gives estimates of the mean and standard deviation of each component class of the polymodal distribution, and also the proportions in which the classes are represented. The refinements of the method, described by Cassie (1954) and Harris (1968), were not felt to be useful for the present broad study.

The mean value of h+d for each size-class within the overall size-frequency distribution from each sampling occasion having been estimated thus, it became possible to calculate a measure of relative growth rate for that size-class during each of the intervals between sampling occasions. Assuming that growth was proportional to the volume of the snail, and that the term $(h+d)^3$ was proportional to shell volume, the following relationship applies:

$$(h+d)^3_t = (h+d)^3_0 \cdot g^t$$

where t is the length of the interval in days, and g is a constant. This is more easily handled in the form:

$$\log\ (h+d)^3_t = \log\ (h+d)^3_0 + t\ .\ \log g$$

or: $\log g = (\log\ (h+d)^3_t - \log\ (h+d)^3_0)\ /t$

and hence g can be calculated. A value of unity for g indicates a growth rate of zero (i.e. no actual growth). Positive values indicate growth - the larger the value, the faster the growth. Negative values indicate a reduction in size, but this is obviously meaningless in the present case. A value of g has been calculated in this way for all size-classes within the overall size-frequency distributions, and for all the intervals between sampling occasions.

Since it was not possible always to record reproductive maturity (as indicated by sperm in the hermaphrodite duct) in all ten samples collected on each occasion, an estimate of the overall proportion of mature animals in each 2 mm category of h+d in the combined ten samples was obtained simply by assuming that this was the same as that found in the combined scored samples alone. In a very small number of cases there were animals in a particular 2 mm category in the unscored samples, while none was present in that category among the scored samples. This situation only arose at the large end of the distributions and so the proportion of mature snails in the particular category was estimated as the same as that in the next lower category.

3.2.1.2. Results.

The size-frequency distributions for the combined set of ten samples collected on each sampling occasion during the course of the four years of the study are shown in fig. 3.5. The data upon which they are based are given in appendix 3. The mean and standard deviation of each component class of the polymodal distributions as well as the proportions in which they are represented within each distribution are given in table 3.1. The mean values of each class are indicated on the histograms and have been joined in consecutive distributions to allow easier following of particular cohorts. Table 3.1. also gives the total number of snails collected on each occasion. The following trends are apparent simply from inspection of the series of distributions.

In June 1977, at the start of the study, the distribution was bimodal; that is, it indicated the presence in the population of two size-classes. Between 1 June 1977 and 10 July 1977 growth of both these classes is shown by the shift in the mean of each peak in the distribution. Newly-hatched individuals (recognisable as such) began to appear during August, as shown by the hint of a peak appearing in the distribution of 31 August 1977 at a lower size than that of the juvenile class already present. The probability paper analysis showed that this was a distinct class (table 3.1). The large-size class (adults) had not grown since 10 July 1977. By 20 October 1977 a large number of the new juveniles was present in the samples, and the number of adults was decreasing. (There was also, at about this time, an increase in the number of empty adult shells seen in and around the sample areas; and further, the remaining live adults appeared to have lost weight, were always retracted far into their shells if not active, and (see chapter 8, section 8.3.) posessed extremely thin and fragile shells). The half-grown juvenile class also seemed to be disappearing from the samples at about this time, although some certainly remained. This picture remained constant through the winter (samples of 8 December 1977, 26 January 1978, 16 March 1978) with little, if any, growth taking place. By 4 May 1978 some growth had occurred, and there was an indication that the 'missing' half-grown juveniles of the previous autumn and winter were again being found in the samples. (Most animals showed a thin, newly-secreted section of shell at this time). By 22 June 1978 the distribution had returned to one very similar in its clear bimodality to those of June and July of the previous year. Rapid growth had taken place.

This sequence of events indicated by the first year's sampling was followed without any significant difference for the subsequent year and a half of regular sampling. The less regular samples taken from 15 November 1979 until 2 July 1981 equally do not indicate any important departure from this pattern, except perhaps in the summer of 1980. Between the sampling occasions of 11 July 1980 and 18 October 1980 there appeared to be little or no growth of the half-grown juvenile class, and at the end of this interval these animals were smaller than were the equivalent classes at this time in previous years. This is more clearly seen by inspection of the mean sizes of the respective classes (table 3.1.). This lack of growth in the half-grown juvenile class was confirmed during a mark-recapture experiment (see chapter 5, section 5.4.). Marked juvenile snails were released on 10 July 1980, and on recapture (17 & 18 October 1980) few had grown.

The apparent disappearance of the half-grown juvenile class from the population during the winters was not explained by the results from the soil and vegetation samples taken on 17 January 1979 and 17 March 1979. The size-frequency distributions of these eight samples, and also those of the normal sample previously taken from each area, are shown in fig. 3.6. It is clear that although some animals were overlooked in the vegetation, and others had buried themselves in the soil, the distributions are not different from those of the usual samples, and therefore that the disappearance cannot be explained in this way; that is, the 'missing' animals had neither been overlooked in the vegetation nor buried themselves in the soil in greater relative numbers than had snails in other size-classes. (Snails of all size-classes could not be induced to bury themselves when kept at low temperatures in the laboratory during the winter).

In fact, their disappearance is explained in a different way. On a number of occasions during late autumn, winter and early spring, large groups (over 100 individuals) of half-grown juveniles (only) have been found outside the 0.5 x 0.5 m sample areas. These animals were always attached with strong, dry, white mucus to a hard surface, often stone or concrete under a slight overhang at the base of a wall for instance. An example of one of these groups is shown in fig. 3.7. Some of the half-grown animals did remain, however, in the areas sampled, as shown by the probability paper analysis which indicated that this size-class was continuously represented, if only by a small proportion of the total sample (fig. 3.5. and table 3.1).

The proportions of animals in each size-class within the distributions can only be poor estimates of the proportions in the actual population, because of the inadequacies of the sampling procedure. These include not only the taking of just ten samples on each occasion from a population with very heterogeneous spatial distribution of size-classes (chapter 4, section 4.3.2.1. and chapter 5, section 5.2.), but also the fact that small, particularly newly-hatched, animals would have been overlooked relatively more than larger snails, and thus would be under-represented in the samples. However, half-grown snails and adults were probably sampled fairly completely, and it is clear that during the summer months the proportions of adults and half-grown juveniles were roughly similar to each other. The random sampling carried out in July 1981 (chapter 5, section 5.3.) agrees with this. This suggests that little mortality took place between these stages of the life-cycle, and therefore that most took place at an earlier stage, probably when the recently-hatched snails were very small.

It is thus possible to suggest a general outline of the life-cycle of Theba pisana at Tenby. Snails become adult during July and August, and at this time there are both adults and half-grown individuals within the population. Newly-hatched juveniles begin to appear in the samples during late August and September. As the autumn proceeds the adults die, although a small number may live right through the winter or even longer (the adult size-class is almost continuously present - fig. 3.5.), and the half-grown animals disappear from the samples. High mortality of newly-hatched snails probably occurs in their first winter. The situation remains more or less static until about March when the half-grown animals return to the samples and growth begins again. Growth is rapid during the spring. By summer the half-grown cohort of the previous year is becoming adult and ready to breed, and the previous year's new cohort now consists of half-grown individuals. Some of the previous year's adults may have survived to this time but will be indistinguishable in this type of analysis from newly-adult snails. In general, then, the size-frequency data show that the life-cycle takes two years to complete, and that adults breed only in their second year, and die very soon afterwards.

The data obtained from 4 May 1978 onwards on the presence of spermatozoa in the hermaphrodite duct, as an indication of reproductive maturity, augment those obtained from the size-frequency distributions. The proportions of mature animals within the samples are indicated by the dark areas in each of the histograms in fig. 3.5. (As has been mentioned in the previous section, it was not possible always to record reproductive maturity in all ten samples from each sampling occasion, so some of these proportions are estimates based on those samples in which this has been done. The data upon which these are based are given in appendix 3). As can be seen from the histograms a small number of large individuals posessed sperm in the hermaphrodite duct by May, and by August most animals over about 14 mm diameter (h+d approximately 20 mm) were mature. Animals smaller than this down to a little over 10 mm diameter sometimes posessed sperm, but this appeared to be less and less likely the smaller the animal. Fully-grown animals over about 14 mm diameter, surviving after this time of year, were almost invariably mature, but such large animals were collected less and less often as the autumns and winters progressed, as has been indicated in the description of the size-frequency distributions. There is no sign of sperm resorption before death.

The observations of the development of the albumen gland, as an indicator of the development of the female part of the reproductive system, suggested that it may develop from a very small size to full maturity later than the male part (as indicated by the presence of sperm in the hermaphrodite duct). It has already been shown, however (Cowie, 1980b), that animals of less than 10 mm diameter are able to lay eggs, and must therefore have had a mature albumen gland. In adult animals surviving into late autumn and winter, the albumen gland remained fully developed, but the hermaphrodite duct, although still containing sperm, sometimes appeared to become less opaque and convoluted. On no occasion has copulation been observed in the field; it may be a purely nocturnal event. Oviposition has been observed from early August through to early November, on about a dozen occasions.

These observations both of reproductive condition and of reproductive activity are entirely consistent with the conclusions drawn from the size-frequency distributions.

The values of the relative growth parameter, g, are given in table 3.2 in which those values corresponding to particular cohorts are indicated. These data are also presented graphically in fig. 3.8. It is clear in general from this diagram that there was little growth, if any, during the autumns and winters. Growth began in early spring (perhaps earlier in 1978 than 1979, these being the only two years when sufficient samples were taken to allow a comparison) and by May was well under way. Growth continued to be rapid during June and the early part of July, when it slowed down, and by the start of September had virtually stopped again. There is a suggestion that the spring growth period was longer for the smaller of the two size-classes present, than it was for the larger one, although growth of animals in the larger size-class may have been faster. During this period of growth, the small number of adults entering their third season did not appear to grow further. The growth of newly-hatched individuals seemed to follow no general pattern. The newly-hatched snails of 1977 did not grow from 31 August 1977 to 8 December 1977 but then started their 'spring' growth very early (between 8 December 1977 and 26 January 1978). Those of 1978 grew immediately they appeared (14 September 1978 - 3 November 1978) although this growth was not as rapid as that in any of the spring growth periods; growth then slowed but during no interval over the 1978/1979 winter did no growth take place. The newly-hatched animals of 1979 did not appear until late in the year (15 November 1979, although one very small individual was collected in the samples of 13 September 1979), and after this, sampling was too infrequent to allow any conclusions to be drawn regarding their winter growth. Sampling was also too infrequent during 1980/1981 for any comment to be made on the cohort hatched in 1980. These growth data thus provide some quantification of events already described qualitatively simply from inspection of the size-frequency distributions.

The presence or absence of a thickened peristome did not appear to indicate necessarily that the snail was reproductively mature, except that a fully-grown shell would always show a thickened edge. Snails could be mature (with spermatozoa in the hermaphrodite duct, and a fully-developed albumen gland) but still be within the period of rapid growth in late spring or early summer, with a thin, growing edge. Conversely, juvenile snails, particularly in the winter (non-growing) period, could be immature (no sperm in the hermaphrodite duct, and an undeveloped albumen gland) yet have a thickened edge. A thickened peristome appeared to be correlated with periods of no growth, rather than with reproductive maturity; that these two factors approximately coincide when the snails become adult may be incidental.

The above results have all been obtained by combining the ten samples from all sites on each sampling occasion. It is now worthwhile to consider the variation between sites. The individual size-frequency distributions are not all presented, but the data are available in appendix 2. On many sampling occasions there was much variation between samples, especially in the proportions of each size-class represented (e.g. fig. 3.9.).

This was due largely to differences in behaviour between animals of different classes, such that the proportions of each class collected depended upon the type of vegetation in the sample area at the time of sampling. (See chapter 4, section 4.3. for a more detailed analysis of behavioural differences). Despite this variation, the biennial pattern is apparent in any one series of samples taken during the course of the study (e.g. figs. 3.10. and 3.11.).

However, there may be some variation from site to site in the time breeding starts and in the sizes of animals within each size-class. In the samples of 31 August 1977 (fig. 3.12) there are significantly more snails of under 6 mm h+d at site 2 than at the other sites combined ($\chi^2_1 = 51.13$, $p < 0.001$), suggesting that breeding started earliest at this site in 1977. (There are too few snails at the other sites to do an overall heterogeneity χ^2 test, but in view of the high value of the χ^2 calculated, it is felt that this indicates a significant difference). In the samples of 5 August 1978 (fig. 3.13.) there is a slight hint (not significant) of the appearance of newly-hatched snails first at site 3. The subsequent set of samples (14 September 1978 - fig. 3.14.) shows heterogeneity in the proportions of snails under 6 mm h+d (when samples from each separate site are combined, $\chi^2_5 = 82.65$, $p < 0.001$). Those sites with more newly-hatched snails than expected were sites 1, 2 and 3, suggesting that breeding started earliest at these. In 1979 there was no significant difference between sites in the first appearance of new juveniles, although snails under 6 mm h+d were only present at site 6 in the samples of 13 September 1979 (fig. 3.15.).

Differences in adult size are apparent (e.g. samples of 5 August 1978 and 14 September 1978 - figs. 3.13. and 3.14.), fully-grown snails at sites 2 and 3 being larger than those at sites 1 and 4, with those at sites 5 and 6 intermediate. A tentative suggestion that animals at sites 2 and 3 grow faster and reach a larger size than those at sites 1 and 4, and breed earlier than those at sites 4 and 5 may be justified.

The observations and results presented above relating to the growth and reproduction of T. pisana at Tenby can now be brought together and the life-cycle summarised. Some variation from site to site within the colony can be discerned, but the general trends are clear. Newly-hatched snails, appearing in late summer and autumn, may or may not grow a little immediately; they grow to approximately half-size during a period of rapid growth in the spring of their first year. Growth ceases by late summer and many of these one-year-old snails go into some form of hibernation for the autumn and winter. During their second spring and summer they grow to full adult size and reproductive maturity, and breed towards the end of this period. Most of these now post-breeding adults then die, although it is possible that some may live through their third winter and perhaps longer.

3.2.2. Other localities.

3.2.2.1. Introduction and interpretation.

A number of random samples (every snail found in a given area) has been collected by myself and others from various further colonies of T. pisana both in the U.K. and abroad. They are derived from localities covering (albeit rather sketchily) the whole Mediterranean and Atlantic distribution of the species. Size-frequency distributions have been constructed for each of them and reproductive maturity, as indicated by the presence of spermatozoa in the hermaphrodite duct, has been recorded for some. Unless otherwise stated, all snails were measured within two weeks of collection, as was the case for the samples from Tenby. It must be remembered that in general, terrestrial snails living in temperate climates breed during the summer and hibernate during the winter, whereas Mediterranean snails tend to breed during the winter and aestivate during the summer. Most of the Mediterranean samples were collected while the snails were aestivating.

Duncan (1959) indicated the problems of interpretation encountered when sampling has only taken place for one year; that is, the samples may represent the situation during a particular year, but not be representative of the more general situation in an average year. These problems will obviously be exaggerated when only single samples are available. This has been pointed out by Haskin (1955), who also discussed the three major difficulties encountered when interpreting size-frequency distributions, and in particular those from single samples:

(i) older year-classes may overlap and be indistinguishable

(ii) the age of the smallest year-class is unknown

(iii) A particular year-class may be missed completely in the sample

This third difficulty may be particularly pertinent in the present analysis. The heterogeneity between samples from each sampling occasion at Tenby suggests behavioural differences between year-classes. Such differences have indeed been found at Tenby, where, in the daytime during the summer, adult snails are found largely above the ground-level vegetation and stuck to taller stems, whereas juveniles show a preference for this ground-level vegetation (chapter 4, section 4.3.). Furthermore, during the winter, as described above (section 3.2.1.2.), half-grown snails are found hibernating in groups stuck to hard surfaces, while others remain in the vegetation. It is likely that these types of differential behaviour are common, and also that other differences may occur, for instance in aestivating position during the summer in Mediterranean localities. In such a situation, inexperienced collectors of *T. pisana* would be apt to collect the more obvious size-classes without realising that they were not taking a representative sample of the population as a whole. For instance, if only microhabitats favoured by adults were noticed as containing snails, then a juvenile class might be missed entirely. Furthermore, if the sample area were small, then despite a complete collection by a collector aware of differential behaviour, a class present in the population may not be collected if the sample area did not contain its favoured microhabitat. Thus, without a thorough search of the surrounding area, to discover a missing class, a unimodal sample, although at first sight suggesting annuality, is in fact of no use for inferring the life-cycle.

Samples containing two size-classes, and in which the small animals do not represent the progeny of the large ones, which themselves belong to a single cohort, do indicate some bienniality. Dr. J. Heller (personal communication) believes that such bimodal samples may result from inhibition by faster-growing, and therefore larger, snails, of the growth of slower-growing ones. If this hypothesis is correct, the effect, (possible mediated by mucus - cf. Cameron and Carter, 1979), would perhaps be expected to obtain to a greater extent in denser populations but although I have no good data on population density at the sample sites (except Tenby), the impression gained was not of a trend for dense populations to exhibit bimodality. The hypothesis has not been considered in the following discussion, but cannot be entirely discounted, and adds to the difficulty of interpretation of single samples.

If the sample is considered truly representative of the population, not only in presence or absence of particular size-classes (considered to represent age-classes), but also in the proportions in which they occur, then some further inferences may be possible. (It must always be assumed that small animals are not found as easily as large ones, although this effect may not be very great when collecting adult and half-grown snails; it will be important if newly-hatched animals are present in the population). Bimodal samples of this kind can be divided into three main groups:

(i) Samples containing mostly half-grown snails, but with a small number of large individuals forming a distinct class (some of the samples in this study from Spain (inland), Sardinia and Crete - section 3.2.2.3.). Samples of this type may indicate an entirely biennial population. If this is the case, and the population density is remaining constant, then they further indicate either low recruitment of the cohort now consisting of large animals, or future high mortality of the half-grown animals. The latter disagrees with the picture at Tenby, where most mortality is thought to take place during the first season of growth; but Tenby is climatically very different from Mediterranean localities in particular, and such differences in the life-tables would be possible. Alternatively, such samples may indicate a predominantly annual cycle, and that the small number of large animals consists of those just failing to mature in their first season. These large, but immature snails would therefore neither breed nor subsequently die at the end of this first season, but survive to breed in their second year. These two-year-old snails might be able to breed somewhat sooner in the autumn and winter than the one-year-old ones, since these would have to spend some time growing before they could commence breeding. However, growth is rapid, and it would be difficult to distinguish the progeny of these one- andtwo-year-old snails in size-frequency distributions as used in this study. An entirely annual cycle could be postulated if the small number of large animals in the population was of those which had indeed reached full size and maturity during their first season, but had managed to survive a second year. These animals might be expected to have sperm in their hermaphrodite ducts, since, at Tenby, old animals surviving into an extra season (through a cold winter, rather than a hot, Mediterranean summer) usually did (e.g. January 1979, fig. 3.5.).

(ii) Samples containing two size-classes, represented in similar proportions (some of the samples in this study from Caldey Island - section 3.2.2.2., Balearics, Lesbos and Cyprus - section 3.2.2.3.). Such samples suggest that a large proportion of the animals takes two years to mature. In this respect, these samples are an extension of the type described in (i) above, in which a greater proportion, if not all of the population, fails to mature within its first year. If the population density is assumed to be remaining constant, then not much can be inferred regarding recruitment and mortality, except that there is little mortality of snails larger than about half-size.

(iii) Samples containing mostly large snails, but with a small number of small individuals forming a distinct class (some of the samples in this study from Brittany, Crete and Israel - section 3.2.2.3.). These indicate bienniality with either low recruitment or high mortality of the younger cohort. Both these regimes will result in a reduced number of adults in the following year, and therefore a dwindling population. This kind of distribution cannot be explained by a predominantly annual cycle with variation in growth rate (as in (i) above), since in this case, the smallest individuals would simply be the small end of a unimodal distribution (assuming a continuous distribution of growth rates within a population).

It is clear both from the samples from Tenby and from those from Mediterranean localities described below (e.g. Spanish duneland) that adult snails generally die soon after breeding for the first time. They are semelparous. However, for the short period between the appearance of newly-hatched snails and the death of their parents, the post-breeding adults, there will be an additional size-class present in distributions of the type described above. At this time a biennial population would consist of three size-classes, and an annual population two.

Having described the possible interpretations of single samples of the various kinds found in this study, one can see that definite conclusions are unlikely to be possible in many cases, particularly when samples may not be representative of the overall population, due to differential behaviour of size-classes. The following results and tentative conclusions, mostly derived from single samples, must therefore be treated with a great deal of caution.

3.2.2.2. Sites in the U.K.

At only three localities within the British distribution of T. pisana (chapter 2) were the snails sufficiently abundant to allow samples to be taken. Details of these sampling sites are given in appendix 2. ~~and the size and maturity data are given in appendix 3.~~ All samples were taken by myself.

(i) Caldey Island (near Tenby) - 2 August 1979 - fig. 3.16. Two samples were taken. All snails were measured (h and d), and those with $d > 10.0$ mm were killed and scored for presence of spermatozoa in the hermaphrodite duct. Smaller animals were assumed to be immature. The two size-frequency distributions are similar to each other, and to the distributions of samples from Tenby at about this time of year (fig. 3.5.), all appearing bimodal, and with most large animals mature. The life-cycle is, no doubt, very similar to that of the main Tenby colony, that is, biennial.

(ii) Porthcawl (Mid Glamorgan) - 13 September 1979. Very few snails were seen at Newton (grid reference SS839771), to the east of Porthcawl, and these were all adults (one ovipositing). Breeding is therefore under way in the middle of September, as at Tenby.

On the Kenfig dunes, just north of Porthcawl, T. pisana was not as abundant as in parts of the Tenby colony, but a sample was taken from an area about 5 x 5 m in which most of the snails were sitting on sea holly (Eryngium maritimum L.). The size-frequency distribution of this sample (fig. 3.16.) is unimodal, only fully-grown adults being present in the sample, and so suggesting that it takes only one year for the snails to reach full-size. However, this is a good example of how misleading a single sample may be; a few half-grown juveniles were certainly present in the area around the sample site, although none was taken in the sample itself. Hence, the cycle is probably biennial, rather than annual, at Kenfig, as at Tenby.

(iii) St. Ives (Cornwall) - 31 July 1979 - fig. 3.16.

The size-frequency distribution of this sample is unimodal, and all the snails were mature. The colony is small and the whole area was investigated; there was no sign of juvenile snails, either half-grown or newly-hatched. This therefore suggests that at St. Ives T. pisana reaches maturity after one year, and that it does not breed until late summer. However, J. Humphreys (in litt. 21 III 1980) considered that this failure to find juveniles was not significant, and that the cycle is biennial at St. Ives. It is conceivable that half-grown snails were indeed present and were missed.

3.2.2.3. Sites abroad.

The following results are derived from samples collected by various people including myself (Spain, Sardinia, Milos) from a number of widely separated localities in the non-British parts of the range of T. pisana, obtained as and when the opportunity arose during the course of other activities. The samples cover a wide geographic and climatic range, from the temperate, northern coast of France, to Israel in the eastern Mediterranean. The precise locations of the sampling sites, date of collection, name of collector, and any available information on the habitat characteristics are given in appendix 2. ~~The size-distribution and maturity data are given in appendix 3.~~ Most of the Mediterranean samples were collected during the summer while the snails were aestivating.

(i) Northern France - fig. 3.17.

Two samples from the Channel coast of France have been analysed, one from the Baie du Mont Saint Michel in Normandy, collected in September 1979, and one from near Roscoff in Brittany, collected in July 1980. Five further samples, taken in July 1980, were available from the south coast of Brittany in the Baie du Quiberon area. The samples are almost entirely composed of mature adults (although some contain a few smaller snails which may suggest bienniality) and are therefore uninterpretable in terms of the life-cycle. From the collectors' notes (appendix 2) they were indeed mostly taken from microhabitats favoured by adults (in south Wales).

The maturity of most large individuals at this time of year agrees with that of Tenby snails, and disagrees with that of most of the Mediterranean samples taken during the summer months (Spain, Sardinia, Lesbos, Crete, Cyprus and Israel - see below), and therefore suggests a similar regime to that at Tenby.

(ii) Southern Spain - figs. 3.18. and 3.19.

Samples were taken by myself from the area between Marbella and Fuengirola on the Costa del Sol during late August and early September of both 1978 and 1979. Four samples were taken from the dunes close to the sea: two in 1978 and two in 1979. The population at a single site about 2 km inland from these duneland sites was also sampled in both 1978 and 1979. Reproductive maturity was only scored in the two inland samples, since only these two contained any large snails. In fact, very few of these were mature and so it is reasonable to assume that none of the snails in the other four samples was mature either. On all sampling occasions, all the snails were aestivating on vegetation; none was active, and none was found on the ground. At all sites a thorough search was made of the surrounding area, including, on a number of occasions, particularly at the duneland sites, an attempt to find snails buried in the sand by digging to a depth of about 40 cm. However, on no occasion was a new class, hitherto unrepresented, discovered, and so it is thought that the samples are true representations of the populations at that time.

The size-frequency distributions show that the four duneland samples (fig. 3.18.) contained only a single class, consisting of small juveniles (although the sample taken from site 2 in 1979 had a few slightly larger animals). This is good evidence of an annual life-cycle at these sites. This cycle would start with breeding taking place sometime during the mild but relatively damp winter, the newly-hatched snails growing somewhat, but not to full size, before aestivating over their first summer; the above samples were taken during this time. They would then grow to maturity during the autumn, and themselves breed before dying at the end of their first year.

In contrast to this picture for the duneland populations, the samples from the inland population show clearly bimodal distributions, although the large size-class is much less well represented than the small one, particularly in 1979 (fig. 3.19.). These samples are also considered good representations of the population, and can be explained in a number of ways (section 3.2.2.1.). It is possible that the cycle is annual as in the dunes, but few of the large snails contained spermatozoa in their hermaphrodite ducts as might be expected if they were mature snails surviving a further year after breeding in their first year. The main argument against an entirely annual explanation is that the duneland populations were characterised as such by virtue of the absence of a distinct class of large snails. Since the inland population, sampled at the same time, has a different distribution, its life-cycle must also be somewhat different.

The bimodality of the distributions of these inland samples must, therefore, indicate at least some bienniality. The population may be entirely biennial, with high mortality in the second year of life (but not low recruitment of cohorts adult at the times of sampling, since the two samples were taken in consecutive years from the same site). Alternatively, the population is predominantly annual and the large animals were those just failing to mature in their first year. This latter explanation is favoured since it does not imply a different mortality regime from Tenby; it suggests only a small difference in life-cycle from that of the nearby duneland populations; and it does not leave a low number of adults in a large site (the sample area was about 75 m x 10 m), although their productivity (section 3.3.) would perhaps be large enough to offset this.

It seems, then, that in this part of southern Spain T. pisana exhibits a predominantly annual life-cycle; but inland, where the growing season may be slightly shorter than in the dunes near the sea, some animals may be unable to reach maturity and breed in one year, and therefore are forced into a biennial cycle. It is clear that T. pisana shows some lability in its life-cycle.

(iii) The Balearic Islands - fig. 3.20.

Two samples were available from Mallorca, collected in August 1980. The Camp de Mar sample is unimodal, consisting entirely of mature adults, while that from Ses Coretes is bimodal, large animals within the sample also being mature. That these mature animals in both samples had come out of aestivation and would have soon started breeding is considered likely, despite the fact that the sample was taken in August. Since 1980 was a cool, relatively damp year in the Mediterranean, it is possible that the season of growth and activity, at least in some parts, may have started rather earlier than in a more representative year. The sample from Ses Coretes clearly indicates a biennial life-cycle at that locality. The unimodal sample from Camp de Mar is uninterpretable (section 3.2.2.1.), although it contrasts with the unimodal Spanish duneland samples (annual) in containing only adults rather than only juveniles, suggesting a different regime. It was collected from a microhabitat probably favoured by adults (appendix 2).

Two further samples were available from Mallorca, both collected in late November 1980 from Costa de le Calma. Sample 1 shows a clear bimodality, indicating a biennial life-cycle as above. Sample 2 shows a rather diffuse distribution, but this does not contradict the conclusion derived from sample 1.

Four small samples (one of only two individuals) were available from Menorca, collected during late October 1980, when the snails had come out of aestivation. Two of these samples (Torre d'en Gaumes and Torralba) contain only mature adults and are therefore uninterpretable. The other two (Santa Clementina and Es Grao) contain both mature adults and immature juveniles and may indicate bienniality.

From the limited samples available from the Balearic Islands, it is evident that some, at least, of the populations of _T. pisana_ exhibit a biennial cycle, and that others probably do, although an annual cycle for some populations cannot be ruled out.

(iv) Sardinia - fig. 3.21.

Two samples were taken by myself during the latter half of August 1980: one from near Calasetta, and one from within the city of Cagliari, both in the south of the island. At both these localities, a thorough search was made of the surrounding area in order to try and discover any animals belonging to size-classes possibly under-represented in the samples taken. No such animals were found, and it is therefore thought that the samples are good representations of the size distributions within the populations from which they were taken. It is clear that the size-frequency distributions of both these samples are bimodal, but that the large size-class constitutes only a a small proportion of the population, and further, that only a small number of these large animals was reproductively mature. These distributions appear similar to those of the samples taken at the inland site in southern Spain (fig. 3.18.) but with even fewer large animals, and they can be interpreted in the same way, as showing a predominantly annual cycle.

(v) Greek Islands - figs. 3.22. and 3.23.

A single sample was taken from a small, probably isolated, population in the centre of Mitilini on the island of Lesbos in May 1980. The snails collected were all stuck to bushes but the area inhabited by this population was small, so that all size-classes present were probably fairly represented in the sample. The size-frequency distribution is bimodal, and very few of the larger snails were reproductively mature (fig. 3.22a). Few of the large shells had a thickened edge to the aperture, but also few showed signs of recent, rapid growth. When collected, the snails were all stuck to the plants by a thin , transparent mucus, not a thick, hard, white one. Faeces produced in the collecting boxes, in which no food was provided, were green. These observations all suggest that at the time of collection, the snails were coming towards the end of the winter period of activity, feeding and growth, but that they had not yet entered aestivation. The two modes strongly suggest that this population is predominantly biennial. The large animals in the population in April would presumably be able to breed almost immediately after coming out of aestivation the following autumn, since they would be almost, if not completely, fully-grown by this time.

The single sample, taken by myself, from Adamas on the island

Milos, while the snails were aestivating, also shows a distinct bimodal distribution, again suggesting a biennial cycle (fig. 3.22b).

A similar pattern can be inferred from the samples from Crete (fig. 3.23). Four samples were received from near Malia, all collected within a small area. There is very clear heterogeneity between their size distributions, but it is believed that these samples were all taken from the same overall population, and that this heterogeneity indicates differential behaviour between the size-classes, as at Tenby (chapter 4, section 4.3.). Sample 1 was taken from grass and contained predominantly juveniles; samples 2 and 3 were taken from bushes and contain largely adults. This is broadly consistent with the findings at Tenby, except that sample 4, which also contained predominantly juveniles, was also taken from bushes. Despite this between-sample heterogeneity, it is clear that there are two, well-represented size-classes within this Malia population, and that the life-cycle is probably to a large extent biennial. The samples were taken in late October 1980 and all the large animals were reproductively mature; it is probable that they had come out of their period of summer aestivation. The absence of any newly-hatched snails in the samples suggests that either breeding was only just starting, or these very small animals were overlooked when taking the samples.

Three further samples from Crete, one from Komo and two from Amnissos, were collected in April 1980, but only the empty shells were received. The samples consist almost entirely of large snails, although the two from Amnissos both have a suggestion of the presence of a smaller size-class. They may well be consistent with the samples from Malia.

There is, then, no indication other than bienniality from these samples from Lesbos, Milos and Crete.

(vi) Cyprus - fig. 3.24.

Two samples were taken from near Limassol in August 1977 and one from the same area in August 1978. The area has since been artificially flooded. The large sample of 1978 was randomly divided into two subsamples, and one of these used to score reproductive maturity in the normal way. The snails in the second subsample were not measured until late October and early November, a lapse of two months since their collection. However, twenty of the snails in this subsample, covering a range of size, had been measured within two weeks of collection, according to the normal procedure, and were then left in the same conditions as the remainder until they were all measured. None of these twenty had grown during this period, so it is acceptable to combine the results from both the subsample measured within two weeks of collection, and that measured later. Since none of the snails in the first subsample was reproductively mature, it is also assumed that none of the snails in this second subsample was mature either. The size-frequency distributions for the two samples of 1977, and the single one of 1978 (both subsamples combined) are strikingly bimodal, suggesting a largely biennial cycle at this locality.

(vii) Israel - fig. 3.25.

Samples from Dor and Caesarea (south) on the coast south of Haifa were collected in September 1977, and samples from

Ashqelon (central and southern) on the coast south of Tel Aviv were collected in late May 1980. Despite the difference in the time of year when the samples were taken, all snails were probably aestivating when collected, and all are therefore comparable summer samples in terms of their size-distributions.

The samples from Dor and Caesarea, although containing predominantly large animals, do also contain a distinct class of small ones. This suggests bienniality (section 3.2.2.1.). The sample from central Ashqelon is unimodal with no appearance of even a few small animals, and is therefore uninterpretable. The sample from Southern Ashqelon was not a random sample, in that the collector deliberately included an excess of small individuals (see appendix 2). However, it does contain a high proportion of small animals; they were, therefore, present in this particular population, and this may indicate bienniality.

These limited samples do not allow a definite conclusion regarding the length of the life-cycle at these localities in Israel. However, since most of the snails collected were large, possibly fully-grown, although not mature, and were aestivating at this site, it is clear that breeding would start very soon after the first rains of autumn; there would be need of little growth. In this respect, these populations contrast with the annual, or predominantly annual Spanish and Sardinian ones, in which the summer is spent aestivating as juveniles rather than adults. Perhaps this hints further at a biennial cycle in these parts of Israel.

(vii) Algeria.

A small number of snails was collected from three localities near the coast in December 1977. None was scored for reproductive maturity, and, since so few snails were found, size-frequency distributions are not presented. However, a wide range of sizes was present in the samples (from 11.1 to 33.1 mm h+d), perhaps showing the presence of both adults and growing juveniles at this time of year, as would be expected.

3.2.3. Discussion of the life-cycle.

Table 3.3 summarises the findings of this section on the life-cycle of T. pisana. Despite the difficulties of interpretation discussed above (section 3.2.2.1.), it is clear that there is variation between the patterns exhibited at the localities from which samples have been studied. This agrees with published work on the life-cycle of T. pisana, summarised in table 3.4. In addition, a number of somewhat anecdotal and speculative comments made in passing and bearing on the life-cycle have appeared in the literature. These include observations of new or rapid growth, copulation and oviposition, and of the presence of only one or two size/age classes within the population at a particular time (Tye, 1877; Cooke and Gwatkin, 1878; Cooper, 1893; Bullen, 1905b; Germain, 1908; Taylor, 1912; Wintle, 1925; Basinger, 1927; Pilsbry, 1939; Comfort, 1957; Crowley, 1961; Backhuys, 1972). All are compatible with the conclusions drawn above.

Undoubtedly, individual variation also exists. Some individuals may grow little in a particular season, yet become mature at the normal age, and be capable of reproduction;

this could explain the observation (Cowie, 1980b) of very small animals laying fertile eggs. Perhaps other such animals might grow to full size in a later season, thus extending their life. A similar kind of halting of growth has been seen in the laboratory, animals becoming stunted. Some of these animals grow and breed subsequently, others do not. Stunting occurs when the snails are overcrowded or fed insufficiently, but also for no apparent reason. It may be a mechanism for extending the life-cycle in the wild in unfavourable conditions. Other individuals may grow to full size and maturity quicker than usual if conditions are good. Such departures from the general trend may well occur, but cannot be inferred from size-frequency distribution analysis.

The present study, then, together with published work, shows that the life-cycle of T. pisana is extremely variable. Sacchi (1971, 1977, 1978) and Sacchi and Violani (1977) have suggested that it is annual or biennial, depending upon the length of the period the snails are forced into aestivation, and therefore prevented from growing, during the summer. Thus they considered that bienniality occurs in 'truly mediterranean' localities, and annuality in 'Atlantic' localities, which include areas such as parts of the north Adriatic coast where the summers are relatively damp. Sacchi (1971, 1978) also inferred intermediate conditions as have been observed in the present study (i.e. Sardinia, inland southern Spain). These authors further suggested that nowhere in its range does T. pisana need to hibernate during the winter season for long enough to force it into bienniality. At that time, the life-cycle in the British Isles was not documented, and it is now clear from the present study, that T. pisana becomes less active, and ceases growth during the winter at Tenby, even if it does not fully hibernate; and that its life-cycle there is biennial. However, the conclusions of these authors undoubtedly offer the broad explanation of the variation: an annual cycle, unless the snails are forced into long periods of no growth (either aestivation in the hot, dry, Mediterranean summers, or hibernation in the cool, north Atlantic winters), when the cycle becomes biennial.

Bienniality in south Wales is therefore easily explained by the enforced winter period of no growth. The suggestion of an annual cycle at St. Ives may be incorrect since winters there are only slightly milder than at Tenby. Southern Brittany, if not the northern coast, is a little warmer than south Wales (data for Tenby and Lorient given by Wernstedt, 1972) and may be sufficiently so to sustain an annual cycle. Sacchi (1971) suggested an annual cycle for T. pisana at Roscoff on the north coast of Brittany, but he did not make clear the extent of the sampling upon which this conclusion was based, and so it must be viewed with some caution. Deblock (1962, and referred to by Deblock and Hoestlandt, 1967) suggested that the life-cycle was annual in Normandy and on the Belgian coast. However, the size-frequency distributions he presented are somewhat similar to those obtained in the present study from Tenby, and may be more correctly interpreted in the same way; that is, a biennial cycle with disappearance of one-year-old animals from the samples during the winter. Unfortunately, the size-frequency data for the samples from northern France in the present study are inconclusive.

The Mediterranean situation appears more complex. Using the maps given by Thran and Broekhuizen (1965) and Steinhauser (1970), and data (H.M.S.O., 1958, 1972; Wernstedt, 1972) from stations as near as possible to the sampling sites, an attempt has been made to detect any climatic trends correlating with the annuality/bienniality of the life-cycle. There appears to be a general east-west trend, such that, of the regions in which samples were taken, the coast of Israel, and Cyprus have the highest temperatures, and the Balearic Islands the lowest, the difference in mean daily maximum for each month between Haifa and Mahon (Menorca) being about 5°C during most of the year. The Israeli coast and the island of Cyprus, and Crete as well, also appear to have the shortest growing period, as determined by both the mean monthly precipitation and the mean number of rain days per month, although Malaga (southern Spain), at the very western end of the Mediterranean, also appears to have a very short growing period (particularly as determined by the number of rain-days per month). The Balearic Islands (data for Palma and Mahon) and to a less extent Sardinia (data for Cagliari) are not only the coolest of these Mediterranean stations, but also have the longest growing period. Further, the Israeli coast has the lowest relative humidity during the growing season, while the Balearic Islands and Sardinia have the highest. Other localities are intermediate.

Harpaz and Oseri (1961, and referred to by Avidov and Harpaz, 1969) concluded that the cycle can be either annual or biennial in Israel, and Heller (1982) indicated an annual cycle at his localities in Ashqelon. These were the same ones from which some of the present samples were taken, one of these suggesting bienniality; this slight inconcistency may reflect the inadequacy of conclusions based on single samples or on only one season's sampling (section 3.2.2.1.). The evidence on the length of the life-cycle in Israel is, then, inconclusive, but both the samples from Limassol (Cyprus) and those from Mallorca and Menorca (Balearics) indicate a biennial cycle, even though these localities are at opposite ends of the large-scale climatic trend described above. Samples from intermediate localities (climatically) indicate both predominantly, or entirely, annual cycles (southern Spain, Sardinia), and biennial cycles (Lesbos, Milos, Crete). A biennial cycle was also found in southern France by Bonavita and Bonavita (1962). Clearly, a general trend in climate cannot explain the variation seen in the life-cycle. Kendrew (1953) has discussed climatic variation on a smaller geographical scale within the Mediterranean, such as the differences in rainfall on east and west coasts; but this goes no further towards an explanation. Indeed Sacchi (1978) has already come to the conclusion that macroclimatic differences in the Mediterranean cannot account for the observed variation in the life-cycle of T. pisana.

The ameliorating effects of the sea at sites very close to it (although T. pisana is rarely found far inland), will be superimposed upon the normal regime for a particular area, and will probably increase the length of the growing season by increasing humidity (cf. Bantock and Noble, 1973). This has been suggested as an explanation of the differences between the duneland and inland sites in southern Spain. That these effects are not always sufficient to allow an annual cycle close to the sea, is indicated, for instance, by the samples from Limassol. Furthermore, the samples from southern Spain and the work of Harpaz and Oseri (1961) in Israel, suggest that the life-cycle can change within a few kilometres, and indicate the fine scale on which climatic measurements are required in order to elucidate the precise combination of factors controlling it.

Apart from climatic factors, which are almost certainly the most important in determining the life-cycle, availability of food and calcium (at least in inland localities, away from the coastal sand - Sacchi, 1971) during the growing season could also play a part. The populations could be forced into bienniality if food and calcium were scarce, despite a climatic regime favourable to a long growth season and annuality. I have no data on which to base further discussion of this.

The variation in the life-cycle of T. pisana in the Mediterranean and western Europe which is shown by the studies presented in this chapter cannot, then, be fully explained. Certainly, the length of the growing season, as determined by the local climate, must be of great importance in its control. Such variability has been shown in the life-cycles of other species of snail by Lewis (1968), Potts (1975) and Umiński (1975) in particular, and hinted at by Mordan (1978). Peake (1978), reviewing the information available on terrestrial molluscan life-cycles, thought it to be widespread and often related to climate.

3.3. Laboratory study of egg production.

3.3.1. Experimental materials and methods.

The snails used were all taken from the sample of 10 April 1980 from site 3 at Tenby. It was assumed that all were virgin and healthy at the start of the experiment since they were small (less than 10 mm diameter on collection), growing rapidly, and because all but a very few large animals in the other samples of 10 April 1980 from Tenby contained no spermatozoa in their hermaphrodite ducts. Thirty pairs were set up on 30 April 1980 by taking one animal at random, and then pairing it with one of similar size. Ten single individuals were also set up to test the assumption of virginity, and to see if self-fertilisation took place.

Each pair (or single individual) was kept in a transparent lunch box 17.5 x 11.5 x 6 cm, with a layer of soil about 4 cm in depth. An area of about 7 x 8 cm was cut at one end of the lid of each box and covered with mesh netting material to allow ventilation. The boxes were kept in a room in which the temperature varied from about 10°C at night during cold spells in winter, to about 21°C during the days in summer. There was a small diurnal variation in temperature. Day length was not altered artificially, except that during the winter, artificial lights were kept on most weekdays until about 1700 or 1800 hrs. The soil in the boxes was kept moist, and the animals were fed twice a week on a ground-up mixture of one part calcium carbonate, one part oat breakfast cereal ('Ready Brek') and one part dried skimmed milk ('Marvel'). This mixture was sprinkled onto the dampened, solid part of the box lid. This food appeared to be ample, and on this regime T. pisana has been regularly grown to full adult size in much less than a year in the laboratory.

Eggs were laid in clutches in cavities excavated in the soil by the snails. In most cases clutches were laid either close to the side of the box, or on the bottom of the box, and so could usually be seen without disturbing the soil. The soil in the boxes was never searched and so on a number of occasions, when clutches were not visible from the outside, newly-hatched juveniles emerged from the soil; they were immediately counted and removed. Every clutch of eggs produced by the paired snails was removed; the eggs were counted, and weighed wet and dry (having been dried at 60°C for 4 days, which reduced them to constant weight). Eggs produced by the single individuals were not removed from the boxes, but estimates were made of the numbers in the clutches. This was done in order to check whether these eggs would develop, that is, whether they were self-fertilised, or infertile. The adults were measured (h and d) when they died.

3.3.2. Results.

3.3.2.1. Introduction and interpretation.

Two of the single individuals produced eggs (between October 1980 and January 1981). They were laid in very small groups or as single eggs which were often large and mis-shapen, although one clutch of about 40 and one of about 20 were also laid. None of these eggs was removed from the box, but none hatched. It is assumed that they were infertile and that T. pisana is an obligate outcrosser, as generally thought.

In 5 boxes containing pairs, one individual died when too small to breed (section 3.2.1.), or if large enough, when its partner was too small to breed, or before the start of the laboratory breeding season (section 3.3.2.2., below). These 5 pairs produced no eggs and are not included in the following analysis.

The results for number of clutches laid, clutch size, and total egg production (below) are based on numbers of eggs plus hatchlings, assuming 100% hatching success. Personal observation of laboratory breeding stocks suggested that hatching success was close to 100%, so this will not affect the results seriously. The date of laying of a clutch appearing as hatchlings is taken as 14 days before their first appearance (again based on previous experience). Since the time between hatching and emergence from the soil probably varies within a clutch, hatchlings appearing on consecutive checks of the boxes (2 per week) have been treated as belonging to a single clutch. This probably under-estimates the real number of clutches, but since only 11% of total production was counted as hatchlings, this will not seriously bias the results.

Morph differences have been considered by comparing production of five-banded x five-banded pairs (11) with that of five-banded x unbanded pairs (14). It was not possible to determine which individual had laid a particular clutch, and there were no unbanded x unbanded pairs. (The morphs are described in chapter 6). No correlation of morph (as considered here) with any of the variables discussed below was found, but the small size of the sample precludes detection of the low levels of correlation which might be expected. (A correlation coefficient of 0.3 would have to be based on a sample of 43 to be, significant at the 5% level).

Egg production took place during the 9 months from July 1980 to March 1981. By 1 March 1982 all but 4 snails were dead, and most had died well before this. There are no significant differences between the mean (± 95% confidence interval) date of death (taking 1 July 1980 as day 1, and considering the 4 snails still alive on 1 March 1982 to have died on this date - day 609) of single animals (338 ± 93), paired animals which failed to breed (237 ± 111) and those which bred (258 ± 46). However, the number of animals is small, and the impression gained was that the single animals lived longer.

The following analysis is aimed at obtaining some understanding of the inter-relations of number of clutches per pair, size of clutches, egg weight, date of onset of laying, date a particular clutch was laid, and adult size. Since all these variables are subject to sampling error, and the values of none were chosen or controlled, and since it is an indication of associations between variables rather than functional relationships which is being sought, correlation analysis is the appropriate test (Sokal and Rohlf, 1969). Step-wise multiple correlation has been used where appropriate. This technique requires selection of a dependent variable and then extracts the independent variable capable of explaining the greatest proportion of the variance in the dependent variable. It then selects the independent variable from those remaining which explains the largest proportion of the remaining variance, and so on until all the independent variables have been taken into account and the variance in the dependent variable has been fully partitioned. The multiple correlation coefficient measures the covariation of the dependent variable with all the independent variables which were taken into account. If the independent variables are themselves correlated, interpretation of the results can be difficult. Multiple correlation cannot, then, entirely separate their individual contributions; part of the relationship of the dependent variable with one independent variable may be expressed in the correlation coefficient of another, and thus, the next step of the analysis will underestimate the contribution of the former. Further, small differences in the correlation of the independent variables with the dependent variable could result in either being selected as the more significant, particularly when correlation between independent variables is high (Snedecor and Cochran, 1967; Cohen and Cohen, 1975). These difficulties have been borne in mind throughout the following sections.

In order to incorporate adult size into the analysis, despite not knowing which member of a pair laid a particular clutch, I have used the mid-parent size for each pair (mean h+d, at death, of the two adults). This will tend to smooth out any effect of size, and may obscure a real correlation.

3.3.2.2. Number of clutches.

The mean number of clutches produced per potentially producing pair (25) is 4.8 ± 4.5 (standard deviation), and 5.2 ± 4.4 for those actually producing (23 pairs), with a maximum of 15. The distribution of number per pair (fig. 3.26.) is skewed.

Clutches were laid over a definite season, the first on 14 July 1980 and the last on 20 March 1981, with the modal numbers in October and November (fig. 3.27.). This was similar to the season at Tenby (section 3.2.1.) but extended later, perhaps because of the absence of harsh winter conditions in the laboratory.

All pairs which ultimately laid eggs had laid their first clutch by November 1980 (fig. 3.28.). The date of laying this clutch was negatively correlated with the mid-parent size of the pair (correlation coefficient, $r = -0.49$; $p < 0.02$).

Because number of clutches may be related to both date of onset of laying (date of first clutch) and adult size, these presumably being manifestations of more fundamental genetic or environmental variation, multiple correlation has been used to detect any associations. It has been assumed for the purposes of this analysis that the relations of number of clutches with data of onset of laying and mid-parent size are linear, since inspection of the very diffuse scatter diagrams gives no indication of curvilinear relations. Since the two independent variables are correlated (above), multiple correlation cannot entirely separate their individual contributions to the variance in number of clutches (section 3.3.2.1.). However, they are not very strongly correlated ($r = -0.49$, $p < 0.02$).

The analysis showed a significant negative correlation ($r = -0.50$, $p < 0.02$) of number of clutches with date of onset of laying, but a non-significant correlation with mid-parent size after removal of the covariation due to date of onset of laying. A simple bivariate correlation of number of clutches and mid-parent size was not significant.

This suggests that date of onset of laying is of more importance than adult size in determining the number of clutches laid. Adult size cannot be discounted with certainty because of the correlation with date of onset of laying (section 3.3.2.1.)

This is consistent with a fixed length of the egg-laying season; snails starting late can only lay a small number of clutches before the season ends.

These two factors only accounted for 26% of the variance of number of clutches. The error variance (74% of total) cannot be further partitioned but it is likely that other unknown environmental, physiological or genetic factors may be contributing to it.

3.3.2.3. Clutch size.

The mean number of eggs per clutch is 76.5 ± 54.3 (standard deviation). The distribution of clutch size is shown in fig. 3.29. and is clearly not normal. However, these are very coarse descriptions of the variation. Fig. 3.30. shows the scatter of clutch size against laying date (with 1 July 1980 as day 1). Although there is considerable variation, an overall decrease in clutch size during the course of the season is clear; the correlation coefficient is low (-0.299) but highly significant ($p < 0.001$). However, from inspection of the scatter diagram, it is apparent that the distribution of clutch size against date of laying is not bivariate normal (as required for correlation analysis), but that there are two kinds of clutch, large (type - L) and small (type - S), both decreasing in size as the season progresses. The dotted line in fig. 3.30. divides them. Within each clutch type, size distribution does not differ obviously from normal, and assumption of a linear relationship with date is not unreasonable. Within each type, size and date are then highly correlated (type - L: $r = -0.70$, $p < 0.001$; type - S: $r = -0.71$, $p < 0.001$).

An obvious interpretation of these two types of clutch is that type - S ones are normal single clutches, type - L ones resulting from both snails laying in the same hole. By inspection of the scatters, this cannot be the case, since at any particular date, mean size of type - L clutches is more than twice that of type - S clutches. Furthermore, the snails lay their eggs in a spherical ball in a cavity excavated to leave a gap of about 2 mm between the clutch and its sides. It seems unlikely that a second snail, discovering precisely the same cavity (60% of the clutches are type - L) would excavate around the first clutch, and then add to it, increasing the size of the ball of eggs, rather than lay its own clutch separately. Indeed, I have seen two distinct, large clutches in a dumb-bell shaped cavity, clearly the work of two snails, and the more likely outcome of both laying in the same cavity. The scatter in fig. 3.30. probably represents two different types of clutch laid by individual snails. The minute possibility remains that the bimodality of the scatter is simply a remote and unfortunate statistical coincidence. There is a hint of a tendency for type - S clutches to occur earlier in the season than type - L clutches (combining clutches from July and August 1980, and January, February and March 1981 to obtain adequate expectations, gives $\chi^2_5 = 11.25$; χ^2_5 (0.05) = 11.07). However, from these rather scanty data, there is probably no real difference, since a large contribution to the χ^2 value is due to very late-season clutches, which are rather arbitrarily assigned to type - L since the separating line could be drawn more obliquely, (fig. 3.30.).

Pairs with mid-parent h+d $<$ 30 mm lay fewer type - L, clutches than expected on the null hypothesis of no difference between them and pairs with h+d $>$ 30 mm (χ^2_1 = 7.76, $p < 0.01$), suggesting that in general small snails tend to lay more type - S clutches than large snails.

Pairs which lay only a few clutches (0 - 5) also lay proportionately fewer type - L ones than pairs laying more clutches (6 - 15) (χ^2_1 = 10.38, $p < 0.005$).

It is possible that particular snails lay either type - S or type - L clutches only. However, the pair laying most clutches (15) and perhaps, therefore, involving large contributions from both individuals, only produced one type - S clutch. From the dates snails died it is not possible to say whether one particular snail could lay both types (i.e. laying both types after the death of its partner). In only one pair was an apparently non-random sequence of laying type - S and type - L clutches seen: three type - L, followed by one type - S, one type - L, and then eight type - S. This may suggest that one snail laid four type - L clutches and overlapped only slightly with its partner laying nine type - S.

Sizes of both type - L and type - S clutches have been shown to be correlated with the date they were laid. Clutch size (within each type) might also be related to mid-parent size and date of onset of laying (date of laying the first clutch of any type), as suggested for clutch number (section 3.3.2.2.), and to the number of clutches laid by a pair. This has been analysed separately for type - L and type - S clutches by multiple correlation. Once again the interpretation of the results of the analysis is hindered because of correlation between independent variables: mid-parent size, number of clutches and date of onset of laying are correlated (section 3.3.2.2.), and date of onset of laying is obviously positively correlated with date of laying a particular clutch ($r = 0.37$, $p < 0.001$).

Taking type - L clutches first, the analysis first extracted laying date, as explaining 48% of the variance of clutch size ($r = -0.70$, $p < 0.001$). Mid-parent size showed the only other significant correlation after removal of the covariation due to date of laying ($p < 0.01$). Mid-parent size, date of onset of laying, and number of clutches, together only reduced the unexplained variance by a further 6%

Date of laying was also negatively correlated with size of type - S clutches ($r = -0.71$, $p < 0.001$) and explained 51% of the variance. Mid-parent size, number of clutches, and date of onset of laying only reduced the remaining variance by a further 5%, although in this case date of onset of laying showed the only significant (negative) correlation ($p < 0.05$) after removal of the covariation due to laying date. This reversal of the importance of the independent variables, compared with type - L clutches, may be due to the correlation of onset of laying and mid-parent size, and does not necessarily imply a real difference between the clutch types.

Despite this difficulty, sizes of both type - L and type - S clutches can be seen to be strongly correlated with the date they were laid; date of onset of laying and mid-parent size together also affect clutch size, but they are of less importance. These three factors explain just over half the variance in size of both clutch types; the remaining variance cannot be partitioned further, but may be determined by other unknown factors (cf. clutch number - section 3.3.2.2.).

Among clutches of one type, there is no correlation of clutch size with the number laid by a pair; i.e. pairs do not lay (among, say, their type - S clutches) a few large type - S clutches or many small ones; the same is true within type - L clutches.

3.3.2.4. Egg weight.

Individual eggs were not weighed; therefore the following analysis is based on mean egg weight of each clutch. The mean dry weight per egg (with standard deviation) of the 96 clutches weighted was $8.24 \times 10^{-4} \pm 2.20 \times 10^{-4}$g; mean wet weight was $50.98 \times 10^{-4} \pm 15.35 \times 10^{-4}$g. Dry weight is thus approximately 16% of wet weight.

Treating type - L and type - S clutches separately, mean dry weight per egg for type - L clutches was $7.86 \times 10^{-4} \pm 1.59 \times 10^{-4}$g, and $9.21 \times 10^{-4} \pm 3.03 \times 10^{-4}$g for type - S clutches. Type - S clutches are considerably more variable than type - L clutches (variance ratio test, $F = 3.66$, $p < 0.01$), and their means are significantly different (d - test, $p < 0.05$).

The distributions of dry weight per egg for both clutch types are shown in fig. 3.31. That for type - S clutches appears flatter because of the number of clutches with very high egg weight.

The assumption of normal distributions of mean egg dry weights, and linear relationships with the other variables considered (as in the analysis of clutch size), allows multiple correlation to be used to investigate correlation with laying date, onset of laying (date of first clutch of either type), mid-parent size and clutch size. This was done for each clutch type separately.

Egg weight in type - S clutches was significantly positively correlated with laying date ($p < 0.01$, 27% of total variance explained) and with mid-parent size $p < 0.01$ a further 19% of the total variance explained). Correlations with clutch size and date of onset of laying were not significant, although part of their effects could have been expressed in the correlation coefficients of the two significantly correlated variables (see section 3.3.2.1.). There is no hint, then, within type - S clutches, of more than one strategy for partitioning reproductive output, either with emphasis on large clutches of small eggs, or small clutches of large eggs.

In type - L clutches, no variable showed a significant correlation with egg weight, but the number of pairs of snails is small, and the range of mean egg weight was less than that of type - S clutches.

3.3.2.5. Total egg production.

Mean production of eggs (plus hatchlings) per pair (25 potentially reproducing) was 383 ± 452 (standard deviation), maximum 1512. The distribution is shown in fig. 3.22., and although the data are few, it is clearly not normal, 12 out of the 25 pairs producing fewer than 100. Mean production of the remaining 13 pairs was 706 ± 414.

Seasonality of total production (fig. 3.33.) naturally follows that of laying of clutches (section 3.3.2.2., fig. 3.27.) but with the peak slightly earlier because of the effect of decreasing clutch size during the season (section 3.3.2.3.).

Multiple correlation with mid-parent size and date of onset of laying was carried out separately for pairs producing more than 100 and those producing less than 100 eggs plus hatchlings, because of the non-normality of the distribution of total production. Consequently, there were few pairs in each group and the variances were large. It was not surprising, therefore, that although 20% of the variance could be explained, this was not significant.

3.3.2.6. Summary of results.

(i) No morph differences were found, but because of the design of the experiment, they cannot be ruled out.

(ii) Egg-laying took place during a single definite season, similar to that in the wild, but perhaps a little longer.

(iii) The snails died without breeding for a second season, as in the wild.

(iv) Large snails tended to start laying early in the season, and, probably as a result of this rather than as a direct result of their size, may lay more clutches.

(v) Two kinds of clutch were laid; large ones (type - L) were not the result of both snails of a pair each laying a small clutch (type - S) in the same cavity.

(vi) There was no tendency for either type - L or type - S clutches to be laid earlier in the season.

(vii) Larger snails laid more type - L clutches.

(viii) Only among the type - L clutches was there any indication that larger snails laid larger clutches, and this was not conclusive.

(ix) Larger snails laid larger eggs, but only within type - S clutches.

(x) Among both clutch types, clutches laid later in the season were smaller. Late season type - L clutches could be smaller than early season type - S clutches.

(xi) Among type - S clutches only, eggs laid later were larger.

(xii) There was no correlation between number and sizes of clutches laid by a pair.

(xiii) There was no correlation between number and size of eggs within a clutch.

(xiv) Mean number of clutches laid by a pair was about 5, with a maximum of 15.

(xv) Mean number of eggs per clutch was 76, with a range from 3 to 269

(xvi) Mean egg dry weight was about 8×10^{-4}g, but eggs in type - S clutches were larger than those in type - L clutches.

(xvii) Mean total production per pair was 383, with a maximum of 1512.

3.3.3. Discussion of egg production.

Total production, the product of number and size of clutches, is the most important of the variables investigated, from the point of view of the snails' reproductive potential. This study may well have underestimated it. Death of one member of a pair would prevent its partner producing once it had run out of stored sperm. It is not known how often the snails mate; they may mate prior to laying each clutch, using fresh sperm in preference to stored sperm which may be less viable and only used as a back-up. There may have been some morphological or behavioural incompatibility between some partners which did not reproduce. In the wild, these factors need not prevent a normal, healthy snail from continuing to breed if it finds another partner.

The non-normal distribution of total production per pair (a large number producing less than 100 eggs) may be produced by the effects just mentioned, if there was only partial incompatibility, or if one snail died very early on as was the case in some pairs. Some production may then have occurred without mating, the eggs being infertile (as were those produced by animals set up singly - section 3.3.2.1.). It could also be related to the unnatural environment in which the snails were kept, but if this were the case, it is surprising that some pairs were so productive. It has been suggested (Crow and Morton, 1955) that infertile pairs should be discounted when constructing distributions of total production. In the present experiment, mean egg production (706) of pairs producing more than 100 eggs may be more meaningful than that of all potentially producing pairs (383).

The correlation within type - S clutches of egg dry weight and date of laying may also be due to an abnormality. Sometimes, particularly late in the season, very large rather misshapen eggs were laid in small groups lacking the form and cohesiveness of normal clutches of normal sized eggs. Since they were small, these clutches belonged to type - S rather than type - L, explaining the lack of a similar correlation within the latter. Although 100% hatchability has been assumed (section 3.3.2.1.), it is likely that these eggs would have failed to hatch since similar eggs, occasionally seen in other work on <u>T. pisana</u>, usually disintegrated. They are clearly abnormal, but although constituting only a small proportion of total production (distribution of egg weight has been given in fig. 3.31.), gave rise to the significant correlation. They may only be one extreme of a continuum, but obviously abnormal eggs would be better left out of the analysis of any future study.

The explanation of the two clutch types is obscure. That they are not the result of only one or of both individuals laying in the same cavity has been argued above (section 3.3.2.3.). Type - S clutches constituted 33% of the total number of clutches laid. If they are also due to some kind of abnormality on the part of the snails, it is surprising that they were so prevalent, and also that relationships with other variables similar to those of type - L clutches, were seen. They are not the result of self-fertilisation; eggs laid by single individuals failed to hatch, yet some type - S clutches overlooked in the soil, did hatch, and results of breeding experiments (chapter 6, section 6.2., and Cain, in preparation) were always interpretable in terms of cross-fertilisation rather than self-fertilisation. If type - S clutches were due to an inadequacy of the regime under which the snails were kept, the dichotomous, rather than continuous, variation in clutch size is surprising, unless a threshold mechanism of some sort was operating, perhaps on the physiological or hormonal control of release of batches of eggs. If, as discussed briefly above (section 3.3.2.3.), each snail only lays either type - L or type - S clutches, and this has not been shown, it may be under genetic control. However, the selective advantage of only laying type - S clutches, although these may contain slightly larger eggs (section 3.3.2.5.), is unclear unless many more are laid, which was not the case. The greater variance of egg size in type - S clutches may suggest that something was wrong with at least some of these.

Prior to this study, nothing was known of the number of clutches laid by T. pisana, except that it may lay up to three (Taylor, 1912; Lazaridou-Dimitriadou and Daguzan, 1981). It is clear that some individuals at least, can lay many more than this. Nor was anything known of egg weight. Eggs have been reported as between 1.5 and 3.3 mm in diamter (Taylor, 1912; Basinger, 1927; Dürr, 1946; Pitchford, 1954; Sacchi, 1971; Peake, 1978); most eggs in this study were about 2 mm.

Some scanty knowledge was, however, available for clutch size, some based on casual observation only. This is summarised in table 3.5. As Basinger (1927) suggested it might, clutch size has been shown in this study to vary with both snail size and time of year. Climate, and therefore locality, may well have a further influence. Together, these factors explain the wide range of previous observations. Date of laying was by far the most important factor controlling clutch size in the present study, later clutches being smaller. A similar decrease was found in field studies of Cepaea nemoralis by Wolda (1963) and Wolda and Kreulen (1973). Wolda (1963) tentatively ascribed this to some physiological change in the gonads but Wolda and Kreulen (1973) rejected this because only a slight decrease had been found in a previous laboratory experiment (Wolda, 1965b). They suggested changing quality of food, either in straightforward nutritional value, or in its effect on the hormonal regulation of production, as the likely explanation of the seasonal decrease in clutch size. This cannot explain the results of this study on T. pisana, since food quantity and quality were constant throughout the experiment. Since T. pisana only breeds for a single season, dying at its close, the decrease in clutch size during the season may simply be a reflection of a gradual decrease in general health due to age and/or effort already put into reproduction. It could also be due to gradual reduction in metabolic rate associated with falling temperature from summer to winter, although the change in the laboratory was not very large (section 3.3.1.). The phenomenon is well-known in fresh-water snails (Duncan, 1959), and in other groups of animals, particularly birds (see Wolda, 1963, p.447; Klomp, 1970).

There seems to be a considerable reproductive advantage in being large,despite the lack of correlation of total production and adult size, which was probably due to the paucity of data and to the large variance of the former. Larger snails started to lay earlier in the season and may therefore lay more clutches. They tended to lay more type - L clutches than small snails, and they laid larger eggs (within the type - S clutch group at least). This agrees with the more extensive information available for Cepaea nemoralis (Wolda, 1963, 1967; Wolda and Kreulen, 1973; Oosterhoff, 1977), although in this species larger snails also laid larger clutches.

At no stage, except as a possible explanation of the two clutch types, has genetic control of the variation in production been discussed. Heller and Volokita (1981a) stated without details that in a preliminary experiment on Xeropicta vestalis, an Israeli land snail with a similar shell pattern polymorphism to *T. pisana*, darker (i.e. banded) snails produced more eggs than paler snails. However, this was suggested to be due to their greater ability to absorb solar radiation, rather than a direct effect of the banded allele(s).

In *C. nemoralis*, Wolda (1963) found differences between morphs, but ascribed them largely to environmental effects (Wolda, 1965b, 1967). Heritability of variation in number and size of clutches (independent of shell morph) was considered to be very low. This seems reasonable since natural selection would rapidly eliminate genes for low production (cf. Falconer, 1960; Lewontin, 1965). It is possible that individuals could adopt more than one strategy to fulfil their reproductive potential; that is, to lay either small clutches with large eggs or vice-versa, or to lay many small clutches or a few large ones. Such variation might well be under genetic control, but there is no evidence at present for more than a single very variable strategy.

This study, then, has fulfilled its primary aim of giving an indication of reproductive potential (total production). It has also indicated much, sometimes enigmatic, detail of the partitioning of this productivity, detail which will require further study to be understood adequately.

3.4. General discussion of life-history strategy.

In order to discuss the overall strategy of *T. pisana* in the context of its environment, a comparative approach is necessary. Horn (1978), Stearns (1980) and Begon and Mortimer

(1981) have discussed the difficulties of such an approach, and point out that, when investigating the agreement of the facts with the predictions of theories of life-history strategies, it is probably only legitimate to compare similar species. Thus, *T. pisana* can only be discussed in relation to other snails, and indeed only in relation to similar snails.

Peake (1978) has reviewed the knowledge of life-history strategies within the terrestrial Mollusca. He suggested that within the Helicidae, the only moderately well-known group, the general pattern of strategies, as far as it goes, is in accord with the predictions of *r*/*K* theory: smaller species tend to be annual or biennial, and semelparous, and to produce small young (little is known of the number of young produced); whilst larger species show the opposite trends. According to the theory, smaller (*r* - selected) species would be associated with patchy and unstable environments, but insufficient is known of the snails' habitats for this to be tested.

The present study has shown that *T. pisana* is a semelparous annual or biennial, and that a healthy individual can probably produce, on average, about 350 eggs in its single breeding season. This contrasts strikingly with *Cepaea nemoralis*, the only other species for which there is adequate information to allow a valid comparison. *C. nemoralis*, with considerable variation from place to place, probably takes 2 or 3 years to mature, and breeds for a further 2 or 3 years, producing on average only one clutch of about 60 eggs per season (Wolda, 1963, 1965b, 1967; Cain and Currey, 1968; Wolda and Kreulen, 1973; Oosterhoff, 1977; Williamson, Cameron and Carter, 1977, Williamson, 1979). It is iteroparous and lays relatively fewer, but larger, eggs than *T. pisana*. *C. nemoralis* is not a great deal larger than *T. pisana* but has adopted a considerably different strategy.

By comparison with the rather varied habitats of *C. nemoralis* (woodland rides, hedges, grassland, dunes), those of *T. pisana* (early successional habitats, particularly the more open parts of duneland and waste ground near the sea) are usually much more ephemeral and perhaps more patchy with respect to the snails' trivial and migratory ranges (see Southwood, 1977) although less variable climatically because of their proximity to the sea.

The 'habitat templet' theory of ecological strategies (Southwood, 1977) suggests that more ephemeral (i.e. *r* - type) habitats will select for shorter generation time and higher fecundity; i.e. the ability to reproduce more quickly and exploit the habitat while it lasts. The different strategies of *C. nemoralis* and *T. pisana* agree with these theoretical predictions only if vegetation type is more important than climate.

The variation of the life-cycle (annual or biennial) within *T. pisana* appears to be analogous, at first sight, to that in the cricket *Nemobius sylvestris* (Bosc.), documented by Brown (1978). Bienniality in *N. sylvestris* was interpreted by Southwood (1977) as the 'evolved modification of the organism's time scale to increase the resources available to a single generation', since, in different populations, annuality or bienniality was determined genetically. This is not the case in *T. pisana* since animals from all stocks are annual in the laboratory. Rather, determination of the cycle is flexible; bienniality is forced upon the snails by a growing season too short to allow them to reach maturity in a single year. It would be interesting to see whether such biennials produce fewer or smaller eggs than annuals, perhaps because of the cost of maintenance for a second year; and if, in regions where the growing season is of intermediate length, some individuals reproduce at a small size, others waiting until the following season to grow larger and thus produce more or larger eggs. In contrast to _Nemobius_, _T. pisana_ must have evolved a flexibility of response to fine-scale climatic variation, so that the balance of such factors is optimized in a particular locality.

Such questions as these indicate the potential of _T. pisana_ as research material , and the need for further careful study of its life-history tactics. It has not been possible to set it in the context of the theoretical framework with any great precision. This emphasizes the view expressed in the introduction of this chapter (section 3.1.), that the present most vital requirement of theoretical studies of life-history strategies is a firm base of detailed knowledge of real organisms. Until we have this base, further advancement of the theory, _per se_, will tell us little about pattern in the real world.

Fig. 3.1. aerial view and map of Tenby indicating the positions of the sampling sites.

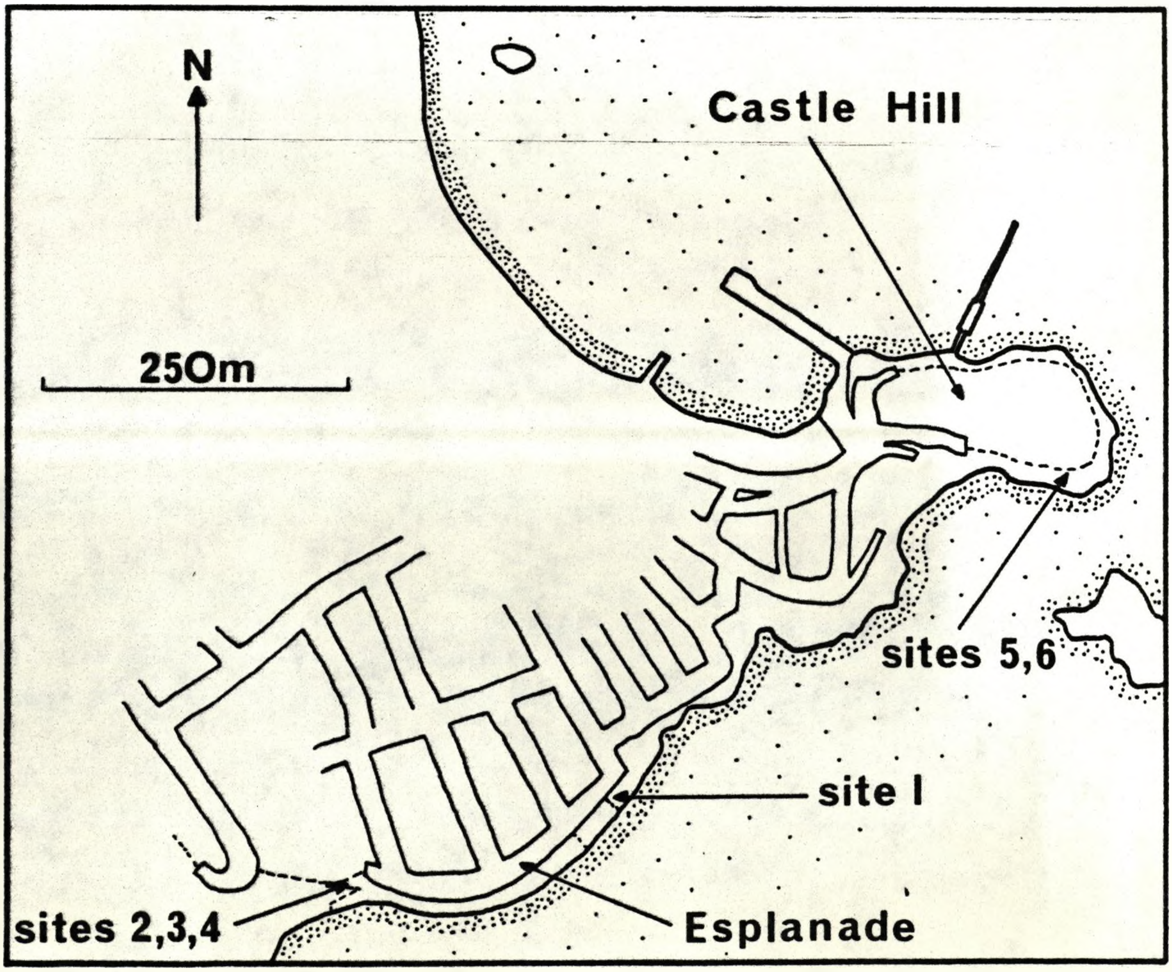


Fig. 3.2. Photograph and sketch map of the area around site 1.

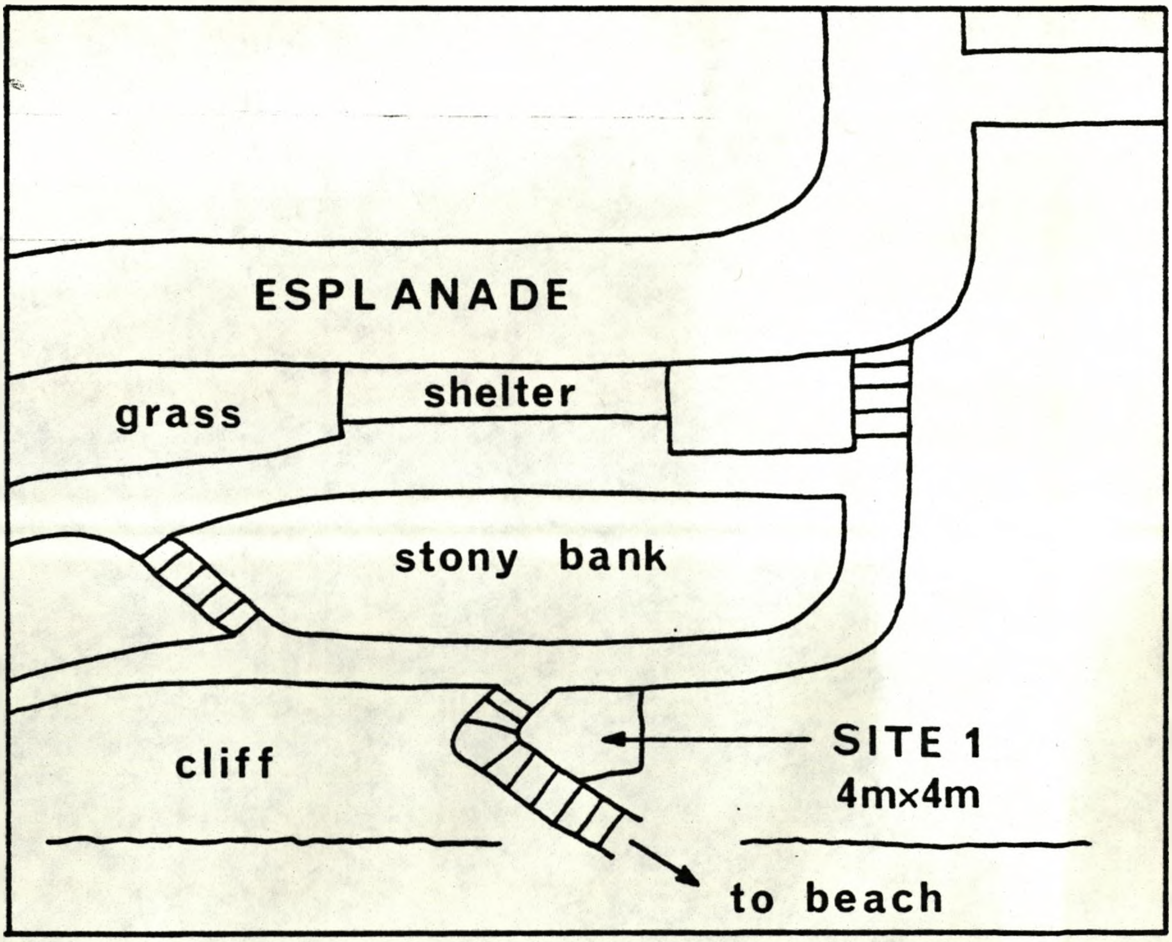


Fig. 3.3. Photograph and sketch map of the area including sites 2, 3 and 4.

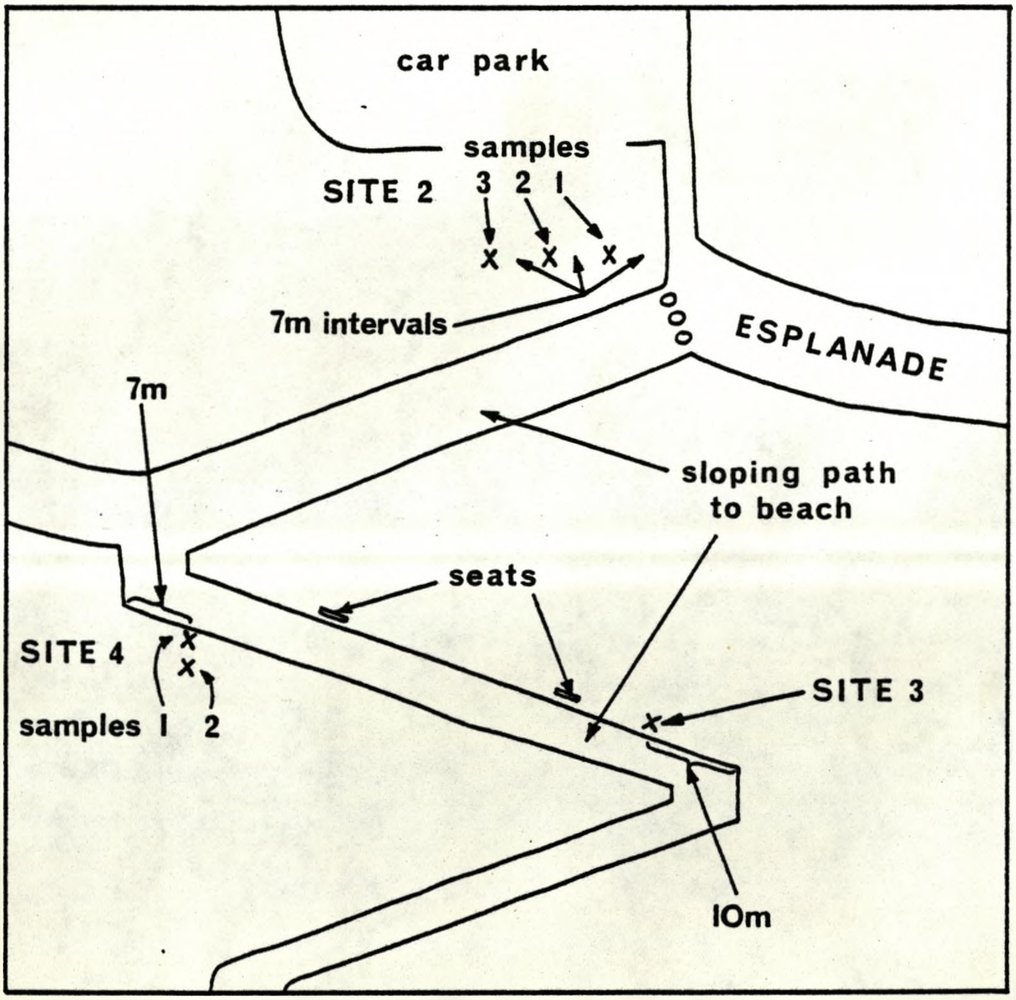
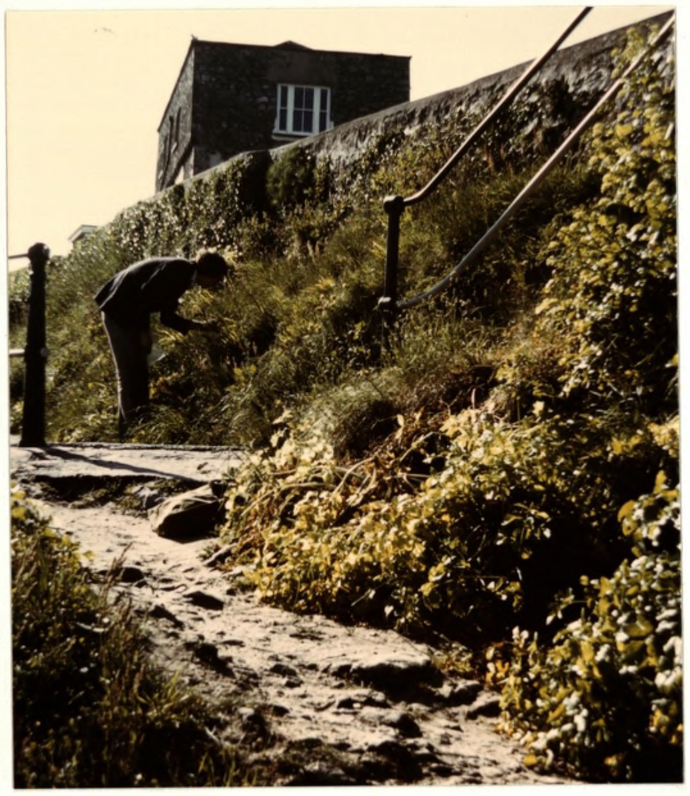


Fig. 3.4. Photograph and sketch map of the area around sites 5 and 6.



