The Population Dynamics of the Natterjack Toad (*Bufo calamita* Laur.) in the north Merseyside sand-dune system.

by

Clifford Adrian Davis M.Sc.

A thesis submitted in part fulfilment
of the degree of Doctor of Philosophy
of the
Council for National Academic Awards

Collaborating Establishment : Nature Conservancy Council.

Department of Biology,
Liverpool Polytechnic,
June 1985

The Population Dynamics of the Natterjack Toad (*Bufo calamita* Laur.) in the north Merseyside sand-dune system by C.A. Davis, M.Sc.

ABSTRACT

Population dynamics of the Natterjack were studied at one of its major British locations, a 40 ha sand-dune site containing 21 freshwater pools near Formby, Merseyside.

The animal was sampled throughout its life cycle. Female fecundity was determined and mortality estimated for juvenile stages. Adult populations were estimated using mark-recapture analysis and spawn counts. Histological analysis of phalangeal sections provided information on adult growth and mortality. Spawn strings were monitored to hatching. Larval and metamorphosing tadpole populations were sampled by quadrat. The relative importance of mortality factors was quantified for ova and larvae using key-factor analysis. Adults were also studied after the breeding season.

Sympatric populations of Common Toad (*B. bufo*) larvae are present at Formby. As other workers have claimed these compete with Natterjack larvae, larval thermal physiologies of both species were compared in relation to their likely developmental success under field conditions.

Results indicate that adult mortality rates are higher for males than females, possibly due to reproductive stress during the protracted breeding season. Males have higher growth rates and breed at an earlier age. Female Natterjacks have much higher fecundities than Common Toads.

Mortality of ova is caused by desiccation and fungal infection while larval mortality is attributable to desiccation and predation. Key-factor analysis indicates inconsistency of mortality factors between years. Although low recruitment occurred during the study, there was no evidence for population decline. Common Toad larvae have lower metabolic rates and greater acclimatory abilities than Natterjacks at similar temperatures suggesting that Common Toads are able to cope with a wider range of field temperatures.

A life history strategy for Natterjacks is proposed based on rapid colonisation of, and opportunistic recruitment in, ephemeral water bodies which provide suitable thermal environments and reduced competition and predation. Conservation measures for Merseyside populations are discussed.

ACKNOWLEDGEMENTS

Grateful thanks are due to my supervisor Dr. P.H. Smith for his help and advice during this study. Also I am indebted to Dr. P.E. Wheeler for contributing equipment, and supervision of the larval physiology section of this thesis. Dr. P.S. Gittings, and Dr. M. Begon contributed helpful advice and information during this work, and Dr. T.J. Pitcher kindly supplied the computer program used. Mark-recapture data were processed using computing facilities made available by Dr. M. Hounsome. Weather data were provided by Dr. R. Pegg, and Dr. D. Clarke gave permission to reproduce his data. I would also like to thank Dr. A. Cooke, Dr. A. Arak, Dr. T.J.C. Beebee, and Mr. B. Banks for their help and advice during this study, and to Mr. T. Sutton, and the North West England TAVR Association for permission to carry out field work at the study site. This work was done whilst in receipt of a Natural Environment Research Council research assistantship and I am indebted to Prof. W.G. Hale for the provision of laboratory facilities.

Finally, I wish to acknowledge the expertise, diligence, and above all patience of my typist, Mrs. S. Abraham.

CONTENTS

CHAPTER PAGE

CHAPTER PAGE

4 RESULTS

CHAPTER PAGE

LIST OF TABLES

TABLE PAGE

LIST OF FIGURES

LIST OF PLATES

CHAPTER 1

INTRODUCTION

1.1 The Status of the Natterjack

The Natterjack Toad (*Bufo calamita* Laur.) is the rarest of three anuran species native to Britain. Due to the large decline in numbers it has experienced since the 1940's (Beebee, 1973) it has recently received special legal protection. Originally this was conferred by the Conservation of Wild Creatures and Wild Plants Act, 1975, now superseded by the Wildlife and Countryside Act 1981. Under this act it is illegal for any life stage to be killed, injured, taken, sold, or kept in possession except under licence. However, this act can do little to protect the Natterjack's habitat through loss or destruction. Many of the largest remaining colonies have been included within Nature Conservancy Council (NCC) National Nature Reserves (NNR's). In these reserves the habitats are maintained and safeguarded against destruction, which together with appropriate management procedures allow populations to be conserved and enhanced. In addition, all other major colonies are protected by Site of Special Scientific Interest (SSSI) designation. Under the 1981 Act, this ensures the site usage is not changed without notification and consultation. The previous system has on occasion failed to meet this objective, and so the NCC's objective is that all these sites should becomes NNR's unless a comparable level of safeguard is, or can be, assured by other means (NCC, 1983).

The numbers of adult Natterjacks in Britain are not accurately known. Beebee (1976) estimated the population as less than 30,000.

Cooke (1980) gives a figure of 20,000. Cooke (1981) attempted to classify the British colonies into size classes. These figures are summarised in Table 1.

1.2 Distribution of the Natterjack

1.2.1 Distribution in Europe

The distribution of the Natterjack is well documented, the earliest recorded limits to its range described by Boulenger (1898). Frazer (1983) points out it is a more westerly counterpart to *B. viridis* which occupies a similar ecological niche. Found only in Europe, it is a western species becoming less widespread and more localised to the north and east (Fig.1). The species reaches its northernmost limit in southern Scotland, west Sweden, and parts of Russia. It is widely distributed in Spain and Portugal, these countries forming the southernmost limits to its range. Beebee (1983a) states that Spanish specimens have been found at altitudes of 1700 m in the Cantabrian mountains, and has apparently been found at an altitude of 2600 m in the Pyrenees. It is found in France, the Benelux countries, Switzerland, and West Germany. Beebee (1979a) lists 10 colonies occurring in western Soviet Russia.

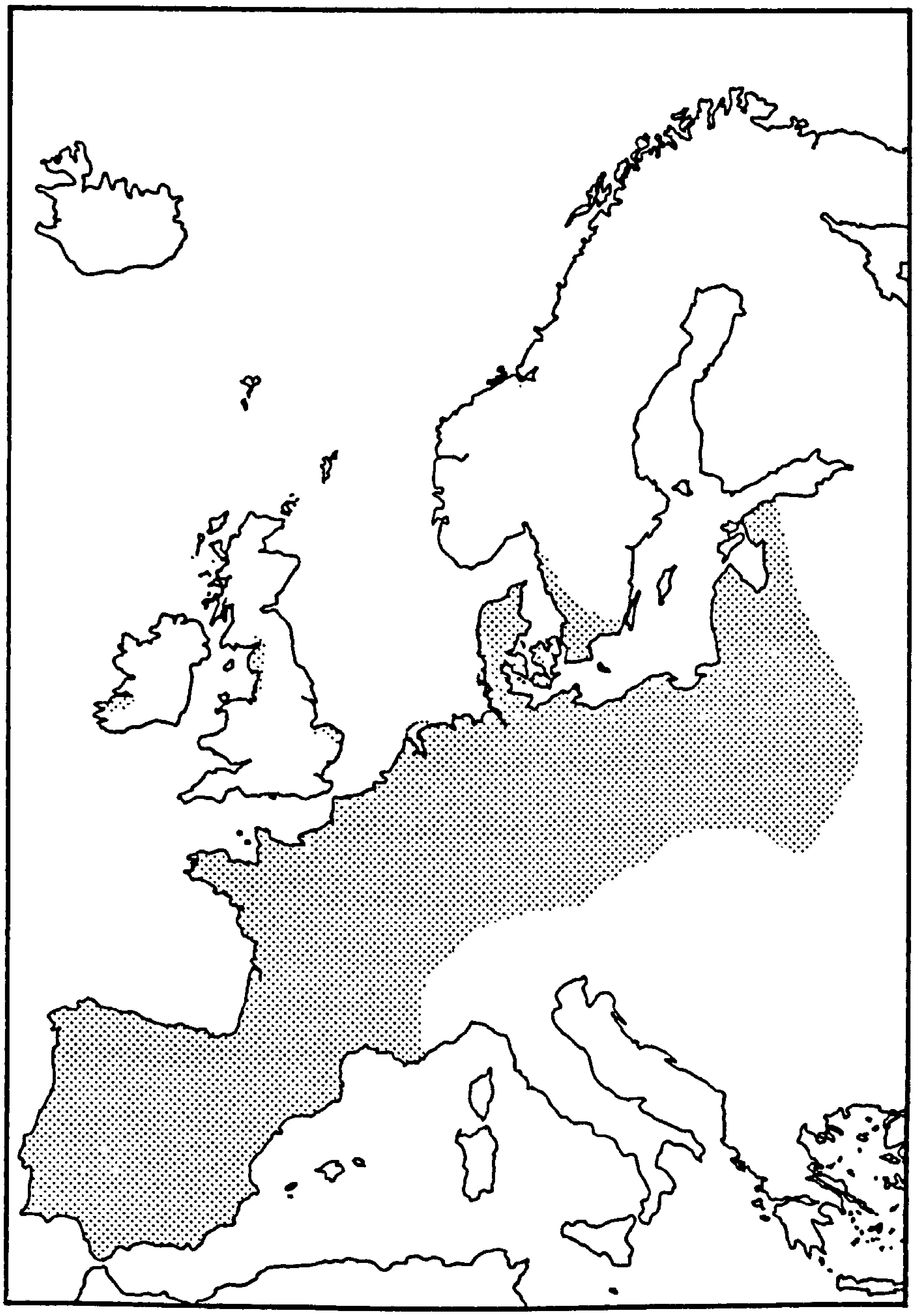
1.2.2 Distribution in the British Isles

Beebee (1978) suggests that the Natterjack entered Britain about 7000-5000 years ago during a climatic optimum, but the species was restricted to the southern coast due to forest cover. Deforestation by

Table 1. Estimated size of Natterjack populations in Britain (Cooke, 1981)

County/region	Site	Estimated size of adult population
Lincs	Saltfleetby	10
Norfolk	Holkham	100
"	Winterton	100's
"	Syderstone	10's (-100)
Hants	Woolmer	10's
Merseyside	Redrocks	10's (-100)
"	Hightown	10's
"	Cabin Hill/Altcar	1000's
"	Formby	100's
"	Ainsdale	1000's
"	Birkdale	100's
Lancs	Cockerham	10's (-100)
Cumbria	North Walney	100's
"	Sandscale	100's
"	Roanhead	10's
"	Dunnerholme	10's
"	Sandwide	10's/100's
"	Lady Hall	10's
"	Millom	1000
"	Haverigg	100's
"	Kirksanton	10's
"	Annaside	10's
"	Eskmeals	1000's
"	Ravenglass	1000's
"	Windscale	100's
"	Braystones	10's
"	Workington	10's
"	Allonby	10's
"	Mawbray Gravel Works	100's
"	Wolsty	10's
"	Silloth	100's
Dumfries & Galloway	North Solway Coast	1000's

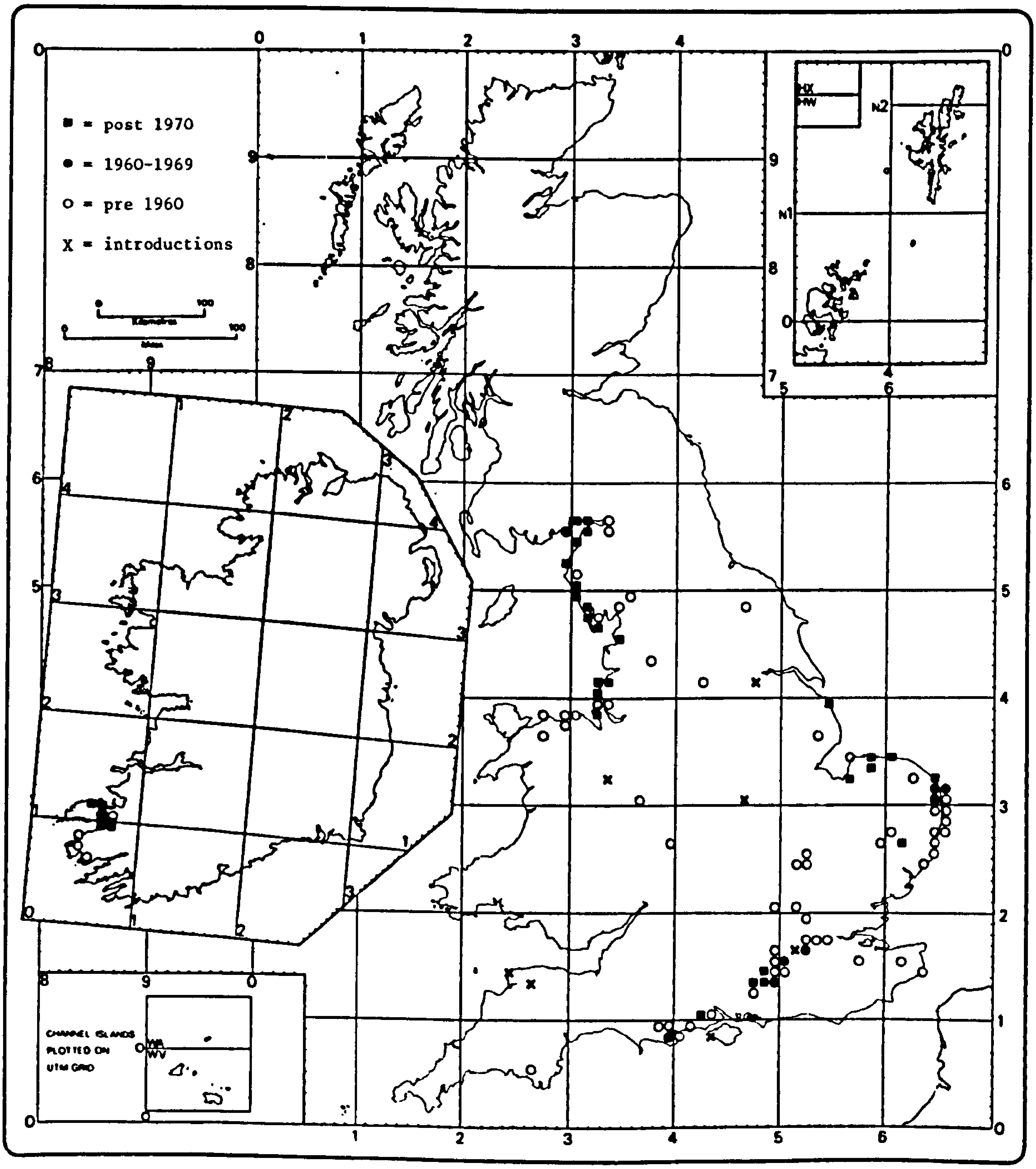
Figure 1. European distribution of the Natterjack Toad (*Bufo calamita*)



man, reaching a peak about 3000 B.P., then allowed the species to spread northwestwards forming a "corridor" through the country. Spellerberg (1975) who earlier described colonization of Britain takes the view that herptiles spread around the coast. The alternative theory is proposed by Yalden (1980). Examination of pollen and climatological histories for Britain show that the distribution of the Natterjack is more likely to represent a post-glacial spread occurring around 9500 B.P. During this period the low sea-level allowed the animals' access into Britain from Europe via a land bridge. A similar connection stretching from north-east Donegal to the island of Islay and Jura in south-west Scotland allowed the animals' access to Ireland (George, 1962). During this period, a rapid improvement in climate, coupled with a lack of forest cover after the last retreat of the ice, provided open conditions suitable for northwards colonization. Subsequent development of forest cover, together with climatic deterioration restricted the animal to refugia of open habitats such as dune systems, and heathlands produced by forest clearance. The development of open habitats during the Neolithic probably permitted an extension of range, particularly in southern England.

The past distribution of the Natterjack in Britain is shown in Fig. 2. Before 1960 the Natterjack occurred on the coastal dunes of north Wales, Merseyside, Cumbria, East Anglia and Lincolnshire, and on the coastal merse of the Scottish Solway (NCC, 1983). However, it has disappeared from the Suffolk, Hampshire and north Wales coasts. Inland heath colonies were centred around London and East Anglia, of which all but 3 are extinct. Cooke & Banks (1983) list 38 colonies currently in

Figure 2. British distribution of the Natterjack.


■ = post 1970
● = 1960-1969
○ = pre 1960
X = introductions
0 100
Kilometres
0 100
Miles
CHANNEL ISLANDS
PLOTTED ON
UTM GRID
WA
WV
HX
HW
N1
N2

Britain. In Ireland there are only 2 colonies still in existence in County Kerry. Gresson & O'Dubhda (1974) state that Natterjacks appear always to have been restricted to this area of Ireland.

In Britain the declines of Natterjacks have been greater on heaths than in coastal areas (Beebee, 1977). In 1976, Beebee reported the elimination of Natterjacks on the north Wales coast through holiday developments. Heathland has been lost through housing development and agricultural reclamation (Frazer, 1983). Afforestation and self-seeding of pine into unmanaged heathlands is probably an important cause of habitat loss, indeed the early stages of afforestation may favour Common Toads (*B. bufo*) producing adverse competitive interactions (Beebee, 1977). Mathias (1971) had previously shown that cooler, shady conditions favour the growth and development of Common Toads over Natterjacks. Beebee *et al* (1982) report the loss of 2 heathland ponds due to acidification for unknown reasons. Collection by humans may have been detrimental to the Natterjack at sites such as Frensham, Surrey and extensive gassing of rabbit burrows may also have had an effect (Prestt *et al*, 1974).

1.2.3 Distribution on Merseyside

The north Merseyside population is considered to be one of the largest in Britain (Table 1), although even here the Natterjack may have undergone a decline. Reliable population estimates are not available, and so its past and present status is difficult to assess. Hardy (1939) describes it as abundant near Ainsdale but does not give any numbers, while Simms (1966) stating that there were three main breeding concentrations between 1961 and 1964 gives neither numbers nor locations. Beebee (1976) claims the population on Merseyside in the 1930's was "hundreds of thousands". Prestt *et al* (1974) give an estimate of 10,000 adults in 1970, while Corbett & Beebee (1975) suggest less than 5,000. It is not clear how any of these estimates were obtained. The apparent decline of Natterjack populations in the 1970's was attributed to local drainage lowering surface water tables and thereby causing the loss of Natterjack breeding pools (Corbett & Beebee, 1975; Beebee, 1977). However Smith (1978a) suggested that the trend towards drier slacks was mainly due to infilling of old slacks with blown sand and organic matter, coupled with a low rate of production of new slacks. This trend was exacerbated in the 1970's by a lowering of the sand dune water-table due to a series of years with lower "effective" rainfall (Campbell, 1978) i.e. precipitation minus evapotranspiration. A study of water relations on the north Merseyside sand dune system by Clarke (1980) confirms this hypothesis.