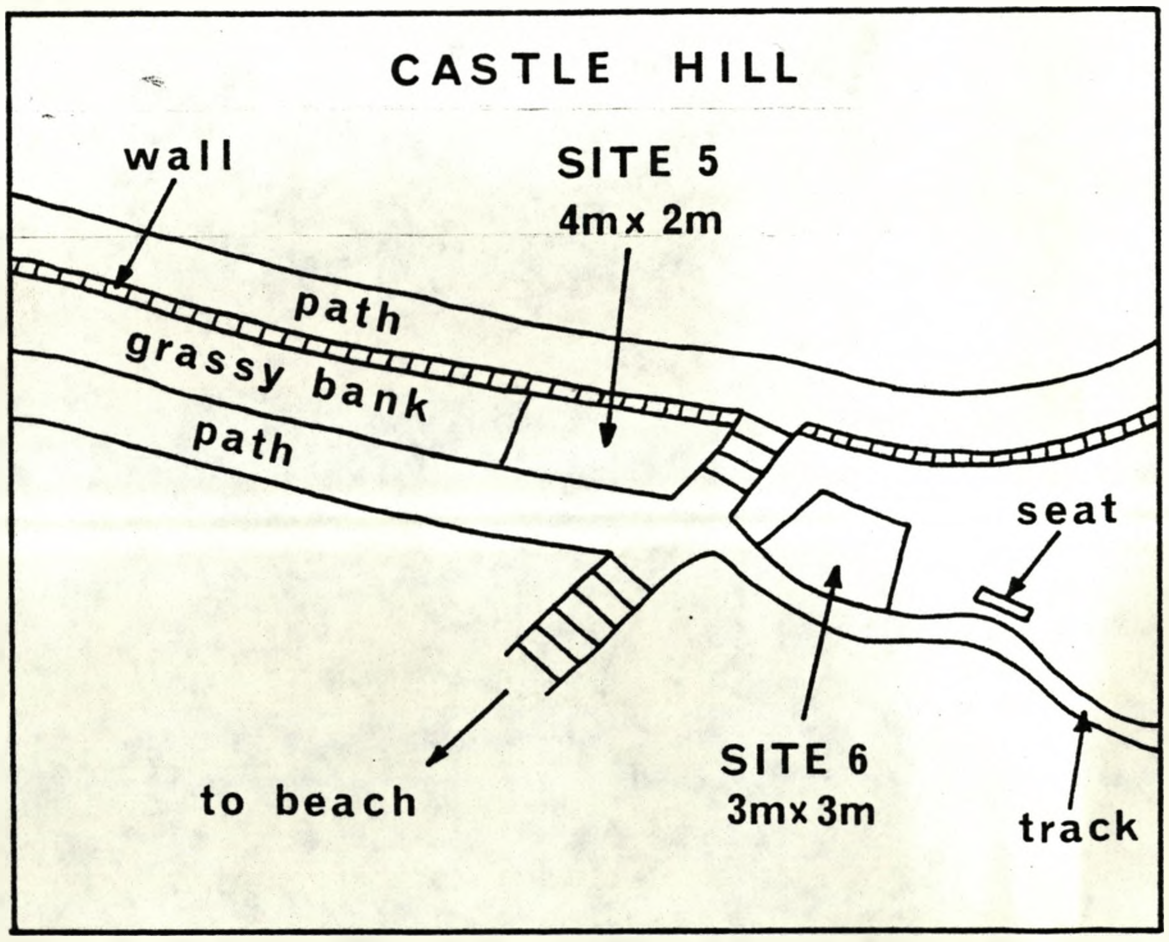
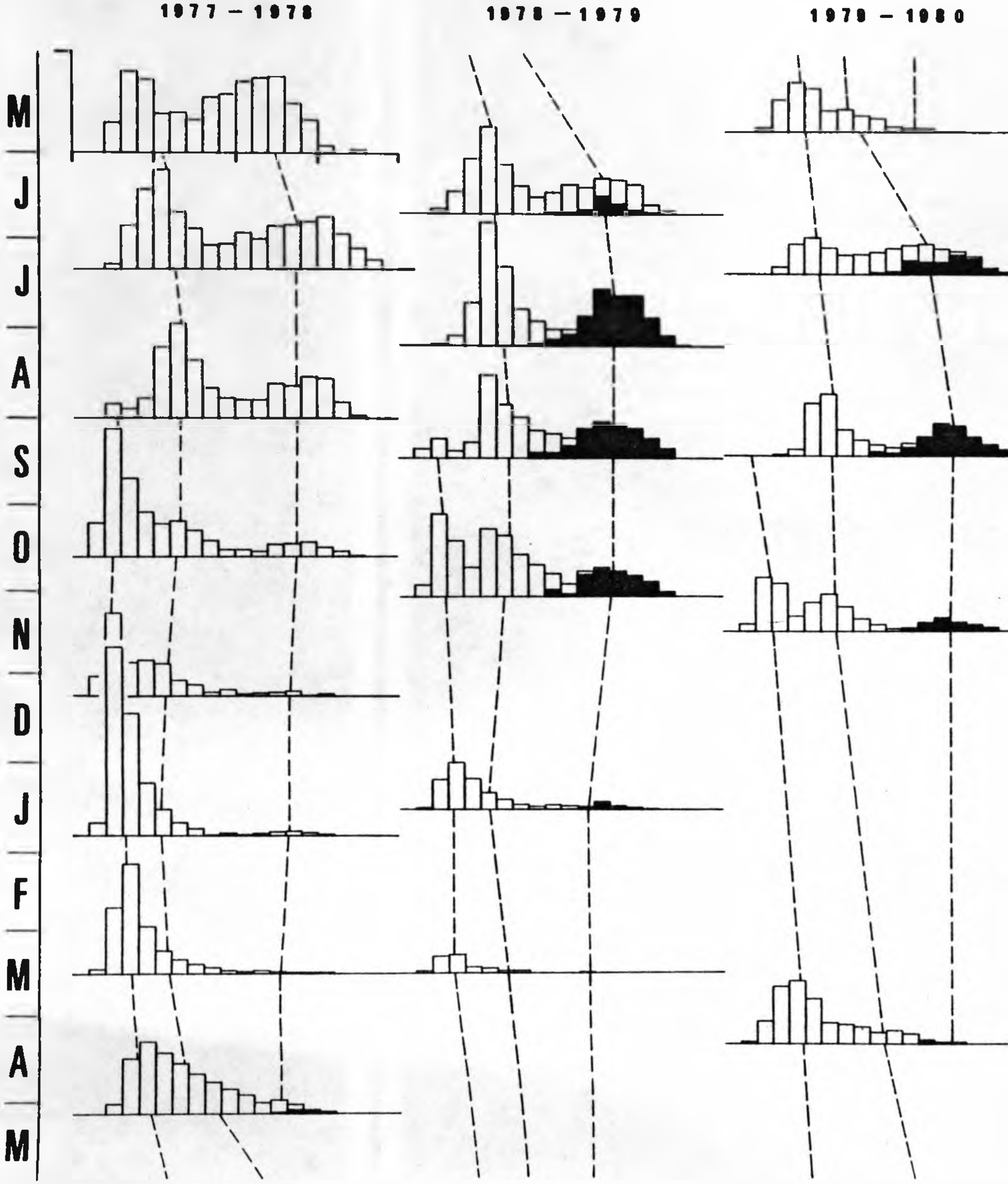
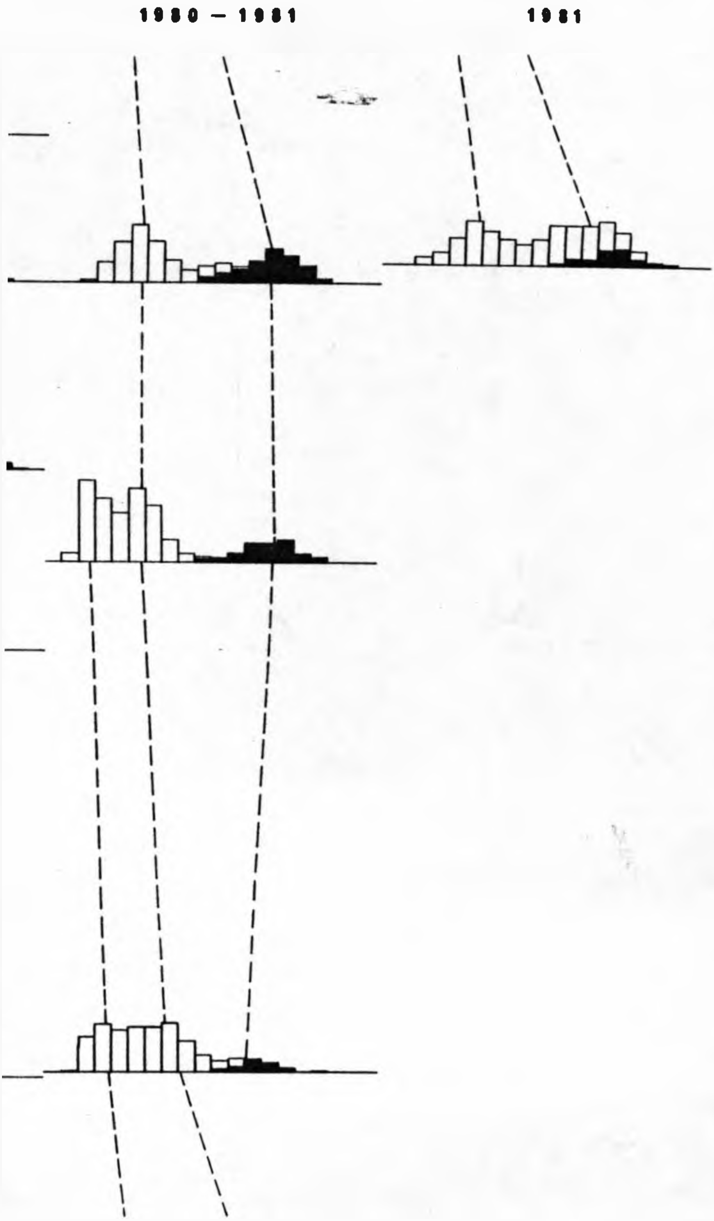
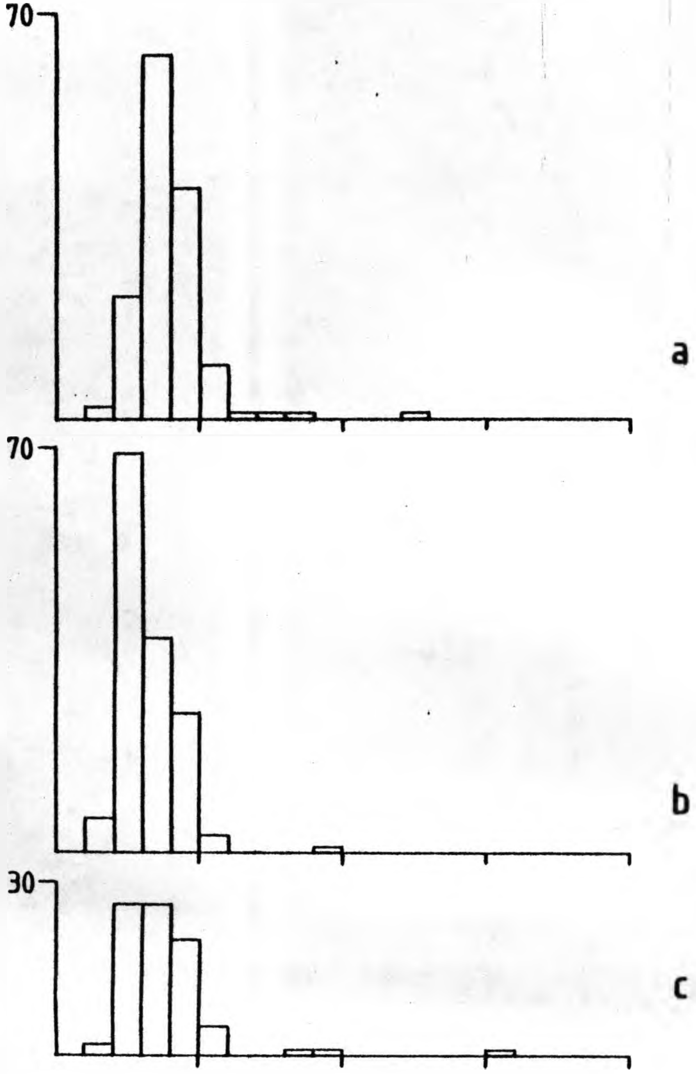


Fig. 3.5. Size-frequency distributions of all samples combined for each sampling occasion, over the complete course of the study at Tenby. From May 1978, reproductive maturity was scored, and the proportions of mature animals in each sample are shown by the solid areas. The dotted lines join up the mean sizes of each size class. The scale is given in the first histogram; the division on the vertical axis represents 300 snails; the horizontal axis is divided into intervals of 10 mm (h+d).


1977 – 1978
1978 – 1979
1979 – 1980
M
J
J
A
S
O
N
D
J
F
M
A
M


1980 – 1981
1981


70
a
70
b
30
c

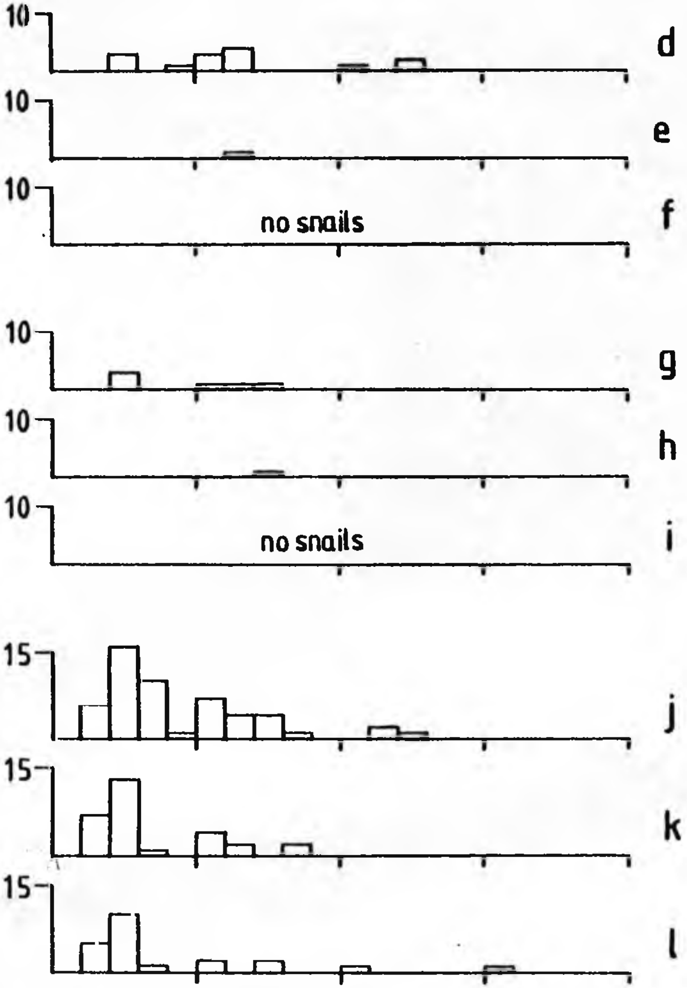

10
d
10
e
10
no snails
f
10
g
10
h
10
no snails
i
15
j
15
k
15
l

Fig. 3.7. A group of 'hibernating' snails. Only half-grown snails are present. Some have been removed to show the rings of hard, dry, white mucus.

Fig. 3.8. Graph of the changes in the value of the relative growth parameter, g, during the life of each cohort within the study period at Tenby. The cohorts are represented in the following way:

- - - - - - - - - -	cohort hatched in 1975
————————	cohort hatched in 1976
....	cohort hatched in 1977
—.—.—.—.—	cohort hatched in 1978
————————	cohort hatched in 1979
— — — — — — — — —	cohort hatched in 1980

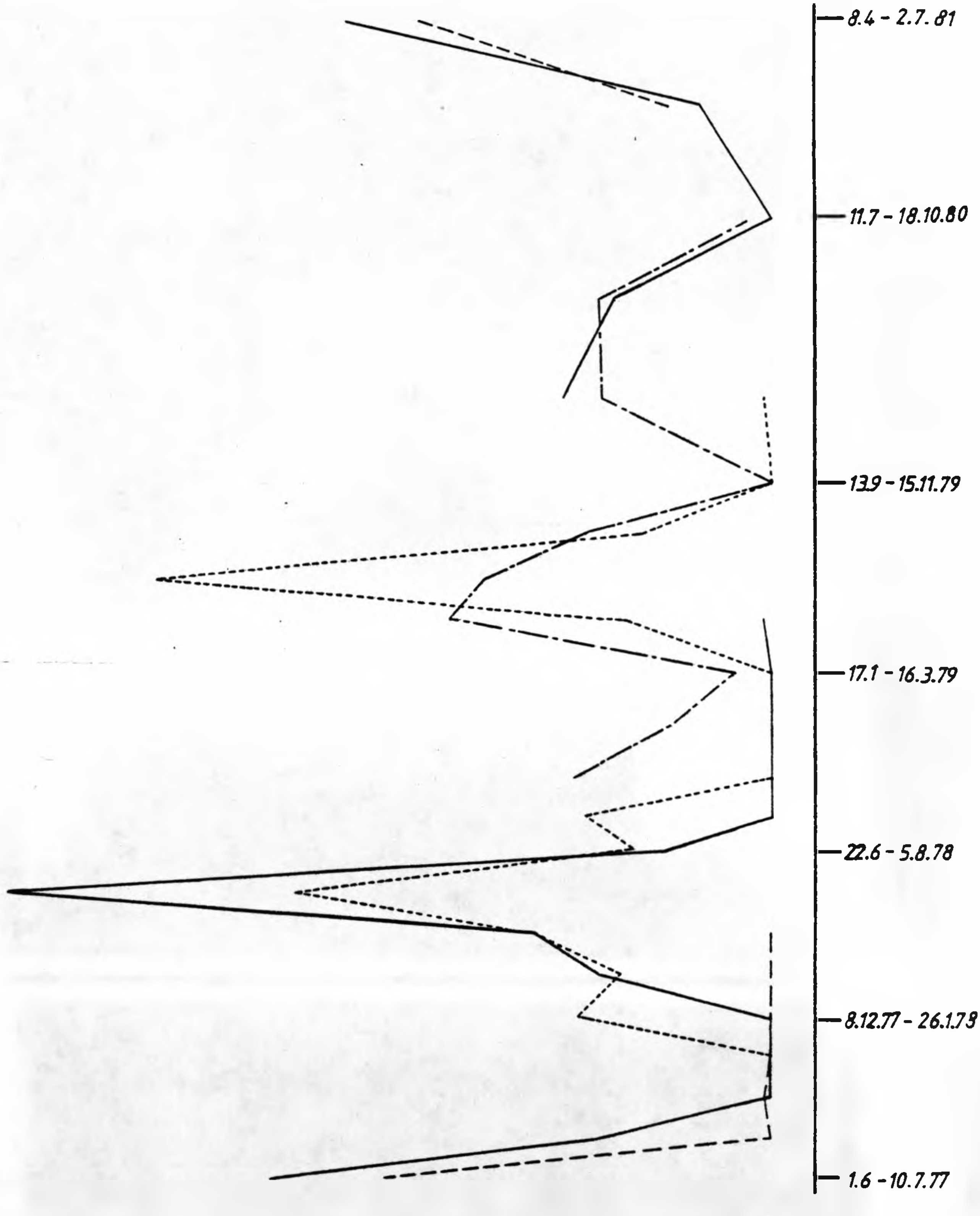

8.4 - 2.7.81
11.7 - 18.10.80
13.9 - 15.11.79
17.1 - 16.3.79
22.6 - 5.8.78
8.12.77 - 26.1.78
1.6 - 10.7.77
1·03
1·02
1·01
1·00
g

Fig. 3.9. Size-frequency distributions of the ten samples taken from Tenby on 18 X 80 , to show the between-sample heterogeneity in proportions of each size-class represented.

a - site 1, sample 1
b - site 1, sample 2
c - site 2, sample 1
d - site 2, sample 2
e - site 2, sample 3
f - site 3
g - site 4, sample 1
h - site 4, sample 2
i - site 5
j - site 6

The numbers of snails are indicated on the vertical axis; the horizontal axis is divided into 10 mm intervals of h+d. Reproductive maturity was scored in all samples and is indicated by the solid areas.

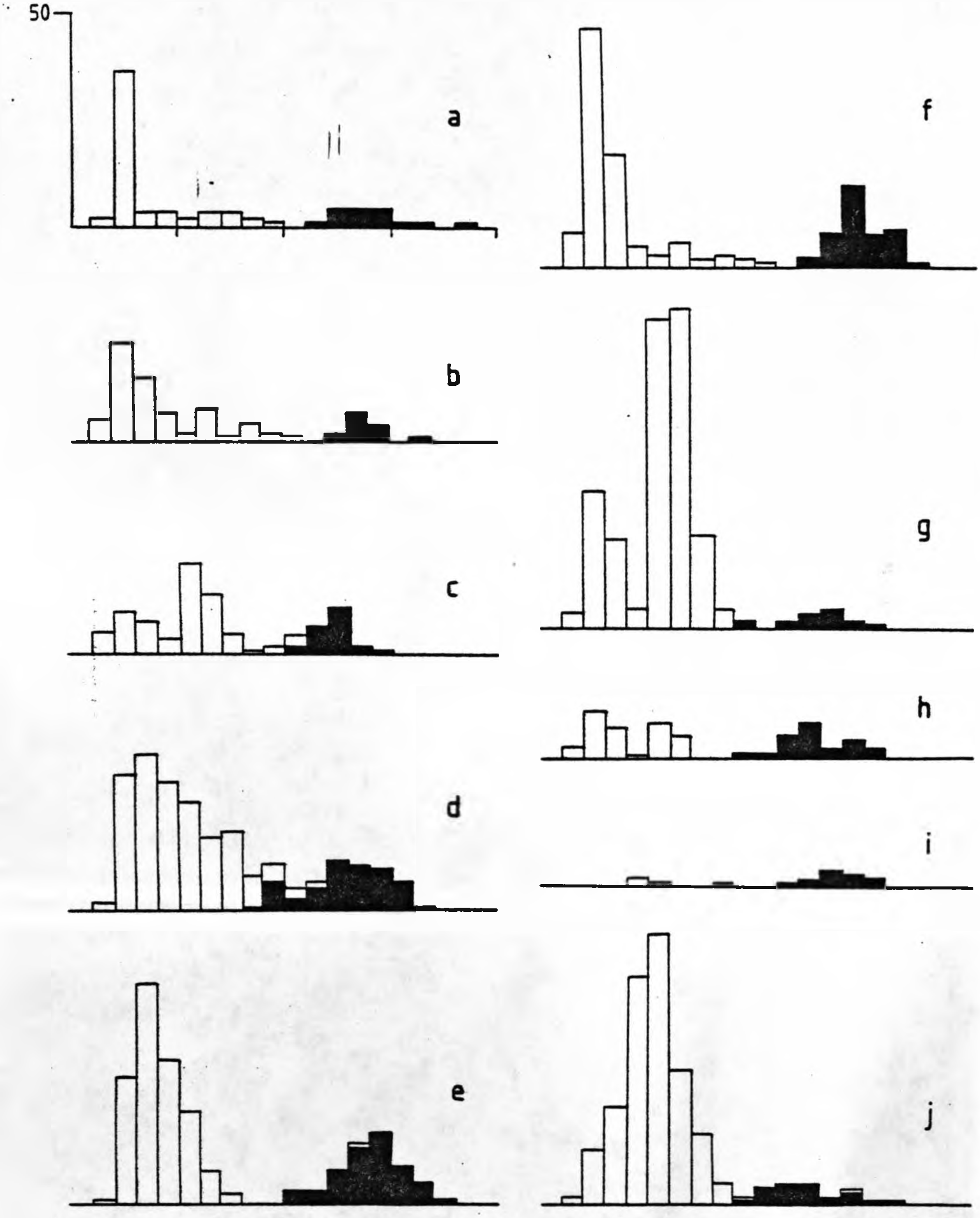
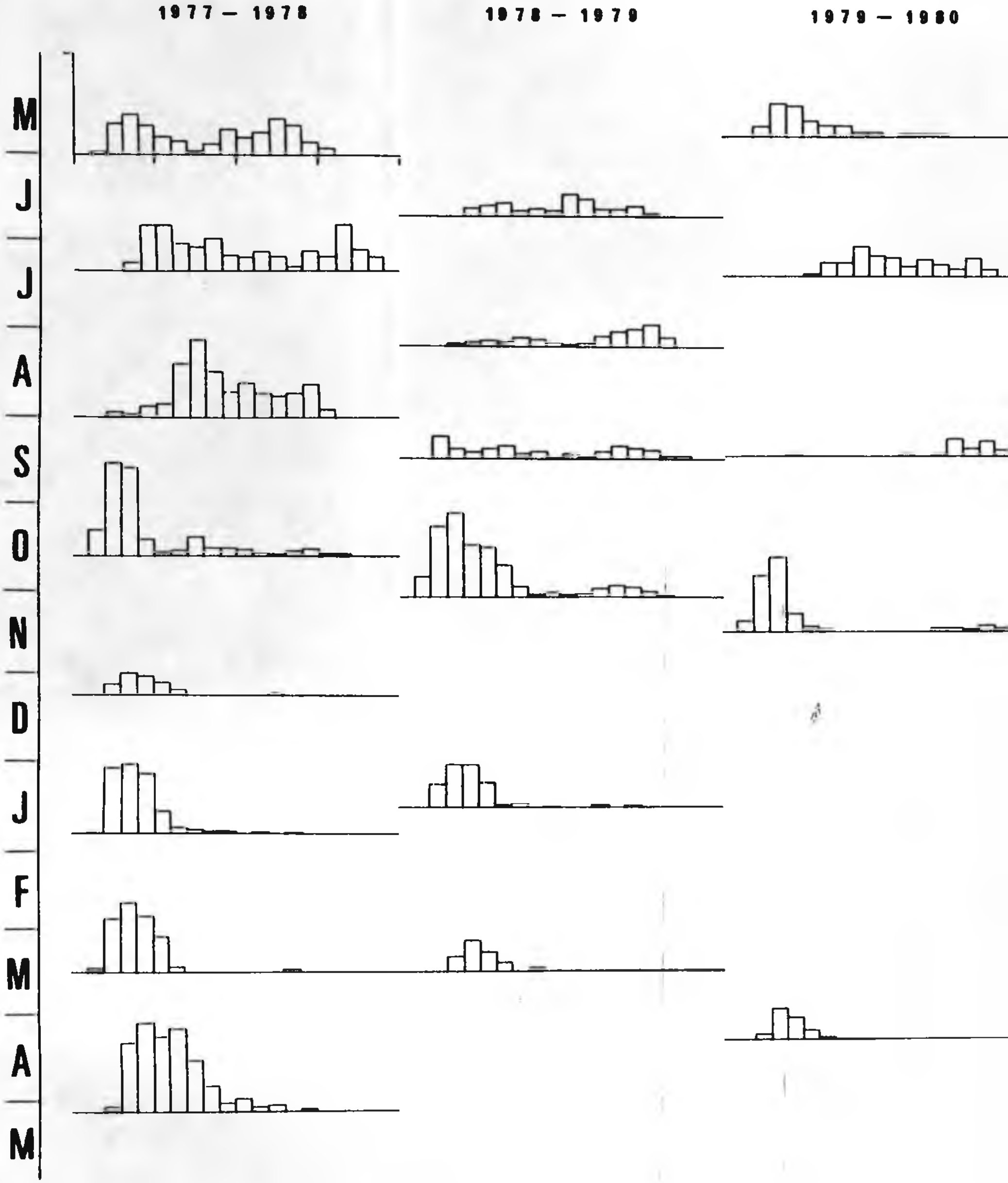

50
a
b
c
d
e
f
g
h
i
j

Fig. 3.10. Size-frequency distributions of samples taken from site 2 (sample 1) during the course of the study. (Reproductive maturity is not indicated). The scale is given in the first histogram, that of June 1977: the single division on the vertical axis represents 60 snails; the horizontal axis is divided into intervals of 10 mm (h+d).


1977 – 1978
1978 – 1979
1979 – 1980
M
J
J
A
S
O
N
D
J
F
M
A
M

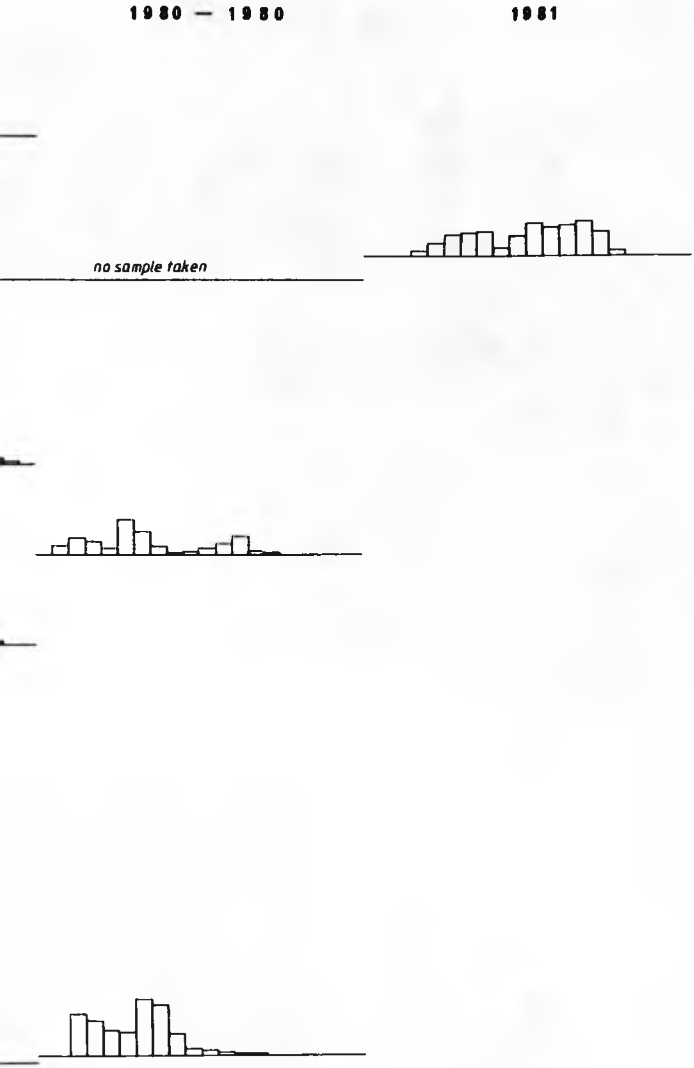
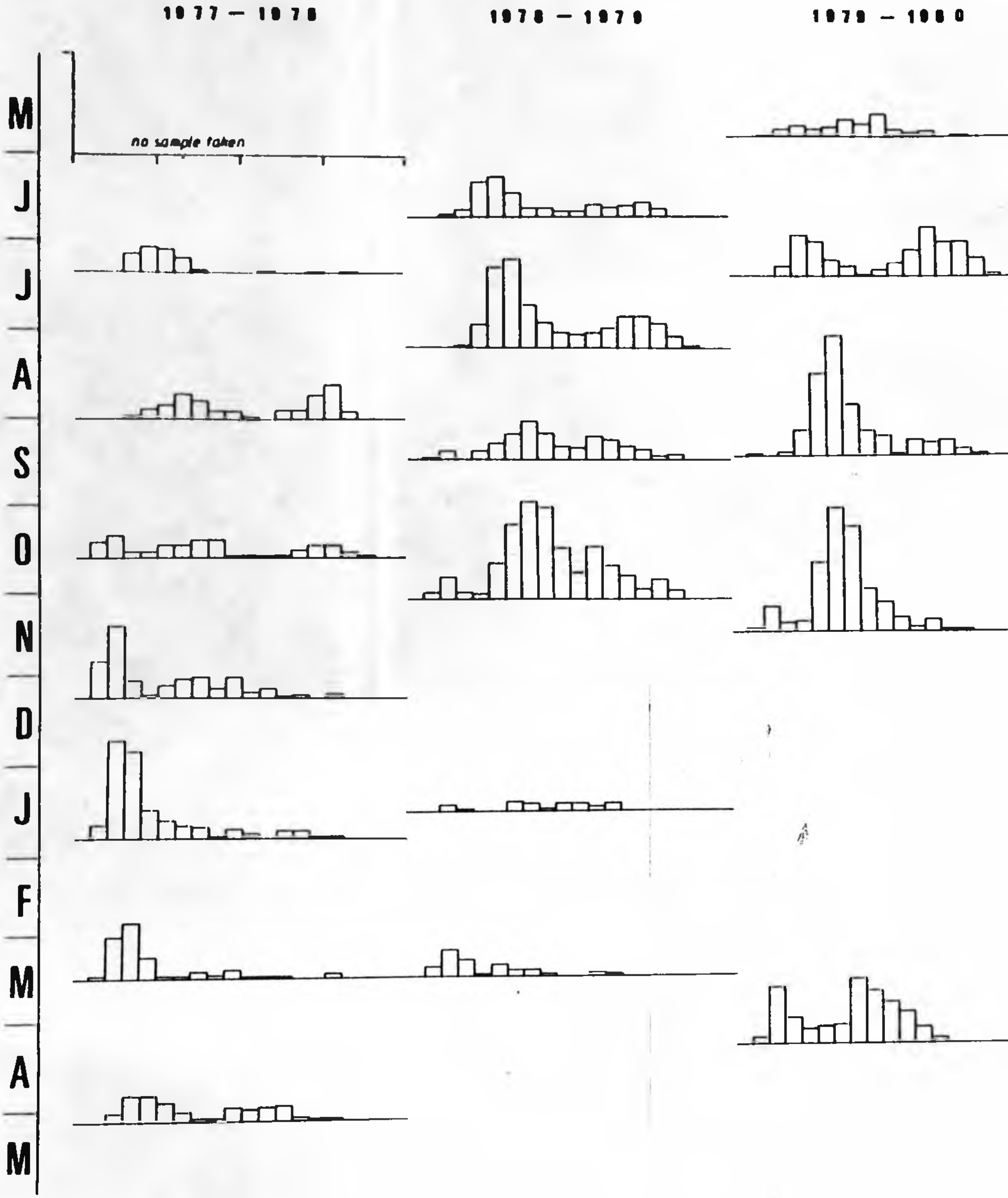

1980 — 1980
1981
no sample taken

Fig. 3.11. Size-frequency distributions of samples taken from site 6 during the course of the study. (Reproductive maturity is not indicated). The scales are as in fig. 3.10.


1977 – 1978
1978 – 1979
1979 – 1980
M
J
J
A
S
O
N
D
J
F
M
A
M
no sample taken

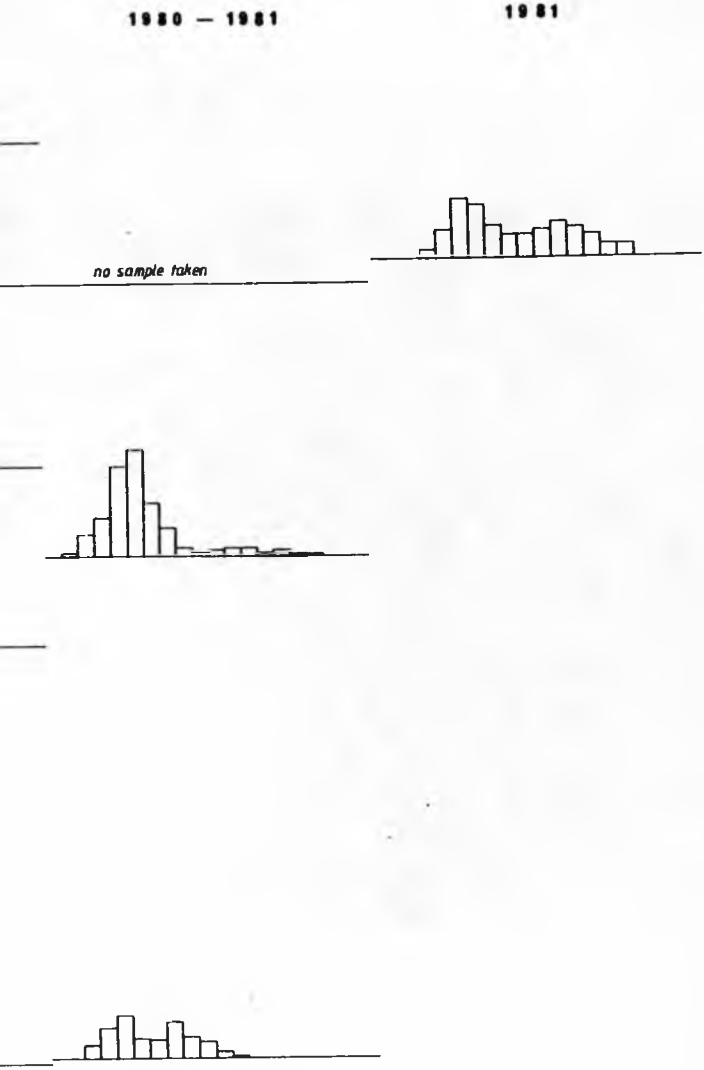

1980 — 1981
1981
no sample taken

Fig. 3.12. Size-frequency distributions of the ten samples taken from Tenby on 31 VIII 77. Reproductive maturity not scored. Scales and order of the histograms are as in fig. 3.9.

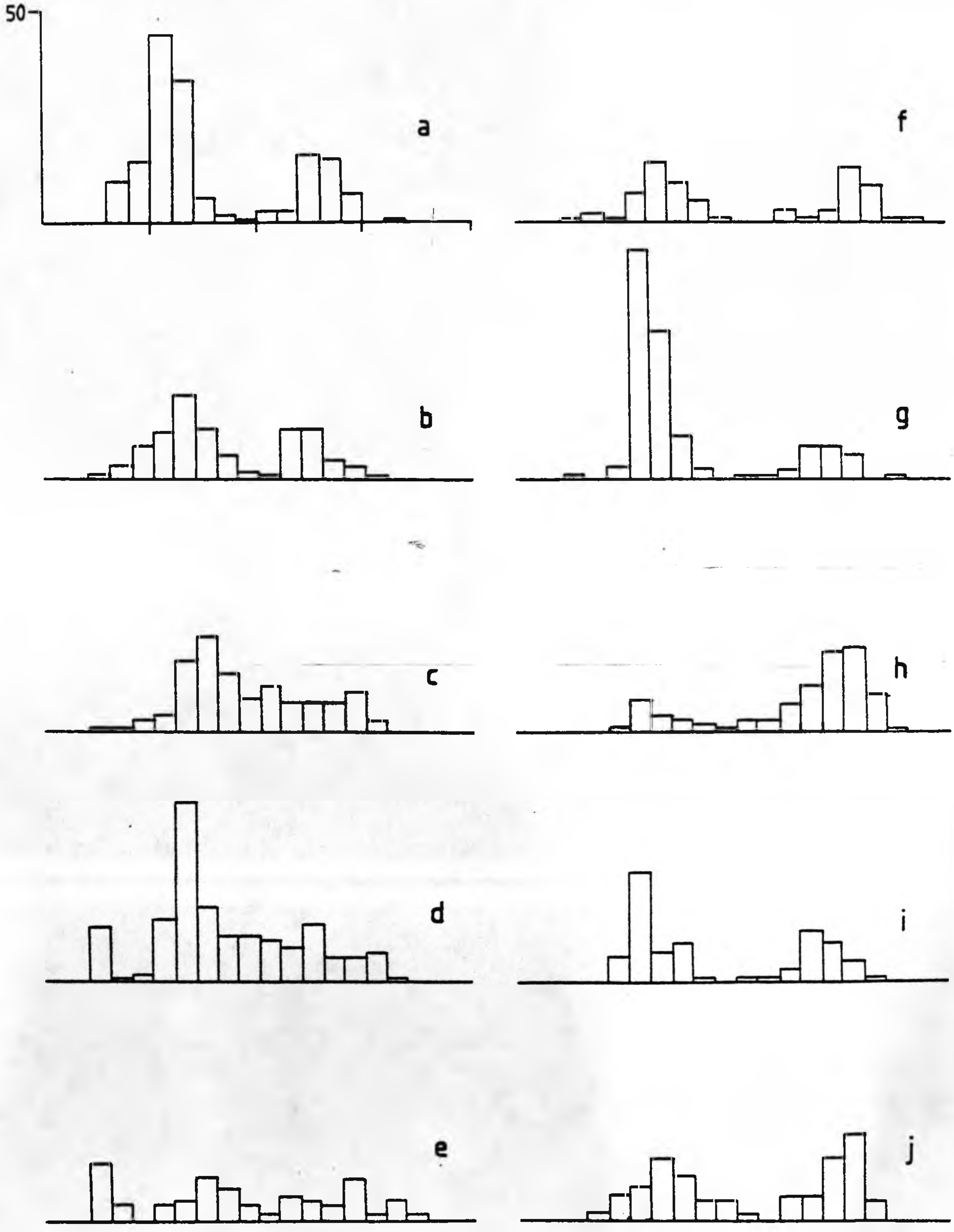


Fig. 3.13. Size-frequency distributions of the ten samples taken from Tenby on 5 VIII 78. Reproductive maturity scored only in site 1, sample 1, site 2, sample 3. Scales and order of the histograms are as in fig. 3.9.

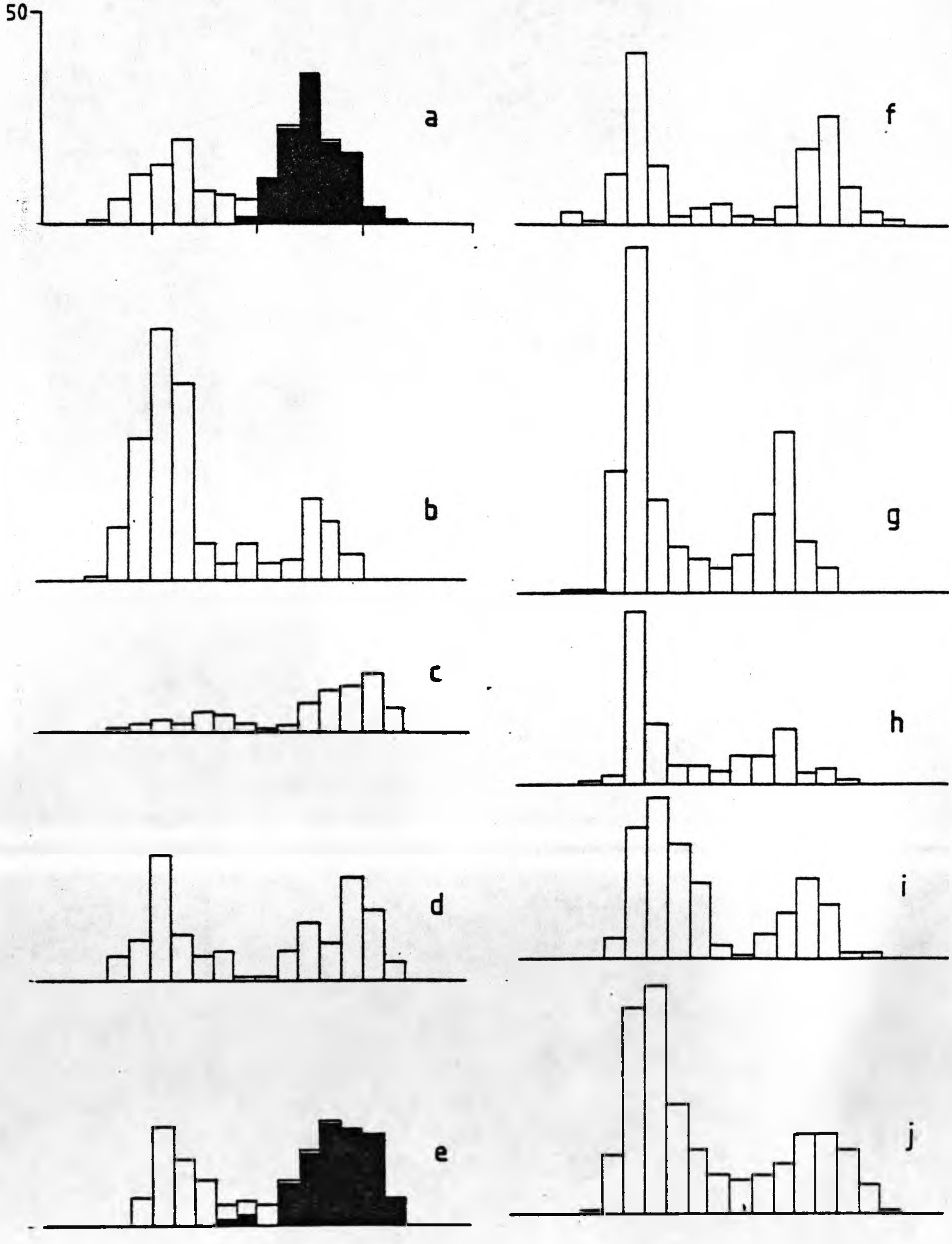


Fig. 3.14. Size-frequency distributions of the ten samples taken from Tenby on 14 IX 78. Reproductive maturity scored only in site 1, sample 1, site 2, sample 3. Scales and order of the histograms are as in fig. 3.9.

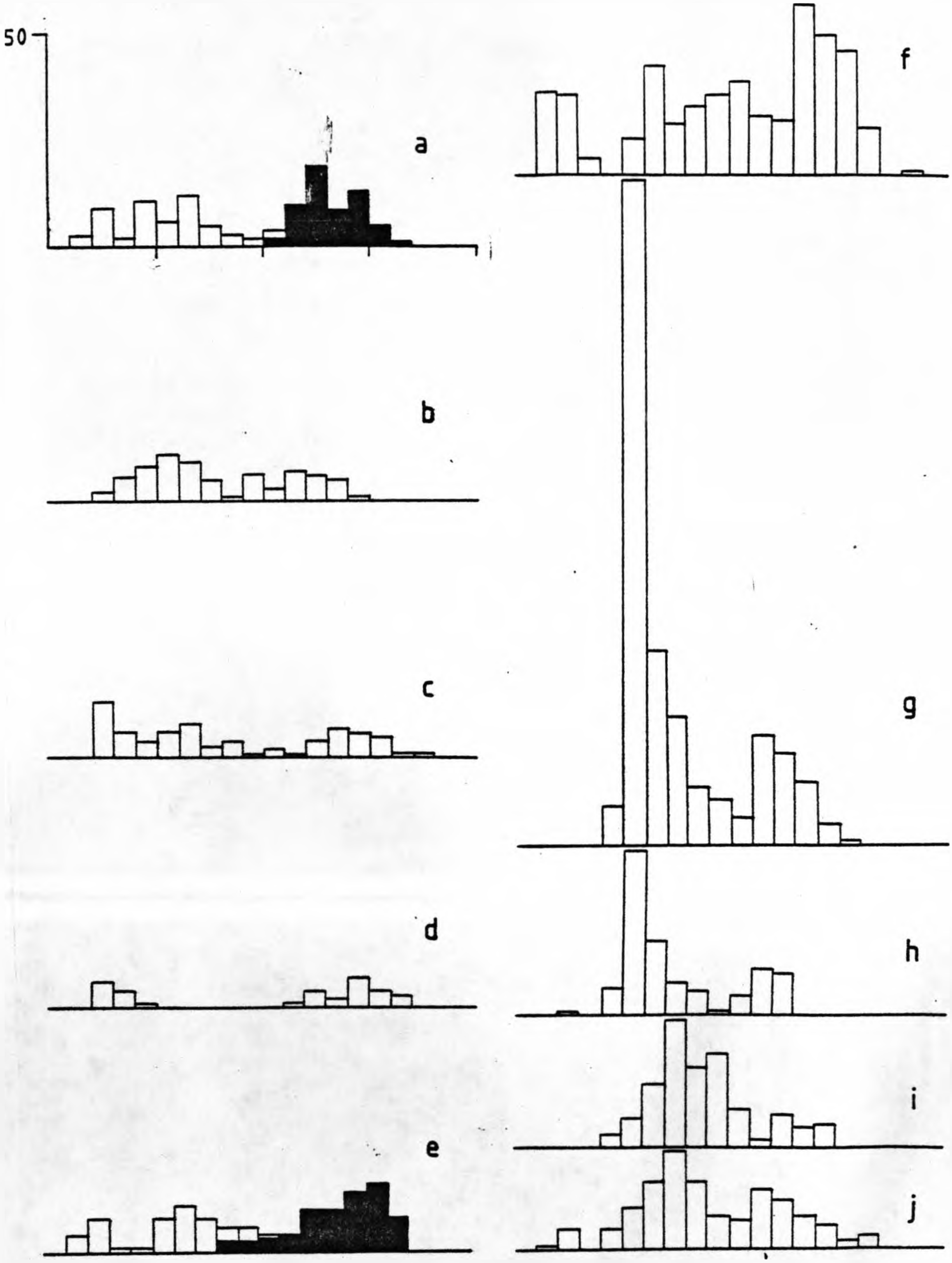


Fig. 3.15. Size-frequency distributions of the ten samples taken from Tenby on 13 IX 79. Reproductive maturity scored only in site 1, sample 1, site 2, sample 3. Scales and order of the histograms are as in fig. 3.9.

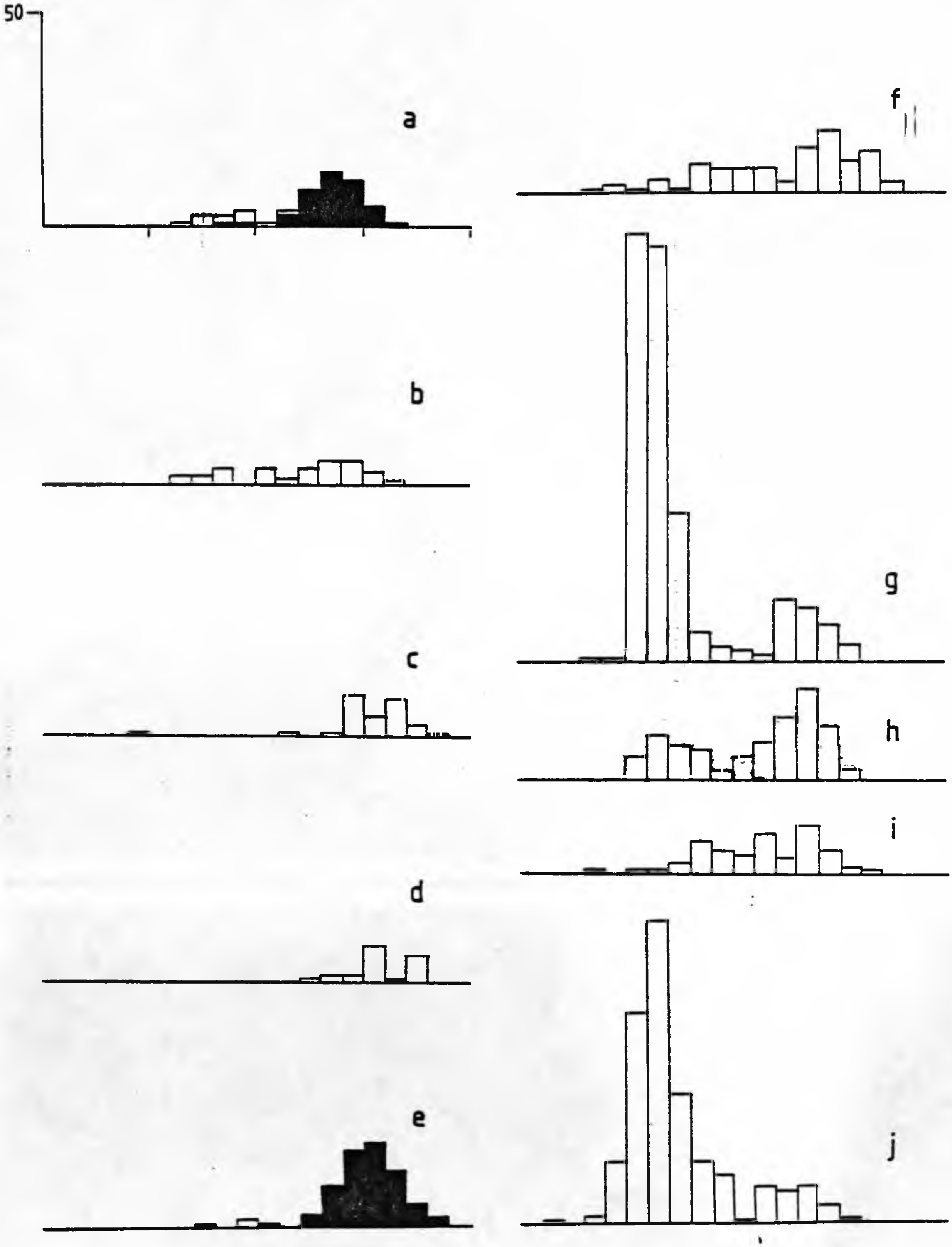


Fig. 3.16. Size-frequency distributions of samples from

a - Caldey Island 1 (maturity scored) 2 VIII 79
b - Caldey Island 2 (maturity scored) 2 VIII 79
c - Kenfig, Porthcawl (maturity not scored
    13 IX 79
d - St. Ives (maturity scored) 31 VII 79

The scales in this and all following histograms in this chapter are as in fig. 3.6.
The dates in this and all following figure legends in this chapter are the dates the samples were collected.

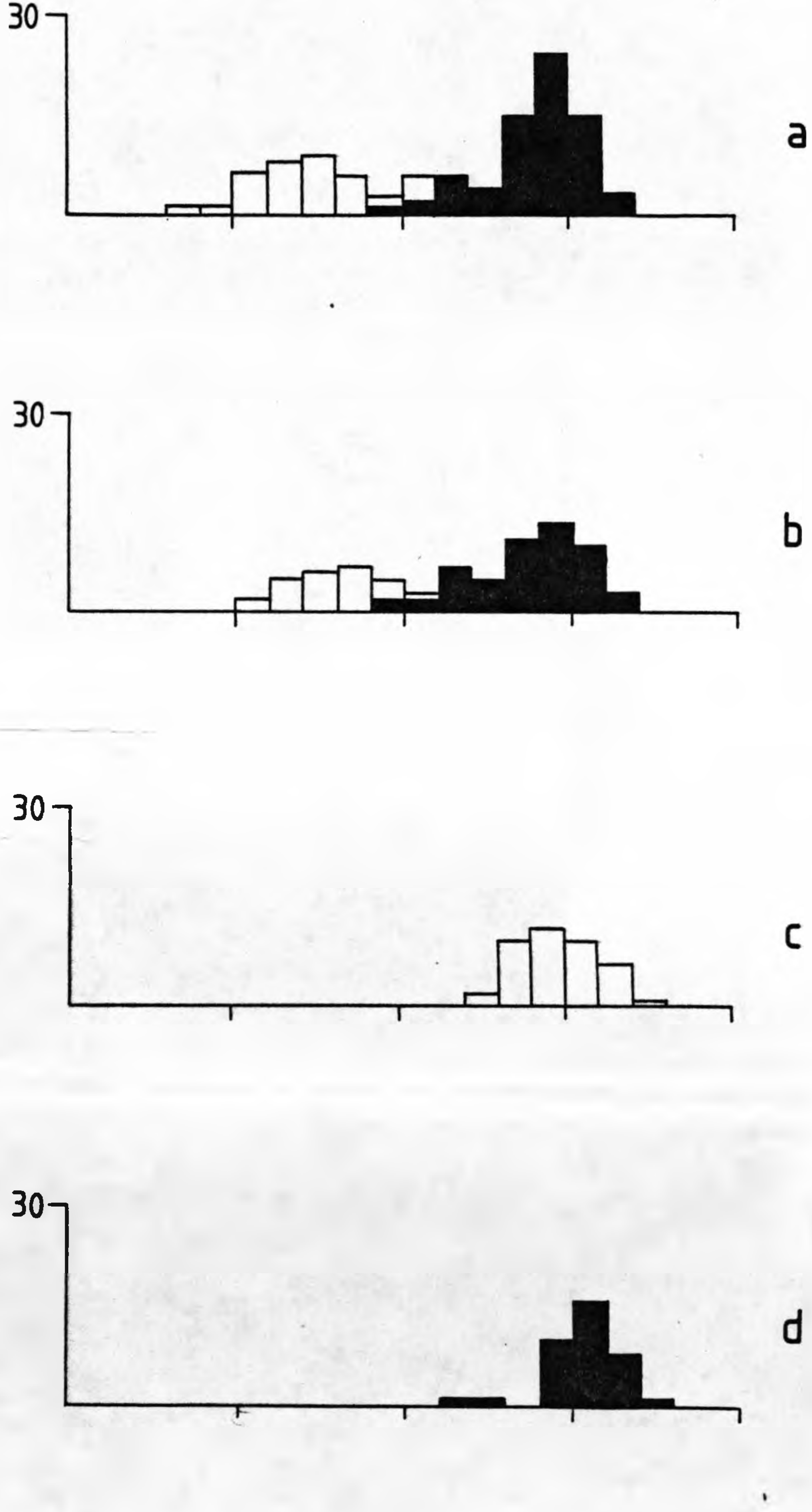

30
a
30
b
30
c
30
d

Fig. 3.17. Size-frequency distributions of samples from

a - Baie du Mont St. Michel September 1979
b - Brittany site 1 (Roscoff) July 1980
c - Brittany site 2 (Quiberon area) July 1980
d - Brittany site 3 " "
e - Brittany site 4 " "
f - Brittany site 5 " "
g - Brittany site 6 " "

(maturity scored in all samples)

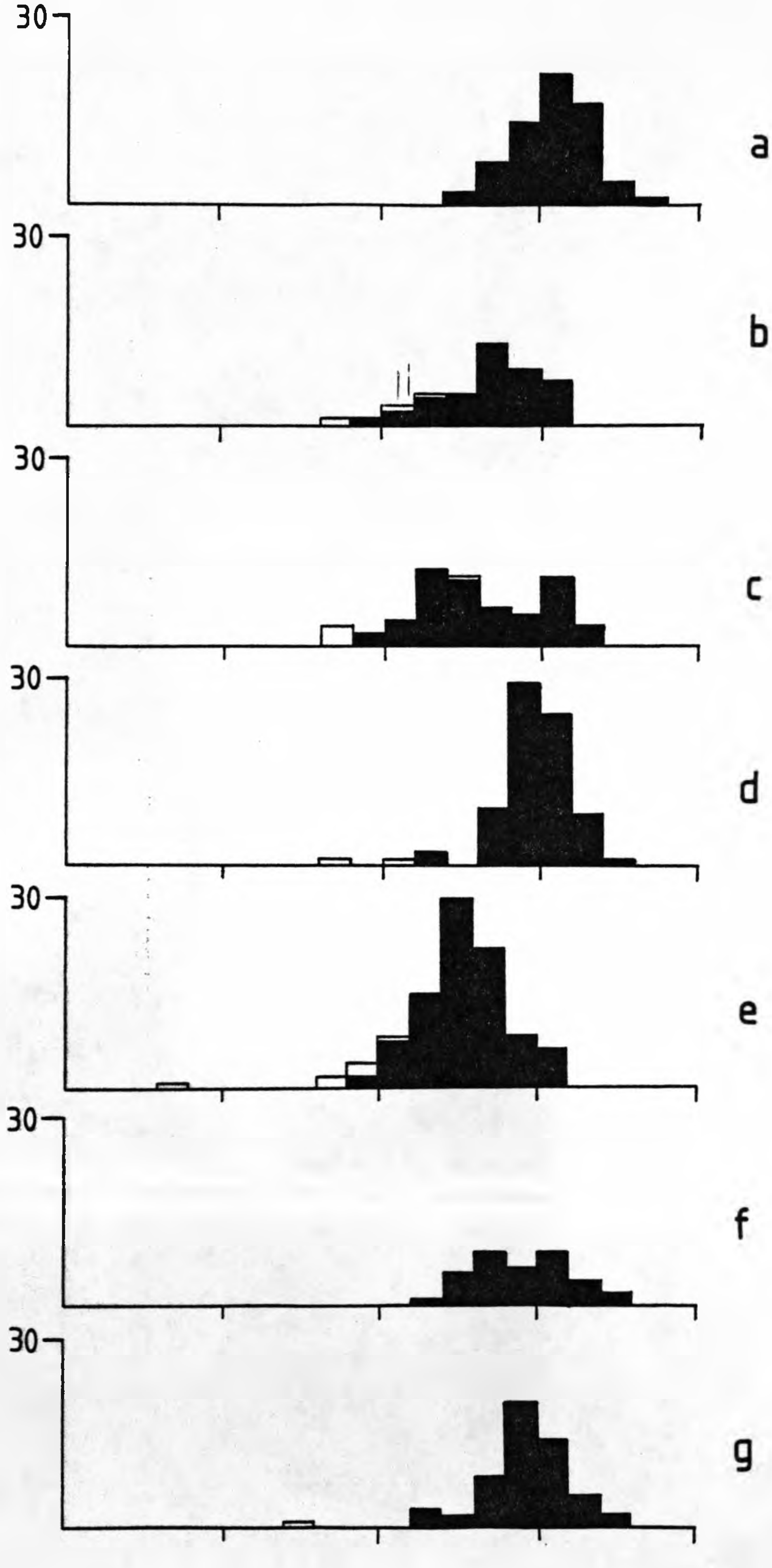

30
a
30
b
30
c
30
d
30
e
30
f
30
g

Fig. 3.18. Size-frequency distributions of samples
from Spanish duneland
a - site 2 (Elviria) 2 IX 78
b - site 3 (Elviria) 6 IX 78
c - site 2 (Elviria) 27 VIII 79
d - site 4 (Puerto Cabopino) 26 VIII 79
(maturity not scored in any sample)

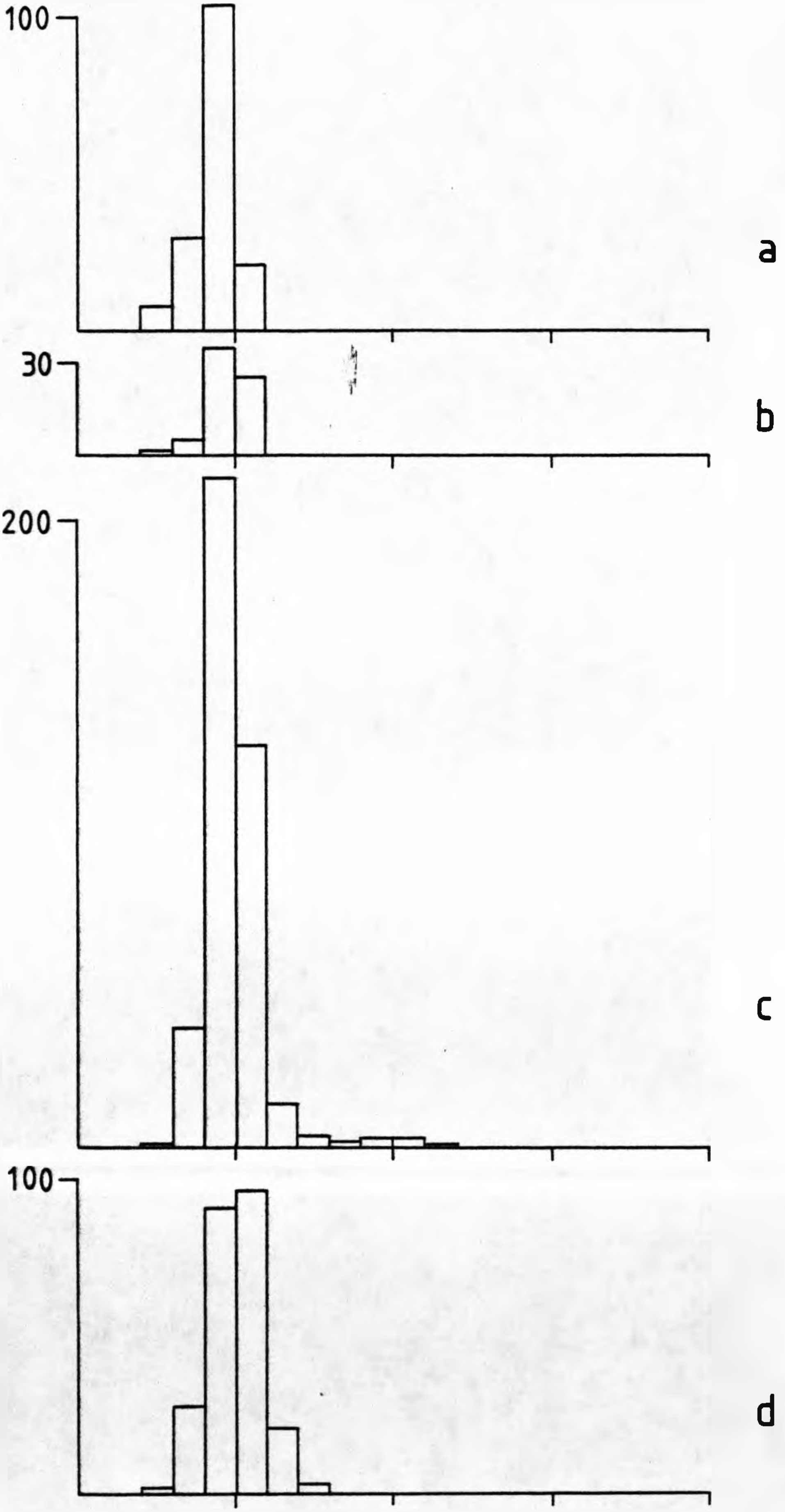

100
a
30
b
200
c
100
d

Fig. 3.19. Size-frequency distributions from Spanish inland site (Elviria, site 1)

a - 28-31 VIII 78 (maturity ~~not~~ scored)

b - 22-29 VIII 79 (maturity scored)

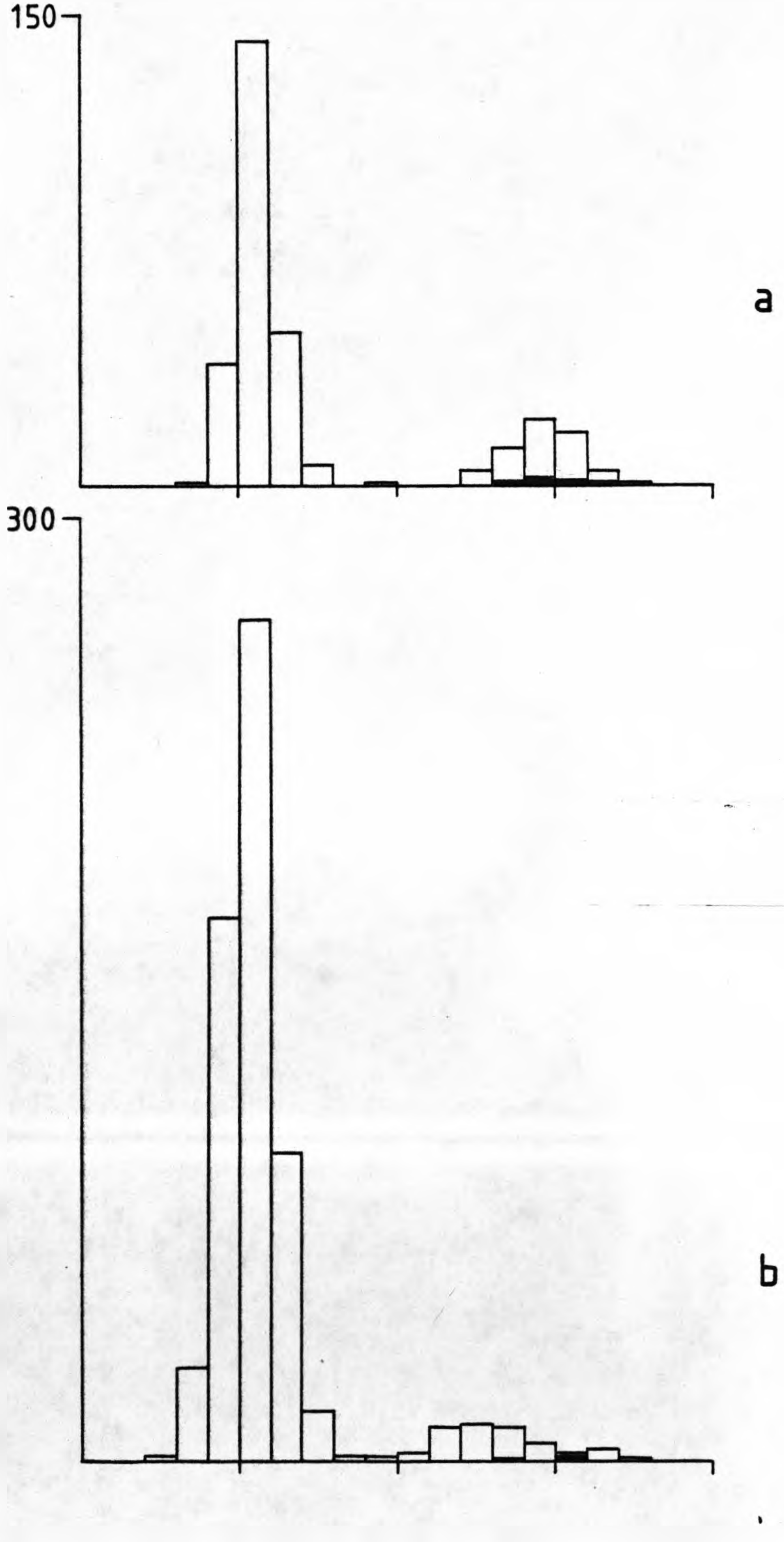

150
a
300
b

Fig. 3.20. Size-frequency distributions of samples from the Balearic Islands

a - Mallorca, Camp de Mar August 1980
b - Mallorca, Ses Coretes August 1980
c - Mallorca, Costa de la Calma 2 22 XI 80
d - Mallorca, Costa de la Calma 1 21 XI 80
e - Menorca, Santa Clementina 23 X 80
f - Menorca, Es Grao 23 X 80
g - Menorca, Torre d'en Gaumes 22 X 80
h - Menorca, Torralba 25 X 80
(maturity scored in all samples)

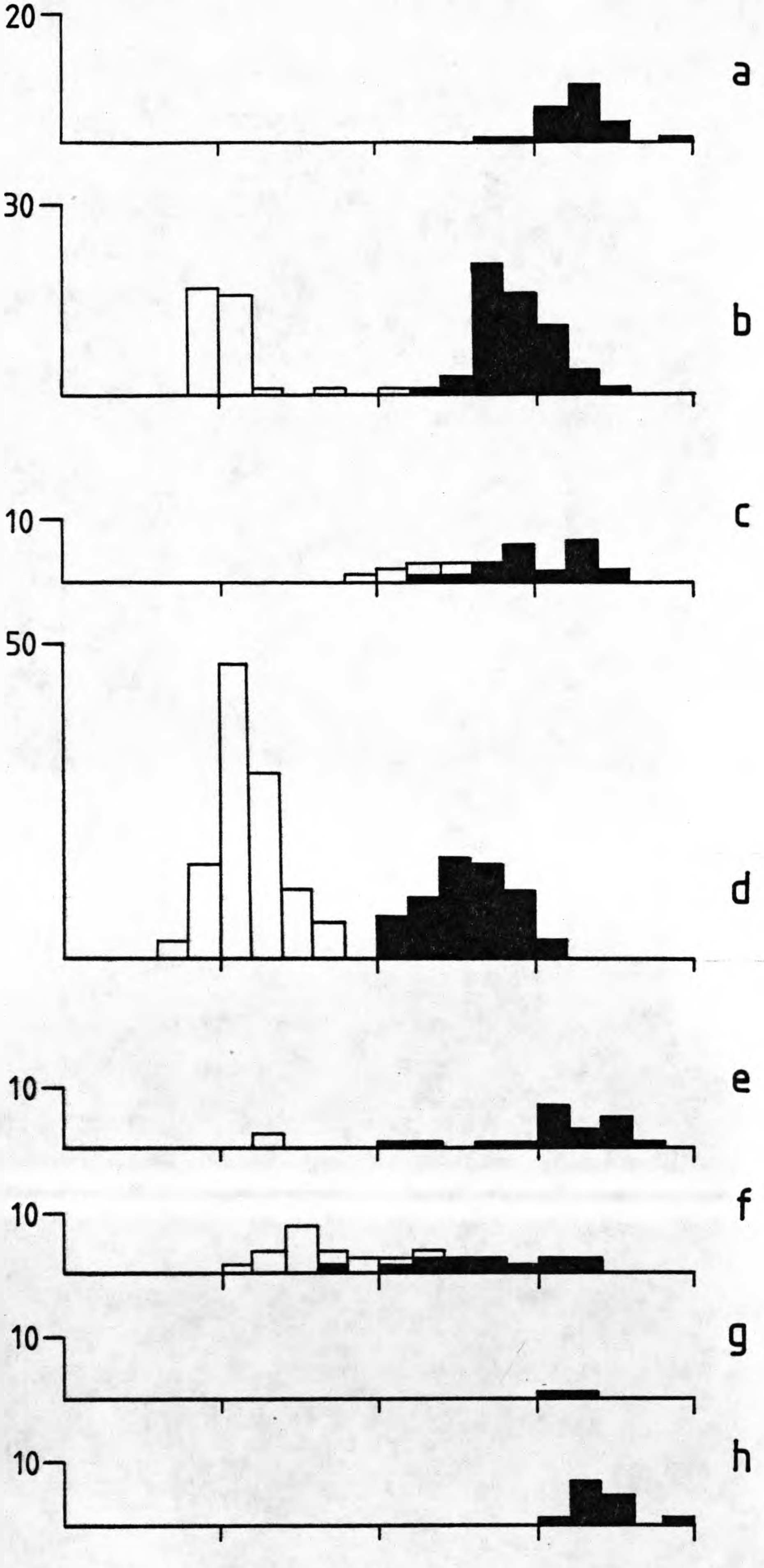

20
a
30
b
10
c
50
d
10
e
10
f
10
g
10
h

Fig. 3.21. Size-frequency distributions of samples from Sardinia

a - Calasetta 19 VIII 80

b - Cagliari 25 VIII 80

(maturity scored in both samples)

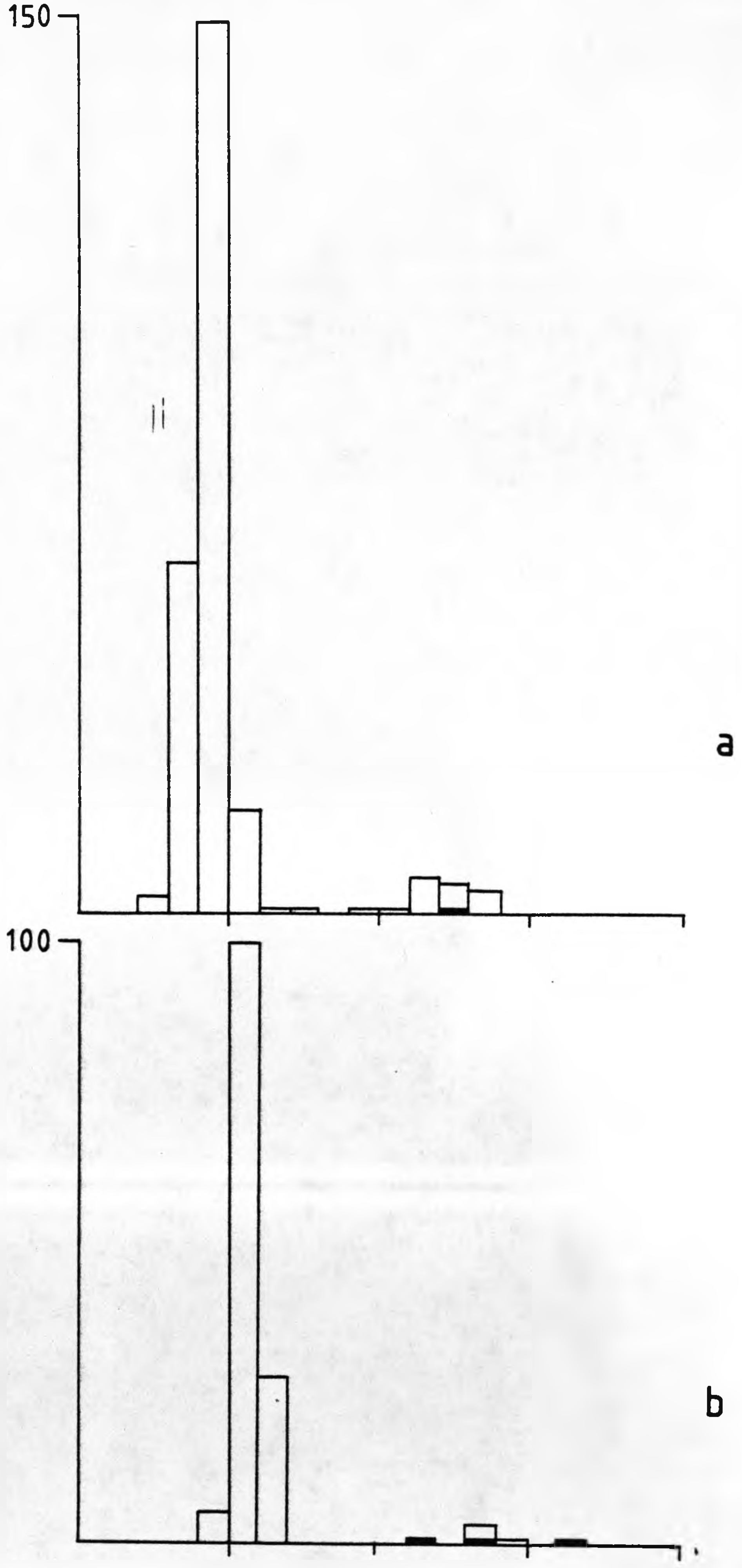
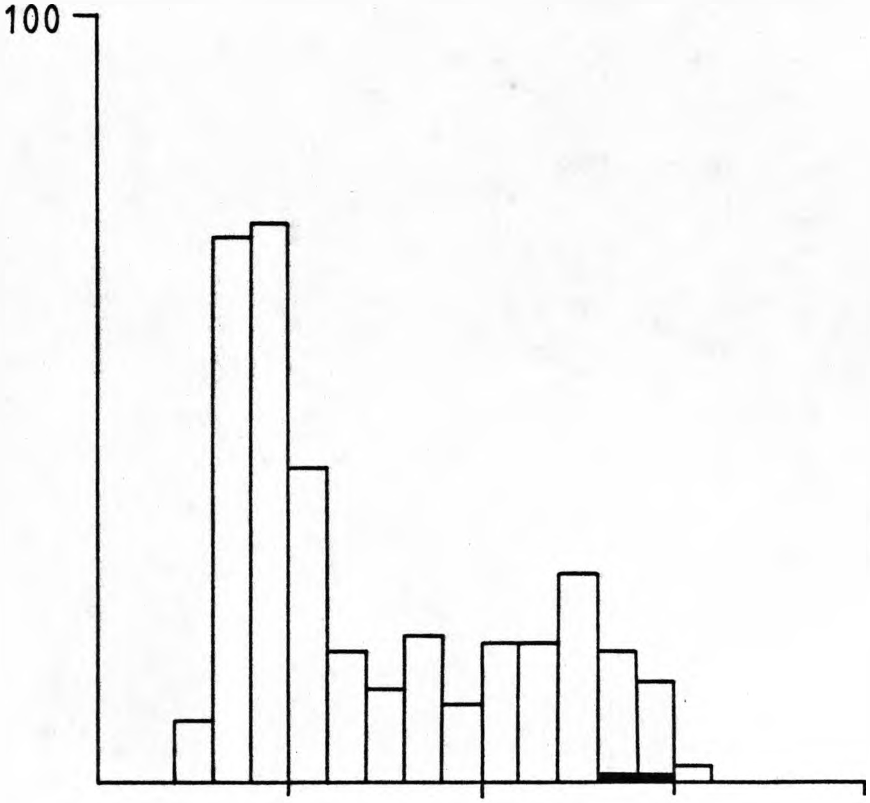

150
a
100
b

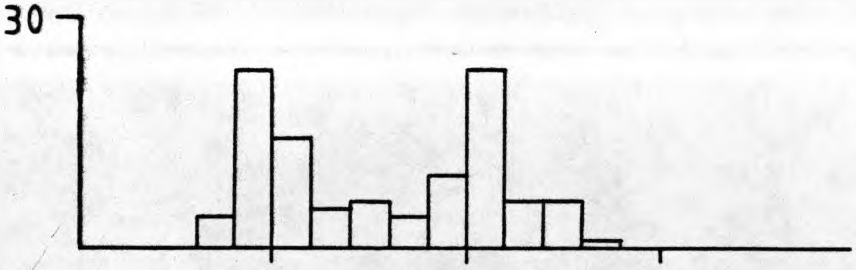
Fig. 3.22. Size-frequency distributions of samples from Lesbos and Milos

a - Lesbos 18 V 80 (maturity scored)

b - Milos 4 IX 81 (maturity not scored)



a



b

Fig. 3.23. Size-frequency distributions of the samples from Crete

a - Malia sample 1 (maturity scored) October 1980
b - Malia sample 2 " "
c - Malia sample 3 " "
d - Malia sample 4 " "
e - Amnissos sample 1 (maturity not scored) April 1980
f - Amnissos sample 2 " "
g - Komo (maturity not scored) April 1980

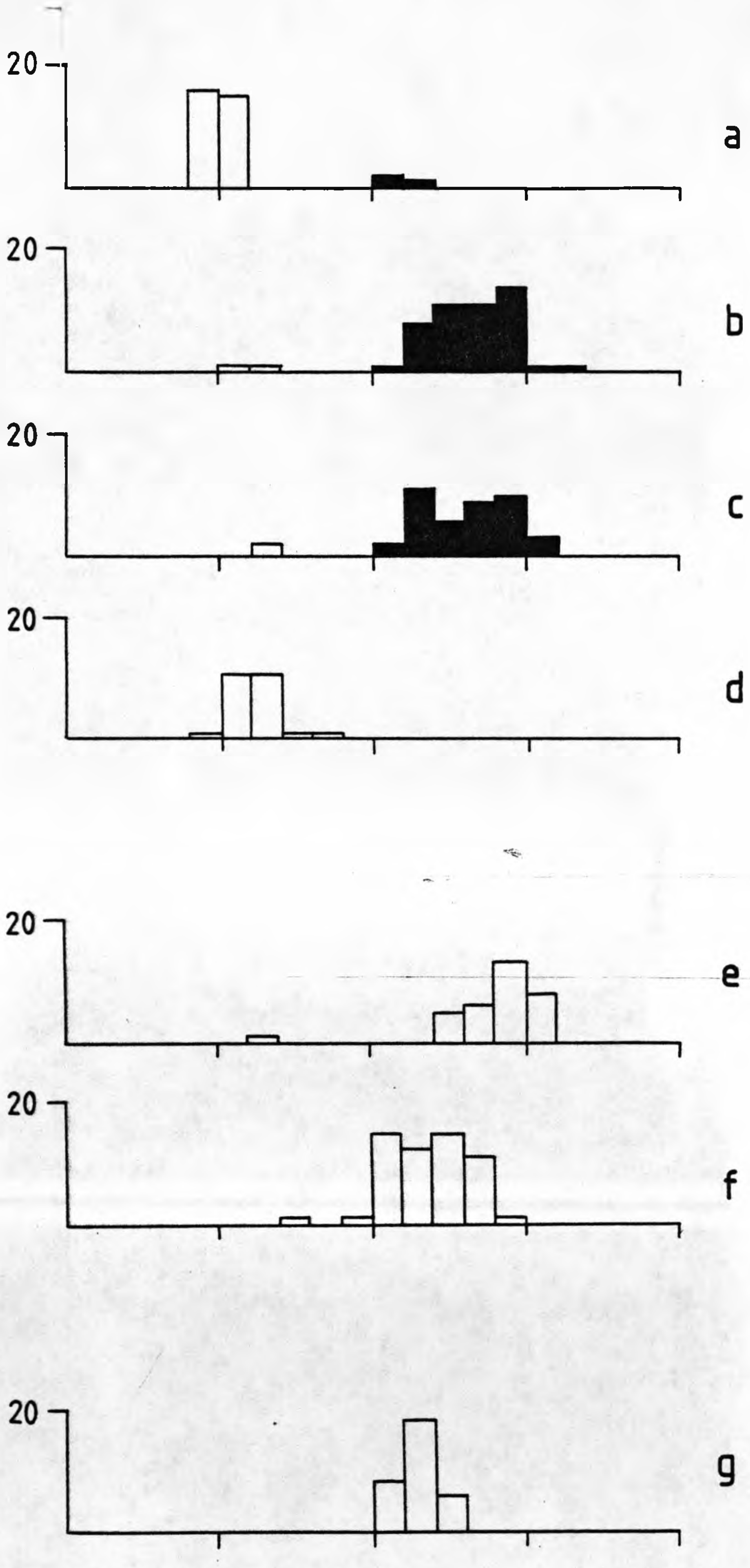

20
a
20
b
20
c
20
d
20
e
20
f
20
g

Fig. 3.24. Size-frequency distributions of the samples from Limassol (Cyprus)

a - sample 1 August 1977 (maturity not scored)
b - sample 2 August 1977 (maturity not scored)
c - August 1978 (maturity scored)

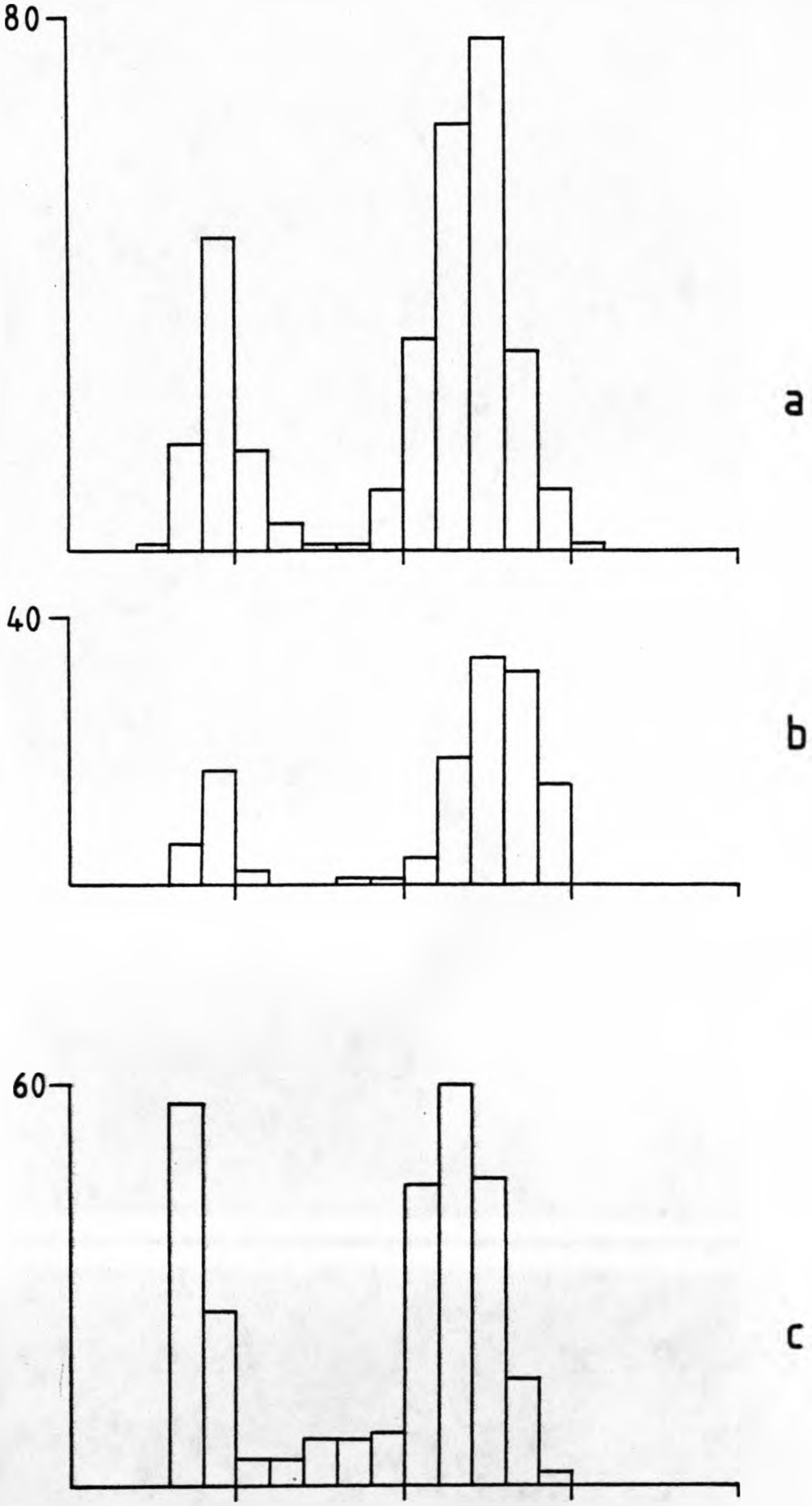

80
a
40
b
60
c

Fig. 3.25. Size-frequency distributions of the samples from Israel

a - Dor (maturity not scored) 4 IX 77

b - Caesarea, south (maturity not scored) 4 IX 77

c - Ashqelon, central (maturity scored) 22 V 80

d - Ashqelon, south (maturity scored - not random sample) 22 V 80

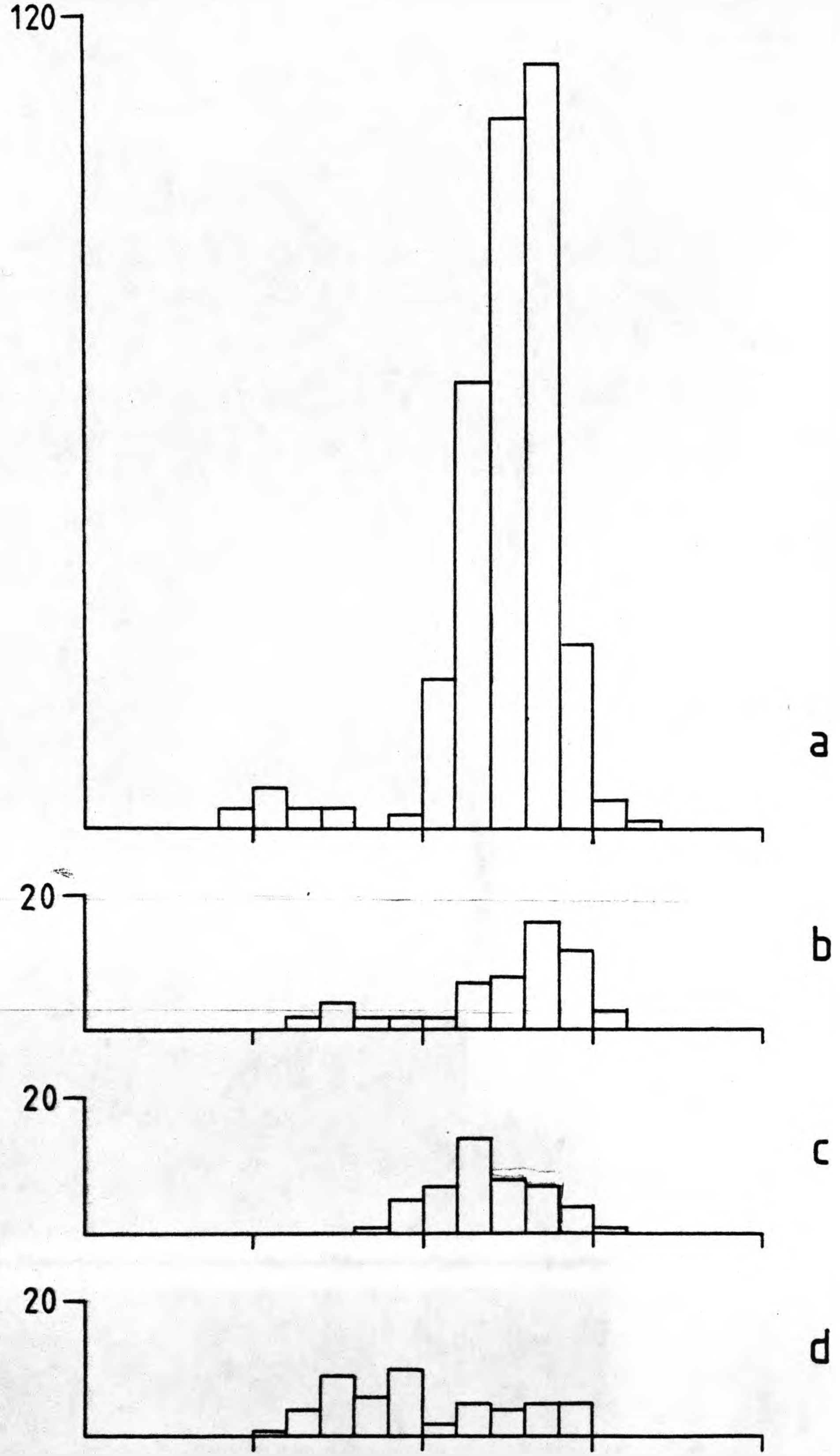

120
a
20
b
20
c
20
d

Fig. 3.26. Distribution of number of clutches per pair.

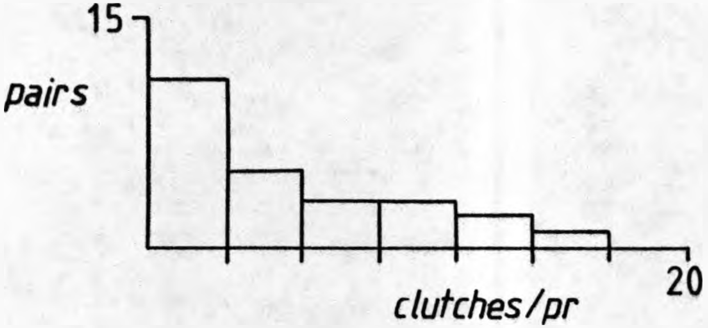


Fig. 3.27. Seasonality of clutch production.

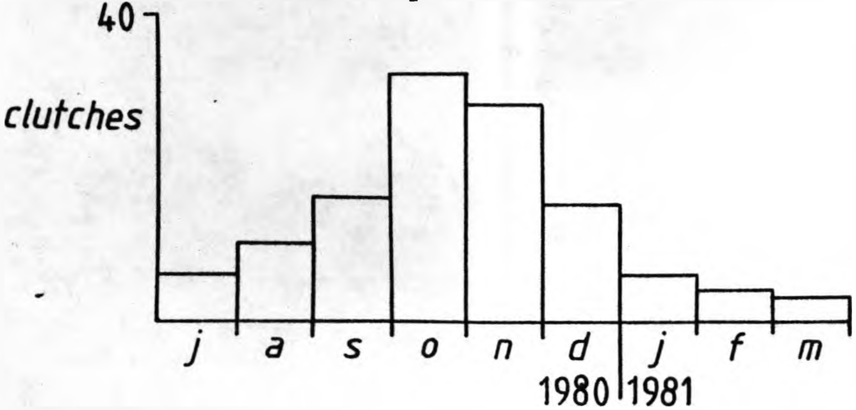


Fig. 3.28. Date of onset of laying.

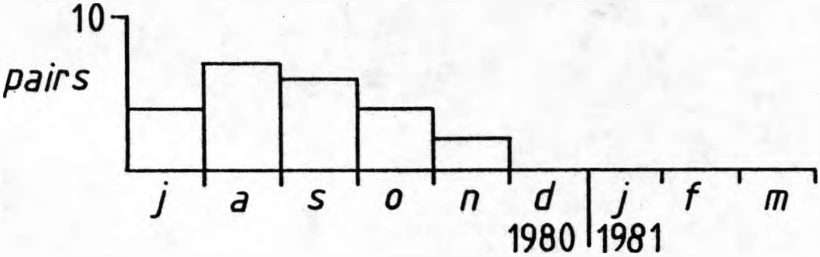


Fig. 3.29. Distribution of clutch size.

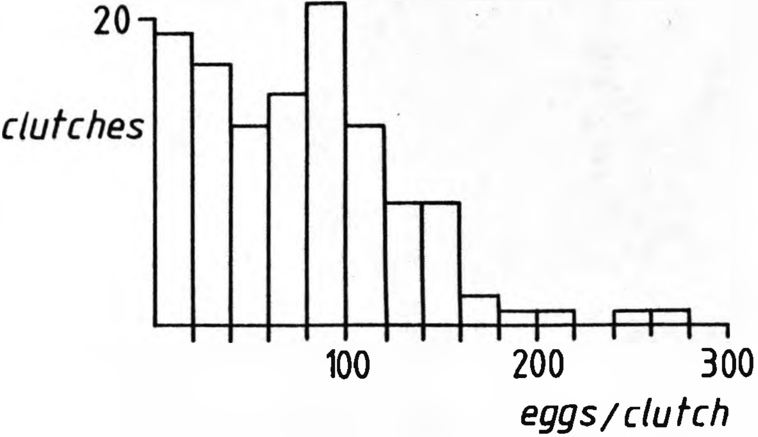


Fig. 3.30. Scatter diagram of individual clutch size against laying date. The dotted line divides type-L and type-S clutches.

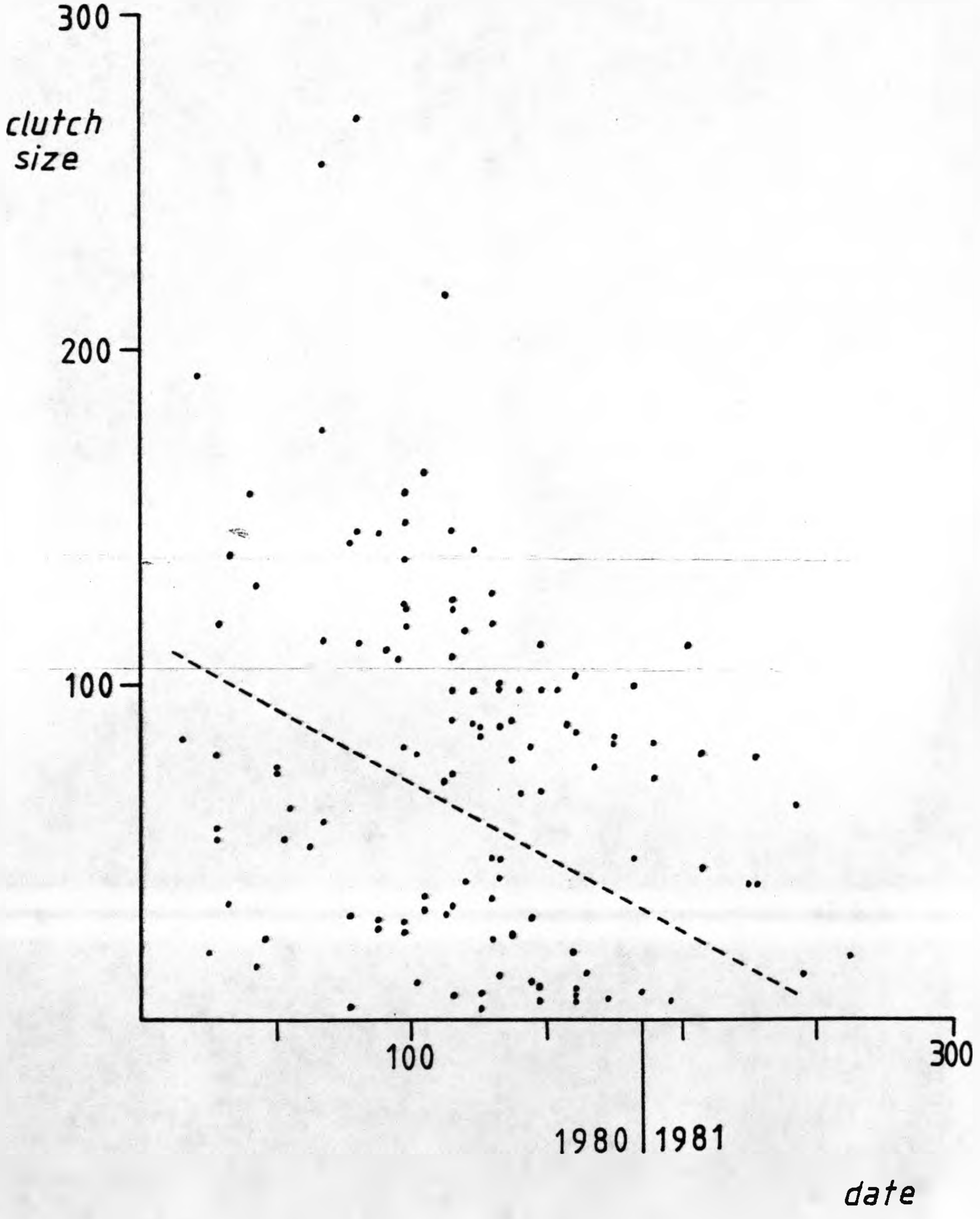


Fig. 3.31. Distribution of mean clutch dry weight per egg.

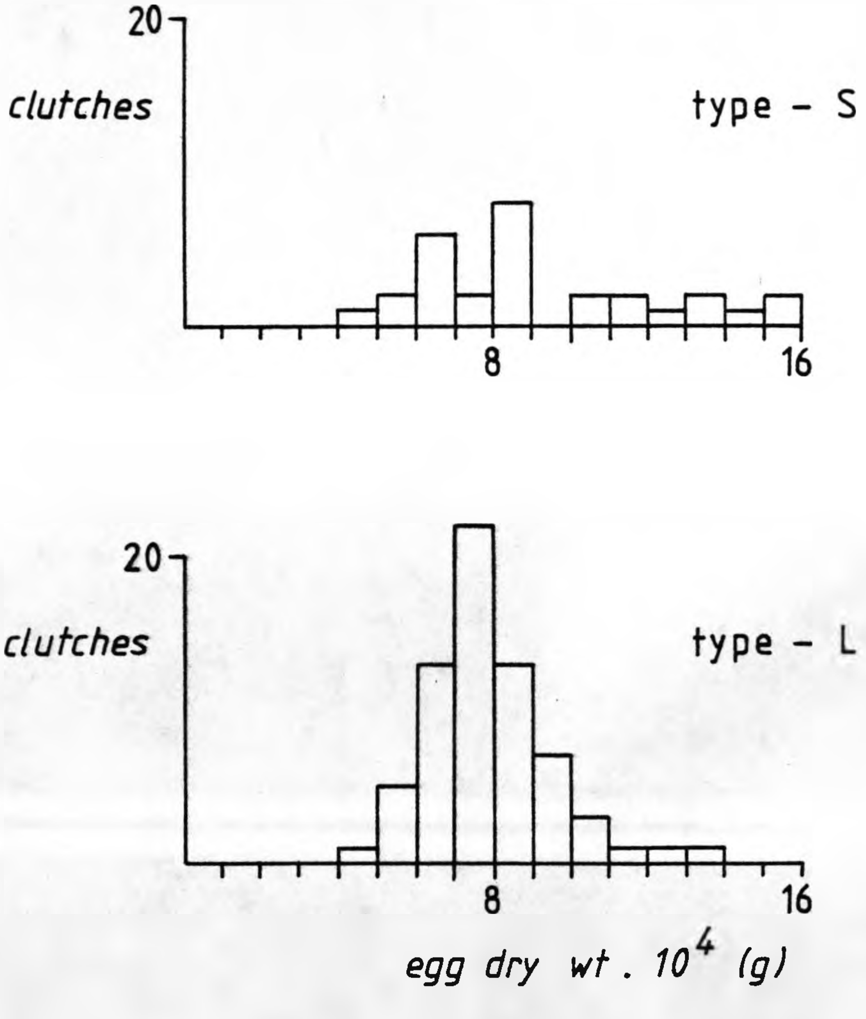


Fig. 3.32. Distribution of total production per pair (23 productive pairs).

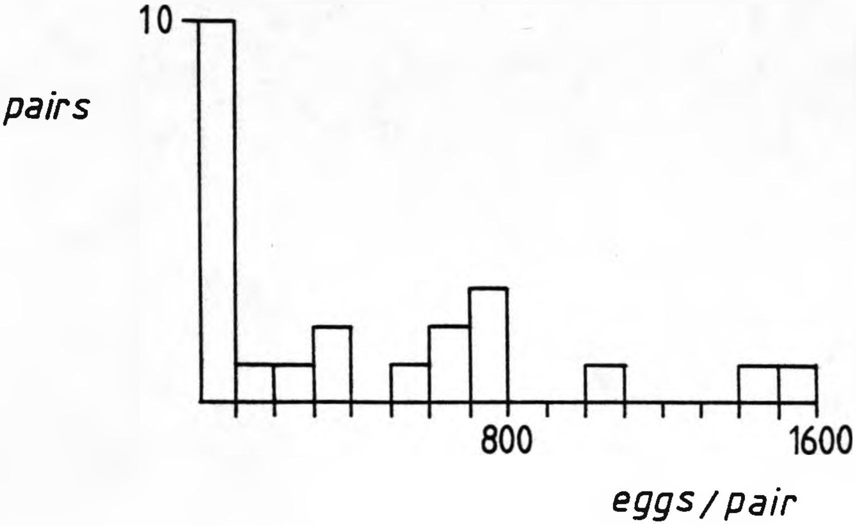


Fig. 3.33. Seasonality of egg production.

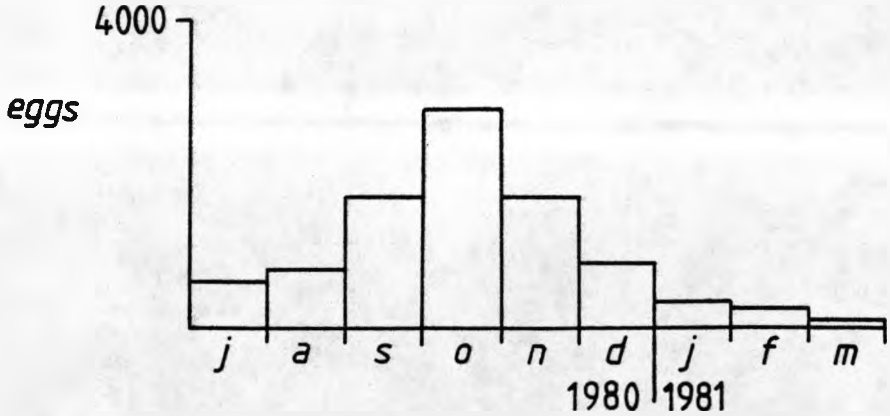


Table 3.1.

Percentage of sample within each class, and
mean ± standard deviation of h+d for each class.

Collection date	two or three classes within samples			Total collected
	← smallest		largest →	
(1) 1.6.77	34% 8.7±1.8	66% 21.9±4.3		1095
10.7.77	52% 11.8±3.0	48% 27.7±4.5		2091
(2) 31.8.77	3.5% 5.2-6.0±0.9	59% 13.6±2.5	37.5% 27.7±3.1	1564
20.10.77	53% 5.5±1.5	33% 13.0±3.6	14% 27.8±3.3	1449
8.12.77	45% 5.0±1.0	48.5% 11.7±3.5	6.5% 26.5±3.2	813
26.1.78	74% 5.8±1.0	21.5% 10.1±3.4	4.5% 26.1±3.4	1352
16.3.78	70% 6.5±1.3	26.5% 11.5±4.2	3.5% 25.2±4.0	906
4.5.78	28% 7.8±1.3	62.5% 13.8±4.2	9.5% 24.8±2.7	1224
22.6.78	56% 11.2±2.5	44% 24.6±3.4		1369
5.8.78	57% 12.3+2.5	43% 26.5+3.3		1736
14.9.78	8% 4.8±1.4	54% 13.8±2.2	38% 26.4±3.3	1406
3.11.78	28% 5.6±1.1	46% 13.5±3.0	26% 26.1±3.1	1669
17.1.79	52% 6.3±1.1	32.5% 10.6±2.8	15.5% 23.4±3.3	507
16.3.79	79.5% 6.5±1.5	17% 13.4±1.9	3.5% 23.3±1.3	195
24.5.79	58% 9.2±1.6	35% 15.7±2.7	7% 23.5±2.5	691
11.7.79	38% 11.4±2.2	62% 24.8±4.0		996
(3) 13.9.79	0.1% 3.6	56.9% 13.7±2.3	43% 28.2±3.2	979
15.11.79	40.5% 5.9±1.2	43% 13.4±3.4	16.5% 28.0±3.5	853
10.4.80	78% 9.5±2.4	20.7% 19.7±2.6	1.3% 28.4±1.6	873
(4) 11.7.80	58% 11.9±2.9	42% 26.0±3.5		632
18.10.80	34% 5.7±1.1	46% 11.8±3.0	20% 27.1±3.2	1415
8.4.81	38% 7.4±1.1	48% 14.2±2.6	14% 24.1±2.6	1042
2.7.81	39% 11.7±3.2	61% 24.8±3.6		1229

(1) only five samples taken

(2) only one point on probability paper for smallest class

(3) smallest class represented by one snail only

(4) only six samples taken

Table 3.2.

Values of the relative growth parameter, g.

interval between sampling occasions	days	two or three size-classes			cohort hatched in
		← smallest		largest →	
1.6.77 - 10.7.77	39	1.0237	1.0182		
10.7.77 - 31.8.77	52		1.0082	no growth	
31.8.77 - 20.10.77	50	no growth (1)	no growth	1.0002	
20.10.77 - 8.12.77	49	no growth	no growth	no growth	
8.12.77 - 26.1.78	49	1.0091	no growth	no growth	
26.1.78 - 16.3.78	49	1.0070	1.0080	no growth	
16.3.78 - 4.5.78	49	1.0112	1.0112	no growth	1975
4.5.78 - 22.6.78	49	1.0224	1.0360		
22.6.78 - 5.8.78	44	1.0064	1.0050		
5.8.78 - 14.9.78	40		1.0087	no growth	
14.9.78 - 3.11.78	50	1.0093	no growth	no growth	
3.11.78 - 17.1.79	75	1.0047	no growth	no growth	
17.1.79 - 16.3.79	58	1.0016	no growth	no growth	
16.3.79 - 24.5.79	69	1.0152	1.0069	1.0004	1976
24.5.79 - 11.7.79	48	1.0135	1.0290		
11.7.79 - 13.9.79	64		1.0087	1.0060	
13.9.79 - 15.11.79	63	1.0238 (2)	no growth	no growth	
15.11.79 - 10.4.80	147	1.0098	1.0079	1.0003	1977
10.4.80 - 11.7.80	92	1.0074	1.0091		
11.7.80 - 18.10 80	99		no growth	1.0013	
18.10.80 - 8.4.81	172	1.0046	1.0032	no growth	1978
8.4.81 - 2.7.81	85	1.0163	1.0199		

(1) assumed, not calculated, because the mean size on 31.8.77 could only be narrowed down to the range 5.2-6.0 mm

(2) based on only one shell on 13.9.79

Table 3.3.

Summary of the life-cycle at the localities studied.

Region	Locality	Life-cycle
United Kingdom	Tenby	biennial
	Caldey Island	biennial
	Porthcawl	biennial
	St. Ives	? annual
Northern France	B. du Mont St. Michel	?
	Roscoff	?
	Quiberon	?
Southern Spain	Elviria / Calahonda	predominantly annual
Balearic Islands	Mallorca	biennial
	Menorca	? biennial
Sardinia	Calasetta	predominantly annual
	Cagliari	predominantly annual
Greek Islands	Mitilini (Lesbos)	biennial
	Adamas (Milos)	biennial
	Malia (Crete)	biennial
	Komo (Crete)	?
	Amnissos (Crete)	?
Cyprus	Limassol	biennial
Israel	Dor	? biennial
	Caesarea	? biennial
	Ashqelon	? biennial

Table 3.4.

Summary of published work on the life-cycle of *T. pisana*.

authors	locality	life-cycle
Bonavita and Bonavita (1962)	southern France	biennial
Deblock (1962) and referred to by Deblock and Hoestlandt (1967)	northern France	annual
	Belgium	annual
	Morocco	annual
Harpaz and Oseri (1961) and referred to by Avidov and Harpaz (1969)	Israel	annual or biennial
Heller (1982)	Israel	annual
Sacchi (1971, 1977, 1978) and Sacchi and Violani (1977)	Italy, Spain, northern France	annual or biennial or more complex

Table 3.5.

Summary of published work on clutch size in *T. pisana*.

authors	number of clutches looked at	clutch size
Basinger (1927)	12	52 - 226 (mean 120)
Dürr (1946)	40	5 - 109 (mean 46)
Fleming (work quoted by Basinger, 1927)	?	25 - 30
Joubert and Walters (1951)	?	up to 50
McLean (1922), referred to by Basinger (1927)	?	10 - 40
Pitchford (1954)	1	40 - 50
Sacchi (1971)	?	c. 50 but very variable
de Stefani (1913), referred to by Basinger (1927)	many	rarely more than 90 (mean 50 - 70)

Chapter 4

Temperature and Desiccation Relations

4.1. Introduction.

Ectothermic animals use both behavioural and physiological adaptations to control their internal temperatures, and to avoid or withstand extreme environmental temperatures (for reviews see papers in Whittow, 1970). This chapter presents the results of an investigation of the thermal and desiccation relations of adult and juvenile T. pisana from Tenby in terms of both the upper lethal ambient temperature limits in laboratory experiments, and the field and laboratory behaviour of snails with respect to microclimate. Snails from southern Spain have been compared with Tenby snails in order to see whether individuals from very different climatic regimes are adapted differently to them.

4.2. Temperature Tolerance.

4.2.1. Methods.

The following procedures were adopted for all experiments. Snails were exposed to high ambient temperatures by putting them in open glass tubes and partially immersing these in constant-temperature water baths. If the snail had formed an epiphragm, this was removed prior to the experiment . A small piece of cotton wool was placed in the bottom of the tube and the snail put on this so that it was not in contact with the glass of the tube. A second piece of cotton wool was then placed loosely on top of the snail to prevent it moving and to provide some insulation, but still to allow it to breathe. The tubes were immersed to such a depth that the water level in the bath was well above this upper layer of cotton wool. The temperature inside each tube was not monitored, but was assumed to be the same as that in a control tube with no snail but with a mercury-in-glass thermometer placed so that the bulb was in the position usually occupied by the snail. The upper piece of cotton wool was put around the thermometer stem. A thermostat in the water, controlling the heating element, held the temperature in this tube within 0.1°C of that required for each experiment. The water was kept in vigorous motion by means of an electric pump, so that the temperature was uniform throughout the bath, and the arrangement of the tubes in each bath was randomized. After immersion, it took about 20 minutes for the air in a tube to reach the required temperature. It is not known how different the time taken for a snail to reach this would be, but addition of 20 minutes immersion to the intended exposure time was used as a standard procedure.

The time taken for snails to cool back to room temperature following exposure has not been taken into account; it will be longer, the larger the snail. After an experiment, snails were allowed to recover in plastic lunch boxes with a layer of damp soil; they were not fed.

The humidity of the air surrounding the snails was not controlled, but was assumed to be approximately the same in all cases, and to be fairly low, since the upper piece of cotton wool was the only barrier between the snail and the laboratory air. Although this introduced desiccation tolerance as a confounding factor, it was considered to approach conditions in the field more closely than would very high humidity. In one experiment, humidity was deliberately increased to near saturation in order to investigate this; drops of water were put into the tube prior to introduction of the lower piece of cotton wool, thus keeping the atmosphere surrounding the snail humid but without allowing free water to make contact with the snail.

A preliminary experiment using adult snails from Tenby (collected 4th November, 1978) was carried out (25th April, 1979) to find the approximate range of temperature over which mortality would start to occur. Temperatures of 36°, 43° and 50°C, and exposure times of 1, 2 and 3 hours were used, 5 snails each being exposed to these six regimes. Because of the difficulty of determining whether a snail was dead immediately after the experiment, the results were scored in four ways:

(i) no movement after a recovery period of 90 minutes.

(ii) no movement after 24 hours.

(iii) death after 5 days.

(iv) death after 2 weeks.

More snails had moved after 24 hours than after 90 minutes, but it was difficult to determine which of the immobile ones had died. After 5 days, dead snails were decaying badly and so mortality was easily scored. This was used in future experiments as the most convenient method, since no further snails were dead at 2 weeks. The results of this preliminary study are presented in fig. 4.1.

Following this, a larger experiment (experiment 1 - table 4.1.) was carried out with 10 adult snails per regime. These had been collected from Tenby on 11th July, 1979 and were then fed and dampened twice a week, keeping them regularly active until the time of the experiment. Temperatures used were at 2°C intervals from 39 to 49°C, and for exposure times of 1, 2, 3, 4 and 8 hours. The results were scored in terms of no movement after 1 and 24 hours, and mortality after 5 days.

Experiments on Tenby snails (summarised in table 4.1.) were then carried out following the same procedure, but with fewer temperatures, usually only one exposure time (3 hours), but often with more snails per regime in order to reduce the variation seen in the results of experiment 1, particularly at low temperatures (see below, section 4.2.2.). All snails were kept regularly active, as above, unless otherwise stated. These experiments were aimed at investigating differences in tolerance between adults and juveniles (using snails from summer samples with two distinct size classes - chapter 3, section 3.2.1.2.), differences due to the snails' condition in the laboratory prior to the experiment (inactive, by being kept in dry boxes without food, or regularly active, as above), and differences due to increased humidity in the experimental glass tubes (see above). All these experiments (and those described below) used snails of all shell colour/pattern morphs selected at random from the samples. Experiment 4 used snails of only the unbanded and dark five-banded morphs (see chapter 6), keeping the results separate in order to detect any morph differences. A further experiment (experiment 5 - table 4.1.) was carried out using 30 snails of each of three narrow size ranges ($d > 13.0$ mm, $9.0 < d < 10.5$ mm, $5.5 < d < 7.0$ mm), corresponding to adults, medium juveniles, and small juveniles, and exposing them at 44°C for 4 hours, in order to investigate further any size dependence in tolerance.

Experiments 6 and 7 (table 4.1.) were performed on juvenile snails (of a similar size to the Tenby juveniles used) collected in southern Spain (Elviria duneland sites - see appendix 2) while they were aestivating. Some of these were used without breaking their aestivation; others were stimulated into regular activity, as above, for a few weeks prior to the experiment.

4.2.2. Results.

The results of the main experiment (experiment 1 - table 4.1.) on Tenby adults are presented in fig. 4.2. (no movement after 1 hour), fig. 4.3. (no movement after 24 hours), and fig. 4.4. (mortality after 5 days). Since some of the lines for different regimes are coincident on these graphs and the full information cannot therefore be obtained from them, the actual results are available in table 4.2.

Fig. 4.2. shows that very few animals exposed to temperatures of 43°C and above moved during the first hour of recovery, but that many of those exposed to lower temperatures (39 and 41°C) did. No clear distinction between the five different exposure times is apparent in the scores of movement after 1 hour. After 24 hours more snails had moved and differences between exposure times are apparent, a trend of less movement of snails exposed for longer periods being indicated (fig. 4.3). As in the preliminary experiment described above (section 4.2.1.), there is little difference between the scores of no movement after 24 hours and mortality after 5 days (fig. 4.4.), except that a few individuals which had moved subsequently died. At 39 and 41°C some mortality did occur, but appeared not to bear

any relation to exposure time or temperature. At 43°C mortality was clearly dependent upon exposure time, and at 45°C all snails died except two exposed for only 1 hour. At 47 and 49°C all snails died. In all cases there are too few points in the transition zone between little and complete mortality, to allow statistical analysis, using probit transformations, of the differences between exposure times, but the results are consistent, and consonant with biological expectation. Clearly, the upper lethal limit lies in a fairly narrow range between about 42 and 46°C and within this range is dependent on exposure time.

Because of the apparently random variation in percentage mortality at 39 and 41°C (fig. 4.4), and the narrow range of temperature over which intermediate percentage mortalities occurred for each exposure time, it is not possible to calculate accurate LD_{50} values (the temperature at which 50% mortality occurs for a given exposure time) by the normal procedure (Woolf, 1968). However, approximate calculations give values of LD_{50} from 42.2°C for 8 hour exposure to 43.5°C for 1 hour exposure.

There is some indication of slight differences in tolerances between experiments 2, 3 and 4 (figs. 4.5. - 4.7.), all using Tenby snails. This may have been due to prior treatment, for instance different laboratory temperatures, or to a physiological change dependent on time of year (Cloudsley-Thompson, 1970, p.63); these experiments were carried out at different times of year, and used snails collected on different occasions and kept in the laboratory for different lengths of time.

However, despite this, a number of definite results do emerge. Experiments 2 and 3 (figs. 4.5. and 4.6.) showed that in the normal dry conditions in the experimental tubes, juveniles were significantly more tolerant at all temperatures ($p < 0.01$ - difference between two sample proportions - Goldstein, 1964, p.101); the difference in approximate LD_{50} values being between 1.5 and 2°C. In humid tube conditions (experiment 2, fig. 4.5.) this difference was reduced, although juveniles may still have been marginally more tolerant (the only significant difference ($p < 0.01$) was at 42°C). Experiment 5 (fig. 4.8.) also showed that adults were less tolerant than medium-sized juveniles ($p < 0.01$); very small juveniles appeared less tolerant than the approximately half-grown ones, but this difference was not significant. There were no significant differences between snails forced into inactivity in the laboratory (probably equivalent to aestivation in the wild) and regularly active snails (experiment 3, fig. 4.6.); nor between snails of different morphs (experiment 4, fig. 4.7.).

Only juveniles were obtained from Spain, but these were of approximately the same size as the Tenby juveniles used. Availability dictated that fewer regimes and fewer snails per regime were possible. However, experiments 6 and 7 (figs. 4.9. and 4.10.) clearly indicate a much higher tolerance than the experiments with Tenby snails. LD_{50} values would be in the region between 45 and 50°C. There is no clear difference between the results of the two experiments, one using snails whose field aestivation had not been broken (experiment 6, fig. 4.9.), and the other using snails induced into activity in the laboratory (experiment 7, fig. 4.10.).

4.2.3. Discussion of temperature tolerance.

Experiment 2, using both dry and humid atmospheres in the tubes, suggests that the mechanism of heat resistance involves evaporative cooling. In an atmosphere of high humidity, adults and juveniles are similarly tolerant. In a dry atmosphere evaporative cooling can take place when the shell aperture is not sealed (Hogben and Kirk, 1944); the snail's temperature is thus lower than that of the ambient air, and tolerance of a particular ambient temperature is raised. Similar results have been found in experiments on other groups of animals (e.g. crabs and isopods - McWhinnie, 1967). This effect would be greater in smaller snails due to their larger aperture surface area/volume ratio (Cameron, 1981), and so the higher tolerance of the juveniles in the present study is probably an incidental concomitant of their small size, rather than a physiological difference. This may also explain the results of Garcia (1978), who showed for Cepaea nemoralis that juveniles lost relatively more weight than adults when exposed to high ambient temperatures, but that adults suffered higher mortality.

Evaporative cooling cannot be relied on as a means of tolerating high temperatures in a dry atmosphere for long periods because of the consequent desiccation, although despite the greater difficulty of evaporating, it may be used by snails in more humid climates (as suggested by Heatwole and Heatwole, 1978). Juvenile snails, as used in the present study, although more tolerant over a period of 3 hours, would be more susceptible over longer periods to death from desiccation. Smaller individuals of a species may generally have lower resistance to desiccation than larger ones (e.g. drosophilids - Barker and Barker, 1980). Indeed, very small snails (exposed for 4 hours) may be less tolerant of high temperature (fig. 4.8.) than approximately half-grown juveniles, probably because lethal desiccation takes place more rapidly the smaller the animal. Exposure times of a few hours only, and the use of dry experimental tubes in this study probably approach more closely the natural situation, in which snails are only exposed to the highest ambient temperatures for a few hours during the middle of the day, when relative humidity is rarely near 100% and usually lower.

Only very little evaporation can take place through the shell (Machin, 1967; Cameron, 1970a), and so little evaporative cooling is possible if the aperture is sealed, as during aestivation (Hogben and Kirk, 1944). Andrewartha (1964) and Schmidt-Nielsen, Taylor and Shkolnik (1971) have documented the low rates of water loss during aestivation of Cernuella virgata and Sphincterochila boissieri (Charpentier) respectively; and in addition, the mantle collar epithelium of Otala lactea (Müller) is known to be particularly impermeable during periods of inactivity and aestivation (e.g. Machin, 1972; Newell and Machin, 1976; Newell and Appleton, 1979). In this situation, tolerance differences between animals of different sizes will be less pronounced, since evaporative cooling will be largely prevented. However, Cloudsley-Thompson (1970, p.45.), has suggested that during periods of aestivation, some animals may show raised temperature tolerances, and this would seem most appropriate for species which aestivate in positions exposed to high temperatures. No evidence of this was found in the present study.

The results show that the tolerance of T. pisana, a Mediterranean snail, is intermediate between that of desert species (Sphincterochila boissieri; Trochoidea seetzeni (Charpentier) - Yom-Tov, 1971a; Schmidt-Nielsen, Taylor and Shkolnik, 1972) and more temperate or mesic species (Helix pomatia L. - Hogben and Kirk, 1944; H. aspersa Müller - Grainger, 1975; Cepaea nemoralis (L.) - Richardson, 1974; Arianta arbustorum (L.) - Grainger, 1969). They are similar to those obtained for T. pisana in South Africa by McQuaid, Branch and Frost (1979). In their experiments, which used aestivating adults, 50% mortality occurred between 44 and 46°C for exposure of 3 hours in 100% relative humidity, but tolerance would presumably have been greater in a dry experimental atmosphere, perhaps approaching the values obtained for the Spanish juveniles used in the present study. Indeed Dürr (1946), also working with T. pisana from South Africa, reported 50% mortality at 50°C with 56% R.H. The South African habitat and climate are more similar to those of southern Spain than of south Wales, and indeed the present study indicates a lower tolerance in Tenby snails than in Spanish snails.

If acclimation to laboratory temperatures was rapid, as suggested for vertebrates by Fry (1967) and for insects by Cloudsley-Thompson (1970, p.59), the snails used in the present study were probably similarly acclimated at the times of the experiments. Therefore, the differences found may have a genetic basis rather than be due to acclimation to different climatic regimes. Such differences have been found in drosophilids by Parsons (1980); and Cloudsley-Thompson (1970, pp. 66-69), reviewing the temperature relations of latitudinally separated populations of arthropods, considered them to be genetic adaptations.

4.3. Field and laboratory behaviour.

4.3.1. Methods.

4.3.1.1. Field behaviour.

It is well known that many snails of mediterranean habitats, including T. pisana (e.g. McQuaid, Branch and Frost, 1979), avoid the heat of the ground by climbing up plants. Even at Tenby such behaviour was clearly exhibited during the summer months (fig. 4.11.). Preliminary observations suggested that there were differences in daytime resting position between adults and juveniles. As differences between snails of the various shell-pattern morphs (chapter 6) might also occur, both these aspects were investigated. The area used for the study was between the western end of the Esplanade and the Burrows, demarcated by the sloping path down to the beach, the Jubilee Gardens at the top, and the small cafeteria/amusement arcade towards the bottom of the cliff (fig. 3.3., chapter 3).

All the observations were carried out during three consecutive summer days in 1980 (10, 11, 12 July) and two in 1981 (3, 4 July) with similar dry but not extremely warm or sunny weather. At this time of year only two size classes are present in the Tenby populations: adults, or near-adults, and approximately half-grown juveniles (chapter 3, section , 3.2.1.2.). These classes are not completely distinct, there being some snails of intermediate size present, but there are no newly-hatched snails. Many snails were clearly associated with two species of tall plant; alexanders (Smyrnium olusatrum), an umbellifer, and sea radish (Raphanus maritimus), a crucifer. The records were all taken from individual plants of these species. Only inactive snails were recorded, although during the daytime in summer when it is dry, very few are active.

In 1980, the following observations were made for each individual resting on the first 15 plants observed with snails:

(i) whether it was adult or juvenile (or in some cases intermediate)

(ii) its morph (dark five-banded, yellow five-banded, unbanded - see chapter 6).

(iii) its height above the ground surface (to the nearest cm).

and for those snails resting on vertical stems,

(iv) which quadrant (NE, NW, SW, SE) of the approximately circular stem it was resting on, taking the position of the aperture as a standardized means of recording this.

Records were also taken of snails in the low vegetation (up to about 20 cm high and mostly grass with some bindweed and other broad-leaved plants) overhung by each of these 15 tall plants:

(i) whether adult or juvenile (or intermediate)

(ii) morph.

All the above records were made, except those from the low vegetation, from a further 17 tall plants. Thus records were available from 32 plants with respect to snails on the stems, and from 15 combinations of tall plants and low vegetation.

In 1981, two adjacent slopes of different aspect (190° and 250°) were chosen from within the general area of the 1980 work. Morph and resting position (stem quadrant) were recorded, for adult snails only, on 11 stems on each of the two slopes and on each of the two days.

4.3.1.2. Laboratory behaviour.

An attempt has been made to elucidate the cues used by the snails to select or avoid particular quadrants of the stems used for resting sites in the wild, in the hope that this might give some support to reasons suggested for any preferences. In order to do this, a cylindrical wooden pole 2.75 cm in diameter was stuck vertically in soil, extending 50 cm above the soil surface, thus simulating in the laboratory a stem of one of the tall plants used by the snails in the field.

Prior to an experiment the pole was dampened. Ninety snails (60 dark five-banded,30 unbanded - all collected from the area of the field study) were then placed on the soil surface near the pole and allowed to crawl up it. If snails moved away from the pole they were returned to its base, so that eventually most snails crawled upwards. After 2 hours, when most had stopped crawling and stuck themselves to the pole by mucus round their shell apertures, the positions of their apertures were recorded (four quadrants of the pole, denoted clockwise A, B, C, D). Snails on the horizontal top of the pole, stuck onto other snails, or still crawling were not scored. The complete set-up was shielded from draughts, and from any light except from directly above, by placing it in a tall cardboard box with a base about 0.5 x 0.5 m. This constituted the control experiment.

Four further regimes were used:

(i) light shone towards quadrant A - 40 W light bulb (to simulate the sun), 0.5 m from the pole, and shone from a height about half-way up the pole - one side of the box replaced with clear plastic, to prevent draughts and any convectional heating from the lamp (there was no temperature gradient in the box).

(ii) light shone towards C - as in (i)

(iii) air blown towards A - hair-dryer blowing air at room temperature (to simulate a gentle horizontal breeze) - two opposite sides of the box removed, allowing a through current.

(iv) air blown towards C - as in (iii)

Each of these regimes (control, light from two directions, wind from two directions) was used five times, thus constituting a total of 25 experiments. The same 90 snails were used in each experiment. Between each, the pole was washed to remove any mucous trails left by the snails. The order of the 25 experiments was randomized.

4.3.2. Results.

4.3.2.1. Field behaviour.

The observations of intermediate-sized snails, being too few to allow separate analysis, have been combined with those of juvenile snails.

No morph differences were detected in preference for low vegetation or tall stems, in aspect on these stems, nor in height above the ground. The following results have thus been obtained by combining the observations for all morphs.

Since there was some heterogeneity between plants (those including records from the low vegetation - 15) in the proportions of adults and juveniles associated with each, each has been considered separately when investigating preferences of these adults and juveniles for the stems or for the low vegetation beneath the plants. The results are presented in table 4.3. The null hypothesis that there were no preferences is shown to be incorrect for 9 plants in which more adults and fewer juveniles were found on the stems, and more juveniles and fewer adults were found in the low vegetation, than would be expected on such a hypothesis. We would not expect 9 out of 15 to be significant by chance even at the 5% level, and some are more significant than this. This same trend is apparent (but not significant) for all the remaining 6 plants. There is clearly a tendency for adults to be associated with the tall stems of alexanders and sea radish, and a preference in the juveniles for the low vegetation overhung by these tall plants.

The data (from 1980 only) are too few to detect heterogeneity between individual plants (32 plants) in the height distributions of the snails on the stems. However, when the combined data for each of the three days are examined, there is heterogeneity between observations taken on different days. Therefore, these are kept separate. Figs. 4.12 and 4.13. show the height distributions for adults, and for juveniles plus intermediates, respectively. The snails tend to avoid the lowest parts of the stems, and to sit just above the level of the low vegetation which rarely exceeded 20 cm in height. There is no significant difference between the distributions of adults and juveniles, but the numbers of the latter are much smaller.

The data are also too few to check for heterogeneity between plants in the proportions of the adult snails sitting on each of the four aspects of vertical stems. When the records of 1980 are combined for each of the three days, there is no heterogeneity between those from the different days. Therefore, the data from all 32 plants have been lumped, and the results are presented in table 4.4. The data of 1981 for the plants combined from each slope for each day are also available in table 4.4. Taking each slope separately, the results from the two days are significantly different (190° slope - $\chi^2_3 = 80.0$, $p < 0.001$; 250° slope - $\chi^2_3 = 19.3$, $p < 0.001$). Those of 3 VII 81 for the two slopes show no significant difference ($\chi^2_3 = 4.1$), but those of 4 VII 81 do ($\chi^2_3 = 73.5$, $p < 0.001$). All (1980 and 1981) are significantly different from a random distribution around the stems (table 4.4.). Despite this heterogeneity, in all cases the highest number occurred on the NE side. The lowest numbers occurred on either the southern or western sides. There are too few data for juveniles to allow a comparable conclusion, although there is a similar overall trend.

4.3.2.2. Laboratory behaviour.

Taking each experiment individually, there were no significant differences in behaviour of the two morphs. Therefore the following results relate to both combined. There was no significant heterogeneity within each set of 5 experiments, so the results of each set can be combined (table 4.5.). Furthermore, there was no significant difference between the two sets with the light when the data from one set were reversed to allow comparability with those of the other; similarly for the two sets with wind.

The numbers on each quadrant in the control experiments do not depart significantly from the random expectation of equal numbers on each, but they do in the light experiments ($\chi^2_3 = 18.7$, $p < 0.001$) and the wind experiments ($\chi^2_3 = 77.6$, $p < 0.001$). The snails seek the most shaded or the least exposed side of the pole; and the response to the wind seems more pronounced than that to the light. They avoid most the quadrant directly facing the wind, but in the light experiments they appear to show the greatest avoidance of the quadrant to the right of the light (when looking at the pole from the position of the light source), whichever direction the light was shone from. This means that they avoid most the positions in which the underside is exposed to the light (since they usually come to rest with the shell aperture uppermost - see below, section 4.3.3.); the reason for this is not clear. They do also avoid the quadrant directly facing the light.

4.3.3. Discussion of behaviour.

It is well-established (e.g. Geiger, 1965; McQuaid, Branch and Frost, 1979) that when the sun shines on bare ground, the ground surface and the air adjacent to it reach a higher temperature than the air higher up. This is exemplified by data, from a site in southern Spain (Elviria, site 1 - appendix 2), of air temperature at ground level and 1 m above it, recorded hourly at 20 positions during a rather hazy day in late August (fig. 4.14.). If the ground is covered with thick, low vegetation, temperatures are highest at the top of this layer of vegetation, and lower both within it and in the air above it. If the ground cover is relatively sparse, the temperature profile approximates that over bare ground, although the air at ground level may not be as hot as in the absence of vegetation (Geiger, 1965). This appears to be the case at the Tenby study area, within which temperatures, recorded at 20 positions at intervals during a clear, but not very warm, and rather windy day in July, were higher in the low vegetation than in the air 1 m up adjacent to the tall stems (fig. 4.15.).

The selection, by adult *T. pisana* at Tenby, of summer daytime resting positions (they do not aestivate at Tenby) up the stems of alexanders and sea radish can be seen, therefore, as avoidance of high air temperatures near the ground. The distinct tendency to cluster on the stems, seen both in the field at Tenby and in the laboratory experiments, is explained by McQuaid, Branch and Frost (1979) as a further mechanism of thermal regulation, using the shade provided by other snails.

Direct solar radiation is partially reflected by the shell (Yom-Tov, 1971a), but some is absorbed by it and can then be conducted to the snail's body, and some is transmitted directly to the body (Emberton and Bradbury, 1963). Since the study site had aspects ranging from S to W, and was also obscured from the direct morning sun by the curve of the cliffs, the more westerly sides of the stems would be expected to receive most sun. Furthermore, Geiger (1965, p.383) showed that in general in the northern hemisphere the west-facing rather than the south-facing sides of tree trunks (or vertical stems) reached the highest temperatures. The prevailing winds in south-west Britain are onshore south-westerlies (Lamb, 1964). It is clear that the southern and western sides of the stems receive the most heat and are the most exposed, and indeed it is these which are avoided by the snails. Since the laboratory experiments showed that the snails avoided both light and and wind, the avoidance of the southern and western aspects of vertical stems can be explained as avoidance not only of high temperatures, in this case due to direct radiation, but also of the desiccating effects of the wind. The snails are still active well after dawn, and so both light and wind cues are available to them when choosing their resting positions.

Although the laboratory study suggested that wind elicited a more pronounced avoidance response, the relative importances of wind and light in the field cannot be determined since a light bulb does not have the same spectral characteristics as the sun. In fact, in the field the response to sunlight could be more important than to wind direction. The significant differences between the results from the different days and slopes in the field study could result from a crude response to the direction of sunlight, with superimposed fine adjustment due to wind direction.

Sacchi (1971) described *T. pisana* in the Mediterranean as aestivating preferentially on the shaded side of power poles, but gave no data. McQuaid, Branch and Frost (1979) gave data, pooled from five telegraph poles and presumably obtained on a single occasion, suggesting that *T. pisana*, introduced from the northern hemisphere to South Africa, aestivated on the more shaded sides. However, Pomeroy (1968), with data from only three power poles but obtained on two occasions from each (although with few data for the second occasion), suggested that *Cernuella virgata*, also introduced, to Australia, from the northern hemisphere, avoided the shaded sides. He explained this as the result of an inbuilt indentification of the northern side, perhaps implying a magnetic sense, an adaptive response evolved in the northern hemisphere, resulting in non-adaptive behaviour in the southern hemisphere. However, because of the pronounced tendency of *T. pisana* (and *C. virgata* - Pomeroy, 1968), to cluster on the stems,and possible very local differences in wind direction, data from five poles or fewer may be insufficient on which to base a general conclusion. Indeed, although Pomeroy combined the data from his three poles on the first occasion (his table 2) they are, in fact, heterogeneous ($\chi^2_6 = 79.0$, $p < 0.001$). The relative importance of wind and light may be different at different localities. In the hot climates in which these workers obtained their results, insolation may well be more important than wind, particularly as aestivating snails would be stuck down hard onto the substrate, but they discussed their data with no reference to the desiccating effects of the latter, and a combination of the two could perhaps explain the results more consistently. Clearly however, T. pisana, at least, is not restricted by any inbuilt identification of a particular compass direction; no such inflexibility has evolved in this species; it is capable of appropriate gross behaviour depending on which hemisphere it is in, and smaller-scale adjustment, to accommodate local insolation or wind patterns, as at Tenby.

McQuaid, Branch and Frost (1979) also found that most snails aestivated with the peripheral edge of the shell aperture uppermost so that the air-space in the body whorl (between body and aperture) was interposed between the most strongly insolated part of the shell and the snail's body. (This is also the case at Tenby). They suggested that it was a further adaptation to aestivation in exposed sites. This air-space acts (in Sphincterochila boissieri) as an insulation device against conduction from the substrate on which the snail is resting (Schmidt-Nielsen, Taylor and Shkolnik, 1971). Newell (1958a,b) showed that winkles on vertical surfaces come to rest with the head uppermost, a similar position to that just described for T. pisana, perhaps for reasons of stability. However, the upward-facing attitude of aestivating or inactive T. pisana may be simply a result of the snails climbing up the stems and coming to rest with no further adjustment of their orientation. Similarly, the incidental observation, during the present study, that snails tend to rest on the undersides of sloping stems, may be due simply to their finding themselves in these positions more often as they climb up the main stems and out along the side stems. The advantages of these behaviours in relation to solar radiation may be incidental, although selection will operate to prevent their changing.

Those juveniles which ascend the stems of alexanders and sea radish during the day-time show similar preferences in both height and aspect to the adults, but the majority of juveniles remain in the low vegetation beneath these tall plants. Both the leaves and stem surfaces of living alexanders and sea radish are eaten by <u>T. pisana</u> at Tenby (personal observations), but many helicids are known to prefer dead or senescent plant tissue (see e.g. Boycott, 1934; Mason, 1970; Williamson and Cameron, 1976) which tends to be found on or near the ground surface, although some wind-damaged tissue may be available higher up. Other broad-leaved plants, which probably form part of the diet of <u>T. pisana</u> at Tenby do not grow tall as do the alexanders and sea radish, but, with grass, are constituents of the low vegetation preferred by the juvenile snails as resting sites. Growing juveniles no doubt require an easily accessible source of suitable food. The alexanders and sea radish, particularly their hard stems, may only be appropriate for adult snails. The length of time available for feeding may be particularly important for juveniles (Pomeroy, 1969), and so the time and energy required to descend and ascend the tall stems would be wasteful. Furthermore, since snails are known to be least active in conditions of low humidity (Wells, 1944; Pomeroy, 1969; Bailey, 1975; Cameron and Williamson, 1977), the higher humidity in the low vegetation would mean that the nocturnal period of activity could be lengthened somewhat if the snails remained within it.

As has been inferred above, (section 4.2.3.) juveniles are more prone to desiccation than adults, and so the preference may be for the higher humidity, per se, in the low vegetation . On the stems above it, the desiccating effects of the less humid air will be further enhanced by the greater wind speeds (Geiger, 1965; McQuaid, Branch and Frost, 1979).

Since juvenile shells are thinner than adult shells (chapter 8, section 8.3.), and thinner shells transmit more light (Emberton and Bradbury, 1963) and probably, therefore, more heat, to the animal, the juvenile shell may be inadequate protection from insolation if the animal is exposed up the stems rather than remaining in the somewhat more shady lower vegetation. If this were the case, adult snails could escape the heat of the ground, but juveniles would be forced to tolerate it. This explanation is perhaps less likely than the two suggested above, since in Mediterranean habitats, all snails are forced off the ground to aestivate, and all tolerate the insolation they are thus exposed to (personal observations); and at Tenby, in the absence of low vegetation, juveniles do climb the stems (personal observations). It is possible that if juveniles are forced to climb up high, they may suffer greater mortality, but no evidence is available for this.

4.4. General Discussion.

The climbing and orientation behaviour of T. pisana must be absolutely necessary in mediterranean habitats where the air temperature at ground level even on a fairly hazy day (fig. 4.14.), may exceed the upper lethal temperature (figs. 4.9. and 4.10.). This applies to both adults and juveniles, and indeed I have never seen either aestivating on the open ground surface (neither has it been reported - e.g. Germain, 1930; Sacchi, 1971, 1974). Even when off the ground, some mortality may occur, and in particularly hot summers can be considerable (Johnson, 1981). The alternative heat-avoidance strategy of hiding in shady places or burying underground has been reported on a few occasions for T. pisana (Jeffreys, 1862; Dürr, 1946; Sacchi, 1974; Humphreys, 1976), but the authors all noted that few individuals employed it. However, it is well-known in many other species (see e.g. Pomeroy, 1968; Yom-Tov, 1971b), and indeed, half-grown juvenile T. pisana at Tenby use such a strategy for avoidance of low temperatures during the winter when they hibernate (chapter 3, section 3.2.1.2.). Even at the northern limits of its range, where it does not aestivate, the daytime climbing behaviour of T. pisana in the summer may still be necessary to avoid the heat of the ground, although perhaps not as vital as in hotter localities. The temperatures measured in the low vegetation at Tenby (fig. 4.15.) did not approach the lethal limits, but they were not taken on a particularly hot day. Temperatures on bare ground would be much hotter. Richardson (1974) has suggested that Cepaea nemoralis (from a climatically similar locality), although only slightly less tolerant of high temperatures than T. pisana from Tenby, can be killed by overheating if it finds itself on the ground surface and exposed to the sun on a hot day. In fact, temperatures somewhat below the upper lethal limit must be avoided since the sub-lethal effects of exposure to high temperatures will be important (Cowles, 1965).

The apparent absence of any morph differences in either temperature tolerance or behaviour needs discussion. The present study of temperature tolerance has been concerned only with ambient temperature, and there is no *a priori* reason to assume that snails of different morphs would necessarily have different tolerances. Both Sedlmair (1956) and Lamotte (1959, 1966) have shown tolerance differences between morphs of *Cepaea nemoralis* and *C. hortensis* (Müller), but the effects of exposure to ambient temperature may have been confounded in these experiments with those due to direct radiation from the heat source. Further, Lamotte (1966) showed differences in tolerance when snails of different morphs were exposed under a light bulb; but the radiation characteristics of light bulbs may not mimic those of the sun sufficiently accurately for much reliance to be placed on these results. However, differences between different colour forms in internal temperature when exposed to sunlight are known in many groups of animals including snails (Clarke, 1967; Heath, 1975; Garcia, 1978). Darker forms attain higher temperatures than paler ones, and so animals living in hotter climates tend to be paler in order to reflect more radiation (e.g. Yom-Tov, 1971a). In cooler climates, ectothermic animals may be darker in order to absorb more radiation, allowing longer periods of activity (Kettlewell, 1973). This has been suggested for *C. nemoralis* by Jones (1973 a,b). Further, seasonal changes in climate and energy requirements may force an animal to adjust its reflectivity during growth (the work of Heller and Volokita (1981a,b) on the Israeli snail *Xeropicta vestalis*). Diurnal variation in colour as a temperature-regulating mechanism is also known (e.g. in crabs - Wilkens and Fingerman, 1965). Since these various studies show that shells of different morphs will reflect different amounts of radiation, and thus under equivalent conditions, the snails would attain different internal body temperatures, differences in temperature-regulating behaviour might be expected, particularly if snails of different morphs show no difference in tolerance of such high internal temperatures (experiment 4, table 4.1., fig. 4.7.). Correspondent differences in behaviour of different morphs of C. nemoralis and C. hortensis in temperature gradients have been found by Sedlmair (1956) and Lamotte (1959). Differences have also been found in C. nemoralis under more natural conditions in outdoor cages by Tilling (reported by Jones, 1980).

T. pisana is near the northern limit of its range at Tenby, and body temperatures may rarely approach the upper lethal limit. Indeed, the shells of Tenby snails are generally darker (although the banded/unbanded polymorphism is retained - see chapter 6) than those from Mediterranean habitats (chapter 6, section 6.5.), which suggests that they may be adapted for increased absorption of solar radiation (see also the discussion of geographical distribution in chapter 2, section 2.4.2.). However, the climbing and orientation behaviour, a vital adaptive response in the hotter climates in which T. pisana evolved (chapter 1, section 1.3.), is retained at Tenby even though it may be less necessary. Differences in behaviour between morphs would then be less pronounced, and the failure to find them may have been due to the coarseness of the observations taken.

Furthermore, only a few aspects of behaviour have been investigated in this study; there may in fact be no morph differences in these anywhere in the species' range. Johnson (1981) has shown morph differences in choice of aestivating site, more-banded snails seeking shadier habitats, and further differences may exist in other, uninvestigated facets of the snails' temperature/desiccation-related behaviour, such as the time the snails leave their daytime resting sites for the period of nocturnal activity, and the time they subsequently return. Livshits (1981) has shown differences in burrowing activity, migration and preference for shade between banded and unbanded morphs of Brephulopsis bidens (Kryn.) and related these to their different thermal tolerances. Wolda (1965a) showed morph differences in tree-climbing behaviour of C. nemoralis, and these may be related to temperature and/or desiccation regimes (cf. Jaremovic and Rollo, 1979).

Fig. 4.1. Preliminary experiment

a - % mortality after 5 days
b - % not moved after 24 hours
c - % not moved after 1 hour

- - - - - - 1 hr exposure
.... 2 hr exposure
——————— 3 hr exposure

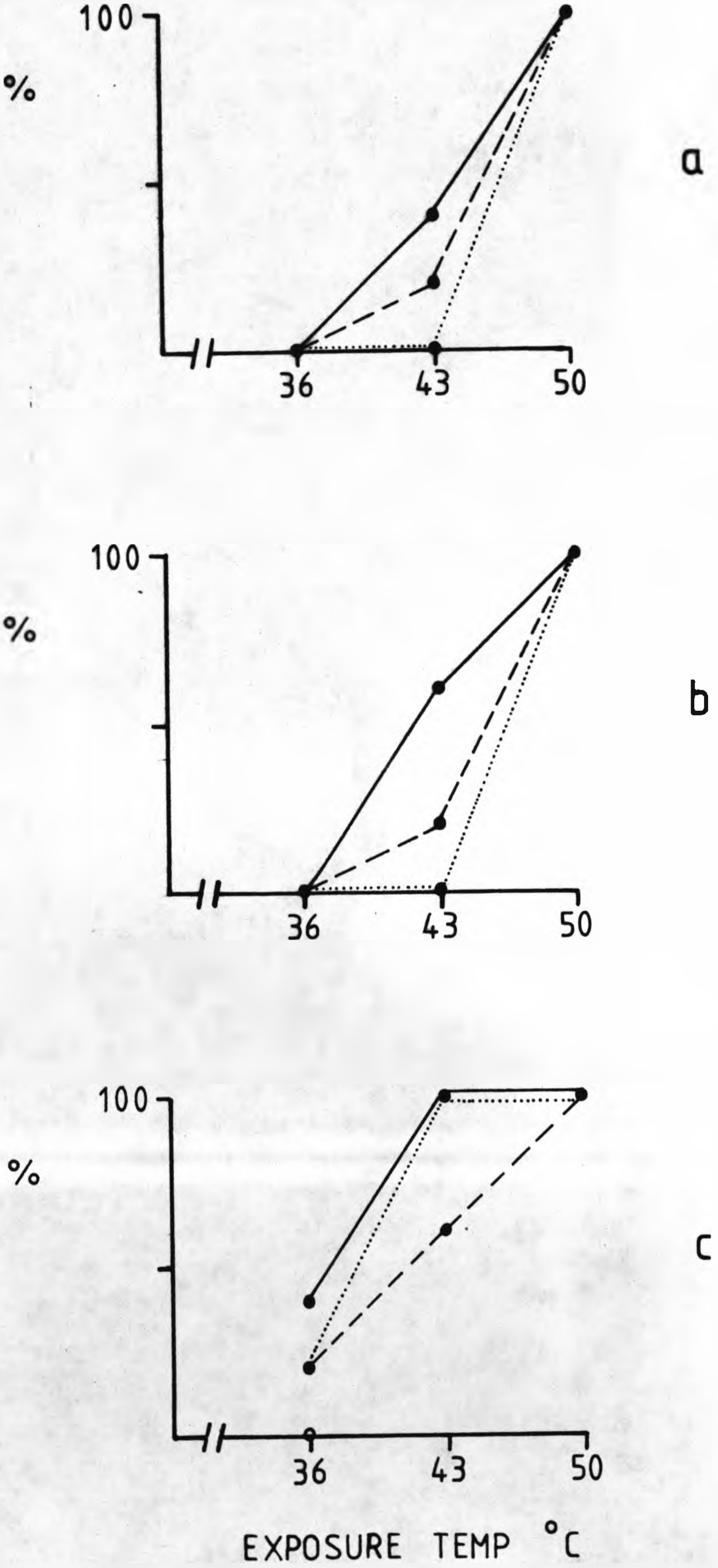
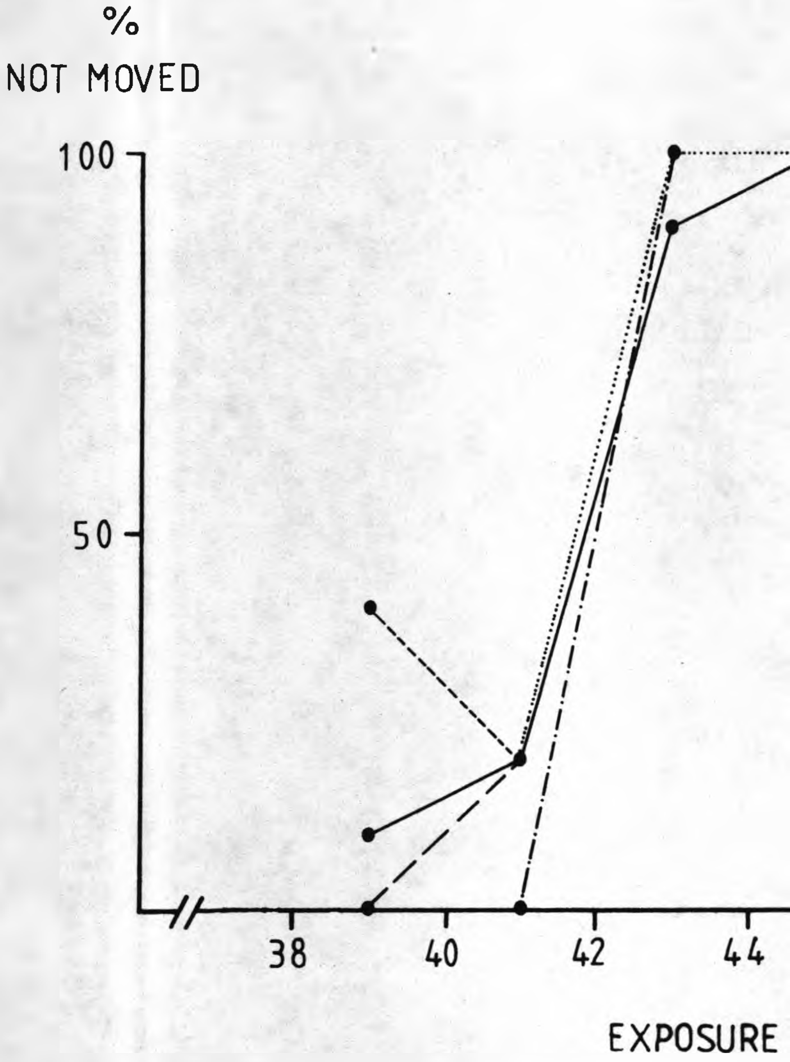

100
%
36
43
50
a
100
%
36
43
50
b
100
%
36
43
50
c
EXPOSURE TEMP °C

Fig. 4.2. Experiment 1 - no movement after 1 hr.



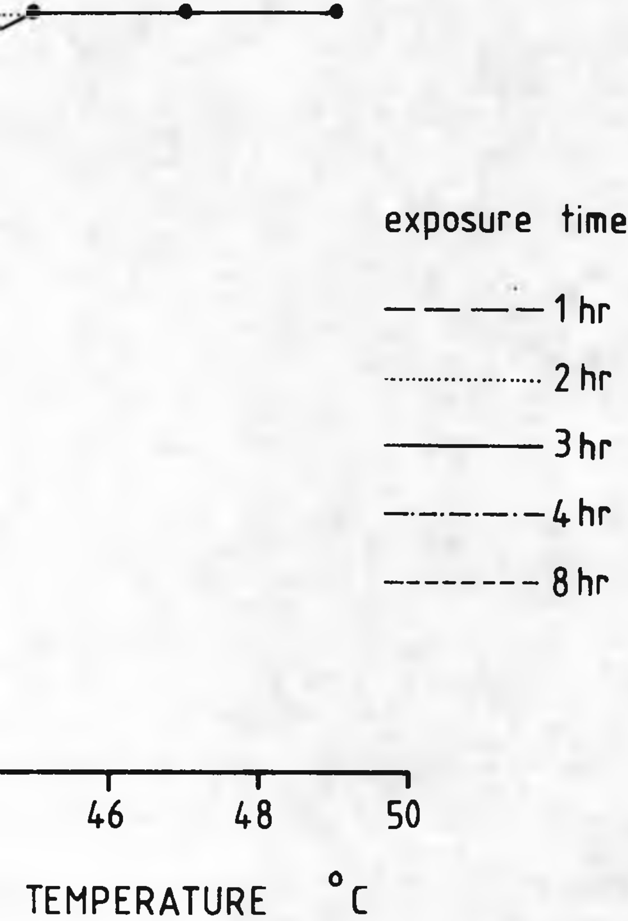

exposure time
1 hr
2 hr
3 hr
4 hr
8 hr
46
48
50
TEMPERATURE °C

Fig. 4.3. Experiment 1 - no movement after 24 hr.

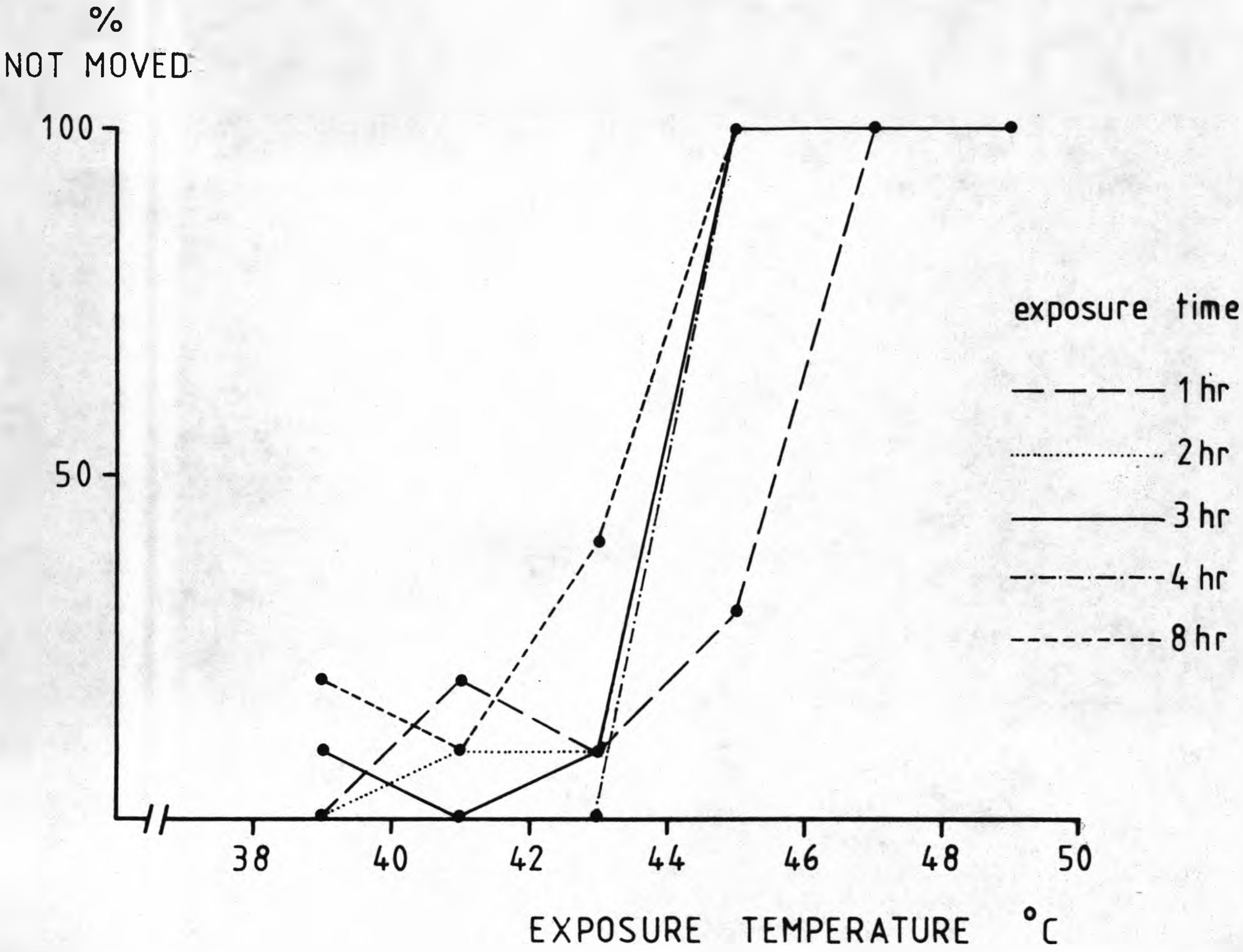


Fig. 4.4. Experiment 1 - mortality after 5 days.

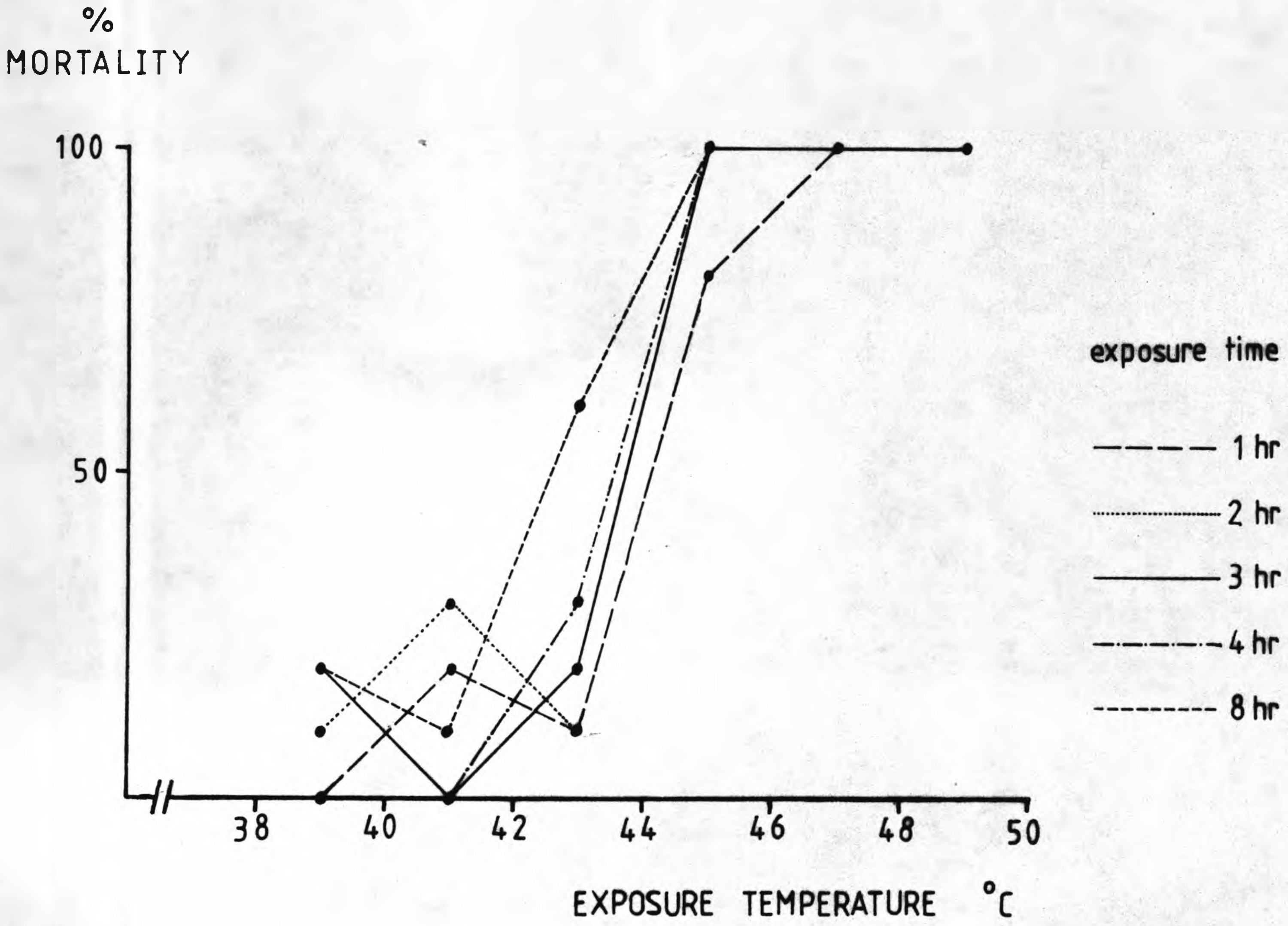


Fig. 4.5. Experiment 2 - Tenby adults and juveniles; dry and humid tubes; mortality after 5 days

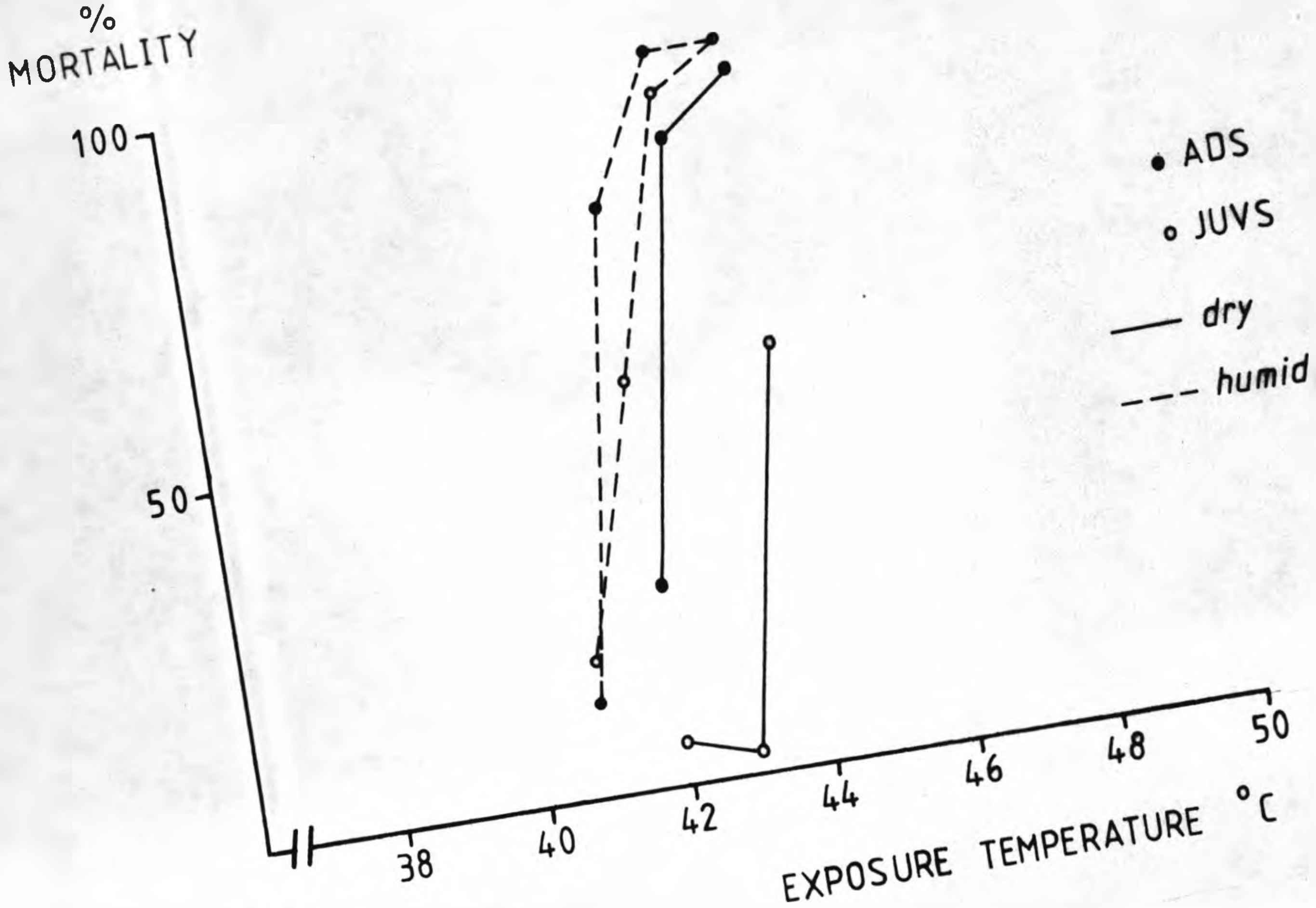
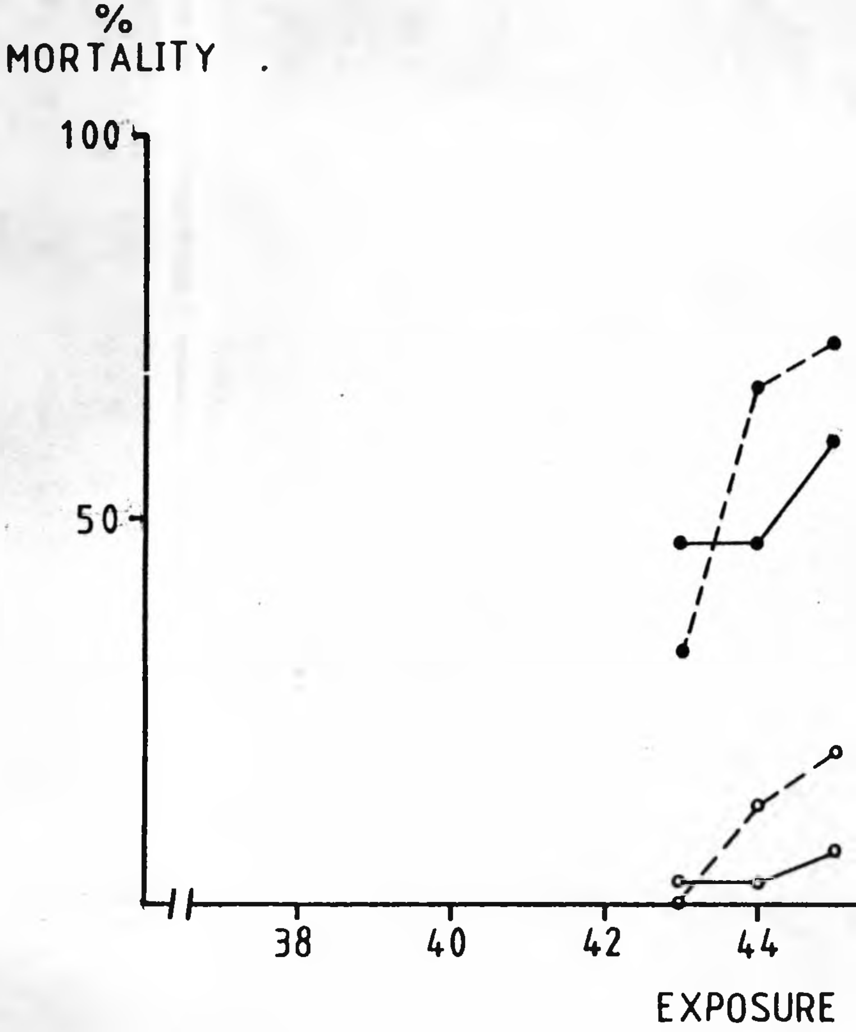


Fig. 4.6. Experiment 3 - Tenby adults and juveniles; mortality after 5 days.



laboratory aestivated and active;

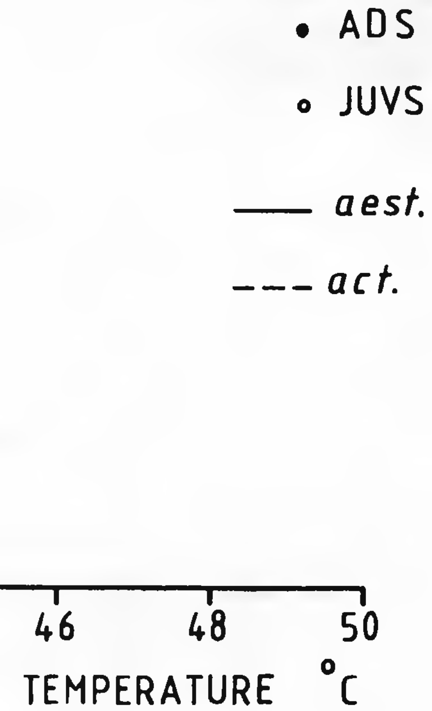


Fig. 4.7. Experiment 4 - Tenby adults; different morphs; mortality after 5 days.