The earliest reference to Natterjacks on Merseyside appears to be that of Byerley (1856). He describes it as more common than the "ordinary toad" at Southport, and common at Bootle. Greening (1888) studied the animals at Wallasey in Wirral, "where this toad abounds". The national status of the animal is given as "local rather than rare" and it is described as being abundant at Formby.

In an important paper, Standen (1914) describes visits to a colony at West Kirby, Wirral where he found all life stages of the species present at the same time. As well as giving a description of the animal and its biology, he makes this significant statement:

"The Natterjack, in disappearing from many of its ancient habitats, is but sharing the fate of many other interesting members of our local fauna in being pushed out by the inexorable advance of bricks and mortar, and by agricultural improvements, etc. No true lover of Nature can repress a feeling of regret that this is so, but the fact remains, and one can only hope it may still hold its own in some of the more remote corners of our coast".

He concludes by arguing that it may be justified to remove a number of Natterjacks from the vicinity of growing seaside towns to more suitable areas where they would be comparatively free from molestation.

During the early 1900's the Natterjack's decline on Wirral through loss of habitat due to the building of golf links is described by Coward (1910,1917). During the course of construction, Natterjack breeding pools were drained for land reclamation. Perry (1934) blames the gradual decrease of the West Kirby colony upon picnickers and collectors.

Many early descriptions of the Natterjack on Merseyside can be found (Hardy, 1939; Perry, 1945; Ellison, 1959; Simms, 1966) but in most cases only single colonies are described and no attempts are made to assess the abundance of the populations at these sites.

Cook (1976) and Smith & Payne (1980) describe the distribution of sites in north Merseyside and the numbers of spawn strings found. Cook (1976) lists 52 wet sites between Southport and Crosby, and gives descriptions of their physical characteristics. Of these, at least 39 were used for spawning in 1976, with over 450 spawn strings being laid. Smith & Payne (1980) list 132 wetland sites in the same area, and give a figure of 2001 spawn strings deposited. Of these, they noted that the highest proportion of strings were laid in the Ainsdale NNR (47%) and the next most important site was Cabin Hill/ Altcar Rifle Range (18%).

1.3 The Biology of the Natterjack

Reviews of the basic biology and ecology of the Natterjack have been published by Smith (1964), Beebee (1979a,1983a) and Frazer (1983), but a detailed population dynamics study seems not have been attempted.

Beebee (1979) showed that they occupy a variety of habitat types although Natterjacks show a marked preference for dry, sandy soils in which they can easily burrow (Smith, 1964). The earliest reference to this habitat feature appears to be that of Jenyns (1835). Preferred breeding sites are characterised by being shallow, exposed, often ephemeral in nature, with little or no aquatic vegetation. This was recognised as early as the 1800's (Newman, 1869; Warner, 1884; Greening, 1888). In Britain the pH of breeding pools range from 5.5 to 8.0, although in East Anglia and in heathland pools values as low as 4.0 have been recorded (Beebee, 1983a). Ionic strengths and ionic contents are not clearly correlated with use by Natterjacks (Mathias, 1971).

Mathias (1971) using mark-recapture showed extensive individual variation in home range. He showed that after the breeding season each toad may occupy a home range of 200-600 m for some time, and then move to a new site up to 1400 m distant. No territoriality was detected and translocation experiments revealed no homing instinct. Flindt & Hemmer (1968) used mark-recapture to demonstrate that only 17.5% of a population was still present in the study area one year later. Smith & Bownes (1978) marked 536 toads. The following breeding season they recaptured 86, of which 44% were at the original site and 34% in the same general area, while 22% had moved to more distant sites up to 2.2 km distant.

Behavioural studies by Arak (1983) of breeding Natterjacks at Ainsdale, Merseyside have shown that male mating success is related to body size and call frequency. Other aspects of breeding behaviour e.g. the tendency towards satellitism by smaller males was investigated. Similar laboratory studies on Common Toads have been carried out by Davies & Halliday (1977,1978,1979). In a previous study at Ainsdale, Mathias (1971) showed that differences in breeding behaviour between Natterjacks and Common Toads reduced the possibility of interspecific mating. He failed to observe any relationship between Natterjack activity and weather conditions. However a relationship has been found by Blankenhorn (1972). Thus, as is described by Smith & Flynn (1977), there is more breeding activity on mild, damp nights than on cool, windy ones. During the breeding season Natterjack mating behaviour is primarily nocturnal in contrast with the more diurnal *B. viridis* (Flindt & Hemmer, 1967) and Common Toad (Mathias, 1971).

Smith (1974) studied hybridization between Common Toad and

Natterjacks. Under controlled conditions he demonstrated 5% viability although the progeny showed gross deformities. In the field he found 9% viability although again the offspring were deformed. None survived to adulthood.

An early study of Natterjack physiology was carried out by Standen (1914). He showed that immersion in 50% sea water was "speedily fatal" to toadlets, but spawn and tadpoles seemed not to be affected by occasional influxes of salt water into breeding pools. Mathias (1971) studied temperature and salinity tolerances in larval and adult Natterjacks. He found that Natterjacks were able to develop under slightly more saline conditions than Common Toads. The maximum tolerance of the latter was 2.9‰ - 4.3‰ while for Natterjacks it was 4.3‰ - 5.6‰. He also showed that larval Natterjacks had a critical thermal maximum of 29-33°C whereas Common Toads survived only 20-25°C. These experiments were concerned mainly with critical maxima, death or failure to develop being taken as criteria for observations. The manner in which these factors acted upon the animal were not investigated. This contrasts with many American studies on other anuran species (e.g. Zweiffel, 1968; Brattstrom, 1970; Hutchinson & Hill, 1978; Feder, 1982) in which oxygen consumption and the acclimation abilities were measured. These are possibly more relevant to an animal which may undergo large shifts in temperature in the wild. The effect of pH on larvae (Beebee & Griffin, 1977), iron precipitates, and organic pollution from decaying matter (Mathias, 1971) have been studied. Roberts (1981) showed the Natterjack could breed successfully in pools polluted with organic wastes from a denatured tobacco waste tip in the Merseyside dunes.

Beebee (1979a) has collected many references on the breeding biology of Natterjacks, detailing differences in timing and length of the breeding seasons through its geographical range. Estimates of egg production have been made (Mertens, 1964; Kowalewski, 1967; Curry-Lindahl, 1975; Kadel, 1975) and Hemmer & Kadel (1971) demonstrated that the number of eggs laid is proportional to female size. Population age structure and survival has not been investigated in Natterjacks. This contrasts with studies of a population of Common Toads in mid-Wales (Gittings *et al*, 1980; Gittings, 1983) which have quantified recruitment.

Mark-recapture studies have been used to estimate the sizes of Natterjack breeding populations (Flindt & Hemmer, 1968; Blankenhorn *et al*, 1969; Heusser & Meisterhans, 1969; Mathias, 1971; Smith & Flynn, 1977) but in some of these (Mathias, 1971; Smith & Flynn, 1977) problems associated with sampling are thought to have given underestimates of population size.

Only one detailed study of larval survival has been made (Kadel, 1975). He attempted to estimate survival rates by following the fates of 32 spawn strings (116,000 ova). He demonstrated 90% survival to hatching and 0.3% survival to metamorphosis. Larval mortality factors reported include desiccation of breeding pools and pollution of pools by cattle (Bridson, 1978), fungal infection (Smith, 1974) and predation by other amphibian species (Heusser, 1970,1971). Kadel (1975) attempted to quantify these, but he did not examine differences in larval survival between years or the changes in relative importance of different mortality factors. Laboratory studies of predation by invertebrates (Mathias, 1971) and vertebrates (Kadel, 1975) upon Natterjack tadpoles are difficult to relate to field conditions. Metamorphosis has been quantified for Natterjacks (Beebee & Beebee, 1978) but this was under laboratory conditions with minimal predation of larvae.

1.4 Aims of this project

As already noted, the Natterjack toad is a nationally endangered species, specially protected by the Wildlife and Countryside Act, 1981. While much information is available concerning the environmental requirements and general ecology of the species, many aspects are poorly understood. In particular there is a lack of detailed population dynamics studies. The need for such studies was recently confirmed by the NCC's Herpetological Review (NCC, 1983). It stresses the need for long term investigation of population dynamics and trends, particularly for important sites. "Natural" population regulating factors including catastrophic factors should be considered, and the way in which these can be modified by management.

The north Merseyside coast has the largest population of Natterjacks in Britain (Cooke, 1982) but despite much general survey work since 1972, conservation management of the species is not based upon a sound understanding of population dynamics.

Cabin Hill/Altcar Rifle Range forms a virtually isolated group of approximately 21 breeding sites which are thought to hold the largest breeding population of Natterjacks in Britain (Cooke, 1982). Many data have been collected almost annually since 1972 on distribution and breeding success. These data form an appropriate baseline on which to develop a more intensive study. A proposed golf course development at Cabin Hill (see Chapter 2) means information is urgently required as a basis for managing the Natterjack population and its habitats. A detailed population dynamics study of the Cabin Hill Natterjacks was therefore considered appropriate. It was hoped that knowledge gained would assist conservation of the species both in Merseyside and in other parts of Britain.

CHAPTER 2

SITE DESCRIPTION

2.1 Introduction

The study site chosen for this project is a section of the north Merseyside sand-dune system between Hightown and Formby (Grid Reference SD 285055), (Fig. 3). The area studied during the breeding season contains 21 freshwater wetlands of varying size within fixed grassy dunes, the largest being approximately 450 m x 50 m. This, together with three others, is a borrow pit formed in 1970/71 during the excavation of a sea defence bank, indeed most of the wet sites appear to be of artificial origin. A footpath which flooded regularly from 1981 onwards was also included in surveys. During the post-breeding period a 2.5 km length of the adjacent sand dunes and foreshore between Formby coastguard lookout and the River Alt estuary was studied. The northern edge of the site is bordered by mixed woodland while the eastern and western edges are bounded by cultivated farmland and Liverpool Bay respectively (Fig. 4).

The site contains two areas of land under different ownership. The southern area of approximately 12 ha forms part of the Territorial Army Volunteer Reserve Training area at Altcar. The northern part, known locally as Cabin Hill, contains about 28 ha of land owned by the Trustees of the Formby Settlement. This forms part of an area subject to planning consent for the proposed Liverpool Bay Golf Course. Throughout this thesis the site will be referred to as Cabin Hill. The relative positions of the wetsites and the numbering system adopted for this study are shown in Plate 1.

Figure 3. Sketch map of Merseyside showing the location of the study site. Built up areas west of the Liverpool-Southport railway line are shown hatched. *Inset*: North-west England showing location of sketch map.

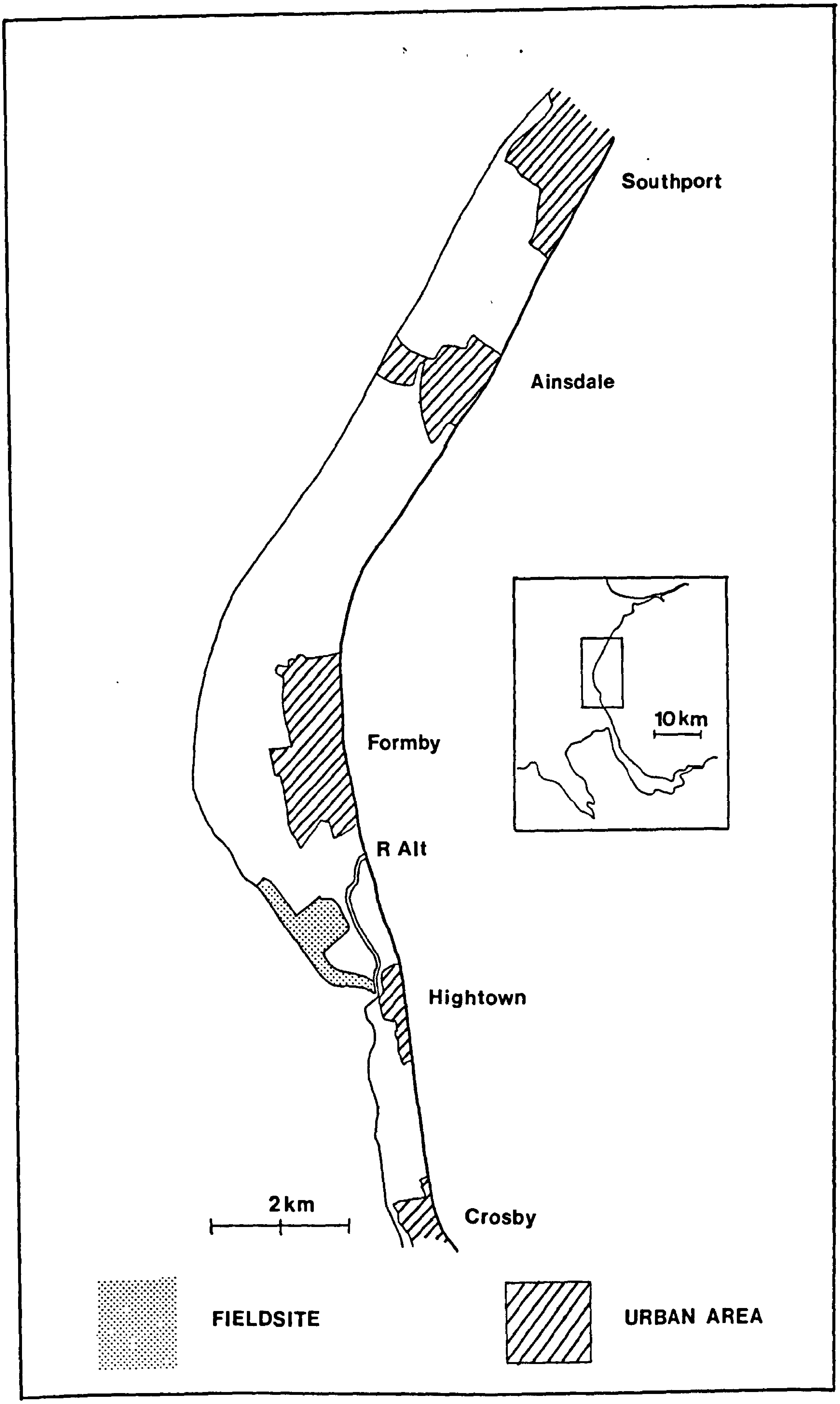

Southport
Ainsdale
Formby
R Alt
Hightown
Crosby
10 km
2 km
FIELDSITE
URBAN AREA

Figure 4. The Cabin Hill study site.

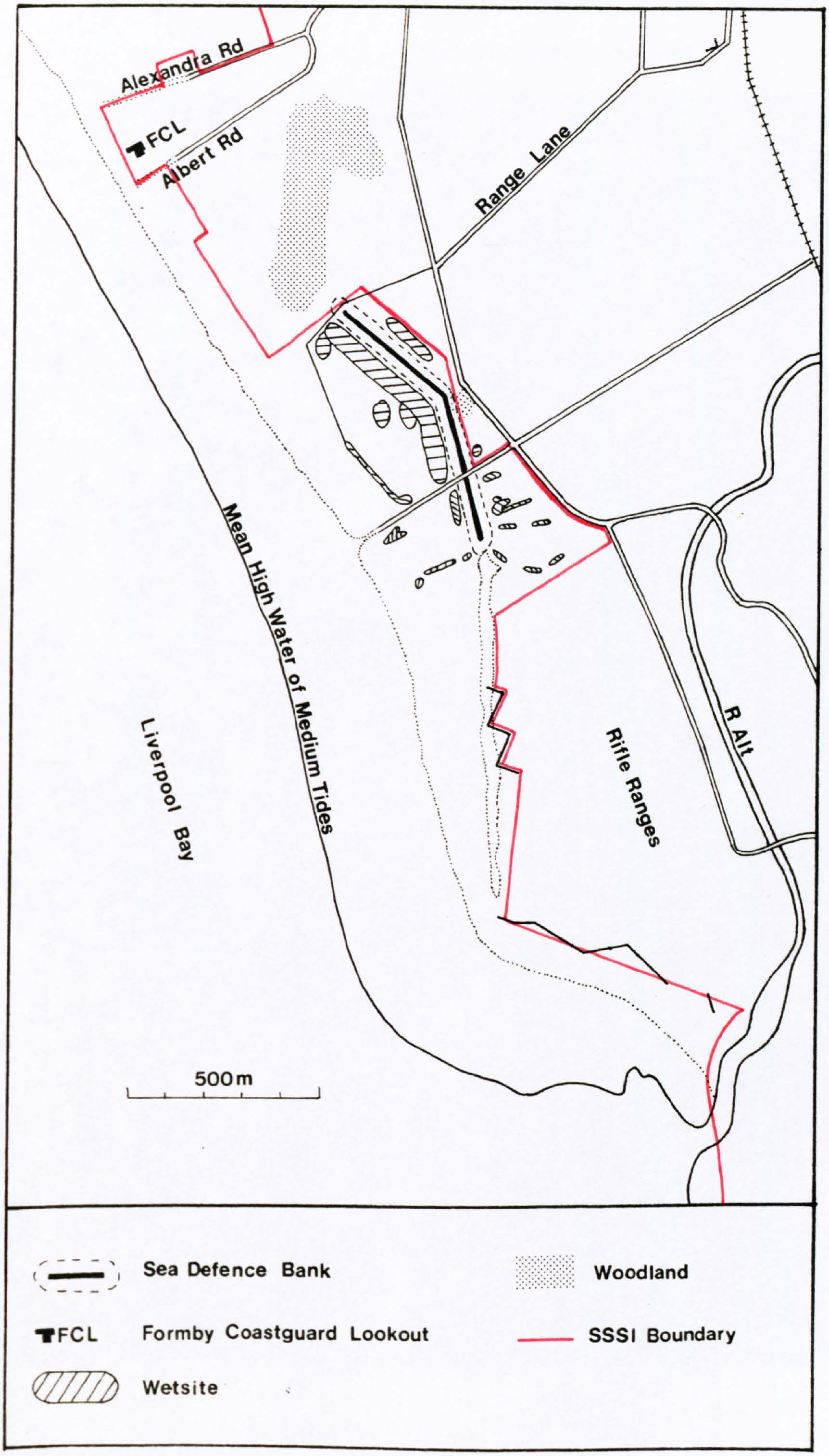

Alexandra Rd
FCL
Albert Rd
Range Lane
Mean High Water of Medium Tides
Liverpool Bay
Rifle Ranges
R Alt
500m
Sea Defence Bank
Woodland
FCL Formby Coastguard Lookout
SSSI Boundary
Wetsite

Plate 1. Aerial photograph of Cabin Hill breeding pools. *Overlay* the numbering system used during the study.