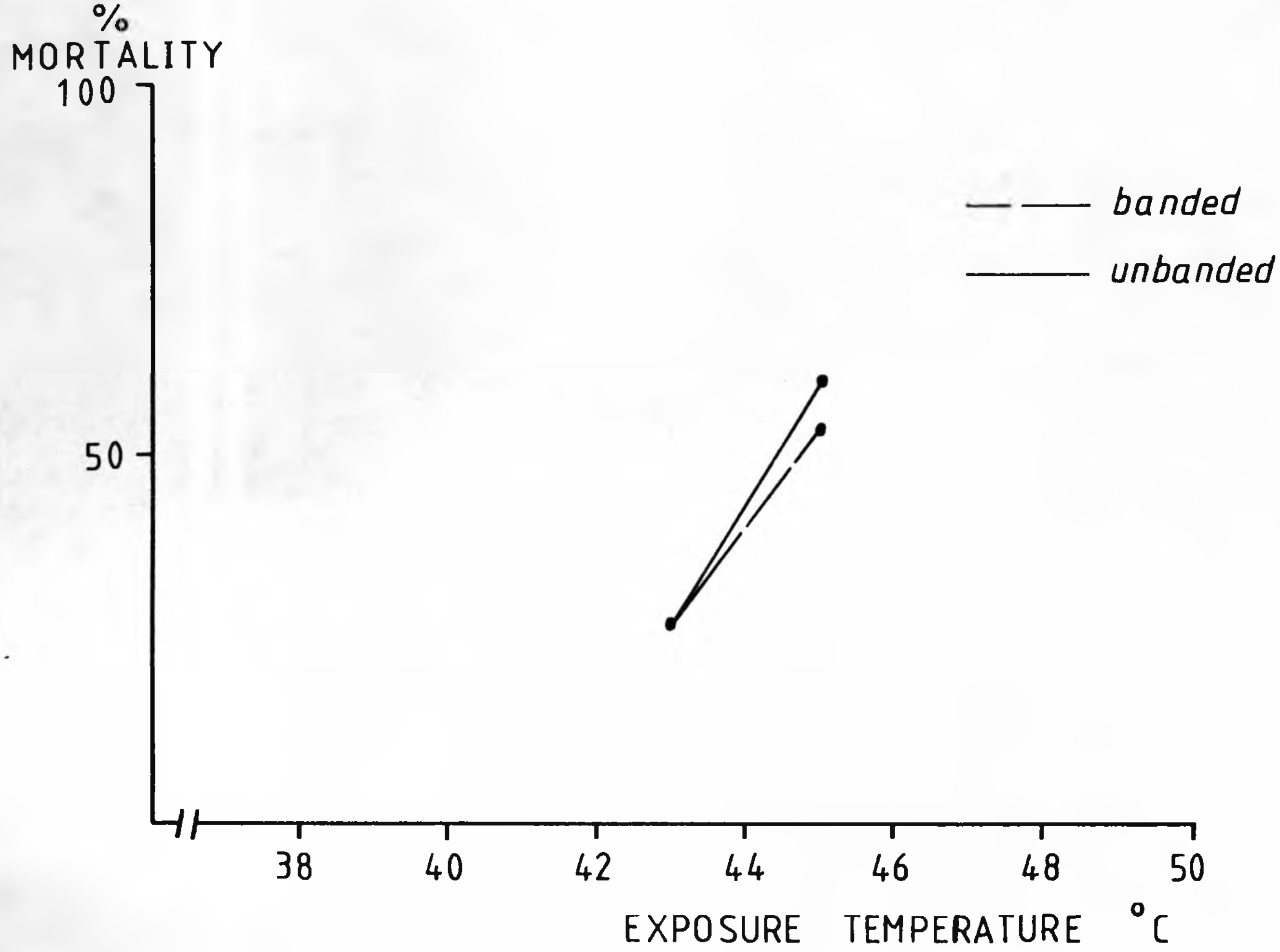


Fig. 4.8. Experiment 5 - Tenby snails; three narrow size ranges; mortality after 5 days.

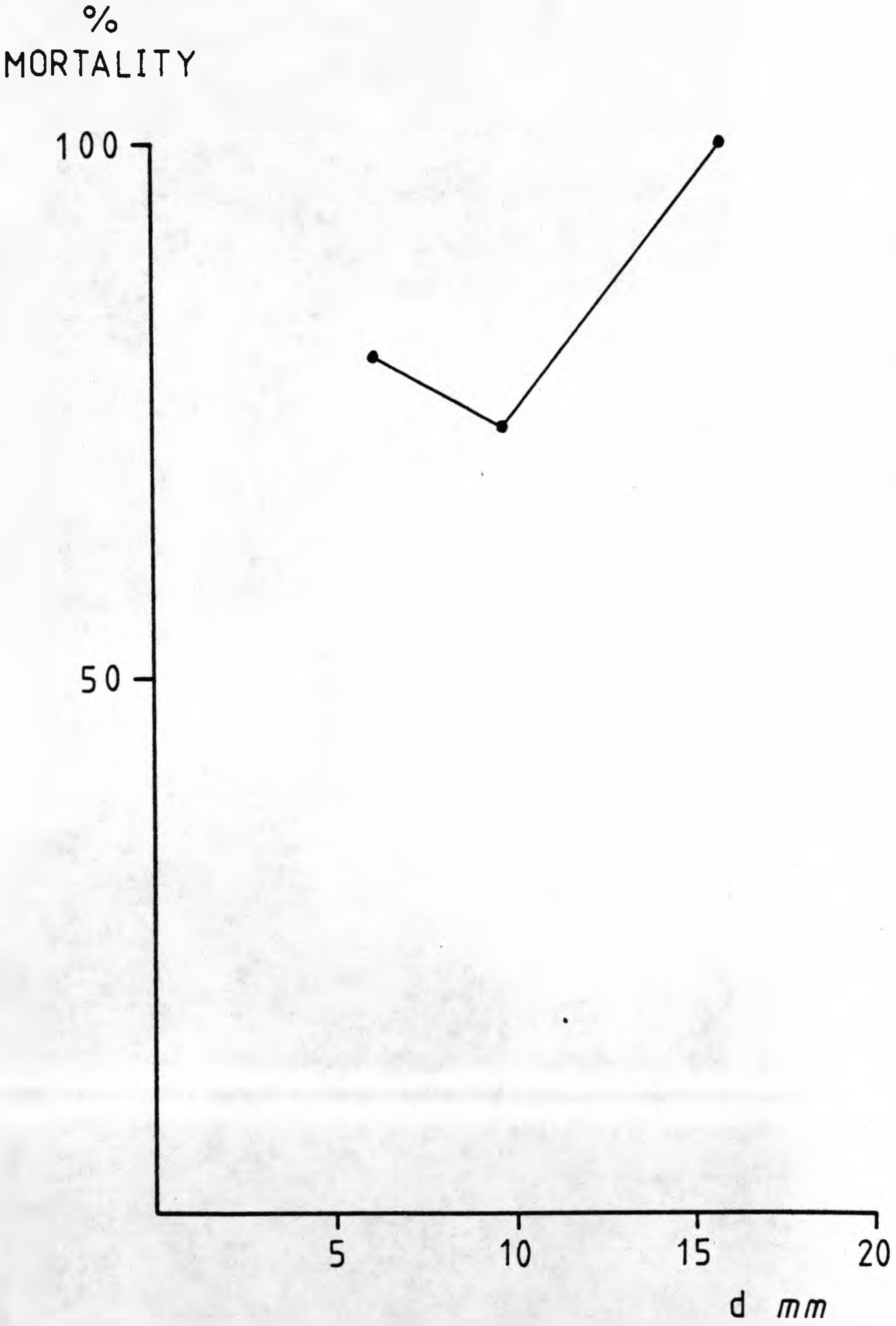


Fig. 4.9. Experiment 6 - Spanish juveniles; aestivating; mortality after 5 days.

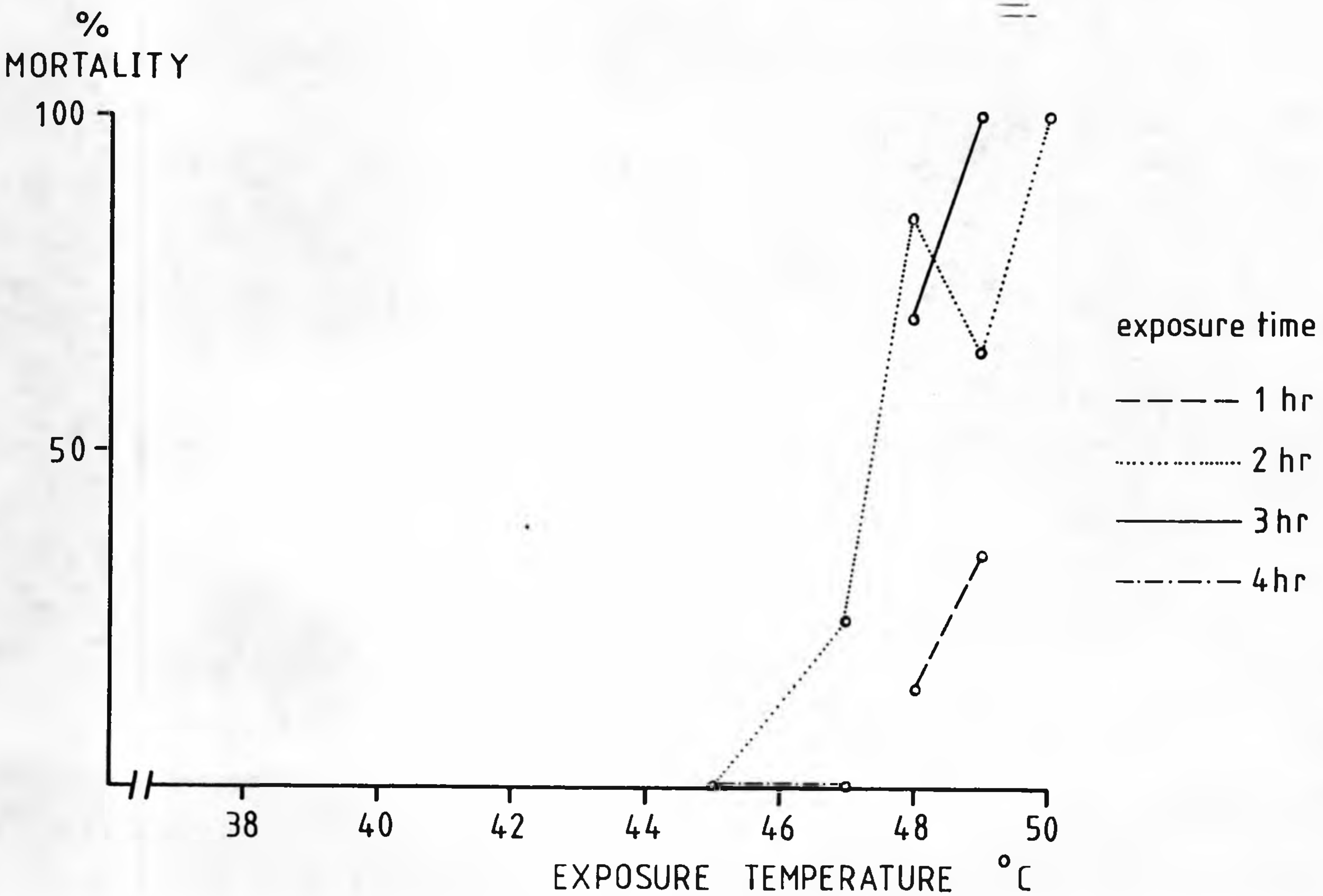
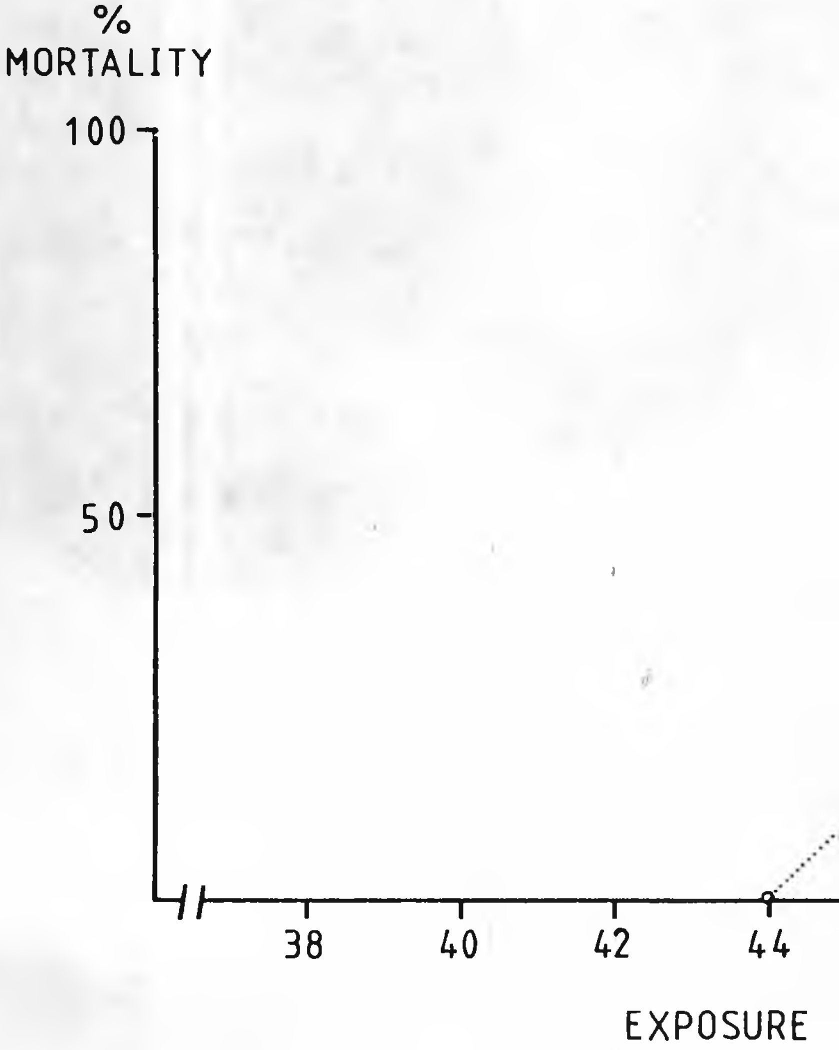


Fig. 4.10. Experiment 7 - Spanish juveniles; active



; mortality after 5 days.

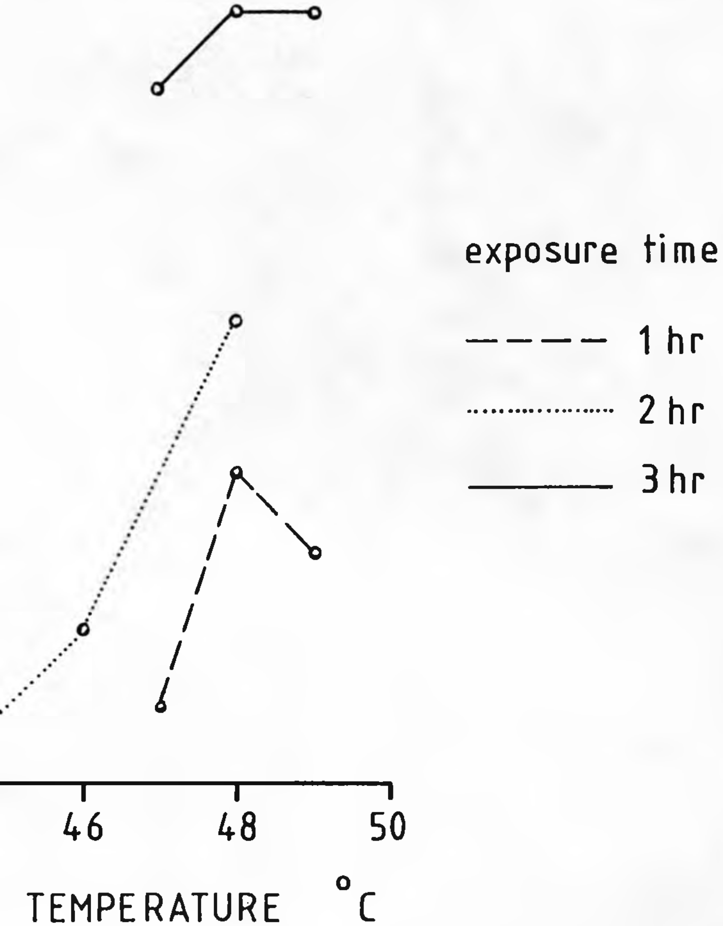


Fig. 4.11. Adult snails resting during the daytime on stems of alexanders at Tenby.

Fig.4.12. HEIGHT DISTRIBUTION OF ADULT *T. PISANA* ON STEMS - 10,11,12·7·80

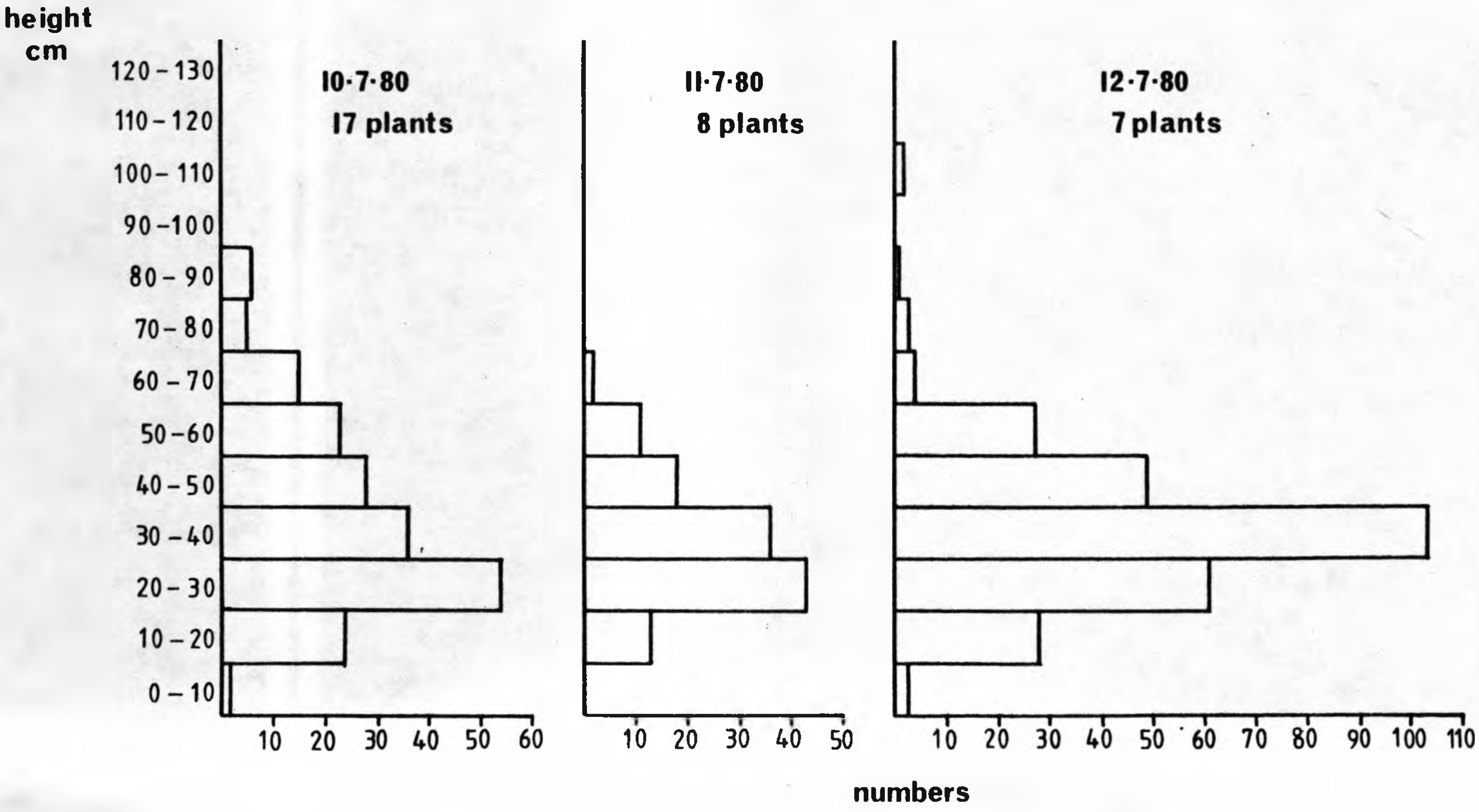


Fig. 4.13. HEIGHT DISTRIBUTION OF JUVENILE (& INTERMEDIATE) T. PISANA ON STEMS - 10,11,12·7·80

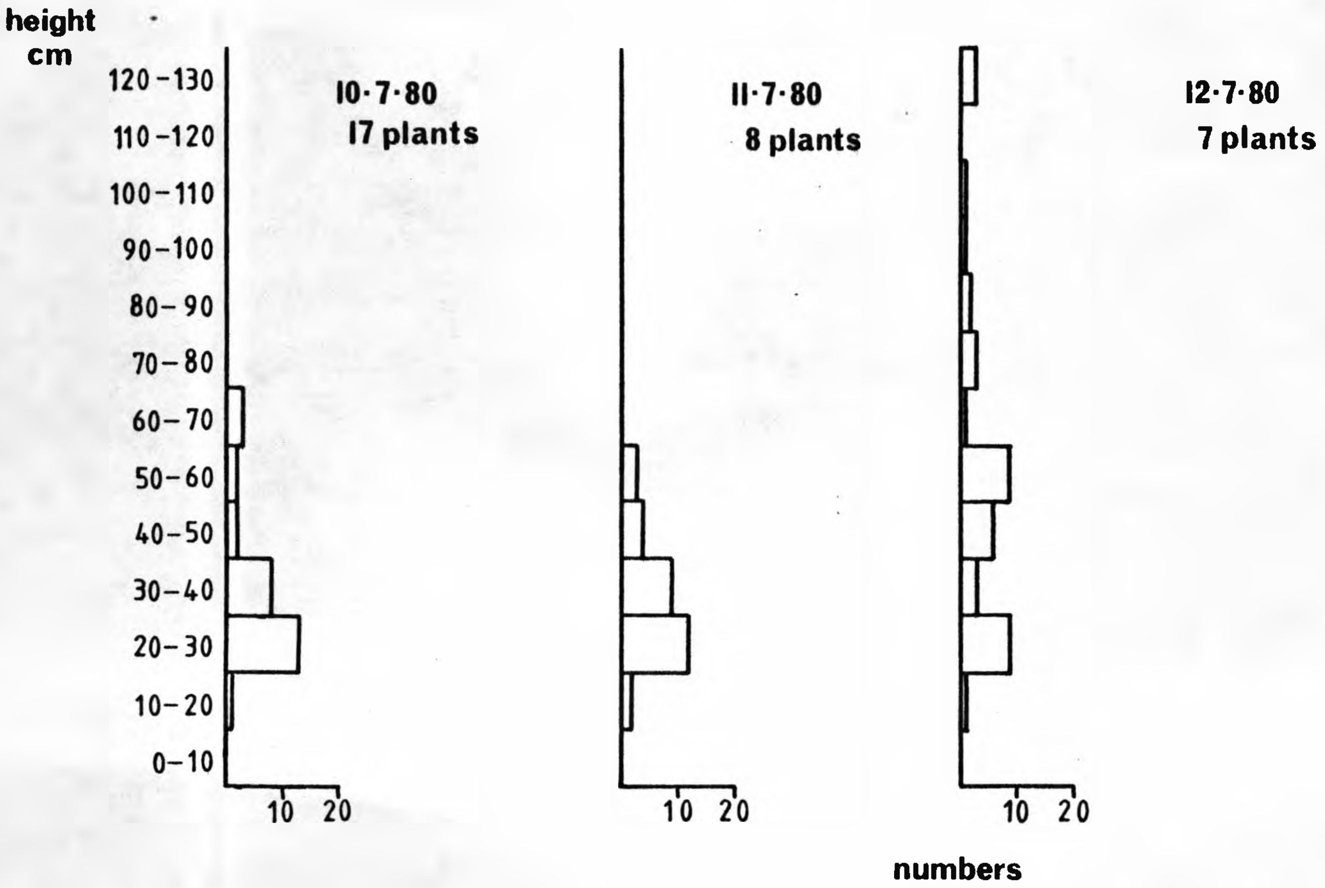


Fig. 4.14. air temperatures at ground level and 1 m up - Spain.

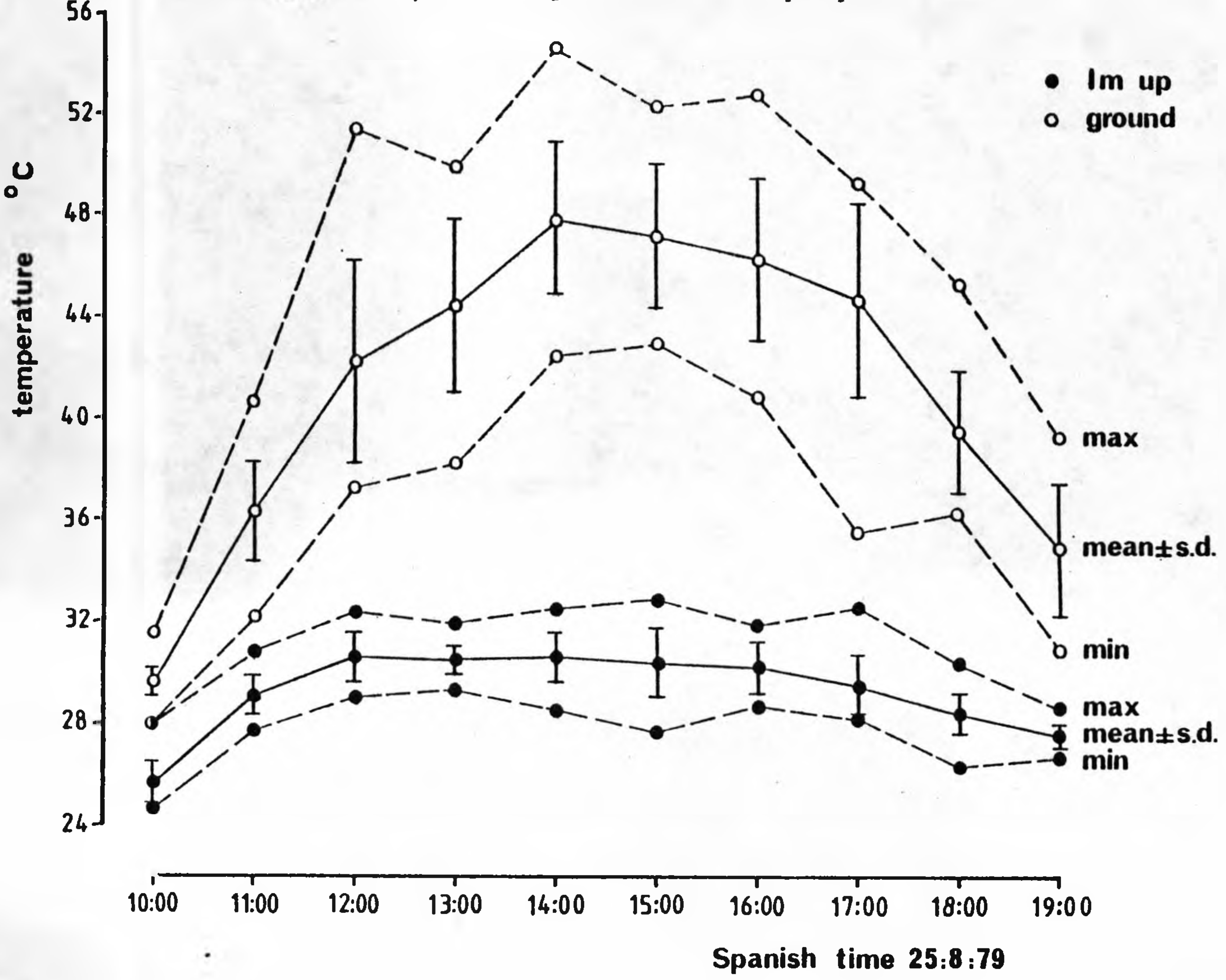


Fig. 4.15. air temperatures at ground level and 1 m up - Tenby.

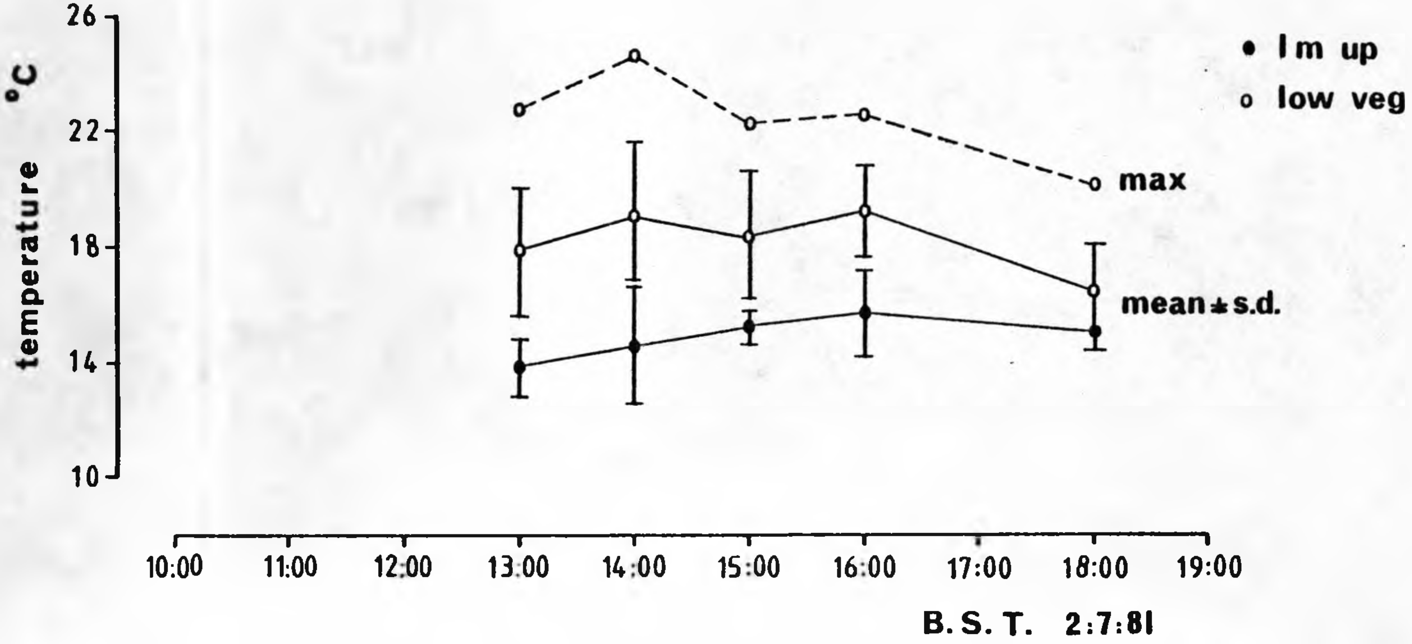


Table 4.1.

Summary of temperature tolerance experiments.

experiment	collection locality	collection date	experiment date	snails	pre-treatment and experimental set-up	number per regime	fig.
1	Tenby	11.7.79	8,9.8.79	adults	regularly active - main experiment	10	4.2. - 4.4.
2	Tenby	11.7.79 13.9.79	31.10.79 - 8.11.79	adults and ½ - grown juvs.	regularly active - dry and humid tubes	adults 25 juvs. 36	4.5
3	Tenby	13.9.79	12,13.12.79	adults and ½ - grown juvs.	regularly active & lab. aestivated	adults 15 juvs. 30	4.6
4	Tenby	2.7.81	4.8.81	adults - unbanded and dark banded	regularly active	unbanded 15 banded 15	4.7
5	Tenby	11.7.79	12.8.79	three narrow size ranges	regularly active	each class 30	4.8.
6	Spain	27.8.79	5,7.9.79	juveniles	kept dry between collection and experiment - wild aestivation not broken	45° - 10 47° - 4 48° - 20 49° - 20 50° - 4	4.9
7	Spain	27.8.79	24.10.79	juveniles	regularly active	10	4.10.

Table 4.2.

Results of experiment 1.

exposure temperature °C	exposure time 1 hr	2 hr	3 hr	4 hr	8 hr
	number not moved after 1 hr				
39	0	0	1	0	4
41	2	2	2	0	2
43	9	10	9	10	10
45	10	10	10	10	10
47	10	10	10	10	10
49	10	10	10	10	10
	number not moved after 24 hr				
39	0	0	1	0	0
41	2	1	0	0	1
43	1	1	1	0	4
45	3	10	10	10	10
47	10	10	10	10	10
49	10	10	10	10	10
	mortality after 5 days				
39	0	1	2	0	2
41	2	3	0	0	1
43	1	1	2	3	6
45	8	10	10	10	10
47	10	10	10	10	10
49	10	10	10	10	10

Table 4.3.

Preference of adults (a) and juveniles plus intermediates (j) for tall stems or low vegetation.

date	plant	snails	tall stems	low veg.	p
11.7.80	1	a	10	25	<0.05
		j	0	12	
	2	a	12	25	n.s.
		j	0	5	
	3	a	15	11	n.s.
		j	4	5	
	4	a	43	6	<0.001
		j	15	22	
	5	a	4	10	n.s.
		j	0	3	
	6	a	7	28	n.s.
		j	1	19	
	7	a	14	7	<0.05
		j	1	6	
	8	a	18	12	<0.001
		j	9	42	
12.7.80	9	a	122	8	<0.001
		j	13	43	
	10	a	90	21	<0.001
		j	14	61	
	11	a	9	19	<0.05
		j	1	21	
	12	a	7	8	n.s.
		j	2	12	
	13	a	7	13	n.s.
		j	5	19	
	14	a	12	13	<0.001
		j	0	48	
	15	a	34	14	<0.001
		j	4	18	

Table 4.4.

Preference of adults for the four quadrants of stems, with significance of departure from random distribution.

date	aspect of slope	NE	NW	SW	SE	χ^2	p
10,11,12.7.80	mixed	132	63	95	120	28.8	<0.001
3.7.81	190°	155	61	51	121	75.8	<0.001
3.7.81	250°	137	38	30	102	103.6	<0.001
4.7.81	190°	194	147	50	39	158.5	<0.001
4.7.81	250°	100	58	58	93	19.5	<0.001

Table 4.5.

Preferred quadrants on the wooden pole in the laboratory.

Experiments	A	B	C	D
control	102	107	93	92
light towards A	83	99	121	79
light towards C	113	74	96	105
wind towards A	50	84	149	104
wind towards C	142	117	70	92

Chapter 5

Population Structure and Effective Population Size

5.1. Introduction.

Knowledge of population structure is essential for estimating the relative efficacy of natural selection and random drift in the determination of genetic diversity. This chapter presents the results of a study of T. pisana in the Tenby colony. The dispersion (the pattern of spatial distribution) of the snails has been measured so that population density estimates obtained from samples can be correctly understood. Dispersal has also been measured, to obtain some idea of the potential for colony extension or colonisation of new areas, and, when combined with density estimates, to allow estimation of the neighbourhood size. Estimates of the effective population size are then obtained and discussed.

5.2. Dispersion.

Individuals may be dispersed randomly within the habitat; they may be over-dispersed (towards a regular pattern); or they may be aggregated. From the numbers of individuals in a series of random samples of appropriate size, the deviation from randomness may be tested. If dispersion follows a Poisson distribution, the variance to mean ratio of the numbers in the samples is equal to unity. Departure towards regularity gives a ratio of less than unity, and towards aggregation (contagiousness), of greater than unity. The significance of the departure from a Poisson distribution (i.e. random dispersion) can be tested by the index of dispersion (Southwood, 1978):

$$I_D = \frac{S^2 (n - 1)}{\bar{x}}$$

in which $\bar{x}$ is the mean, S^2 is the variance, and n is the number of samples taken. I_D is approximately distributed as χ^2 with n - 1 degrees of freedom (Seber, 1973; Southwood, 1978). Greig-Smith (1964), Southwood (1978) and Seber (1973) have discussed this and other measures of dispersion, and their limitations. The simple index, above, although not independent of density and quadrat size (Skellam, 1952) is appropriate in the present study.

The study of T. pisana at Tenby was carried out in July, 1981 when there were two distinct size classes within the population. At this time the trough between these classes in the size-frequency distribution of samples combined from all sites at Tenby (chapter 3, fig. 3.5.) occurred at approximately 18 mm (h + d); i.e. snails of 18 mm and over belong to the adult class, smaller snails belonging to the half-grown juvenile class (see chapter 3). Thirty random quadrats (0.25 x 0.25 m) were thrown within the area of about 25 x 5 m which constitutes site 2 (see appendix 2), and the numbers of snails in each of the two size classes found in each quadrat were recorded. Little difficulty was encountered in allocating snails by eye to one or other of these classes. Such a sampling procedure may be prone to some personal bias; edges of the site are often undersampled (Greig-Smith, 1964; Southwood, 1978). However, the method is sufficiently accurate for the present study. The numbers in each sample and the calculated values of $\bar{x}$, S^2 $S^2/\bar{x}$ and I_D for the adult and juvenile snails are presented in table 5.1. The values of I_D (582 for adults, 77 for juveniles) indicate aggregation, and the significant difference of the variances (247 for adults, 34 for juveniles; F - test, $p < 0.02$) suggests that the large snails were more aggregated than the small ones.

Aggregation has previously been reported both for T. pisana (Lazaridou-Dimitriadou and Daguzan, 1981) and for other species of snail (e.g. Baker, 1968; Pomeroy, 1969; Crook, 1980), and is consistent with the observed behaviour of the snails in the field. It can result in two ways: selection of preferred areas within the habitat, and/or some form of interaction between individuals (e.g. Hamilton, 1971). The latter may be important on a very small scale; T. pisana forms clusters on the stems it uses as resting sites, perhaps benefiting from the shade of other snails (McQuaid, Branch and Frost, 1979; chapter 4 of this thesis). However, the aggregation observed in this study is almost certainly due to selection of particular plants for resting positions (and perhaps also for food). The greater aggregation of the larger snails is probably a result of their preference for the tall stems of alexanders (at this site), whereas the juveniles, remaining in the lower vegetation which covers most of the study area, are less restricted (chapter 4, section 4.3.).

5.3. Density.

The 30 quadrat samples used to estimate dispersion at site 2 have also been used to estimate population density. These data give mean population density estimates of 197 m^{-2} for the larger snails and 203 m^{-2} for the smaller snails at site 2. Three samples, large enough for the study of the life-cycle (see chapter 3, section 3.2.1.1.), were also taken at the same time from areas of high density at this site (the aggregations described above - section 5.2.). The ratio of mean density obtained from the 30 quadrat samples to mean density obtained from these three samples has been used to convert densities calculated from life-cycle samples (from aggregations) taken at other times and from other sites (listed in appendix 2), to overall population densities comparable with that obtained from the 30 quadrat samples from site 2. These can only be very rough estimates since the degree of aggregation may differ from time to time and place to place, and the life-cycle samples may not all have been taken from biologically similar aggregations. Further, Zippin (1956) has shown that such removal methods of estimating population density are not very precise. At the time when the quadrat samples were taken (July, 1981), the large snails recorded in the quadrats approximately corresponded to those snails with $h + d \geqslant 18.0$ mm taken in the life-cycle samples (see above - section 5.2.). Since the snails begin to breed during August (chapter 3), these snails of 18 mm and over roughly constitute the breeding adult population for that year, important in the estimation of effective population size. Separate estimates of density of snails over and under 18 mm have been made at each site, and only for the period between 22nd June and 31st August of each of the years in which samples were taken. At sites where more than one sample was taken on a particular sampling occasion, and/or in years when there was more than one occasion between these dates, the samples were combined by taking the mean value.

The resulting estimates are presented in tables 5.2. and 5.3. (The data upon which they are based are available in appendix 3). Ranging from mean values of 39 to 202 m^{-2} (adults) and 13 to 436 m^{-2} (juveniles), these are within the very broad range of estimates given by Basinger (1927), Hickson (1972), Lazaridou-Dimitriadou and Daguzan (1981), Johnson (1981). Hickson's estimates (6 - 33 m^{-2}) are of total population density in duneland areas which, from his descriptions, were probably more sparsely vegetated than the Tenby sites, and more similar to the Spanish sites (described in appendix 2), where population density, although not estimated, was certainly lower than at Tenby. Johnson's estimates (2.6 - 4.0 m^{-2}), also low, were of adults only, and from a similar habitat. Lazaridou-Dimitriadou and Daguzan gave values of 1 - 9 m^{-2} in duneland, and 110 - 1200 m^{-2} in a more densely vegetated habitat. These figures are extremes for a whole year, and include both adults and juveniles; the higher figure of 1200 m^{-2} probably occurred during the breeding season. Basinger's estimate of well over 200 m^{-2} (21 per square foot) includes all age classes; his remark about the La Jolla colony describes well the main areas inhabited by T. pisana at Tenby:

> ' ... it is hardly putting it too strongly to say that Helix pisana occurred on, under, and in everything'.

Certainly, T. pisana is well known (e.g. Taylor, 1912; Germain, 1929, 1930) for its ability to reach densities much higher than many other species of terrestrial snail (e.g. Helix aspersa Müller - Potts, 1975; Crook, 1980; Cepaea nemoralis (L.) - estimates of various authors, summarised by Williamson, Cameron and Carter, 1977; Aegopinella nitidula (Draparnaud) - Mordan, 1978; Caracolus carocollus (L.) - Heatwole and Heatwole, 1978). Higher densities, approaching those attained by T. pisana, have been reported for species of Cerion Röding by Woodruff (1978), for Candidula intersecta (Poiret) (= Helicella caperata (Montagu)) by Baker (1968), and for Cernuella (= Helicella) virgata (da Costa) by Pomeroy (1969), although in both the latter cases the highest densities were only attained immediately after breeding. However, Pomeroy (1968) did give a photograph of aestivating C. virgata in South Australia which suggested that it existed in similar abundance to T. pisana; indeed both species have become pests in this region (chapter 1, section 1.3.).

5.4. Dispersal.

Dispersal of T. pisana at Tenby was measured by releasing snails marked with a spot of enamel paint on the shell apex from a central release point. Release of individually marked animals from where they are found is theoretically preferable in this kind of study, since it reduces the effects of unnatural dispersal due to disturbance, overcrowding at the release point, and situation of the release point in an unfavourable microhabitat (Cowie, 1980a). However, this was not practicable in the present study; 200 near adults and 200 approximately half grown juveniles were released (during the afternoon of 9th July, 1980) from within a 10 cm radius of a marker stake at each of two sites (sites 2 and 6 - appendix 2). The snails had been collected from these sites immediately prior to release. Marked snails were recovered the following afternoon and the distances travelled by those that were found were recorded. The snails were then returned to within 10 cm of the marker stakes. Dispersal distances were again measured after about 100 days (17, 18 October, 1980). On this occasion only live snails were returned to the release points, dead ones being removed from the sites to avoid recording them on subsequent occasions. Further searches were made on 8th April, 1981 and 2nd, 3rd July, 1981.

The results obtained after one day and 100 days are presented as histograms (figs. 5.1. and 5.2.). Following Kerster (1964) and Greenwood (1976), variance of dispersal along one axis (required for the estimation of effective population size) has been calculated as half the variance of dispersal in all directions (absolute or radial dispersal), which was measured, from the relation used by Cowie (1980a, after Dobzhansky and Wright, 1943):

$$\text{Variance of absolute dispersal} = \frac{\sum r^2 f}{n-1}$$

in which r is the median value of each 10 cm class in the histograms, f is the number of observations in each class, and n is the total recaptures. These variances are given in table 5.4. If dispersal from the release points were random (i.e. it followed a random-walk, Brownian motion or diffusion model), the histograms would appear as half normal distributions with the vertical axis being at the release point (Fletcher, 1974; Taylor, 1978). Dispersal of organisms has often been found to be non-random (e.g. Dobzhansky and Wright, 1943; Cowie , 1980a) and described by logarithmic curves of the exponential family (Freeman, 1977; Southwood, 1978; Taylor, 1978). Furthermore, if dispersal were random, and rate of dispersal constant, variance of dispersal would increase linearly with time (Lamotte, 1951; Greenwood, 1974). Although in all cases (table 5.3.) the variances in this study are greater over 100 days than over one day, they are not 100 times greater. In fact, it was clear that after one day most snails had moved away from the release points to particular patches of vegetation; after 100 days, many were still in these patches. Clearly, a mathematical analysis of the distributions of dispersal distances in this study is inappropriate. After a further six months (October, 1980 - April, 1981) only six marked snails were found (four juveniles, one of which had grown, at site 2, and two empty juvenile shells at site 6) and all were within 1 m of the release points. In July, 1981 (the final search), one marked snail was found at each site, both within 1 m of the release point.

These results suggest that the release points were situated in less than favourable microhabitats, and that the high dispersal after one day resulted from the snails moving away until they found a more favourable one, even if only 20 cm away. Having found such an area they tended to remain there. It could also result from overcrowding at the release points, although this produced no significant effect in a study of dispersal in two other species of snail (Cowie, 1980a). There was a suggestion that snails may have tended to move away from the release points in particular directions, but no data were collected to test this. The differences in dispersal between the two sites, and between the larger and smaller snails at each site, reflect the distances the preferred areas were from the release points, and the different microhabitat preferences of the two size classes (chapter 4, section 4.3.). (Differences in dispersal of snails in different microhabitats has also been shown by Cowie (1980a) for Cernuella virgata). The bimodal appearance of the adult distribution after one day at site 2 simply reflects the distances from the release point of two preferred areas, not one, as for the juveniles, and for both at site 6. Adults can certainly move faster than juveniles, but this is unlikely to be important since dispersal distances were well within the capabilities of both, even allowing for the contorted nature of the paths taken. Although snails which had moved very great distances were less likely to be found than those which had moved only short distances, rapid dispersal from the unfavourable release points may mean that the estimates of variance of dispersal are over-estimates, release points in favourable areas, or with less crowding, giving lower values.

The values of variance of dispersal obtained in this study are of a similar magnitude to those given by Hickson (1972) for T. pisana in South Africa (0.159 - 1.052 m^2, for 1 - 3 weeks). They are also similar to those given by Cowie (1980a) for Candidula intersecta (0.052 - 0.175 m^2, for one day) and Cernuella virgata (0.172 - 2.479 m^2, for one day), and to those calculated from the data of Paul (1978) for Trichia plebeia (Draparnaud) and Aegopinella nitidula (table 5.5.). All these estimates, although for shorter periods, are much smaller than those given by Greenwood (1974) for Cepaea nemoralis (30 - 100 m^2 per year) and by Crook (1980) for Helix aspersa (17 - 45 m^2 per year). However, although larger' snails can move faster than smaller ones, this may be of minor importance since H. aspersa appears to disperse less than C. nemoralis despite being much larger. This may result from some form of homing behaviour or restriction of activity to limited areas as has been described for a number of species of terrestrial mollusc (Pollard, 1975b; Potts, 1975; Heatwole and Heatwole, 1978; Cook, 1979a,b). Habit may be more important than speed, and T. pisana, although not a great deal smaller than C. nemoralis, appears to be very sedentary by comparison. However, this may not be the case in all habitats of T. pisana; Johnson (1981) showed that although most of his snails remained within 5 m of the release points, a small number travelled much further (40 m in one case) over the winter active season at his Australian site. His populations were rather sparse, and it may be that in habitats which can only support small numbers, T. pisana must move greater distances to obtain food, mates, etc.

Dürr (1946) described a similar experiment to that reported here, carried out in South Africa. He concluded that T. pisana showed a 'reluctance to migrate'. Humphreys (1976) provided some evidence that T. pisana is rather sedentary at St. Ives. However, this study was based on only a small number of snails, and, since the St. Ives colony is restricted by physical barriers (car park, footpaths, mown areas of turf), his results may indicate the general habit of T. pisana there, but fail to show the occasional wandering individual. This criticism can be levelled at all these studies, since snails moving long distances from the release point are less likely to be recaptured than those moving only a short distance, and indeed it is the distance moved by the former which will give an indication of the colonising potential of the species. Although no snails were recovered more than 3 m from the release points, the present study shows that adult T. pisana can travel at least 1.6 m overnight. Hickson (1972) gave an estimate of 35 years for 5 per cent of his population to travel 50 m. This estimate, however, was based on movement of snails during the relatively dry summer when they would be least active, and, as Hickson acknowledged, the measurements were taken in vegetation, whereas snails on the bare sand would probably travel much faster than he had shown. For colonisation of a new area from an existing colony as densely populated as that at Tenby, a much smaller proportion than 5 per cent needs to travel to it. Indeed Johnson and Black (1979) have calculated the rate of linear expansion of an introduced colony of T. pisana on Rottnest Island off Western Australia for a period of over 50 years, and gave a figure of 21 m per year. Paul (1978) and Cowie (1980a) have both commented that some other species may be able to colonise a new area rapidly. Although Cowie's study was not carried out in a habitat suitable for T. pisana, one of the species in this study, Cernuella virgata, is often found in such habitats (e.g. sand dunes). C. virgata was shown to be capable of travelling at least 3 m overnight; and indeed Pomeroy (1969) has indicated that it can colonise new areas at a rate of about 50 m per year. It is clear that T. pisana, despite its generally sedentary habit, is capable of rapid colonisation.

5.5. Effective population size.

If the population is sufficiently small, fluctuation in gene frequency can result from genetic drift. Wright (1931) introduced the concept of the 'effective' population size, as the size of the ideal population equivalent genetically to a real population. Developing this concept, he used the terms 'neighbourhood' and 'panmictic unit' to mean the population from which the parents of an individual can be considered to be drawn, and that in which mating is potentially at random (Wright, 1943, 1946, 1951). Dobzhansky and Wright (1943, p.335) estimated the neighbourhood area as the area of a circle of radius $\sqrt{2}\,\sigma$, where σ is the standard deviation of dispersal per generation along a single axis. Later, Wright (1946) doubled this estimate, such that it became the area of a circle of radius 2σ. Thus,

$$\text{Neighbourhood area} = 4\pi\sigma^2$$

Hence, if d is the density of the breeding population, neighbourhood number (N) for a 2-dimensional population is given by the relation

$$N = 4\pi\sigma^2 d \text{ (Wright, 1969)}$$

The variance of dispersal along a single axis for T. pisana at Tenby has been estimated for a period of 100 days during the active season as between 0.489 and 1.601 m^2 (section 5.4., table 5.4.). The snails are active at Tenby from about early April until late October (7 months), although some activity takes place all year round. Since they die soon after breeding, the lifetime and generation time are approximately equivalent, and equal to about two years (chapter 3). Therefore, if variance of dispersal increased in proportion to elapsed time, and adult and juvenile dispersal were similar, its value per generation would be about four times that for 100 days. Since the snails appear fairly sedentary (section 5.4.), this would probably be an over-estimate, although nothing is known of dispersal of newly-hatched juveniles. Since it is important to obtain a minimum estimate of neighbourhood size (Begon, Krimbas and Loukas, 1980), the values of variance obtained for 100 days, although themselves probably over-estimates for this shorter period (see section 5.4.), will be used as the minimum estimates of the true variance of dispersal per generation. Variance per generation is therefore taken as lying between 0.489 m^2 (100 days, site 6, juveniles) and 6.404 m^2 (4 x 100 days, site 2, adults). These values give a neighbourhood area of between 6.1 and 80.5 m^2, which combined with the estimates of breeding adult density (section 5.3., table 5.2), give the neighbourhood number (N) for each year treated separately as between 240 and 16257 (table 5.6.).

The effective population number (N_e) may depart from the neighbourhood number (N) under certain conditions (see Murray, 1964; Wright, 1969; Greenwood, 1974). The effects on the present study are now dealt with in turn.

(i) sex-ratio not unity.

The term sex-ratio is redundant in a hermaphrodite species such as <u>T. pisana</u>.

(ii) non random fertilisation.

In an obligate outbreeding hermaphrodite fertilisation is not completely at random since self-fertilisation is ruled out.

In this case N_e will differ, but only slightly, from N:

$N_e \simeq N + 0.5$ (Wright, 1969, p.212)

Clearly this is of no importance in the present study.

Non-random fertilisation could also be caused by non-random mate selection. Assortative mating, effectively by increasing inbreeding, will reduce the estimate of N_e; disassortative mating will increase it. Unfortunately the quantitative effects of non-random mating have only been discussed in relation to gene frequencies, and not effective population size (Wright, 1969; Crow and Kimura, 1970). It has not been investigated in T. pisana, but neither Lamotte (1951) nor Wolda (1963) could find any evidence for it in Cepaea nemoralis in terms of shell colour variation and shell size; this is the only information available for snails. It may occur, if at all, only to a very small extent, and as Greenwood (1974) remarks, it may only cause effective number to depart by a few percent from the actual number.

(iii) non-random dispersal.

Dispersal is certainly not random (section 5.4). However, Wright (1951) remarked in passing that N_e was determined 'largely irrespective of the form of the distribution curve' (of dispersal), and later (Wright, 1969) showed that it varied little with changing kurtosis (at least in a two-dimensional habitat). It appears unlikely that non-random dispersal in the present study will alter the estimate of N_e greatly, particularly as extreme values have been used in arriving at an estimate of the neighbourhood number. It is possible that juvenile dispersal, particularly in the early stages after hatching, would be greater than measured in this study. However, this would increase the value of N_e and it is the minimum estimate which is important in showing whether drift could play a significant role.

(iv) fluctuating population size.

When density is fluctuating, the effective number is given by the harmonic mean of the number in successive generations, this enhancing the importance of the smaller values (Wright, 1938, 1940; Crow and Morton, 1955). Implicit in this is the assumption that, although population size is fluctuating, the fluctuation occurs around a constant average (see Wright, 1969, p.214), and indeed there is no obvious indication of an overall long-term trend from the (very approximate) estimates of population density used in this study (section 5.3., tables 5.2. and 5.3.). The reduction of the importance of the years with low population densities, because of multiple mating and sperm storage, has been ignored in the present study, since, although not negligible, it is likely to be of less importance in the approximately semelparous T. pisana than in the iteroparous C. nemoralis discussed by Murray (1964). Besides, it can only increase the estimate of N_e and the importance of a minimum estimate has already been noted. T. pisana is not absolutely biennial at Tenby, since some individuals probably reach maturity in only one year, others probably require three (chapter 3); the adult populations of two consecutive years are thus not entirely separate. However, in order to combine the values of N from each year, and to take account of fluctuations of density (if any), it seems a reasonable approximation to take the harmonic means of the estimates for 1977, 1979 and 1981, and of the estimates for 1978 and 1980. This has been done for each site separately, and ranges obtained by taking the means of the lower estimates, and the means of the higher estimates of N for each year (table 5.6.). The values obtained are given at the bottom of table 5.6.

(v) non-random variation in family size.

The family size is the number of individuals reaching reproductive maturity contributed to by each adult. In a population of cross-fertilising hermaphrodites (equivalent to a population of dioecious organisms - Wright, 1969) the mean family size will be 2 if the population size is constant; and if the contribution from each parent varies randomly according to a Poisson distribution (Falconer, 1960), the variance will also be 2 . If it is not, this may affect N_e considerably, since:

$$N_e = \frac{4N}{2 + V_f} \quad \text{(after Wright, 1969)}$$

in which V_f is the variance of family size. Direct information on V_f cannot easily be obtained from natural populations, but Crow and Morton (1955) have derived formulae relating it to the initial production of offspring, which is usually much easier to investigate. They produced two models, one based on random mortality of offspring between birth and maturity, and one based on mortality in family units. Greenwood (1974) combined these two models by introducing a term, U, denoting the proportion of the juvenile mortality occurring in family units, assuming a constant population size. He gave his formula as:

$$V_f = 2 + 4\ (V/M + (M - 2)U - 2) \big/ (M(1 - U) + 2U) \quad ,$$

correctly, it should read:

$$V_f = 2 + 4\ (V/M + (M - 2)U - 1) / (M(1 - U)+2U)$$

in which M and V are the mean and variance of the number of offspring produced. Since I have data on egg rather than juvenile production, I shall use U to denote egg as well as juvenile mortality. Values of the mean and variance of the number of eggs produced per pair (and therefore the number contributed to by each adult) have been obtained in a laboratory study (chapter 3, section 3.3.). The minimum estimate of the mean was 383 and the variance 204117. Greenwood (1974) argued that for *C. nemoralis* U would be unlikely to exceed 0.5 and was probably nearer 0.3, since firstly, genetic correlation between offspring of a single parent is low because of multiple mating; secondly, it is rare for whole clutches of eggs to die; and thirdly, juveniles disperse quickly after hatching so that each member of a clutch would not be subject to identical hazards. With regard to *T. pisana*, it has been inferred from breeding experiments (A. J. Cain, personal communication; my own observations) that it may mate with more than one partner. In the laboratory, hatchability seemed high (probably about 90%), and whole clutches rarely died. Most mortality probably occurs after hatching (see also chapter 3, section 3.2.1.2.). Although nothing is known about dispersal of newly-hatched *T. pisana*, on the basis of the adult and half-grown juvenile dispersal (section 5.3.) it may be less than for *C. nemoralis*. However, the value of N_e is robust to differences in U, particularly when U is low, and the value of 0.3 used by Greenwood seems to be appropriate for this study. Inserting these values of

M(383), V(204117) and U(0.3) into Greenwood's equation, we obtain $V_f = 11.62$. This yields a range of N_e from 93 (site 5, lowest estimate of $\tilde{N} = 317$) to 3329 (site 2, highest estimate of $\tilde{N} = 11337$).

At all stages of this study, the need for a minimum estimate of N_e has been borne in mind. It seems highly unlikely that dispersal variance per generation would be lower than the minimum estimate used, and although the estimates of density are approximate, the lowest has been used. However, the assumption of constant population size over the long term, although not contradicted by these estimates of density (tables 5.2. and 5.3.), may not be valid. The total numbers of snails collected from all sites on each sampling occasion of the life-cycle study (chapter 3, table 3.1), may suggest a slightly decreasing population. This would lower the estimate of N_e by an amount dependent upon whether it were the inbreeding effective number or the variance effective number (see Wright, 1969, p.211) which was being considered. Wright (1969, p.219) gave these as:

$$\text{Inbreeding} \quad N_e = \frac{N\bar{k}}{(\bar{k} - 1 + V_f/\bar{k})}$$

$$\text{Variance} \quad N_e = \frac{2N}{(1 + V_f/\bar{k})}$$

in which $\bar{k}$ is the mean family size. When population size is constant, as assumed above (i.e. $\bar{k} = 2$), these are equal. If the population were decreasing by 25% per generation ($\bar{k} = 1.5$), this would lower the minimum estimate of the inbreeding effective number to 58, and that of the variance effective number to 72 (for $\tilde{N} = 317$, $V_f = 11.62$). The estimate would be further lowered if the assumptions of random fertilisation and random dispersal were not true. Furthermore, if V_f were larger in the field than in the laboratory, because of greater differentials in fecundity and survival, the estimate of N_e would again be lowered.

The minimum estimate of N_e obtained in this study (93) is within the region in which it is difficult to discount drift as a potential force (Wright, 1943; Begon, 1977), particularly if selection coefficients were low; although Greenwood (1974), estimating N_e for C. nemoralis as more than 180, considered that his populations were large from the point of view of stochastic genetic processes. The upper estimate (3329) is, however, effectively infinite as far as such effects are concerned, and in such a population drift would be of no consequence. The true value probably lies somewhere between these estimates, in which case drift would be of little importance. However, in view of the possible further lowering of the minimum estimate of N_e if the Tenby populations are declining, as discussed in the previous paragraph, drift cannot be disregarded as a potential force in at least some parts of the colony.

Fig. 5.1. Distances travelled, grouped into 10 cm intervals, after 1 day

a - site 2 adults (162 recaptures, 81.0%)
b - site 2 juveniles (171 recaptures, 85.5%)
c - site 6 adults (167 recaptures, 83.5%)
d - site 6 juveniles (167 recaptures, 83.5%)

The scales for all are shown in the first histogram. No snails were recaptured dead.

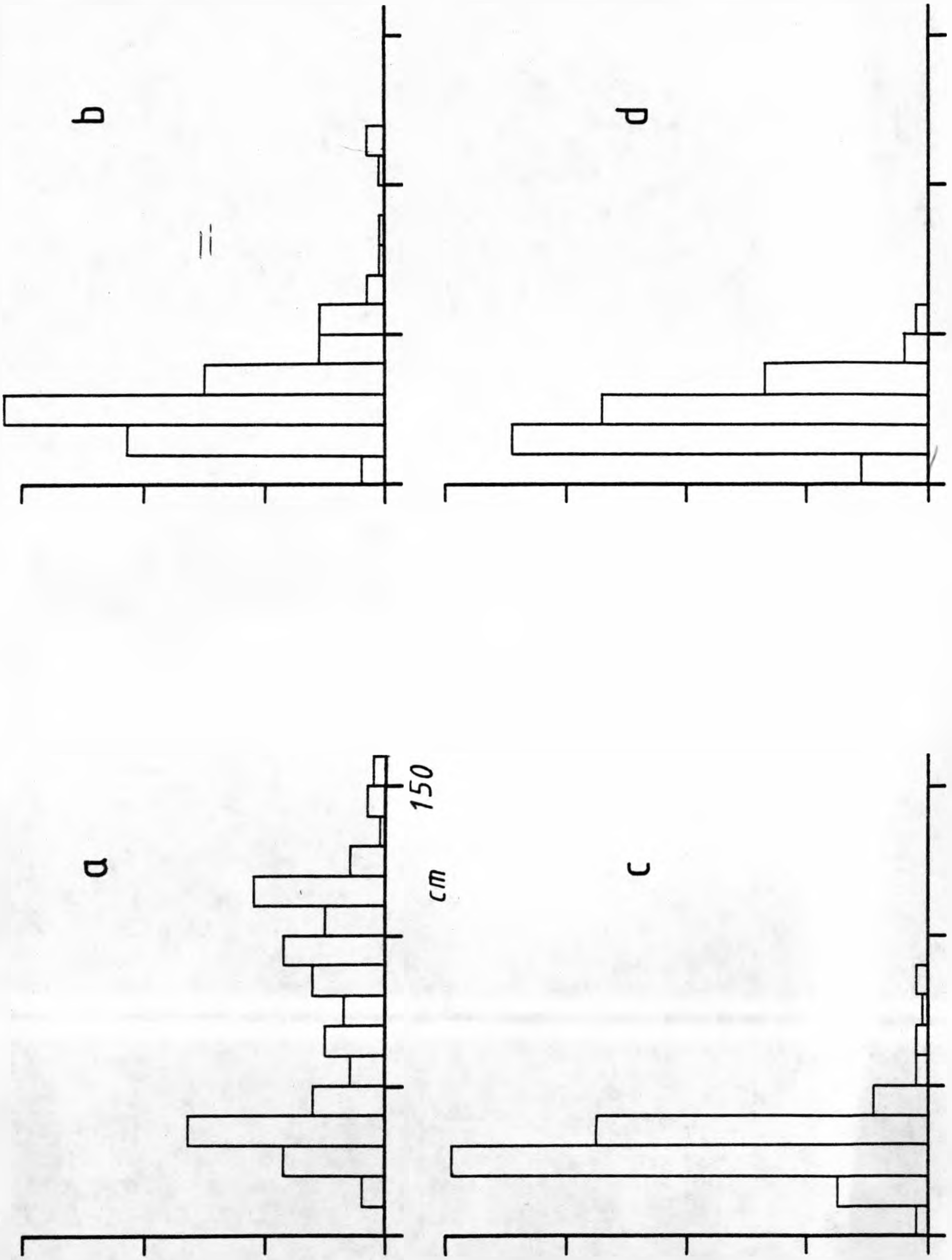
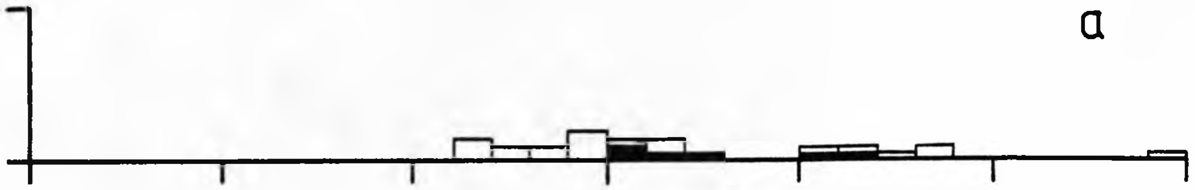

a
b
c
d
60
nos
cm
150

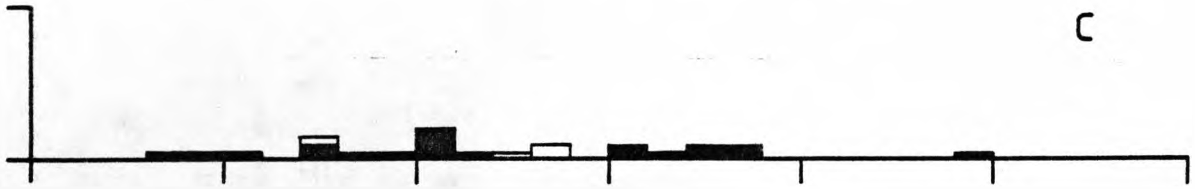
Fig. 5.2. Distances travelled, grouped into 10 cm intervals, after 100 days.

a - site 2 adults (26 recaptures, 13.0%)
b - site 2 juveniles (33 recaptures, 16.5%)
c - site 6 adults (24 recaptures, 12.0%)
d - site 6 juveniles (58 recaptures, 29.0%)

The scales are as in fig. 5.1. Shaded areas indicate snails recaptured dead.


a


b


c

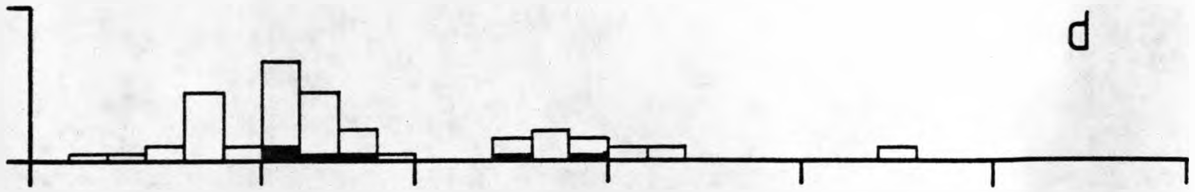

d

Table 5.1.

Numbers of snails in the quadrat samples, with values of $\bar{x}$, s^2, $s^2/\bar{x}$ and I_D.

sample	large snails	small snails
1	4	15
2	23	28
3	8	33
4	7	7
5	3	1
6	2	3
7	5	10
8	2	2
9	0	0
10	14	7
11	3	11
12	4	14
13	14	12
14	26	29
15	4	14
16	25	16
17	37	21
18	62	24
19	0	0
20	0	5
21	9	17
22	0	0
23	17	11
24	3	9
25	2	2
26	55	9
27	22	8
28	1	1
29	9	4
30	9	9
$\bar{x}$	12.3	12.7
s^2	247.0	33.8
$s^2/\bar{x}$	20.1	2.7
I_D	582.4	77.2

Table 5.2.

Estimates of numbers per m^2 (mean ± s.d. if based on more than one sample) of snails with h+d $\geqslant$18.0 mm during summer.

year	sample dates	site 1	site 2	site 3	site 4	site 5	site 6
1977	10.7.77 31.8.77	148±108	180±64	202±141	87±66	52±1	100±130
1978	22.6.78 5.8.78	92±70	126±44	110±1	100±35	98±13	113±64
1979	11.7.79	57±6	94±35	114	69±25	72	181
1980	11.7.80	55±6	-	77	88±3	86	-
1981	2.7.81	39±21	196±59	42	132±82	40	155

Table 5.3.

Estimates of numbers per m^2 (mean ± s.d. if based on more than one sample) of snails with $h+d < 18.0$ mm during summer.

year	sample dates	site 1	site 2	site 3	site 4	site 5	site 6
1977	10.7.77 31.8.77	411±229	417±213	436±274	145±143	113±64	235±100
1978	22.6.78 5.8.78	292±168	153±68	279±44	401±137	318±93	387±178
1979	11.7.79	97±69	77±47	258	198±52	100	223
1980	11.7.80	126±13	-	300	271±9	42	-
1981	2.7.81	154±57	203±144	19	134±52	13	397

Table 5.4.

Estimates of variance of dispersal in one axis, in m^2.

time since release	site 2		site 6	
	adults	juveniles	adults	juveniles
1 day	0.323	0.064	0.052	0.029
100 days	1.601	1.580	0.900	0.489

Table 5.5.

Estimates of variance of dispersal in one axis, in m^2, calculated from the data given by Paul (1978) for _Trichia plebeia_ and _Aegopinella nitidula_.

time since release	_T. plebeia_	_A. nitidula_
12hr 10min	0.099	0.050
23hr 30min	0.088	0.048
47hr 30min	0.212	0.063
108hr 30min	0.628	0.274

Table 5.6.

Estimates of range of N, with $0.900 < \sigma^2 < 6.404\,m^2$, and harmonic means, $\tilde{N}$, derived from them.

year	site 1	site 2	site 3	site 4	site 5	site 6
1977	910-11911	1106-14486	1241-16257	535-7002	320-4185	615-8048
1978	565-7404	774-10141	676-8853	615-8048	602-7887	694-9094
1979	350-4587	578-7565	701-9175	424-5553	442-5795	1112-14567
1980	338-4426	-	473-6197	541-7082	529-6921	-
1981	240-3139	1204-15774	258-3380	811-10623	246-3219	953-12474
$\tilde{N}_{1977,79,81}$	369-4825	866-11337	491-6433	549-7194	317-4154	839-10986
$\tilde{N}_{1978,80}$	423-5540	774-10141	557-7291	576-7534	563-7372	694-9094

Chapter 6

Shell Polymorphism

6.1. Introduction.

Theba pisana is renowned for the immense range of variation in shell pattern which it displays. Previous workers have failed to develop an adequate classification of this variation; for instance, Lamarck virtually gave up trying to describe the variation succinctly (Cain, 1981c); Germain (1929) concluded that all intermediates could be found between the numerous varieties then named; and neither Johnson (1980) nor Heller (1981) were able to do more than split their shells into three and five broad categories respectively. Heller (1981) hinted at some sort of genetic control of the variation, and quoted unpublished work by G. Lewis which indicated that an allele producing an unbanded shell was dominant to an allele for banding. Nothing further has been published regarding the genetics of shell pattern in T. pisana.

The purpose of this chapter is to present the results of a series of breeding experiments using specimens of T. pisana from the Tenby colony; and then, with this as a basis, to investigate the range of variation present in the field at Tenby, comparing this briefly with variation seen in samples from the Mediterranean region.

6.2. Breeding experiments and the genetics of the variation at Tenby.

6.2.1. Methods.

The original stock of breeding animals was derived from the Tenby colony. Only small juveniles were used for breeding since it is known that animals of under 10 mm diameter may be able to mate and breed successfully (Cowie, 1980b; chapter 3, section 3.2.). Further, only rapidly growing individuals were used. These precautions ensured the use of only healthy, virgin snails. Each pair was set up on soil in a plastic lunch box and maintained as described in chapter 3, section 3.3.1. When juveniles appeared, they were separated into a sufficient number of boxes to prevent gross overcrowding, but despite this, some animals became stunted, or growth was uneven, which in some cases masked the true banding pattern. However, most shells could be scored.

6.2.2. Description of banding morphs.

Shells of T. pisana, like those of most helicid species, are pentataeniate, as indicated by Taylor (1912); that is, they possess up to a maximum of five bands. The positions of these bands are shown in fig. 6.1. in which they are numbered in the standard fashion, starting with band 1 nearest the suture. (Heller (1981) has argued that T. pisana is in fact tetrataeniate; either his shells do not possess band 1, or their bands 1 and 2 are fused).

Although it is possible to use a simple banding formula as for Cepaea (see Murray, 1975), this does not by itself describe adequately the complex variation in T. pisana. The multitude of varietal names used within the species (Taylor, 1912) has no basis in the genetics of the variation, and so a new series of vernacular names plus modified formulae (see also Cain, in preparation) has been introduced to describe the consistent genetic forms which have been found. It is hoped that these will largely supersede the old varietal names.

The demarcation of the banding morphs rests heavily upon the results of the breeding experiments discussed below. However, for the sake of clarity, the appearance of each morph is described at this stage, and a selection of each is shown in fig. 6.2. The major division is between unbanded and five-banded shells; these two groups are then subdivided. In all groups, if growth is halted (for instance by overcrowding in the breeding box) but subsequently restarts, the pattern may appear to change abruptly. In all such cases, the shells were scored as belonging to the pattern before the change.

1. Unbanded

(i) Plain 00000 - The early whorls lack bands, but virtually all shells acquire some banding on later whorls. Lower bands, especially band 5, may begin earlier than the upper ones. There is much variation in the timing of the start of these bands (see fig. 6.2.). (To avoid the introduction of an over-complex nomenclature, these shells are scored as unbanded, although they may be different genetically from completely unbanded shells. This is discussed further below (section 6.6.)).

(ii) Dotty 00000 - In all respects similar to plain, except for the presence of a row of dots along, or just above, the keel of the shell, i.e. at the lower edge of band 3. This form, therefore, does not completely lack banding pigment on the upper whorls, but in order to obtain comprehensible results from the breeding programme it is necessary to consider both plain and dotty individuals as within the unbanded class. Shells with the faintest hint of dots have been scored as dotty.

2. Five-banded

(i) Dark 12345 - All bands are present. Each is more or less broken up longitudinally into fine, dark brown lines, which may themselves be broken transversely into dots and dashes, augmented with feathering along their edges, or fused to varying extents producing arrow-head shapes and blocks. This lineolation appears to be superimposed upon a yellowish-buff background band-colour, darker than the remainder of the shell. In most shells, dark lineolations are present on the upper bands (1 and 2 particularly) and on band 5 from the first whorl. Band 4 is the last to acquire them (usually during the third whorl).

(ii) Yellow 12345 - All bands are present, but only as the yellowish-buff background stripe. The bands are usually broken up transversely to some extent, and thus appear as a sequence of rather ill-defined blocks. No dark lineolations are superimposed, although there may be a hint of them in some shells, on both earlier and later whorls.

(iii) Intermediate forms (fig. 6.3.) - It is not clear whether any of these strictly constitutes a morph. The bands may be completely lineolate, but the lineolations being barely darker than the yellowish background stripe; with intermediates between this and the dark lineolate form (dark 12345). Alternatively, there may be very few lineolations, yet these very dark; again with many intermediates between this and the dark, fully lineolate form.

6.2.3. Relationships between banding morphs.

The results of all the matings are presented in table 6.1. They can only be understood in terms of a minimum of three loci:

1. Unbanded/five-banded

Combining all types of unbanded shells and all banded shells, in two classes, matings TP152, TP156 and TP180 (unbanded x unbanded) each show a good 3:1 ratio of unbanded to banded progeny. Matings TPR212 and F9 (unbanded x banded) gave only unbanded progeny. Clearly, unbanded is dominant to five-banded. The segregation is confirmed by matings TPR213, F11, F15, F16, F19, F20 and F29 (unbanded x banded) which gave 1:1 ratios. No banded x banded mating gave any unbanded progeny. No matings are difficult to interpret.

2. Plain/dotty

The 3:1 segregations in the progeny of matings TP155, TP171, TP172 and TP178 indicate that plain is dominant to dotty. The segregation is confirmed by 1:1 ratios in the progeny of TP160 and F9, and by both 3:1 and 1:1 ratios within the unbanded class of further matings in which other morphs appear: TP152 (3:1), TP156 (3:1), TP180 (1:1), F16 (1:1), F19 (1:1) and F29 (1:1). Matings, F11, F15 and F20 show the segregation but the numbers are too low to be sure of the ratio.

Since plain, dotty and banded individuals appear together in the progeny of these matings, a minimum of two loci must be involved. If plain and dotty are allelic, and banded is at a second locus, then the results of matings TP152 and TP156 can be explained as 9:3:4 ratios of plain: dotty: banded: TP180 a 3:3:2 ratio; F16 and F19 1:1:2 ratios. F11, F15, F20 and F29 are similar but with rather few progeny. In none of these matings is the effect of the dotty allele exhibited in the banded progeny; five-banded is presumably epistatic to dotty.

Four matings present difficulties of interpretation which, however, can be resolved. Mating TP156 is of a clearly dotty individual mated with one in which it is difficult to be sure of the presence of dots, these perhaps lie obscured in the suture. Despite one or both these parents being dotty, the progeny show a 3:1 ratio of plain to dotty. Since, therefore both parents must have been heterozygous (plain/dotty), in a small number of cases there must be penetrance of the dotty allele of heterozygotes, such that an animal which according to its genotype should appear plain, is in fact phenotypically dotty. This hypothesis can also be used to explain the results of matings TPR212 and TPR213 (both dotty x banded) Either (i) there is penetrance of the dotty allele in the unbanded parents, combined with a low number of dotty individuals (especially in TPR212) in a 3:1 ratio within the unbanded progeny (i.e. both parents were heterozygous plain/dotty); or (ii) the unbanded adult was in fact dotty genotypically as well as phenotypically (and the banded parent homozygous plain), and there was penetrance of the dotty allele in some of the progeny, which must all, in this case, be heterozygous plain/dotty. Either way, there must be penetrance of the recessive allele of heterozygotes. Since there is no clear bias towards plain in the numbers of progeny in the majority of these matings, either (i) penetrance of the dotty allele of heterozygotes does not occur in all matings, or (ii) it is balanced by non-expression of dotty in some dotty homozygotes; certainly the dots can be extremely faint and it may only be a small step to not being expressed at all. Indeed, the only logical explanation of the fourth difficult mating, TP180, is that one parent was homozygous dotty but failed to express the dotty phenotype; the other parent would then have been heterozygous plain/dotty, thus giving the 1:1 ratio within the unbanded progeny.

3. Dark/Yellow

This is the most difficult locus to interpret because of the occurrence in some matings of forms intermediate between dark and yellow. However, within other matings the banded progeny are all very similar to each other, and are either yellow (TP169) or dark (TP152, TP156, TP180, TP183, TPR216, TPR217, TPR220, TPR227, F28, F30). In no mating do the banded progeny all belong to a well-defined intermediate group. The two extremes of the range of banding are thus defined by the above matings and can be considered as morphs. In only one mating (TP154) is there a clear-cut segregation and evidence of a dominance relationship within the banded class: the 3:1 ratio of dark to a yellow form (both varying little) indicates that dark is dominant. However, the yellow progeny, although varying little, show hardly any overlap with the yellow form of TP169 (which defines the yellow extreme of banding), the latter being slightly paler and with less indication of lineolation. This is suggestive of a further morph. A complication is that both parents of TP154 belong to the yellow form in their progeny and not to the dark form which appeared in much greater numbers. This kind of problem has been encountered above when dealing with the plain/dotty locus, and may perhaps again be explained by penetrance of a recessive allele in a heterozygote. That two such individuals were crossed may simply be an unlikely coincidence.

The remaining matings all gave some banded progeny of intermediate appearance. In no case was there a well-defined division between these and the dark or yellow progeny, either or both of which were present in all of these matings. However, there is still a slight indication of some form of genetic control. The matings which gave only yellow and intermediate (no dark) progeny (TPR213, F26) or very few dark progeny (F1) had one yellow parent. Both those matings lacking yellow progeny (F11, F15), although with low numbers, and those with only few yellow progeny (TPR218, F5, F29) have at least one dark parent. Those with a more even spread (F16, F19, F24) have either dark or yellow. F20 has too few progeny to allow comment. It appears that a number of banding-modifier alleles are involved, perhaps at a different locus (or loci) from the dark/yellow locus. In matings where the dark and yellow forms are well defined, non-modifying alleles must be present at this locus (or loci).

Matings F16 and F19 show a 1:1 segregation of unbanded: five-banded, and both dark and yellow forms appear within the banded class. Since the banded parent of F16 was yellow, and that of F19 dark, these results are incompatible with unbanded, dark and yellow all being at the same locus, assuming no penetrance irregularities. Furthermore, since plain and dotty also segregate within the unbanded progeny of these matings, they cannot be at the same locus as dark and yellow. Indeed, matings F16, F19, F20 and F29 (all unbanded x banded) gave all four classes of progeny and can only be explained in terms of a minimum of three loci, with other possible loci modifying the five-banded class further. There is no evidence of linkage in any mating, since unbanded is epistatic to dark and yellow, and five-banded is epistatic to dotty and plain.

6.2.4. Lip colour morphs - descriptions and relationships.

Strictly, T. pisana does not form a well marked lip (see chapter 3, section 3.2.1.2.) but for the sake of simplicity the thickening of the shell around the aperture will be described here as such. It may be pink, white, or within a range from white to a very pale brownish colour (fig. 6.4.). Those with a pink lip are, in most cases, clearly sepearable from the others. Shells with only a small area of pink around the columella have been scored as pink, as have those with only very pale pink.

The results of all the matings are given in table 6.2. Because some (or all) shells of a mating were too small, fewer matings were scored for lip colour than for banding pattern, and the total scored for lip colour in a particular mating was in most cases less than for banding pattern. A number of matings of pink to pink gave only pink-lipped progeny (TP154, TP155, TP160, TPR213, TPR227), and of non-pink to non-pink gave only non-pink progeny (TP172, TP178, TP183, TPR217, TPR218, TPR221, F5 F16, F19, F24 F26). Ratios of 1:1 were obtained, in matings TP152, TP156 and TP169, which were of pink to non-pink parents. TP180 and F11 probably belong in this group but the numbers of progeny were low. These matings simply indicate that both pink and non-pink breed true or segregate. The remaining four matings in which it was possible to score lip colour (in others no snails were large enough) gave conflicting results. TP171 (pink x non-pink) and F29 (pink x non-pink) gave all non-pink progeny, suggesting non-pink as the dominant allele; but TPR216 and F1 (both pink x pink) gave 3:1 ratios of pink to non-pink (with quite large numbers in F1), suggesting pink as the dominant allele. It seems reasonable to accept these 3:1 ratios as correct, in which case the scoring of the parents of TP171 and F29 may have been incorrect. However, if pink is dominant, both parents of both these matings must have been homozygous non-pink and penetrance of pink in the absence of an allele for pink seems unreasonable. If one parent in these matings was heterozygous pink/non-pink, a 1:1 ratio in the progeny would be expected. The actual results would therefore imply penetrance failure in half of them, but this is inconsistent with the results of the other matings. These results cannot be further explained.