20
3
50 m
19
1
2
4
21
5
15
6
7
8
9
18
10
P
16
14
11
17
12
13

2.2 Topography

The Merseyside sand-dune system is the fourth largest in Britain, much of which is given Grade 1 (nationally important) status in the Nature Conservation Review (Ratcliffe, 1977). Smith (1980a) describes the areas as "one of the finest examples of a calcareous west-coast dune system, being extremely rich floristically and including many rare species". The Cabin Hill area shows features of classic dune succession except for localised damage at beach access points. Detailed ecological surveys of the area have been carried out by Smith (1978a,1980a).

The embryo dunes form a broad belt up to 45 m wide in places. These rise to a maximum height of approximately 10 m OD and have a mean slope angle of 9°, range 5-14°. There is a sharp boundary between the embryo dunes and the intertidal zone. A slope or "bank" of 57° separates the intertidal zone (4.5 m OD) from the embryo dunes (7.0 m OD) over a distance of about 1 m.

The embryo dunes are backed by mobile dunes which rise to an average height of 16.5 m OD although there are two dunes 200 m south of Albert Road which reach a height of 23 m OD. The latter are within an area of severe damage caused by sandwinning in the 1940's. The mobile dunes form a belt approximately 30 m wide in which slope angles are steeper than within the embryo dunes, mean 24°, range 17-45°. Smith (1980a) notes that in several places a series of parallel ridges, running approximately north-south, can be detected but local sand movement has often erased this original pattern of dune formation.

The mobile/fixed dune transition is up to 100 m wide in places, being absent only where active sand deflation from the mobile dunes is taking place (Smith, 1980a). Following Smith (1980a) this is described as a distinct community. The maximum height of the dunes along their seaward edge is 9.5 m OD, with a mean slope of 13°, range 4-25°.

The fixed dunes give way to almost level ground within the training area and behind the sea defence bank. Along their seaward edge the fixed dunes rise to a height of 8.0 m OD while the training area lies at approximately 6.5 m OD. Small blow-outs occur in the fixed dunes, most being near to beach access points and possibly induced by trampling (Smith, 1980a). Dune slacks are also present in an area north of Albert Road and while some of these have been formed by sand extraction others appear to be natural features.

The sea defence bank is 650 m long and 35 m wide at its base. From its southernmost point it runs in a NNE direction for 320 m after which it runs NE. The sides slope at 15° and it has a maximum height of 8.7 m. Associated with the bank are borrow pits which flood and form part of the Natterjack breeding area (pools 1,3,4,15). With very few exceptions, all the areas which flood at Cabin Hill are man-made in origin, although pool 18 has been modified by vehicle activity. The majority of sites appear to be areas created by vehicle activity, some of which have been deepened by hand-digs in subsequent years. Topographical information for all wet-sites studied is given in Table 2. Depth contour maps are given in Appendix 1.

2.3 Soils

The soils of the Merseyside sand dune system have been classified as belonging to the Ainsdale association (Hall & Folland, 1970).

Table 2. Summary of breeding site information

Pool No.	Slack type	Origin	Approx area (m^2)	Comments
1	Semi-aquatic	Borrow pit	16250	2 scrapes added 1976
2	"	Semi-natural	5000	*Salix* dominance
3	"	Borrow pit	4125	
4	"	"	1250	
5	Wet	Vehicle activity	550	
6	"	"	300	
7	Semi-aquatic	"	300	
8			700	Deepened by M.O.D., 1977
9	Wet	"	350	
10	Semi-aquatic	"	600	Deepened by M.O.D., 1977,
11	"	"	325	"
12	"	"	150	Declared out of bounds, M.O.D., 1982
13	"	"	175	
14	"	"	275	Deepened by N.W.W.A. 1978
15	"	Borrow pit	2000	
16	"	Vehicle activity	759	Deepened by N.W.W.A. 1978
P	Wet	Footpath	300	
17	"	Mine craters	16*	
18	"	Semi-natural	2000	
19	"	Natural	1800	"Mature" vegetation dominated by *Salix repens*
20	"	Natural	1500	
21	"	Vehicle track	900	

*750 m^2 in 1981

These are formed on incoherent calcareous sand thus producing an alkaline soil. Clarke (1980) found 2-4% $CaCO_3$ by weight in dune sand. The pH values quoted below are taken from Smith (1980a). The embryo dunes comprise raw, mobile sand with little or no organic matter, and a high pH (8.55). The mobile dunes are also characterised by unconsolidated raw sand with a high pH (8.1-8.2). As in the embryo dunes there is much bare sand and a low frequency of plant roots. In the mobile/fixed dune transition the soil profiles are immature, mainly raw sand. Again, high pH's are recorded (8.2-8.5) however there are areas with a high frequency of *Festuca rubra*, in which accumulation of organic matter can be detected, with a lower pH (7.9). On the fixed dunes organically rich, but weakly structured pararendzina soils form which have a pH of 7.8-8.2 in the A horizon. In the seasonally flooded wet-sites ground-water and peaty gley soils form. These consist of surface accumulations of organic matter, sometimes peaty in nature, over grey, structureless sand with prominent rusty mottles.

Clarke (1980) found that the particle size structure of the dune soils is highly sorted with a mean size of 0.19 mm, and a porosity of approximately 40%.

2.4 Climate

The north Merseyside climate is maritime in nature but the coastline has a fairly low average rainfall of 81-84 cm yr^{-1} (Hall & Folland, 1967). Savidge, Heywood & Gordon (1963) give figures for mean annual rainfall in South Lancashire from 1916 to 1950. Their figures show mean rainfall of 89 cm on the coast. The average seasonal sequence is a cool, wet winter, a relatively dry spring and summer becoming progressively warmer, succeeded by a warm and often wet late summer and autumn. However, considerable variation occurs between years. The following figures taken from Clarke (1980) show this variation clearly.

Table 3. Monthly rainfall totals at Southport (expressed in mm) (Clarke, 1980)

Year	Jan.	Apr.	Jul.	Oct.
1957	64	10	118	114
1960	166	42	112	76
1963	12	54	32	98
1966	34	78	53	124
1969	74	111	70	154
1972	70	62	71	38
1975	134	48	62	34
1977	57	47	20	92

Weather data for this study were obtained from the Ainsdale Sand Dunes National Nature Reserve, courtesy of Dr. R. Pegg, University of Liverpool. These are given in Figs. 5 and 6. During this study considerable variation in weather patterns was experienced.

In 1981 a mild winter was followed by a very wet spring and an absence of drought. During November 1980-January 1981 a total rainfall of 262 mm was recorded, while from February 1981-April 1981 the total precipitation was 258.9 mm. The wettest month during this period was March, when 171.7 mm rainfall was experienced.

The weather in 1982 returned to more "normal" conditions,

Figure 5. Total monthly rainfall for the study period (data from Ainsdale NNR recording station). Numerals above histograms indicate the number of days on which rain fell during each month.

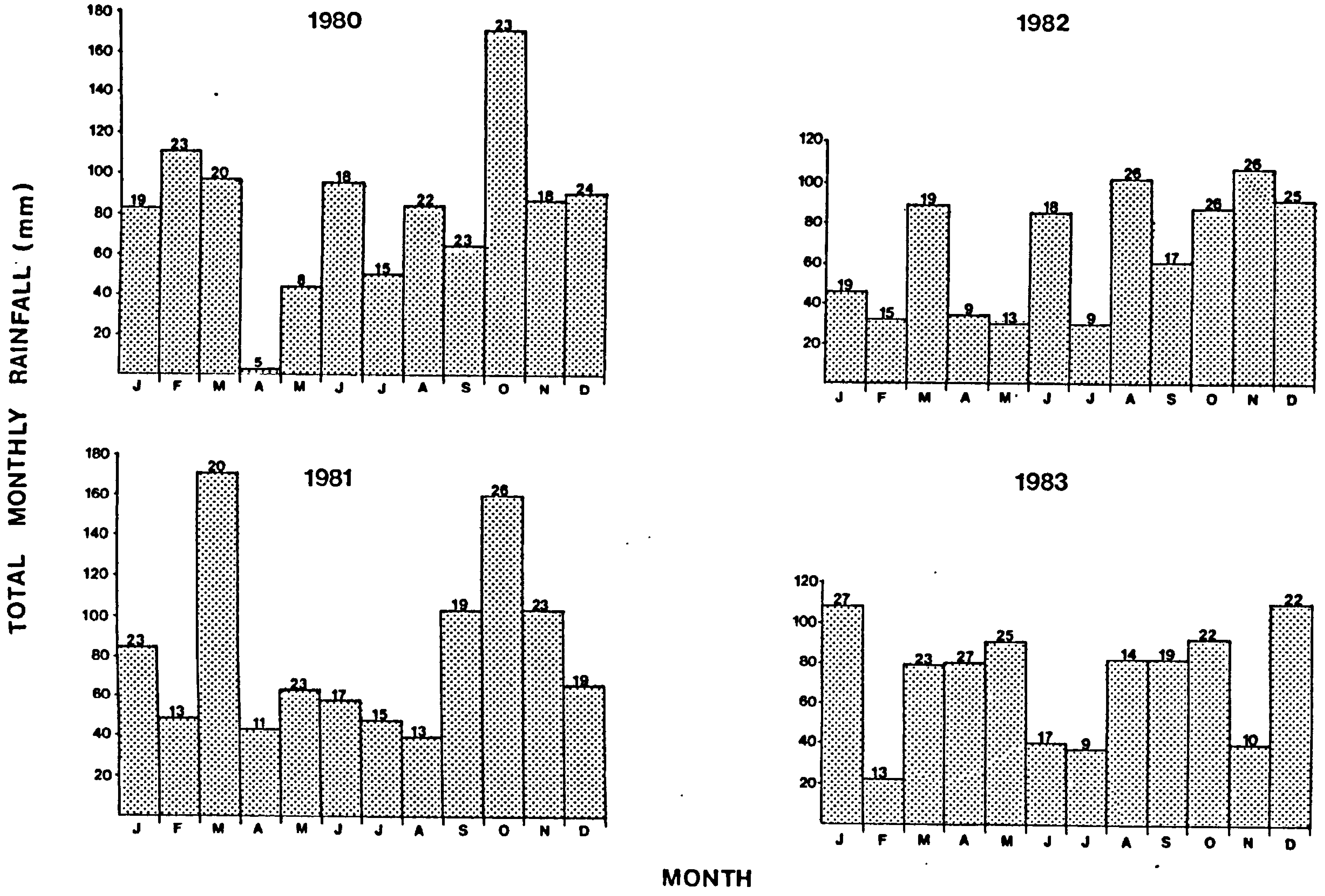
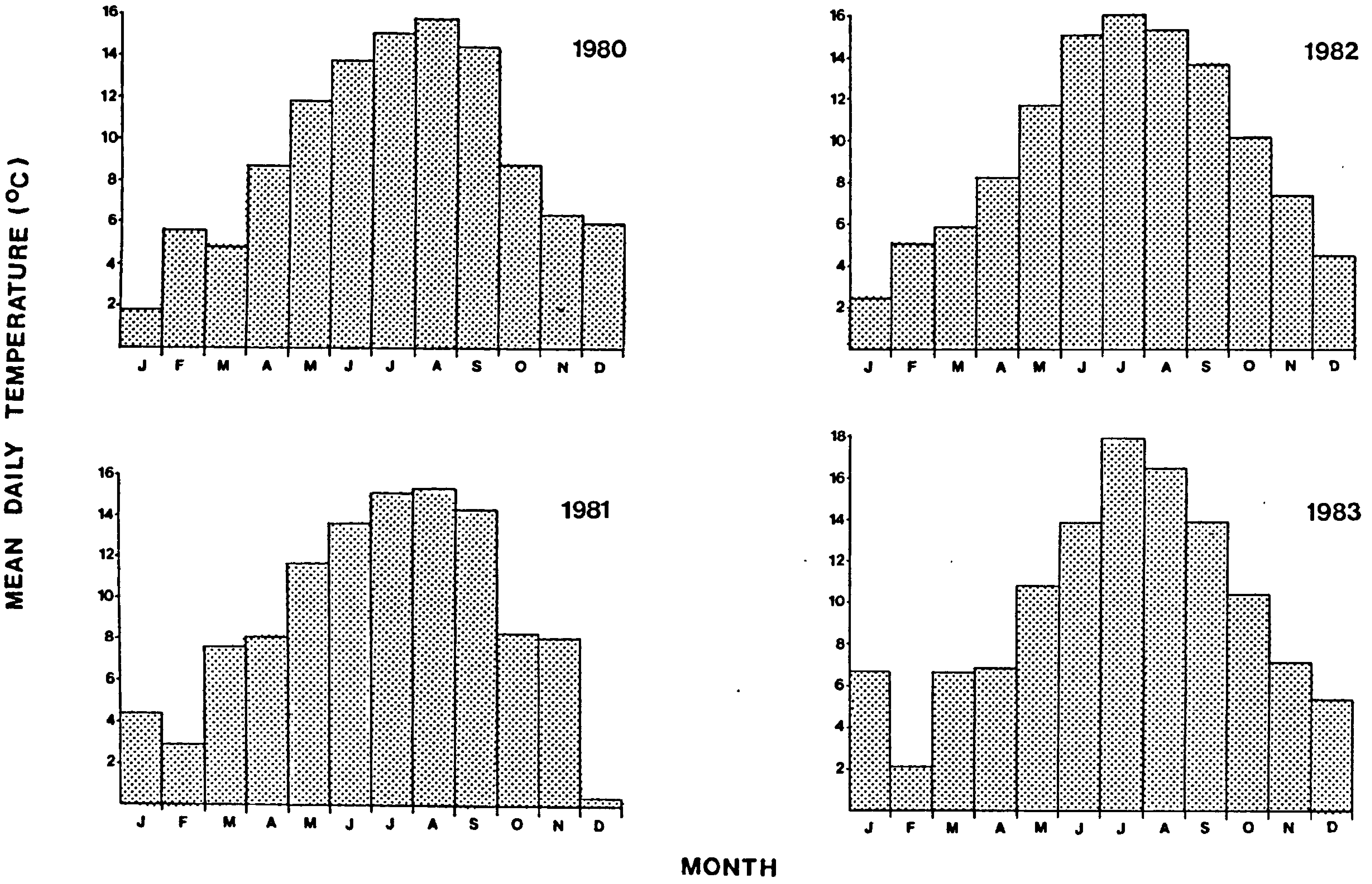

TOTAL MONTHLY RAINFALL (mm)
MONTH
1980
19 23 20 5 8 18 15 22 23 23 18 24
1981
23 13 20 11 23 17 15 13 19 26 23 19
1982
19 15 19 9 13 18 9 26 17 26 26 25
1983
27 13 23 27 25 17 9 14 19 22 10 22
J F M A M J J A S O N D
180 160 140 120 100 80 60 40 20

Figure 6. Mean daily temperatures for the study period (data from Ainsdale NNR recording station).


1980
1981
1982
1983
16
14
12
10
8
6
4
2
18
J
F
M
A
M
J
J
A
S
O
N
D
MEAN DAILY TEMPERATURE (°C)
MONTH

characterised by a spring drought. Little rain fell throughout April and early May (total 65.4 mm), and during late May and June the weather was hot and sunny (average daily temp. 16.6°C).

A mild, dry winter in 1982/83 was followed by a spring drought during March. However between late March and May there was heavy rain (75 mm). The following summer was hot and dry, punctuated by occasional thunder storms.

2.5 Hydrology

Clarke (1980) studied groundwater balance at Ainsdale Sand Dunes NNR. Prolonged observations have shown that water-table trends are similar throughout the dune system, so Clarke's study is also relevant to Cabin Hill. He found seasonal variations in the level of the water-table. From 1972 to 1977 inclusive there was a mean amplitude of approximately 60 cm. The water-table was at its highest in late winter and early spring, and at its lowest in early autumn. He also found that the size of dune ridges has an important effect on the water levels of adjacent slacks. Large ridges catch more water and thus raise small slacks considerably.

Comparison of annual trends in groundwater levels with weather data from Southport showed that rainfall is the "dominant factor in changes of groundwater levels at Ainsdale". Clarke demonstrated cyclical variations in the weather. Thus there were wet periods during the early 1960's and late 1960's, and relatively dry periods during the mid 1950's, mid 1960's and mid 1970's. However, seasonal changes in individual years were not well explained by rainfall alone. Total moisture storage and the rates of evapotranspiration from slack floors were also important in affecting groundwater balance and hence slack water levels. Local water abstraction had no observable effect on groundwater levels.

Variations in groundwater level can have considerable effects upon the associated slacks leading to premature desiccation or excessive flooding. Clarke (*op. cit.*) gives figures for changes in the annual water table, measured at the same sites, for the years 1972-1980 (Table 4).