Since pink and non-pink occur equally in the banding classes segregating in individual matings, pink/non-pink lip colour must be at a further unlinked locus.

6.2.5. Penetrance.

The results of five of the thirty-two matings described above have been explained by penetrance of a recessive allele in heterozygotes (TP154 - dark/yellow, and TP156, TPR212, TPR213 - all plain/dotty), or by lack of expression of a recessive allele even when homozygous (TP180 - dotty). Such phenomena are rare, but not unknown in Cepaea (Cain, King and Sheppard, 1960; Wolda, 1969; A. J. Cain, personal communication). Their occurrence in T. pisana may be more extensive than this study has shown, since penetrance of a recessive allele in heterozygotes may be balanced in the progeny by its non-expression in homozygotes, such that no radical departures from expected ratios become apparent. The phenomena may occur in further morphs not discussed in this study (A. J. Cain, in preparation). Clearly, in any future work, the progeny of a mating must be scored first regardless of the appearance of the parents, which may be misleading.

6.3. Variation in the field at Tenby.

6.3.1. Methods.

Samples taken at the six main sites (details in chapter 3, section 3.2.1.1. and appendix 2) of the five year sampling programme at Tenby (1977-1981, see chapter 3, section 3.2.1.1.)

have been used to estimate frequencies at these sites of the morphs determined in the breeding experiments (section 6.2.). Since T. pisana at Tenby is biennial and approximately semelparous, breeding in late summer and then dying, samples taken in late spring to mid-summer show a clear bimodal distribution of shell size (chapter 3, fig. 3.5.). Only these bimodal samples, taken between 24 May and 31 August, have been used in the present study of morph frequencies. Probability paper analysis (chapter 3, section 3.2.1.1.) could not be performed on individual samples, since these were not large enough, but has allowed the position of the trough in the (bimodal) size-frequency distributions of the combined samples on each sampling occasion to be estimated. Shells in each sample were allocated to the adult or juvenile size class if they had h+d larger or smaller respectively than the value at the lowest point of the trough in the distribution of the combined samples.

Adults were than scored as (i) plain unbanded, (ii) dotty unbanded, (iii) dark five-banded, (iv) intermediate five-banded and (v) yellow five-banded. Allocation to one of the banded classes was by comparison with the yellow and dark bred material (section 6.2.1.3.). Shells falling between the ranges exhibited within these clutches (yellow - TP169; dark - TP152, TP156, TP180, TP183, TPR216, TPR217, TPR220, TPR227, F28, F30) were scored as intermediate. Juveniles were simply scored as banded, since there is variation in the size at which the shell darkens; a small juvenile could be mis-scored as yellow, dark lineolations appearing somewhat later in its growth. All shells could be readily scored according to this scheme.

6.3.2. Results.

The morph scores for each sample are available in appendix 4. Considering adults and juveniles separately, all samples taken at a particular site during a particular year are homogeneous in morph frequencies (heterogeneity χ^2 tests), and the data have therefore been pooled. Percentages of (i) unbanded, (ii) plain (within the unbanded class), (iii) dark (within the five-banded class), and (iv) yellow (within the five-banded class) are given in table 6.3. Figs. 6.5. and 6.6. show some of these data graphically; the remainder follows a very similar pattern. The results are summarised in figs. 6.7., 6.8. and 6.9. The values for each year at a particular site (adults and juveniles) mostly fall within a fairly narrow range. Extreme values are almost all from small samples with consequently large confidence limits.

There are no significant differences (heterogeneity χ^2 tests on the actual numbers) between sites in any year in the frequencies of plain and dotty within the unbanded shells (either adults or juveniles), nor of dark, intermediate and yellow within the five-banded class (adults only, juveniles not scored). However, there is significant heterogeneity between sites in the frequencies of unbanded and five-banded shells in both adults and juveniles ($p \ll 0.05$ on most occasions). The sites fall clearly into two groups: 1,5 and 6, and 2,3 and 4. Comparing within sites and within years, adult and juvenile frequencies of all morphs are homogeneous. At some sites, there is heterogeneity between years in some morph frequencies (site 1, juveniles, unbanded/banded, $p < 0.001$; site 2, adults, plain/dotty, $p < 0.005$; site 2, adults, dark/intermediate/yellow, $p < 0.025$; site 4, juveniles, plain/dotty, $p < 0.001$), and this is more than would be expected by chance (Cooper, 1968). However, there is no pattern to these differences, and indeed, the 95% confidence limits of the percentages for all the years at any particular site almost all overlap. There is no general trend in changes of morph frequencies at any site in either adults or juveniles; they remain similar over the five years. (Sign tests on the differences between the 1977 and 1981 percentages for each morph showed no significant trend). The heterogeneity is not understood.

Although comparison within sites and within years indicates no heterogeneity between adults and juveniles in the frequency of unbanded shells, there is a slight suggestion from fig. 6.7. that it may be higher in the juveniles. Direct comparison of adults and juveniles in a particular year shows that there is a higher percentage of unbandeds in the juveniles than in the adults (Wilcoxon's signed-ranks test: $p < 0.02$). However, being essentially biennial and semelparous, one-year-old and two-year-old snails may belong to somewhat different populations genetically. Therefore, the percentage unbanded in the adults of each year was also compared with that in the juveniles of the previous year (i.e. the population from which the adults were derived) at each site. This showed a significant decrease in the proportion of unbandeds from one-year-old to two-year-old snails ($p < 0.02$). The 20 possible comparisons are illustrated graphically in fig. 6.10. There is a clear tendency for the points to fall above the line of equal adult and juvenile percentage unbanded.

Similar comparisons were carried out for plain and dotty within the unbandeds, but the slight tendency for the proportion of plain to decrease from one-year-old to two-year-old snails, suggested by fig. 6.8., was not quite significant at the 95% level.

6.3.3. Discussion of variation at the main Tenby sites.

The small but significant indication overall of a greater proportion of unbanded shells in the one-year-old (juvenile) class than in the two-year-old (adult) class, suggests selection in the second year, at least, of life. (It is not possible to obtain sufficiently reliable scores for very young shells to allow any possible selection to be detected in the first year of life). This would be expected if, at the northern edge of the species' range, animals capable of absorbing more solar radiation (i.e. those with banded shells) were at an advantage (see chapter 2, section 2.4.2. and chapter 4, section 4.4. for further discussion of this with respect to climate, distribution and thermal relations). This advantage might be expected to result in banded snails growing to a larger size than unbandeds, but no indication of this had been found in comparisons (by t - tests) of mean size of banded and unbanded shells within both one-year-old and two-year-old cohorts of late summer samples (when adults were fully grown).

It is also possible that selection is by visual predation, banded shells being more cryptic (at least to the human eye - Heller, 1981). Certainly, both avian and mammalian predators are present in the vicinity. If visual predation is a factor, it could act in a density or frequency dependent manner (e.g. Clarke, 1972, 1975) as discussed for Cepaea by Jones, Leith and Rawlings (1977) and Clarke, Arthur, Horsley and Parkin (1978). No correlation has been found between the degree of selection (as indicated by the difference in proportion of unbandeds in adults and juveniles), and either the adult or juvenile population densities at each of the sites (chapter 5, section 5.3.). These estimates of density are very variable and may not be sufficiently accurate to justify a definite conclusion about density dependence. There is no indication of frequency dependent selection, since fig. 6.10. does not show any tendency for points to be at different distances from the equal percentage line, or on opposite sides of it, according to morph frequency (cf. Cook, 1965). Indeed at the high densities at which T. pisana exists at Tenby, apostasy may be of little importance (Greenwood, 1969).

The possible selection favouring dotty over plain unbandeds is in the expected direction if snails with more banding are at an advantage.

Since the Tenby colony was probably introduced within the last few hundred years (chapter 2, section 2.4.3), it is possible that gene frequency equilibrium has not been reached, and the porportion of banded snails is gradually increasing because of selection, but that this trend was not picked up in the five years of this study. Alternatively, gene frequencies may be stable, and the selective advantage during the second year of life of the banded snails is balanced by selection favouring unbandeds during their first year, or by greater productivity of unbanded snails, although no indication of the latter has been found (chapter 3, section 3.3.2.), and besides, it is contrary to expectation if banded snails can absorb more energy from the sun (cf. Heller and Volokita, 1981a).

The proportions of unbanded shells within both adults and juveniles are clearly different at sites, 1, 5 and 6, and sites 2, 3 and 4. Sites 2, 3 and 4 are close together (at the western end of the South Cliff) and may all be located within a single population (see chapter 5 for a discussion of effective population size at these sites). Sites 5 and 6 are close to each other (on Castle Hill, beyond the eastern end of the South Cliff) and could certainly be within a single population. The population at site 1 (towards the western end of the South Cliff) must be distinct from the others, despite its congruence in morph frequency with sites 5 and 6. It is likely, therefore, that the six sites are located within three populations (at least): at site 1, at sites 2, 3 and 4, and at sites 5 and 6. There are no obvious differences between these three groups of sites, although no special study has been made of habitat characteristics. The greatest apparent difference is between site 3 and and rest, site 3 being the least exposed and most shaded, yet its morph frequencies are no different from sites 2 and 4, which are as exposed as the others. It is not possible to give reasons for the differences and similarities in morph frequencies between the sites. They may be due to the founder effect, bottlenecks, or to selection by factors unknown.

6.4. Variation at other British localities.

Samples have been taken, or records made in the field, at a number of other sites both in and around Tenby, and elsewhere in the British distribution of T. pisana (detailed in chapter 2). At all but two localities (dealt with individually below), shells could be readily scored according to the scheme of morphs developed for the main six Tenby sites.

The scores are given in appendix 4. Within Tenby, both banded and unbanded shells were usually present, but sometimes in different proportions than at the main six sites. In the unbanded class, frequencies of plain and dotty shells were similar to those at the six main sites, as were frequencies of dark, intermediate and yellow shells within the banded class. Outside Tenby (Caldey Island, Saundersfoot, Stackpole Warren, Porthcawl-Newton) only banded shells, mostly dark, were found, except at Saundersfoot where they were yellow and intermediate only.

At all these localities, shell colour is pale yellowish-buff to off-white, and banded shells always have darker apices than unbandeds. Apex colour is probably very closely linked to the unbanded/banded locus, and not a pleiotropic effect of it, since shells from other localities may have the opposite combinations of unbanded/banded and apex colour (see below, Porthcawl - Kenfig, and section 6.5.). If sufficient time has elapsed since the founding of these colonies for crossing over to have taken place, this large linkage disequilibrium implies selection maintaining the association of dark apex with banded and pale apex with unbanded at these localities.

At Porthcawl - Kenfig and St. Ives the shells did not fit the Tenby scoring scheme. The sample from Kenfig (fig. 6.11.) contains both five-banded and unbanded shells, but there is no clear distinction between them as at Tenby. At Tenby, banded shells are banded right from the apex, even if without dark lineolation; their apices are dark, and the shell colour is pale yellowish-brown. At Kenfig, there is a continuum from shells with bands right from the apex, via those with bands starting later, to those with no bands at all; most shells have a pale apex, and the shell colour is much more white. The shells appear similar to those from Normandy (Baie du Mont St. Michel) rather than to any British ones (see below, section 6.5.1.). The elucidation of the control of this variation must await breeding experiments. This is the only British locality outside Tenby at which unbanded shells have been found.

At. St. Ives only two forms, both five-banded, are present (fig. 6.12.): one with full pigmentation, and one described as sub-hyalozonate by Cain (in preparation). They occur in roughly equal proportions in the population. The banding pattern of both forms appears the same, the sub-hyalozonate almost, but not entirely, lacking pigment in both bands and shell background. It appears very white, and effectively unbanded, usually with a very pale apex, although with the animal inside the shell it is considerably darkened. The normally pigmented form is intermediate in darkness of the bands, but more reminiscent of some of the shells from Brittany than of those from Tenby in pattern (see below). The normally pigmented form is dominant to the sub-hyalozonate (Cain, in preparation). Fig. 6.13. shows banded shells from Tenby, Kenfig and St. Ives for comparison.

6.5. Variation at non-British localities.

6.5.1. Northern France and the Channel Islands.

Locations of all sites in Brittany, Normandy and the Channel Islands are given in appendix 2.

The Breton samples consist largely of banded shells, two of them wholly so. Not unexpectedly, the proportions of unbanded and banded shells appear different at the different sites. All the banded shells are five-banded. There is some variation between sites in the overall appearance of these banded shells, but, although all are similar to some of the intermediate banded shells from Tenby, none is quite the same. The band lineolations are less continuous than at Tenby, and the shells have a more speckled appearance. In fact the normally pigmented shells from St. Ives resemble these extremely closely.

Further forms, not seen in Britain, are present at low frequency in some of these samples from Brittany, (cf. Sacchi and Gaudiosi, 1961). A true hyalozonate, as well as sub-hyalozonate, appears as both banded and unbanded, showing it to be controlled at a different locus. As unbanded, it is extremely white, and the apex colourless. The distinction between hyalozonate and sub-hyalozonate is clear in the bandeds but less so in the unbandeds.

The single sample from Guernsey, consisting of normally pigmented five-banded shells only, shows, not unexpectedly, great similarity to the Breton samples.

The single sample from Normandy is different from those from Brittany, showing strong similarities to that from Porthcawl - Kenfig, in that it is difficult to draw a line between unbanded, late-banded, and banded shells, and the background shell colour is whiter. Shells with dark and pale apices are present, within both the unbanded and banded classes.

In some shells in all these northern French samples there is a slight tendency, not seen in Britain, except, perhaps, at Porthcawl - Kenfig, for band 3 to be emphasized, so that it appears rather darker and less broken up than bands 1 and 2.

6.5.2. The major region of the distribution of *T. pisana*.

Forms clearly similar in banding pattern to those found in northern Europe are known from this area, which includes the Mediterranean, and the Atlantic coasts of north Africa and the southern Iberian peninsula. However, many other forms are also known, although most samples contain only some of them. A good selection of the immense range has been illustrated by Taylor (1912), although his pictures show little fine detail. Forms with band 3 heavily emphasized and with 1 and 2 very much reduced or absent, are common, as are forms with bands reduced to flecks, these flecks sometimes apparently superimposed on a yellowish background band; a common form of this type having heavy flecks on the upper surface of the shell on bands 1 and 2 and not on band 3. Forms with only bands 4 and 5, and 5 only, are well-known, and some shells appear truly unbanded, even lacking the very late bands often found towards the shell aperture of unbanded shells from Tenby.

The other major difference between shells from this region and those from the north, is that the background shell colour can often be very white, although buff or off-white colours, as in the British and French samples, are sometimes found. Tan and pink varieties are also known.

Apex colour varies from nearly black to almost colourless (colourless in hyalozonate forms), and different apex colours appear to segregate in some samples (table 6.4) in both banded and unbanded shells, showing that they are not pleiotropic effects of the unbanded/banded locus, as Tenby material could suggest (section 6.4.). Linkage disequilibria between banding and apex colour in some samples (table 6.4.) may imply selection favouring particular combinations, the predominant associations being of banded with dark apex, and unbanded with pale. A single cross (TPR202) of two unbanded shells with pale apices, from Lesbos, gave a 3:1 ratio of pale:dark (62 pale:25 dark) in the progeny (all unbanded); dark is thus recessive to pale (fig. 6.14).

6.6. Discussion.

The variation of T. pisana makes sorting of large samples into distinct forms extremely difficult without knowledge of the genetic control. We are only beginning to understand this control; it may be much more complex than that of the more limited variation in Cepaea.

This study has broadly characterised genetically the relatively simple variation at Tenby, and Cain (in preparation) has investigated the genetics of some forms from the Mediterranean, northern France, and St. Ives. Few crosses have been made between animals from these different regions, and so, although some forms are clearly not present at certain localities, it is impossible to be sure whether slightly different forms are indeed different morphs, or simply the same morph expressed against rather different genetic backgrounds. For instance, all the five-banded shells from Britain and northern France, and some from the Mediterranean, although having distinct regional characters in the styling of the pattern, may not be distinct morphs. Similarly, unbanded shells from Tenby with some banding appearing very late on the body whorl in many cases, may be the same morph as completely unbanded shells from elsewhere, but expressed against a different background. On the other hand, they may be different morphs; in which case the nomenclature may have to be modified, and the Tenby morph designated as something other than unbanded. The genetic control of this kind of subtle variation may be complicated.

Since variation in natural selection may be even more localised in T. pisana than in Cepaea (Heller, 1981), and furthermore, differential habitat selection by different morphs may enhance the large differences in morph frequency over short distances (Johnson, 1980, 1981), it is not possible to use single samples to give morph ratios for a whole region. However, it is still possible to detect differences and similarities between localities. The clear similarities between shells from St. Ives, Guernsey and Brittany, and between shells from Porthcawl - Kenfig and Normandy, back up the suggestion from other evidence that T. pisana has been introduced only very recently to these British sites (chapter 2, section 2.4.3.). All other British shells bear strong resemblance to those from Tenby, and may be the result of introductions from there. Tenby shells, although similar to those from northern France, bear no striking resemblance to either these or to Mediterranean shells. It is possible that T. pisana, although probably introduced to Tenby as well as to the other British localities, may have been there long enough (chapter 2, section

2.4.3.) for selection to have given rise to a range of variation characteristic of this locality.

In general, these northern European populations exhibit less variation than those in the Mediterranean. Assuming that *T. pisana* originated in the Mediterranean region (perhaps in Morocco - chapter 1, section 1.3.), it is probable that the reduced number of forms seen in the northern populations (probably artificially introduced), results from the founder effect and/or natural selection of the small number of forms capable of withstanding the more temperate conditions (cf. introduced colonies of *C. nemoralis* in North America - Brussard, 1975). Some Mediterranean localities also only have a small number of forms, probably for similar reasons, if the species spread from a small area of origin in the western Mediterranean.

Fig. 6.1. Five-banded shells with the bands numbered in the standard fashion.

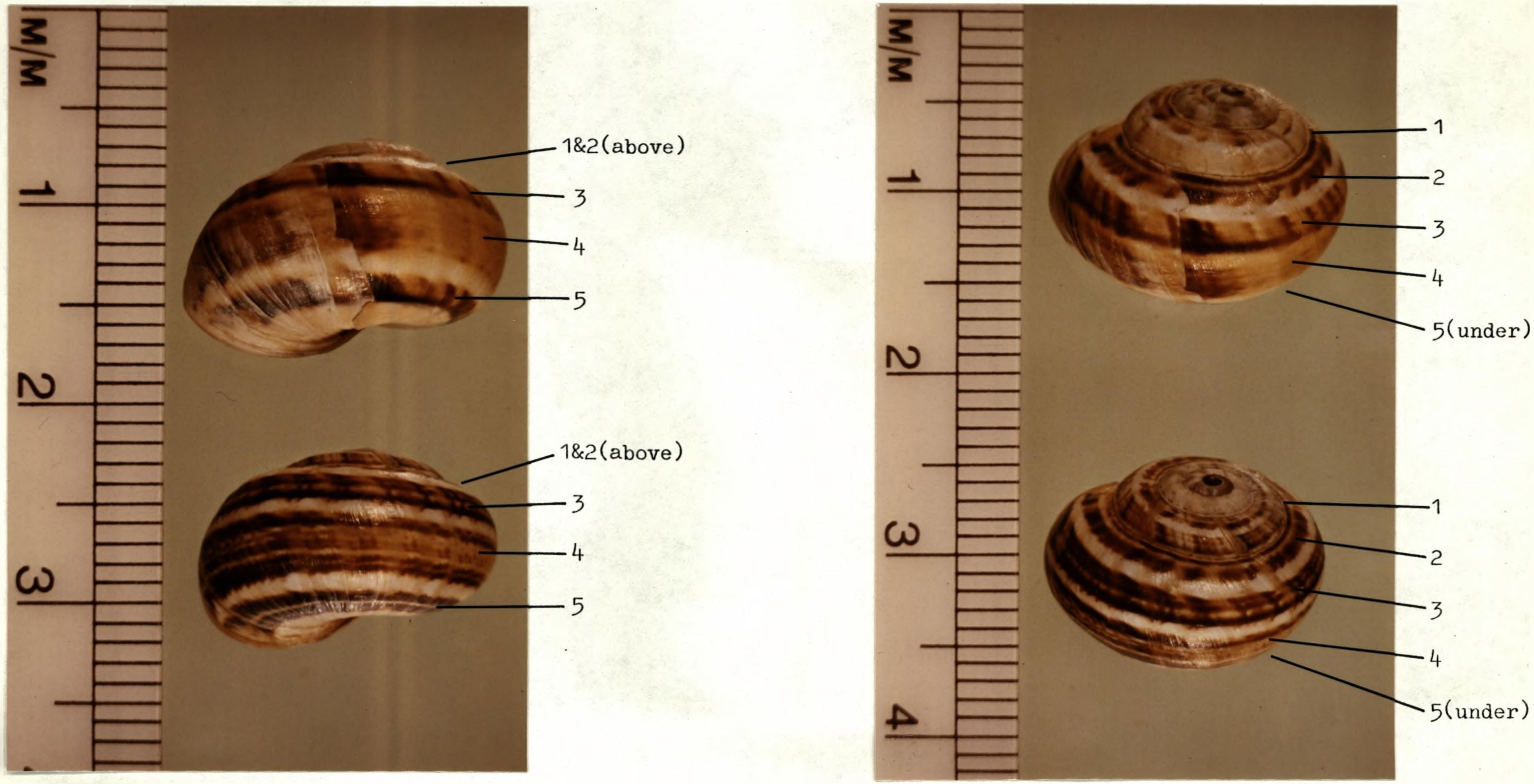


Fig. 6.2. The four main morphs at Tenby. a - adults, b - juveniles.

In both a and b : top row - plain 00000
second row - dotty 00000
third row - dark 12345
bottom row - yellow 12345


b


a

Fig. 6.3. Five-banded shells to show the range of variation.
yellow - left
intermediate - centre
dark - right
(five-banded progeny of mating F19).

Fig. 6.4. Banded and unbanded shells from Tenby to show pink (top row) and non-pink (bottom row) lip colour.

Fig. 6.5. Morph percentages, with 95% confidence limits, over five years. Site 1 adults.

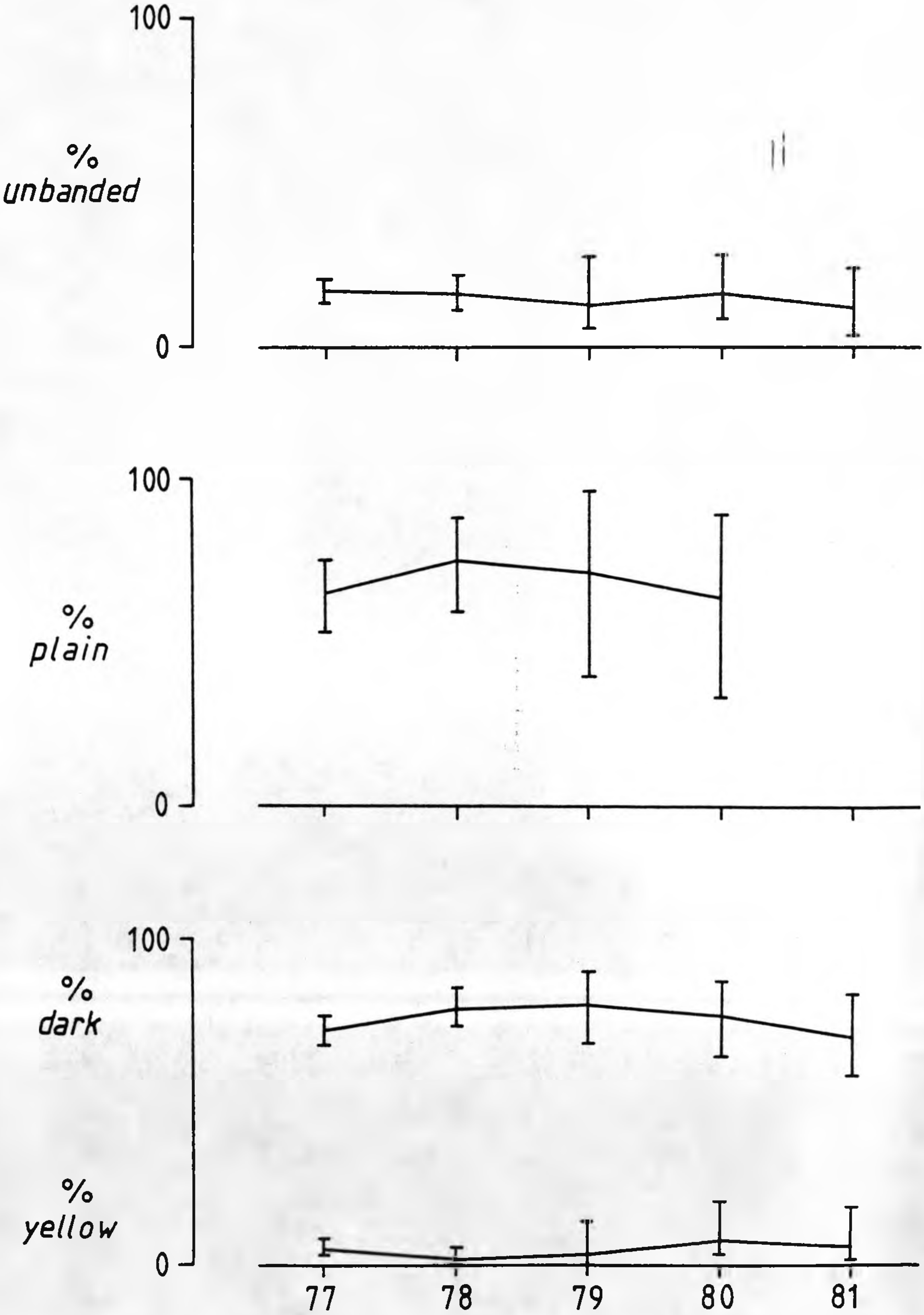


Fig. 6.6. Morph percentages, with 95% confidence limits, over five years. Site 4 juveniles.

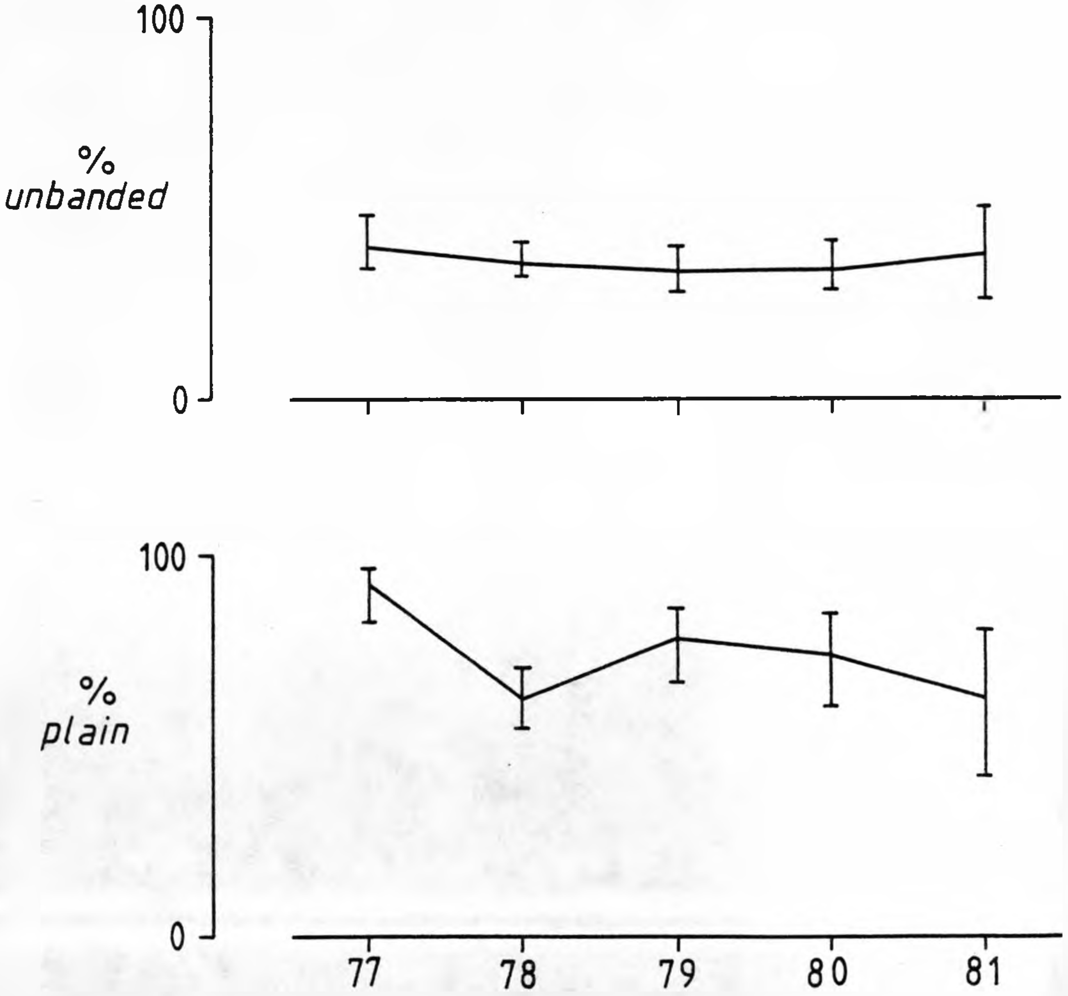
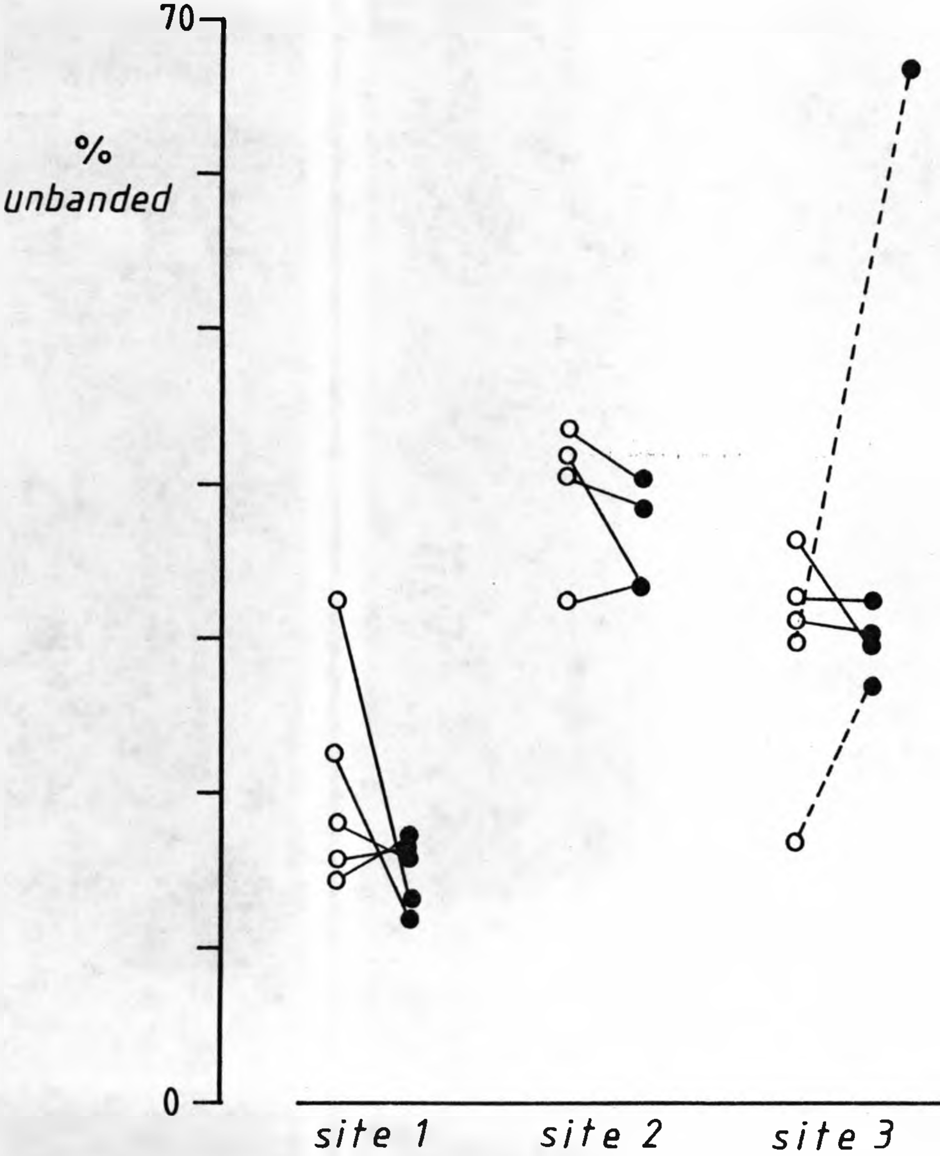


Fig. 6.7. Percentage unbanded, with values for adults (closed circles) and juveniles (open circles) connected for each year. Connections by broken lines are for years when the adult and/or juvenile value was based on a sample of less than 30.


70
%
unbanded
0
site 1
site 2
site 3

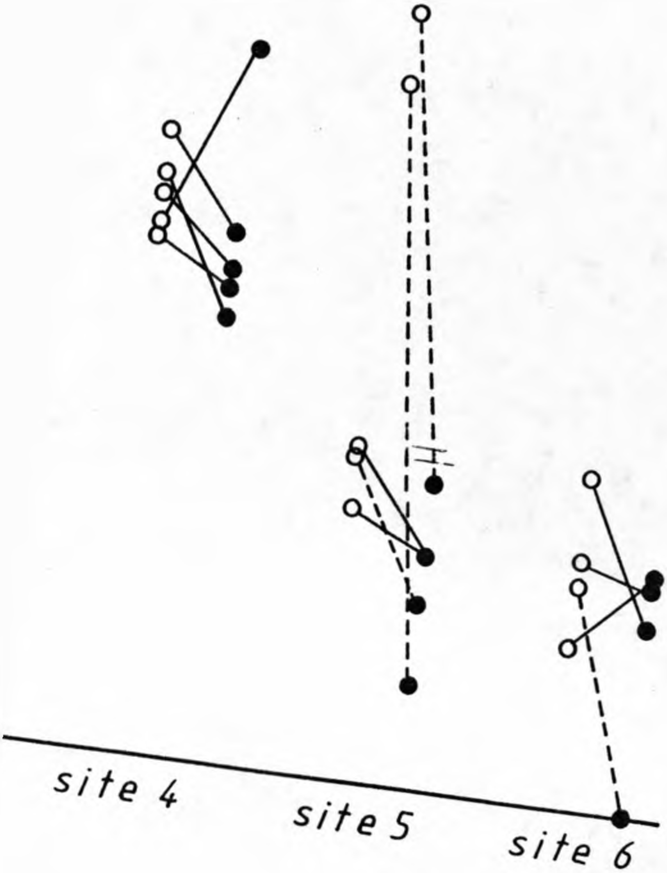
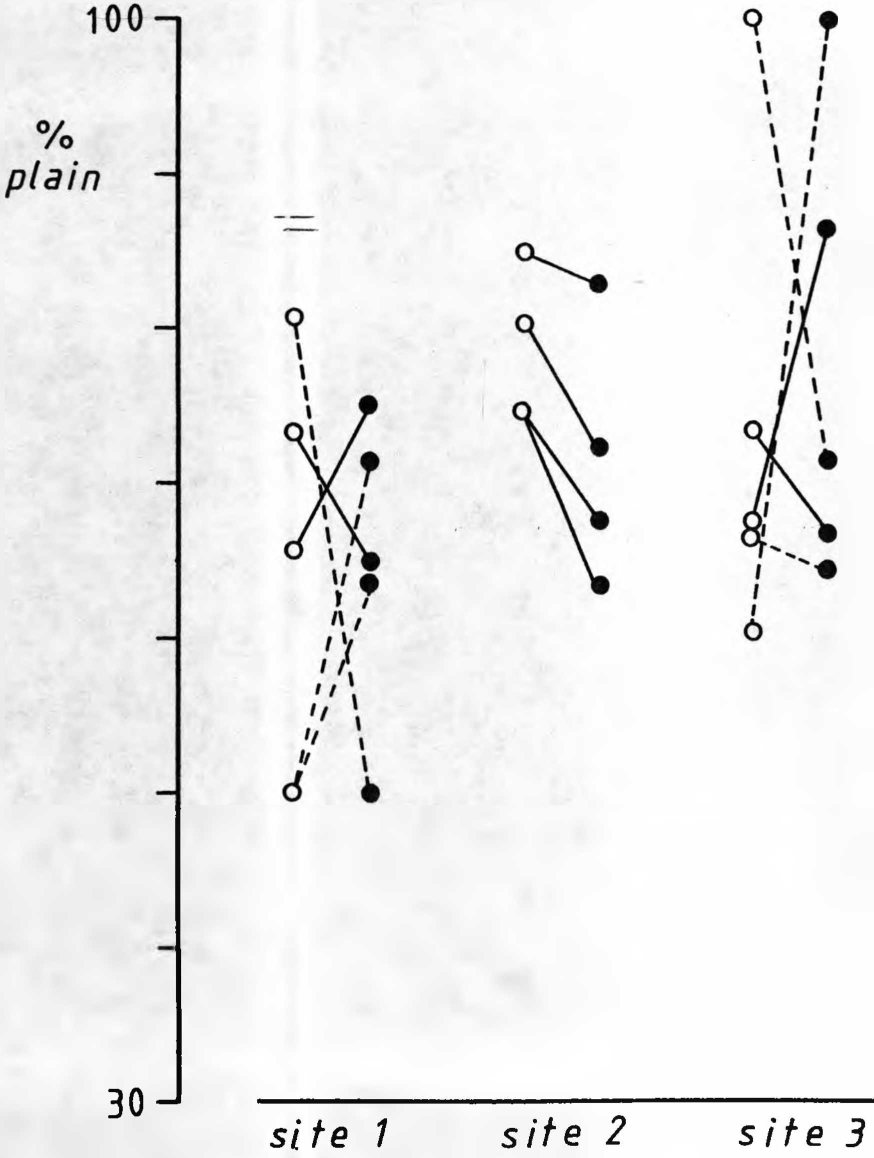

site 4
site 5
site 6

Fig. 6.8. Percentage plain within the unbanded class, symbolised as in fig. 6.7. (The unconnected juvenile point for site 6 is for 1979 when no unbanded adults were sampled at this site).


100
%
plain
30
site 1
site 2
site 3

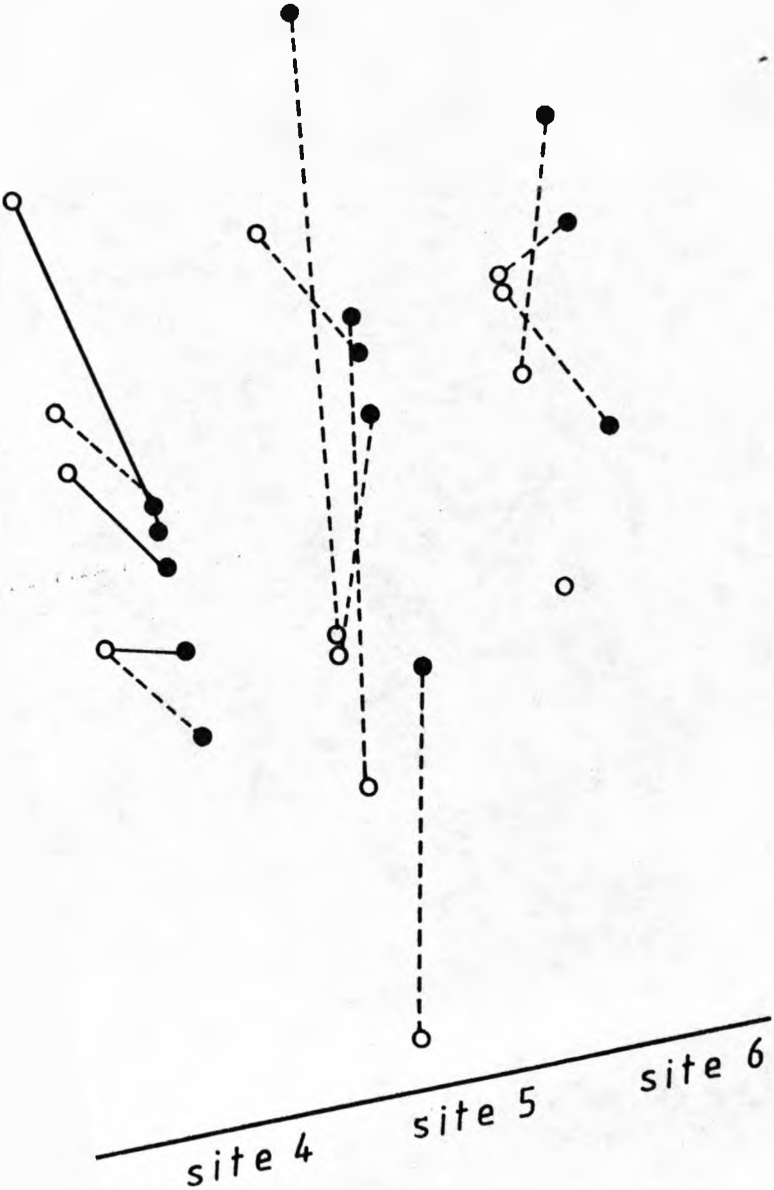
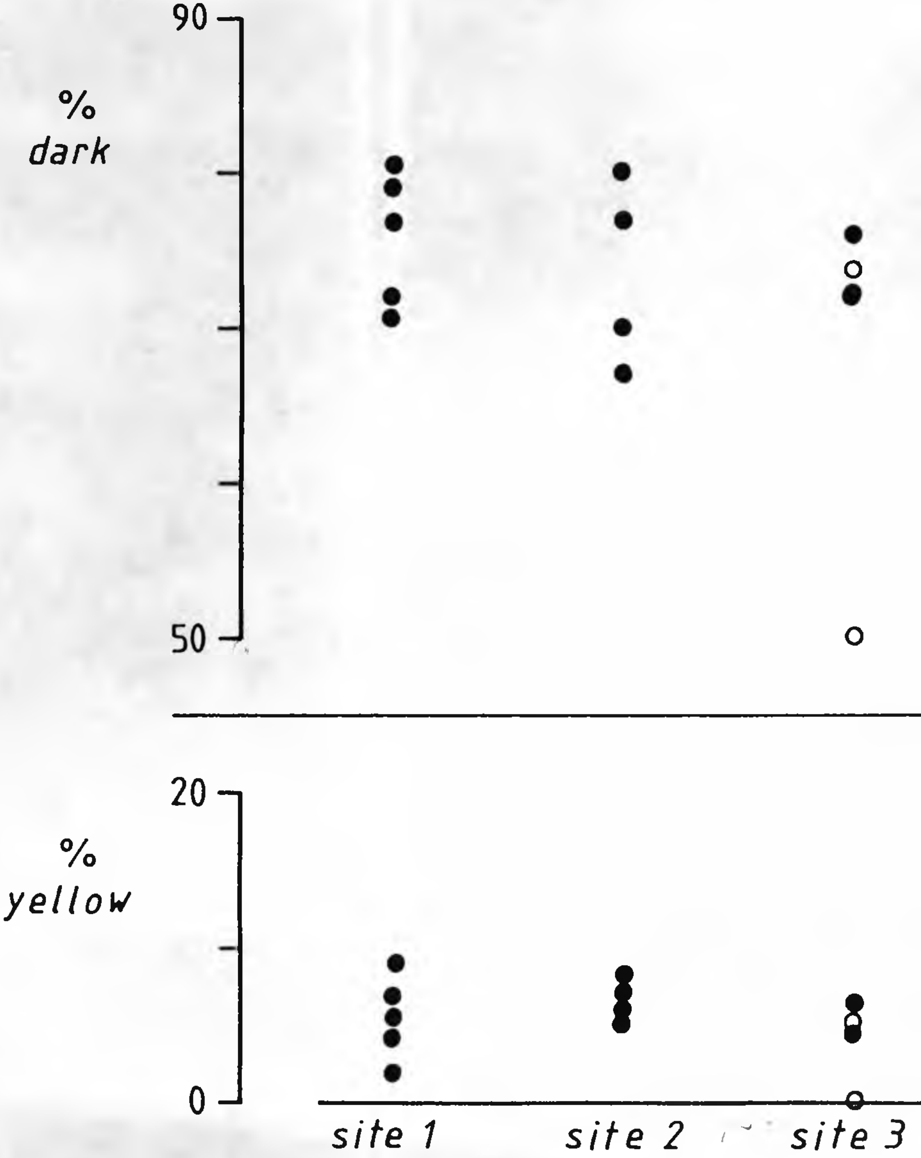

site 4
site 5
site 6

Fig. 6.9. Percentages of dark and yellow within the banded class (adults only scored). Closed circles represent percentages based on over 30 individuals, open circles those on under 30.


90
% dark
50
20
% yellow
0
site 1
site 2
site 3

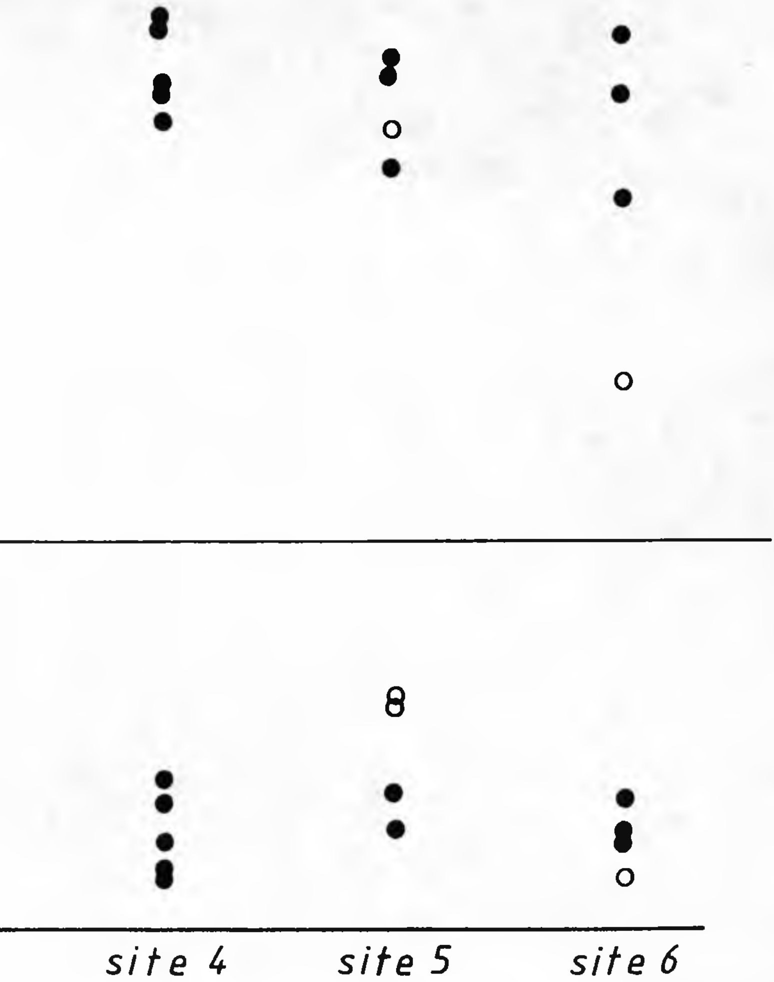

site 4
site 5
site 6

Fig. 6.10. Scatter diagram of percentage unbanded in the adults of each year against that in the juveniles of the previous year at each site, with the line of equal percentages drawn in. Open circles when the adult or juvenile sample was of less than 30.

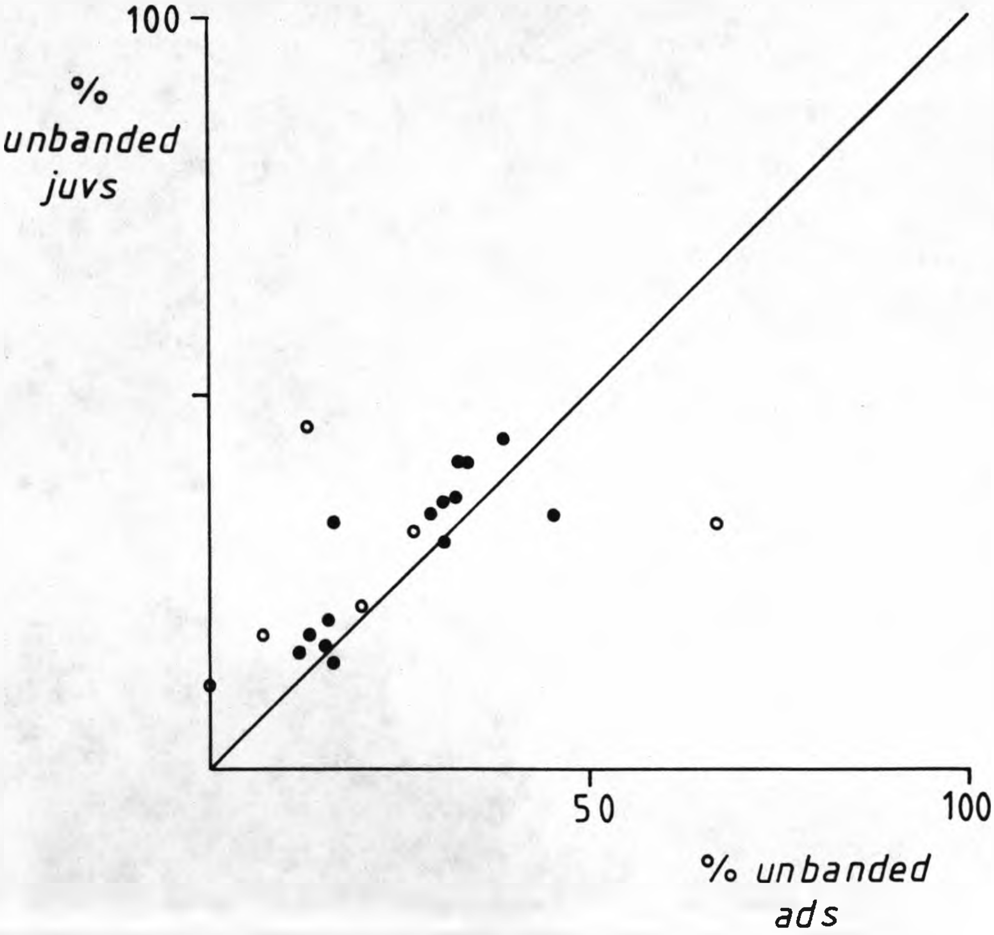


Fig. 6.11. Complete sample from Porthcawl - Kenfig.

Fig. 6.12. Complete sample from St. Ives.

Fig. 6.13. Banded shells from St. Ives (top), Tenby (middle) and Kenfig (bottom).

Fig. 6.14. Shells from the progeny of mating TPR202 with pale apices (upper row) and dark apices (lower row).

Table 6.1.

Results of breeding experiments - banding pattern.

Mating	Parental phenotypes	Progeny phenotypes					
		unbanded		banded			
		plain	dotty	dark	intermed.	yellow	total
TP152	plain x plain	16	3	8			27
TP154	yellow x yellow			81		39	120
TP155	plain x plain	24	2				26
TP156	?dotty x dotty	93	41	44			178
TP160	plain x dotty	188	159				347
TP169	yellow x yellow					154	154
TP171	plain x plain	77	29				106
TP172	plain x plain	12	4				16
TP178	plain x plain	26	6				32
TP180	plain x plain	35	50	28			113
TP183	dark x intermed.			75			75
TPR212	dotty x yellow	43	5				48
TPR213	dotty x yellow	23	5		8	13	49
TPR216	dark x dark			122			122
TPR217	dark x dark			11			11
TPR218	dark x dark			25	16	1	42
TPR220	dark x dark			77			77
TPR221	dark x yellow			10	7	16	33
TPR227	dark x dark			38			38
F1	intermed. x yellow			4	53	47	104
F5	dark x intermed.			16	11	2	29
F9	plain x dark	101	105				206
F11	plain x dark	4	5	4	4		17
F15	plain x dark	4	2	1	2		9
F16	dotty x yellow	36	35	22	14	23	130
F19	plain x dark	23	25	16	23	9	96
F20	plain x dark	5	5	3	1	3	17
F24	dark x intermed.			7	19	18	44
F26	intermed. x yellow				30	31	61
F28	dark x dark			4			4
F29	dotty x dark	22	14	10	8	4	58
F30	dark x dark			28			28

Table 6.2.

Results of breeding experiments - lip colour.

Mating	Parental phenotypes	Progeny phenotypes	
		pink	non-pink
TP152	pink x non-pink	13	13
TP154	pink x pink	64	
TP155	pink x pink	1	
TP156	pink x non-pink	26	27
TP160	pink x pink	65	
TP169	pink x non-pink	27	32
TP171	pink x non-pink		48
TP172	non-pink x non-pink		16
TP178	non-pink x non-pink		18
TP180	pink x non-pink	2	9
TP183	non-pink x non-pink		25
TPR213	pink x pink	16	
TPR216	pink x pink	15	7
TPR217	non-pink x non-pink		5
TPR218	non-pink x non-pink		27
TPR221	non-pink x non-pink		12
TPR227	pink x pink	17	
F1	pink x pink	62	24
F5	non-pink x non-pink		17
F11	pink x non-pink	2	3
F16	non-pink x non-pink		34
F19	non-pink x non-pink		16
F24	non-pink x non-pink		9
F26	non-pink x non-pink		37
F29	?pink x non-pink		10

Table 6.3.

Percentages of morphs, with 95% confidence limits.

Site	Year	% unbanded		% plain		% dark	% yellow
		ADS.	JUVS.	ADS.	JUVS.	ADS.	ADS.
1	1977	$17.1^{13.7}_{20.9}$	$14.5^{11.3}_{18.2}$	$64.9^{53.0}_{75.4}$	$73.8^{61.1}_{84.1}$	$71.9^{67.0}_{76.3}$	$5.6^{3.5}_{8.4}$
	1978	$15.9^{11.4}_{21.3}$	$17.9^{14.2}_{22.2}$	$75.0^{58.8}_{87.7}$	$65.6^{52.9}_{76.9}$	$79.0^{72.5}_{84.5}$	$2.1^{0.6}_{5.3}$
	1979	$13.2^{5.5}_{26.6}$	$32.6^{22.3}_{44.4}$	$71.4^{39.0}_{96.2}$	$50.0^{16.0}_{84.0}$	$80.4^{67.8}_{90.4}$	$4.4^{0.5}_{14.4}$
	1980	$16.4^{8.6}_{27.3}$	$15.4^{8.3}_{25.2}$	$63.6^{32.9}_{88.9}$	$50.0^{21.0}_{79.0}$	$76.8^{63.7}_{86.9}$	$8.9^{3.0}_{19.6}$
	1981	$12.0^{4.5}_{24.3}$	$22.6^{14.6}_{32.4}$	50.0	$81.0^{58.4}_{94.5}$	$70.5^{57.3}_{82.6}$	$6.8^{1.4}_{18.1}$
2	1977	$40.2^{36.4}_{44.2}$	$43.6^{39.9}_{47.5}$	$82.7^{77.7}_{87.3}$	$85.1^{80.8}_{89.6}$	$76.9^{72.3}_{81.0}$	$5.1^{3.2}_{7.7}$
	1978	$38.7^{34.3}_{43.2}$	$40.6^{34.9}_{46.5}$	$72.3^{65.2}_{78.6}$	$80.4^{71.9}_{87.2}$	$69.9^{64.4}_{74.9}$	$7.2^{4.6}_{10.7}$
	1979	$33.7^{24.5}_{43.8}$	$32.6^{24.8}_{41.1}$	$63.6^{46.0}_{79.4}$	$74.4^{60.8}_{86.1}$	$80.0^{68.4}_{88.8}$	$6.2^{1.8}_{14.9}$
	1980	-	-	-	-	-	-
	1981	$33.5^{28.8}_{38.5}$	$41.7^{33.9}_{49.9}$	$67.5^{58.5}_{75.6}$	$74.6^{62.2}_{84.6}$	$66.8^{60.5}_{72.7}$	$8.4^{5.3}_{12.6}$
3	1977	$29.5^{21.7}_{38.4}$	$36.3^{28.0}_{45.3}$	$66.7^{50.5}_{81.3}$	$73.3^{60.4}_{85.0}$	$72.1^{61.5}_{81.1}$	$4.7^{1.3}_{11.4}$
	1978	$32.4^{24.7}_{40.8}$	$32.7^{25.8}_{40.3}$	$86.4^{73.7}_{94.8}$	$67.3^{53.4}_{79.2}$	$76.1^{66.1}_{84.4}$	$6.5^{2.5}_{13.6}$
	1979	66.7	$30.2^{22.4}_{38.9}$	100.0	$60.5^{45.8}_{75.3}$	50.0	0.0
	1980	$30.4^{18.5}_{42.8}$	$31.6^{22.5}_{41.9}$	$64.3^{41.9}_{86.6}$	$66.7^{47.2}_{82.7}$	$71.9^{53.7}_{86.2}$	$6.3^{0.8}_{20.7}$
	1981	$26.9^{11.6}_{47.5}$	$16.7^{0.4}_{59.7}$	$71.4^{39.0}_{96.2}$	100.0	$73.7^{51.4}_{90.6}$	$5.3^{0.1}_{25.3}$
4	1977	$34.4^{28.2}_{41.1}$	$40.5^{33.2}_{48.0}$	$68.9^{57.2}_{79.0}$	$91.7^{82.8}_{96.8}$	$73.8^{65.8}_{80.7}$	$5.7^{2.5}_{10.8}$
	1978	$33.0^{27.6}_{38.8}$	$36.5^{32.2}_{41.0}$	$61.1^{50.3}_{71.0}$	$62.0^{54.4}_{69.2}$	$78.1^{71.4}_{83.8}$	$3.8^{1.6}_{7.7}$
	1979	$30.9^{19.6}_{44.7}$	$33.7^{27.1}_{40.6}$	$70.6^{45.6}_{89.5}$	$77.6^{66.0}_{86.7}$	$79.0^{64.7}_{90.3}$	$7.9^{1.7}_{20.9}$
	1980	$46.4^{36.9}_{56.0}$	$34.1^{27.1}_{41.8}$	$66.7^{51.4}_{79.3}$	$73.7^{60.4}_{84.3}$	$74.6^{61.7}_{84.9}$	$3.4^{0.5}_{11.7}$
	1981	$29.0^{22.2}_{36.5}$	$37.7^{26.6}_{50.0}$	$55.3^{40.0}_{70.0}$	$61.4^{41.0}_{79.7}$	$72.2^{63.1}_{80.0}$	$9.6^{4.9}_{16.4}$

continued...

Table 6.3. (continued).

Percentages of morphs, with 95% confidence limits.

Site	Year	% unbanded		% plain		% dark	% yellow
		ADS.	JUVS.	ADS.	JUVS.	ADS.	ADS.
5	1977	$15.3^{10.6}_{21.0}$	$22.1^{13.0}_{33.6}$	$77.4^{59.1}_{90.4}$	$86.7^{59.5}_{98.3}$	$69.2^{61.8}_{76.0}$	$8.7^{5.0}_{13.9}$
	1978	$15.5^{9.7}_{23.0}$	$17.8^{12.7}_{25.0}$	$73.7^{51.4}_{90.6}$	$58.8^{42.1}_{75.0}$	$75.0^{65.6}_{82.9}$	$8.7^{4.0}_{16.0}$
	1979	$7.1^{0.2}_{31.8}$	$45.5^{17.0}_{73.9}$	100.0	$60.0^{14.7}_{94.7}$	$71.4^{47.3}_{91.3}$	$14.3^{1.8}_{39.7}$
	1980	$13.2^{5.5}_{24.8}$	$21.4^{4.3}_{46.6}$	$57.1^{11.0}_{81.0}$	33.3	$76.1^{63.4}_{87.0}$	$6.5^{1.4}_{17.3}$
	1981	$20.0^{6.8}_{40.7}$	50.0	$80.0^{28.4}_{99.5}$	50.0	$75.0^{56.3}_{94.3}$	$15.0^{3.2}_{37.9}$
6	1977	$14.9^{10.8}_{20.2}$	$16.1^{10.2}_{23.7}$	$69.7^{52.0}_{84.3}$	$80.0^{56.4}_{94.3}$	$73.9^{67.0}_{80.0}$	$5.3^{2.5}_{9.5}$
	1978	$15.8^{10.3}_{23.0}$	$11.0^{7.5}_{15.5}$	$90.5^{69.8}_{98.8}$	$74.1^{54.3}_{88.8}$	$77.7^{69.0}_{84.9}$	$6.3^{2.6}_{12.4}$
	1979	$0.0^{0.0}_{11.8}$	$14.7^{5.0}_{30.7}$	-	$60.0^{14.7}_{94.7}$	$55.2^{36.0}_{74.0}$	$3.5^{0.1}_{17.6}$
	1980	-	-	-	-	-	-
	1981	$12.4^{6.6}_{20.6}$	$21.7^{14.8}_{29.0}$	$83.3^{53.7}_{97.9}$	$80.8^{60.8}_{93.4}$	$67.1^{56.1}_{76.7}$	$8.2^{3.4}_{16.2}$

The 95% confidence limits have been calculated using the tables given by Sokal and Rohlf (1973), supplemented by Goldstein (1964).

No samples were taken at sites 2 and 6 in 1980, and there were no adult unbandeds in the 1979 sample at site 6.

Confidence limits have not been given where sample sizes were too small to allow their calculation.

Table 6.4.

Examples of apex colour scores in unbanded and banded shells ($d > 12$ mm) from various localities (site details in appendix 1).

sample	unbanded		banded	
	dark apex	pale apex	dark apex	pale apex
Lesbos	21	50	26	0
Amnissos 2 (Crete)	0	48	8	0
Elviria, site 1 1978 (S. Spain)	7	48	2	4
Elviria, site 1 1979	4	39	3	4

Chapter 7

Mantle Colour Variation

7.1. Introduction.

Variation in body colour is known in Cepaea nemoralis, Trichia striolata (Pfeiffer), and Monacha cantiana (Montagu), and its genetic control is partially understood (e.g. Cain, 1959a, b, 1971; Wolda, 1969; Chatfield, 1977; Burke, 1979). Personal observation of a range of other species of terrestrial snail suggests that such variation is a widespread phenomenon, but little information is available. This chapter presents a description of variation in mantle collar colour in T. pisana from a range of localities broadly covering its distribution. Details of sampling sites are available in appendix 2.

7.2. Methods.

Mantle collar colour was scored by matching to plates in a colour atlas (Villalobos-Dominguez and Villalobos, 1947) giving scores of hue (1 to 38), saturation (0 to 12) and intensity (0 to 20). All matching was done under fluorescent light with blinds drawn across windows to achieve standard lighting conditions. Snails were scored with the animal retracted, the foot withdrawn and covered by the mantle collar, and with the latter close to the shell aperture and thus illuminated without shadow from the shell itself. Most snails could be induced to rest with the mantle collar in this position by keeping them in sufficiently humid conditions prior to scoring.

There is some variation in colour over the exposed mantle. Colour was therefore scored in a standard area (fig. 7.1.) which had a fairly uniform appearance over a large enough region to make comparison with the atlas possible.

Despite these standardizing precautions, some error was involved, particularly when the colour to be matched fell between plates on the atlas. There may also be some very small bias in matching, such that particular plates are chosen more often than their close neighbours on the chart, introducing some polymodality into the data. However, although variation in hue (usually between 6 and 8) and saturation (usually between 2 and 5) was low, intensity varied from extremely dark (0) to very pale (18). For this reason, I have concentrated entirely on the latter.

Preliminary observation of a sample from Caldey Island, near Tenby (Caldey Island, sample 1), indicated that intensity changes with size. The sample was taken on 2 VIII 1979 and all animals were scored on 10 VIII 1979. The scatter of intensity against shell size is shown in fig. 7.2. Large animals are clearly darker than small ones, although the relationship is not linear. Snails with $d < 10$ mm were subsequently allowed to grow in the laboratory until 8 XI 1979, when some had grown considerably and others hardly at all. The scatter of intensity against shell size for these snails is given in fig. 7.3. Clearly, those which had grown had darkened, while those which had remained small had also remained pale. The change is thus due largely to size and not age, and this is not an artefact due to selection favouring darker or paler forms during life.

This difference in intensity in large and small snails was confirmed in sample 2 from Caldey Island (fig. 7.4.). Similar differences were found in samples from Sardinia, Majorca and Menorca, although less pronounced in some (e.g. Majorca, fig. 7.5.). Because of this difference, only snails with $d > 10$ mm were scored in subsequent samples.

7.3. Results.

The values of hue, saturation and intensity for all animals scored are available in appendix 5. Mean values of intensity (with mean d and number of snails scored) for each sample are given in tables 7.1. 7.2. and 7.3. (only snails with d$>$10 mm scored unless otherwise stated). These can only be considered as approximate descriptions of mantle colour at each locality since different samples showed different degrees of variability. Some examples of distributions are given below.

7.3.1. Tenby and other British localities.

Snails collected on two sampling occasions at Tenby were scored. Those of 18 X 1980 were darker than those of 2 VII 1981 (table 7.1.). The change from pale to dark during growth takes place over a narrow size range (fig. 7.2.), and although there is not much difference in shell size between these two sets of samples, it is probable that the 2 VII 1981 snails were paler because they were not quite fully grown.

At all other British localities, except St. Ives, snails were also very dark, although some variation between sites may exist (table 7.2.). The St. Ives sample stands out as particularly pale despite mean shell size being larger than in Tenby samples.

7.3.2. Non-British localities.

Table 7.3. gives details of all foreign samples. Some

examples of distribution of intensity within samples, to show the variability, are given in figs. 7.6., 7.7. and 7.8. Plotting mean intensity against mean size (only snails with $d > 10$ mm), for all foreign samples, indicates two distinct groups (fig. 7.9.), with a strong correlation of intensity and size within each, (group with intensity < 6, $r = -0.80$, $p < 0.001$; group with intensity > 6, but not including the two samples from southern Spain with intensity > 12, $r = -0.88$, $p < 0.001$). It is legitimate to divide the scatter in this way because the points fall very clearly into two groups, and because a size/intensity correlation has already been found within some of these samples. Two samples, both from southern Spain (Elviria and Benalmadena), belong to neither group; they contain extremely pale animals. The lower scatter (dark) contains the samples from northern France, Calasetta (Sardinia), Lesbos and some of the Balearic samples. The upper scatter (pale) contains the samples from Israel, Limassol (Cyprus), Cagliari (Sardinia) and the remainder of the Balearic samples. All the British samples, except that from St. Ives, would fall within, or perhaps just below the lower scatter; the St. Ives sample probably falls within the upper scatter, but may be rather paler.

7.4. Discussion.

It is likely that variation in mantle colour is under at least partial genetic control. Heritability of body colour in Cepaea has been estimated from the data of Wolda (1969) as about 40% (Clarke, Arthur, Horsley and Parkin, 1978). Mantle colour of T. pisana in the samples studied falls into two groups, dark and pale, with a third possible group, extremely pale. Snails usually begin life pale and at this stage there is little difference between populations; darkening may be controlled by a gene (or genes) determinining its rate. The large variation within populations suggests that the control is polygenic as suggested for C. nemoralis by Cain and Sheppard (1952), or due to a small number of major genes (cf. Murray, 1963; Cain, Sheppard and King, 1968; Wolda, 1969) with rather variable expression, or a combination of these. Whichever is correct, it is rather surprising that the populations studied fall into two groups with no intermediates. This argues for the involvement of major genes, but then some samples might be expected to show polymodal distributions of intensity. In fact none does clearly; all populations appear monomorphic, which would suggest very strong modal selection. It is not possible to discuss this further without a much more extensive survey and genetic data from breeding experiments.

The reasons for the variation are obscure. Darkening with increased size, in contrast to C. nemoralis which shows no such change, at least when above about one third grown (Cain and Sheppard, 1952; A. J. Cain, personal communication), may be due to a more or less gradual production of pigment during growth; but very small animals can be quite dark on occasion, so this is not a very rigid constraint. The difference between adults and juveniles may be related to their different microhabitat (and microclimate) preferences, but these differences have only been studied at Tenby (chapter 4, section 4.3.) and may not be universal.

Both visual selection (Cain and Sheppard, 1952; Cain and Currey, 1963) and climatic selection (Burke, 1979) have been put forward as mechanisms controlling the extensive body (not mantle) colour variation in Cepaea. In T. pisana there is a hint of a correlation of intensity of mantle colour with overall climatic variation, although the number of localities studied is small. All the populations sampled from Britain and northern France belong to the dark scatter, except that at St. Ives which may be derived from a small founding population (chapter 2, section 2.5.3. and chapter 6, section 6.6) from one tail of the distribution of mantle colour in Brittany. All other populations with pale mantles are Mediterranean. This suggests some climatic control, although there is no clear correlation with overall climatic variation within the Mediterranean. There may indeed be an overall correlation, but obscured by local or microclimatic patterns (cf. life-cycle parameters - chapter 3, section 3.2.3., and shell thickness - chapter 8, section 8.4.).

If climate does determine mantle colour to any extent, the reason for this is not clear. Certainly, if its effect is due to the reflective or absorptive properties of surfaces of different colour, then the paler mantles of Mediterranean snails would be expected. However, T. pisana is largely nocturnal and its mantle is rarely exposed to the sun; it is difficult to see how incident solar radiation could be important in determining its colour.

Even when active, little mantle is exposed. If visual selection by nocturnal predators were important (or indeed, if climatic selection could operate via occasional daytime activity), one would expect colour variation of soft parts to involve the much more exposed head/foot at least as much as the mantle, which it does not, the former being universally fairly pale, although with some variation (personal observation).

Cain (1982) has suggested tentatively that while selective pressures for crypsis and/or reflectance will be important in controlling variation of the upper shell surface, they may be relaxed for the under side. Greater polymorphism, or at least a contrasting pattern on the under side, may thus become possible, and this is indeed found in many groups of terrestrial snails. If, having discovered a snail, a predator fails to take it cleanly, but dislodges it from its resting position, so that it falls to the ground landing either way up, a contrasting pattern or range of patterns on the under side may hinder generation of a search image. Since the mantle is exposed when a sitting snail falls with its apex down, it is possible that variation in mantle colour is related to this phenomenon (called heterosematism by Cain). If this is so, then it is surprising, with the wide range of mantle intensity available within the species, that populations are monomorphic.

Clearly, none of these theories for the control of mantle colour variation is satisfactory, but without further study it is not possible to suggest a more adequate one.

Fig. 7.1. Diagram of a snail to show the position at which mantle collar colour was scored.

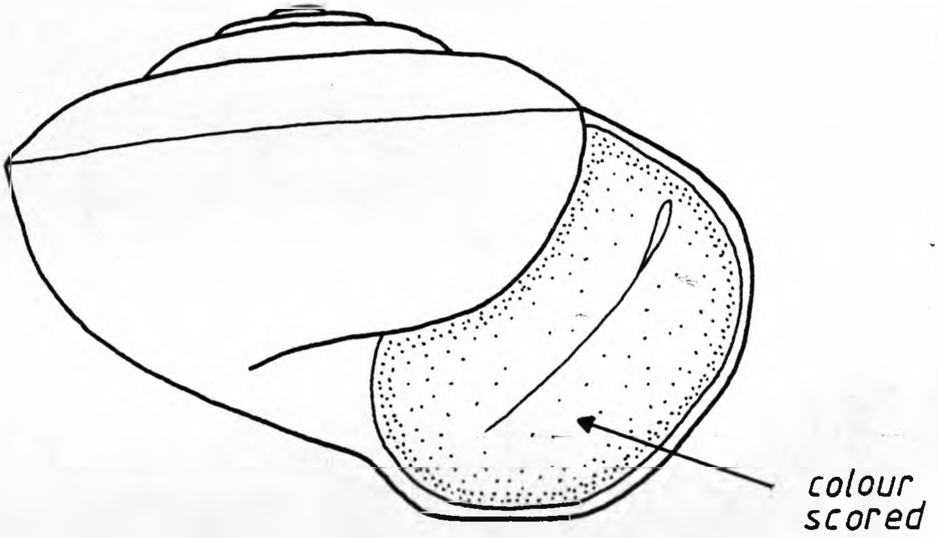


Fig. 7.2. Scatter diagram of intensity against shell size.
Caldey Island sample 1 - scored 10 VIII 79.

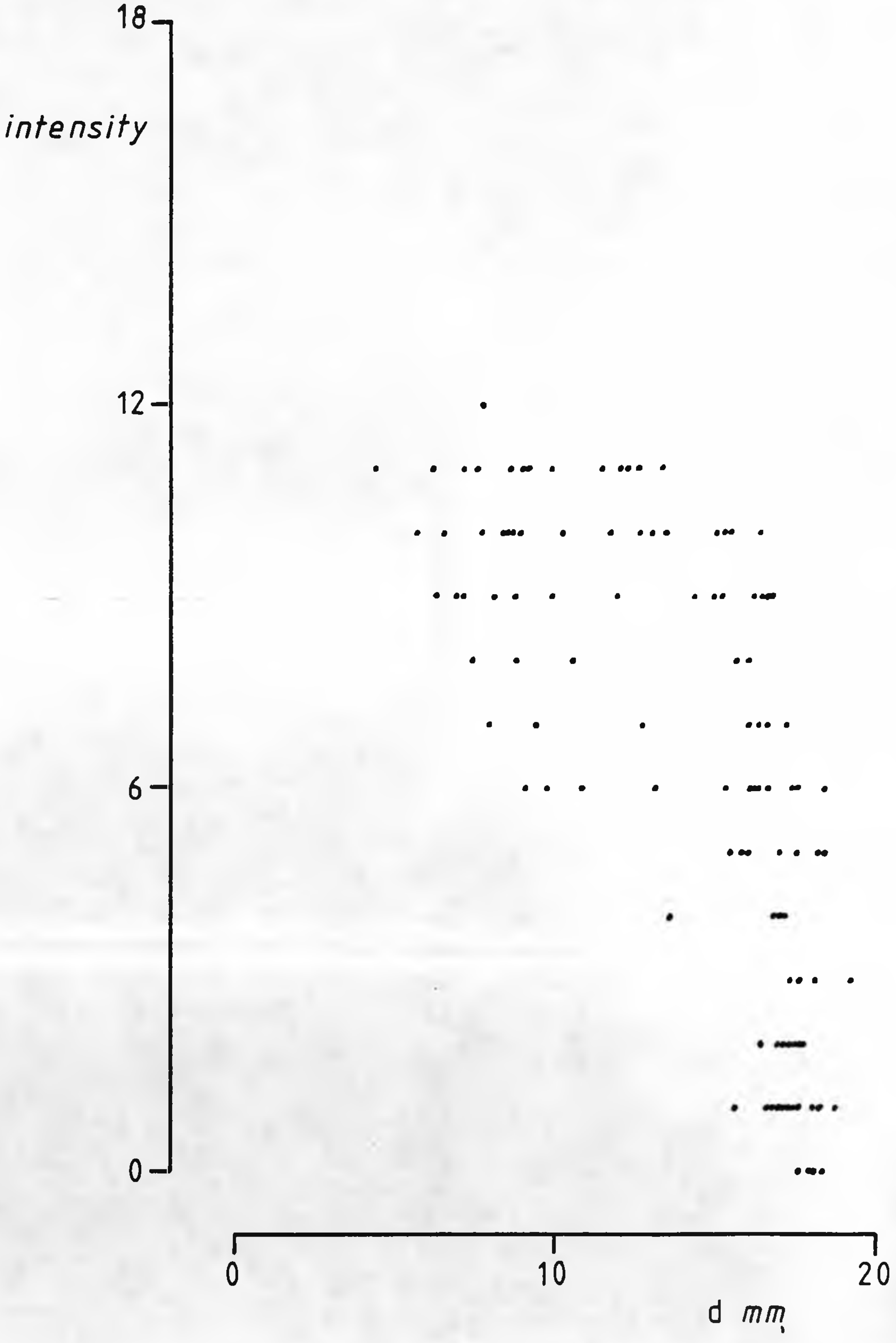


Fig. 7.3. Scatter diagram of intensity against shell size.
Caldey Island sample 1 - scored 8 XI 79.

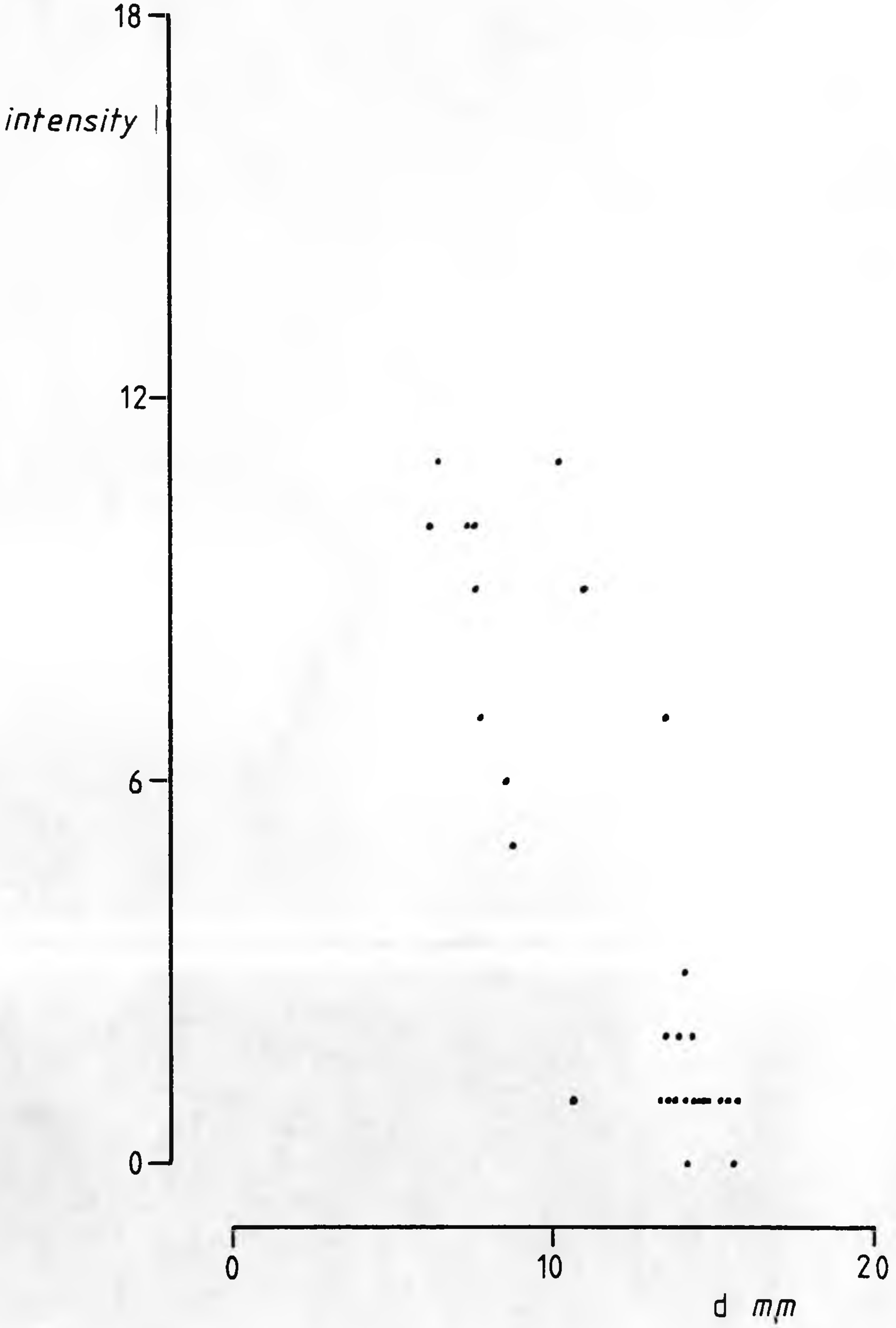


Fig. 7.4. Distribution of mantle colour intensity
Caldey Island sample 2
a - snails with d >10.0 mm
b - snails with d <10.0 mm

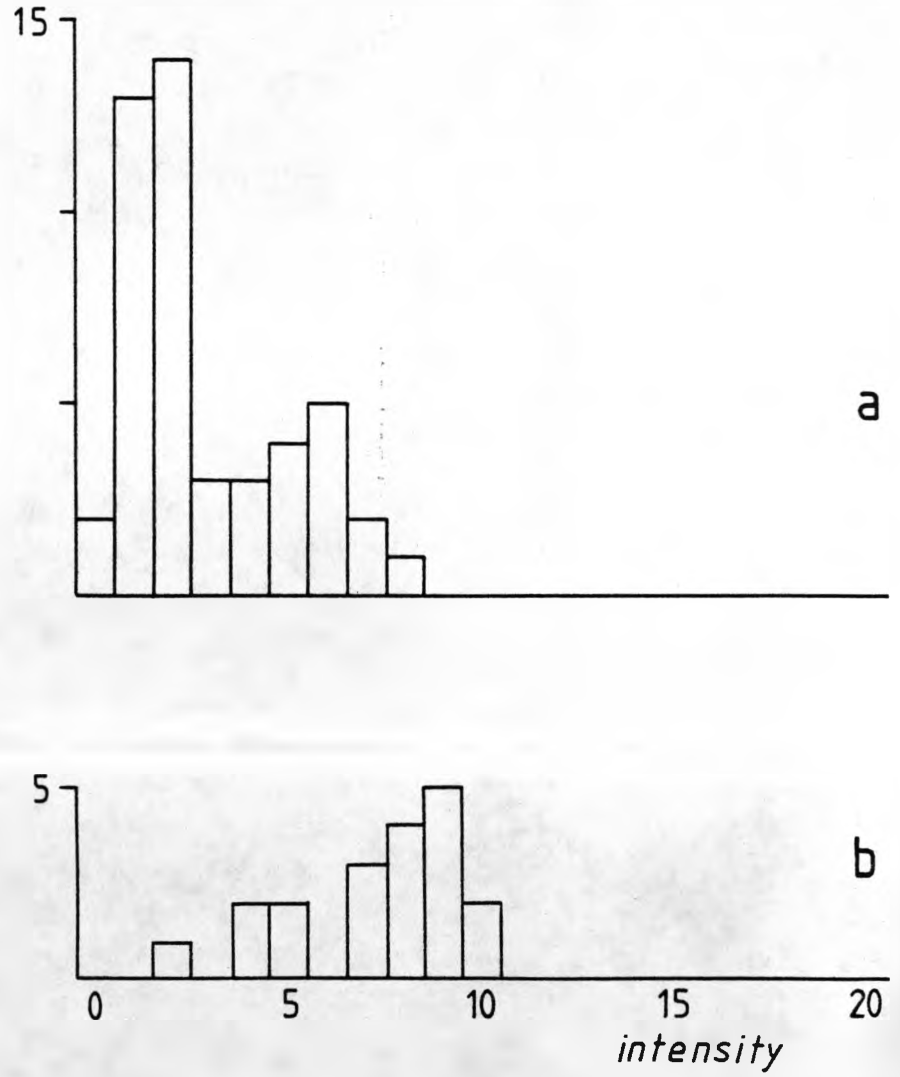
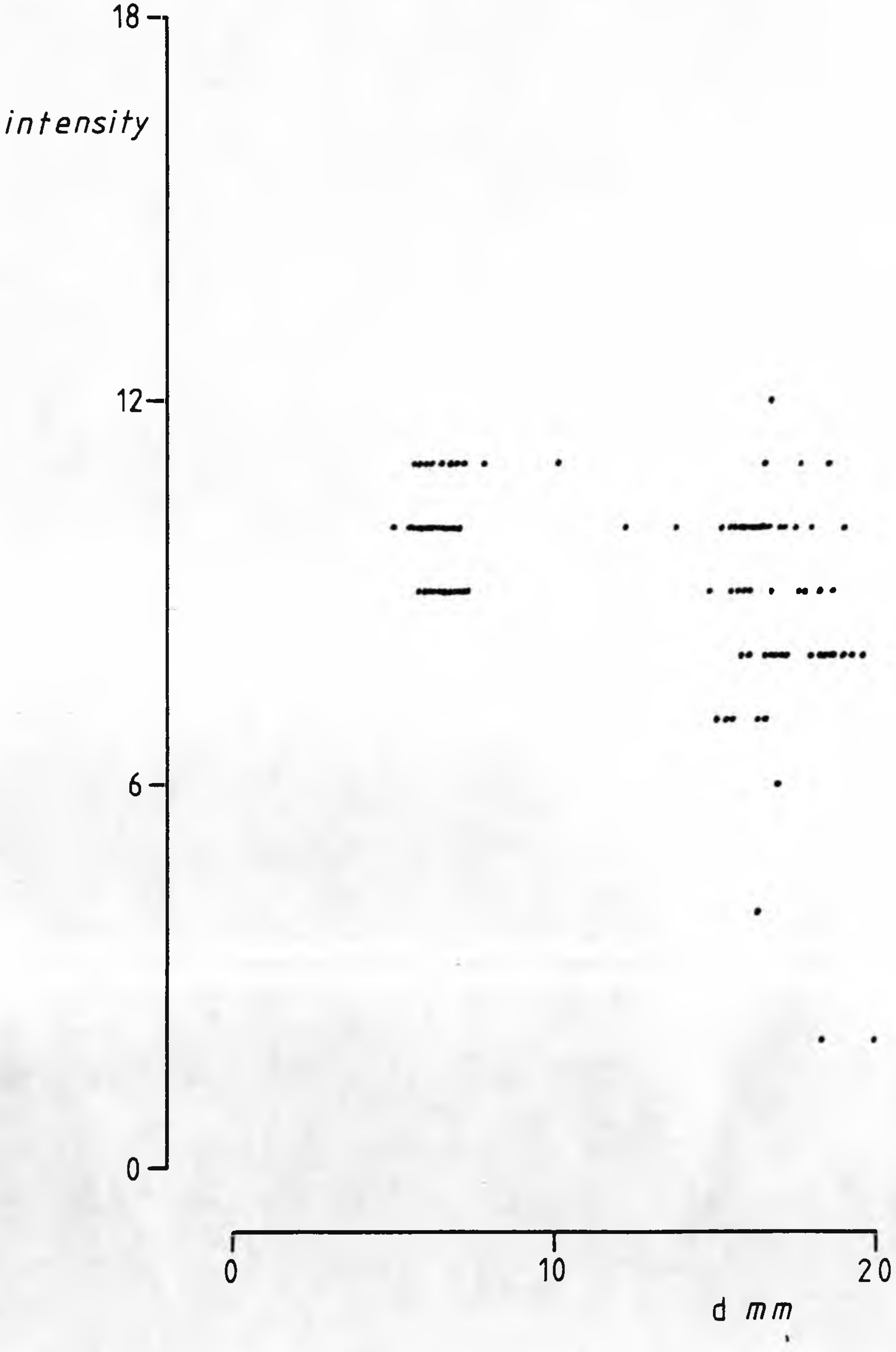


Fig. 7.5. Scatter diagram of intensity against shell size.
Mallorca - Ses Coretes.



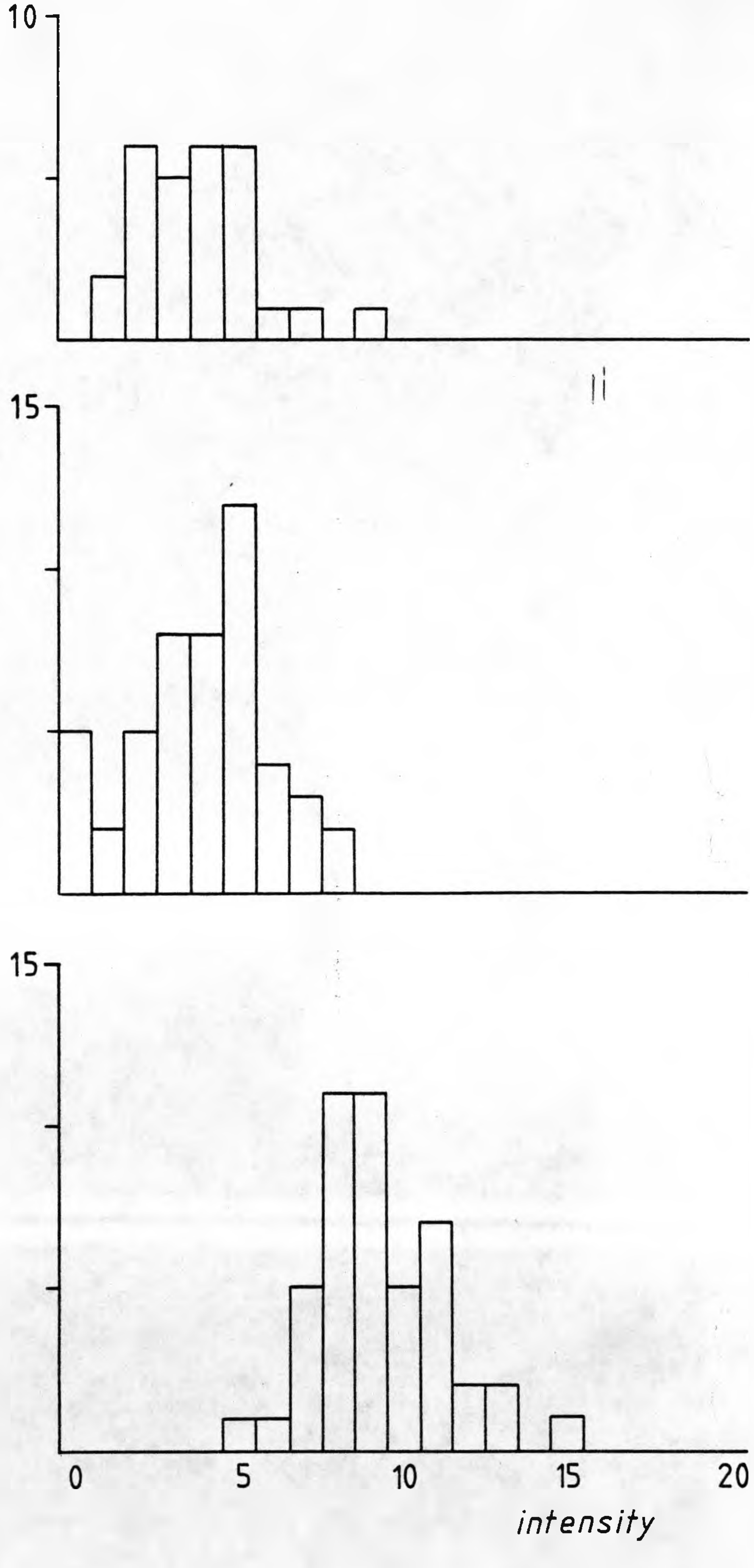

10
ii
15
15
0
5
10
15
20
intensity

Fig. 7.9. Scatter diagram of mean intensity against mean shell size for non-British samples (snails with d>10.0 mm).

- ● samples from northern France
- ⊙ samples from the Balearics
- ○ other samples

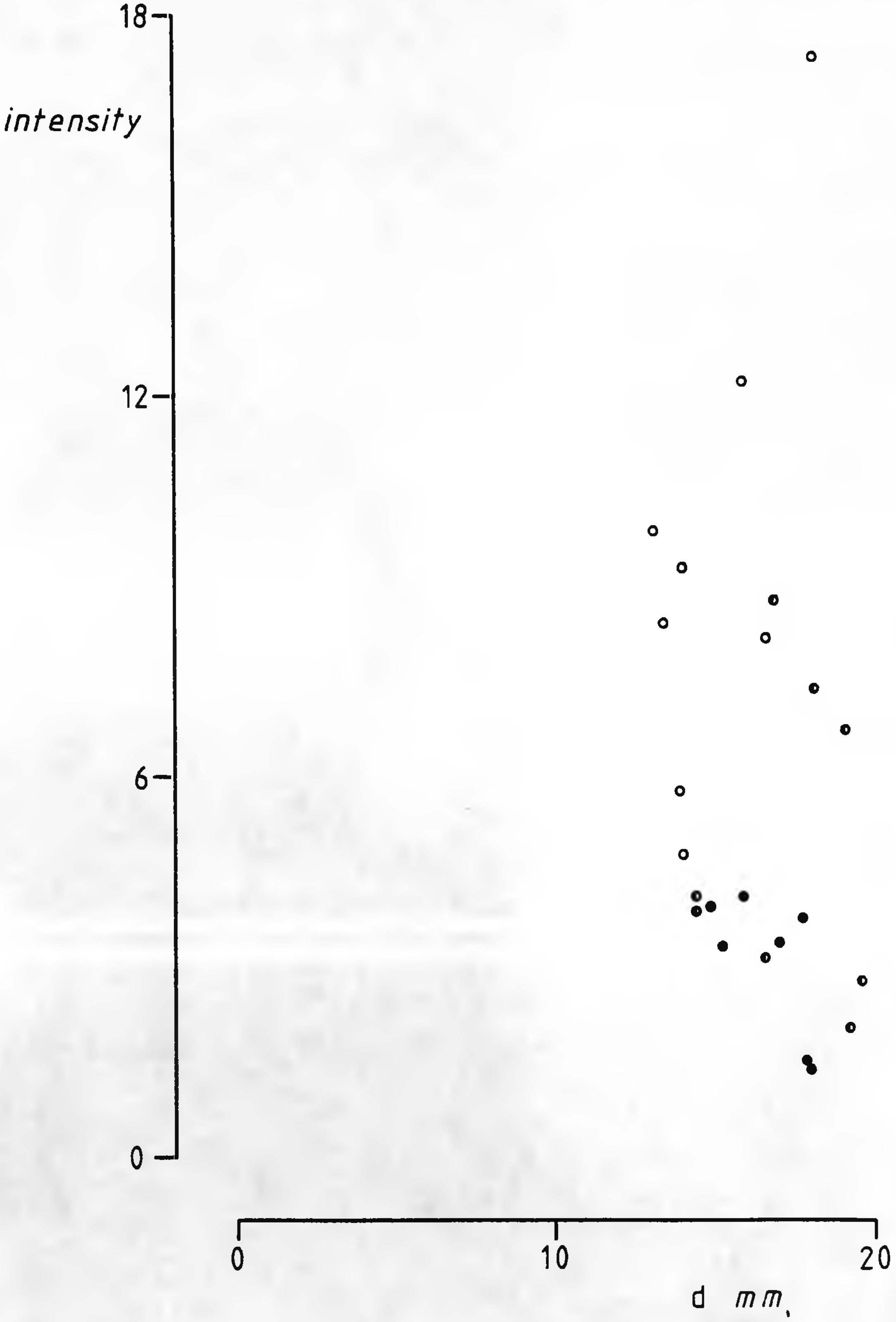


Table 7.1.

Mean mantle intensity of Tenby samples, with mean size of scored snails and number in sample.

collection date	site	sample	intensity	size (d)	number
18.10.80	1	1	2.26	15.22	19
	1	2	1.75	14.30	20
	2	1	1.63	13.58	27
	2	2	2.43	14.07	70
	2	3	0.82	16.29	60
	3	-	1.24	16.49	50
	4	1	2.25	13.38	16
	4	2	0.55	14.78	20
	5	-	0.42	15.63	12
	6	-	1.58	14.08	26
2.7.81	1	1	4.00	13.58	16
	1	2	3.56	13.99	36
	2	1	4.33	14.03	110
	2	2	3.82	13.10	177
	2	3	3.73	14.45	102
	3	-	6.00	15.97	27
	4	1	3.41	15.34	119
	4	2	2.76	15.64	46
	5	-	3.20	14.78	25
	6	-	3.18	13.54	106

Table 7.2.

Mean mantle intensity of British samples (not main Tenby sites) with mean size of scored snails (d$>$10.0 mm unless otherwise stated) and number in sample.

sample	intensity	size (d)	number
Tenby - Narberth Road	1.43	18.36	7
Saundersfoot - site 1	3.00	19.88	8
Saundersfoot - site 2	1.90	17.25	10
Porthcawl - Newton	0.00	20.76	8
Porthcawl - Kenfig	0.57	17.55	30
St. Ives	9.89	18.07	35
Caldey Island - sample 1:			
d$>$10.0 mm, scored 10.8.79	5.51	15.87	77
d$<$10.0 mm, scored 10.8.79	9.45	7.95	29
d$>$10.0 mm, scored 8.11.79	2.24	13.89	21
d$<$10.0 mm, scored 8.11.79	8.50	7.49	8
Caldey Island - sample 2:			
d$>$10.0 mm	2.85	15.50	47
d$<$10.0 mm	7.26	8.83	19

Table 7.3.

Mean mantle intensity of non-British samples, with mean size of scored snails ($d > 10.0$ mm unless otherwise stated) and number in sample.

sample	intensity	size (d)	number
Baie du Mont St. Michel	1.35	18.16	60
Brittany: site 1	3.33	15.13	40
site 2	3.88	14.73	56
site 3	1.46	17.94	74
site 4	4.14	15.74	86
site 5	3.75	17.76	28
site 6	3.36	17.01	53
Elviria (S. Spain), site 1	12.19	15.84	43
Benalmadena (S. Spain)	17.33	17.93	4
Majorca: Camp de Mar	6.71	19.00	21
Ses Coretes ($d > 10.0$ mm)	8.67	16.72	56
Ses Coretes ($d < 10.0$ mm)	9.94	6.29	33
Costa de la Calma 1 ($d > 10.0$ mm)	3.86	14.42	49
Costa de la Calma 1 ($d < 10.0$ mm)	6.23	7.16	105
Costa de la Calma 2	3.07	16.52	29
Menorca: Torralba	2.71	19.66	14
Torre d'en Gaumes	2.00	19.20	2
Santa Clementina	7.35	18.09	20
Es Grao ($d > 10.0$ mm)	4.12	14.41	17
Es Grao ($d < 10.0$ mm)	10.15	8.77	13
Calasetta (Sardinia) ($d > 10.0$ mm)	4.76	13.98	17
Calasetta ($d < 10.0$ mm)	9.16	5.70	32
Cagliari (Sardinia) ($d > 10.0$ mm)	7.83	16.53	6
Cagliari ($d < 10.0$ mm)	10.37	7.21	30
Lesbos	5.72	13.89	108
Limassol (Cyprus)	8.42	13.34	86
Ashqelon (Israel): central	9.24	13.93	46
southern	9.82	13.04	22

Chapter 8

Shell Thickness

8.1. Introduction.

Most evaporative water loss from the body of an inactive snail takes place through the shell aperture, unless the snail seals its peristome to a hard surface, when evaporation through the shell itself is important (Machin, 1967). This experimental work of Machin (1967) also showed that shell thickness was greater in species living in hot and dry environments and exposed to the sun. This was seen as an adaptation for reducing water loss. Variation in shell thickness within a single species living in a range of climatically different habitats might therefore also be expected. Indeed both Rensch (1932) and Bar (1978) have suggested that thickness in T. pisana increases with increasing aridity or exposure to the sun (see also Sacchi, 1971). Pollard (1975a) also has shown, for Helix pomatia L., that shell thickness is correlated with climatic factors.

Following these findings, the thickness of shells from Tenby and also from other localities in northern France and the Mediterranean, was investigated in an attempt to describe this phenomenon more generally, for a large part of the range of T. pisana.

8.2. Methods.

Thickness was measured within two weeks of the snails being collected. It was assumed that this short period would allow only negligible further deposition or resorption of shell material. Shell thickness was measured once for each shell, at a point ¼ of a whorl back from the aperture and half-way between the suture and the periphery (the keel in juvenile shells) (fig. 8.1.).

This avoided the thickened peristome and (in juveniles) the keel which is also thicker than the main part of the shell (fig. 8.2.). A piece of shell including this point (previously marked) was removed from the shell and thickness measured using a micrometer with conical measuring points, designed specially for measuring curved surfaces (fig. 8.3.). This method of measuring thickness at a single standard point on each shell (Murray, 1966; Bar, 1978) rather than averaging thickness over the whole shell (Machin, 1967), or weighing the shell (Rensch, 1932), was considered best, not only for obtaining a measure of thickness itself rather than a measure only proportional to thickness but also for obtaining data from the large number of shells used in the study.

Shell thickness was measured in some, or all, of the samples taken from Tenby on all sampling occasions from 14 September, 1978 until 18 October, 1980 (chapter 3, section 3.2.1.1.). Most of the samples from the Mediterranean and northern France (chapter 3, section 3.2.2.3., and appendix 2) were also used. In most of these samples, thickness of shells with $h + d < 7.0$ mm was not measured. Scatter diagrams of thickness (t) against size (h + d) have been plotted, and the mean shell thickness of shells in each 2 mm category of h + d has been calculated.

8.3. Results.

The results are not all presented here, but the means and standard deviations of the values of shell thickness (t) for each 2 mm category of h + d of all the samples analysed are available in appendix 6.

There is considerable within-sample variation in thickness, and indeed also within each 2 mm size category of a particular sample. Some of this variation is undoubtedly due to the increased thickness of the repaired parts of damaged shells, where this included the point at which thickness was measured. However, most is natural variation among healthy, undamaged individuals. In few samples is a straightforward relationship between shell thickness and shell size apparent over the whole range of size. Therefore, the usual method (Calow, 1975; Williamson, 1976) of analysing the relationship between two such measures, by transforming the scatter diagrams to logarithmic co-ordinates and calculating a single regression for each sample using the constants of these regressions for between-sample comparisons, has not been used.

Since most data are available from the Tenby samples, these will be dealt with first. Small shells (up to about 12 mm are usually thinner than large ones (above about 24 mm h +d). Examples of this are given in figs. 8.4., 8.5. and 8.6. Within the small shells of a sample there was usually a clear increase in thickness with increase in size. A similar, but less clear relationship was also sometimes apparent within the large shells (as also found by Bar, 1978). Intermediate-sized shells were often thinner than the larger small shells, so that the complete relationship over the whole range of shell size often appeared stepped (figs. 8.4., 8.5. and 8.6). A partial explanation of this is that intermediate-sized snails were those undergoing rapid growth (chapter 3, section 3.2.1.2.). If this were the case, they were thinner because the newly-added and unthickened part of the shell could include the point, ¼ of a whorl back from the aperture, at which thickness was measured.

Shell material is resorbed during breeding, mostly from those inner parts of the shell enclosed by later whorls, but also to some extent from the inner surface of parts not enclosed. This is clear from my own observations of the condition of live adult shells taken during and after the breeding season at Tenby, and also of dead adult shells seen at these times. It may also take place in Israel (Heller, 1982), and other species have been shown to use the shell as a calcium reserve (Wagge, 1951; Chan and Saleuddin, 1974). Thus, mean thickness of adults will be greatest during the short period between the completion of growth and the start of breeding. There is considerable variation in the length of this period; indeed some animals may breed before they are fully grown (Cowie, 1980b). Mean thickness of a particular 2 mm category of h + d will thus depend to some extent on the time of year. This is clear from a comparison between figs. 8.4., 8.5. and 8.6. Despite these difficulties of analysis, it can be said that at Tenby, mean adult thickness lies between about 0.08 mm and 0.20 mm, albeit with considerable individual variation.

None of the samples from northern France and the Mediterranean suggests a radical departure from this pattern (e.g. Brittany, fig. 8.7.; southern Spain, fig. 8.8.; Lesbos, fig. 8.9.; Cyprus, fig. 8.10.). Most of these samples were taken during periods of no growth when shell thickness would be near its greatest, and thus intermediate-sized shells would not be especially thin. No trends can be seen which correlate with large-scale climatic trends in the Mediterranean (chapter 3, section, 3.2.3.); and furthermore, there is clearly no great difference in mean shell thickness between shells taken from localities as different climatically as south Wales and Israel.

8.4. Discussion.

Williamson (1976) found seasonal differences in the shell weight/shell size relationship of Cepaea nemoralis and related this to periods of rapid growth, and possibly to periods of shell thickening prior to hibernation. He also showed that, although the log-log relationship of shell weight to shell size was linear over most of the range of size, departure from linearity was evident for snails of under 5 mm diameter. Clearly, these effects, and also shell resorption during breeding, complicate the shell thickness/shell size relationship in T. pisana. During this study, it has only been possible to suggest some trends within the relationship, and to indicate a range of mean adult thickness of between about 0.08 mm and 0.20 mm. This range encompasses all the samples analysed, from both Atlantic and Mediterranean localities, south Wales and Israel being the climatic extremes.

My results from Israel do not agree with those of Bar (1978) who showed a correlation between shell thickness and aridity along two transects in Israel. He gave figures of mean shell thickness for his five samples of between 0.37 mm and 0.79 mm, with a range of from 0.25 mm to 0.95 mm for individual shells. These values are far higher than any obtained in the present study, including those from Israel (maximum thickness in my Israeli samples was 0.23 mm and this was the only shell with a thickness over 0.20 mm). Both Bar's samples and those from Israel in the present study were taken during the summer period of aestivation, and so should be comparable, with no complications due to growth or breeding, and furthermore the shells were probably near their maximum thickness. The only differences are that Bar measured the thickness of his shells at a position on the under surface and just behind the thickened peristome, rather than on the upper surface and ¼ of a whorl back from the aperture; and that he used a caliper with flat measuring surfaces rather than a specially designed micrometer with conical measuring points. In order to test whether these differences in method could explain the differences in the results, the shells of the Caesarea sample of the present study (the sample with highest mean thickness amongst the Israeli samples) were measured using Bar's method, and indeed using the same model of caliper. The results showed that although the under surface just behind the peristome was slightly thicker than the upper surface ¼ of a whorl back from it, and the use of the caliper rather than the micrometer exaggerated shell thickness, the effect was small when compared with the difference between the results obtained in the two studies. The values obtained in the present study could not be increased by the use of Bar's methods to become similar to the results he obtained. It is possible that he did not completely avoid the thickened peristome. As well as this difference in the results of Bar's study and the present study, there is no indication from the present samples that shells from the south (Ashqelon) are thicker than those from the north of Israel (Dor and Caesarea).

Rensch (1932) also suggested a relationship between shell thickness (weight) and insolation in T. pisana, but gave no details of the time of year his samples were collected. He compared only within two groups of localities, viz. southern France, Algeria and Egypt; and Venice and Sicily. His values are not strikingly variable, and indeed if comparisons are made between the two groups (and there is no reason for keeping them separate), in particular between Sicily and Algeria, then the relationship breaks down, shells from Sicily being heavier than those from Algeria, although Rensch's hypothesis would suggest the opposite should occur. His study clearly shows that there is some variation in thickness from place to place, but it is not related to any obvious, large-scale climatic factor, and in this respect agrees with the results of the present study. In view of this the results of Bar's study are all the more enigmatic.

What variation there is in mean shell thickness of T. pisana from locality to locality is, then, not clearly related to large-scale climatic trends. It may be related to more local climate, and in this respect may be similar to the variation in the life-cycle (chapter 3, section 3.2.3.). It may also be related to availability of calcium, as suggested by Sacchi (1971), although he gave very little supporting data (cf. Taylor, 1895; Oldham, 1929, 1934; Murray, 1966). Snails living very close to the sea would have spray, sea shells and shell sand as an extra source, a source not available to populations further inland. This effect would change markedly within a few hundred metres of the shore. Since shells from localities as strikingly different climatically as south Wales and Israel do not show marked differences in shell thickness, it is possible that calcium availability is more important than local climate in controlling shell thickness.

Fig. 8.1. Diagram of shell to indicate position of measurements.

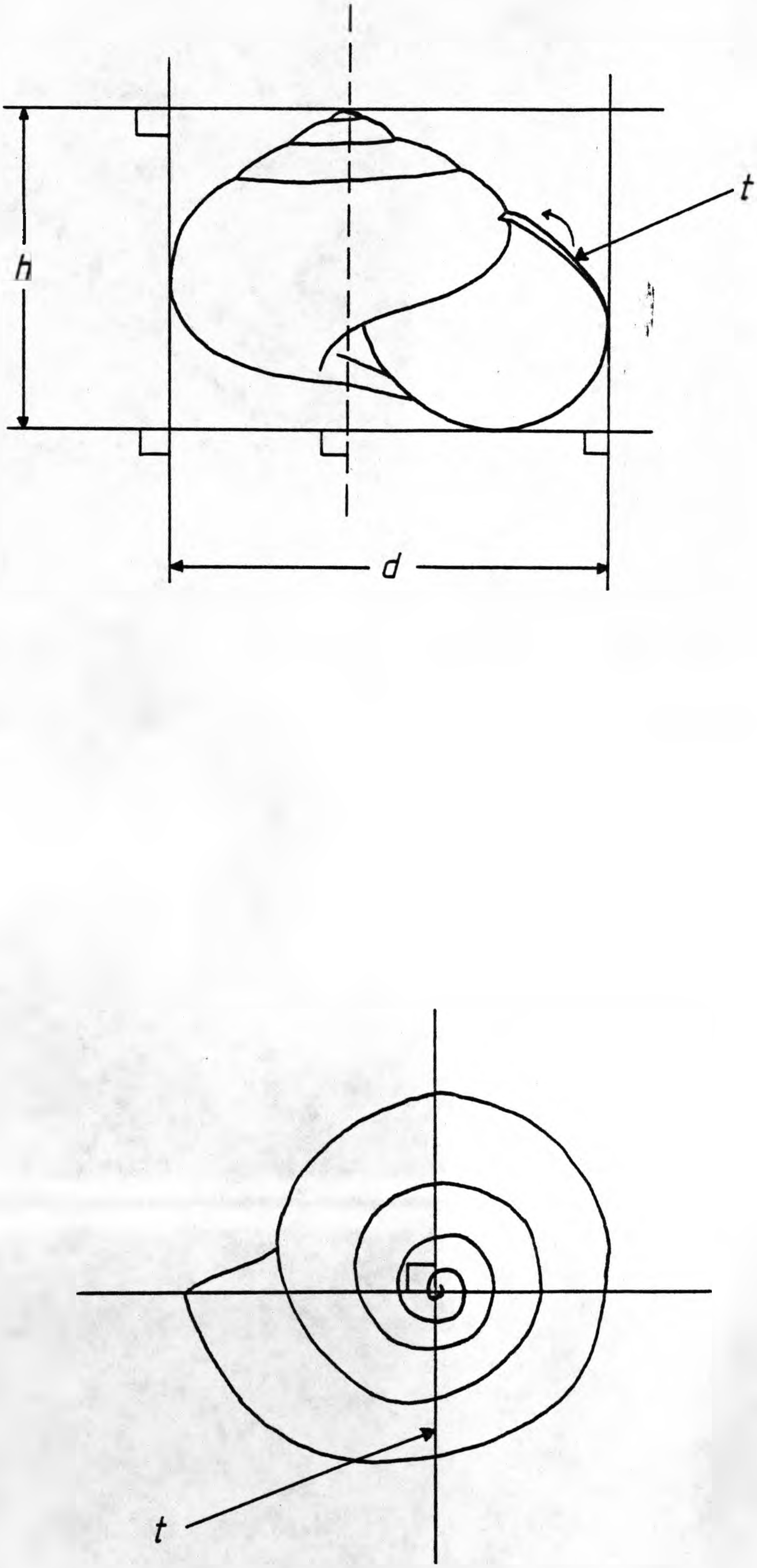


Fig. 8.2. Juvenile shell to show the slight thickening at the keel.

Fig. 8.3. Diagram of Micrometer.

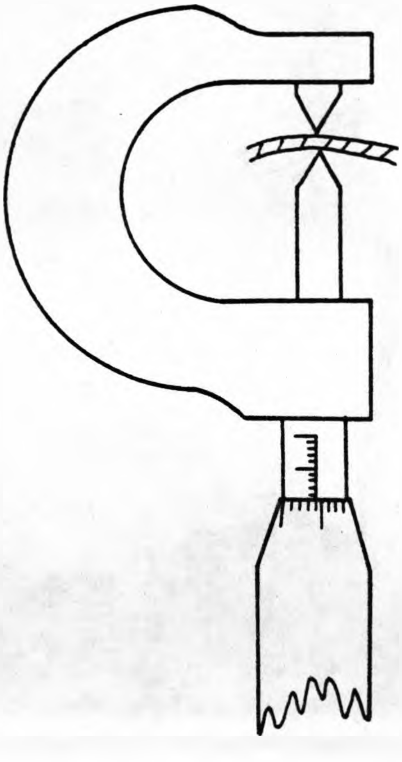


Fig. 8.4. Variation of shell thickness (t) with shell size (h+d).
Tenby 17 I 79.

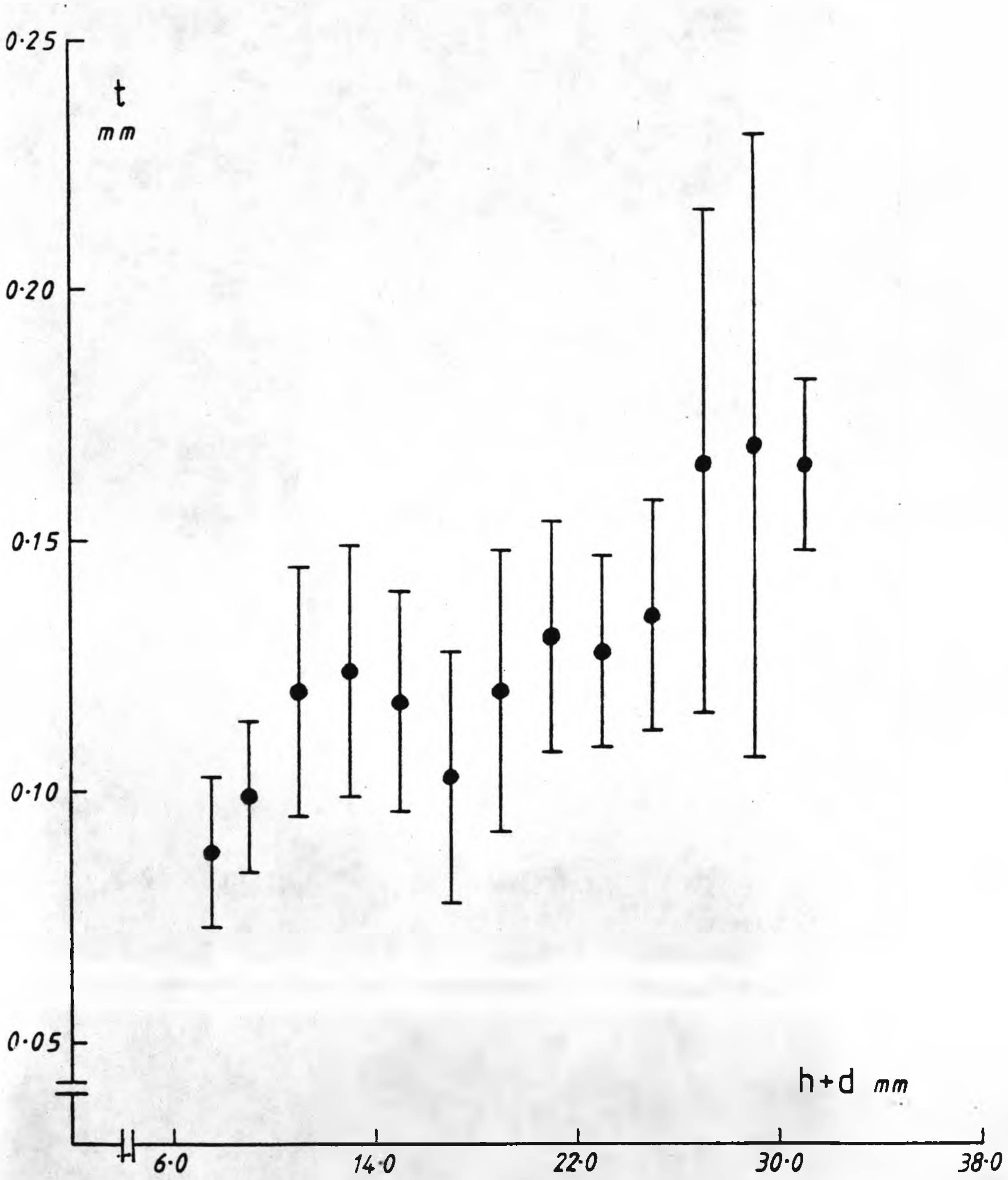


Fig. 8.5. Variation of shell thickness (t) with shell size (h+d).
Tenby 11 VII 80.

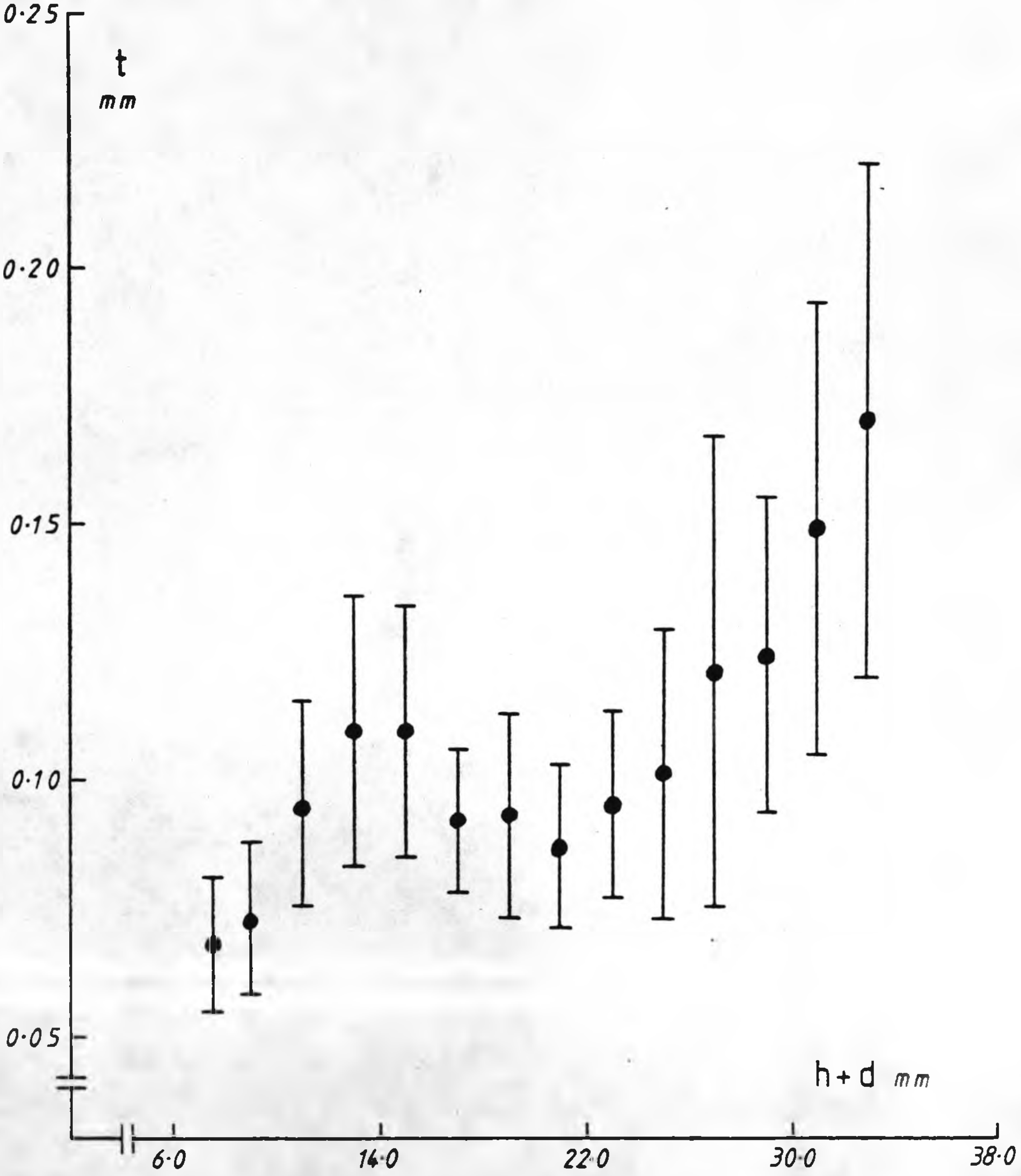


Fig. 8.6. Variation of shell thickness (t) with shell size (h+d).
Tenby 18 X 80.

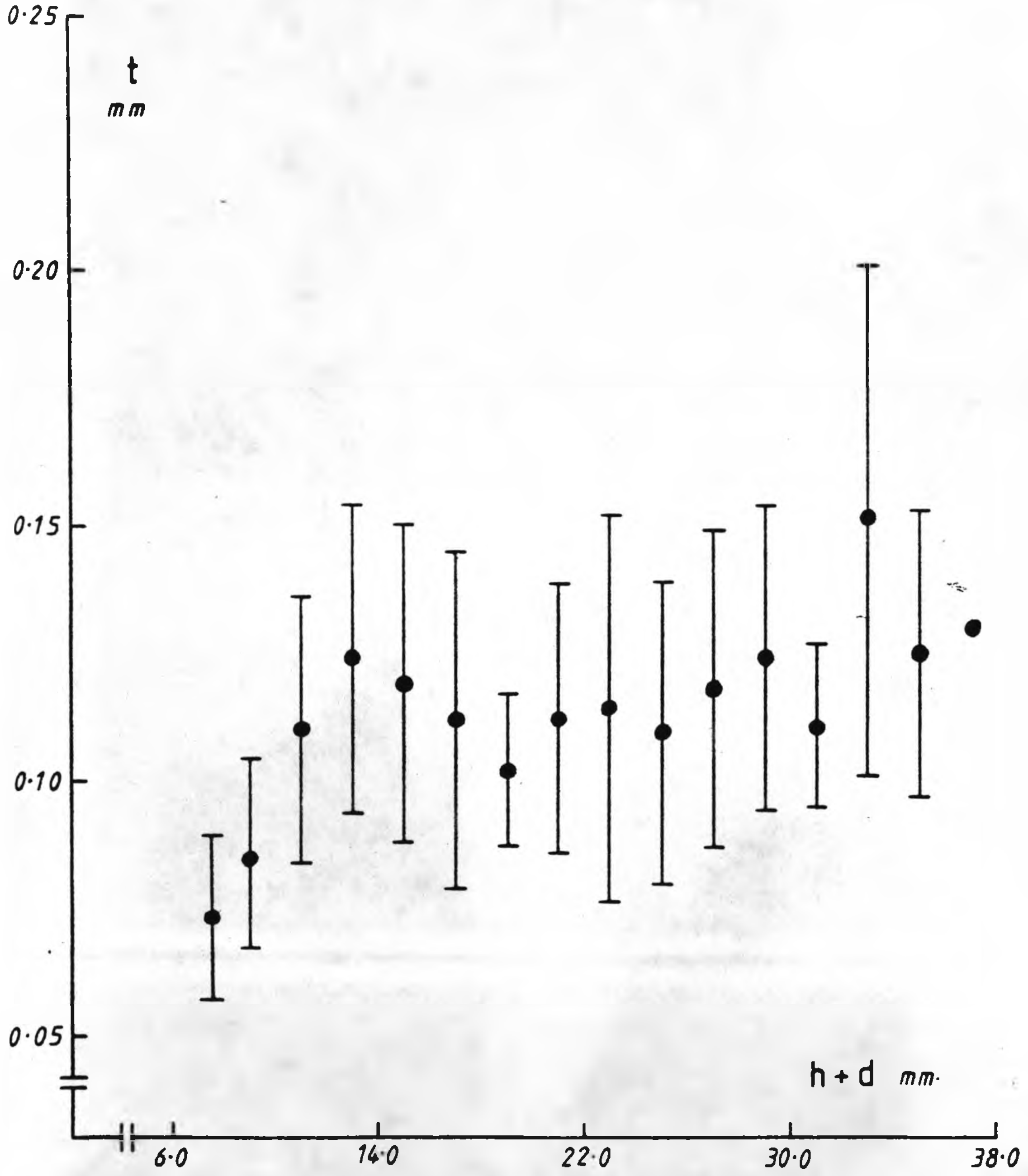


Fig. 8.7. Variation of shell thickness (t) with shell size (h+d).
Brittany sites 2, 3, 4, 5 and 6 July 1980.

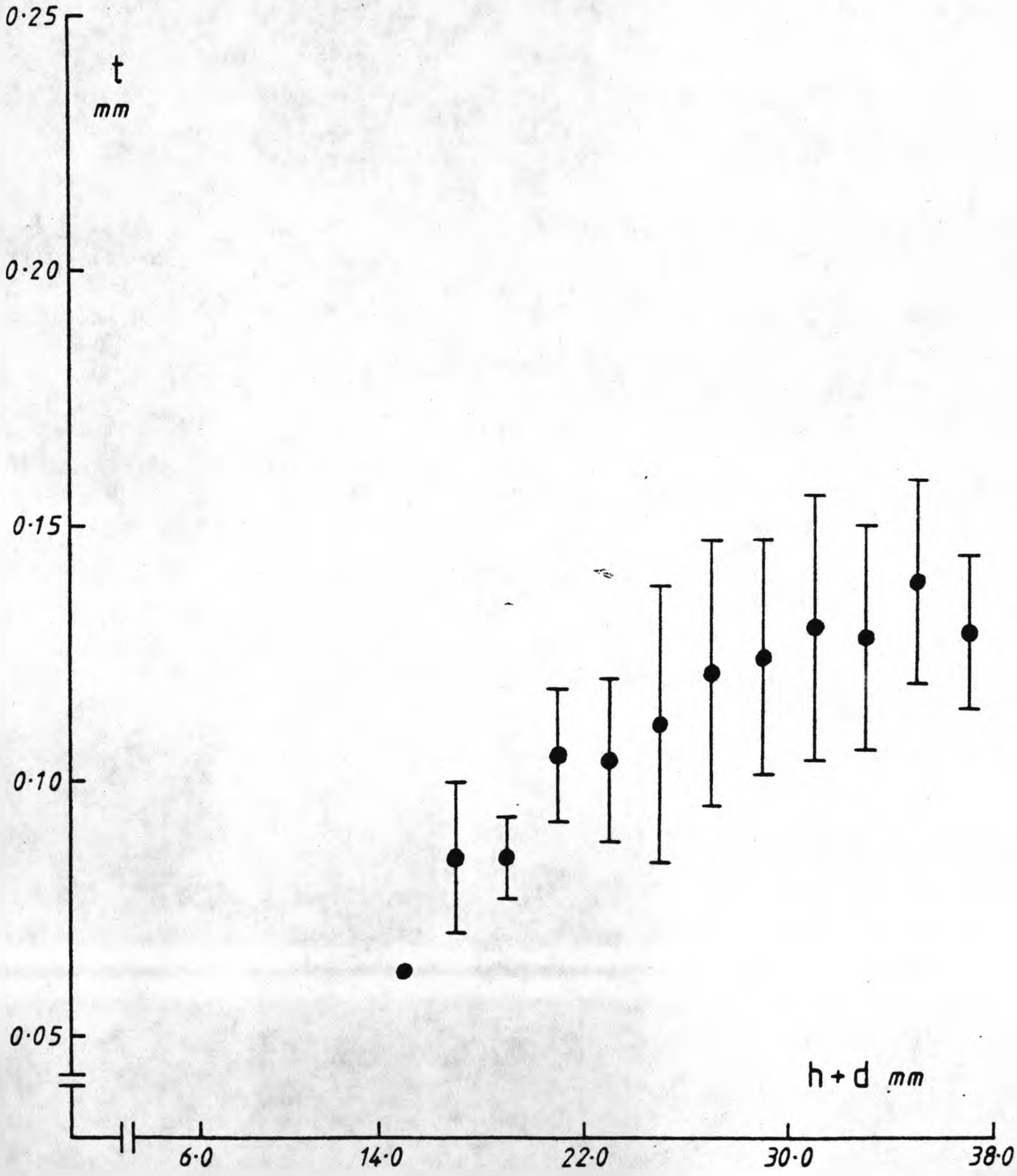


Fig. 8.8. Variation of shell thickness (t) with shell size (h+d). Elviria, southern Spain site 1 28-31 VIII 78.

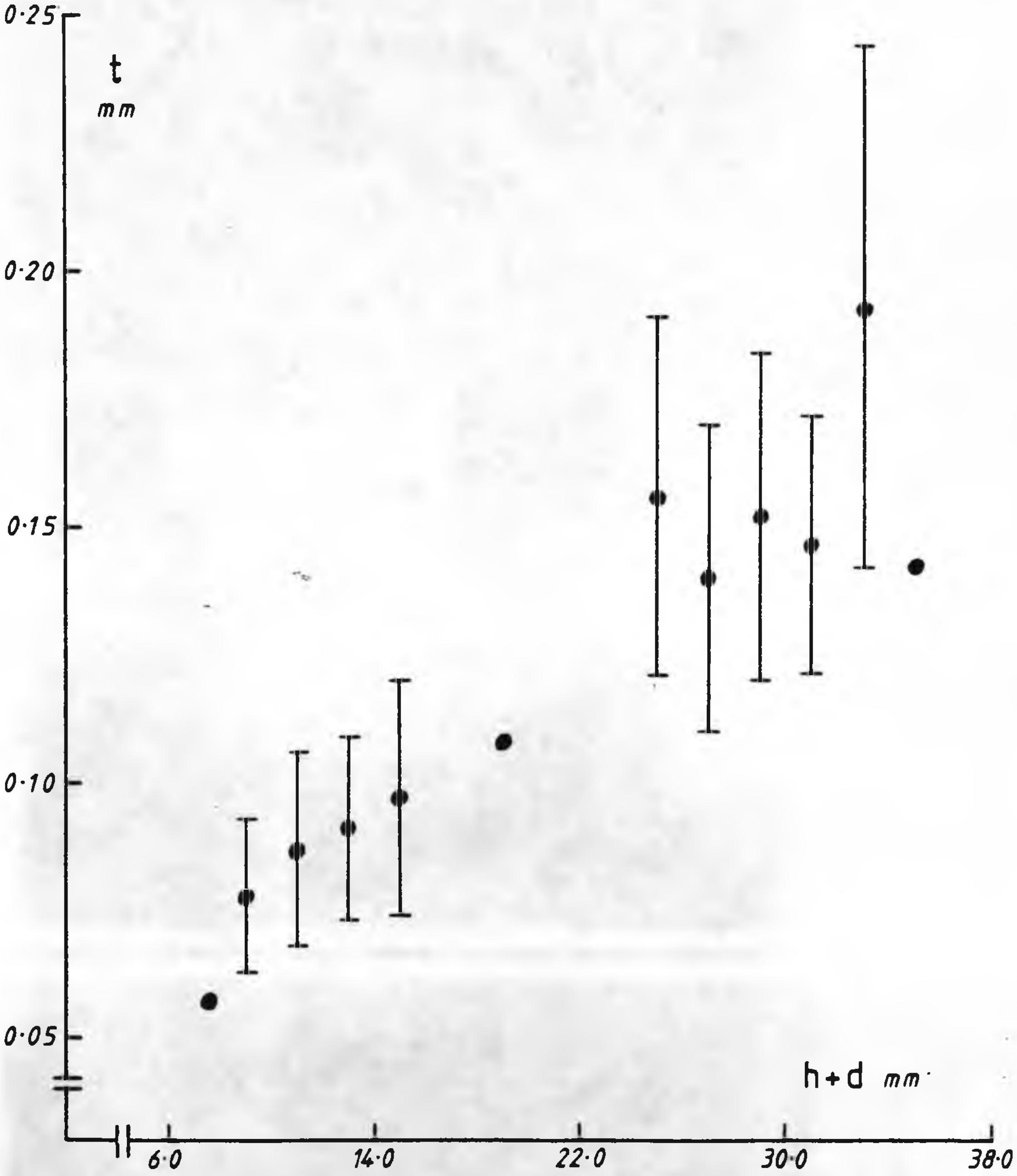


Fig. 8.9. Variation of shell thickness (t) with shell size (h+d).
Mitilini, Lesbos 18 V 80.

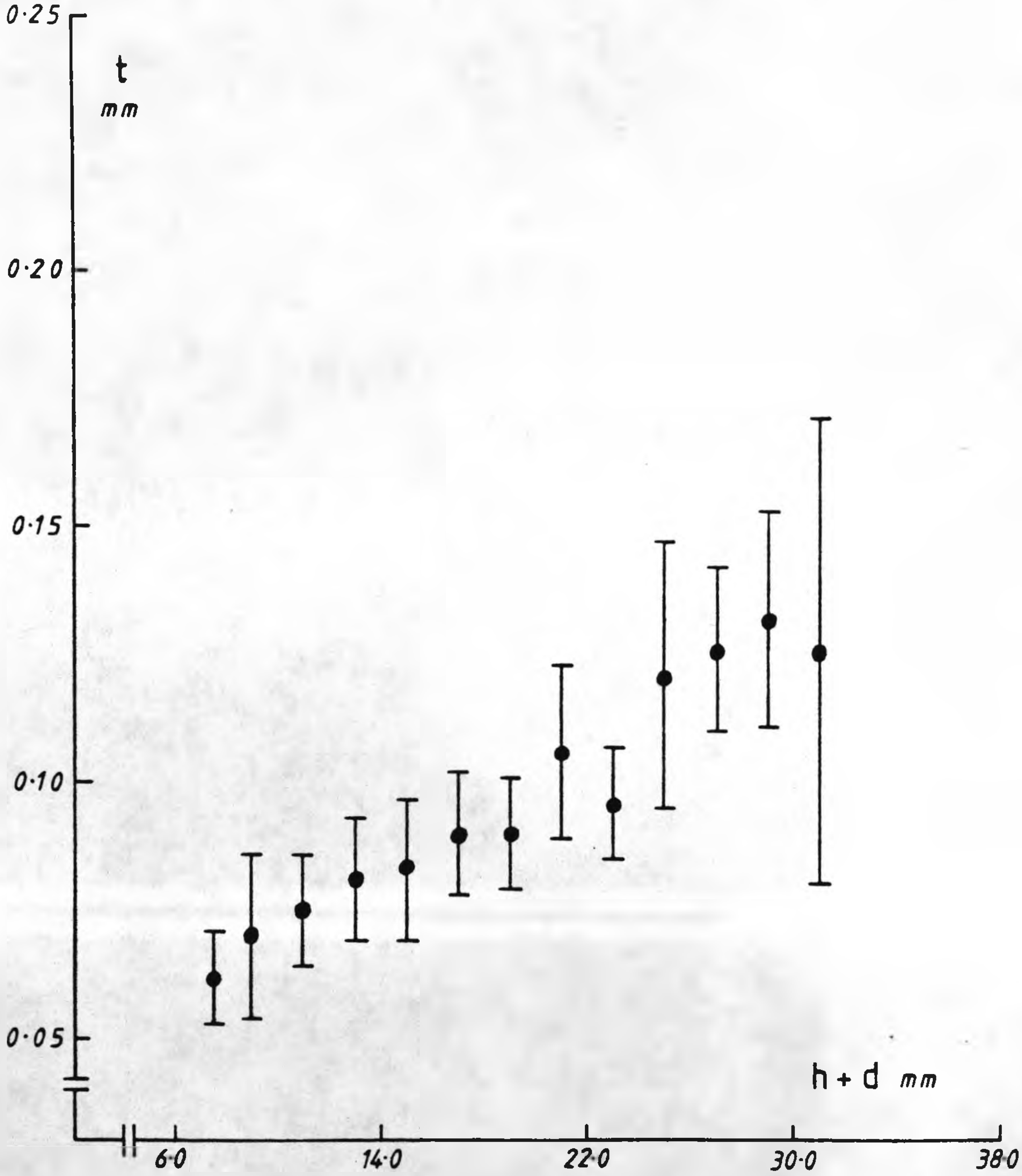
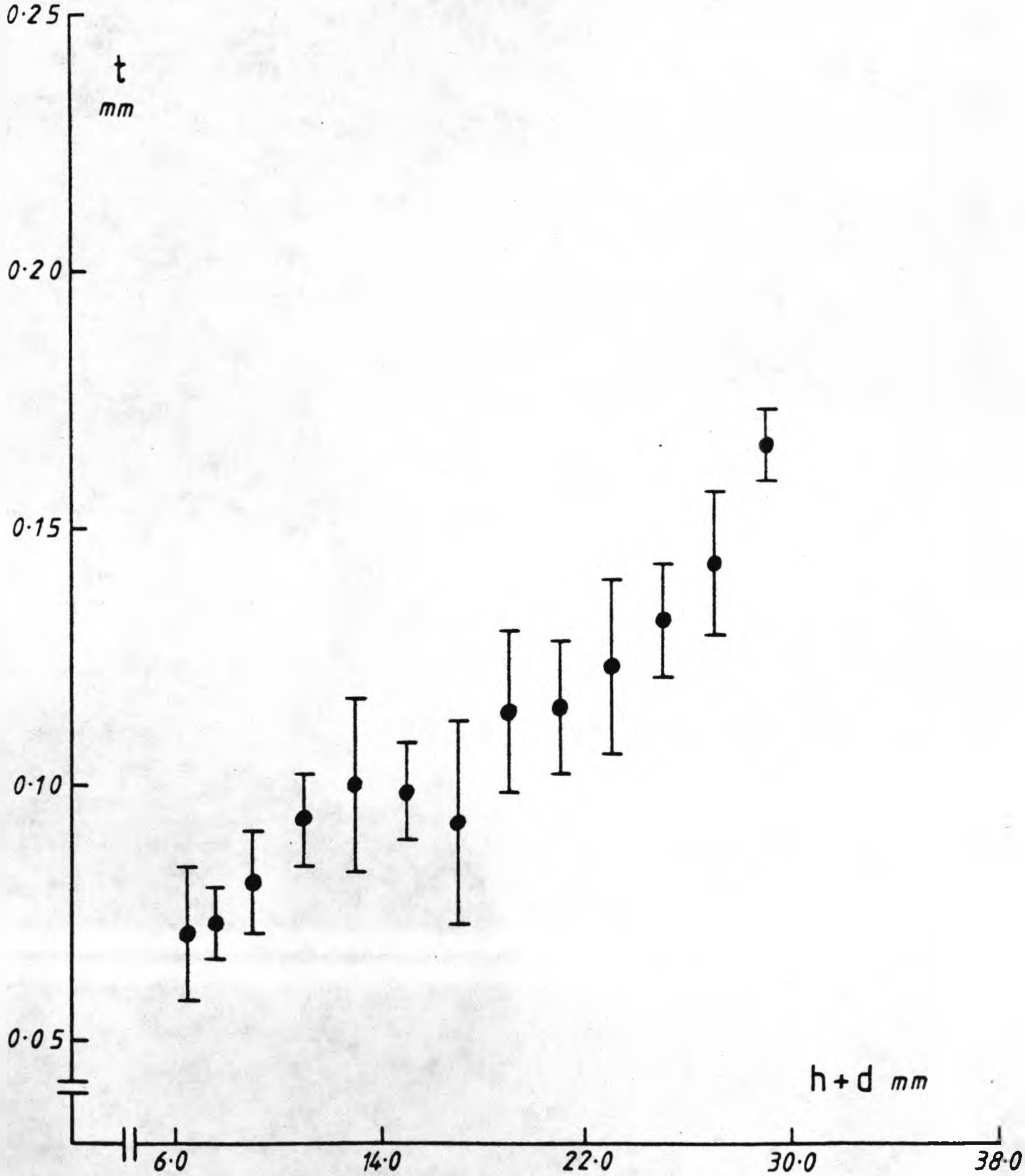


Fig. 8.10. Variation of shell thickness (t) with shell size (h+d).
Limassol August 1978.



Chapter 9

General Considerations

The aims of this thesis (chapter 1) were threefold: first, to add to the very limited ecological knowledge available for T. pisana; second, with this as a base, to describe and investigate the control of the profuse variation it exhibits, particularly in shell pattern; and third, to gain some understanding of the role of both macro- and micro- climate in its biology. The work carried out has already been discussed at length in each chapter. The purpose of this chapter is to bring these rather diverse studies together and consider their more general consequences, and to comment on some questions still remaining to be answered.

Basic ecological knowledge of an organism is essential before sound conclusions can be drawn regarding the significance of variation. Of fundamental importance is a clear understanding of population structure in space and time, especially life-history strategy (chapter 3), micro-habitat preference (chapter 4), and dispersion, dispersal, density and effective population size (chapter 5).

T. pisana is shown to be a highly productive, semelparous annual or biennial. Populations may be extremely dense, and individual snails appear rather sedentary by comparison with some other species of snail. There is a distinct tendency to aggregate in small patches within the general habitat, adults and juveniles having different micro-habitat preferences. When necessary, however, they can probably disperse long distances, and this, combined with their essentially '*r* - type' life-history strategy, means that they are well adapted to making full use of their common duneland habitat.

Combining this information on spatial population structure and life-history strategy allows a conservative estimate of effective population size to be calculated. Despite their high densities, their generally sedentary habit means that N_e may be sufficiently low at some times in some places for genetic drift to be possible; at least, it cannot be discounted totally.

This ecological knowledge has provided a framework for genetic and ecogenetic studies. The investigation of the variation in shell pattern in the Tenby colony (chapter 6), with the work of Cain (in preparation), provides the first information to become available on the genetics of T. pisana, and allows the first adequate classification of the variation. Because of the variability in expression of the morphs, which results in the often apparently continuous range found in field samples, further advances in characterisation of the variation will only come from breeding experiments.

Mantle collar colour variation at a number of localities has simply been described (chapter 7). It is undoubtedly controlled genetically, at least in part, but details of this control must also await breeding experiments.

The description of the Tenby morphs allowed random samples from there to be scored. The reasons for the differences in the frequency of unbanded at different sites, maintained over five years, remain unknown. Natural selection may well be maintaining them, but superimposed upon this is an overall tendency for five-banded snails to be at a selective advantage during at least the second year of their life. This may be balanced by a contrasting advantage (in favour of unbandeds) earlier in life; alternatively, if the Tenby population is of recent origin (chapter 2), equilibrium may not yet have been attained. Further work to show that the phenomenon is real will be invaluable; this study has barely skimmed the surface of what may prove to be an important finding: natural selection actually operating in the wild in this species.

Predation may be at too low a level (but see below) to be the selective agent giving banded snails an advantage. If banded snails can absorb more incident solar energy than unbandeds, this may be more important. It is certainly tempting to suggest this as the reason for the generally darker appearance (despite the retention of the unbanded/banded polymorphism) of Tenby shells compared with Mediterranean shells. The same may apply to mantle colour variation since northern populations have dark mantles.

Climate clearly has a profound effect on almost every aspect of T. pisana's biology investigated in this study. The distribution in Britain in only the south-west points immediately to the importance of climate at this, the northern edge of its range (chapter 2). Winter cold may be the limiting factor since the distribution follows isotherms of mean winter temperature, although absence from the extreme south-west of Ireland may be due to this area being too damp for an essentially Mediterranean species. Its local distribution at Tenby, on only south facing slopes (those remaining warmest in winter) emphasizes the importance of temperature in restricting its distribution (cf. Helix pomatia L. - Pollard, 1975b). Restriction to south facing slopes may also be related to summer energy requirements, only these slopes receiving sufficient total incident radiation to allow full size and reproductive maturity to be attained in two years. The seeking of the shadier parts of the microhabitat during summer (chapter 4), may still suggest that temperatures rise too high on some occasions.

Temperature and humidity regimes determine the length of the growing season; if short, the life-cycle is forced into bienniality. This will tend to occur at the climatically determined edges of the range, both in the north where the cold winters are too long to allow annuality, and in the south where the length of the hot, dry summers prevents it. Furthermore, well within the range, variation in local climate, for instance related to the distance from the sea, causes variation in the cycle. In order to quantify this, detailed studies, including measurements of local climate, are necessary at a range of localities. The inadequacies of the present study due to the haphazard availability of samples from sites other than Tenby have been discussed already (chapter 3, sections 3.2.2.1. and 3.2.3.).

Differences in tolerance of high temperatures by snails from Tenby and southern Spain correspond to the different prevailing temperature regimes of these regions, and may be genetically determined (chapter 4). It would be valuable to know whether there is an appropriate difference in low temperature tolerance also, as intolerance of winter cold may be the factor limiting the northern distribution of <u>T. pisana</u>. Temperature tolerances of adults and juveniles at Tenby differ, and correspond to their particular micro-climate or micro-habitat requirements, although the difference is an automatic concomitant of smaller animals having a relatively larger surface area over which evaporative cooling can operate.

Variation in shell thickness is not high between populations, and does not show any clear relation to overall climate. Greater variation exists within populations; leaving aside variation due merely to temporal patterns of growth and absorption of calcium for reproduction, this is partly related to shell size. There may also be some genetic control of thickness; this is not known. What inter-population variation there is, may be more dependent on local climatic pattern or availability of calcium, than on large-scale climatic trends.

These principal findings of the thesis leave a number of obvious, important questions unanswered. Foremost amongst these is the explanation of the extremely high densities often achieved by _T. pisana_, and the factors regulating them.

T. pisana has been considered (chapter 3, section 3.4.) as an '_r_ - selected' species adapted to obtaining the maximum from an ephemeral habitat while it lasts. As such, it should be found at many population densities (Southwood, May, Hassell and Conway, 1974), as indeed it is (chapter 5, section 5.3.). When population density is low, mortality will be largely density-independent; but when density is high (as at Tenby during the course of this work), regulation by density-dependent factors, albeit with much overshoot, will be important (Southwood, May, Hassell and Conway, 1974)

Extrinsic factors (predation, parasitism, disease) surely operate at Tenby, but their effects have not been investigated. Nothing is known of the effects of parasitism or disease on the population dynamics of terrestrial snails. Little is known of the effects of predation, but both Yom-Tov (1970) and Mordan (1977) have considered it significant in very different habitats. Predation, at least, does occur at Tenby. Avian and mammalian predators are present (e.g. jackdaws, rats); also, attack by an unknown organism, perhaps another snail (Oxychilus draparnaudi (Beck), a partially carnivorous snail, is present), leaves a neat hole about 1 mm in diameter in the shell. At first sight, it seems surprising that more animals do not take advantage of the vast numbers of T. pisana available and flock to a feast. However, it only requires 10 jackdaws, each taking 10 snails per day during the snails' active season (about 7 months), to remove 20,000 snails from the colony during this period. As Cain (in press b) points out, many other species of birds may also take snails, particularly juveniles, which they swallow whole, and especially during the breeding season when they require calcium for egg production. In such a situation, predation may be intense but unnoticed by the observer. It is clearly not legitimate to discount the importance of predation on colonies of T. pisana.

At such high densities it is possible that intrinsic factors are influencing population density. It is tempting to suggest that intra-specific competition for food is the regulating factor. This has been considered likely for some populations of Cernuella virgata by Pomeroy (1969) and Butler (1976), and of Cepaea nemoralis by Carter, Jeffery and Williamson (1979, and references therein) who emphasized food quality rather than total available biomass; but a major gap in the ecological knowledge of T. pisana is the lack of information regarding its food requirements. However, when compared with many other species of land snail, in particular C. nemoralis, which seem to show at least a preference for dead or senescent vegetation within their rather generalist food requirements (see Carter, Jeffery and Williamson, 1979), T. pisana may be even more of a generalist. At Tenby it is often seen eating healthy, growing alexanders, sea radish and sea beet in particular, as well as dead and dying material. This readiness to take a very wide range of food is one of the suite of characters considered by ecological theory to contribute to the strategy of an 'r - selected' or 'weed' species (Southwood, 1977; Lawton and McNeill, 1979). This could explain why C. nemoralis, perhaps with a narrower preference, does not attain such high densities or levels of biomass (densities of 50 adults m^{-2} would be very high and extremely rare for C. nemoralis - A. J. Cain, personal communication) in regions where it is the dominant (non-helicelline) helicid of duneland. Being such a food generalist may explain the restriction of T. pisana to early successional habitats, since plants occurring later in a succession are, in general, more protected from attack, and thus require greater specialisation on the part of the herbivore (Lawton and McNeill, 1979).

Populations of T. pisana may only be regulated by their food supply, when close to the carrying capacity of their habitats. Population regulation below the carrying capacity has been suggested for C. nemoralis and other species (Yom-Tov, 1972; Williamson, Cameron and Carter, 1976), and a mechanism for this, the inhibitory effect of conspecifics' mucus on growth and reproductive output, has been suggested by Oosterhoff (1977) and Cameron and Carter (1979). Indeed, an inverse correlation of population density and shell size has been found by Williamson, Cameron and Carter (1976) in the wild. Regulation below the carrying capacity may not take place in T. pisana; it may be more tolerant of its own mucus than C. nemoralis (juvenile T. pisana will grow healthily in laboratory breeding boxes, at much greater densities than C. nemoralis will). This is reasonable if, as a 'weed' species, T. pisana has evolved a strategy to get the maximum out of an ephemeral habitat while it lasts, rather than to maintain a more consistent level in a more predictable, stable habitat. One can go no further without detailed studies addressing the specific problems of the determination of abundance and its regulation in T. pisana.

However, it does lead on to a further consideration. A number of other species coexist with T. pisana at the main Tenby sites, although in relatively small numbers (Helix aspersa, Cernuella virgata, Cochlicella acuta, Ashfordia granulata, Oxychilus draparnaudi). At other sites, particularly that near the railway bank, further species were found (C. nemoralis, C. hortensis, Trichia striolata - see fig. 9.1.). Faced with the very high densities of T. pisana at these sites, how do these other species survive? Some probably coexist by having rather different diets: zonitids are probably part-carnivorous (Mason, 1970; Mordan, 1977); helicellines may be more microphagous (Pomeroy, 1969). However, C. nemoralis, C. hortensis, H. aspersa and T. striolata are known to depend largely on herbaceous material (Carter, Jeffery and Williamson, 1979, and references therein; Chatfield, 1976). At some sites, particularly where T. pisana is less plentiful (e.g. the railway bank site), slightly different preferences within this general diet may allow coexistence. Elsewhere, these four species are probably virtually excluded by T. pisana.

There appears to be a geographical succession within the large helicids of European Atlantic duneland. H. aspersa is known from these habitats (McMillan, 1966), but by far the commonest large herbivorous helicid of duneland in Britain is C. nemoralis. In the north of Scotland, C. hortensis replaces it, and in the very north, even Arianta arbustorum may occur on dunes (Cain, Cameron and Parkin, 1969). These differences in range on duneland mirror the known climatic preferences and tolerances of these three species (e.g. Cameron, 1970a, b, c.). T. pisana is the dominant duneland species further south in France, and in much of the Mediterranean; it can well be thought of as the next species in the sequence. The change from pure C. nemoralis to pure T. pisana colonies, beginning in the south-west of Britain, will surely be as complex as the relationship between C. nemoralis and C. hortensis (Arthur, 1978, 1980). It may be due to inter-specific competition, but this cannot be asserted on distributional evidence alone (Cain, Cameron and Parkin, 1969; Cain, in press b). A thorough sampling programme down the coast of France, with this in mind, would be rewarding.

In a series of papers, Cain (1977a, 1978a, b, 1980, 1981a, b) has suggested a possible mechanism by which snails with similar, generalist food requirements may coexist with little inter-specific competition for food. Differences in sites of activity, with particular emphasis on the preferred angle of inclination of the surface on which the snails crawl was considered as an important dimension of the 'niche hypervolume' (Hutchinson, 1957) of a particular species. Cain and Cowie (1978) and Cameron (1978) have provided some data tending to support Cain's suggestion that snails with a height: diameter ratio (h/d) greater than unity, would, for mechanical reasons, prefer more vertical surfaces, while those with h/d <1 would prefer more horizontal ones. Tattersfield (1982) has presented evidence from a range of species in different habitats and argues that the relationship is considerably complicated by preference for substrate-type.

Adult *T. pisana* are globular, but somewhat flatter (lower value of h/d) than *Cepaea* spp. and *H. aspersa*; the significance of this remains unknown. The striking change in shape undergone by *T. pisana* during growth (fig. 9.2.), which involves a considerable change in h/d (fig. 9.3.), may be related to differences in the niche occupied by different growth stages (chapter 4 - and see the work on other species by Pollard, 1975b, and Roth and Eng, 1980). During the summer at Tenby, juvenile *T. pisana* are found near the ground, whereas the adults tend much more to climb up stems of plants; juveniles are flatter than adults, and this is thus in accord with Cain's hypothesis. Woodruff (1978) has indicated a similar pattern in species of *Cerion* which change shape even more markedly during growth, and Cain (1981a) has suggested that this could explain Cerion's dominance of Caribbean juxta-littoral malacofaunas, a whole guild of differently shaped species occupying the equivalent niches in western Europe. The significance of the keel in T. pisana is not clear; it may be a mechanism for strengthening a flatter shell. In a preliminary study (Cowie, unpublished) using information given by Germain (1930) on the terrestrial mollusc fauna of France, and by Thiele (1931) on those of Europe, North Africa and the Near East, no significant correlation was found between the posession of a keel throughout life or only as a juvenile (like T. pisana) and either habitat type or geographical range of the species involved. However, the number of species may be too small to detect any association.

The remaining questions to be asked relate to the shell pattern variation. Why is variation in T. pisana so complex? Why is the expression of particular morphs so variable, and complicated by penetrance irregularities? These questions cannot be answered at present, but it is worth making a few suggestions. Many Mediterranean snails which sit out during the day exposed to the sun tend to have much more broken patterning, particularly on the upper surfaces of their shells, than do species of more temperate habitats. They also tend to be less colourful, most of the pattern being brown on a white or pale background shell colour (e.g. compare Eobania vermiculata (Müller) and Otala lactea (Müller) with Cepaea). The variation in T. pisana closely resembles that of various helicellines which sit out (e.g. Xeropicta vestalis - see Heller and Volokita, 1981a, b), and also that of the unrelated helminthoglyptid genus Micrarionta, some species of which (e.g. M. levis (Pfeiffer)) occur on dunes in Baja California. This suggests a possible relation to habit or habitat. Perhaps, when sitting out in mediterranean habitats amongst the dried-up vegetation of summer, a very broken pattern is favoured for crypsis, while in the more temperate or mesic habitats (consisting of blades of grass, living plant stems, etc.) of Cepaea (which burrows during the winter when the vegetation is dead), a bolder pattern is favoured for crypsis. Reasons for having paler background shell colours in more insolated habitats have been discussed previously (chapter 4). Further speculation on these questions seems unproductive.

This thesis, then, has provided increased knowledge of the basic ecology and behaviour of what has become, in some parts of the world, an economically important species of snail. This knowledge is essential for the investigation of the causes of genetic and phenotypic variation in what is potentially an important species for ecogenetic research. It has also provided an understanding of some of the complex ways in which climate can fundamentally affect a whole suite of aspects of an organism's biology. I feel that Theba pisana, with its immense variation, high population densities, and the ease with which it is maintained and bred in the laboratory, could become as important as Cepaea nemoralis in increasing our understanding of ecogenetic principles. This thesis is only a beginning, but, I hope, should provide a basis for further work.

Fig. 9.1. Complete sample from the Railway Bank site (Tenby), including Helix aspersa (adults and juveniles), Cepaea nemoralis and C. hortensis (adults and juveniles), Trichia striolata, Candidula intersecta and T. pisana.

Fig. 9.2. Photographs of adult (top) and juvenile (bottom) shells, magnified to the same diameter, to show the change in shape.

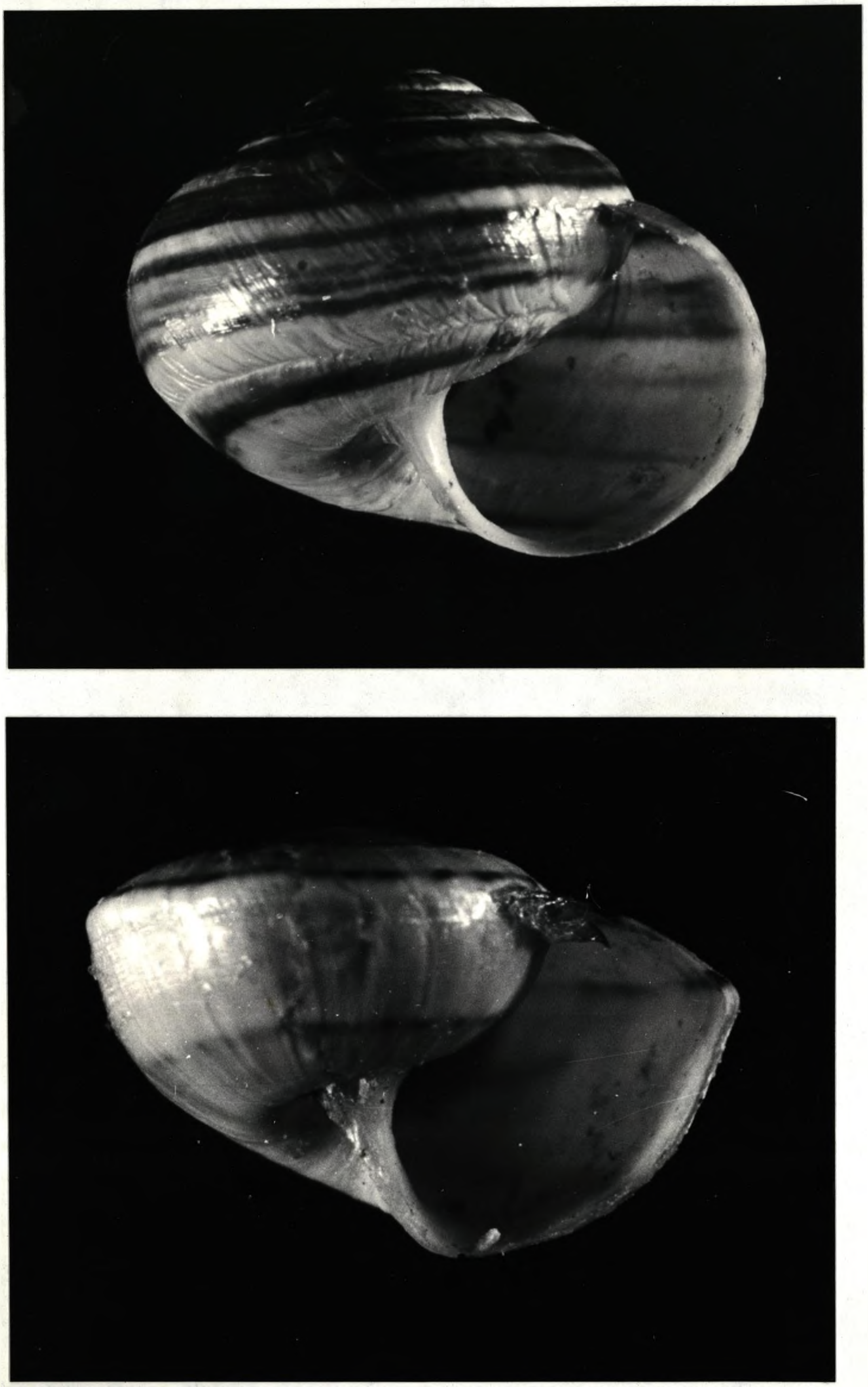
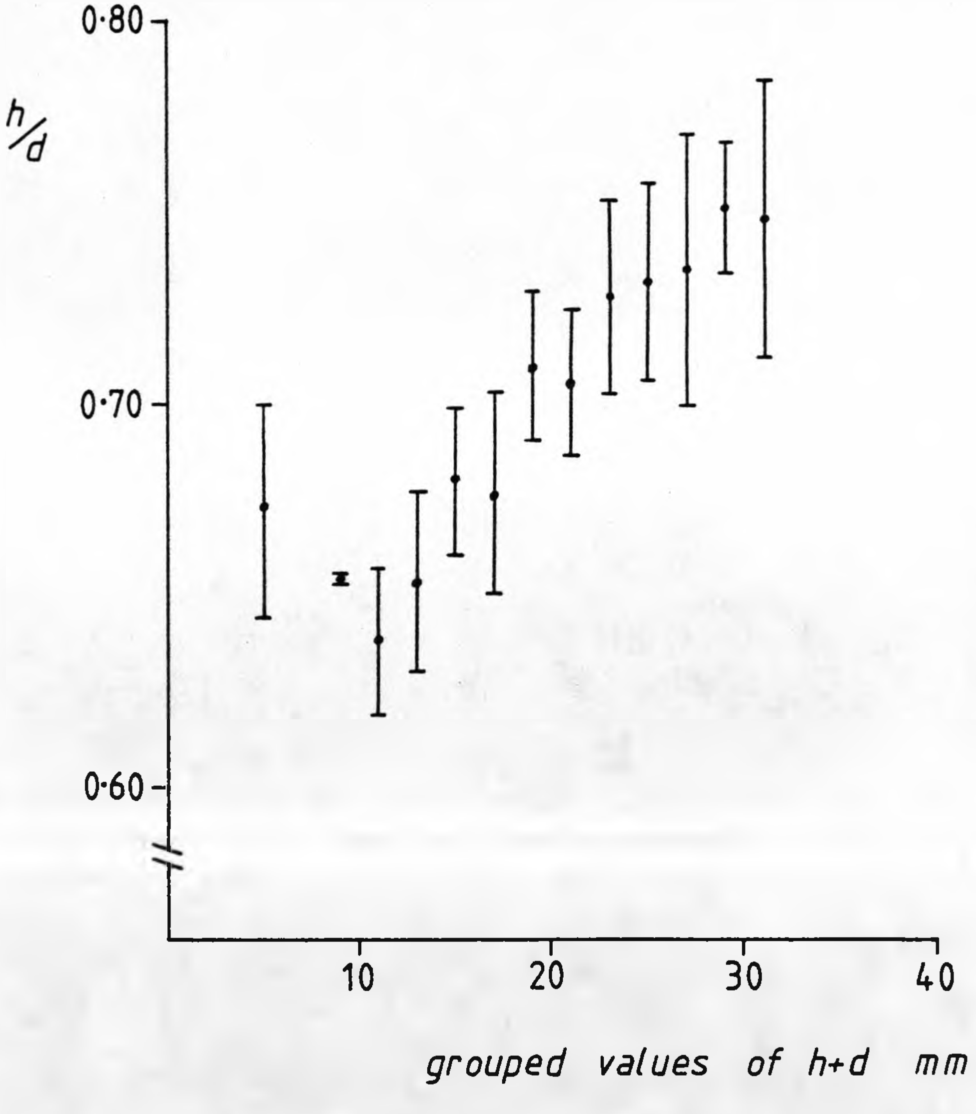


Fig. 9.3. The change in spire index (h/d) with change in shell size. (Tenby site 2 sample 2 31 VIII 77).



Appendices

Appendix 1 - Nomenclature.

Theba pisana has been given various common names, most referring either to its often white shell or to its usual habitat, *viz*: the White Snail (Basinger, 1927), the Grey Snail (Dürr, 1946), the White Garden Snail (Joubert and Walters, 1951; Harpaz and Oseri, 1961), the Italian White Snail (Lim and Jenkins, 1972), the White Sand-hill Snail (Turk, 1972), the Sandhill Snail (Barrett, 1975; Heller, 1981). It was first described scientifically in the early eighteenth century by Petiver who gave it a polynominal name including *pisana*. Juvenile specimens in the Linnean collections may have been intended to represent Linnaeus's *Helix leucas*, but the evidence for this is not sufficiently definite for this name to take precedence over the first incontrovertible binominal name, *Helix pisana*, given to it in 1774 by O. F. Müller (see Jeffreys, 1862; Taylor, 1912; Turk, 1966). Since then it has been ascribed to various genera, *viz*; *Teba*, *Carocolla*, *Xerophila*, *Cochlea*, *Tropidocochlis*, *Euparypha*, and *Theba*. Some modern authors (e.g. Sacchi, 1974) retain it within *Euparypha* but it is more usually placed within *Theba*.

By the start of the twentieth century, no less than 27 species, all attributable to *pisana*, had been described (see Germain, 1908). The most notable confusion came from Bourguignat and the 'Nouvelle Ecole' (Dance, 1970), who went so far as to describe juvenile shells posessing a parietal tooth as a different species, *Helix catocyphia*; and more normal juveniles as *Helix aestivalis* and *Helix hyperplatae* (see Taylor, 1912; Germain, 1929). Extensive synonymies have been given by Germain(1908, 1929, 1930) and Kennard and Woodward (1926). It was Taylor and Germain who brought order back to the situation, and now, _Theba pisana_ is an easily recognisable, if highly variable, species.

Appendix 2 - Details of sampling sites.

1. The main six sites at Tenby.

A map of Tenby indicating the sampling sites, and sketch maps and photographs of their precise positions, have been given in the main body of the thesis (figs. 3.1., 3.2., 3.3. and 3.4., chapter 3). Further details of each site are now listed.

Site 1. About a quarter of the way along the Esplanade from the eastern end, at the very edge of the cliff-top, and just below the public gardens. Flanked on one side by a stone wall, and on another by the steps leading down to the beach.

Vegetation: sea-beet (*Beta vulgaris* L.), buck's horn plantain (*Plantago coronopus* L.), rock samphire (*Crithmum maritimum* L.), alexanders (*Smyrnium olusatrum* L.), bindweed (*Convolvulus arvensis* L.), dock (*Rumex* sp.), grass. Also some small planted shrubs, on which snails were never found and which did not overshadow the site to any great extent.

Ground cover: sparse, and became more so during the course of the study.

Aspect: south   Slope: steep

Soil: sandy soil   Exposure: exposed

Samples: Sample 1 always a metre or two away from the wall, sample 2 adjacent to the wall.

Site 2. The area between the Rectory Field car park and the sloping path down to the beach from the western end of the Esplanade.

Vegetation: alexanders, brambles (Rubus sp.), some nettles (Urtica dioica L.), sea radish (Raphanus maritimus Sm.), bindweed, grass, some rock samphire and buck's horn plantain.

Ground cover: usually well covered

Aspect: south Slope: slight

Soil: Sandy soil Exposure: exposed

Samples: sample 1 always about 7 m from the eastern end of the bank, samples 2 and 3 at approximately 7 m successive intervals going south-westward along the line of the bank (i.e. away from the end of the Esplanade).

Site 3. Adjacent to the sloping path to the beach from the western end of the Esplanade, on the landward side of the path about 10 m up from the second hairpin bend the path makes on its way down to the beach.

Vegetation: alexanders, sea radish, bindweed, dock, some wallflowers (Cheiranthus cheiri L.), some grass, wild cabbage (Brassica oleracea L.) in 1977 and 1980 only.

Ground cover: fairly sparse

Aspect: south Slope: fairly steep

Soil: sandy soil Exposure: overhung by shrubs and small trees but open to the south

Sample: sampling position shifted within a 2 x 2 m area occasionally as a result of changes in vegetation cover and hence, presence of snails.

Site 4. The top of the open area between the second and third sections of the sloping path indicated in the descriptions of sites 2 and 3 (above).

Vegetation: mostly grasses, also alexanders, bindweed, red valerian (*Centranthus ruber* (L.) D.C.), sea radish, ribwort plantain (*Plantago lanceolata* L.)

Ground cover: thick

Aspect: south Slope: sample 1 almost horizontal, sample 2 fairly steep.

Soil: sandy soil Exposure: exposed

Samples: sample 1 always adjacent to the path and about 7 m down from the first hairpin bend, sample 2 about 3 or 4 m below this.

Site 5. Castle Hill. Bank about 2 m high adjacent to the main path round the hill, and topped by a stone wall.

Vegetation: mostly grass, also buck's horn plantain, kidney vetch (*Anthyllis vulneraria* L.)