Table 4. Annual water table changes at Ainsdale, 1972-1980 (from Clarke, 1980)

Year	Max. water table depth (relative to ground level (cm). Well 4)
1972	-14
1973	-31
1974	-18
1975	-6
1976	-21
1977	+20
1978	-11
1979	+10
1980	+20

Fluctuations in the water table at Cabin Hill occurred during the study period. The highest water table yet recorded in the dune system occurred in 1981. Many of the pools were deeper, larger in area, and persisted for a longer period than previously known. Thus pools 6,7, 8 and 9 formed one continuous water body, as did pools 16 and 17, the latter two connected by a flooded footpath (P). Site 17 was flooded to such an extent that it formed a sheet of water reaching to the grenade practice range. In previous years it had consisted of a series of small pools in old land-mine craters. Slacks 1,2 and 20 were also joined. The maximum recorded depth for pool 1 was 110 cm. The majority of pools persisted until mid/late June although others held water until late July. Some pools e.g. 1,7,8,14,16 did not dry out that year. A summary of maximum depths and persistance of all pools during the study period is given in Table 5. In 1982 pool levels were considerably lower than the previous year, the maximum depth for pool 1 was recorded as 80 cm. The pools also persisted for a shorter period, with many drying by mid April. Pools 16 and 17 were not connected, although the footpath between them did hold water for a short period. The mild, dry winter of 1982/83 resulted in a low water table at the beginning of the breeding season. The maximum recorded depth for pool 1 was 75 cm. During March the pool levels dropped but levels were restored during wet weather in late March and April. During the subsequent hot weather the pools dried fairly rapidly, many sites being dry by early/mid June.

2.6 Vegetation

2.6.1 Dune Vegetation

Smith (1980a) has described the main vegetation types in the dunes south of Formby Point, including part of the study area. The embryo dunes are dominated by *Agropyron junceiforme* with occasional clumps of *Elymus arenarius*. Strand line species such as *Atriplex hastata* and *Cakile maritima* can be found in some years. The mobile dunes are

Table 5. Maximum depths and persistence of breeding pools during the study period

Pool	Max. depth (cm)			Pools dried		
No.	1981	1982	1983	1981	1982	1983
1	110	96	90	*	*	*
2	62	-	-	Mid July	Mid May	Early June
3	56	40	34	"	Late May	*
4	52	36	27	"	Mid May	Late May
5	35	20	15	Mid June	Early May	Late June
6	20	8	10	Mid June	Late April	Late June
7	77	50	39	*	Early May	*
8				*	*	*
9	20	20	13	Mid June	Late April	Early June
10	68	50	44	Late June	Early July	*
11	59	44	35	*	Early June	*
12	33	-	-	Mid June	Late April	-
13	54	-	-	Late June	-	-
14	73	60	48	*	*	*
15	50	34	27	Late July	Early June	Mid July
16	97	80	74	*	*	*
17	38	23	25	Late June	Late April	Mid June
P	40	25	17	Early June	Mid April	Mid June
18	35	20	15	Late June	Late April	Mid June
19	35	-	-	Mid June	Early April	Early June
20	38	-	-	Mid July	Mid April	Late May
21	30	-	-	Late June	Mid April	Mid June

* Pool did not dry out completely.

\- Unrecorded

characterised by *Ammophila arenaria* with scattered clumps of *Elymus arenarius*, *Eryngium maritimum* and *Euphorbia paralias*. Further inland, the transitional zone between the mobile and fixed dunes is characterised by an increased species diversity dominated by *Festuca rubra* and *Ammophila arenaria*. In some sheltered areas *Hypochoeris radicata*, *Leontodon taraxacoides* and the shrubs *Populus gileadensis* and *Salix fragilis* can be found. Fixed dunes are characterised by an almost complete sward, and abundant *Festuca rubra* and *Poa pratensis*. *Salix repens* is also present in damper areas. Associated species include *Carex arenaria*, *Rhinanthus minor*, *Cerastium* spp., *Lotus corniculatus*, *Ononis repens* and *Rubus caesius*. Cattle are kept within the fenced area on the northern half of the field site for most of the year. Grazing pressure leads to, and maintains, a shorter fixed dune turf. However no particular effect on species composition has been noticed.

2.6.2 Slack vegetation

Ranwell (1972) has suggested a simple classification of dune slacks based on the average water table and associated vegetation type:

1. Semi-aquatic: Water table never more than 0.5 m below the soil surface; flooding from autumn to spring; amphibious hydrophytes represented in the flora.
2. Wet slack: Water table never more than 1 m below the soil surface; the bulk of the flora mesophytic; bryophytes particularly abundant; relatively few grass species.
3. Dry slack: Water table between 1 m and 2 m below surface at all seasons; grasses abundant.

Cabin Hill contains examples of semi-aquatic and wet sites, containing a high diversity of at least 87 vascular plants (see Appendix 2).

Although the slacks share many plants in common it is possible to make a generalised description of the different vegetation. Thus semi-aquatic slacks contain species such as *Eleocharis palustris*, *Equisetum palustre*, *Galium palustre*, *Juncus inflexus*, *J. gerardi*, *Hydrocotyle vulgaris*, *Mentha aquatica*, *Ranunculus flammula* and *Samolus valerandi*. Many of the wet slacks are dominated by *Salix repens*, *Agrostis stolonifera* and *Juncus articulatus*. On the margins *Epipactis palustris* and *Parnassia palustris* can be found.

Vegetation is also dependent upon slack depth and age. Thus there is a difference in the vegetation of newly formed "slacks" such as no. 21 and "mature slacks" such as nos. 2, 19 and 20. This is largely a matter of lower relative cover and degree of scrub invasion in the "younger slacks". Typical colonisers of bare sand in new slacks and excavated scrapes are *Agrostis stolonifera*, *Anagallis tenella*, *Carex serotina*, *Eleocharis quinqueflora*, *Juncus articulatus* and *Samolus valerandi*. However, many colonisers are apparently poor competitors and are replaced by other species as the slack matures (Smith, 1978a). The deeper areas in slacks often support emergent aquatic species such as *Iris pseudacorus* and submerged aquatic plants such as *Chara* spp.

2.7 Proposed Liverpool Bay Golf Course - Planning background

In 1975 the Mount Rule Land Company submitted a planning application for a golf course in the southern part of Formby Point. The affected area, in the ownership of the company, consisted of sand-dunes north of Range Lane, together with adjacent agricultural land. In 1976, a further application included a small area owned by the Trustees of Formby Settlement at Cabin Hill adjacent to Range Lane. This did not affect any Natterjack breeding sites, and outline planning permission was granted by Sefton Municipal Borough Council.

In 1979 an application for detailed planning permission was made which now included the whole of the Cabin Hill site, an option to lease that area having been agreed between the golf course company and the Trustees. However a revised SSSI schedule had been prepared by the Nature Conservancy Council, including Cabin Hill in the newly established Altcar Sand Dunes and Foreshore SSSI. The 1979 application did not include land previously granted outline planning permission in 1976. The NCC opposed this application and discussions were held between all the interested parties. In September 1979 planning permission was granted on the basis of a detailed agreement between the NCC and the company. This placed constraints on many aspects of construction and operation and required the golf course company to lease an area containing most of the Natterjack breeding sites to NCC for establishment of a National Nature Reserve. However, apparently due to financial difficulties, golf course construction did not begin.

By 1983 the option to lease Cabin Hill had expired and the NCC made it known that they proposed to negotiate directly with the Trustees a lease for the whole of their Cabin Hill holdings, including the frontal dunes. They would then sublet those areas not needed for the NNR to the Company. Meanwhile, research had indicated a larger area would be needed that than previously agreed with the Company.

Therefore the Company has modified its course layout to take account of these new requirements.

At the time of writing, NCC has indicated that it is generally satisfied with the new design, subject to a number of points of detail which must be clarified before a revised planning application can be submitted to the local authority.

In the summer of 1984, NCC signed a lease with the Trustees for the whole of the Cabin Hill dunes and began wardening and managing the site.

CHAPTER 3

METHODS

3.1 Adults (Breeding Season)

3.1.1 Introduction

Several methods are available for determining the size of Natterjack populations (Beebee, 1979a). Direct methods involve counts of adults gathering at breeding pools; counting the number of calling males; counting the number of spawn strings deposited. Indirect methods use mark-recapture surveys.

Smith & Flynn (1977) censused adult Natterjacks using newly excavated breeding sites at Ainsdale. In this case the sites were easy to search and all toads discovered were marked. However, up to 8 return visits to the same site over a period of 5 weeks revealed a majority of unmarked toads on each occasion. They concluded that only a small proportion of toads using those sites were discovered on each visits and that the maximum direct count for each site gave a gross underestimate of the likely population size. Smith & Payne (1980) concluded that the use of direct counts was likely to give underestimates of adult population numbers for the following reasons:

1. Many breeding sites are large and well-vegetated and therefore difficult to search.
2. Adult Natterjacks move between water bodies during the breeding season (Mathias, 1971), therefore a proportion of the population will probably be absent from the breeding sites at any particular time.
3. Adult activity seems to be related to prevailing weather conditions,

many more toads being found on mild, damp nights than cool, windy ones (Smith & Flynn, 1977).

4. The numbers of adults assembling at breeding waters increases early in the season then declines. The peak of activity may last only for a few days (Mathias, 1971) and its timing is difficult to predict.

The use of counting calling males at the breeding sites has little value for estimating population size, as it is not possible to distinguish more than 10 individuals in a breeding chorus (P.H. Smith pers. comm.). This was confirmed (pers. obs.) when attempts were made to count calling males.

Counting spawn strings can only give an estimate of the number of females spawning. The method also has certain problems associated with it (Beebee, 1979a). Underestimates will be given if spawn strings are missed and if part of the female population does not take an active part in breeding. Overestimates will be obtained in cases of multiple spawning or if broken strings are mistaken for two. The method can therefore can only give a rough estimate of the number of females present.

Mark-recapture has been used extensively for estimating the sizes of anuran populations (Jameson, 1955; Pearson, 1955; Smith & Flynn, 1977; Smith & Bownes, 1978; Gittings *et al*, 1980; Gittings, 1983) although many marking methods have been used. The most popular method has been toe-clipping (Hamilton, 1934; Storm & Pimentel, 1954; Jameson, 1955; Pearson, 1955; Pyburn, 1958; Turner, 1960; Frazer, 1966; Mathias, 1971; Smith & Flynn, 1977; Smith & Bownes, 1978; Schaub & Larsen, 1978), whereby toes are removed singly or in combination.

However, as Collier (1970) mentions, this can result in inflammation of the digits. Clarke (1972) found a reduction in captures of *B. woodhousei fowleri* with increasing numbers of toes clipped. He concluded that the effect was mainly due to the absence of toes rather than the open wound. This indicated that the toads were more dependent upon their agility than was previously assumed by investigators using this technique. Jaw tags (Raney, 1940; Raney & Ingram, 1941) also lead to increased mortality due to wounding and infection of marked animals. Numbered and colour coded waistbands (Breder *et al*, 1927; Savage, 1934; Frazer, 1966) are useful but can prove slow to fit or can be lost. Moore (1954) attempted to affix numbered 'running shorts' but this proved inoperable especially at night in heavy rain. Smith (1964) mentions tattoing the web of the foot but gives no indication of performance. Wisnieswki *et al* (1980) describe the use of a 'Panjet' marker to inject alcian dye intracutaneously in Common Toads. This method had previously been used successfully by fisheries biologists (Kelly, 1967; Hart & Pitcher, 1969), and had proved useful with small or immature specimens as well as large, adult fish (Riley, 1966; Hart & Pitcher, 1969; Smith, 1970; McIlwain & Christmas, 1975). Wisnieswski *et al* (1980) found the method was successful in Common Toads. Injuries caused by the technique were minimal (0.0005%) and individuals were recaptured bearing marks for the current and previous breeding seasons. They indicated that the method might be considered for long term studies, although they noted that, where combinations of marks were used, failure of one mark could produce spurious results. However, due to its ease of use, longevity of mark, and low injury rate this method was chosen to estimate the Natterjack population at Cabin Hill.

3.1.2 Methods

During the breeding season visits were made between 19.30 and 02.00 hrs to search for toads. Each pool was circuited in turn and toads located using a hand-held torch. This was Smith & Flynn's (1977) method 3 whereby captures were randomised with respect to time. When toads were captured they were sexed using the presence or absence of nuptial pads (Smith, 1964), weighed and snout-vent length to the nearest mm recorded. They were then given an individual mark using an Alcian dye (obtained from E. Gurr Ltd.) injected by a 'Panjet' inoculator obtained from F.H. Wright Dental Manufacturing Co., Kingsway West, Dundee, Scotland. A marking scheme adapted from Wisniewski *et al* (1980) was used, toads being marked ventrally using combinations of up to 8 marking positions on the legs (Fig. 5). Each point was given a numerical value so that a binary coding scheme could be employed (point 1 = 1, point 2 = 2, point 3 = 4, point 4 = 8 etc.). This meant that a total of 255 toads could be marked with one colour dye. This marking scheme was extended by using two extra marking positions on the upper legs (denoted by X's in Fig. 7). Thus toads 256-510 were given an extra colour mark on the upper left leg.

To facilitate searching, the 21 pools comprising the site were divided into zones, although with changing environmental conditions and rates of pools drying this scheme and the number of visits had to be modified between years (Table 6).

Figure 7. The marking scheme adopted for mark-recapture surveys (see text 3.1.2 for explanation).

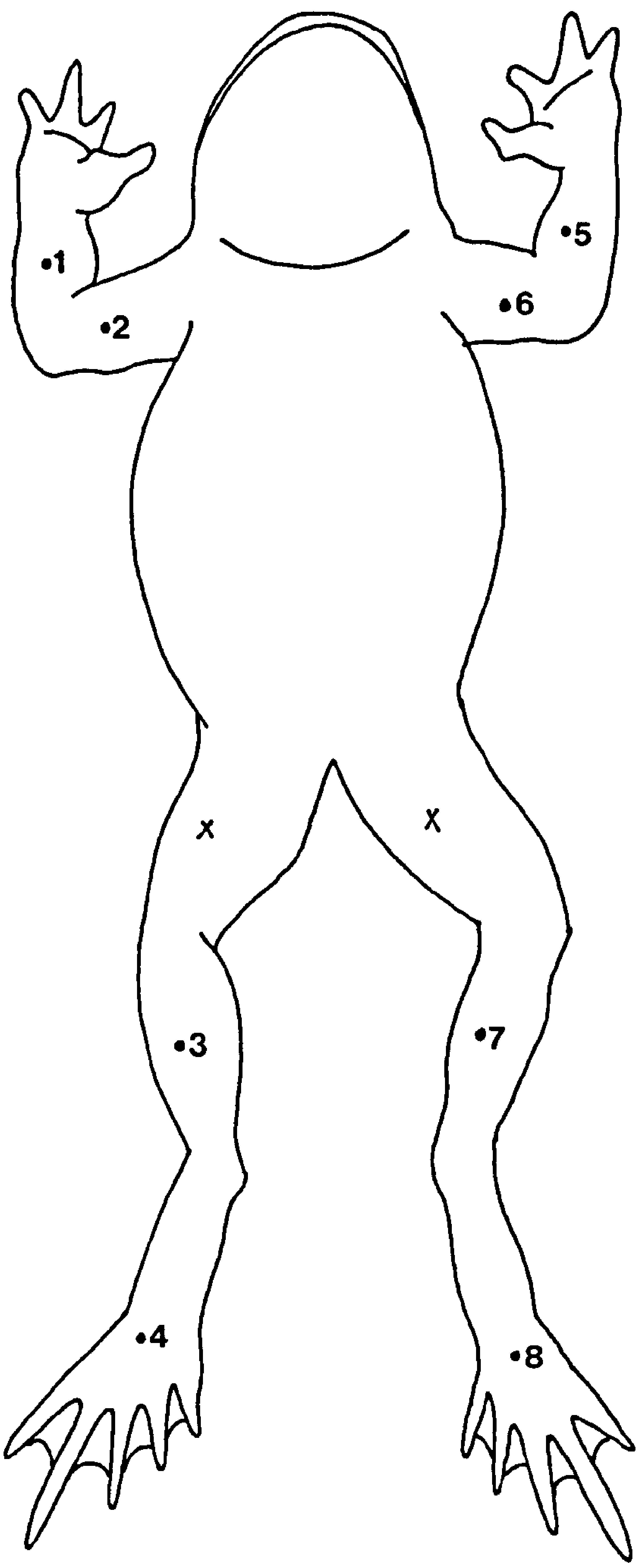

1
2
5
6
x
x
3
7
4
8

Table 6. Mark-recapture schemes adopted during the study period

Year	Mark-Recapture Period	Sub area	Pool No.'s	No. recapture occasions
1981	28/3-30/6	1	5-14	8
		2	16,P,17,18	8
		3	3,4,15	8
		4	1,2,19,20,21	8
1982	17/4-25/4	1	3,4,15	8
	11/5-18/5	2	1,2,20	7
	23/5-28/5	3	8,10,14,16	5
1983	28/4-1/5	1	1,2,3	3
	11/5-17/5	2	8,10,14,15,16	6

Difficulties were experienced in 1983 due to mechanical problems encountered with the 'Panjet'. Thus the number of recapture occasions was reduced so that the whole site could be investigated as soon as possible.

Results were submitted for analysis by the MARKREC computer programme developed by Dr. M.V. Hounsome of Manchester University Museum. The methods considered for use in this study were those of Manly & Parr (1968), Jolly (1965), and Fisher & Ford (1947). Begon (1979) reviews the mathematical requirements of each method. The disadvantage of the Manly-Parr method is that it requires a large extensive sample for the initial capture with correspondingly large numbers of multiple-recaptures for reliable estimates (approximate sampling intensity of 40%). The Fisher-Ford method requires considerably fewer data than Manly-Parr. Bishop & Sheppard (1973) found that the Fisher-Ford method was more accurate than the Manly-Parr and Jolly methods when sampling intensities were low (< 12%), survival rates were low (approximately 0.5) and/or population sizes were low (< 1000). However, the method assumes a constant and age-independent survival rate. For such a study as the present one (i.e. within-year captures over a short period) the daily survival rate is more a measure of the availability for capture and as this can vary with Natterjacks due to the effects of weather upon calling (Smith & Flynn, 1977), this method was discounted in favour of the Jolly stochastic model (1965).

3.2 Determination of Population Age Structure

3.2.1 Introduction

Length-frequency analysis using probability graph paper can be used to detect age-groups in animal populations (Harding, 1949, Cassie, 1954). However, using this method to distinguish cohorts of Natterjacks at Cabin Hill proved unsuccessful as inflexion points denoting year groups were not clearly definable.

An alternative method of determining age is to use annual growth zones (Peabody, 1961). Schroeder & Baskett (1968) used growth marks on the posterior limb of the pterygoid bone to study age in a population of *Rana catesbeiana*. They found that this method was useful for estimating post-metamorphic age up to 6 years. Barbault *et al* (1979) used growth rings in femoral sections to distinguish age-groups of *B. pentoni*. This method has also been employed to study *Triturus vulgaris* and *T. cristatus* (Hagström, 1977) and

T. alpestris (Smirna & Roček, 1976). Growth rings occur in specimens exhibiting different rates of bone growth between summer feeding and winter hibernating periods. They consist of relatively broad periosteal bone layers separated by narrow resting lines representing the hibernation period.

The disadvantage of all these methods is that they necessitate killing the animals being studied. An alternative method is to use phalangeal sections (Hemelaar & Van Gelder, 1980; Gittings *et al*, 1982), which allows the collection of samples by toe-clipping living animals. Clarke (1972) found mortality in toe-clipped *B. woodhousei fowleri* increased with the number of toes removed. Removal of single toes from a small sample of Natterjacks (47♀♀, 33♂♂) was not expected to have any major adverse effects upon the population at Cabin Hill.

3.2.2 Methods

During the 1983 breeding season, samples were collected after mark-recapture visits were completed. Captured toads were sexed, weighed, and measured for snout-vent length before a hind toe was removed using dissecting scissors. The toes were labelled for future identification and stored at -20°C until analysis. Following Gittings *et al* (1982) each toe was boiled in tap water for 30 mins to remove skin and muscles, and placed in Gooding and Stewards' decalcifying fluid overnight (Carleton & Short, 1954). After decalcifying, the toes were serially dehydrated in alcohol, and following clearing in xylene, embedded in paraffin wax. Sections 20 μ thick were cut using a Cambridge rocking microtome. Gittings *et al* (1982) used freezing microtomy techniques, but initial trials with this method gave unreliable results. Although the whole toe was sectioned, only sections from the central region of the diaphysis were used for age analysis, as growth rings are absent or incomplete in the epiphysis (Hemelaar & Van Gelder, 1980). The sections were counter-stained using Ehrlich's haemotoxylin and Eosin, mounted in DPX, and examined at x100 magnification. The growth rings stained pink/light purple and the resting lines dark purple. The age of each toad was determined by counting the number of darkly stained resting lines per section. All complete sections were counted for each sample. For toads collected during the breeding season before any current-year's growth has occurred, the outer margin of the bone is regarded as an additional resting line (Hemelaar & Van Gelder, 1980; Gittings *et al*, 1982).

3.3 Spawn and environmental factors

3.3.1 Introduction

A literature survey revealed few quantitative investigations of anuran spawn survival. Herreid & Kinney (1966) investigating survival of *Rana sylvatica* larvae carried out direct counts of eggs in spawn masses. They counted eggs in 52 masses and found a mean number of 778 eggs per mass. However, observations by Smith (1977,1978b,1979, 1980b) at Cabin Hill suggested that larger numbers of Natterjack spawn strings could be expected during this study. For the years 1977-1980 he found totals of 109, 366, 224, and 222 spawn strings respectively. As it was intended that the maximum possible number of strings be investigated it was felt that direct counting would prove too time consuming. Licht (1974) investigating *R. aurora* and

R. pretiosa populations estimated the survival of spawn by holding an egg mass in his hand and counting 100 eggs at random. It was felt that a modification of this method would allow estimates of egg numbers and survival to be made during this study.

3.3.2 Methods

During daily visits to Cabin Hill, each pool was circuited and searched for spawn strings. When found, the developmental stage was noted, and each string was marked using an individually numbered plastic peg. This allowed subsequent observations to be made on the fate of each string. Before estimating egg numbers, the following variables were noted: water depth; depth of spawn; distance of spawn from shoreline; substrate/vegetational type; % vegetation cover; vegetation height. Water pH was measured using a WPA Environmental Multi-Probe kit. This also allowed later measurement of water temperature and oxygen concentration to be made during 24 hour monitoring. Spawn was identified using guidelines by Smith (1964).

To estimate egg numbers, each string was gently lifted from the pool bottom and floated into a shallow plastic tray, where it was untangled and measured using a 30 cm rule, the string being folded to allow measurement. Three 15 cm sections were then chosen at random and all the eggs within each counted. From these counts the mean number eggs cm^{-1} was calculated which, multiplied by the total length of the string gave an estimate of the total number of eggs present. Strings were then returned to where they were found. The total number of dead eggs was counted directly rather than estimated in cases where numbers were low. However, where the majority of the string was affected, the number of dead eggs was estimated. The accuracy of this method was checked by counting eggs in large sections of strings chosen randomly, and comparing this number with the estimated value. The method was found to overestimate by an average of 8%, but this was not considered to be unreasonable. In those cases where the spawn could not be measured e.g. too entangled with vegetation the stage of development was noted, the length estimated visually, and a mean number of eggs cm^{-1} for that stage of development used to estimate the total number for that string.

Four stages of development were described: blastula, tail bud, tailed, hatched. The first 3 are equivalent to stages 1-17, 18-19, 20-23 of Pollister & Moore's (1937) table for anuran development. 'Hatched' refers to tadpoles during the period before they become free swimming. In subsequent visits to the site the strings were not removed again, however the developmental stage was described and any further mortality noted by measuring lengths of spawn affected by fungus (*Saprolegnia*).

3.4 Female fecundity and body size

3.4.1 Introduction

A simple technique for determining fecundity is to kill a sample of females and count eggs in the dissected ovaries. This well established method has been used in many studies of fish populations (e.g. Macer, 1974; Wilkinson & Jones, 1977; Babiker & Ibrahim, 1979; Davis, 1979). However, it was desirable to use a method which did not involve killing individuals. Caging spawning females was chosen as it allowed data on body size and egg number to be collected, after which females could be released.

3.4.2 Methods

Cages with an open base measuring 25 cm x 25 cm x 30 cm were made from wire mesh. In the evening, the combined weight of pairs found in amplexus was determined without separating the individuals. A cage was placed over each pair and secured to the floor of the pool with skewers. The following day the post-spawning weight of the male was measured. This was subtracted from the combined weight to give an estimate of initial female weight including the weight of spawn. It was assumed that male weight loss during spawning was negligible. This method was used as initial attempts, involving separating pairs before weighing, resulted in cessation of breeding activity. However, pairs could be handled and weighed while still amplexed without causing undue disturbance. Egg numbers were estimated using the method described in Section 3.3.2.

3.5 Tadpoles and invertebrate predators

3.5.1 Introduction

Several methods have been used to undertake quantitative surveys of larval amphibian survival. Whitaker (1971) and Licht (1974) used hand nets to collect tadpoles. However this type of sampling does not produce results easily comparable with other workers, and the numbers of tadpoles caught only gave crude estimates of relative changes in numbers of tadpoles in the pond. Mark-recapture surveys have been used to estimate the sizes of tadpole populations using different methods of marking. Warburg *et al* (1979) used tail clipping to mark tadpoles of *Salamandra salamandra*. It is possible however, that this method may lead to increased predation of the study organism by causing difficulty in locomotion. Neutral Red staining of tapoles has been used by several workers (Herreid & Kinney, 1966; Wijnands, 1972; Guttman & Creasey, 1973), however Cooke (1978) found that the staining regimes used in these studies were "too severe" when used on Common Frogs (*R. temporaria*) particularly if population estimates were made on several occasions during one season, and led to increased mortality, possibly due to selective predation of stained tadpoles. Cecil & Just (1979) working with *R. catesbeiana* were able to inject acrylic dyes under the skins of tadpoles. Calef (1973) used funnel traps in 1000 m^2 quadrats, and captive populations to relate the numbers caught per day to the density of tadpoles present. He then multiplied his estimated density by the area of the quadrat and summed the number of quadrats used. However this method is problematical since it assumes that trapping occurs over a known area (1000 m^2). Also it is not certain that trapping will occur even if tadpoles are present.

In view of the problems associated with the above methods, a continuous qaudrat survey technique was used. This offers the advantages of giving information on tadpole distribution, causing no tadpole mortality, and allowing other species of amphibians and invertebrates to be monitored concurrently.

3.5.2 Methods

Tadpole numbers were estimated using a stratified-random sampling technique. Samples were taken randomly using a $0.25\,m^2$ quadrat with net walls within depth strata (0-10 cm, 10-20 cm etc.) charted from transects of all the pools made at the beginning of the study period. Continuous depth readings taken at fixed points allowed the changing depth strata to be plotted and their areas to be calculated. The number of samples taken per pool was varied according to a fixed index of precision (20%). The advantage of this method is that it takes into account changes in the areas of the pools. The number of quadrats needed was calculated from Elliot (1971) using the equation:

$$n = 25\left(\frac{1}{\bar{x}} + \frac{1}{K}\right)$$

where n = number of quadrats required

$\bar{x}$ = mean number of tadpoles per quadrat

K = index of clumping in population.

As tadpoles remained within a few centimetres of the pool bottoms, estimates of numbers were expressed per m^2 rather than per m^3. The numbers of possible invertebrate predators e.g. dytiscids, odonatans were taken concurrently during quadrat surveys. Identifications were made using a standard text (Macan, 1979). Tadpoles were identified using guidelines by Smith (1964) and Smith (1974).

3.6 Thermal relations in Natterjack and Common Toad larvae

3.6.1 Introduction

Beebee (1979b) used a mathematical model to investigate sympatric populations of Natterjacks and Common Toads. He showed that after introduction, Common Toad populations increased while Natterjacks declined, although the rate of disappearance was slower for dune sites than heath sites. He attributed this to predation of Natterjack larvae by Common Toad larvae, but did not consider other factors, in particular the physiological requirements of the two species. In an earlier paper Beebee (1977) showed that increasing usage of heathland pools by Common Toads is related to afforestation of sites. This may lead to a change in physical conditions which differentially favour metamorphic success of Common Toads.

Noland & Ultsch (1981) investigated the importance of temperature and dissolved oxygen concentrations on microhabitat selection by tadpoles of *R. pipiens* and *B. terrestris*. They related laboratory studies of critical thermal maxima (CTM), defined as the mean temperature at which locomotor activity became disorganised and the animals lost their ability to escape from conditions that lead to their death (Hutchison, 1961), and oxygen consumption to physical conditions in the field. Noland & Ultsch (*op cit*) found differences in thermal and oxygen requirements for the two species, and also differences in the physical parameters of their habitats. They suggested that *B. terrestris* is adapted to high temperatures while *R. pipiens* is better adapted to variations in oxygen availability. Mathias (1971) found that Common Toad tadpoles had lower CTM (25-28°C), and could develop at lower temperatures than Natterjacks, suggesting that Common Toads would fare better in cooler pools.

Monitoring over a 24 hour period at Cabin Hill revealed fluctuations in pool temperatures (13-23.5°C) and oxygen concentrations (3.8-17.8 ppm). In view of this it was decided to study thermal dependence of oxygen requirements of Common Toads and Natterjacks and its role in the relative breeding success of the two species. Investigations were made into thermal preferanda of larvae; the effects of temperature upon larval oxygen consumption and growth; and also the ability of both species to acclimate to changes in temperature. The following questions were asked:

1. Is there any difference in the effect of temperature upon metabolic rate (oxygen uptake) between Natterjacks and Common Toads, and what implication does this have for metamorphic success under conditions experienced during development in the field?
2. What implication does this have for reproductive strategies chosen by each species?

3.6.2 Method

Animals: For each species, 10 freshly laid spawn strings were chosen randomly from Cabin Hill. In the laboratory these were held in 5 l plastic beakers containing aerated, dechlorinated tap water at 15°C. The water was changed every two days, and dead spawn removed as it appeared. On hatching, 6 groups of 50 tadpoles were transferred to a constant 10°C environment. Another 6 groups were held at 20°C. All were contained in 5 l plastic beakers on a 12 hr photoperiod. The water was changed weekly and tadpoles fed on lettuce and *Elodea canadensis*.

Growth studies: Samples of 25 randomly chosen tadpoles at each acclimation temperature were weighed at weekly intervals. Larvae were weighed in milligrams using a Stanton Unimatic CL 51 balance.

Individuals were removed from water filled petri dishes using an inverted pasteur pipette, placed on filter paper and gently blotted. They were then transferred to the balance, weighed, and replaced in water. The tadpoles did not appear to suffer any adverse effects from this treatment, measurements being made as rapidly as possible to minimise stress. Observations were also made with 2 groups of 10°C acclimated Common Toad tadpoles shifted to 20°C during week 3.

Oxygen consumption: Oxygen consumption was measured at weekly intervals using a polarographic electrode; the Y31 Biological Oxygen Monitor 53 (Yellow Springs Instruments, Ohio). This consists of 4 removeable glass reaction chambers (20 mm dia. x 70 mm length) surrounded by a water jacket. A Clark-type electrode is mounted in a lucite plunger, shaped so that all air can be expelled from the chambers by a slot on the side of the plunger. The electrode has a platinum cathode and silver anode bathed in potassium chloride solution and separated from the reaction chamber by a membrane. When operating, the current flowing between the electrodes is directly proportional to the oxygen concentration of the medium within the reaction chamber. The output (0-10 mV) was recorded using a Servegor 120 chart recorder. Relative oxygen consumption values obtained during experimentation were converted to actual oxygen consumption using tables of oxygen concentrations in water at the experimental temperatures. Clark-type electrodes require a continuous movement of liquid over the membrane to maintain steady-state readings. Normally this is achieved by using 18 mm dia. magnetic stirrers. However, to prevent excessive disturbance of tadpoles, these were replaced by 15 mm sections of wire agitated by an under-assembly magnetic stirrer. This, together with random locomotory movement by the tadpoles, was considered adequate to prevent any localised reduction of oxygen concentration around the electrode which might have affected readings. The temperature of the chambers was held constant with an accuracy of ± 0.1°C using a Haake F3 heater-cooler unit.

Controls of 2 mls fully aerated water were used to calibrate the chart recorder at maximum deflection for both experimental temperatures. Sterile water was used to prevent oxygen uptake by micro-organisms influencing the results. Five randomly chosen tadpoles from each acclimation temperature were used for oxygen consumption readings. Each tadpole was introduced into the reaction chamber containing 2 ml of sterile, aerated water, the electrode inserted, and all air bubbles expelled. For each tadpole, the oxygen consumption was measured at 10°C and 20°C for 15 mins, after which the tadpole was weighed (see above) and returned to the holding vessel. For the final set of measurements (week 5) oxygen consumptions were measured at 5°C intervals between 5°C and 30°C. This allowed oxygen requirements to be measured across a full range of temperatures which might be encountered in the field.

During week 6, thermal preferanda of both species were measured. A temperature gradient was created in a 2 m section of 7.5 cm dia. plastic guttering, using a thermostatic heater set at 40°C at one end of the gutter, and cracked ice at the other. Ten tadpoles were placed equidistant along the length of the gradient. To reduce movements associated with foraging behaviour by the tadpoles, *Elodea canadensis* was placed uniformly along the gutter. After 50 mins the temperature of the water adjacent to each tadpole was recorded using a 0-50°C thermometer. The tadpoles were removed and then placed equidistant along the gradient. This was repeated a maximum of 5 times for each tadpole after which the tadpoles were returned to the holding vessels.

3.7 Metamorphosis

Previous workers (Storm & Pimentel, 1954; Whitaker, 1971) have successfully used combinations of fences and sunken traps around breeding pools to study the emergence of metamorphosing anurans. Unfortunately, public access to the site, and army activity on the training areas precluded the use of this sampling method at Cabin Hill. Initial attempts at using pitfall traps and board traps around the edges of the pools did not produce reliable results. Because of these difficulties, metamorphosing toadlets were estimated indirectly by monitoring the numbers of 4-legged tadpoles within the pools, during the course of quadrat surveys (described in section 3.5.2). Searches were also made around the pools for fully metamorphosed toadlets.

3.8 Other amphibians

Although primarily concerned with Natterjacks, observations concerning breeding biology of other amphibians (Common Frogs, Common Toads) at Cabin Hill were maintained for the study period by Dr. P.H. Smith and myself. Common Frog spawn numbers were estimated visually, but only the presence or absence of Common Toad spawn was recorded. Presence or absence of larvae was recorded for both species, and metamorphosis estimated visually. Quadrat surveys of Common Toad tadpoles were undertaken during the course of this study using the method described previously (section 3.3.2).

3.9 Adults (Post-breeding season)

From previous observations (Mathias, 1971; P.H. Smith *in litt*) adult Natterjacks were seen to move away from the breeding pools and disperse along the frontal dunes after the breeding season. A second mark-recapture scheme was undertaken to provide details of adults' movements along the fore-dunes and also provide a more accurate population estimate by reducing the heavy bias towards males at the breeding sites. Accordingly a 2.5 km stretch of dunes adjacent to the breeding area was searched for toads. This ran from Formby Coastguard Lookout in the north to the River Alt estuary in the south. To facilitate searching, driftwood was placed on the dunes in the hope of attracting toads which are known to shelter under flat objects (P.H. Smith *in litt*). The dunes were marked off at 100 m intervals by posts driven into the ground so that capture positions could be identified. On capture, the same procedure as that used in the breeding season was employed. The toads were sexed, weighed, and snout-vent length to the nearest mm noted. The animals were then given an individual mark using the 'Panjet' inoculator, and released.

CHAPTER 4

RESULTS

4.1 Population estimation, 1981-83 Breeding season

4.1.1 Data analysis for the study period

Male and female capture data for the study period are given in Table 7. Overall capture rates were low, with an excess of males. This is due to males remaining longer at the breeding pools than females which visit briefly to spawn (Smith, 1964). The female data did not lend themselves to mark-recapture analysis, and so population estimates were only calculated for the male breeding population. This problem has been encountered by previous workers (Smith & Flynn 1977; Smith & Bownes, 1978).

4.1.2 Testing the assumption of Jolly's (1965) Stochastic Method

Mark-recapture models contain underlying mathematical assumptions. The results are thus only explainable in biological terms if these assumptions are valid. If these requirements are not fulfilled, interpretation of results proves difficult, and a different method of population estimation may have to be applied (Caughley, 1980). Jolly's (1965) method makes the following assumptions:

1. All marks are permanent and noted upon capture.
2. All individuals, whether marked or not, have an equal chance of capture.
3. Capturing, handling, and marking one or more times has no effect upon an individual's chance of dying/emigrating.