Ground cover: dense

Aspect: south Slope: steep

Soil: sandy soil Exposure: exposed

Sample: always at the seaward end of the bank beside the small flight of steps leading to the mowed, grassy area which covers the top of the hill.

Site 6. Close to site 5. The area just the other side of the small flight of steps.

Vegetation: alexanders, sea-beet, birdsfoot-trefoil (*Lotus corniculatus* L.), some dock, grass.

Ground cover: variable

Aspect: south Slope: quite steep

Soil: very sandy Exposure: exposed

Sample: position shifted within a 3 x 3 m area depending on the presence of vegetation.

2. Sites elsewhere in the U.K.

Other sites at Tenby have been described adequately in chapter 2. Further samples have been taken from the following localities:

(i) Caldey Island Collector: R. H. Cowie

Date: 2.8.79

Dunes behind Priory Bay (National Grid reference SS 139 969) Two samples from 1 x 1 m areas, sample 1 from bindweed, sample 2 from grass.

(ii) Porthcawl Collector: R. H. Cowie

Date: 13.9.79

Kenfig dunes (approx. Grid reference SS 787 807)

One sample from a 5 x 5 m area. Most snails on sea holly (*Eryngium maritimum* L.).

(iii) St. Ives Collector: R. H. Cowie

Date: 31.7.79

Sample from an area c.4 x 2 m within the primary colony (see chapter 2; Humphreys, 1976) (grid reference SW 521 411)

(iv) Guernsey Collector: J. Cooper

Date: 1981

'They were collected from an area of sandy grass and dune at the north of Port Soit'. (J. Cooper *in litt.* 8 I 1982).

3. Sites abroad.

The following details are those given by the various collectors of samples from localities outside the U.K. They vary in comprehensiveness, many are simply odd comments made in correspondence or by word of mouth, but they do provide useful information. Where details have been given in litt. and not altered by myself, they are indicated in quotes. The name of the collector and the dates of collection are given and photographs of sites are presented where available.

(i) Northern France

1. Normandy Collector: M. A. Carter

Date: September, 1979

'Sample taken from St. Benoit des Ondes in the Bay of Mont Saint Michel. a sea-bank c. 10 m x 2 m. mostly on low bushes and fennel. ? 50 m - 100 m. from high tide mark'.

2. Brittany Collector: R. A. D. Cameron

Date: July, 1979

The sample sites have been re-numbered for the purposes of this thesis. Dr. Cameron's site numbers are given in parentheses.

Site 1 (4) 'Roscoff: (North coast). On edge of municipal camp site c. 3 km. W. of town. Summit of dune crest c. 5 m above beach (or more). sand presumably blown onto rocks; very narrow strip of dune veg. backed by turf of camp site. Lush veg. of tussocky marram and tall herbs, including nettles, ragwort etc. area sampled c. 5 m^2. Other helicids - *C. acuta*, *H. aspersa*, *C. nemoralis*, *C. intersecta* much in evidence'.

Site 2 (1) 'Near camp site at Kervert' (not named on Michelin 1: 200,000 map but just north of St. Gildas-de-Rhuys). 'In badly eroded dunes (tourist pressure) partly fenced off for restoration. c. 50 m. inland from H. T. M. on dunes c. 3 - 4 m. high sloping down smoothly away from sea to marshes inland. Sparse marram + ½ bare-sand and ½ ground cover of stonecrop - Sedum spp. with a few other plants (mostly Eryngo spp.) area collected c. 4 m^2.'

Site 3 (2) 'Suscinio beach. Similar locality to 2 (1). not so eroded, but on back slope to marshes. c. 100 m. from H. T. M. Less marram, and more dense veg. with much sea holly and other Eryngo spp. and mosses. Snails from four bushes of sea holly very close together: area collected c. 2 m^2.'

Site 4 (3) 'Ile de Houat: on centre part of big eastern beach; c. 10 m from H. T. M. on seaward front of dunes. Marram sparse, but much Bindweed, Sea Holly spp., Cudweeds, Sand sedge, mosses, Jersey pinks etc. and c. 25% bare sand (rather well stabilized). Snails from c. 2 m^2.'

Site 5 (5) 'Quiberon dunes. c. 300 m. inshore of Atlantic beach; Massive dune system, largely stabilized, but eroded by cars, and German activities in WWII. Turf vegetation with some scrub and occasional marram patches. and varied dicot veg. including cudweeds and sea holly and thyme. Snails from edge of old german block-house/ gun emplacement on sea holly and under bits of old bucket etc. veg. patchy. area searched c. 30 - 40 m^2.

T. pisana rather hard to find'.

Site 6 (6) 'Quiberon peninsular. Bare roadside plot by main road in Penthièvre on E. side of road. much bare sandy soil and ruderal vegetation including some thistles and dune veg. but most snails found on wooden fence posts of neighbouring 'garden' (veg. inside much same as out!) Area searched c. 4 m^2.
(Whole town built on sand, Quiberon was once an island)'.

(ii) Southern Spain

Elviria - Calahonda Collector: R. H. Cowie

Site 1 Dates: 28-31.8.78, 22-29.8.79

Behind the house belonging at the time to Mr. and Mrs. R. V. Corsgreen: 'Alachar', at La Alqueria, Elviria. A photograph is given of the area sampled (fig. A2.1.), which was c. 75 x 10 m. Vegetation mostly dead bushes and fairly sparse grass, but some succulent, evergreen plants. Snails found mainly stuck to the woody stems of shrubs with a hard, white secretion; some, particularly small ones, stuck to dead grass stems. None found alive on the ground,none seen active during the times of collection. Other snail species present: Otala lactea, Rumina decollata, Helix aspersa, Cochlicella spp. and unidentified Helicellinae, probably including Cernuella virgata.

Site 2 Dates: 2.9.78, 27.8.79

The general area of this site and site 3 (below) is shown in fig. A2.2. Dunes c. 100 m. from sea just west of the Don Carlos Hotel, Elviria. 2.9.78 - area sampled c. 0.5 x 0.5 m. from the dead branches of a shrub. Most snails stuck firmly to the branches/stems. 27.8.79 - area sampled c. 2 x 2 m. again from a small group of shrubs, there being little other vegetation at this site.

Site 3. Date: 6.9.78

Dunes c. 100 m. further west than site 2 (above). Area sampled c. 0.5 x 0.5 m. Very similar to site 2.

Site 4. Date: 26.8.79

Dunes c. 100 m. from the sea, just west of Puerto Cabopino, Calahonda. Area sampled c. 2 x 2 m. Similar to sites 2 and 3.

(iii) The Balearic Islands

1. Mallorca Collector: M. A. Carter

Date: August, 1980

Two samples, one from Camp de Mar in the south-west corner of the island and about 600 m from the sea; one from Ses Coretes in the south-east corner and about a mile inland. 'Both were collected from fennel on road-side strips about 1 m wide and less than 10 m long'.

2. Mallorca Collector: J. Whitelaw

Two samples from south-west Mallorca at Costa de la Calma, a little south-east of Paguera.

Sample 1. Date: 21.9.80

Sample from an area of about 3 x 3 m, about 20 m from the sea and about 5 m above sea level. 'The site was level, and covered with grass 15 - 30 cm. high. There was some cast-up eel-grass in the herbage so I imagine there is quite a bit of salt spray in the winter. Most snails were on the ground, and at least two other species were present'.

Sample 2.   Date: 22.9.80

About 400 m due east of sample 2. 'The habitat was rough herbage - senecios, umbellifers, grass, including what appeared to be pampas grass, and occasionally young pines. On average the vegetation was about 1 m high. The ground was level. The site was probably about 15 m above sea level. The population seemed more diffuse than at the first site (sample 1 - above), with many fewer small snails. Several other species were present. The snails were active and largely up on the vegetation - many in the umbellifer heads. There was evidence of predation on many empty shells found on the ground;' a smallish hole in the shell of the body whorl.

3. Menorca   Collector: C. R. C. Paul

Details given in person by Dr. Paul:

Santa Clementina   Date: 23.10.80

North of Mahon, towards the north-east coast of the island - about 3 km. inland.

Es Grao   Date: 23.10.80

North of Mahon, on the north-east coast - less than 100 m. from the sea - sample collected from stems of vegetation.

Torre d'en Gaumes   Date: 22.10.80

West of Mahon, south of Alayor - c. 3 k. inland.

Torralba   Date: 25.10.80

West of Mahon, south of Alayor - c. 5 km. inland - sample collected after a rainy night - snails active, some ovipositing in mid-morning.

(iv) Sardinia.

1. Calasetta Collectors: R. H. Cowie,
C. Inglesfield

Date: 19.8.80

Sample from salt-marsh vegetation (rushes and some shrubs and grass) beside a large salt pan/lagoon. Vegetation up to c. 1 m high. All snails stuck to the vegetation with a thick, hard, white secretion. Area sampled c. 5 x 3 m, about 150 m from the sea. A sketch map of the area, and one of the sample site are given in fig. A2.3., with a photograph of the site.

2. Cagliari. Collector: R. H. Cowie

Date: 25.8.80

Sample from the large spiky plant shown in the photograph (fig. A2.4.). Situated within the city, just under the old town wall, aspect approximately south-west. Site was c. 1.5 km. from the sea.

(v) Greek Islands.

1. Mitilini, Lesbos. Collectors: J. Whitelaw and
I. Denholm

Date: 18.5.80

Details given in person by Dr. Whitelaw:

A sketch map of the area is given in fig. A2.5. The plants in the raised flower beds were evergreen, laurel-like bushes and a spiky plant. There was no greenery within 100 - 200 m. suggesting that the colony was very isolated. All snails were stuck to the plants with a thin, clear secretion.

2. Adamas, Milos. Collector: R. H. Cowie

Date: 4.9.81

c. 100 m. east of Adamas - Plaka road. c. 200 m. from sea. behind 'Hotel Chronis'. Area sampled c. 1 m^2. Dry vegetation up to 1 m. high alongside narrow dirt road (fig. A2.6.).

3. Crete.

Malia Collector: J. Osborne

Date: October, 1980

About 27 km. east of Heraklion

Sample 1 'on grasses'

Sample 2 'all clustered on bushes'

Sample 3 ' all clustered on thorn - like bushes'

Sample 4 'from bushes'

Komo Collector: G. Lewis

Date: April, 1980

'35°N 24°45'E On shortish grass on gentle slope running down to sea - facing due west. About ½ mile from sea but exposed to it. Substrate - sprinkling of blown sand on dryish earth - crumbly and broken. Snails no further inland than blown sand reached'.

Amnissos Collector: G. Lewis

Date: April, 1980

About 18 km. east of Heraklion.

'35° 30'N 25° 12'E between coast road and shore.

1st sample - On *Carpobrotus* sp. (probably *edulis*) - thick mat. About 50 m. from top of shore in vicinity of house? hotel - confined almost entirely to the *Carpobrotus*.

2nd sample - To east of 1st sample - ~ 100 m. East. On rather tussocky grassy area - but with some (~ 30%) exposed sandy soil, and about 20 m - 50 m from top of beach/shore. Fewer here than on Carpobrotus'.

(vi) Cyrpus

Limassol. Collector: P. Karayiannis

Dates: August, 1977, August, 1978.

Description given in person by Dr. Karayiannis:

On the coast south-west of Limassol. Samples from small sand-dune in salt-marsh c. 100 m. from shore. Ground very hard and sandy with crystalline salt. Small halophytic bushes.

(vii) Israel. Collector: J. Heller

Dor	Date: 4.9.77
Caesarea (south)	Date: 4.9.77
Ashqelon (central)	Date: 22.5.80
Ashqelon (south)	Date: 22.5.80

Dr. Heller writes of the sample from Ashqelon (south):

'They are not a random sample, but rather an assorted collection so that you will get an idea of the variety of different morphs at the site. I put in a lot of semi-adult-sized ones, so that you can start breeding from them ...'

(viii) Algeria Collector: A. J. Cain

Date: December, 1977.

Rhegaia	4 snails.
Douaouda Marine	1 snail.
Dunes de la plage familiale, Zeralda	14 snails.

Fig. A2.1. Elviria - Calahonda. Site 1.

Fig. A2.2. Elviria - Calahonda. The general area including sites 2 and 3.

Fig. A2.3. Sketch maps and photograph of the Calasetta site.

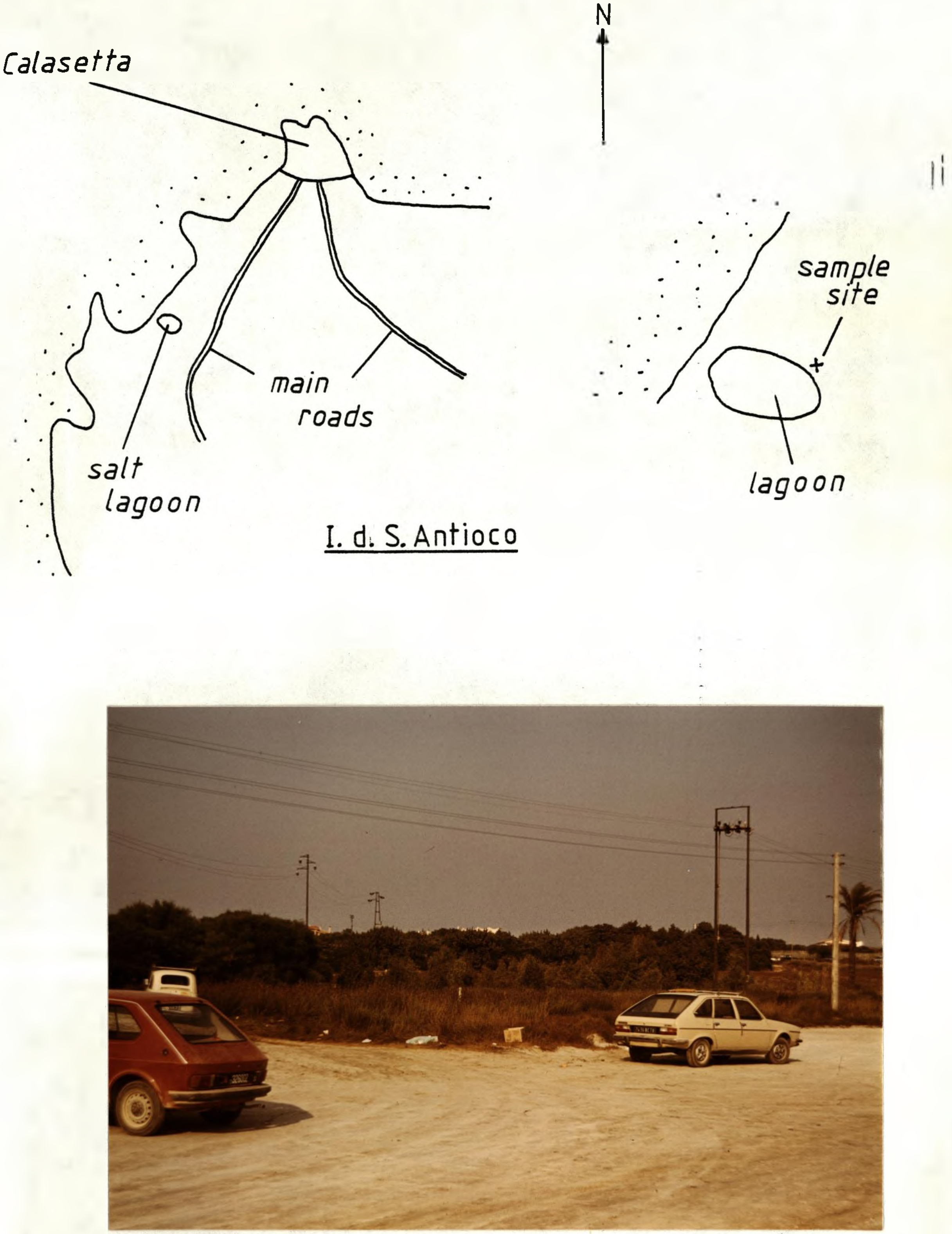


Fig. A2.4. The sampling site in Cagliari, Sardinia.

Fig. A2.5. Sketch map of the Mitilini (Lesbos) sample site.
X marks the position of the site.

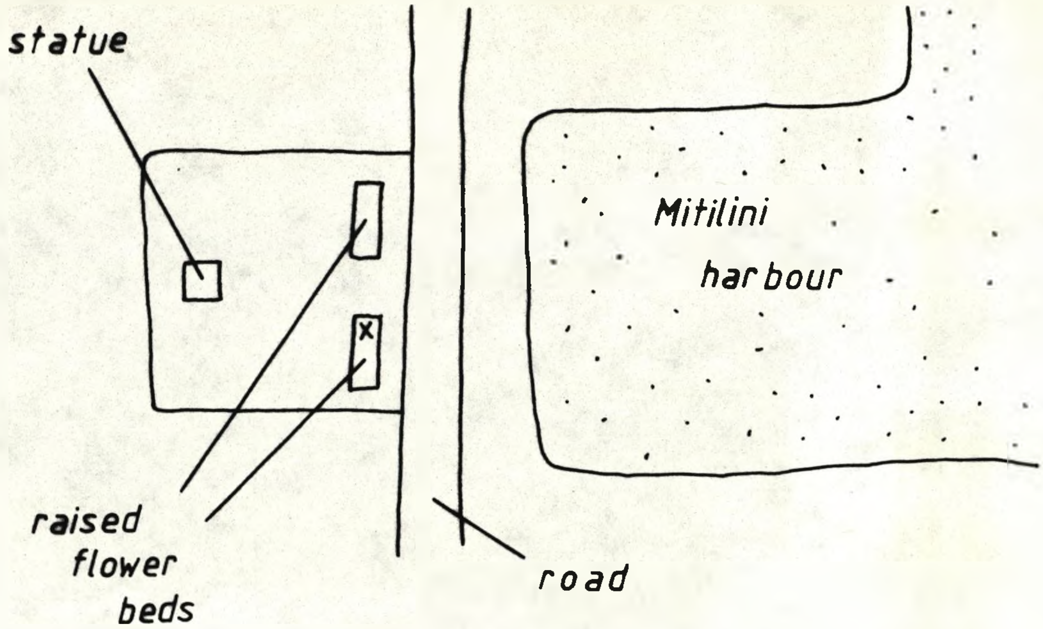


Fig. A2.6. Photograph of the Adamas (Milos) sample site.

Appendix 3 - Tenby size-frequency data.

The tables available in this appendix (one table for each sampling occasion at Tenby) give the numbers of snails in each 2 mm category of h + d present in each of the samples taken. An asterisk above the sample designation indicates that the snails in that sample were scored for reproductive maturity (sperm in the hermaphrodite duct). In such a sample, the numbers given in parentheses are those of mature snails.

Tenby 1 June 1977

h+d	site 1 sample 1	site 1 sample 2	site 2 sample 1	site 2 sample 2	site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9			1								1
4.0-5.9		9	18	17					1		45
6.0-7.9	6	25	23	63	no sample taken	no sample taken	no sample taken	no sample taken	5	no sample taken	122
8.0-9.9	3	17	17	64					10		111
10.0-11.9	5	10	10	30					4		59
12.0-13.9	6	9	7	32					7		61
14.0-15.9	8	10	2	26					3		49
16.0-17.9	29	9	6	23					17		84
18.0-19.9	26	11	15	20					17		89
20.0-21.9	35	8	10	29					25		107
22.0-23.9	26	7	13	36					30		112
24.0-25.9	22	3	21	35					35		116
26.0-27.9	12	2	17	30					14		75
28.0-29.9	6		7	24					12		49
30.0-31.9			4	7					1		12
32.0-33.9											
34.0-35.9									3		3
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	184	120	171	436					184		1095

Tenby 10 July 1977

h+d	site 1 sample 1	site 1 sample 2	site 2 sample 1	site 2 sample 2	site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9											
4.0-5.9	4	7				4		1			16
6.0-7.9	24	48	4	4		32		3	6	11	132
8.0-9.9	33	56	28	19	8	71		9	2	15	241
10.0-11.9	27	57	28	64	8	68	1	22	8	14	297
12.0-13.9	5	20	16	76	25	12	2	8		9	173
14.0-15.9	15	16	13	40	19	8	2	6	2	2	123
16.0-17.9	1	24	20	5	17		1	2	3		73
18.0-19.9	7	19	8	8	20	5	2	2	4		75
20.0-21.9	28	24	7	11	20	12	1	3	2		108
22.0-23.9	8	25	12	9	19	4	3	1	3	2	86
24.0-25.9	28	44	9	12	17	8	6		6		130
26.0-27.9	13	35	3	11	19	27	15	5	6		134
28.0-29.9	12	25	12	19	12	36	27	2	8	1	144
30.0-31.9	7	8	8	23	8	57	43	1	3		158
32.0-33.9		3	28	24	15	28	5		1	2	106
34.0-35.9			13	21	17	11	1				63
36.0-37.9			8	12	8						28
38.0-39.9						1					1
40.0-41.9					3						3
total	212	411	217	348	235	384	109	65	54	56	2091

Tenby 31 August 1977

h+d	site 1 sample 1	site 1 sample 2	site 2 sample 1	site 2 sample 2	site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9											
4.0-5.9		1	3	25	14	1	1				45
6.0-7.9	10	3	1	3	4	2				4	27
8.0-9.9	15	8	7	4		3	3	1	6	12	59
10.0-11.9	45	11	8	29	4	13	54	8	26	16	214
12.0-13.9	34	20	33	87	5	28	35	4	7	31	284
14.0-15.9	6	12	47	36	11	19	10	3	9	21	174
16.0-17.9	2	6	28	21	8	9	2	2	1	11	90
18.0-19.9	1	2	16	23	4	3		1		9	59
20.0-21.9	3	1	21	20	2		1	3	1	4	56
22.0-23.9	3	12	15	16	6		1	3	1		57
24.0-25.9	16	12	13	28	5	5	2	7	3	12	103
26.0-27.9	15	5	15	12	4	3	8	11	12	12	97
28.0-29.9	7	3	20	12	10	5	8	19	9	31	124
30.0-31.9		1	5	13	2	27	6	20	5	41	120
32.0-33.9	1			3	5	17		9	1	11	47
34.0-35.9					2	3	1	1			7
36.0-37.9						1					1
38.0-39.9											
40.0-41.9											
total	158	97	232	332	86	139	132	92	81	215	1564

Tenby 20 October 1977

h+d	site 1 sample 1	site 1 sample 2	site 2 sample 1	site 2 sample 2	site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9	18	6	16	1	7	16	15	2	15	10	106
4.0-5.9	99	50	57	16	20	29	56	13	33	14	387
6.0-7.9	2	11	54	60	49	4	23	19	3	4	229
8.0-9.9	2	16	10	47	49	2	3	3		4	136
10.0-11.9	4	12	2	16	21		17	11	12	8	103
12.0-13.9	4	14	3	23	4	1	26	19	8	8	110
14.0-15.9	3	8	12	10	1	1	13	7	18	11	84
16.0-17.9	2	6	5	12		2	3	7	3	11	51
18.0-19.9	2	3	5	5	2			1	5	1	24
20.0-21.9	1	4	4	4	2	3	1	3		2	24
22.0-23.9	5	3	2	4		2	1			1	18
24.0-25.9	14	8	1	4	1	3		1	3	2	37
26.0-27.9	14	10	3					31	5	5	40
28.0-29.9	10	7	4			7	1	1	6	8	44
30.0-31.9	3	3	1			15		1	1	8	32
32.0-33.9	1	1	1			11		1	2	4	20
34.0-35.9						2				2	4
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	184	162	180	202	156	98	159	91	114	103	1449

Tenby 8,9 December 1977

h+d	site 1 sample 1	site 1 sample 2	site 2 sample 1	site 2 sample 2	site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9	10	8		2		4	5	1	11	22	63
4.0-5.9	48	28	6	19	1	18	40	33	17	43	253
6.0-7.9	5	5	13	36		9	12	5	5	11	101
8.0-9.9	8	2	11	76	1	3	1	4	1	2	109
10.0-11.9	11	4	7	54	1	1		6	5	8	97
12.0-13.9	13	2	3	7		3	2	10	6	12	58
14.0-15.9	7			1		5	2	1	6	13	35
16.0-17.9	3			2		2	1			6	14
18.0-19.9	1					4	3		1	13	22
20.0-21.9	1					3				4	8
22.0-23.9	4	1								6	11
24.0-25.9	4	2	1			3		2		1	13
26.0-27.9	7	1		1		1		1	1	2	14
28.0-29.9		1				2			3		6
30.0-31.9					1	5				3	9
32.0-33.9											
34.0-35.9											
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	122	54	41	198	4	63	66	63	56	146	813

Tenby 26,27 January 1978

h+d	site 1 sample 1	site 1 sample 2	site 2 sample 1	site 2 sample 2	site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9	16	3	1	1	1	7				8	37
4.0-5.9	49	79	38	20	18	226	36	9	40	58	573
6.0-7.9	17	22	41	42	5	96	51	34	8	52	368
8.0-9.9	12	7	36	26	5	14	29	13	1	17	160
10.0-11.9	17	2	14	16	2	3	9	3	3	11	80
12.0-13.9	8	3	3	2		3	8	1	2	8	38
14.0-15.9	2		2	1			5	2	6	7	25
16.0-17.9	1		1			1			1	1	5
18.0-19.9			1						1	6	8
20.0-21.9				1			1			3	5
22.0-23.9	5	1	1				1				8
24.0-25.9	6			1						5	12
26.0-27.9	5		1					1	3	5	15
28.0-29.9	7					1			2	1	11
30.0-31.9	1	1				2	1		1	1	7
32.0-33.9											
34.0-35.9											
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	146	118	139	110	31	353	141	63	68	183	1352

Tenby 16 March 1978

h+d	site 1 sample 1	site 1 sample 2	site 2 sample 1	site 2 sample 2	site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9	1		2			8			3	2	16
4.0-5.9	13	9	32	20	2	52	19	13	15	25	200
6.0-7.9	10	7	42	38	4	117	47	32	5	33	335
8.0-9.9	2		34	9	8	23	38	17		13	144
10.0-11.9	2	3	21	1	6	10	19	7		2	71
12.0-13.9	3	9	3	2	2	4	19			2	44
14.0-15.9	4	4				5	7	4		4	28
16.0-17.9	3	3				5	4	4		2	21
18.0-19.9						5			1	5	11
20.0-21.9	1				1	3	1			1	7
22.0-23.9	1	1			1	4	1		1	1	10
24.0-25.9	3	2								1	6
26.0-27.9	3	1	1								5
28.0-29.9	2	1				1					4
30.0-31.9							1			3	4
32.0-33.9											
34.0-35.9											
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	48	40	135	70	24	237	156	77	25	94	906

Tenby 4,5 May 1978

h+d	site 1 sample 1	• site 1 sample 2	site 2 sample 1	site 2 sample 2	• site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9						1					1
4.0-5.9	2	1	3	2		7		2	8	5	30
6.0-7.9	19	23	42	9	5	13	11	12	17	15	166
8.0-9.9	10	21	54	11	13	28	36	19	11	15	218
10.0-11.9	6	16	46	16	21	18	33	17	1	11	185
12.0-13.9	2	5	50	11	22	7	28	14	8	6	153
14.0-15.9	3	5	31	7	24	10	23	13	5	2	123
16.0-17.9	6	3	16	11	19	6	18	1	14	2	96
18.0-19.9	5	4	6	5	14	8	12		13	8	75
20.0-21.9	4		8	6	5	10	9	1	6	7	56
22.0-23.9	5	1	3	2	2	3	8	1	2	8	35
24.0-25.9	11	1	4	1	7(1)	5	2	1	2	9	43
26.0-27.9	8			1	3(1)	5	4	5	2	2	30
28.0-29.9	1	1(1)	1			1	1	1	1	1	8
30.0-31.9		1(1)			2(1)					1	4
32.0-33.9											
34.0-35.9											
36.0-37.9					1(1)						1
38.0-39.9											
40.0-41.9											
total	82	82	264	82	138	122	185	87	90	92	1224

Tenby 22,23 June 1978

h+d	• site 1 sample 1	site 1 sample 2	site 2 sample 1	• site 2 sample 2	site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9											
4.0-5.9	13					1				2	16
6.0-7.9	29	4		2	2	7	3	3	10	5	65
8.0-9.9	11	12	5	6	7	32	15	19	35	22	164
10.0-11.9	10	22	7	16	21	30	52	55	24	25	262
12.0-13.9	2	13	8	13	13	12	21	47	3	15	147
14.0-15.9	1	3	3	7	8	8	18	29	2	6	85
16.0-17.9	5	1	4	6	6	6	8	6	4	6	52
18.0-19.9	4(1)	2	3	10	12	4	10	12	3	4	64
20.0-21.9	3(1)	5	13	12	19	4	18	9	6	3	92
22.0-23.9	9(2)	1	10	9(1)	9	7	11	5	12	8	81
24.0-25.9	8(6)	3	4	14(5)	23	13	10	11	16	6	108
26.0-27.9	8(3)	3	4	13(3)	17	17	13	8	15	7	105
28.0-29.9	5(3)	2	6	17	10	15	2	8	14	9	88
30.0-31.9		1		10(2)	2	8	2	2	1	5	31
32.0-33.9			1	3	3		1				8
34.0-35.9											
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	108	72	68	138	153	164	184	214	145	123	1369

Tenby 5 August 1978

h+d	• site 1 sample 1	site 1 sample 2	site 2 sample 1	site 2 sample 2	• site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9											
4.0-5.9	1	1				3	1				6
6.0-7.9	6	13	1	6		1	1	1		1	30
8.0-9.9	12	34	2	10	7	12	29	3	5	14	128
10.0-11.9	14	60	3	30	24	41	82	41	31	49	375
12.0-13.9	20	47	2	11	16	14	22	14	38	54	238
14.0-15.9	8	9	5	6	11	2	11	4	27	26	109
16.0-17.9	7	4	4	7	5(1)	4	8	4	18	15	76
18.0-19.9	6(2)	9	2	1	6(2)	5	6	3	3	9	50
20.0-21.9	11(11)	4	1	1	5	2	9	7	1	8	49
22.0-23.9	23(22)	5	2	7	11(10)	1	19	7	6	9	90
24.0-25.9	36(36)	19	7	14	18(17)	4	38	13	11	12	172
26.0-27.9	20(19)	14	10	9	25(24)	18	12	3	19	19	149
28.0-29.9	17(17)	6	11	25	23(23)	26	6	4	13	19	150
30.0-31.9	4(4)		14	17	22(22)	9		1	1	15	83
32.0-33.9	1(1)		6	5	6(6)	3			1	7	29
34.0-35.9						1				1	2
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	186	225	70	149	179	146	244	105	174	258	1736

Tenby 14 September 1978

h+d	site 1 sample 1	site 1 sample 2	site 2 sample 1	site 2 sample 2	site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9	3				4	20				1	28
4.0-5.9	9	2	13	6	8	19		1		5	63
6.0-7.9	2	6	6	4	1	4					23
8.0-9.9	11	8	4	1	1		10	7	3	5	50
10.0-11.9	6	11	6		8	9	156	39	7	10	252
12.0-13.9	12	9	8		11	26	46	18	15	16	161
14.0-15.9	5	5	3		8	12	30	8	30	23	124
16.0-17.9	3	1	4		6(2)	16	14	6	19	16	85
18.0-19.9	2	6	1		6(2)	19	11	1	22	8	76
20.0-21.9	4(2)	3	2		4(3)	22	7	5	9	7	63
22.0-23.9	10(10)	7	1	1	4(4)	14	26	11	2	14	90
24.0-25.9	19(19)	6	4	4	10(10)	13	22	10	8	12	108
26.0-27.9	9(9)	5	7	2	10(10)	40	15		5	8	101
28.0-29.9	13(13)	1	6	7	14(14)	33	5		6	6	91
30.0-31.9	5(5)		5	4	16(16)	29	1			2	62
32.0-33.9	1(1)		1	3	8(8)	11				3	27
34.0-35.9			1								1
36.0-37.9						1					1
38.0-39.9											
40.0-41.9											
total	114	70	72	32	119	288	343	106	126	136	1406

Tenby 3,4 November 1978

h+d	site 1 sample 1	• site 1 sample 2	site 2 sample 1	site 2 sample 2	• site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9	6	2	13	4		6		1		4	36
4.0-5.9	34	36	43	36	7	40	36	1	8	13	254
6.0-7.9	7	7	51	29	24	17	20	1	9	4	169
8.0-9.9	6	3	31	8	23	2	12	1	2	3	91
10.0-11.9	12	15	30	3	12		94	16	4	22	208
12.0-13.9	13	10	20	3	5	2	48	20	21	45	187
14.0-15.9	2	7	7		5	1	20	9	19	59	129
16.0-17.9	1	7	1	1	1		6	1	23	56	97
18.0-19.9	1	5(2)	3	2	4(1)	1	2	7	18	31	74
20.0-21.9		3(1)	1		3	4	4		9	16	40
22.0-23.9	7	6(6)	2	1	2(1)		20	5	7	32	82
24.0-25.9	18	17(17)	5	3	3(2)	4	12	3	5	20	90
26.0-27.9	20	15(15)	7	3	5(5)	8	3	1	5	14	81
28.0-29.9	14	6(6)	6	7	10(10)	11	3	1	2	6	66
30.0-31.9	4	5(5)	3	6	6(6)	10			1	12	47
32.0-33.9			1	1	7(7)	2			1	5	17
34.0-35.9					1(1)						1
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	145	144	224	107	118	108	280	67	134	342	1669

Tenby 17,18 January 1979

h+d	• site 1 sample 1	• site 1 sample 2	• site 2 sample 1	• site 2 sample 2	• site 2 sample 3	• site 3	• site 4 sample 1	• site 4 sample 2	• site 5	• site 6	total
0.0-1.9											
2.0-3.9					2	2					4
4.0-5.9	1	6	14	3	21	31	7	3	1	4	91
6.0-7.9		6	26	8	63	19	17	1	2	1	143
8.0-9.9			26	20	40	4	1	1			92
10.0-11.9		1	15	3	9	3	15	3			49
12.0-13.9		3	1	1	1	2	11	4		6	29
14.0-15.9	1	2	2		1	4				5	15
16.0-17.9	2	2			1	3				2	10
18.0-19.9	1	3	1	1		1	1		1	5	14
20.0-21.9				1		3	1(1)	1		5	11
22.0-23.9	1						3(2)			3(2)	7
24.0-25.9	2(2)	3(3)	1(1)	1(1)	1	3(2)	4(4)	2(2)	2	5(2)	24
26.0-27.9	2(2)	2(1)				4(4)	1(1)		1		10
28.0-29.9			1(1)			3(3)			2(1)		6
30.0-31.9				1(1)		1(1)					2
32.0-33.9											
34.0-35.9											
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	10	28	87	39	139	83	61	15	9	36	507

Tenby 16,17 March 1979

h+d	• site 1 sample 1	• site 1 sample 2	• site 2 sample 1	• site 2 sample 2	• site 2 sample 3	• site 3	• site 4 sample 1	• site 4 sample 2	• site 5	• site 6	total
0.0-1.9											
2.0-3.9	1									6	7
4.0-5.9	4	3	9	2	2	5	12	3		16	56
6.0-7.9	2		19	7	5	5	8	2	1	10	59
8.0-9.9			12	10						1	23
10.0-11.9	1	1	5	1			3	1		7	19
12.0-13.9	2	1		2		1				4	10
14.0-15.9	1	1	2				2	1		4	11
16.0-17.9				1		1				1	3
18.0-19.9											
20.0-21.9							1				1
22.0-23.9				1(1)	1			1		2(1)	4
24.0-25.9										1(1)	2
26.0-27.9											
28.0-29.9											
30.0-31.9											
32.0-33.9											
34.0-35.9											
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	11	6	47	24	8	12	26	8	1	52	195

Tenby 24 May 1979

h+d	• site 1 sample 1	• site 1 sample 2	• site 2 sample 1	• site 2 sample 2	• site 2 sample 3	• site 3	• site 4 sample 1	• site 4 sample 2	• site 5	• site 6	total
0.0-1.9											
2.0-3.9											
4.0-5.9	1		5			5	1	1		1	14
6.0-7.9	1	1	19	4	3	21	14	23	7	4	97
8.0-9.9	12	8	18	7	5	36	23	30	2	6	147
10.0-11.9	2		9	9	8	39	22	38	1	4	132
12.0-13.9	1	2	6	9	2	14	4	28		5	71
14.0-15.9	1	2	6	6	4	16	7	19	2	10	73
16.0-17.9	2	4	2	9	3	2	7	16	2	7	54
18.o-19.9	4	3	2	1	3	1	9	8	2	13	46
20.0-21.9				1			1	10	5	4	21
22.0-23.9		2	1			1	1	5	3	2(1)	15
24.0-25.9			1	2			3	1	4	3	14
26.0-27.9	2		1						2		5
28.0-29.9		1								1	2
30.0-31.9											
32.0-33.9											
34.0-35.9											
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	26	23	70	48	28	135	92	179	30	60	691

Tenby 11 July 1979

h+d	• site 1 sample 1	site 1 sample 2	• site 2 sample 1	site 2 sample 2	site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9											
4.0-5.9		1				1		1			3
6.0-7.9	4					9	1	3		6	23
8.0-9.9	13	4		1		18	10	14	5	25	90
10.0-11.9	12	2	1	3		13	36	13	11	21	112
12.0-13.9	8	2	8	8	1	14	18	3	10	10	82
14.0-15.9	3	3	8	10	5	9	6	7	4	6	61
16.0-17.9	5	3	18	7	1	16	2	9	1	1	63
18.0-19.9	5(2)	3	13	11	4	10	4	10	3	4	67
20.0-21.9	4(2)	7	12	15	3	13	7	7	5	8	81
22.0-23.9	6(6)	8	6	16	6	10	4	12	4	16	88
24.0-25.9	7(6)	4	10(1)	6	3	10	5	11	8	30	94
26.0-27.9	3(3)	8	7(2)	5	4	13	5	9	4	21	79
28.0-29.9	6(6)	5	5(3)	5	5	7	5	4	9	21	72
30.0-31.9	2(2)	3	11(9)	9	1	6	2	1	9	11	55
32.0-33.9			5(4)	5	5	1			3	2	21
34.0-35.9				2	2	1					5
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	78	53	104	103	40	151	105	104	76	182	996

Tenby 13 September 1979

h+d	• site 1 sample 1	site 1 sample 2	site 2 sample 1	site 2 sample 2	• site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9										1	1
4.0-5.9											
6.0-7.9						1	1		1	2	5
8.0-9.9			1			2	1			15	19
10.0-11.9						1	101	5	1	50	158
12.0-13.9	1	2				3	98	10	1	73	188
14.0-15.9	3	2			1	1	35	8	3	31	84
16.0-17.9	3(1)	4				7	7	7	8	15	51
18.0-19.9	4(1)				2	6	4	2	6	12	36
20.0-21.9	1	4			1(1)	6	3	5	5	1	26
22.0-23.9	4(3)	2	1			6	2	9	10	9	43
24.0-25.9	9(9)	4		1	3(3)	3	15	14	4	8	61
26.0-27.9	13(13)	6	1	2	10(10)	11	13	21	12	9	98
28.0-29.9	11(11)	6	10	2	18(18)	15	9	12	6	4	93
30.0-31.9	5(5)	3	5	9	20(20)	8	4	2	2	1	59
32.0-33.9	1(1)	1	9	1	13(13)	10			1		36
34.0-35.9			3	7	5(5)	3					18
36.0-37.9			1		2(2)						3
38.0-39.9											
40.0-41.9											
total	55	34	31	22	75	83	293	95	60	231	979

Tenby 15,16 November 1979

h+d	• site 1 sample 1	• site 1 sample 2	• site 2 sample 1	• site 2 sample 2	• site 2 sample 3	site 3	site 4 sample 1	site 4 sample 2	site 5	site 6	total
0.0-1.9											
2.0-3.9	1	3	6			1	4	1		2	18
4.0-5.9	10	4	34	16	1	34	34	10	5	15	163
6.0-7.9	3	5	45	28	4	16	34	4	1	5	145
8.0-9.9			11	19		3	4	2		6	45
10.0-11.9		2	2	4		2	31	1	1	42	85
12.0-13.9			1	1			27	8		75	112
14.0-15.9				1			7	1	1	64	74
16.0-17.9				1			6	1	1	26	35
18.0-19.9	1			1				1	1	18	22
20.0-21.9								4	1	8	13
22.0-23.9	1(1)	1(1)		1			3	1	3	3	13
24.0-25.9	2(2)	2(2)		2(2)	1(1)		8	3		7	25
26.0-27.9	7(7)	6(6)	2(2)	4(4)		1	10	1	4	1	36
28.0-29.9	10(10)	6(6)	2(2)	2(2)			8			1	29
30.0-31.9	2(2)	6(6)	1(1)	1(1)	1(1)	6	2		1		20
32.0-33.9			3(3)	3(3)	1(1)	5			1		13
34.0-35.9			2(2)		1(1)						3
36.0-37.9					1(1)	1					2
38.0-39.9											
40.0-41.9											
total	37	35	109	84	10	69	178	38	20	273	853

Tenby 10 April 1980

h+d	• site 1 sample 1	• site 1 sample 2	• site 2 sample 1	• site 2 sample 2	• site 2 sample 3	• site 3	• site 4 sample 1	• site 4 sample 2	• site 5	• site 6	total
0.0-1.9											
2.0-3.9										4	4
4.0-5.9	3		4	1	2	7	8	11	1	34	71
6.0-7.9	2	7	19	11	13	40	21	44	1	16	174
8.0-9.9	5	10	14	18	12	42	23	52	7	9	192
10.0-11.9	1	5	6	2	8	58	11	35		11	137
12.0-13.9		1	1	2	2	22	5	17		12	62
14.0-15.9		2				7	1	6	2	39	57
16.0-17.9	2					2	1	11	2	32	50
18.0-19.9		1		1				4	3	25	34
20.0-21.9				1				7	13	19	40
22.0-23.9							1	6(1)	11	10(1)	28
24.0-25.9	3(1)					1(1)	1(1)	1	3	3(2)	12
26.0-27.9	2(2)						1(1)		2		5
28.0-29.9	2(2)						3(2)				5
30.0-31.9						2(2)					2
32.0-33.9											
34.0-35.9											
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	20	26	44	36	37	181	76	194	45	214	873

Tenby 11 July 1980

h+d	• site 1 sample 1	• site 1 sample 2	site 2 sample 1	site 2 sample 2	site 2 sample 3	• site 3	• site 4 sample 1	• site 4 sample 2	• site 5	site 6	total
0.0-1.9											
2.0-3.9											
4.0-5.9	1	2				3					6
6.0-7.9	4	8	n	n	n	12	7	5		n	36
8.0-9.9	8	11	o	o	o	25	9	19		o	72
10.0-11.9	10	4				23	35	29	2		103
12.0-13.9	6	5	s	s	s	19	23	19	2	s	74
14.0-15.9	4	6	a	a	a	6	10	7	6	a	39
16.0-17.9	3	6	m	m	m	5	2	3	3	m	22
18.0-19.9	8	3(2)	p	p	p	2	8(4)	7(6)	3	p	31
20.0-21.9	6(2)	4(2)	l	l	l	3	9(9)	8(7)	4	l	34
22.0-23.9	3(1)	2(2)	e	e	e	3(3)	9(9)	8(8)	4(1)	e	29
24.0-25.9	3(1)	2(2)				8(7)	8(8)	13(13)	5(4)		39
26.0-27.9	6(6)	10(9)	t	t	t	10(10)	13(13)	9(9)	12(11)	t	60
28.0-29.9	5(5)	6(4)	a	a	a	9(9)	7(7)	8(8)	13(13)	a	48
30.0-31.9	4(4)	4(4)	k	k	k	11(11)	2(2)		10(10)	k	31
32.0-33.9	2(2)		e	e	e	2(2)		1(1)	3(3)	e	8
34.0-35.9			n	n	n					n	
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	73	73				141	142	136	67		632

Tenby 18 October 1980

h+d	• site 1 sample 1	• site 1 sample 2	• site 2 sample 1	• site 2 sample 2	• site 2 sample 3	• site 3	• site 4 sample 1	• site 4 sample 2	• site 5	• site 6	total
0.0-1.9											
2.0-3.9	2	5	5	2	1	8	3	3		2	31
4.0-5.9	37	23	10	32	30	56	32	11		13	244
6.0-7.9	3	15	8	37	52	26	21	7		23	192
8.0-9.9	3	7	4	31	34	5	5	1	2	54	146
10.0-11.9	2	2	21	26	22	3	73	8	1	64	222
12.0-13.9	3	8	14	18	8	6	75	5		32	169
14.0-15.9	3	1	5	19	2	2	22			17	71
16.0-17.9	2	4	1	9(1)		3	5		1	5	30
18.0-19.9	1(10)	2	2	11(7)		2(2)	2(2)	1(1)		2(1)	23
20.0-21.9		1	4(2)	6(3)	3(3)	1		1(1)		4(1)	20
22.0-23.9	1(1)		7(7)	7(6)	3(3)		2(2)	5(5)	1(1)	5(5)	31
24.0-25.9	4(4)	2(2)	11(11)	12(12)	8(8)	2(2)	4(4)	8(8)	2(2)	5(5)	58
26.0-27.9	4(4)	7(7)	2(2)	11(11)	14(13)	8(8)	5(5)	2(2)	4(4)	2(2)	59
28.0-29.9	4(4)	4(4)	1(1)	10(10)	17(17)	19(19)	2(2)	4(4)	3(3)	4(3)	68
30.0-31.9	1(1)			7(7)	9(9)	8(8)	1(1)	2(2)	1(1)	1(1)	30
32.0-33.9	1(1)	1(1)		1(1)	5(5)	9(9)				1(1)	18
34.0-35.9					1(1)	1(1)					2
36.0-37.9	1(1)										1
38.0-39.9											
40.0-41.9											
total	72	82	95	239	209	159	252	58	15	234	1415

Tenby 8 April 1981

h+d	• site 1 sample 1	• site 1 sample 2	• site 2 sample 1	• site 2 sample 2	• site 2 sample 3	• site 3	• site 4 sample 1	• site 4 sample 2	• site 5	• site 6	total
0.0-1.9											
2.0-3.9								1			1
4.0-5.9	7	6	25	13	18	10	11	9		8	107
6.0-7.9	12	6	21	27	19	8	11	10	5	18	137
8.0-9.9	11	5	15	15	18	11	7	7	8	25	122
10.0-11.9	5	7	14	26	12	9	26	13	7	12	131
12.0-13.9	9	1	34	26	2	5	20	18	5	11	131
14.0-15.9	10	7	30	21	3	4	17	23	6	22	143
16.0-17.9	10	6	13	7	1	2	12	24		13	88
18.0-19.9	7	4	4	1		1	2	14	2	10	45
20.0-21.9	4(1)	5	3	9(2)		1	2(1)	2	1	4	31
22.0-23.9	7(2)	5	2(1)	3		2	4(2)	10(8)	2	1	36
24.0-25.9	7(7)	8(4)	1(1)	2(2)			3(2)	14(13)			35
26.0-27.9	8(8)	5(5)	1	1			2(1)	5(5)	2(1)		24
28.0-29.9	3(3)	1(1)					1(1)	5(4)			10
30.0-31.9											
32.0-33.9							1(1)				1
34.0-35.9											
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	100	66	163	151	73	53	119	155	38	124	1042

Tenby 2 July 1981

h+d	• site 1 sample 1	• site 1 sample 2	site 2 sample 1	site 2 sample 2	site 2 sample 3	• site 3	site 4 sample 1	• site 4 sample 2	• site 5	• site 6	total
0.0-1.9											
2.0-3.9											
4.0-5.9	18	3		1	1						23
6.0-7.9	9	6	3	8		2	1			5	34
8.0-9.9	10	6	8	22	2		7	5		17	77
10.0-11.9	8	9	13	21	4	1	25	14		36	131
12.0-13.9	9	2	14	16	2	1	13	8	2	32	99
14.0-15.9	5	4	15	17	2	1	7	3	2	19	75
16.0-17.9	1	5	5	25	10	1				14	61
18.0-19.9	2	6	12	27	11		2		1	14	75
20.0-21.9	4(1)	3	20	49	14	2	6	1	4	17	120
22.0-23.9	3(3)	5	17	33	14	5(1)	13	6(4)	4	21	121
24.0-25.9	3	8(1)	19	22	8	2	30	6(4)	6(1)	18(1)	122
26.0-27.9	1	3(1)	21	15	15	3(1)	41	14(9)	2	13(2)	128
28.0-29.9	2(1)	4(1)	15	13	21	2	18	14(10)	6(4)	7(1)	102
30.0-31.9		3(1)	3	4	12	4(1)	7	4(4)	2(1)	7(2)	46
32.0-33.9		1(1)		1	1	4(1)	2	1(1)			10
34.0-35.9				1		4(2)					5
36.0-37.9											
38.0-39.9											
40.0-41.9											
total	75	68	165	275	117	32	172	76	29	220	1229

Appendix 4 - Morph frequencies.

Frequencies of morphs (described in chapter 6) are given for all Tenby samples taken from 24 May to 31 August in each year of the sampling programme. Data are also given for samples collected at other British localities, whatever their date of collection.

Tenby - 1 June 1977

site	sample	age class		UNBANDED			BANDED				grand total
			plain	dotty	total	dark	intermed.	yellow	unknown	total	
1	1	ad	17	9	26	101	33	5		139	165
		juv	3	4	7				11	11	18
1	2	ad	3	2	5	32	13	3		48	53
		juv	7	1	8				55	55	63
2	1	ad	33	4	37	45	5	1		51	88
		juv									
2	2	ad	71	15	86	94	17	7	14	132	218
		juv	71	14	85				102	102	187
2	3	ad			no sample taken						
		juv									
3	-	ad			no sample taken						
		juv									
4	1	ad			no sample taken						
		juv									
4	2	ad			no sample taken						
		juv									
5	-	ad	17	4	21	85	24	8		117	138
		juv							1	1	1
6	-	ad	20	8	28	97	33	4		134	162
		juv	2	1	3				18	18	21

Tenby - 10 July 1977

site	sample	age class	UNBANDED			BANDED					grand total
			plain	dotty	total	dark	intermed.	yellow	unknown	total	
1	1	ad	8	2	10	29	9	2		40	50
		juv	5	4	9				42	42	51
1	2	ad	9	7	16	50	18	4		72	88
		juv	10		10				105	105	115
2	1	ad	18	3	21	24	6	1		31	52
		juv	19	3	22				30	30	52
2	2	ad	14	6	20	31	10	4		45	65
		juv	38	8	46				63	63	109
2	3	ad	26	6	32	29	13	1		43	75
		juv	10	2	12				25	25	37
3	-	ad	19	10	29	46	13	4		63	92
		juv	22	8	30				57	57	87
4	1	ad	23	13	36	54	11	2		67	103
		juv	3		3				3	3	6
4	2	ad	3	2	5	6	1	1		8	13
		juv	19	4	23				26	26	49
5	-	ad	5	2	7	16	8	3		27	34
		juv	3	1	4				16	16	20
6	-	ad	1		1	2	1	1		4	5
		juv	8	1	9				43	43	52

Tenby - 31 August 1977

			UNBANDED			BANDED					
site	sample	age class	plain	dotty	total	dark	intermed.	yellow	unknown	total	grand total
1	1	ad	6	4	10	25	4	5		34	44
		juv	16	5	21				92	92	113
1	2	ad	5	2	7	21	4	1		26	33
		juv	4	2	6				55	55	61
2	1	ad	12	4	16	15	4	1		20	36
		juv	30	6	36				43	43	79
2	2	ad	17	2	19	16	4	3		23	42
		juv	39	6	45				62	62	107
2	3	ad	12	2	14	15	4			19	33
		juv	12	1	13				21	21	34
3	-	ad	5	2	7	16	7			23	30
		juv	11	4	15				22	22	37
4	1	ad	4	5	9	10	6	1		17	26
		juv	35	1	36				68	68	104
4	2	ad	21	3	24	34	11	4		49	73
		juv	9	1	10				9	9	19
5	-	ad	2	1	3	18	6	4		28	31
		juv	10	1	11				36	36	47
6	-	ad	2	2	4	40	5	5		50	54
		juv	6	2	8				43	43	51

Tenby - 22,23 June 1978

site	sample	age class	UNBANDED plain	dotty	total	BANDED dark	intermed.	yellow	unknown	total	grand total
1	1	ad	7		7	27	6			33	40
		juv	8	5	13				52	52	65
1	2	ad	2		2	12	3			15	17
		juv	3	3	6				50	50	56
2	1	ad	8	6	14	20	4	3		27	41
		juv	5	1	6				15	15	21
2	2	ad	21	8	29	39	19	2		60	89
		juv	19	7	26				23	23	49
2	3	ad	21	10	13	47	16	3		66	97
		juv	14	5	19				37	37	56
3	-	ad	21	3	24	36	8	3		47	71
		juv	18	14	32				56	56	88
4	1	ad	11	7	18	41	8	1		50	68
		juv	21	19	40				71	71	111
4	2	ad	20	9	29	40	9	3		52	81
		juv	29	19	48				83	83	131
5	-	ad	6	2	8	45	11	5		61	69
		juv	5	5	10				61	61	71
6	-	ad	8		8	27	6	1		34	42
		juv	6	1	7				73	73	80

Tenby - 5 August 1978

site	sample	age class	UNBANDED plain	dotty	total	BANDED dark	intermed.	yellow	unknown	total	grand total
1	1	ad	11	5	16	75	20	4		99	115
		juv	7	3	10				55	55	65
1	2	ad	7	4	11	36	7			43	54
		juv	24	11	35				137	137	172
2	1	ad	21	8	29	18	6	2		26	55
		juv	6	2	8				9	9	17
2	2	ad	16	8	24	41	10	4		55	79
		juv	7	4	21				48	48	69
2	3	ad	46	11	57	39	12	7		58	115
		juv	29	3	32				32	32	64
3	-	ad	17	3	20	34	8	3		45	65
		juv	19	4	23				57	57	80
4	1	ad	19	12	31	44	9	2		55	86
		juv	41	21	62				97	97	159
4	2	ad	5	7	12	18	7	1		26	38
		juv	15	6	21				46	46	67
5	-	ad	8	3	11	33	6	4		43	54
		juv	15	9	24				96	96	120
6	-	ad	11	2	13	60	12	6		78	91
		juv	14	6	20				146	146	166

Tenby - 24 May 1979

site	sample	age class	UNBANDED			BANDED					grand total
			plain	dotty	total	dark	intermed.	yellow	unknown	total	
1	1	ad	1	1	2	5	1			6	8
1	2	ad	2		2	2	4			6	8
1	1&2	juv	1	2	3	19	8	1		28	31
2	1	ad	1		1	4	1			5	6
		juv	11	3	14				30	30	44
2	2	ad	2	1	3	6				6	9
		juv	10	4	14				27	27	41
2	3	ad	1		1	4		1		5	6
		juv	3	2	5				18	18	23
3	-	ad	1		1	1	1			2	3
		juv	23	15	38				88	88	126
4	1	ad	5		5	12	2	2		16	21
		juv	17	5	22				49	49	71
4	2	ad	7	5	12	18	3	1		22	34
		juv	35	10	45				83	83	128
5	-	ad	1		1	10	2	2		14	15
		juv	3	2	5				6	6	11
6	-	ad				16	12	1		29	29
		juv	3	2	5				29	29	34

Tenby - 11 July 1979

site	sample	age class	UNBANDED			BANDED					grand
			plain	dotty	total	dark	intermed.	yellow	unknown	total	total
1	1	ad	2	1	3	30	2	2		34	37
		juv	3	2	5				37	37	42
1	2	ad				not scored					
		juv									
2	1	ad	17	11	28	38	8	3		49	77
		juv	8	2	10				14	14	24
2	2	ad				not scored					
		juv									
2	3	ad				not scored					
		juv									
3	-	ad				not scored					
		juv									
4	1	ad				not scored					
		juv									
4	2	ad				not scored					
		juv									
5	-	ad				not scored					
		juv									
6	-	ad				not scored					
		juv									

Tenby - 11 July 1980

site	sample	age class		UNBANDED			BANDED				grand total
			plain	dotty	total	dark	intermed.	yellow	unknown	total	
1	1	ad	5	2	7	22	6	1		29	36
		juv	4	3	7				29	29	36
1	2	ad	2	2	4	21	2	4		27	31
		juv	2	3	5				37	37	42
2	1	ad			no sample taken						
		juv									
2	2	ad			no sample taken						
		juv									
2	3	ad			no sample taken						
		juv									
3	=	ad	9	5	14	23	7	2		32	46
		juv	20	10	30				65	65	95
4	1	ad	16	10	26	23	7			30	56
		juv	25	7	32				54	54	86
4	2	ad	18	7	25	21	6	2		29	54
		juv	17	8	25				56	56	81
5	-	ad	4	3	7	35	8	3		46	53
		juv	1	2	3				11	11	14
6	-	ad			no sample taken						
		juv									

Tenby - 2 July 1981

site	sample	age class	UNBANDED plain	dotty	total	BANDED dark	intermed.	yellow	unknown	total	grand total
1	1	ad	1	1	2	12		1		13	15
		juv	12	1	13				47	47	60
1	2	ad	2	2	4	19	10	2		31	35
		juv	5	3	8				25	25	33
2	1	ad	25	13	38	49	14	6		69	107
		juv	12	1	13				35	35	48
2	2	ad	36	15	51	68	32	9		109	160
		juv	29	13	42				46	46	88
2	3	ad	20	11	31	42	13	5		60	91
		juv	6	2	8				7	7	15
3	-	ad	5	2	7	14	4	1		19	26
		juv	1		1				5	5	6
4	1	ad	19	15	34	60	14	8		82	116
		juv	8	6	14				26	26	40
4	2	ad	7	6	13	23	7	3		33	46
		juv	8	4	12				17	17	29
5	-	ad	4	1	5	16	1	3		20	25
		juv	1	1	2				2	2	4
6	-	ad	10	2	12	57	21	7		85	97
		juv	21	5	26				94	94	120

Tenby - extra sites

sample, date	age class	UNBANDED plain	dotty	total	BANDED dark	intermed.	yellow	unknown	total	grand total
St. Cath's Is.	ad	8	5	13	19	1	1		21	34
11.7.80	juv	1		1	1			1	2	3
Fundrome	ad	8	2	10	15	8	5		28	38
4.11.78	juv									
Railway bank	ad	19	3	22	30	7	3		40	62
24.5.79	juv	1		1	4				4	5
Marsh Road	ad	16	11	27	16	1			17	44
4.11.78	juv	14	4	18	7			1	8	26
Marsh Road	ad	21	13	34	12	1			13	47
24.5.79	juv	21	6	27	8	1		4	13	40
Marsh Road (1)	ad	13	1	14	1	1		1	3	17
4.8.78	juv	3		3				1	1	4
Marsh Road (2)	ad	12	10	22	8	1			9	31
4.8.78	juv	1		1				1	1	2
Narberth Road	ad				7				7	7
4.11.78	juv									

U.K. sites (not Tenby)

sample, date	age class	UNBANDED plain	dotty	total	BANDED dark	intermed.	yellow	unknown	total	grand total
Caldey Is. 1	ad				73	5			78	78
2.8.79	juv				22	4		2	28	28
Caldey Is. 2	ad				48	7			55	55
2.8.79	juv				10			12	22	22
Saundersfoot 2	ad					1	2		3	3
4.8.78	juv									
Saundersfoot 1	ad					3	5		8	8
4.11.78	juv									
Saundersfoot 2	ad					4	6		10	10
4.11.78	juv									
S'pole Warren	ad			no sample taken, but all animals seen were banded						
	juv									
P'cawl, Newton	ad				8				8	8
13.9.79	juv									
P'cawl, Kenfig	ad			sample does not fit this scheme - see ch. 6						
	juv									
St. Ives	ad			sample does not fit this scheme - see ch. 6						
	juv									

Appendix 5 - Mantle collar colour scores.

Colour scores of all individuals scored are given in this appendix. Scores for each individual are given in a group of three numbers, the first is hue, the second is saturation, and the third is intensity. The superscript used in the designation of saturation (e.g. 6°) in the colour atlas (see chapter 7) is omitted since this tabular presentation has sufficient clarity.

In some instances, there appeared to be no colour in the mantle, it was simply a shade of grey; or it was so dark that any colour present could not be discerned. In such cases, only intensity was scored, and hue, saturation and intensity have been given the same value in the tables (e.g. 5 5 5).

TENBY site 1 sample 1 18 X 80

0 0 0   0 0 0   6 4 2   6 4 2   6 2 2   6 5 4   6 4 5
6 4 7   6 4 5   6 5 4   0 0 0   6 3 3   6 2 1   6 1 1
6 3 3   1 1 1   6 3 3   0 0 0   0 0 0

TENBY site 1 sample 2 18 X 80

6 1 7   6 2 3   0 0 0   0 0 0   6 3 3   6 3 1   7 3 8
0 0 0   6 2 1   6 3 3   6 2 1   7 2 1   6 2 2   6 3 2
6 3 3   0 0 0   0 0 0   0 0 0   0 0 0   0 0 0

TENBY site 2 sample 1 18 X 80

6 2 2   6 3 1   6 2 2   6 2 1   0 0 0   6 2 1   6 2 2
0 0 0   6 1 1   6 3 1   6 2 1   5 3 2   0 0 0   6 3 4
6 1 1   0 0 0   5 2 2   6 2 2   6 2 4   0 0 0   6 3 1
5 3 2   6 5 4   6 2 3   6 1 1   7 3 2   7 1 4

TENBY site 2 sample 2 18 X 80

0 0 0   0 0 0   6 1 1   0 0 0   0 0 0   7 1 1   6 1 1
0 0 0   6 1 1   0 0 0   0 0 0   7 2 2   0 0 0   0 0 0
0 0 0   0 0 0   6 2 1   6 2 3   6 3 3   0 0 0   0 0 0
6 1 1   0 0 0   6 3 2   0 0 0   0 0 0   0 0 0   6 3 5
6 3 2   6 3 3   7 3 1   6 4 3   6 2 1   7 3 9   6 2 1
7 2 8   6 3 1   6 2 1   6 2 2   6 4 7   0 0 0   7 2 6
6 3 3   7 1 1   6 4 6   6 2 2   0 0 0   0 0 0   7 2 2
7 2 7   6 2 1   6 4 8   6 3 1   6 3 4   6 3 3   7 3 10
6 2 1   7 3 11   6 3 6   6 3 6   6 2 1   7 3 7   7 2 3
7 2 7   6 2 2   6 2 1   6 2 3   7 2 1   6 2 1   7 2 6

TENBY site 2 sample 3 18 X 80

0 0 0   0 0 0   0 0 0   0 0 0   6 2 1   6 3 1   0 0 0
6 3 1   0 0 0   6 3 2   7 4 8   0 0 0   6 3 3   0 0 0
6 3 1   6 3 1   0 0 0   0 0 0   0 0 0   0 0 0   0 0 0
0 0 0   0 0 0   0 0 0   0 0 0   6 3 1   6 2 1   6 2 1
6 3 1   6 2 1   6 1 1   0 0 0   0 0 0   5 5 2   6 5 3
0 0 0   0 0 0   0 0 0   0 0 0   0 0 0   0 0 0   0 0 0
6 2 2   6 2 2   6 2 2   6 2 3   0 0 0   0 0 0   6 2 3
6 2 1   0 0 0   6 2 1   0 0 0   6 2 1   6 2 2   0 0 0
0 0 0   6 3 1   6 1 1   6 2 1

TENBY site 3 18 X 80

6 1 1   0 0 0   0 0 0   6 2 2   0 0 0   6 1 1   0 0 0
6 1 1   6 3 3   0 0 0   0 0 0   6 1 2   6 1 1   0 0 0
0 0 0   0 0 0   6 1 1   0 0 0   6 3 2   0 0 0   7 1 2
0 0 0   6 2 1   0 0 0   0 0 0   6 1 1   0 0 0   0 0 0
6 1 2   6 2 3   6 1 1   0 0 0   6 2 2   0 0 0   0 0 0
0 0 0   0 0 0   0 0 0   0 0 0   0 0 0   6 1 1   6 2 1
6 3 5   0 0 0   0 0 0   6 1 2   6 3 5   7 3 4   7 4 11
7 3 7

TENBY site 4 sample 1 18 X 80

0 0 0   0 0 0   6 2 2   6 1 1   0 0 0   0 0 0   5 2 2
0 0 0   6 4 7   0 0 0   6 2 1   6 3 1   6 4 4   6 2 3
6 3 6   6 3 9

TENBY site 4 sample 2 18 X 80

0 0 0   5 3 2   6 2 2   6 1 1   0 0 0   6 1 1   6 2 1
0 0 0   6 1 1   0 0 0   6 1 1   0 0 0   0 0 0   6 1 1
0 0 0   0 0 0   0 0 0   0 0 0   0 0 0   6 2 1

TENBY site 5 18 X 80

```
0 0 0    0 0 0    0 0 0    6 1 1    0 0 0    0 0 0    6 2 1
0 0 0    0 0 0    6 2 1    0 0 0    6 2 2
```

TENBY site 6 18 X 80

```
0 0 0    0 0 0    0 0 0    6 2 1    6 2 1    0 0 0    6 4 5
0 0 0    6 3 3    0 0 0    0 0 0    0 0 0    6 4 2    0 0 0
0 0 0    0 0 0    6 4 2    5 3 2    6 2 2    6 3 8    6 3 1
6 3 6    6 3 1    6 3 1    6 1 1    6 4 5
```

TENBY site 1 sample 1 2 VII 81

```
6 1 2    6 3 3    6 2 2    6 2 2    6 4 4    7 3 9    7 2 2
7 2 7    7 2 2    6 3 3    7 3 10   7 2 3    7 2 2    7 1 1
7 2 8    7 2 4
```

TENBY site 1 sample 2 2 VII 81

```
0 0 0    0 0 0    7 2 5    0 0 0    7 2 6    7 1 1    7 2 2
7 1 1    7 2 4    7 2 1    7 2 3    7 2 7    7 2 5    7 2 4
7 2 3    7 1 2    7 1 1    7 1 2    7 2 3    6 3 4    7 2 2
7 3 8    7 3 7    7 2 3    7 2 4    7 3 6    0 0 0    0 0 0
7 2 3    6 2 8    7 2 4    7 2 6    7 2 3    7 3 9    7 2 4
7 2 8
```

TENBY site 2 sample 1 2 VII 81

```
6 4 4    6 2 8    6 2 4    6 4 8    6 2 3    7 2 2    7 2 7
7 2 8    7 2 7    6 2 3    6 3 3    6 3 6    6 3 4    0 0 0
7 1 1    7 2 4    6 3 5    6 4 7    7 2 5    7 3 6    7 2 7
6 3 6    6 2 3    1 1 1    7 2 8    6 2 5    6 3 3    6 2 2
7 1 1    6 2 6    7 2 6    7 1 2    7 3 8    7 1 2    6 3 4
7 2 7    7 1 1    7 2 1    7 1 1    6 3 4    7 4 9    7 2 6
```

8 2 12	6 3 3	6 1 2	6 2 2	6 1 5	7 2 7	3 3 3
3 3 3	6 4 4	7 2 8	6 1 1	7 2 8	3 3 3	7 2 3
7 3 5	7 3 4	7 2 3	7 3 7	6 2 6	7 2 8	6 2 7
6 2 3	6 3 5	6 1 2	7 3 8	6 2 4	6 2 4	7 2 8
6 1 2	6 1 3	6 2 3	7 2 5	6 1 1	6 3 3	6 2 4
7 3 6	6 4 5	0 0 0	2 2 2	6 2 1	7 2 8	6 3 3
6 1 2	7 4 4	2 2 2	6 1 3	6 2 5	7 2 7	6 1 3
6 3 4	6 3 4	6 3 3	6 3 4	6 3 3	6 4 4	7 1 1
6 2 2	7 1 2	6 2 3	7 2 6	7 2 5	7 2 7	7 3 6
7 3 6	7 2 5	7 2 6	7 2 4	7 2 4		

TENBY site 2 sample 2 2 VII 81

7 3 7	6 3 3	6 3 3	6 3 3	6 1 2	6 3 3	6 1 1
6 3 5	6 2 3	6 3 3	6 2 3	6 3 3	6 2 1	6 2 4
6 2 3	6 4 5	6 3 5	6 4 5	6 3 3	6 3 8	6 3 4
6 4 4	6 4 5	6 3 5	6 3 3	6 3 4	6 2 2	6 4 4
6 4 5	6 4 4	6 1 2	6 2 3	6 3 6	6 2 2	6 4 4
6 2 2	6 1 4	6 4 6	6 3 5	6 4 5	6 4 4	6 2 1
6 4 4	6 2 2	6 4 4	6 2 1	6 1 1	6 3 7	0 0 0
6 2 2	6 4 6	0 0 0	6 3 4	6 2 6	6 3 4	6 2 4
6 4 5	6 2 3	6 2 5	6 2 4	6 2 4	7 2 6	6 3 4
6 2 5	6 4 6	6 2 2	7 2 6	6 2 6	7 2 5	6 2 4
6 2 3	6 4 4	6 3 3	6 2 2	6 1 3	6 3 5	6 3 3
0 0 0	7 3 7	6 3 5	6 2 2	6 2 2	6 4 4	6 4 5
6 4 6	6 3 6	7 3 7	7 3 7	6 2 3	6 2 3	6 3 4
6 4 4	6 4 4	6 3 4	7 3 7	6 3 3	6 1 3	6 3 3
7 3 5	6 2 1	6 3 3	6 4 5	6 2 3	6 3 5	6 3 3
6 4 4	6 4 4	6 4 5	6 1 1	6 2 3	7 2 6	6 2 3
6 2 2	6 3 5	6 2 3	6 2 4	6 2 3	0 0 0	6 3 3
7 2 6	7 2 3	7 3 5	6 3 4	6 2 2	6 3 4	6 3 4
6 3 3	6 3 7	6 2 5	6 4 4	6 2 2	7 2 7	0 0 0
6 3 6	6 2 2	6 3 3	6 4 5	6 2 2	6 3 3	6 4 5
6 4 5	6 3 2	7 3 8	7 2 2	6 3 3	6 3 1	6 2 2
6 1 1	6 3 8	0 0 0	7 3 6	6 2 2	6 4 5	6 2 2
6 1 1	6 3 4	7 2 5	6 4 5	6 4 5	6 3 3	6 4 5
7 4 7	7 4 8	6 1 2	6 3 3	6 2 3	7 3 6	7 2 5

1 1 1	7 3 8	6 2 3	6 3 3	6 4 5	7 3 7	7 3 6
0 0 0	6 3 7					

TENBY site 2 sample 3 2 VII 81

7 3 5	6 2 3	6 2 2	5 2 2	6 2 2	7 2 6	5 2 2
6 2 2	6 3 3	6 3 3	7 2 8	6 1 3	6 2 5	6 1 1
6 1 1	6 1 3	6 4 4	6 1 3	7 2 3	6 3 5	6 3 4
6 1 1	7 2 5	7 1 1	7 3 7	6 2 2	6 2 4	7 2 6
7 2 5	7 2 5	7 2 6	6 2 2	6 3 3	7 2 6	6 4 4
6 3 5	6 3 3	6 1 1	7 3 7	6 2 3	7 3 7	6 3 6
7 2 7	6 3 3	6 2 3	7 1 1	6 2 3	6 3 6	6 3 3
6 1 2	6 2 3	7 3 6	6 1 1	6 4 6	6 2 8	6 3 3
6 3 4	6 2 1	6 2 2	6 2 3	6 2 2	6 4 6	6 4 4
0 0 0	6 3 4	6 4 4	0 0 0	6 3 3	6 4 4	6 2 1
6 2 3	6 4 4	6 2 3	6 4 7	6 2 2	6 4 6	6 2 1
6 2 5	6 1 1	6 2 3	6 2 4	6 3 4	6 1 2	6 4 4
6 3 4	6 4 5	6 4 5	6 2 2	6 1 1	6 2 3	7 2 6
6 2 2	6 4 5	7 3 8	6 3 3	6 4 4	6 4 6	6 1 3
6 4 6	6 3 4	6 3 4	7 3 8			

TENBY site 3 2 VII 81

6 1 3	6 1 2	6 1 2	7 3 9	6 2 9	6 2 2	0 0 0
6 1 1	7 3 7	6 3 8	7 3 6	6 3 8	7 3 10	7 2 7
6 3 5	7 3 6	7 3 7	7 2 7	6 3 3	7 3 7	7 3 6
7 3 8	7 4 9	7 2 7	7 3 7	7 3 7	7 4 9	

TENBY site 4 sample 1 2 VII 81

6 1 2	6 4 4	6 4 4	6 4 7	6 2 1	7 2 10	6 3 3
7 2 9	6 3 3	6 4 6	6 2 2	6 3 7	6 3 5	6 5 4
6 4 5	6 4 4	7 2 8	6 2 2	6 5 4	6 2 3	7 2 10
6 1 2	6 2 1	0 0 0	6 1 2	6 3 3	6 4 5	7 1 4
6 2 1	6 3 2	6 4 4	6 3 5	7 1 1	6 2 4	6 2 1
6 3 3	6 4 4	6 2 4	6 3 5	6 3 3	7 2 6	6 3 3
7 2 8	6 3 3	6 2 2	6 2 5	6 3 6	6 1 2	6 4 5

2 2 2	6 2 2	6 1 3	6 4 3	6 5 3	6 3 3	6 1 3
6 4 5	6 3 4	7 1 6	6 1 3	6 2 4	6 4 5	6 1 1
6 1 2	6 4 5	6 3 3	6 3 4	6 4 4	5 3 3	6 2 3
6 2 2	6 2 3	6 4 4	6 3 3	6 3 3	6 2 2	6 3 3
6 4 4	6 2 4	6 2 7	5 1 2	6 3 3	6 3 3	6 4 4
6 3 1	6 1 2	0 0 0	6 2 4	7 2 6	6 2 4	1 1 1
6 2 3	6 4 4	6 3 3	6 3 4	6 3 3	6 4 5	6 4 7
6 3 1	6 2 3	6 2 2	6 3 3	6 2 5	6 3 3	0 0 0
6 1 1	6 3 3	6 4 4	6 2 1	6 3 3	6 2 3	6 2 1
6 2 2	0 0 0	1 1 1	6 3 3	6 1 1	6 1 1	6 3 3

TENBY site 4 sample 2 2 VII 81

6 4 4	6 2 3	7 3 4	0 0 0	6 2 2	6 2 4	7 2 6
7 3 5	1 1 1	6 2 4	6 2 1	6 3 1	7 2 6	7 2 3
6 4 4	6 3 2	6 3 3	7 3 5	7 3 5	2 2 2	0 0 0
6 1 1	7 1 1	6 2 1	0 0 0	6 1 1	0 0 0	6 2 6
6 3 5	0 0 0	0 0 0	7 2 5	0 0 0	0 0 0	6 2 6
6 3 6	7 1 1	0 0 0	6 3 4	6 3 4	6 1 1	6 3 5
7 3 3	6 3 3	7 2 3	7 3 6			

TENBY site 5 2 VII 81

7 1 2	0 0 0	0 0 0	6 3 5	6 1 1	0 0 0	7 1 3
6 1 1	6 1 1	6 3 7	0 0 0	6 3 3	6 3 4	6 4 4
6 3 5	6 1 1	6 3 5	6 3 4	6 4 7	7 1 1	7 1 3
7 3 7	7 1 3	7 3 8	7 3 5			

TENBY site 6 2 VII 81

6 3 3	6 2 2	6 1 1	6 2 2	6 2 2	6 2 4	2 2 2
7 2 4	7 2 6	7 2 2	7 2 1	6 2 1	7 2 5	6 1 1
7 3 6	0 0 0	7 3 3	7 1 1	7 1 1	6 1 1	6 3 4
1 1 1	6 2 2	6 2 3	6 2 3	6 2 2	6 1 1	6 3 4
6 1 3	6 2 3	6 3 1	6 2 3	6 2 3	6 2 3	6 2 3
6 1 2	6 3 3	7 3 6	6 4 4	6 2 3	6 2 1	7 1 1
7 2 5	7 2 3	6 3 4	6 2 2	6 2 2	6 3 5	6 2 3
7 2 7	7 2 7	7 2 1	7 2 4	7 2 2	7 2 2	7 2 3

0 0 0 6 1 1 7 2 8 1 1 1 7 2 1 6 3 3 7 2 6
6 2 1 6 2 2 7 2 7 7 3 6 6 3 3 6 3 3 6 3 3
6 2 2 6 4 4 7 2 4 6 3 3 7 3 7 6 4 4 6 2 2
0 0 0 6 3 3 6 2 2 7 3 7 6 3 3 6 3 3 6 2 2
6 2 3 7 2 6 6 3 3 6 1 3 6 4 4 6 4 5 6 2 2
6 3 3 7 3 7 6 3 4 6 3 3 6 3 3 7 3 4 6 3 3
6 2 3 7 3 8 6 2 2 6 2 4 6 5 4 7 3 8 6 3 3
6 3 3

TENBY Narberth Road 4 XI 78

5 2 1 6 2 2 6 2 2 5 2 2 5 2 1 5 2 1 5 1 1

SAUNDERSFOOT site 1 4 XI 78

5 2 3 5 3 3 6 2 2 5 2 3 5 2 2 5 2 4 6 2 3
6 4 4

SAUNDERSFOOT site 2 4 XI 78

5 3 3 6 1 1 6 1 1 6 2 1 6 2 2 6 2 2 6 2 2
6 2 2 6 3 3 5 2 2

PORTHCAWL Newton 13 IX 79

0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0

PORTHCAWL Kenfig 13 IX 79

0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0
1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 6 2 2 0 0 0
0 0 0 6 2 2 6 2 4 0 0 0 6 1 1 7 1 1 0 0 0
6 2 1 7 2 2

ST. IVES 31 VII 79

7 3 10	7 2 8	7 2 9	7 3 10	7 3 10	7 3 10	7 3 10
7 3 9	7 3 10	7 3 10	7 3 11	7 2 11	8 4 12	7 3 8
7 3 9	7 3 10	7 4 11	7 3 9	7 3 10	8 3 9	7 3 10
8 3 8	8 4 12	7 2 8	8 4 11	7 2 9	8 4 11	7 4 11
8 3 11	7 3 10	7 4 10	8 3 9	7 3 9	8 4 10	7 4 11

CALDEY IS. sample 1 2 VIII 79 d>10.0 mm, scored 10 VIII 79

7 4 1	6 2 3	6 4 7	7 3 2	6 2 2	7 2 7	7 2 5
7 1 1	6 3 5	7 3 10	8 1 10	0 0 0	7 2 9	7 3 9
7 3 9	7 2 1	7 2 5	6 4 5	6 2 3	7 2 4	8 1 9
7 2 5	7 2 10	7 2 1	7 2 2	6 2 2	6 4 4	7 3 9
6 3 5	7 3 1	7 3 1	7 3 6	7 2 6	7 2 6	7 1 1
6 4 6	6 3 3	7 1 1	0 0 0	6 3 3	6 1 2	7 2 6
7 2 9	7 2 5	7 2 8	7 3 10	6 3 6	7 2 6	7 3 7
7 3 6	7 2 2	7 1 1	7 3 7	7 3 10	7 1 1	7 2 1
7 3 8	7 3 4	7 3 9	7 3 4	8 2 11	7 3 6	7 3 11
7 3 10	8 4 11	0 0 0	7 2 1	7 2 2	7 4 10	7 3 9
8 3 11	8 4 11	7 2 8	7 4 10	8 4 10	7 3 7	7 3 9

CALDEY IS. sample 1 2 VIII 79 d<10.0 mm, scored 10 VIII 79

8 3 9	7 3 8	7 2 6	7 3 11	8 3 7	8 3 9	8 3 10
7 3 11	7 3 11	8 3 11	7 3 10	7 4 9	7 4 12	7 3 11
7 4 11	7 3 11	8 3 8	7 3 7	7 3 9	7 3 9	7 3 11
8 3 10	8 3 10	8 4 8	7 2 6	7 3 10	7 2 6	7 3 10
8 3 10						

CALDEY IS. sample 1 2 VIII 79 d>10.0mm, scored 8 XI 79

7 1 1	7 1 1	7 2 1	7 1 1	6 2 2	7 1 1	0 0 0
6 1 1	5 2 3	7 1 1	0 0 0	6 2 2	6 1 1	6 4 7
6 2 2	6 2 1	1 1 1	7 1 9	7 1 1	7 1 1	7 2 11

CALDEY IS. sample 1 2 VIII 79 d<10.0 mm, scored 8 XI 79

7 2 6   7 3 10   5 5 5   7 4 10   7 3 11   7 3 10   7 2 7
7 2 9

CALDEY IS. sample 2 2 VIII 79 d>10.0 mm

7 3 5   7 1 1   7 1 1   7 3 3   7 2 1   7 3 2   6 2 2
6 2 2   6 2 1   7 1 1   6 2 2   6 2 1   6 3 2   7 3 1
7 3 2   7 3 1   6 3 2   7 2 1   7 2 1   7 3 2   7 1 1
6 3 2   6 3 3   7 1 1   6 3 2   7 3 4   7 3 5   8 3 7
7 3 6   7 3 6   7 3 2   7 1 1   7 2 8   8 3 7   7 3 6
8 2 4   8 3 5   7 3 4   7 2 5   7 3 2   7 3 6   7 3 6
7 3 2   7 3 3   7 3 2   7 2 1   7 1 1

CALDEY IS. sample 2 2 VIII 79 d<10.0 mm

8 2 4   7 2 2   8 2 4   8 4 9   7 4 8   7 3 9   7 3 8
7 3 9   7 3 7   7 3 8   7 3 7   7 4 10   7 3 9   7 3 7
7 3 9   7 3 5   7 3 5   7 3 8   7 3 10

BAIE DU MONT ST. MICHEL

0 0 0   7 1 1   7 1 1   7 1 1   7 1 2   6 2 1   0 0 0
6 2 1   6 2 2   6 1 1   6 2 2   6 2 2   6 1 1   6 3 2
6 2 3   6 2 3   6 2 3   6 2 1   6 2 2   0 0 0   6 1 3
6 3 3   0 0 0   6 3 3   6 3 3   6 2 2   6 2 3   6 1 1
6 2 1   6 2 1   6 2 2   1 1 1   6 1 1   0 0 0   1 1 1
6 1 1   6 2 1   0 0 0   6 2 2   6 1 2   1 1 1   6 2 1
6 1 1   6 2 4   0 0 0   6 1 1   0 0 0   6 3 3   6 1 1
6 1 1   0 0 0   0 0 0   6 1 1   6 1 1   6 2 1   0 0 0
6 1 1   6 1 1   6 2 3   0 0 0

BRITTANY site 1

6 1 1   6 2 1   6 2 4   8 3 13   6 2 2   6 3 3   6 2 1
6 2 2   7 2 10   6 2 4   7 3 10   6 2 2   6 3 5   6 1 1

6 3 6	7 2 4	0 0 0	6 1 2	6 1 1	5 3 3	6 2 3
6 2 2	6 2 2	6 1 2	0 0 0	0 0 0	6 1 3	6 1 1
6 2 1	0 0 0	6 2 3	6 2 2	6 2 1	6 1 3	6 3 3
6 2 2	6 1 3	7 3 11	7 2 10	7 2 6		

BRITTANY site 2

6 3 7	6 2 2	6 3 6	6 2 3	5 2 2	7 2 8	7 3 9
6 2 3	6 3 5	6 2 3	6 3 4	6 2 2	6 2 3	7 3 7
6 2 1	6 2 5	6 2 5	6 1 3	6 1 3	7 2 9	6 2 2
6 1 2	7 2 3	7 2 2	6 2 2	7 2 5	7 3 6	6 2 1
6 4 4	6 1 3	7 2 3	7 2 3	7 4 9	7 3 5	6 2 2
6 2 3	6 3 4	6 2 3	0 0 0	7 3 5	6 3 3	6 2 1
7 3 10	7 2 3	7 2 3	7 2 8	6 2 1	6 2 2	6 3 4
7 2 2	7 2 6	6 2 4	0 0 0	6 3 3	6 4 7	6 3 3

BRITTANY site 3

6 2 1	1 1 1	6 2 1	6 1 1	6 3 2	6 1 1	6 1 1
6 2 2	6 2 3	6 3 3	6 1 1	6 2 2	6 2 3	6 2 2
6 2 2	6 1 1	6 1 1	6 2 2	6 3 3	6 1 1	6 1 1
7 3 2	6 3 2	2 2 2	6 2 1	7 3 1	0 0 0	0 0 0
6 2 1	7 2 5	6 3 2	7 3 1	7 2 2	0 0 0	8 3 2
7 2 1	0 0 0	7 1 1	7 3 3	1 1 1	0 0 0	0 0 0
7 2 3	7 3 8	0 0 0	6 3 3	7 1 1	7 1 1	7 3 2
7 3 2	0 0 0	0 0 0	0 0 0	6 2 2	8 4 2	6 3 3
7 5 3	7 3 2	7 3 2	7 2 2	6 2 3	0 0 0	7 2 1
6 3 1	7 3 1	7 2 1	0 0 0	7 2 1	0 0 0	6 3 2
0 0 0	0 0 0	0 0 0	0 0 0			

BRITTANY site 4

7 3 9	6 4 3	6 3 3	6 5 5	7 3 8	6 3 3	6 2 2
6 4 4	6 3 3	6 4 4	7 3 7	5 4 3	6 3 5	6 3 6
7 3 7	6 4 7	6 3 3	7 3 8	6 3 3	6 4 4	6 3 3
7 3 1	6 5 7	7 4 7	6 5 4	7 4 10	7 4 7	6 3 3
7 4 6	6 2 5	7 3 1	7 2 1	0 0 0	7 2 2	6 3 5

7 3 3	6 5 5	7 2 1	6 4 5	6 4 4	6 5 5	6 2 2
7 3 5	6 3 3	6 5 4	6 5 3	6 3 4	7 4 7	6 5 3
6 4 3	6 3 3	6 3 4	7 2 3	7 5 9	6 2 3	6 2 3
6 4 4	6 5 5	6 3 2	7 3 1	7 3 6	6 3 2	6 4 4
6 3 3	7 3 9	6 3 1	6 5 2	7 2 2	7 3 8	6 4 3
7 3 6	6 4 4	6 3 4	7 2 6	6 5 5	7 3 2	6 5 3
6 4 3	6 6 5	6 3 3	6 4 4	7 3 1	7 3 7	6 4 3
7 2 3	6 3 3					

BRITTANY site 5

5 2 4	6 1 2	6 3 5	6 2 4	6 4 4	6 3 4	6 3 5
6 4 5	7 2 7	6 2 2	6 3 4	6 3 5	6 3 9	6 2 4
6 2 2	6 1 1	6 4 6	6 3 3	6 2 3	6 2 3	7 2 5
6 1 1	6 1 2	6 1 2	6 2 3	6 3 3	6 3 5	6 2 2

BRITTANY site 6

7 3 7	6 3 5	6 1 2	6 4 6	6 3 6	6 2 9	6 3 5
6 2 2	6 3 4	7 3 6	7 2 6	6 2 1	7 2 6	6 1 2
7 2 3	6 3 3	6 3 3	6 2 2	7 2 6	0 0 0	6 1 1
6 4 6	6 2 4	6 2 2	6 1 2	6 2 1	6 3 4	6 3 5
6 3 6	7 2 5	6 1 3	0 0 0	6 3 1	6 2 2	6 2 3
6 1 2	6 2 2	0 0 0	2 2 2	6 2 2	6 2 3	7 4 6
6 3 6	0 0 0	6 3 4	6 2 4	6 2 1	6 3 3	6 1 3
6 3 1	6 1 1	6 3 5	6 4 4			

ELVIRIA site 1 1979

7 4 13	7 3 14	7 3 12	7 3 12	7 3 12	7 3 11	8 2 12
8 5 14	7 3 12	7 3 11	7 2 8	7 4 13	7 3 8	7 2 9
7 4 13	7 4 14	7 3 13	7 3 10	7 4 13	7 4 14	7 4 13
7 5 14	7 3 11	7 2 9	7 3 12	7 4 13	7 5 14	7 4 13
7 3 11	7 5 15	7 4 11	7 3 13	7 3 12	7 3 12	7 4 12
7 3 11	7 4 14	7 3 11	7 5 14	7 3 12	7 4 13	7 4 14
7 4 12						

BENALMADENA

8 6 18	8 4 17	8 6 17

MAJORCA Camp de Mar

6 5 5	6 5 6	6 4 7	6 3 3	6 3 3	6 5 5	6 4 9
6 4 8	6 4 5	5 4 5	6 4 7	6 5 9	6 4 9	5 3 5
6 4 8	6 5 7	6 5 7	6 4 7	6 4 9	6 4 9	6 4 8

MAJORCA Ses Coretes $d > 10.0$ mm

6 4 8	6 3 8	6 4 7	7 2 8	7 3 10	6 3 11	7 2 8
6 4 9	7 3 9	6 2 6	6 3 8	6 2 8	7 3 10	6 2 9
6 3 10	7 3 11	6 3 8	6 3 7	6 2 8	6 3 8	5 2 8
7 4 11	6 3 9	6 4 12	6 3 9	7 1 2	7 1 4	7 3 10
7 1 2	7 3 9	7 3 10	7 4 10	6 3 9	7 3 10	6 3 7
6 4 9	7 3 9	6 3 8	6 4 8	7 3 10	7 3 10	6 4 9
7 3 10	5 3 7	7 2 8	7 3 10	6 4 10	7 3 10	6 4 10
7 3 10	7 2 8	6 4 7	6 4 10	6 3 8	6 3 10	7 3 11

MAJORCA Ses Coretes $d < 10.0$ mm

7 3 11	7 3 11	7 3 10	7 3 10	7 3 11	7 3 10	7 3 10
7 3 9	7 3 10	7 3 9	7 3 10	7 3 10	7 3 11	6 4 9
6 4 9	6 4 9	6 3 10	7 3 11	7 3 10	7 3 11	6 3 10
6 4 9	7 3 11	7 3 9	7 3 10	7 3 10	7 3 11	6 4 11
6 4 10	6 4 9	6 3 9	6 4 9	6 3 9		

MAJORCA Costa de la Calma sample 1 $d > 10.0$ mm

6 5 6	6 5 3	0 0 0	0 0 0	6 4 5	6 3 3	6 4 7
6 3 2	6 3 8	0 0 0	6 2 5	5 4 4	6 4 6	6 3 3
6 3 3	6 2 1	0 0 0	6 5 6	6 5 6	6 4 4	5 3 2
6 6 5	6 3 3	6 5 5	5 4 4	6 3 3	5 4 5	6 1 1
6 5 5	6 5 5	6 5 7	0 0 0	6 3 3	6 4 8	6 6 5
5 4 2	6 5 5	6 5 4	6 4 5	6 5 5	5 3 3	5 3 2

6 5 5   6 5 7   5 4 4   6 5 4   6 4 4   7 3 8   6 2 2
6 5 4

MAJORCA Costa de la Calma sample 1 d<10.0 mm

6 4 8   6 3 10   6 4 9   6 2 2   6 4 9   6 5 12   6 2 2
6 3 3   6 4 8   6 4 11   6 3 3   6 4 8   6 4 7   7 2 2
7 3 10   7 3 9   6 3 3   6 2 2   6 2 3   6 3 7   6 4 4
6 5 5   6 4 6   6 3 8   6 3 9   6 4 9   7 3 9   6 2 3
6 2 2   7 4 11   6 3 10   6 3 3   6 2 1   7 3 9   6 2 3
6 1 1   6 4 7   6 4 4   7 3 9   7 3 9   6 2 2   6 4 9
6 3 3   7 2 1   6 3 2   6 4 8   6 2 2   6 4 8   6 4 5
6 1 1   6 4 6   6 4 7   7 4 10   6 4 5   6 4 4   6 3 3
6 4 10   6 4 4   7 3 10   6 4 4   6 2 2   6 4 10   6 4 4
7 4 9   6 1 2   6 3 3   6 2 1   6 2 6   6 4 9   6 4 5
6 3 3   7 2 9   7 2 9   6 4 5   0 0 0   7 3 10   6 4 5
6 3 11   6 4 5   6 2 2   6 3 8   6 3 8   5 3 3   5 3 4
6 3 3   6 4 6   5 4 5   7 5 10   7 3 10   7 3 10   7 3 3
6 4 7   7 3 8   7 3 9   7 3 10   7 3 9   7 4 11   7 3 8
6 5 10   6 4 6   7 5 11   7 3 8   7 4 10   6 4 5

MAJORCA Costa de la Calma sample 2

6 5 3   6 4 2   7 2 1   5 3 1   6 4 2   6 2 2   0 0 0
6 4 4   6 4 4   6 3 7   6 3 7   6 5 3   0 0 0   6 2 2
6 2 1   7 2 2   6 2 2   6 3 3   6 4 9   6 5 6   6 3 1
5 3 3   5 3 3   6 5 4   6 6 5   6 5 4   6 3 1   6 3 3
6 3 4

MENORCA Torralba

5 3 2   6 3 3   5 3 3   6 4 5   6 3 3   5 2 1   6 4 4
6 3 1   5 3 1   6 4 6   5 2 3   5 2 3   6 2 2   6 2 1

MENORCA Torre d'en Gaumes

5 2 3   6 2 1

MENORCA Santa Clementina

6 4 5	6 4 9	7 4 9	7 2 8	6 4 8	6 5 6	6 4 7
6 4 7	6 4 7	7 3 7	6 3 10	6 3 8	7 4 9	6 4 8
6 4 6	6 4 9	7 4 10	7 3 3	6 3 4	6 3 7	

MENORCA Es Grao d>10.0 mm

6 4 10	5 2 3	6 2 3	6 4 7	6 1 2	5 2 4	5 1 1
6 3 2	6 2 1	6 2 2	6 1 1	6 1 3	6 3 6	6 2 2
7 2 9	7 3 11	5 2 3				

MENORCA Es Grao d<10.0 mm

7 2 6	7 3 12	6 3 10	7 4 13	7 2 8	7 4 12	7 4 13
7 3 10	7 4 12	7 3 9	7 3 8	6 3 9	6 3 10	

SARDINIA Calasetta d>10.0 mm

7 3 9	7 2 6	6 2 5	6 2 3	6 1 4	7 2 9	6 2 3
6 3 5	6 3 4	7 1 2	6 1 3	6 3 8	6 2 4	6 1 4
6 2 3	6 2 3	6 3 6				

SARDINIA Calasetta d<10.0 mm

6 3 7	6 3 3	7 3 9	7 3 10	6 3 10	7 3 10	7 3 10
7 3 9	7 3 8	6 4 8	6 4 8	6 3 10	6 4 10	7 3 9
7 3 10	7 4 10	7 3 9	7 3 10	7 3 9	7 3 9	7 3 9
7 3 10	7 3 10	7 3 9	7 3 9	7 3 10	7 3 9	7 3 10
7 3 9	7 3 10	7 3 10	7 3 10			

SARDINIA Cagliari d>10.0 mm

6 2 4	6 3 12	6 3 8	6 2 8	6 3 6	6 3 9

SARDINIA Cagliari d $<$10.0 mm

7 3 9	7 3 11	7 4 9	7 3 10	7 3 11	7 3 10	7 3 10
7 3 11	7 4 10	7 3 12	7 4 11	7 4 10	7 3 11	7 4 9
7 3 12	7 3 11	7 3 9	7 3 10	7 4 9	7 3 9	7 3 10
7 3 12	7 3 10	6 4 9	7 3 10	7 3 10	7 3 12	7 3 10
7 3 12	7 3 12					

LESBOS

5 2 6	6 1 9	6 1 6	7 2 12	6 2 6	7 2 9	6 2 8
6 3 6	6 3 6	4 4 4	6 2 9	6 3 5	6 3 6	6 2 5
6 1 9	6 2 4	6 1 5	6 1 4	5 5 5	7 7 7	6 2 7
7 3 8	4 4 4	5 2 3	6 1 4	6 3 6	6 1 4	6 3 4
6 3 5	3 3 3	5 5 5	6 3 3	6 2 8	6 2 7	6 3 3
6 2 5	6 2 6	6 6 6	7 2 10	6 2 3	6 3 6	3 3 3
6 2 6	7 2 9	6 3 5	6 1 3	6 1 4	7 2 8	1 1 1
7 2 8	0 0 0	6 2 3	6 2 8	6 3 6	7 2 9	6 2 2
7 2 6	3 3 3	6 2 5	6 3 5	6 3 7	6 2 3	6 2 1
6 4 6	6 2 3	7 3 5	7 2 8	7 2 4	7 2 6	6 1 6
7 3 10	7 3 7	6 3 6	6 3 7	7 2 5	6 3 5	6 4 5
7 3 4	6 2 5	7 2 7	7 3 8	7 3 9	7 3 11	7 3 5
6 3 5	6 3 4	5 4 5	7 3 10	7 2 6	6 2 2	7 4 9
7 2 6	6 1 5	6 2 2	7 3 9	5 5 5	6 3 6	6 3 6
7 2 11	5 5 5	6 3 7	6 2 4	6 3 7	6 2 8	6 3 3
6 2 3	6 2 3	6 3 11	4 4 4			

LIMASSOL

7 3 9	6 5 4	6 6 3	6 5 10	7 4 9	6 4 8	7 4 11
7 4 11	7 5 9	6 5 7	6 5 10	6 5 7	7 3 9	7 4 10
6 4 7	7 5 10	6 5 9	6 4 10	7 4 11	7 5 11	6 5 5
6 3 4	6 5 7	6 4 6	6 4 8	6 5 6	6 4 7	6 5 4
6 5 4	6 4 6	7 3 8	6 5 4	6 5 6	6 5 8	6 5 10
6 4 10	6 5 11	6 5 7	6 4 10	6 5 11	6 4 8	6 5 10
6 5 8	6 5 9	6 4 9	6 5 8	6 5 8	6 5 9	6 5 9
6 5 8	6 5 8	7 4 11	6 5 9	7 4 11	6 4 4	6 4 6

7 3 10	7 3 11	7 3 11	7 3 11	7 3 12	7 3 11	7 3 11
7 3 11	7 3 12	7 3 11	7 2 10	8 3 11	7 3 11	7 3 11
7 3 12	7 3 11	7 3 12	7 3 12	7 3 11	7 3 12	7 3 12
7 3 12	7 3 11	7 3 12	7 3 11	7 3 11	7 3 11	7 3 11
7 3 11	7 3 10					

ASHQELON central

7 3 8	7 3 7	7 4 8	7 3 11	7 4 13	7 4 11	7 3 10
7 3 9	7 3 10	8 4 11	8 4 9	7 4 9	7 4 11	8 6 15
8 4 12	7 3 8	7 6 9	7 3 8	7 6 7	7 3 8	7 5 9
7 3 7	7 4 12	7 4 11	7 5 8	7 3 9	7 4 10	7 5 9
7 3 7	7 3 10	7 3 7	7 4 8	6 5 6	7 4 8	7 4 11
7 4 8	7 3 9	7 3 11	8 5 13	7 4 9	7 4 9	7 5 8
6 5 5	7 4 8	7 5 10	7 4 9			

ASHQELON southern

8 5 15	7 3 13	7 6 10	7 4 12	7 3 9	7 3 9	7 3 10
7 4 10	7 4 10	7 3 8	7 3 8	7 3 11	7 4 10	7 4 11
7 4 11	7 3 9	7 4 9	8 2 8	7 5 9	7 3 11	7 4 9
6 5 4						

Appendix 6 - Shell thickness data.

Mean shell thickness (with standard deviation) of shells in each 2 mm category of h + d is given for all British and foreign samples measured. Thickness was measured in the following Tenby samples only:

14.9.78	site 6.
3.11.78	site 1 sample 2
17.1.79	all samples
16.3.79	all samples
24.5.79	all samples
11.7.79	site 1 sample 1, site 2 sample 1
13.9.79	site 1 sample 1, site 2 sample 3
15.11.79	site 1 samples 1 & 2, site 2 samples 1, 2 & 3
10.4.80	all samples except snails with $d < 10.0$ mm at site 3
11.7.80	site 1 samples 1 & 2, site 3, site 4 samples 1 & 2, site 5
18.10.80	all samples

Tenby

h+d	14.9.78	3.11.78	17.1.79	16.3.79	24.5.79	11.7.79	13.9.79
6.0-7.9			0.088±0.015	0.083±0.013	0.054±0.005		
8.0-9.9	0.072±0.010	0.069±0.005	0.099±0.015	0.093±0.016	0.068±0.015	0.074±0.008	
10.0-11.9	0.102±0.019	0.087±0.014	0.120±0.025	0.102±0.023	0.066±0.018	0.088±0.014	
12.0-13.9	0.120±0.015	0.106±0.017	0.124±0.024	0.104±0.012	0.078±0.030	0.081±0.020	
14.0-15.9	0.120±0.015	0.095±0.024	0.118±0.022	0.105±0.021	0.089±0.034	0.067±0.026	0.110±0.033
16.0-17.9	0.137±0.022	0.095±0.017	0.103±0.025	0.128±0.008	0.072±0.021	0.068±0.017	0.105±0.012
18.0-19.9	0.128±0.027	0.112±0.015	0.120±0.028		0.079±0.021	0.068±0.018	0.112±0.037
20.0-21.9	0.122±0.035	0.107±0.018	0.131±0.023		0.088±0.024	0.069±0.012	0.126±0.047
22.0-23.9	0.120±0.027	0.125±0.026	0.128±0.019	0.127±0.036	0.099±0.032	0.084±0.021	0.101±0.026
24.0-25.9	0.112±0.018	0.105±0.018	0.135±0.023	0.125±0.003	0.136±0.041	0.076±0.017	0.112±0.039
26.0-27.9	0.116±0.029	0.113±0.040	0.166±0.051		0.104±0.016	0.092±0.026	0.112±0.063
28.0-29.9	0.110±0.011	0.124±0.032	0.169±0.062		0.194±0.044	0.099±0.027	0.106±0.024
30.0-31.9	0.130±0.012	0.193±0.072	0.165±0.017			0.092±0.021	0.104±0.022
32.0-33.9	0.124±0.020					0.096±0.015	0.112±0.020
34.0-35.9							0.121±0.011
36.0-37.9							0.108±0.028
38.0-39.9							

Tenby

h+d	15.11.79	10.4.80	11.7.80	18.10.80
6.0-7.9	0.077±0.016	0.066±0.016	0.068±0.013	0.073±0.016
8.0-9.9	0.072±0.013	0.069±0.018	0.073±0.015	0.085±0.020
10.0-11.9	0.084±0.010	0.072±0.020	0.095±0.021	0.110±0.026
12.0-13.9	0.142±0.025	0.080±0.032	0.109±0.027	0.124±0.030
14.0-15.9		0.087±0.030	0.110±0.024	0.119±0.031
16.0-17.9		0.096±0.032	0.092±0.014	0.112±0.033
18.0-19.9	0.117±0.030	0.099±0.030	0.093±0.020	0.102±0.015
20.0-21.9		0.103±0.027	0.087±0.016	0.112±0.026
22.0-23.9	0.140±0.046	0.125±0.030	0.095±0.018	0.114±0.038
24.0-25.9	0.102±0.041	0.134±0.031	0.102±0.029	0.110±0.029
26.0-27.9	0.110±0.470	0.126±0.033	0.121±0.046	0.118±0.031
28.0-29.9	0.115±0.037	0.132±0.039	0.124±0.031	0.124±0.030
30.0-31.9	0.123±0.033	0.111±0.011	0.149±0.044	0.111±0.016
32.0-33.9	0.128±0.030		0.170±0.050	0.152±0.049
34.0-35.9	0.117±0.045			0.125±0.028
36.0-37.9				
38.0-39.9				

St. Catherine's Island (Tenby); northern France

h+d	St. Cath's Island	Roscoff	B. du Mont St. Michel	Baie du Quiberon
6.0-7.9				
8.0-9.9				
10.0-11.9				
12.0-13.9				
14.0-15.9				
16.0-17.9				0.085±0.015
18.0-19.9				0.085±0.008
20.0-21.9		0.073±0.017		0.105±0.013
22.0-23.9		0.076±0.005		0.104±0.016
24.0-25.9		0.093±0.038	0.107±0.001	0.111±0.027
26.0-27.9	0.089±0.034	0.100±0.026	0.122±0.013	0.121±0.026
28.0-29.9	0.119±0.024	0.091±0.015	0.113±0.021	0.124±0.023
30.0-31.9	0.135±0.013	0.090±0.015	0.136±0.020	0.130±0.026
32.0-33.9	0.115±0.024		0.138±0.016	0.128±0.022
34.0-35.9	0.117±0.029		0.173±0.070	0.139±0.021
36.0-37.9	0.135±0.008			0.129±0.015
38.0-39.9				

Mediterranean sites - Spain and the Balearics

h+d	Elviria 1979 site 1	Mallorca Camp de Mar	Mallorca Ses Coretes	Mallorca Costa de la Calma	Menorca sites combined
6.0-7.9				0.081±0.012	
8.0-9.9	0.078±0.015		0.090±0.015	0.097±0.024	
10.0-11.9	0.087±0.019		0.126±0.024	0.110±0.023	
12.0-13.9	0.091±0.018			0.120±0.026	0.093±0.025
14.0-15.9	0.097±0.023			0.116±0.026	0.102±0.010
16.0-17.9				0.134±0.022	0.107±0.008
18.0-19.9					
20.0-21.9				0.133±0.026	0.099±0.007
22.0-23.9				0.139±0.027	0.082±0.006
24.0-25.9	0.156±0.035		0.119±0.021	0.148±0.047	0.095±0.011
26.0-27.9	0.149±0.030		0.129±0.022	0.169±0.045	0.112±0.031
28.0-29.9	0.152±0.032		0.137±0.017	0.140±0.038	0.132±0.013
30.0-31.9	0.147±0.025	0.159±0.008	0.143±0.028	0.173±0.068	0.144±0.023
32.0-33.9	0.193±0.051	0.156±0.013	0.155±0.006	0.146±0.033	0.166±0.033
34.0-35.9		0.175±0.015		0.148±0.021	0.155±0.024
36.0-37.9					
38.0-39.9					

Mediterranean sites - Sardinia, Lesbos and Crete

h+d	Sardinia Calasetta	Sardinia Cagliari	Lesbos	Crete Malia	Crete Komo	Crete Amnissos
6.0-7.9	0.068±0.010		0.062±0.009			
8.0-9.9	0.082±0.014	0.098±0.021	0.070±0.016	0.087±0.013		
10.0-11.9	0.107±0.013	0.122±0.019	0.075±0.011	0.093±0.012		
12.0-13.9		0.132±0.018	0.081±0.012	0.089±0.007		
14.0-15.9			0.083±0.014			
16.0-17.9			0.090±0.012			
18.0-19.9			0.090±0.011			
20.0-21.9			0.106±0.017	0.116±0.034	0.118±0.024	0.089±0.012
22.0-23.9	0.146±0.018		0.096±0.011	0.116±0.050	0.143±0.023	0.106±0.019
24.0-25.9	0.158±0.018		0.121±0.026	0.127±0.011	0.137±0.021	0.113±0.018
26.0-27.9	0.162±0.018	0.179±0.033	0.126±0.016	0.134±0.016		0.119±0.014
28.0-29.9			0.132±0.021	0.141±0.020		0.148±0.027
30.0-31.9			0.126±0.046	0.162±0.029		0.153±0.024
32.0-33.9						
34.0-35.9						
36.0-37.9						
38.0-39.9						

Mediterranean sites - Cyprus and Israel

h+d	Cyprus Limassol	Israel Ashqelon both sites	Israel Dor	Israel Caesarea
6.0-7.9	0.072±0.009			
8.0-9.9	0.081±0.010		0.099±0.031	
10.0-11.9	0.093±0.009		0.123±0.012	
12.0-13.9	0.100±0.017	0.070±0.011	0.117±0.021	0.075±0.013
14.0-15.9	0.099±0.009	0.081±0.005	0.138±0.037	0.083±0.008
16.0-17.9	0.093±0.020	0.090±0.013		0.095±0.006
18.0-19.9	0.114±0.016	0.093±0.019	0.088±0.009	0.091±0.020
20.0-21.9	0.115±0.013	0.093±0.017	0.084±0.017	0.094±0.012
22.0-23.9	0.123±0.017	0.099±0.021	0.097±0.019	0.114±0.020
24.0-25.9	0.132±0.011	0.102±0.015	0.111±0.024	0.114±0.015
26.0-27.9	0.143±0.014	0.114±0.021	0.116±0.022	0.126±0.033
28.0-29.9	0.166±0.007	0.118±0.015	0.117±0.023	0.118±0.015
30.0-31.9			0.119±0.015	0.133±0.027
32.0-33.9				
34.0-35.9				
36.0-37.9				
38.0-39.9				

References

References marked with an asterisk have not been seen personally.

Adam, W. 1947. Revision des Mollusques de la Belgique. I Mollusques terrestres et dulcicoles. Mémoires du Musée Royal d'Histoire Naturelle de Belgique. 106 1-297 6pl.

Adams, L.E. 1896. The collector's manual of British land and freshwater shells. 2nd edition. 214+xii pp. 9 pl. Leeds, Taylor Brothers.

Adams, L.E. 1902. The census of the British land and freshwater Mollusca. J. Conch., Lond. 10 217-237.

Alder, J. 1837. Notes on the land and fresh-water Mollusca of Great Britain, with a revised list of species. Mag. Zool. Bot. 2 101-119.

Alzona, C. 1971. Malacofauna Italica. Catalogo e bibliografia dei Molluschi viventi, terrestri e d'acqua dolce. Atti Soc. ital. Sci. nat. Museo civ. Stor. nat. Milano. 111 1-433.

Andrewartha, H.G. 1964. How animals live in dry places. Proc. Linn. Soc. N.S.W. 89 287-294.

Armitage, H.M. 1949. Bureau of Entomology. Thirtieth annual report. Calif. Dept. Agric. Bull. 38 157-216.

Arthur, W. 1978. Morph-frequency and co-existence in Cepaea. Heredity 41 335-346.

Arthur, W. 1980. Further associations between morph-frequency and coexistence in Cepaea. Heredity 44 417-421.

Avidov, Z. & Harpaz, I. 1969. Plant pests in Israel. Jerusalem, Israel Universities Press.

Backhuys, W. 1972. Notes on Theba pisana ustulata (Lowe, 1852) the land-snail of the Salvage Islands. Basteria 36 117-130.

Backhuys, W. 1975. Zoogeography and taxonomy of the land and freshwater molluscs of the Azores. xii+350 pp. 97 figs. 32 pl. Amsterdam, Backhuys & Meesters.

Bailey, S.E.R. 1975. The seasonal and daily patterns of locomotor activity in the snail Helix aspersa Müller in relation to environmental variables. Proc. Malac. Soc. Lond. 41 415-428.

Baillie, W. 1887. Colonizing land and freshwater shells in East Sutherland. J. Conch.,Lond. 5 192.

Baillie, W. 1889. Colonizing land and freshwater shells at Brora, East Sutherland. J. Conch., Lond. 6 15.

Baker, R.E. 1968. The ecology of the wrinkled snail, Helicella caperata Mont. on the Braunton Burrows sand dune system. Proc. Malac. Soc. Lond. 38 41-54.

Bantock, C.R. & Noble, K. 1973. Variation with altitude and habitat in Cepaea hortensis (Müll.). Zool. J. Linn. Soc. 53 237-252.

Bar, Z. 1978. Variation and natural selection in shell thickness of Theba pisana along climatic gradients in Israel. J. Moll. Stud. 44 322-326.

Barker, J.F. & Barker, A. 1980. The relation between body size and resistance to desiccation in two species of Zaprionus (Drosophilidae). Ecol. Ent. 5 309-314.

Barrett, B.W. 1972. Theba pisana in Guernsey, 1971. J. Conch., Lond. 27 391-396.

Barrett, B.W. 1975. The sandhill snail Theba pisana (Müller) in Jersey. Bull. Annuel de la Soc. Jersiaise 21 409-412.

Basinger, A.J. 1927. The eradication campaign against the white snail (Helix pisana) at La Jolla, California. Calif. Dept. Agric. Bull. 16 51-77.

Beaufort, L.F.de 1951. Zoogeography of the land and inland waters. viii+208 pp. London, Sidgewick & Jackson.

Begon, M.(E.) 1977. The effective population size of a natural Drosophila subobscura population. Heredity 38 13-18.

Begon, M.(E.), Krimbas, C.B. & Loukas, M. 1980. The genetics of Drosophila subobscura populations. XV. Effective size of a natural population estimated by three independent methods. Heredity 45 335-350.

Begon, M.(E.) & Mortimer, M. 1981. Population Ecology. A unified study of animals and plants. vii+200 pp. Oxford, Blackwell.

Beirne, B.P. 1952. The origin and history of the British fauna. x+164 pp. London, Methuen.

Berry, R.J. 1979. The Outer Hebrides: where genes and geography meet. Proc.Roy. Soc. Edinb. B 77 21-43.

Bett, J.A. 1960. The breeding season of slugs in gardens. Proc. Zool. Soc. Lond. 135 559-568.

Biberson, P. & Jodot, P. 1965. Faunes de mollusques continentaux du Pleistocene de Casablanca (Maroc). Publ. Serv. géol. Maroc. 25 115-169.

Bonavita, A. & Bonavita, D. 1962. Contribution à l'étude écologique d'Euparypha pisana Müller des rivages Méditerranéens de la Provence. Note préliminaire. Publ. Staz. Zool. Napoli 32 suppl. 189-204.

Boycott, A.E. 1934. Habitats of land Mollusca in Britain. J. Ecol. 22 1-38.

Bronson, M.T. 1979. Altitudinal variation in the life-history of the golden-mantled ground-squirrel (Spermophilus lateralis). Ecology 60 272-279.

Brown, V.K. 1978. Variation in voltinism and diapause intensity in Nemobius sylvestris (Bosc.) (Orthoptera: Gryllidae). J. Nat. Hist. 12 461-472.

Brussard, P.F. 1975. Geographic variation in North American colonies of Cepaea nemoralis. Evolution 29 402-410.

Bullen, R.A. 1905a. Notes on Pleistocene and Recent shells from Crete. Proc. Malac. Soc. Lond. 6 307-308.

Bullen, R.A. 1905b. Notes on land and fresh-water shells from the Alhambra ditch, Granada, Andalucia, Spain; on recent land shells from various localities near Carmona, Province of Sevilla; and on land, fresh-water and marine shells from Holocene deposits, Carmona. Proc. Malac. Soc. Lond. 6 309-313.

Bullen, R.A. 1910. Notes on (I) Pleistocene, (II) Holocene, (III) Recent non-marine shells from Mallorca; (IV) marine shells associated with the Holocene deposits; (V) marine shells from Alcudia, Mallorca; (VI) non-marine shells from Manresa, Cataluña. Proc. Malac. Soc. Lond. 9 118-122.

Burke, D.P.T. 1979. Variation in Western Irish populations of Cepaea nemoralis (L.). Ph.D. thesis, University of Liverpool.

Butler, A.J. 1976. A shortage of food for the terrestrial snail Helicella virgata in South Australia. Oecologia (Berl.) 25 349-371.

Butler, A.J. & Murphy, C. 1977. Distribution of introduced land snails on the Yorke Peninsula, South Australia. Trans. Roy. Soc. South Australia 101 91-98.

Cain, A.J. 1959a. An undescribed polymorphism in Hygromia striolata (C. Pfeiffer). J. Conch., Lond. 24 319-322.

Cain, A.J. 1959b. Inheritance of mantle colour in Hygromia striolata (C. Pfeiffer). J. Conch., Lond. 24 352-353.

Cain, A.J. 1971. Undescribed polymorphisms in two British snails. J. Conch., Lond. 26 410-416.

Cain, A.J. 1977a. Variation in spire index of some coiled gastropod shells, and its evolutionary significance. Phil. Trans. Roy. Soc. Lond. B 277 377-428.

Cain, A.J. 1977b. The uniqueness of the polymorphism of Cepaea (Pulmonata: Helicidae) in Western Europe. J. Conch., Lond. 29 129-136.

Cain, A.J. 1978a. Variation of terrestrial gastropods in the Philippines in relation to shell shape and size. J. Conch., Lond. 29 239-245.

Cain, A.J. 1978b. The deployment of operculate land snails in relation to shape and size of shell. Malacologia 17 207-221.

Cain, A.J. 1980. Whorl number, shape, and size of shell in some pulmonate faunas. J. Conch., Lond. 30 209-221.

Cain, A.J. 1981a. Possible ecological significance of variation in shape of Cerion shells with age. J. Conch., Lond. 30 305-315.

Cain, A.J. 1981b. Variation in shell shape and size of helicid snails in relation to other pulmonate faunas of the palaearctic region. Malacologia 21 149-176.

Cain, A.J. 1981c. The development of systematic ideas of variation illustrated by malacology. In History in the service of Systematics. (eds. Wheeler, A. & Price, J.H.). 151-156. London, Society for the Bibliography of Natural History.

Cain, A.J. 1982. Heterosematism in land snails. Malacologia in press.

Cain, A.J. in press a. On Homology and Convergence. In Problems of phylogenetic reconstructions. (eds. Joysey, K.A. & Friday, A.E.). Systematics Association Special Volume No. 21. London & New York, Academic Press.

Cain, A.J. in press b. Ecology and ecogenetics of terrestrial molluscan populations. In Biology of the Mollusca (ed. Wilbur, K.M.). vol. 5 Ecology (ed. Russell-Hunter, W.D.).

Cain, A.J. in preparation. Genetics of some morphs in the land snail Theba pisana. Malacologia.

Cain, A.J., Cameron, R.A.D. & Parkin, D.T. 1969. Ecology and variation of some helicid snails in Northern Scotland. Proc. Malac. Soc. Lond. 38 269-299.

Cain, A.J. & Cowie, R.H. 1978. Activity of different species of land-snail on surfaces of different inclinations. J. Conch., Lond. 29 267-272.

Cain,A.J. & Currey, J.D. 1963. Area effects in Cepaea. Phil. Trans. R. Soc. Lond. B 246 1-81.

Cain, A.J. & Currey, J.D. 1968. Studies on Cepaea III. Ecogenetics of a population of Cepaea nemoralis (L.) subject to strong area effects. Phil. Trans. R. Soc. Lond. B 253 447-482.

Cain, A.J., King, J.M.B. & Sheppard, P.M. 1960. New data on the genetics of polymorphism in the snail Cepaea nemoralis L. Genetics 45 393-411.

Cain, A.J. & Sheppard, P.M. 1952. The effects of natural selection on body colour in the land snail Cepaea nemoralis. Heredity 6 217-231.

Cain, A.J., Sheppard, P.M. & King, J.M.B. 1968. Studies on Cepaea I. The genetics of some morphs and varieties of Cepaea nemoralis (L.). Phil. Trans. R. Soc. Lond. B 253 383-396.

Calow, P. 1975. Length - dry weight relationships in snails: some explanatory models. Proc. Malac. Soc. Lond. 41 357-375.

Cameron, R.A.D. 1970a. The survival, weight loss and behaviour of three species of land snail in conditions of low humidity. J. Zool. 160 143-157.

Cameron, R.A.D. 1970b. The effect of temperature on the activity of three species of Helicid snail (Mollusca: Gastropoda). J. Zool. 162 303-315.

Cameron, R.A.D. 1970c. Differences in the distribution of three species of helicid snail in the limestone district of Derbyshire. Proc. Roy. Soc. Lond. B 176 131-159.

Cameron, R.A.D. 1978. Differences in the sites of activity of coexisting species of land mollusc. J. Conch., Lond. 29 273-278.

Cameron, R.A.D. 1981. Functional aspects of shell geometry in some British land snails. Biol. J. Linn. Soc. 16 157-167.

Cameron, R.A.D. & Carter, M.A. 1979. Intra- and interspecific effects of population density on growth and activity in some Helicid land snails (Gastropoda: Pulmonata). J. Anim. Ecol. 48 237-246.

Cameron, R.A.D. & Williamson, P. 1977. Estimating migration and the effects of disturbance in mark-recapture studies on the snail *Cepaea nemoralis* L. *J. anim. Ecol.* *46* 173-179.

Carter, M.A., Jeffery, R.C.V. & Williamson, P. 1979. Food overlap in co-existing populations of the land snails *Cepaea nemoralis* (L.) and *Cepaea hortensis* (Müll.). *Biol. J. Linn. Soc.* *11* 169-176.

Cassie, R.M. 1954. Some uses of probability paper in the analysis of size frequency distributions. *Aust. J. mar. freshwat. Res.* *5* 513-522.

Chan, W. & Saleuddin, A.S.M. 1974. Evidence that *Otala lactea* (Müller) utilizes calcium from the shell. *Proc. Malac. Soc. Lond.* *41* 195-200.

Chappell, H.G., Ainsworth, J.F., Cameron, R.A.D. & Redfern, M. 1971. The effect of trampling on a chalk grassland ecosystem. *J. appl. Ecol.* *8* 869-882.

Charlesworth, J.K. 1930. Some geological observations of the origin of the Irish fauna and flora. *Proc. R. Irish Acad.* *B* *39* 358-390.

Chase, E.P. 1915. *Helix pisana* Muller in California. *The Nautilus* *29* 72.

Chatfield, J.E. 1976. Studies on food and feeding in some European land molluscs. *J. Conch., Lond.* *29* 5-20.

Chatfield, J.E. 1977. Observations on variation in the mantle of the land snail *Monacha cantiana* (Montagu) (Pulmonata: Helicidae). *J. Conch., Lond.* *29* 219-222.

Clapham, A.R., Tutin, T.G. & Warburg, E.F. 1962. *Flora of the British Isles*. 2nd. edn. xlviii+1269 pp. Cambridge, University Press.

Clarke, B.(C.) 1972. Density-dependent selection. *Am. Nat.* *106* 1-13.

Clarke, B.(C.) 1975. Frequency-dependent and density-dependent selection. In *The role of natural selection in human evolution*. (ed. Salzano, F.M.). 187-200. North-Holland Publishing Company.

Clarke, B.(C.), Arthur, W., Horsley, D.T. & Parkin, D.T. 1978. Genetic variation and natural selection in pulmonate molluscs. In *Pulmonates* vol.2a (eds. Fretter, V. & Peake, J.). 219-270. London, New York, San Francisco, Academic Press.

Clarke, K.U. 1967. Insects and temperature. In *Thermobiology* (ed. Rose, A.H.). 293-352. London and New York, Academic Press.

Cloudsley-Thompson, J.L. 1970. Terrestrial Invertebrates. In *Comparative physiology of thermoregulation*. (ed. Whittow, G.C.). 15-77. New York, London, Academic Press.

Cockerell, S.C. 1885. *Helix pisana* var. *alba* at Rush, Co. Dublin. *J. Conch., Lond*. *4* 368.

Cockerell, T.D.A. 1886. Notes on some varieties of British shells. *J. Conch., Lond*. *5* 79-80.

Cockerell, T.D.A. 1921. *Helix pisana* in Porto Santo. *Proc. Malac. Soc. Lond*. *14* 196-197.

Cohen, J. & Cohen, P. 1975. *Applied multiple regression/correlation analysis for the behavioural sciences*. xxi+490 pp. John Wiley & Sons, New York, Toronto, London, Sydney.

Cole, L.C. 1954. The population consequences of life-history phenomena. *Quart. Rev. Biol*. *29* 103-137.

Comfort, A. 1957. The duration of life in molluscs. Proc. Malac. Soc. Lond. 32 219-241.

Companyo, L. 1863. Histoire naturelle du département des Pyrénées-Orientales. vol. 3. 942 pp. 1 pl. Perpignan, J.-B. Alzine.

Connolly, M. 1916. Notes on the South African non-marine Mollusca. Ann. S. Afr. Mus. 13 179-190.

Cook, A. 1979a. Homing in the Gastropoda. Malacologia 18 315-318.

Cook, A. 1979b. Homing in the slug Limax pseudoflavus. Anim. Behav. 27 545-552.

Cook, L.M. 1965. A note on apostasy. Heredity 20 631-636.

Cook, L.M., Jack, T. & Pettitt, C.W.A. 1972. The distribution of land molluscs in the Madeiran Archipelago. Boletin do Museu municipal do Funchal 26 5-30.

Cooke, A.H. 1916. A new British locality for Helix (Euparypha) pisana, Müll. Proc. Malac. Soc. Lond. 12 4.

Cooke, A.H. & Gwatkin, H.M. 1878. A list of shells taken at Guernsey, Sark, and Herm, in September, 1877. Quart. J. Conchol. 1 321-333.

Cooper, D.W. 1968. The significance level in multiple tests made simultaneously. Heredity 23 614-617.

Cooper, J.E. 1893. Notes on Helix pisana in the Channel Islands. J. Conch., Lond. 7 265.

Corbet, G.B. 1961. Origin of the British insular races of small mammals and of the 'Lusitanian' fauna. Nature, Lond. 191 1037-1040.

Cowie, R.H. 1980a. Observations on the dispersal of two species of British land snail. J. Conch., Lond. 30 201-208.

Cowie, R.H. 1980b. Precocious breeding of Theba pisana (Müller) (Pulmonata: Helicidae). J. Conch., Lond. 30 238.

Cowles, R.B. 1965. Hyperthermia, aspermia, mutation rates and evolution. Q. Rev. Biol. 40 341-367.

Crook, S.J. 1980. Studies on the ecological genetics of Helix aspersa (Müller). Ph.D. thesis, University of Dundee.

Crow, J.F. & Kimura, M. 1970. An introduction to population genetics theory. xiv+591 pp. New York, Evanston, London, Harper & Row.

Crow, J.F. & Morton, N.E. 1955. Measurement of gene frequency drift in small populations. Evolution 9 202-214.

Crowley, T.E. 1961. Theba pisana (Müller) in Guernsey. J. Conch., Lond. 25 15-17.

Cundall, J.W. 1889. A list of shells taken at Tenby, September 1888. J. Conch., Lond. 6 102-106.

Dance, S.P. 1970. 'Le fanatisme du nobis': a study of J.-R. Bourguignat and the 'Nouvelle École'. J. Conch., Lond. 27 65-86 4 pl.

Deblock, R. 1962. Recherches biologiques sur un Gastropode pulmoné Mediterranéen Euparypha pisana Müll aux limites nordiques de son extension. Thesis for the Diplome d'études superieures, Laboratoire de Zoologie de la Faculté Libre des Sciences de Lille.

Deblock, R. & Hoestlandt, H. 1967. Données biologiques sur le Gastropode littoral Theba pisana Müller aux limites septentrionales de son extension. C. R. Acad. Sc. Paris 265 893-896.

Deevey, E.S. 1949. Biogeography of the Pleistocene. Part 1. Europe and North America. Bull. geological Society of America 60 1315-1416.

* De Stefani, T. 1913. Helix pisana and the damage it is capable of doing to citrus trees. Translated from Nuovi Annali di Agricoltura Siciliana. Anno II; N.S. Fasc. I Palermo by Harry S. Smith, California Citrograph 8 35,36,57 1922.

Dobzhansky, Th. & Wright, S. 1943. Genetics of natural populations. X. Dispersion rates in Drosophila pseudoobscura. Genetics 28 304-340.

Duncan, C.J. 1959. The life cycle and ecology of the freshwater snail Physa fontinalis (L.). J. anim.Ecol. 59 97-117.

Dundee, D.S. 1974. Catalog of introduced molluscs of Eastern North America (North of Mexico). Sterkiana 55 1-37.

Dürr, H.J.R. 1946. A contribution to the morphology and bionomics of Theba pisana (Müller) (Gastropoda: Helicidae). Sci. Bull. Dep. Agric. S. Afr. no. 257 34 pp

Ellis, A.E. 1926. British Snails. 1st. edn. 275 pp. 14 pl. Oxford, Clarendon Press.

Ellis, A.E. 1951. Census of the distribution of the British non-marine Mollusca. J. Conch., Lond. 23 171-244.

Ellis, A.E. 1969. British Snails. 2nd. edn. 298 pp. 14 pl. Oxford, Clarendon Press.

Emberton, L.R.B. & Bradbury, S. 1963. Transmission of light through shells of Cepaea nemoralis (L.). Proc. Malac. Soc. Lond. 35 211-219.

Evans, J.G. 1972. Land snails in archaeology - with special reference to the British Isles. 436 pp. London, New York, Seminar Press.

Falconer, D.S. 1960. *Introduction to quantitative genetics*. ix+365 pp. Edinburgh & London, Oliver & Boyd.

Fletcher, B.S. 1974. The ecology of a natural population of the Queensland Fruit Fly, *Dacus tryoni*. V. The dispersal of adults. *Aust. J. Zool*. *22* 189-202.

Forbes, E. 1846. On the connection between the distribution of the existing fauna and flora of the British Isles and the geological changes which have affected their area, especially during the epoch of the Northern Drift. *Mem. geol. Surv. U.K*. *1* 336-432.

Forbes, E. & Hanley, S. 1853. *A history of British Mollusca and their shells*. vol. 4. vi+301 pp. 133 pl. London, John van Voorst.

Freeman, G.H. 1977. A model relating numbers of dispersing insects to distance and time. *J. appl. Ecol*. *14* 477-487.

Fry, F.E.J. 1967. Responses of poikilotherms to temperature. In *Thermobiology* (ed. Rose, A.H.). 376-409. London, New York, Academic Press.

Gammon, E.T. 1943. Helicid snails in California. *Calif. Dept. Agric. Bull*. *32* 173-187.

Garcia, M.C.L.R. 1977. Écophysiologie de l'escargot *Cepaea nemoralis* (L.) (Helicidae): quelques conséquences de l'échauffement par l'énergie rayonnée. *Arch. Zool. exp. gén*. *118* 495-514.

Geiger, R. 1965. *The Climate near the Ground*. xiv+611 pp. Cambridge, Mass., Harvard University Press.

Germain, L. 1908. Étude sur les Mollusques recueillis par M. Henri Gadeau de Kerville pendant son voyage en Khroumirie (Tunisie). In *Voyage zoologique en Khroumirie (Tunisie)*. (Gadeau de Kerville, H.). 129-277. Paris, J.-B. Baillière et fils.

Germain, L. 1929. Les Helicidae de la Faune française. Archives du museum d'histoire naturelle de Lyon 13 1-484.

Germain, L. 1930. Mollusques terrestre et fluviatiles, pt. 1. Faune Fr. 21 1-477.

Gloyne, C.P. 1878. Remarks on the geographical distribution of the terrestrial Mollusca. Quart. J. Conchol. 1 283-320.

Godwin, H. 1975. The history of the British flora. 2nd edn. x+541 pp. xxviii pl. Cambridge, University Press.

Goldstein, A. 1964. Biostatistics. ix+272 pp. New York, Macmillan; London, Collier - Macmillan.

Gosse, P.H. 1856. Tenby: a sea-side holiday. xx+408 pp. London, John van Voorst.

Gould, S.J. 1969. An evolutionary microcosm: Pleistocene and Recent history of the land snail P. (Poecilozonites) in Bermuda. Bull. Mus. comp. Zool. Harvard 138 406-531.

Grainger, J.N.R. 1969. Heat death in Arianta arbustorum. Comp. Biochem. Physiol. 29 665-670.

Grainger, J.N.R. 1975. Mechanism of death at high temperatures in Helix and Patella. J. Thermal Biology 1 11-13.

Gray, J.E. 1840. New edition of W. Turton's A manual of the land and fresh-water shells of the British Islands. ix+324 pp. 12 pl. London, Longman, Orme, Brown, Green & Longmans.

Gray, J.E. 1857. New edition of W. Turton's A manual of the land and freshwater shells of the British Islands. xvi+335 pp. 12 pl. London, Longman, Brown, Green, Longmans & Roberts.

Greenwood, J.J.D. 1969. Apostatic selection and population density. Heredity 24 157-161.

Greenwood, J.J.D. 1974. Effective population numbers in the snail Cepaea nemoralis. Evolution 28 513-526.

Greenwood, J.J.D. 1976. Effective population number in *Cepaea*: a modification. *Evolution* *30* 186.

Greig-Smith, P. 1964. *Quantitative plant ecology*. 2nd edn. xii+256 pp. London, Butterworths.

Hamilton, W.D. 1971. Geometry for the Selfish Herd. *J. Theoret. Biol.* *31* 295-311.

Harding, J.P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. mar. biol. assoc. U.K.* *28* 141-153.

Harpaz, I. & Oseri, Y. 1961. *Crop-damaging snails in Israel and their control*. iv+44 pp. Tel Aviv, Citrus Marketing Board; Rehovot, Hebrew University of Jerusalem, Faculty of Agriculture.

Harris, D. 1968. A method of separating two superimposed normal distributions using arithmetic probability paper. *J. anim. Ecol.* *37* 315-319.

Hart, A. & Begon, M.(E.) 1982. The status of general reproductive-strategy theories, illustrated by winkles. *Oecologia (Berl.)* *52* 37-42.

Haskin, H.H. 1955. Age determination in molluscs. *Trans. N.Y. Acad. Sci.* *16* 300-304.

Heath, D.J. 1975. Colour, sunlight and internal temperatures in the land-snail *Cepaea nemoralis* (L.). *Oecologia (Berl.)* *19* 29-38.

Heatwole, H. & Heatwole, A. 1978. Ecology of the Puerto Rican camaenid tree-snails. *Malacologia* *17* 241-316.

Heginbotham, C.D. 1946. Wiltshire mollusc collectors. *Wiltshire Archaeological and Natural History Magazine* *51* 457-463.

Heller, J. 1981. Visual versus climatic selection of shell banding in the landsnail *Theba pisana* in Israel. *J. Zool.* *194* 85-101.

Heller, J. 1982. Natural history of Theba pisana in Israel. J. Zool. 196 475-487.

Heller, J. & Tchernov, E. 1978. Pleistocene landsnails from the coastal plain of Israel. Israel J. Zool. 27 1-10.

Heller, J. & Volokita, M. 1981a. Gene-regulation of shell banding in a land snail from Israel. Biol. J. Linn. Soc. 16 261-277.

Heller, J. & Volokita, M. 1981b. Shell-banding polymorphism of the land snail Xeropicta vestalis along the coastal plain of Israel. Biol. J. Linn. Soc. 16 279-284.

Hickson, T.G.L. 1972. A possible case of genetic drift in colonies of the land snail Theba pisana. Heredity 29 177-190.

H.M.S.O. 1952. Climatological atlas of the British Isles. iv+139 pp. London.

H.M.S.O. 1958. Tables of temperature, relative humidity and precipitation for the world. Part V Asia. ix+129 pp. London.

H.M.S.O. 1972. Tables of temperature, relative humidity, precipitation and sunshine for the world. Part III. xiv+228 pp. London.

Hogben, L. & Kirk, R.L. 1944. Studies on temperature regulation. I. The Pulmonata and Oligochaeta. Proc. R. Soc. B 132 239-252.

Horn, H.S. 1978. Optimal tactics of reproduction and life-history. In Behavioural ecology: an evolutionary approach. (eds. Krebs, J.R. & Davies, N.B.). 411-429. Oxford, Blackwell.

Huddesford, G. 1770. New edition of Lister's Historiae sive synopsis methodicae conchyliorum et tabulanum anatomicanum. 13+iv+6+7+12+77 pp. 1059 pl. 22 tbl. Oxonii, Typographeo Clarendoniano.

Humphreys, J. 1976. Field observations on Theba pisana (Müller) (Gastropoda: Helicidae) at St. Ives, Cornwall. J. Conch., Lond. 29 93-106.

Humphreys, J. 1980. The land and freshwater Mollusca of St. Ives, Cornwall. Part I. Shell-bearing species. J. Conch., Lond. 30 155-166.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology. 22 415-427.

Jackson, J.W. 1925. The distribution of Margaritana margaritifera in the British Isles. J. Conch., Lond. 17 270-278.

Jaremovic, R. & Rollo, C.D. 1979. Tree climbing by the snail Cepaea nemoralis (L.): a possible method for regulating temperature and hydration. Can. J. Zool. 57 1010-1014.

Jeffreys, J.G. 1833a. A synopsis of the Testaceous Pneumonobranchous Mollusca of Great Britain. Trans. Linn. Soc. Lond. 16 323-392.

Jeffreys, J.G. 1833b. A supplement to the 'Synopsis of Testaceous Pneumonobranchous Mollusca of Great Britain'. Trans. Linn. Soc. Lond. 16 505-523.

Jeffreys, J.G. 1862. British Conchology. vol.1. cxiv+341 pp. 8 pl. London, John van Voorst.

Johnson, M.S. 1980. Association of shell banding and habitat in a colony of the land snail Theba pisana. Heredity 45 7-14.

Johnson, M.S. 1981. Effects of migration and habitat choice on shell banding frequencies in Theba pisana at a habitat boundary. Heredity 47 121-133.

Johnson, M.S. & Black, R. 1979. The distribution of Theba pisana on Rottnest Island. The Western Australian Naturalist 14 140-144.

Jones, J.S. 1973a. Ecological genetics of a population of the snail Cepaea nemoralis at the northern limit of its range. Heredity 31 201-211.

Jones, J.S. 1973b. The genetic structure of a southern peripheral population of the snail Cepaea nemoralis. Proc. R. Soc. Lond. B 183 371-384.

Jones, J.S. 1980. Evolutionary genetics of snails. Nature, Lond. 285 283-284.

Jones, J.S., Leith, B.H. & Rawlings, P. 1977. Polymorphism in Cepaea: a problem with too many solutions? Ann. Rev. Ecol. Syst. 8 109-143.

Joubert, C.J. & Walters, S.S. 1951. The control of snails and slugs. Farm. S. Afr. 26 379-380.

Kendrew, W.G. 1953. The climate of the continents. 4th edn. 607 pp. Oxford, Clarendon.

Kennard, A.S. 1923. The Holocene non-marine Mollusca of England. Proc. Malac. Soc. Lond. 15 241-259.

Kennard, A.S. & Woodward, B.B. 1901. The post-Pleistocene non-marine Mollusca of the south of England. Proc.Geol. Ass. 17 213-260.

Kennard, A.S. & Woodward, B.B. 1926. Synonymy of the British non-marine Mollusca (Recent and post-Tertiary). xxiv+447 pp. London, British Museum (Natural History).

Kerney, M.P. 1966. Snails and Man in Britain. J. Conch., Lond. 26 3-14.

Kerney, M.P. 1967. Distribution mapping of land and freshwater Mollusca in the British Isles. J. Conch., Lond. 26 152-160.

Kerney, M.P. 1968. Britain's fauna of land Mollusca and its relation to the post-glacial thermal optimum. Symp. zool. Soc. Lond. 22 273-291.

Kerney, M.P. 1976. Atlas of the non-marine Mollusca of the British Isles. (xi)+199 pp. Cambridge, Institute of Terrestrial Ecology.

Kerney, M.P. & Cameron,R.A.D. 1979. A field guide to the land snails of Britain and north-west Europe. 288 pp. 24 pl. London, Collins.

Kerster, H.W. 1964. Neighbourhood size in the Rusty Lizard, Sceloporus olivaceus. Evolution 18 445-457.

Kettlewell, (H.) B.(D.) 1973. The evolution of melanism. xxiv+423 pp. 72 pl. Oxford, Clarendon.

Kew, H.W. 1893. The dispersal of shells. xiv+291 pp. London, Keegan Paul, Trench, Trübner & Co. Ltd.

* Klomp, H. 1970. The determination of clutch size in birds. A review. Ardea 58 1-124.

Kobelt, W. 1897. Studien zur Zoogeographie: die Mollusken der Palaearkt. Region. viii+344 pp. Wiesbaden, C. W. Kriedel's Verlag.

Lamb, H.H. 1964. The English climate. xi+212 pp. London, English Universities Press.

Lamb, H.H. 1965. Britain's changing climate. In The biological significance of climatic changes in Britain. (ed. Johnson, C.G. & Smith, L.P.). 3-34. London, New York, Academic Press.

Lamb, H.H. 1966. The changing climate. Selected papers. xi+236 pp. London, Methuen.

Lamb, H.H. 1970. Our changing climate. In *The flora of a changing Britain*. (ed. Perring, F.). 11-24. Middlesex, Classey.

Lamotte, M. 1951. Recherches sur la structure génétique des populations naturelles de *Cepaea nemoralis* (L.). *Bull. biol. Fr. Belg. suppl*. *35* 1-238.

Lamotte, M. 1959. Polymorphism of natural populations of *Cepaea nemoralis*. *Cold Spring Harbor Symposium on Quantitative Biology*. *24* 65-86.

Lamotte, M. 1966. Les facteurs de la diversité du polymorphisme dans les populations naturelles de *Cepaea nemoralis* (L.). *Lavori della Società Malacologica Italiana*. 3 33-73.

Lassen, H.H. 1979. Reproductive effort in Danish mudsnails. (Hydrobiidae). *Oecologia (Berl.)* *40* 365-369.

Lawton, J.H. & McNeill, S. 1979. Between the Devil and the deep blue sea: on the problem of being a herbivore. In *Population dynamics* (eds. Anderson, R.M., Turner, B.D. & Taylor, L.R.). 223-244. Oxford, Blackwell.

Lazaridou-Dimitriadou, M. & Daguzan, J. 1981. Étude de l'effet du 'groupement' des individus chez *Theba pisana* (Mollusque Gastéropode Pulmoné Stylommatophore). *Malacologia* *20* 195-204.

Leach, W.E. 1852. *A synopsis of the Mollusca of Great Britain*. xvi+376 pp. 13 pl. London, John van Voorst.

Lewis, G. 1968. *Polymorphism in the shell characters of certain helicid molluscs, particularly the genus Cochlicella*. D.Phil. thesis. Oxford University.

Lewis, T. & Taylor, L.R. 1967. *Introduction to experimental ecology*. xi+401 pp. 4 pl. London, New York, Academic Press.

Lewontin, R.C. 1965. Selection for colonizing ability. In The genetics of colonizing species. (eds. Baker, H.G. & Stebbins, G.L.). 77-94. New York, Academic Press.

Lim, Y.P. & Jenkins, R.B. 1972. The Italian White Snail... Theba pisana (Müller) in South Australia with particular reference to its distribution in the south-east of South Australia. Exp. Rec. Dept. Agric. S. Aust. 6 23-25.

Lindroth, C.H. 1957. The faunal connections between Europe and North America. 344 pp. New York, John Wiley & Sons.

Livshits, G.M. 1981. Survival, behaviour and spatial distribution of shell morphs in apopulation of the snail Brephulopsis bidens (Pulmonata). Oecologia (Berl.) 51 220-226.

Lovell, M.S. 1884. The edible Mollusca of Great Britain and Ireland. 2nd edn. 310 pp. 12 pl. London, L. Reeve & Co.

MacArthur, R.H. & Wilson, E.O. 1967. The theory of island biogeography. xi+203 pp. Princeton, University Press.

Machin, J. 1967. Structural adaptations for reducing water-loss in three species of terrestrial snail. J. Zool. Lond. 152 55-65.

Machin, J. 1972. Water exchange in the mantle of a terrestrial snail during periods of reduced evaporative loss. J. exp. Biol. 57 103-111.

Mallett, G.E. 1962. A study of chromosome numbers in molluscs. D.Phil. thesis. Oxford University.

Manley, G. 1952. Climate and the British Scene. (6th. impression, 1975). 382 pp. 16 pl. Glasgow, Collins, Fontana.

Mason, C.F. 1970. Food, feeding rates and assimilation in woodland snails. Oecologia (Berl.) 4 358-373.

Maton, W.G. 1797. Observations relative chiefly to the natural history, picturesque scenery, and antiquities, of the western counties of England, made in the years 1794 and 1796. vol. 1. xi+336 pp. Salisbury, J. Eaton.

Maton, W.G. & Rackett, T. 1807. A descriptive catalogue of the British Testacea. Trans. Linn. Soc. Lond. 8 17-250 5 pl.

Matthews, J.R. 1937. Geographical relationships of the British flora. J. Ecol. 25 1-90.

Matthews, J.R. 1955. Origin and distribution of the British flora. 176 pp. London, Hutchinson.

* McLean, R.R. 1922. Snail pest at La Jolla. California Cultivator 58 593.

McMillan, N.F. 1966. Arianta arbustorum (L.) living with Helix nemoralis L. on blown sand. J. Conch., Lond. 26 47-48.

McMillan, N.F. 1968. British shells. xii+196 pp. 80 pl. London, New York, Warne.

McQuaid, C.D., Branch, G.M. & Frost, P.G.H. 1979. Aestivation behaviour and thermal relations of the pulmonate Theba pisana in a semi-arid environment. J. Therm. Biol. 4 47-55.

McWhinnie, M.A. 1967. The heat responses of invertebrates (exclusive of insects). In Thermobiology (ed. Rose, A.H.). 353-373. London, New York. Academic Press.

Mead, A.R. 1961. The Giant African Snail: a problem in economic malacology. 257 pp. Chicago, University Press.

Milnes, H. 1889. Helix pisana var. scalariformis. J. Conch., Lond. 6 146.

Mitchell, G.F. & Watts, W.A. 1970. The history of the Erinaceae in Ireland during the Quaternary epoch. In Studies in the vegetational history of the British Isles. (eds. Walker, D. & West, R.G.). 13-21. Cambridge, University Press.

Montagu, G. 1803. Testacea Britannica, or Natural history of British shells, marine, land and freshwater. xxvii+606 pp. 16 pl. (2 vols.) London, J. White.

Mordan, P.B. 1977. Factors affecting the distribution and abundance of Aegopinella and Nesovitrea (Pulmonata: Zonitidae) at Monks Wood National Nature Reserve, Huntingdonshire. Biol. J. Linn. Soc. 9 59-72.

Mordan, P.B. 1978. The life-cycle of Aegopinella nitidula (Draparnaud) (Pulmonata: Zonitidae) at Monks Wood. J. Conch.,Lond. 29 247-252.

Morris, M.G. 1968. Differences between the invertebrate faunas of grazed and ungrazed chalk grassland. II. The faunas of sample turves. J. appl. Ecol. 5 601-611.

Murphy, G.I. 1968. Pattern in life history and the environment. Am. Nat. 102 391-403.

Murray, J. 1963. The inheritance of some characters in Cepaea hortensis and Cepaea nemoralis (Gastropoda). Genetics 48 605-615.

Murray, J. 1964. Multiple mating and effective population size in Cepaea nemoralis. Evolution 18 283-291.

Murray, J. 1966. Cepaea nemoralis in the Isles of Scilly. Proc. Malac. Soc. Lond. 37 167-181.

Murray, J. 1975. The genetics of the Mollusca. In Handbook of Genetics. vol. 3. (ed. King, R.C.). 3-31. Plenum Press.

Newell, G.E. 1958a. The behaviour of Littorina littorea (L.) under natural conditions and its relation to position on the shore. J. mar. biol. Ass. U.K. 37 229-239.

Newell, G.E. 1958b. An experimental analysis of the behaviour of Littorina littorea (L.) under natural conditions and in the laboratory. J. mar. biol. Ass. U.K. 37 241-266.

Newell, P.F. & Appleton, T.C. 1979. Aestivating snails - the physiology of water regulation in the mantle of the terrestrial pulmonate Otala lactea. Malacologia 18 575-581.

Newell, P.F. & Machin, J. 1976. Water regulation in aestivating snails - ultrastructural and analytical evidence for an unusual cellular phenomenon. Cell. Tiss. Res. 173 417-421.

Nobre, A. 1930. Moluscos terrestres, fluviais e das aguas solobras de Portugal. 259 pp. 18 pl. Porto, Ministério da Agricultura.

Noyce, A.G. 1973. The morphology and histology of the genital system of Theba pisana (Müller) (Pulmonata: Helicidae). Ann. Univ. Stellenbosch serie A 48 1-40.

Oldham, C. 1928. Range in Pembrokeshire of Euparypha pisana Müller. J. Conch., Lond. 18 186.

Oldham, C. 1929. The influence of lime on the shell of Arianta arbustorum (L.). Proc. Malac. Soc. Lond. 18 143-144.

Oldham, C. 1934. Further observations on the influence of lime on the shells of snails. Proc. Malac. Soc. Lond. 21 131-138.

Oosterhoff, L.M. 1977. Variation in growth rate as an ecological factor in the land snail Cepaea nemoralis (L.). Neth. J. Zool. 27 1-132.

Parsons, P.A. 1980. Parallel climatic races for tolerances to high temperature - desiccation stress in two Drosophila species. Journal of Biogeography 7 97-101.

Paul, C.R.C. 1978. The ecology of Mollusca in ancient woodland. II. Analysis of distribution and experiments in Hayley Wood, Cambridgeshire. J. Conch., Lond. 29 281-294.

Peake, J. 1978. Distribution and ecology of the Stylommatophora. In Pulmonates vol. 2a (eds. Fretter, V. & Peake, J.). 429-526. London, New York, San Francisco, Academic Press.

Peile, A.J. 1926. The Mollusca of Bermuda. Proc. Malac. Soc. Lond. 17 71-98.

Pennant, T. 1777. British Zoology. 4th edn. 136+vii pp. London, Benjamin White.

Perrot, M. 1939. Sur la position systématique d'Euparypha pisana Muller, d'après l'étude chromosomique. C. R. Soc. phys. Genève. 56 32-35.

Pianka, E.R. 1970. On r- and K-selection. Am. Nat. 104 592-597.

Pianka, E.R. 1972. r and K selection or b and d selection? Am. Nat. 106 581-588.

Pigott, C.D. 1968. Biological flora of the British Isles. Cirsium acaulon (L.) Scop. J. Ecol. 56 597-612.

Pilsbry, H.A. 1939. Land Mollusca of North America. vol.1. pt. 1. xvii+573 pp. Philadelphia, Academy of Natural Sciences.

Pitchford, G.W. 1954. Eggs of Theba pisana (Müller). J. Conch., Lond. 24 22.

Pitchford, G.W. 1973. Theba pisana (Muller) in Guernsey: 1961-1971. The Conchologists' Newsletter No. 46 330-333.

Pollard, E. 1975a. Differences in shell thickness in adult Helix pomatia L. from a number of localities in southern England. Oecologia (Berl.) 21 85-92.

Pollard, E. 1975b. Aspects of the ecology of Helix pomatia L. J. anim. Ecol. 44 305-329.

Pomeroy, D.E. 1968. Dormancy in the land snail Helicella virgata (Pulmonata: Helicidae). Aust. J. Zool. 16 857-869.

Pomeroy, D.E. 1969. Some aspects of the ecology of the land snail Helicella virgata in South Australia. Aust. J. Zool. 17 495-514.

Pomeroy, D.E. & Laws, H.M. 1967. The distribution of introduced snails in South Australia. Records of the South Australian Museum 15 483-494.

Potts, D.C. 1975. Persistence and extinction of local populations of the garden snail, Helix aspersa in unfavourable environments. Oecologia (Berl.) 21 313-334.

Praeger, R.L. 1939. The relations of the flora and fauna of Ireland to those of other countries. Proc. Linn. Soc. Lond. 151 192-213.

Praeger, R.L. 1950. Natural history of Ireland. A sketch of its flora and fauna. 350 pp. London, Collins.

Quick, H.E. 1927. Oecological notes on the Oxwich sand dune area. J. Conch., Lond. 18 119-122.

Quick, H.E. 1943. Land snails and slugs of West Glamorgan. J. Conch., Lond. 22 4-12.

Quick, H.E. 1952. Emigrant British snails. Proc. Malac. Soc. Lond. 29 181-189.

Quick, H.E. 1953. Helicellids introduced into Australia. Proc. Malac. Soc. Lond. 30 74-79.

Rainer, M. 1967. Chromosomenuntersuchungen an Gastropoden (Stylommatophora). Malacologia 5 341-373.

Reid, C. 1899. The origin of the British flora. vi+191 pp. London, Dulau & Co.

Rensch, B. 1932. Über die Abhängigkeit der Grösse, des relativen Gewichtes und der Oberflächenstruktur der Landschneckenschalen von den Umweltsfaktoren. (Ökologische Molluskenstudien I.). Zeitschrift für Morphologie und Ökologie der Tiere. 25 757-807.

Richardson, A.M.M. 1974. Differential climatic selection in natural population of land snail Cepaea nemoralis. Nature, Lond. 247 572-573.

Rimmer, R. 1877. Helix pisana Müller. Quart. J. Conchol. 1 266-268.

Rimmer, R. 1880. The land and freshwater shells of the British Isles. xxxii+208 pp. 10 pl. London, David Bogue.

Roebuck, W.D. 1921. Census of the distribution of British land and freshwater Mollusca. J. Conch., Lond. 16 165-212.

Roth, B. & Eng, L.L. 1980. Distribution, ecology and reproductive anatomy of a rare land snail, Monadenia setosa Talmadge. Calif. Fish and Game. 66 4-16.

Sacchi, C.F. 1955. Fattori ecologici e storici nel polimorfismo delle Euparypha (Helicidae, Helicinae) del Marocco occidentale. Studia Ghisleriana serie III 2 44-66.

Sacchi, C.F. 1965. Ecological and historical bases for a study of the Iberian terrestrial Mollusca. Proc. First Europ. Malac. Congr. 1962. London, Conchological Society of Great Britain and Ireland, Malacological Society of London.

Sacchi, C.F. 1971. Écologie comparée des Gastéropodes Pulmonés des dunes Méditerranéennes et Atlantiques. Natura 62 277-358.

Sacchi, C.F. 1974. Points de vue d'un écologiste sur la physiologie de l'estivation chez l'hélicidé dunicole Euparypha pisana (Müller). Natura 65 117-133.

Sacchi, C.F. 1977. La 'lacune nord-adriatique' et son influence sur l'écologie des gastéropodes dunicoles. Prémisses methodologiques. Atti Soc. ital. Sci. nat. Museo civ. Stor. nat. Milano 118 213-225.

Sacchi, C.F. 1978. Il Delta del Po come elemento disgiuntore nell'ecologia delle spiaggie adriatiche. Boll. Mus. Ven. 29 suppl. 43-73.

Sacchi, C.F. & Gaudiosi, M.R. 1961. Sul significo ecologico dell'azoto conchigliare nella Elicide dunicola Euparypha pisana (Müll.). II. Analisi di fenotipi differenti in una singola popolazione. Lincei - Rend. Sc. fis. mat. e nat. serie VIII 30 571-575.

Sacchi, C.F. & Violani, C. 1977. Ricerche ecologiche sulle elicidi dunicole della Ria di Vigo (Spagna). Natura 68 253-284.

Salisbury, E. 1952. Downs and dunes. Their plant life and its environment. xiii+328 pp. 32 pl. London, G. Bell & Sons.

Schaffer, W.M. 1974. Optimal reproductive effort in fluctuating environments. Am. Nat. 108 783-790.

Scharff, R.F. 1892. The Irish land and freshwater Mollusca. Irish Naturalist 1 3-9, 45-47, 65-67, 87-90, 105-109, 135-138, 149-153, 177-181.

Scharff, R.F. 1905. The origin of the land and freshwater Mollusca at present living in the British Isles. J. Conch., Lond. 11 138-144.

Schmidt-Nielsen, K., Taylor, C.R. & Shkolnik, A. 1971. Desert snails: problems of heat, water and food. J. exp. Biol. 55 385-398.

Schmidt-Nielsen, K., Taylor, C.R. & Shkolnik, A. 1972. Desert snails: problems of survival. Symp. zool. Soc. Lond. 31 1-13.

Seber, G.A.F. 1973. The estimation of animal abundance. xii+506 pp. London, Griffin.

Sedlmair, H. 1956. Verhaltens- , Resistenz- und Gehäuse-unterschiede bei den polymorphen Bänderschnecken Cepaea hortensis (Müll.) und Cepaea nemoralis (L.). Biol. Zentr. 75 281-313.

Shileyko, A.A. 1978. On the systematics of Trichia s. lat. (Pulmonata: Helicoidea: Hygromiidae). Malacologia 17 1-56.

Simpson, G.G. 1952. Probabilities of dispersal in Geologic time. Bull. Amer. Mus. Nat. Hist. 99 163-176.

Skellam, J.G. 1952. Studies in Statistical Ecology. I. Spatial pattern. Biometrika 39 346-362.

Smith, C.J. 1980. Ecology of the English Chalk. xv+573 pp. London, New York, Toronto, Sydney, San Francisco, Academic Press.

Snedecor, G.W. & Cochran, W.G. 1967. Statistical Methods. 6th edn. xiv+593 pp. Iowa, State University Press.

Sokal, R.R. & Rohlf, F.J. 1969. Biometry. xxi+776 pp. San Francisco, W.H. Freeman & Co.

Sokal, R.R. & Rohlf, F.J. 1973. Introduction to Biostatistics. xiii+368 pp. San Francisco, W.H. Freeman & Co.

South, A. 1974. Changes in composition of the terrestrial mollusc fauna. In The changing flora and fauna of Britain (ed. Hawksworth, D.L.). 255-274. Systematics Association Special Volume No. 6. London & New York, Academic Press.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? J. anim. Ecol. 46 337-365.

Southwood, T.R.E. 1978. Ecological methods. 2nd edn. xxiv+524 pp. London, Chapman & Hall.

Southwood, T.R.E., May, R.M., Hassell, M.P. & Conway, G.R. 1974. Ecological strategies and population parameters. Am. Nat. 108 791-804.

Spence, G.C. 1938. Helix pisana Müller. J. Conch., Lond. 21 72.

Stapf, O. 1917. A cartographic study of the Southern element in the British flora. Proc. Linn. Soc. Lond. 129 81-94 5 pl.

Stearns, S.C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51 3-47.

Stearns, S.C. 1977. The evaluation of life history traits: a critique of the theory and a review of the data. Ann. Rev. Ecol. Syst. 8 145-171.

Stearns, S.C. 1980. A new view of life-history evolution. Oikos 35 266-281.

Steinhauser, F. 1970. Climatic atlas of Europe. I. Maps of mean temperature and precipitation. Geneva, W.M.O., Paris, UNESCO, Budapest, Cartographia.

Stelfox, A.W. 1911. A list of the land and freshwater mollusks of Ireland. Proc. Roy. Irish Acad. B 29 65-164.

Stelfox, A.W. & McMillan, N.F. 1966. The distribution in Ireland of very dark forms of Cochlicella acuta (Müller). J. Conch., Lond. 26 51.

Step, E. 1927. Shell life. An introduction to the British Mollusca. New edn. 421 pp. 32 pl. London, New York, Warne.

Stratton, L.W. 1970. Numbers of shells. J. Conch., Lond. 27 171-176.

Stubbs, A.G. 1900. The land and freshwater shells of Tenby, South Wales. J. Conch., Lond. 9 321-328, 358-365.

Swanton, E.W. 1902. South African notes. J. Conch., Lond. 10 194-195.

Tate, R. 1866. A plain and easy account of the land and freshwater mollusks of Great Britain. 244 pp. 11 pl. London, Robert Hardwicke.

Tattersfield, P. 1982. Behavioural aspects of niche separation and population dynamics of terrestrial molluscs. Ph.D. thesis, Birmingham University.

Taylor, D.W. & Sohl, N.F. 1962. An outline of gastropod classification. Malacologia 1 7-32.

Taylor, J.W. 1883. Descriptions of some new varieties of British land and freshwater shells. J. Conch., Lond. 4 28-37.

Taylor, J.W. 1888. Helix pisana var. minor Bourg. J. Conch., Lond. 5 331.

Taylor, J.W. 1890. Helix pisana var tenuis a new variety from Tenby. J. Conch., Lond. 6 281.

Taylor, J.W. 1894-1921. Monograph of the land and freshwater Mollusca of the British Isles. 22 parts. Leeds, Taylor Brothers.

Taylor, J.W. 1928. Helix pisana (Müll.) in S. Australia. J. Conch., Lond. 18 208.

Taylor, J.W. & Roebuck, W.D. 1885. Census of the authenticated distribution of British land and freshwater Mollusca. J. Conch., Lond. 4 319-336.

Taylor, J.W. & Roebuck, W.D. 1889. Census of the authenticated distribution of British land and freshwater Mollusca. In Land and freshwater shells. (Williams, J.W.). 94-112. London, Swan Sonnenschein & Co.

Taylor, J.W. & Roebuck, W.D. 1901. Census of the authenticated distribution of British land and freshwater Mollusca. In Land and freshwater shells. 3rd edn. (Williams, J.W.). 94-112. London, Swan Sonnenschein & Co.

Taylor, R.A.J. 1978. The relationship between density and distance of dispersing insects. Ecol. Ent. 3 63-70.

Thiele, J. 1931. Handbuch der Systematischen Weichtierkunde. vol. 1. vi+778 pp. Reprinted (1963), Amsterdam, Asher.

Thran, P. & Broekhuizen, S. 1965. Agro-climatic atlas of Europe. Amsterdam, London, New York, Elsevier.

Turk, F.A. & Turk, S.M. 1981. Cornish Biological Records 4 25 pp. Redruth, Institute of Cornish Studies.

Turk, S.M. 1966. The rediscovery of Theba pisana (Müller) in Cornwall. J. Conch., Lond. 26 19-25.

Turk, S.M. 1972. A study of the white sand-hill snail Theba pisana. Journal of the Devon Trust for Nature Conservation. 4 138-142.

Turton, W. 1819. A conchological dictionary of the British Isles. xxvii+272 pp. 28 pl. London, John Booth.

Turton, W. 1831. A manual of the land and freshwater shells of the British Islands. viii+150 pp. 10 pl. London, Longman, Rees, Orme, Brown & Green.

Tye, G.S. 1874. List of shells taken at Tenby, Pembrokeshire, at the end of September 1872. *Quart. J. Conchol.* *1* 30-31.

Tye, G.S. 1877. *Helix pisana* Müller. *Quart. J. Conchol.* *1* 230-233.

Tye, G.S. 1878. *Helix pisana* Muller. *Quart. J. Conchol.* *1* 333-334.

Umiński, T. 1975. Life cycles in some Vitrinidae (Mollusca, Gastropoda) from Poland. *Annls. Zool. Warsz.* *33* 17-33.

Van Bruggen, A.C. 1964. The distribution of introduced mollusc species in southern Africa. *Beaufortia. Ser. misc. publ. Zool. Mus. Amst.* *11* 161-169.

Villalobos-Dominguez, C. & Villalobos, J. 1947. *Colour Atlas*. xv+74 pp. 38 pl. Buenos Aires, Libreria el Ateneo Editorial.

Wagge, L.E. 1951. The activity of amoebocytes and of alkaline phosphatases during regeneration of the shell in the snail *Helix aspersa*. *Quart. J. micr. Sci.* *92* 307-321.

Waldén, H.W. 1976. A nomenclatural list of the land Mollusca of the British Isles. *J. Conch., Lond.* *29* 21-25.

Wallén, C.C. 1970. Climates of northern and western Europe. *World Survey of Climatology*. (ed. Landsberg, H.E.). vol. 5. x+253 pp. Amsterdam, London, New York, Elsevier.

Watson, E.V. 1960. A quantitative study of the bryophytes of chalk grassland. *J. Ecol.* *48* 397-414.

Welch, R.J. 1904. Rare or local Irish land and freshwater Mollusca. *J. Conch., Lond.* *11* 16-19.

Wells, G.P. 1944. The water relations of snails and slugs. III. Factors determining activity in *Helix pomatia* L. *J. exp. Biol.* *20* 79-87.

Wernstedt, F.L. 1972. *World climatic data*. 523 pp. Pennsylvania, Climatic Data Press.

Whittow, G.C. (ed.) 1970. Comparative physiology of thermoregulation. vol. 1. Invertebrates and non-mammalian vertebrates. ix+333 pp. New York, London, Academic Press.

Wilbur, H.M., Tinkle, D.W. & Collins, J.P. 1974. Environmental certainty, trophic level and resource availability in life history evolution. Am. Nat. 108 805-817.

Wilkens, J.L. & Fingerman, M. 1965. Heat tolerance and temperature relationships of the fiddler crab, Uca pugilator, with reference to body coloration. Biol. Bull. mar. biol. Lab. Woods Hole. 128 133-141.

Williamson, P. 1976. Size-weight relationships and field growth rates of the landsnail Cepaea nemoralis L. J. anim. Ecol. 45 875-885.

Williamson, P. 1979. Age determination of juvenile and adult Cepaea. J. Moll. Stud. 45 52-60.

Williamson, P. & Cameron, R.A.D. 1976. Natural diet of the landsnail Cepaea nemoralis. Oikos 27 493-500.

Williamson, P.,Cameron, R.A.D. & Carter, M.A. 1976. Population density affecting adult shell size of snail Cepaea nemoralis L. Nature, Lond. 263 496-497.

Williamson, P. Cameron, R.A.D. & Carter, M.A. 1977. Population dynamics of the landsnail Cepaea nemoralis L.: a six-year study. J. anim. Ecol. 46 181-194.

Wintle, W.J. 1922. Note on terrestrial Mollusca from a blown sand deposit on Caldey. Proc. Malac. Soc. Lond. 15 152.

Wintle, W.J. 1925. The non-marine Mollusca of Caldey Island. Proc. Malac. Soc. Lond. 16 171-176.

Wolda, H. 1963. Natural populations of the polymorphic landsnail Cepaea nemoralis (L.). Factors affecting their size and their genetic constitution. Arch. Néerl. Zool. 15 381-471.

Wolda, H. 1965a. Some preliminary observations on the distribution of the various morphs within natural populations of the polymorphic landsnail Cepaea nemoralis (L.). Arch. Néerl. Zool. 16 280-292.

Wolda, H. 1965b. The effect of drought on egg production in Cepaea nemoralis (L.). Arch. Néerl. Zool. 16 387-399.

Wolda, H. 1967. The effect of temperature on reproduction in some morphs of the landsnail Cepaea nemoralis (L.). Evolution 21 117-129.

Wolda, H. 1969. Genetics of polymorphism in the land snail Cepaea nemoralis. Genetica 40 475-502.

Wolda, H. & Kreulen, D.A. 1973. Ecology of some experimental populations of the landsnail Cepaea nemoralis (L.). II. Production and survival of eggs and juveniles. Neth. J. Zool. 23 168-188.

Woodruff, D.S. 1978. Evolution and adaptive radiation of Cerion: a remarkably diverse group of West Indian land snails. Malacologia 17 223-239.

Woolf, C.M. 1968. Principles of biometry. xiii+359 pp. Princeton, Toronto, London, Melbourne, D. Van Nostrand Company, Inc.

Wright, S. 1931. Evolution in mendelian populations. Genetics 16 97-159.

Wright, S. 1938. Size of population and breeding structure in relation to evolution. Science 87 430-431.

Wright, S. 1940. Breeding structure of populations in relation to speciation. Am. Nat. 74 232-248.

Wright, S. 1943. Isolation by distance. Genetics 28 114-138.

Wright, S. 1946. Isolation by distance under diverse systems of mating. Genetics 31 39-59.

Wright, S. 1951. The genetical structure of populations. Ann. Eugen. 15 323-354.

Wright, S. 1969. Evolution and genetics of populations. vol. II. The theory of gene frequencies. vii+511 pp. Chicago & London, Chicago University Press.

Yom-Tov, Y. 1970. The effect of predation on the population densities of some desert snails. Ecology 51 907-911.

Yom-Tov, Y. 1971a. Body temperature and light reflectance in two desert snails. Proc. Malac. Soc. Lond. 39 319-326.

Yom-Tov, Y. 1971b. The biology of two desert snails. Trochoidea (Xerocrassa) seetzeni and Sphincterochila boissieri. Isr. J. Zool. 20 231-248.

Yom-Tov, Y. 1972. Field experiments on the effect of population density and slope direction on the reproduction of the desert snail Trochoidea (Xerocrassa) seetzeni. J. anim. Ecol. 41 17-22.

Zilch, A. 1959-1960. Gastropoda. Teil 2. Euthyneura. xii+834 pp. Berlin, Gebrüder Borntraeger.

Zippin, C. 1956. An evaluation of the removal method of estimating animal populations. Biometrics 12 163-189.