Table 7. Male and female captures, Cabin Hill. Breeding season 1981-83

		No. of toads captured	No. of toads recaptured	No. of recaptures
Males	1981	519	48	49
	1982	521	142	254
	1983	648	180	244
Females	1981	54	2	2
	1982	43	5	9
	1983	118	0	0

4. Capturing, handling, and marking one or more times has no effect upon an individual's subsequent chance of recapture.
5. All individuals, whether marked or not, have an equal chance of dying/emigrating.
6. Sampling periods are short in relation to total time.

In previous mark-recapture surveys of Natterjack populations (e.g. Mathias, 1971; Smith & Bownes, 1978) these assumptions were not tested although difficulties in gathering data were noted. For this study, mathematical tests described by Begon (1979) were used to check the validity of the data. In 1981, low numbers of captures (Table 7) resulted in data unsuitable for this type of analysis. Therefore the following refer to the 1982 data.

1. All marks are permanent and noted correctly on capture.

The Panjet marker has been used successfully in studies of fish populations (e.g. Hart & Pitcher, 1969) and although it has only recently been applied to amphibians (Wisniewski *et al*, 1980) it has proved to be a reliable method of marking. During this study, Panjet marks were clear and easy to read. The three colours used (Alcian blue, green, and yellow) were easily distinguished against the animals' pale ventral surface, and there were no problems in reading code numbers.

2. All individuals, whether marked or not, had an equal chance of capture

Random sampling within the population was investigated using Leslie's (1958) test. Ideally this requires a sample of at least 20 individuals known to have survived 3 intermediate recapture occasions. If the sample is smaller, the test can be applied, but the results may be unreliable.

The analyses for all three sub-areas sampled in 1982 are given in Table 8. Of these, only data for sub-areas 1 and 2 could be used to calculate χ^2 values. Random sampling was confirmed for sub-area 2 but not for sub-area 1. Although in both cases the number of individuals susceptible to sampling (G) was below the ideal minimum, twice as many animals were available in sub-area 2 (G = 12) as sub-area 1 (G = 6). In the case of sub-area 3 where G = 3, no χ^2 values were computable. These results indicate sampling was probably random, but there were too few data to confirm this. Analysis of 1983 recapture data (Table 9) for sub-area 2 (G = 14) supports the hypothesis of random capture ($p > 0.1$).

If capture was non-random, the most probable explanation would be a tendency to recapture territorial males remaining at favoured calling sites. Territoriality has been shown in Natterjacks (Arak, 1983), larger toads being more successful in male-male interactions than smaller toads. Therefore recapture rate of 'larger' individuals could be greater than for 'smaller' males. This was tested by χ^2 analysis using the 1982 data for male captures in sub-area 1. Toads were classified into one of four size groups ($\leq$ 50 mm; 51-55 mm; 56-60 mm; > 60 mm). The analysis is given in Table 10, and shows no particular size group had a greater chance of recapture ($\chi^2 = 4.23$, $p > 0.1$).

The overall conclusion is that capture of Natterjacks was probably random.

Table 8. Leslie's (1958) test for random sampling of male Natterjacks at Cabin Hill, 1982

Sub area 1. G = 6

Day of capture i	No. of captures (g_i)	$(g_i)^2$	No. of recaptures x	Frequency f_x	xf_x	x^2f_x
2	3	9	0	2	0	0
3	2	4	1	1	1	1
4	4	16	2	1	2	4
	9	29	3	2	6	18
				6	9	23

Actual sum of squares $= 23 - \frac{81}{6} = 9.5$

Expected variance $= \frac{9}{6} - \frac{29}{36} = 0.69$

$$X^2 = \frac{9.50}{0.69} = 13.77 \text{ (with 5 d.f.)}$$

$p < 0.05$ (∴ Non-random sampling)

Sub area 2. G = 12

i	(g_i)	$(\bar{g}_i)^2$	x	f_x	xf_x	x^2f_x
2	5	25	0	4	0	0
3	5	25	1	2	2	2
4	5	25	2	5	10	20
	15	75	3	1	3	9
				12	15	31

Actual sum of squares $= 31 - \frac{225}{12} = 12.25$

Expected variance $= \frac{15}{12} - \frac{75}{44} = 0.73$

$$X^2 = \frac{12.25}{0.73} = 16.78 \text{ (with 11 d.f.)}$$

$p > 0.1$ (∴ Random sampling)

Table 8 (continued)

Sub area 3. G = 3

i	(g_i)	$(g_i)^2$
2	3	9
3	3	9
4	3	9
	9	27

x	f_x	xf_x	x^2f_x
0	0	0	0
1	0	0	0
2	0	0	0
	3	9	27
	3	9	27

Actual sum of squares $= 27 - \frac{89}{3} = 0$

Expected variance $= \frac{9}{3} - \frac{27}{9} = 0.$

∴ Captures too small for sensible estimate.

Table 9. Leslie's (1958) test for random sampling of male Natterjacks at Cabin Hill, 1983

Sub area 2. G = 14

i	g_i	g_i^2
2	1	1
3	6	36
4	4	16
	11	53

x	f_x	xf_x	x^2f_x
0	6	0	0
1	5	5	5
2	3	6	12
3	0	0	0
	14	11	17

Actual sum of figures $= 17 - \frac{121}{14} = 8.36$

Expected variance $= \frac{11}{14} - \frac{53}{196} = 0.52$

$$\chi^2 = \frac{8.36}{0.52} = 16.07 \text{ (with 13 d.f.)}$$

$p > 0.1$ ($\therefore$ Random sampling)

Table 10. The effect of size (age) upon an individual's chance of recapture

Size	< 50 mm	50-55 mm	56-60 mm	> 60 mm	Total
Recaptured	4	26	17	1	48
Not-recaptured	15	70	72	15	172
Total	19	96	89	16	220

$\chi^2 = 4.232$ (with 3 d.f.). $p > 0.1$

∴ No size group exhibited a greater recapture rate compared to the rest of the population.

3. Capturing, handling, and marking one or more times has no effect upon an individual's chance of dying/emigrating

Due to the relative novelty of marking amphibians by Panjetting this test was particularly important. Field observations by myself and previous workers (Wisniewski *et al*, 1980) suggest that Panjetting mortality is negligible. Wisniewski *et al* (1980) report < 0.01% marking mortality. During the present study 3 (0.2%) marked toads were found dead, although it was not clear whether this was due to the marking process. The effect of marking was tested by determining whether toads marked for the first time were recaptured as frequently as those already marked (Begon, 1979). The results are given in Table 11.

The results are rather difficult to interpret. Significant and non-significant values were found for all sub-areas (Table 11). Thus in sub-area 1 there was a tendency for toads marked on days 2, 3 and 7 not to be recaptured. This is also true for sub-area 2 (day 4) and sub-area 3 (day 4). However, for all other marking occasions there was no evidence for initial marking mortality. It is important to note that Natterjack captures (and hence recaptures) are affected by the prevailing weather conditions (see below). This may have affected the analysis giving rise to conflicting results. Checks were made around the pools each morning after marking, but no dead, marked animals were found.

It is concluded that there is no strong evidence that marking increased mortality.

Table 11. The effect of marking upon subsequent recaptures of male Natterjacks at Cabin Hill, 1982

Sub area 1

Example: Day 2 captures

	Captured after day 2	Not captured after day 2	Total
1st captured day 2 and released	8	41	49
Recaptured day 2 and released	7	5	12
Captured day 2 and released	15	46	61

$\chi^2 = 7.05$ (with 1 d.f.) $p < 0.001$.

Analysis	χ^2 value	Probability level
Day 3	16.26	< 0.001
Day 4	0.39	> 0.5
Day 5	0.07	> 0.9
Day 7	5.00	< 0.05
Day 8	3.79	> 0.05

Table 11. (continued)

Sub area 2

Analysis	χ^2 value	Probability level
Day 2	1.05	> 0.1
Day 3	2.00	> 0.1
Day 4	8.10	< 0.01
Day 5	3.42	> 0.05
Day 6	0.94	> 0.1
Day 7	2.43	> 0.1

Sub area 3

Analysis	χ^2 value	Probability level
Day 2	0.16	> 0.5
Day 3	0.04	> 0.05
Day 4	4.95	< 0.05
Day 5	0	

4. Capturing, handling, and marking one or more times has no effect upon an individual's subsequent change of recapture

It is possible that individuals caught one or more times are more likely to be caught on subsequent occasions. Thus the hypothesis is that marked animals can be treated as equivalent, regardless of the number of times they have been caught. The analysis is described by Begon (1979). The results are given in Table 12. Because of the low recapture rates all marks were pooled.

Apart from three occasions (days 2, 3, and 7: sub-area 1) there was no apparent tendency for marked animals to be caught more or less times than unmarked toads. The reasons for the significant results are not clear. In each case however, there is a tendency for previously marked toads to appear less often than expected. Begon (1979) states that this test combines 2 factors - survival and catchability. Thus the absence of marked toads could be due to decreased survival. However, in view of the preceding analysis, it seems more likely that the results were due to insufficient data for the days in questions.

5. All individuals, whether marked or not, have an equal chance of dying/emigrating

The basis of this assumption is that survival is age-independent. In a fairly long lived species where captures are maintained over several years this could seriously affect calculations. However in the present study, population estimates were undertaken over short periods (e.g. 9 consecutive days) within years, during which age dependent mortality might not be expected to operate.

Table 12. The analysis of Natterjack recaptures (1982) for independence of mark status

Sub area 1

Example: Day 2 captures

	Times caught previously		Total
	0	1	
Recaptured	5	7	12
Not Recaptured	44	5	49
Released	49	12	61

$\chi^2 = 1.23$ (with 1 d.f.) $p > 0.5$.

Analysis	χ^2	df	Probability level
Day 3	11.94	1	< 0.001
Day 4	1.88	1	> 0.5
Day 5	0.95	1	> 0.1
Day 7	5.00	1	< 0.05
Day 8	3.79	1	> 0.05

Sub area 2

Analysis	χ^2	df	Probability level
Day 2	1.05	1	> 0.1
Day 3	2.00	1	> 0.1
Day 4	2.02	1	> 0.1
Day 5	2.15	1	> 0.1
Day 6	2.57	1	> 0.1
Day 7	1.60	1	> 0.1

Table 12 (continued)

Sub-area 3

Analysis	χ^2	df	Probability level
Day 2	0.16	1	> 0.5
Day 3	0.04	1	> 0.9
Day 4	1.35	1	> 0.1

Thus the assumption that survival is age independent was considered to have been maintained.

6. Sampling periods were short in relation to total time

The maximum sampling duration throughout the study period was 6½ hours. Even as a maximum (27% per day) this was considered an acceptably small proportion of the total time.

4.1.3 The use of Jolly's (1965) method for estimating Natterjack populations.

Previous studies (Mathias, 1971; Smith & Flynn, 1977; Smith & Bownes, 1978) attempted to census Natterjack populations using Manly & Parr's (1968) method. However on the basis of published work, the use of this method is suspect. Mathias (1971) discounted Jolly's (1965) method on the basis that intervals between some samples were long (i.e. 1 year) and therefore mortality could not be assumed to be age-independent. However, age independent mortality can be assumed within years. Also as Begon (1979) states, Jolly's (1965) method is mainly unaffected by age dependent survival when survival is independent of mark status and capture independent of age. The present study shows that these conditions may be fulfilled.

Although he noted differences in male and female behaviour Mathias (1971) combined the sexes for his population estimates, thus violating the assumption that individuals have an equal chance of capture. There also appears to be insufficient data for Manly & Parr's (1968) method. At each of his field sites, Mathias (1971) sampled on 10 occasions over 3 years, with sample sizes ranging from 5-90 (mean = 29). Initial sample sizes for his two sites were 6 and 17 respectively. By indirect calculation he suggested population sizes were 250-1500 and 300-800. If these were correct, data from Robson & Regier (1964) suggests minimum daily sample sizes of 80 were needed for population estimation. Similarly, Mathias' recaptures appear too few for Manly & Parr's (1968) method to be effective (see Mathias, 1971, Appendix 1).

Smith & Flynn (1977) and Smith & Bownes (1978) used Manly & Parr's (1968) method to study Natterjack populations within years. Manly (1970) suggested there should be a minimum of 10 recaptures per sampling occasion but Smith & Flynn (1977) only achieved this once during 8 recapture visits. Smith & Bownes (1978) also had a low recapture rate. Thus it appears that Manly & Parr's (1968) method may be of limited value for censussing Natterjack populations, requiring extensive trapping and recapture data (Begon, 1979).

No mathematical testing of the validity of Natterjack capture data has been attempted previously. Begon (1979) states that these tests are not merely "refinements for the fastidious but should be an essential part of any attempt to apply theoretical capture-recapture models to actual capture-recapture data". However he points out that they must be undertaken in conjunction with specialised or generalised knowledge of a species' ecology and behaviour, and also an appreciation of the extent, and therefore validity, of the data to be analysed. Thus interpretation of these tests must be made with caution, and not solely on the basis of mathematics.

In the present study, although the assumptions of Jolly's (1965) method were violated mathematically in some cases, the overall trend suggested that there were no major discrepancies. Thus Jolly's (1965) method was considered acceptable to estimate the Natterjack population at Cabin Hill.

4.1.4 A Summary of Jolly's (1965) Stochastic Method

Individuals were captured, marked, and released on i days, and the total number captured on any day was n_i. Each marked individual only contributed its most recent mark, m_i. The number of marks at risk in the day i population, M_i, is given by:

$$M_i = m_i + \frac{z_i(r_i + 1)}{(y_i + 1)}$$

where z_i = the number of inviduals marked before day i, not caught on day i, but caught subsequently.

r_i = the number of individuals released on day i.

y_i = the number of r_i that were caught subsequently.

The estimated population size, N_i, is given by:

$$N_i = \frac{M_i(n_i + 1)}{(m_i + 1)}$$

The survival rate from day_i until day_{i+1}, ϕ_i, is given by:

$$\phi_i = \frac{M_i + 1}{(M_i - m_i + r_i)}$$

The overall survival rate is calculated as the geometric mean of all the individual daily survival rates:

$$\phi_o = \sqrt[n]{\phi_i + \phi_{i+1} \; \ldots\ldots + \phi_n}$$

where n = the number of values.

Life expectancy is calculated by:

$$LE = \frac{-1}{\ln \phi_o}$$

The estimated number of additions to be population between day i and day i+1, B_i, is given by:

$$B_i = N_{i+1} - \phi_i(N_i - n_i + r_i)$$

More detailed explanation together with formulae for standard errors may be found in Jolly (1965), and Begon (1979).

4.1.5 The Population Size Estimates

The extracted data required for analyes are given in Tables 13-15.

4.1.6 The 1981 Survey

Recapture data for this year were too few for population estimation within sub-areas, therefore the data were combined (Table 13). Even so, the data showed large fluctuations in captures with many zero counts recorded for m_i and y_i. This affected the calculation of $\hat{M}_i$ and hence $\hat{N}_i$, leading to overestimation of parameters. Considering the equation:

$$M_i = m_i + \frac{z_i r_i}{y_i} \qquad \text{(terms as in section 4.1.4).}$$

As y_i tends towards zero, the value of M_i will tend to increase. When $m_i = 0$, y_i directly influences M_i since:

$$M_i = \frac{z_i r_i}{y_i}$$

Both M_i and m_i are used in the calculation of N_i:

$$N_i = \frac{M_i(n_i + 1)}{(m_i + 1)}$$

Table 13. The 1981 capture-recapture data of adult male Natterjacks analysed by Jolly's (1965) method - all sub areas combined

Day	Captured	Time of release of marks, j							
		1	2	3	4	5	6	7	8
i	n_i	Recaptured marks M_{ij}							
1	193								
2	137	4							
3	150	17	14						
4	1	0	0	0					
5	0	0	0	0	0				
6	43	5	0	1	0	0			
7	42	2	3	2	0	0	0		
8	0	0	0	0	0	0	0	0	
9	2	0	1	0	0	0	0	0	0

Table 14. The 1982 capture-recapture data of adult male Natterjacks analysed by Jolly's (1965) method

Sub area 1 (Pools 3,4,15)

Day	Captured	Time of release of marks, j							
		1	2	3	4	5	6	7	8
i	n_i	Recaptured marks, M_{ij}							
1	49								
2	61	12							
3	51	3	7						
4	44	5	6	6					
5	38	2	0	1	4				
6	0	0	0	0	0	0			
7	24	0	1	2	2	3	0		
8	44	0	0	0	1	5	0	8	
9	35	0	1	0	2	5	0	1	10

Table 14 (continued)

Sub area 2 (Pools 1,2,20)

Day	Captured	Time of release of marks, j							
		1	2	3	4	5	6	7	8
i	n_i	Recaptured marks, M_{ij}							
1	42								
2	34	10							
3	56	8	9						
4	28	1	5	9					
5	65	4	6	12	10				
6	38	2	1	0	2	10			
7	31	1	0	0	1	12	5		
8	26	0	0	3	2	2	2	4	

Sub area 3 (Pools 8,10,14,16)

Day	Captured	Time of release of marks, j				
		1	2	3	4	5
i	n_i	Recaptured marks, M_{ij}				
1	22					
2	28	10				
3	22	0	10			
4	19	0	4	9		
5	12	0	0	2	9	
6	8	0	0	0	2	2

Table 15. The 1983 capture-recapture data of adult male Natterjacks analysed by Jolly's (1965) method

Sub area 1 (Pools 1,3)

Day	Captured	Time of release of marks, j		
		1	2	3
i	n_i	Recaptured marks, M_{ij}		
1	215			
2	200	63		
3	131	26	24	
4	86	7	15	13

Sub area 2 (Pools 8,14,15,16)

Day	Captured	Time of release of marks, j					
		1	2	3	4	5	6
i	n_i	Recaptured marks, M_{ij}					
1	45						
2	41	4					
3	32	15	3				
4	41	5	5	5			
5	38	6	1	3	11		
6	44	0	3	3	9	12	
7	19	1	1	1	2	3	3

Thus where M_i is overestimated, and m_i is small (0), the population on that day, N_i, will be overestimated.

Only two estimates were computable for this year (Table 16). On day 2 N_i was calculated as 4948. However, this is probably not a reliable estimate as the proportion of recaptures (R_i) was only 3%. This produced an overestimate for N_i (See above). By day 3 however, the sampling intensity had increased to 24%. It can be seen (Table 16) that N_i is lower (1605) than previously calculated. A simple Lincoln (1930) estimate at this point gives a population estimate of 1597 which is in close agreement with the Jolly (1965) estimate (formula for the Lincoln (1930) method is given in Begon (1979)). Due to the increase in R, the population estimate is likely to be more reliable than that calculated for day 2, although the standard error (SEN_i) is large (±884) representing 55% of the estimated population value.

The overall survival rate (ϕ_o) was calculated to be 1.08, however a survival rate greater than 1 is biologically impossible. Thus the estimated value is considered to be a combination of the true survival rate which may be close to 1, and a positive error term. The best estimate of ϕ_o is therefore 1.

4.1.7 The 1982 survey

Probably as a result of the shorter sampling periods (Table 6) and the reduced pool sizes, more recaptures were obtained. The proportion of recaptures ranged from 18 to 75% (Table 17), with an overall mean of 42% for the three sampling periods. Zero captures

Table 16. Computation of the 1981 recapture data by Jolly's (1965) method

Day i	Proportion of Recaptures R_i	No. marked Animals at Risk M_i	Total Population N_i	$SE.N_i$	Survival Rate ϕ_i	$SE.\phi_i$	Ingress B_i	$SE.B_i$
1	-	0	-	-	0.924	0.259	-	-
2	0.029	198.3	4948	2555	1.259	0.696	-4614	3764
3	0.238	391.2	1605	884	-	-	-	-
4	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-
6	0.139	-	-	-	-	-	-	-
7	0.142	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	-
9	0.500	-	-	-				

$\phi_o = 1.07$

Table 17. Computation of the 1982 data by Jolly's (1965) method

Sub area 1

i	R_i	M_i	N_i	$SE.N_i$	ϕ_i	$SE.\phi_i$	B_i	$SE.B_i$
1	-	0	-	-				
					1.036	0.270	-	-
2	0.196	50.7	246	85				
					0.882	0.314	203	137
3	0.196	88.0	420	174				
					0.376	0.142	-35	51
4	0.388	48.5	123	41				
					0.425	0.149	108	54
5	0.184	52.0	160	63				
					-	-	-	-
6	-	-	-	-				
					-	-	74	-
7	0.333	43.0	121	45				
					0.361	0.299	50	41
8	0.318	50.8	154	53				
					-	-	-	-
9	0.576	-	-	-				

ϕ_o = 0.661 Life Expectancy = 2.41 days

Sub area 2

i	R_i	M_i	N_i	$SE.N_i$	ϕ_i	$SE.\phi_i$	B_i	$SE.B_i$
1	-	0	-	-				
					0.844	0.134	-	-
2	0.294	35.4	115	31				
					1.085	0.203	82	46
3	0.304	64.5	206	51				
					0.636	0.133	-11	30
4	0.536	65.7	120	28				
					0.813	0.168	36	20
5	0.477	64.0	133	25				
					1.188	0.404	146	77
6	0.368	116.4	304	116				
					0.546	0.263	-43	41
7	0.613	76.6	123	51				
					-	-	-	-
8	0.500	-	-	-				

ϕ_o = 0.821 Life Expectancy = 5.07 days

Table 17 (continued)

Sub area 3

i	R_i	M_i	N_i	$SE.N_i$	ϕ_i	$SE.\phi_i$	B_i	$SE.B_i$
1	-	0	-	-				
					0.455	0.106	-	-
2	0.337	10.0	28	28				
					0.607	0.133	16	5
3	0.500	17.0	33	33				
					0.630	0.138	4	4
4	0.684	17.0	25	25				
					0.768	0.327	4	3
5	0.750	17.7	23	23				
					-	-	-	-
6	0.500	-	-	-				

$\phi_o = 0.604$ Life Expectancy = 1.98 days

For explanation of symbols see Table 16.

were obtained once when the site was not visited. Survival rates varied between 0.36 and 1.19 (1.0). The sampling periods were short enough (maximum duration 9 days) for the actual biological survival to be perfect i.e. 1.0. Therefore it is likely that the estimated survival values reflected the animals' availability for capture between days rather than their actual survival rate. The low life expectancies calculated for sub-areas 1 and 3 (Table 17) suggest a rapid turnover of animals entering and leaving the pools. Life expectancy refers to the duration of marks available for sampling. If there are marked differences in the number of animals available for capture on successive sampling occasions the estimated population values may show large fluctuations accordingly. Previous workers (Smith & Flynn, 1977) have noted fluctuations in numbers of Natterjacks during mark-recapture surveys, the main factors responsible appearing to be climatological. Figure 8 shows the numbers of captures on each sampling occasion together with the prevailing weather conditions during the 24 hours within which sampling occurred. Although some differences may be due to sampling error, the numbers caught and survival rates appear to be lower on windy days. Numbers caught also appear to follow trends in minimum air temperature, with decreasing numbers of toads caught as temperatures fall. No statistical correlations have been attempted as the weather data represent conditions experienced over 24 hour periods at Ainsdale, and are not the actual weather conditions at Cabin Hill during sampling. Also, the recording instruments are situated in a rather sheltered area, so that there may be some difference between actual and recorded conditions (Dr. R. Pegg, pers. comm.). It was noticeable however, that during periods of cool, windy weather or on clear, moonlit

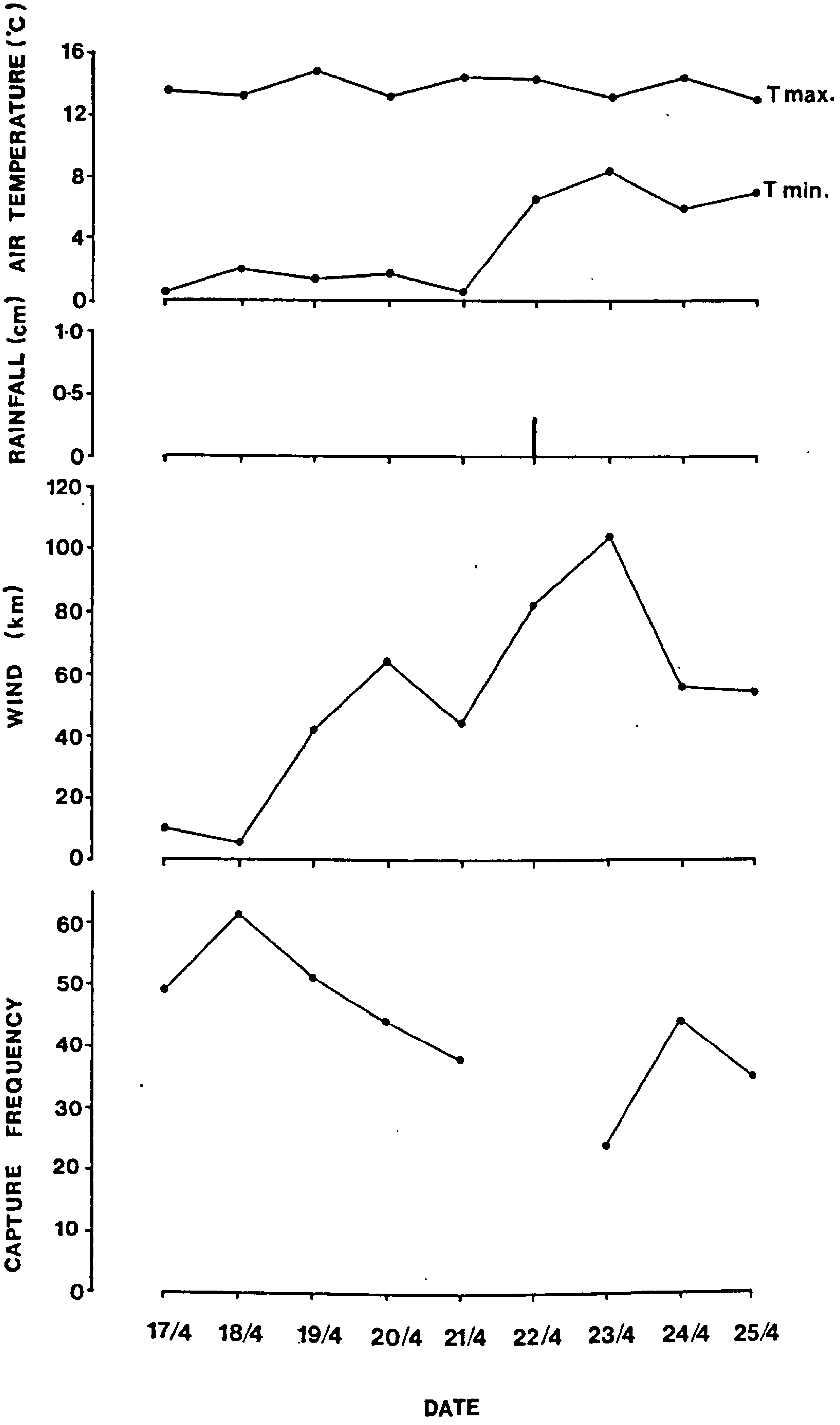
Figure 8. The numbers of male captures and the prevailing weather conditions during the 1982 sampling programme.

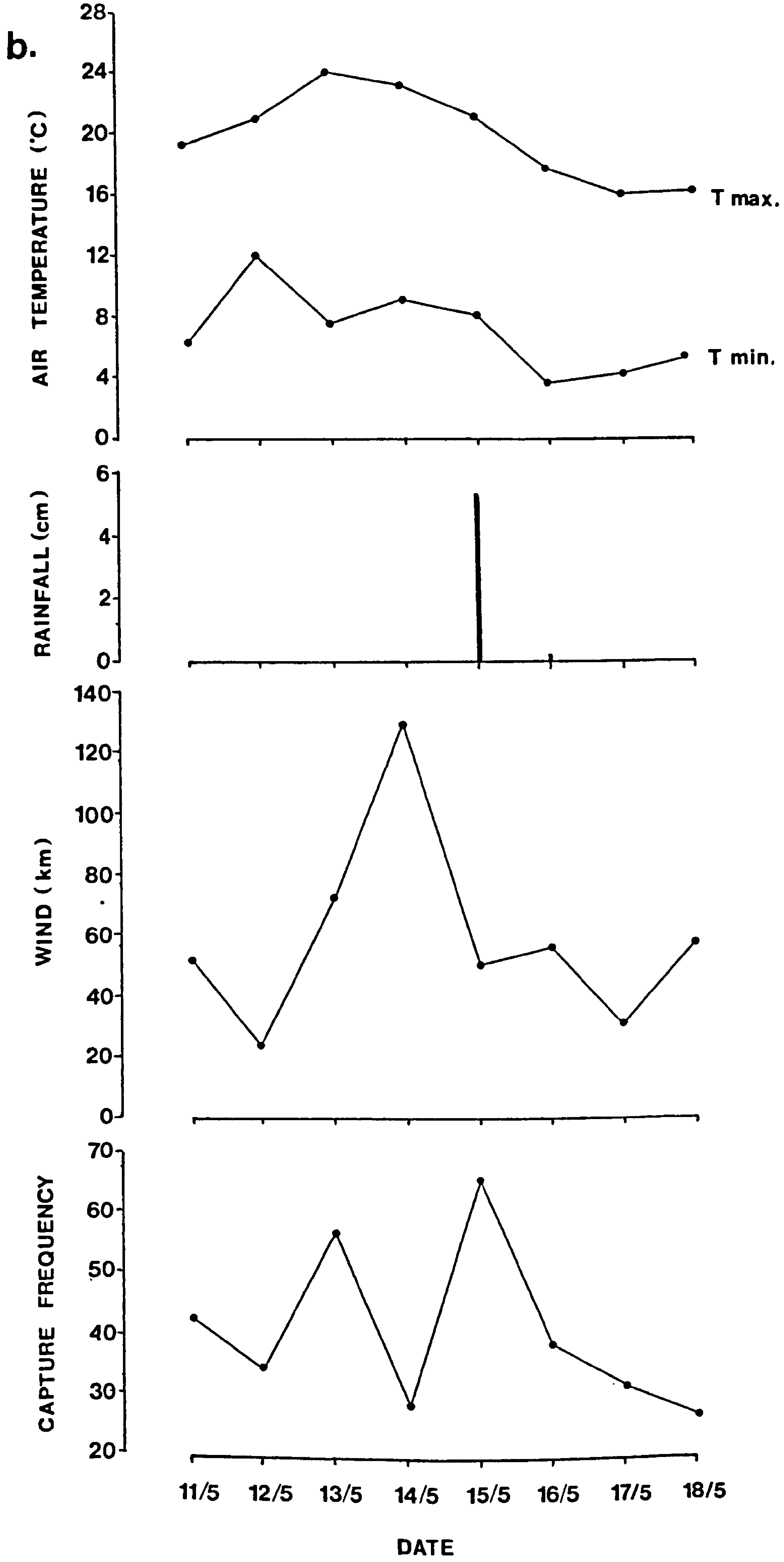
a. Sub area 1 (Pools 3,4,15)

b. Sub area 2 (Pools 1,2,20)

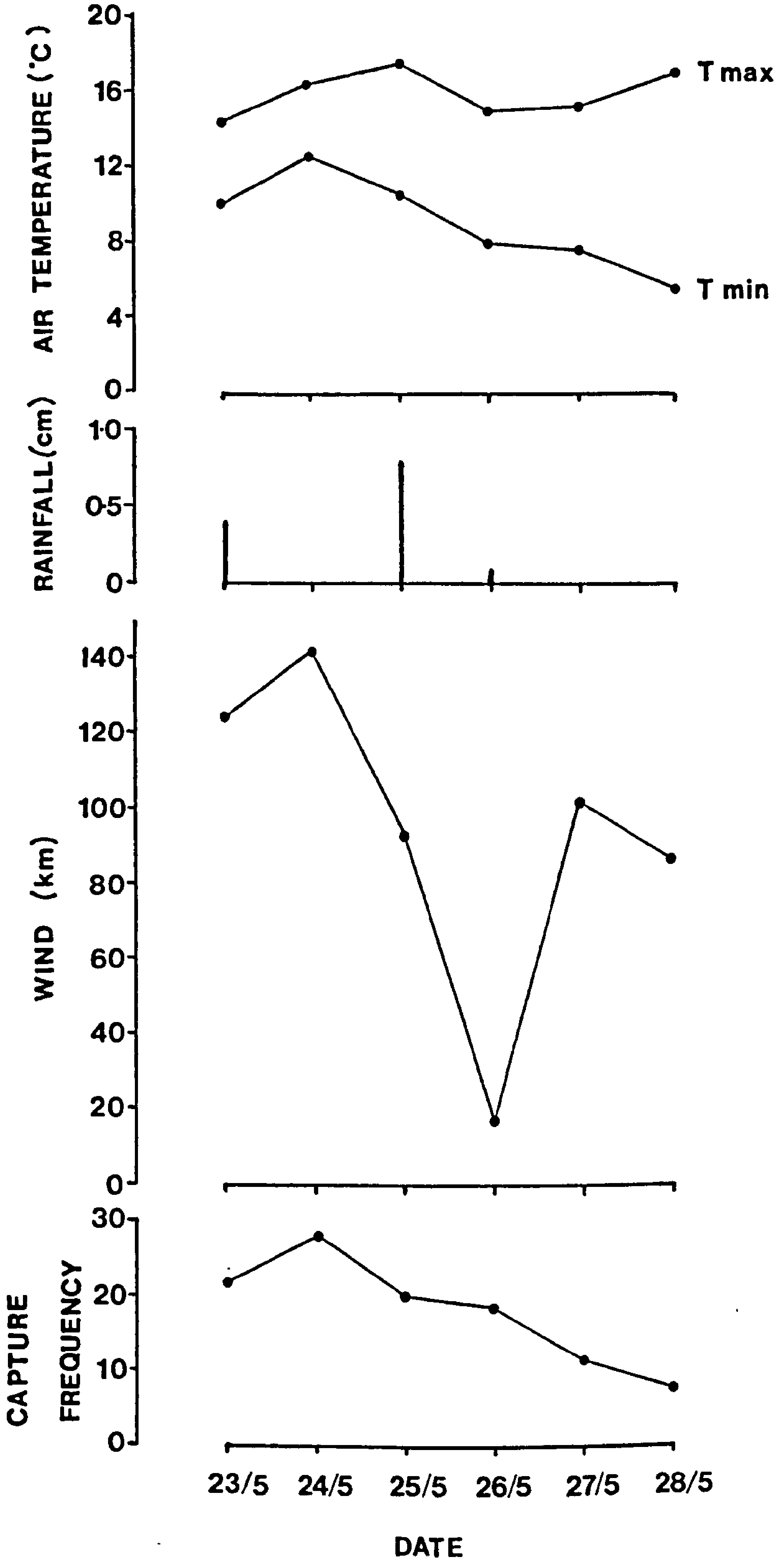
c. Sub area 3 (Pools 8,10,14,16)

a.


AIR TEMPERATURE (°C)
16
12
8
4
0
T max.
T min.
RAINFALL (cm)
1·0
0·5
0
WIND (km)
120
100
80
60
40
20
0
CAPTURE FREQUENCY
60
50
40
30
20
10
0
17/4
18/4
19/4
20/4
21/4
22/4
23/4
24/4
25/4
DATE


b.
AIR TEMPERATURE (°C)
28
24
20
16
12
8
4
0
T max.
T min.
RAINFALL (cm)
6
4
2
0
WIND (km)
140
120
100
80
60
40
20
0
CAPTURE FREQUENCY
70
60
50
40
30
20
11/5
12/5
13/5
14/5
15/5
16/5
17/5
18/5
DATE

c.


AIR TEMPERATURE (°C)
20
16
12
8
4
0
T max
T min
RAINFALL (cm)
1·0
0·5
0
WIND (km)
140
120
100
80
60
40
20
0
CAPTURE FREQUENCY
30
20
10
0
23/5
24/5
25/5
26/5
27/5
28/5
DATE

nights toads were difficult to capture, ceasing calling and hiding when approached.

Maximum population estimates for the 3 sub-areas were 420, 304, and 33 (Table 17). During the sampling periods only 6.6% of marked animals were found to move between sub-areas (Table 18). The population estimates were thus considered "isolated" values for each sub-area i.e. no significant mixing of the populations. Therefore, the maximum estimates were summed to give an overall estimate of 757 ± 212 breeding males at the site.

However, another interpretation of the results may be made. If it is assumed that N_2 is close to the true population value, the total number of animals using the site is given by N_2 plus the sum of entries during the sampling period:

$$T = N_2 + \Sigma B_i .$$

Negative values of B_i are biologically impossible (Begon, 1979) and are interpreted as the true value (close to 0) plus a negative error term. Thus negative values are considered to be zero. Using this method the population sizes of the three sub areas are 681 ± 182, 379 ± 97 and 52 ± 29 respectively, with a total of 1112 ± 208. This value is 47% greater than that calculated by the first method.

4.1.8 The 1983 survey

As in 1982, the proportion of recaptures was high (Table 19). Except for one occasion (day 2, sub-area 2) when only 10% of marked animals were caught, recapture rates varied from 31 to 61% and did not appear to fluctuate as greatly as in 1982. The weather data for

Table 18. Movements of toads between and within sub areas (1982)

Movements between pools

	From	To	Number of toads
Pool No.	1	16	3
	2	1	6
	3	4	3
	3	15	9
	4	1	2
	4	15	1
	8	14	2
	10	16	1
	15	1	5
	15	3	3
	15	4	3
	16	14	2
			40

Movements between sub-areas

		From Sub-area		
		1	2	3
To Sub-area	1	(19)	0	0
	2	13	-	0
	3	0	3	(5)

Table 18. (continued)

% Movements between sub-areas (expressed as a percentage of total marked per sub-area)

		From Sub-area		
		1	2	3
To Sub-area	1	(7.6)	0	0
	2	5.2	-	0
	3	0	1.4	(8.0)

Table 19. Computation of the 1983 data by Jolly's (1965) method

Sub area 1

i	R_i	M_i	N_i	$SE.N_i$	ϕ_i	$SE.\phi_i$	B_i	$SE.B_i$
1	-	0	-	-				
					1.064	0.162	-	-
2	0.315	228.8	721	130				
					0.704	0.197	161	93
3	0.382	257.4	668	188				
					-	-	-	-
4	0.407	-	-	-				

ϕ_o = 0.957   Life Expectancy = 22.89 days

Sub area 2

i	R_i	M_i	N_i	$SE.N_i$	ϕ_i	$SE.\phi_i$	B_i	$SE.B_i$
1	-	0	-	-				
					1.889	0.448	-	-
2	0.098	85.0	721	352				
					0.605	0.172	-308	198
3	0.562	73.8	129	34				
					0.566	0.139	29	26
4	0.366	49.7	132	31				
					0.921	0.192	3	56
5	0.553	69.7	124	29				
					1.349	0.638	21	29
6	0.614	117.0	189	87				
					-	-	-	-
7	0.579	-	-	-				

ϕ_o = 0.865   Life Expectancy = 6.91 days

For explanation of symbols see Table 16.

the sampling period is given in Fig. 9 together with the numbers of captures. As before, the trend was for fewer toads to be caught on cooler, windy nights. The higher rainfall during this period may have contributed to the increase in captures compared to 1982. Mathias (1971) and Smith & Payne (1980) note that toad breeding activity increases during or after a period of rain.

The maximum population estimates for the two sub areas were 721 (Table 19). However in sub area 2 the proportion of recaptures was only 9.8% when this maximum was calculated. On subsequent days the proportion of recaptures increased (mean = 52%) and the population estimates were not only reduced but showed greater similarity (mean = 143). Thus it seems more appropriate to accept the day 6 estimate ($N_i = 189$, $R_i = 61.4\%$) as being a more accurate estimate of maximum population size. Therefore the overall site maximum was 910 ± 156.

By ignoring the day 2 estimate for sub area 2, site usage was calculated thus:

$$T = N_3 + \Sigma B_i .$$

Calculation of site usage in sub area 1 was undertaken using the initial method described (see above). Thus, estimates of 882 ± 160 and 182 ± 76 were derived for the two areas. The total (1064) is 17% greater than the previous estimate (910).

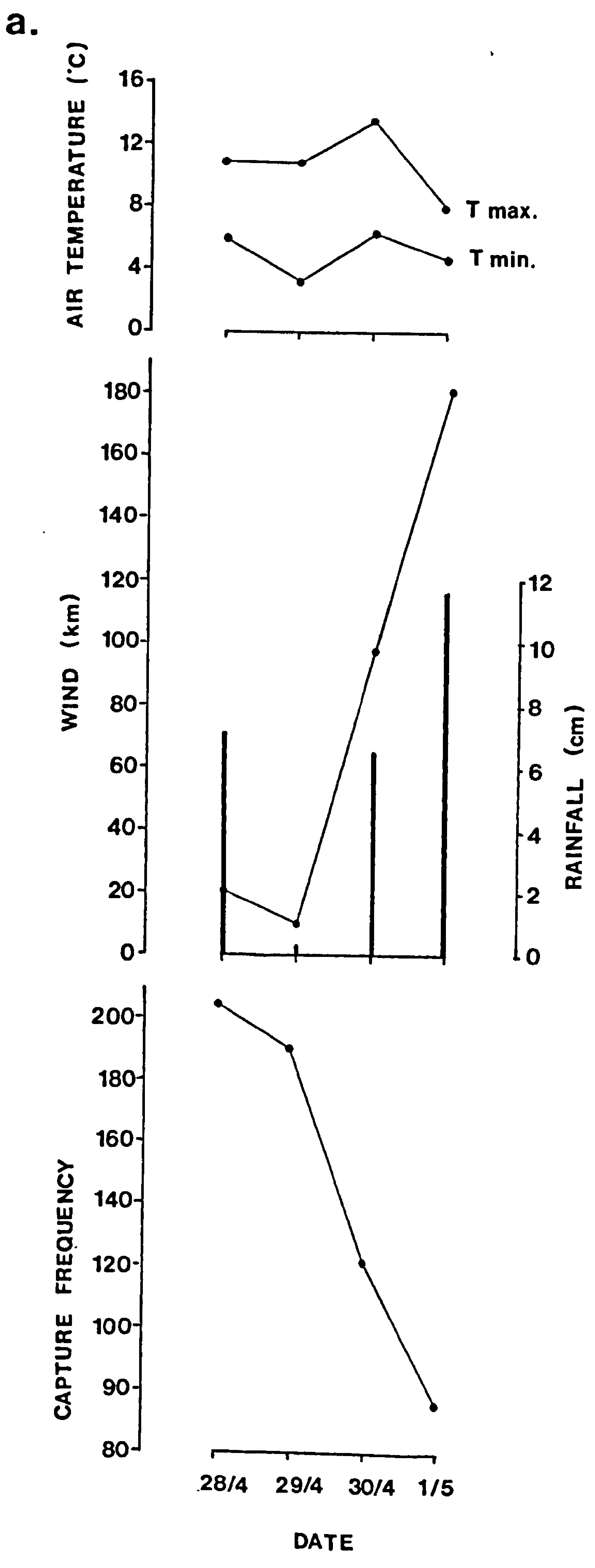
4.1.9 Summary of population estimates at Cabin Hill, 1981-83

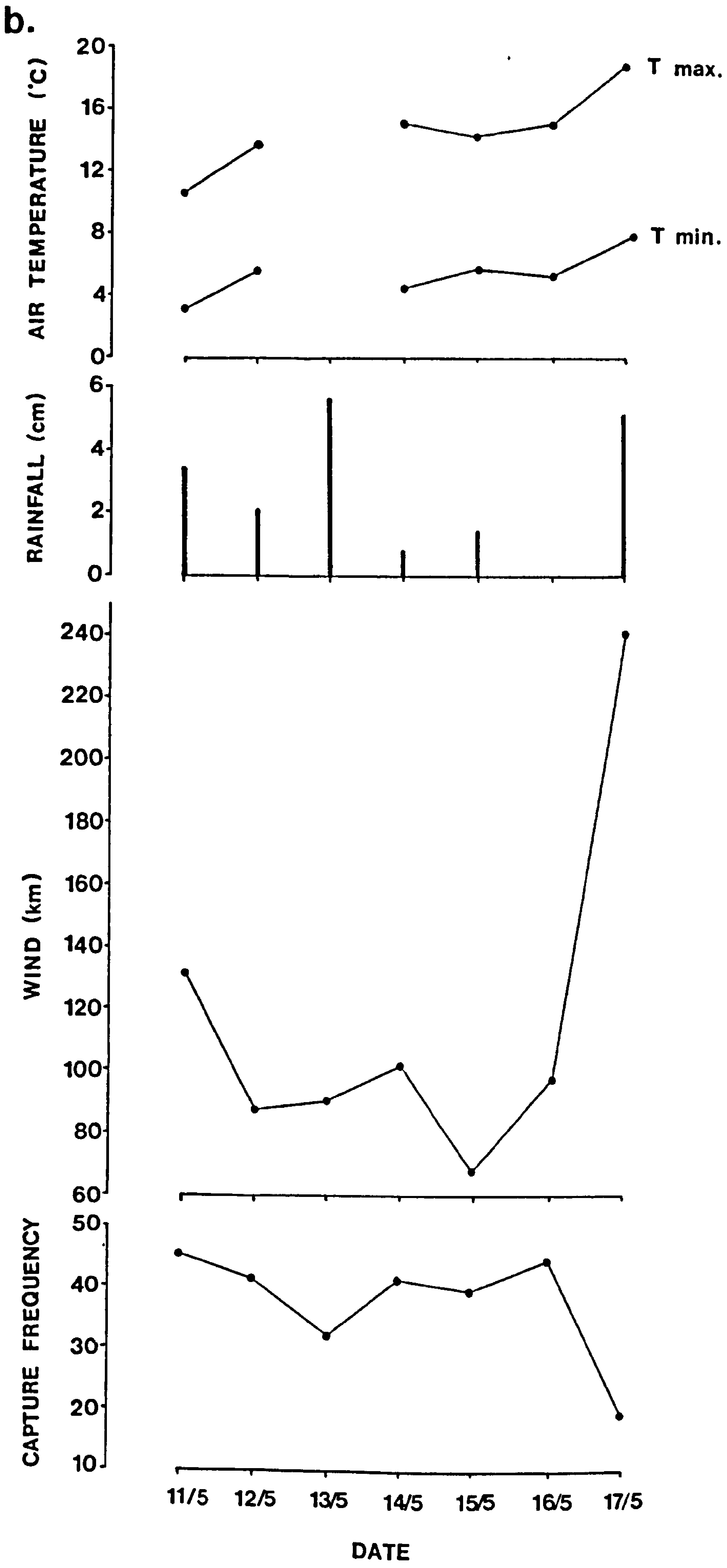
All population estimates are summarised in Table 20. It is important to note that these are not estimates of the total male population at Cabin Hill, but represent the number of individuals

Figure 9. The numbers of male captures and the prevailing weather conditions during the 1983 sampling programme.

a. Sub area 1 (Pools 1,2,3)

B. Sub area 2 (Pools 8,10,14,15,16)


a.
AIR TEMPERATURE (°C)
16
12
8
4
0
T max.
T min.
WIND (km)
180
160
140
120
100
80
60
40
20
0
RAINFALL (cm)
12
10
8
6
4
2
0
CAPTURE FREQUENCY
200
180
160
140
120
100
90
80
28/4
29/4
30/4
1/5
DATE


b.
AIR TEMPERATURE (°C)
20
16
12
8
4
0
T max.
T min.
RAINFALL (cm)
6
4
2
0
WIND (km)
240
220
200
180
160
140
120
100
80
60
CAPTURE FREQUENCY
50
40
30
20
10
11/5
12/5
13/5
14/5
15/5
16/5
17/5
DATE

taking part in breeding. Studies of ageing (section 4.3) suggest that these figures exclude the 1 year old population and part of the 2 year old population.

Table 20. Summary of population estimates at Cabin Hill, 1981-83 (breeding season males)

Year	M	Sub-area mark-recapture estimates	Total	Sub-area "ingress" estimates	Total	% difference
1981	519	1605 ± 884	1605 ± 884	-	-	-
1982	521	420 304 33 ± 174,± 116,± 33	757 ± 212	681 379 52 ± 182,± 97,± 29	1112 ± 208	46.90
1983	648	189 721 ± 87,± 130	910 ± 156	182 882 ± 76,± 160	1064 ± 177	16.92
Mean	563 ± 74		1090		1088	0.18
			834*			23.35

*Mean for 1982 and 1983 only.

The population estimates (Table 20) suggest that the male breeding population at Cabin Hill has remained fairly stable during the study period, with an overall mean of 1090 toads. This figure is only 0.2% greater than mean site usage during this period (1088). However an additional mean population has been calculated for 1982 and 1983 (Table 20). Using this value, mean population size and site usage differ by 23%. The larger population estimates for site usage result from calculations based upon the whole sampling period, as opposed to single maxima. Thus site usage may be closer to the true population size, although it is subject to errors of initial population size (N_2) and ingress (B_i). Therefore this method may not be preferable to summation of maximum population estimates.

The total sub-area maxima (Table 20) show an apparent 50% decrease in population size between 1981 and 1982, followed by a subsequent 20% increase. It is unclear whether these differences are due to actual changes in population size or are a result of sampling error. The mean sample sizes (numbers caught per day) were 15, 33, and 81 for the three years respectively. Comparison with data published by Begon (1979) suggest that the accuracies of population estimates were >0.5, 0.5 and 0.25 respectively. Therefore it seems likely that the differences in annual population estimates (Table 20) were due to a reduction in sampling error during the study period.

4.1.10 Recaptures between years

During 1982 and 1983 few toads marked in previous years were caught. In 1982, 3 males and 1 female marked in 1981 were recaptured, while in 1983, 4 males marked in 1981 and 1982 were captured. These recapture totals are low compared to previous studies. Mathias (1971) marked a total of 339 Natterjacks in 1968 and 1969 of which he recaptured 53 (16%) at least one year later. Of 118 toads marked in 1968, he recaptured 14 (12%) in 1969 and 8 (7%) in 1970. Similarly, of 536 toads marked by Smith & Flynn (1977), 84 (16%) were subsequently captured by Smith & Bownes (1978). Gittings (1983) studying Common Toads obtained recaptures of toads over 5 years. For example, he records that in 1982 15 males were caught bearing marks for each of the previous 4 years (initial number marked = 3873).

There are several possible explanations for my low recapture rates. First, there may be mortality due to the marking process. However it has been shown (present study and Wisniewski *et al*, 1980) that Panjetting causes little or no mortality. Secondly, the colour marks may be lost by rapid fading. However it was found that although marks on recaptured toads had faded, they were still discernible after two years. Dr. P. Gittings (pers. comm.) has found that colour marks on Common Toads remain visible for several years, although he notes that incorrect use of the Panjet may fail to leave a permanent mark.

A third explanation could be migration of toads between Cabin Hill and other Sefton coast populations. Smith & Bownes (1978) found that marked animals were captured up to 2.2 km from their original location, indicating that toads may not necessarily return to the same breeding pools in consecutive years.

Finally, there may be heavy natural mortality within the population, which if reflected in the samples, will reduce the numbers of marked toads available for future sampling. Studies of age structure in the Cabin Hill population (section 4.3) indicate this could be the explanation.

4.1.11 Female population size

As stated previously (section 4.1.1) behavioural differences between the sexes resulted in low captures of female Natterjacks, thus population size could not be estimated by mark-recapture analysis. However, indirect estimates of breeding females can be made, although studies of population age structure (section 4.3) indicate that 1, 2, and some 3 year olds do not breed.

Minimum breeding population size is given by the numbers of females caught annually. However, due to reduced probabilities of capture in relation to males, these figures represent minima which may be a small percentage of the true population size. Using this method, minimum estimates of 53, 43, and 118 (mean = 72) were obtained for the study years (Table 21).

Table 21. Female Natterjack population estimates at Cabin Hill, 1981-83 (Breeding season)

Method	1981	1982	1983	Mean ± 1 SD
Minimum size (No. of of Captures)	54	43	118	72 ± 41
Spawn counts	240	207	427	291 ± 119

Difficulties in relating spawn counts to female population size (Beebee, 1979a) have been discussed (Chapter 3). Daily searches for spawn minimised the likelihood of underestimates from failure to locate strings, and although 6 females were recaptured at the pools, there was no evidence for multiple spawning. This method gives estimates of 240, 207 and 427 females (mean = 291) for 1981-83 (Table 21).

The larger number of spawn strings in 1983 may have been partly due to immigration of individuals from the adjacent Raven Meols population. Smith (1983a) records that during early spring the pools at this site dried completely, although later reflooding allowed spawning. During the early part of the season toads may have migrated to Cabin Hill, attracted by olfactory (Oldham, 1967) or vocal cues (Arak, 1983). Alternatively, the increased number of spawn strings may reflect the entry of a particularly large cohort into the breeding population (section 4.3).

4.1.12 Sex ratios

Sex ratios were calculated using direct counts of both sexes, mark-recapture estimates of males, and spawn counts. The results are summarised in Table 22. Direct counts gave male:female ratios of 5.5-12.1:1 during the study period, with a mean of 9.1:1. An excess of males was also recorded by Mathias (1971), Smith and Flynn (1977) and Smith & Bownes (1978), their ratios being 10:1, 9.2:1 and 6.6:1 respectively. Similarly, Flindt & Hemmer (1968) found a sex ratio of 12:1 although they considered the true ratio to be approximately 4:1.

Table 22. Sex ratio of Natterjack breeding population at Cabin Hill 1981-1983 (Breeding season)

Year	Method		
	Direct counts	Pop. est:spawn counts	Site usage:spawn counts
1981	9.6:1	3.6:1	-
1982	12.1:1	3.8:1	5.5:1
1983	5.5:1	2.1:1	2.1:1
Mean	9.1:1	3.2:1	4:1

The ratios based upon male population estimates and spawn counts are lower than the previous estimates, ranging from 2.1-3.8:1 (mean = 3.2:1). Similar ratios were obtained from male site usage ($N_2 + \Sigma B_i$) and spawn counts. These suggested that male:female ratios were 5.5:1 in 1982 and 2.1:1 in 1983 (mean = 4:1).

4.2 Population estimation, Post-breeding season

Dune surveys began at the end of July each year, and continued until October. Sexes were determined by the presence or absence of nuptial pads (Smith, 1964) and by inspection of the ventral skin which is more rugose in females than males (Beebee, 1983a). Despite daily searches, few toads were caught. Capture totals for 1981-83 were 27, 131 and 59 respectively, with corresponding recaptures of 2, 8, and 2. This contrasts with preliminary surveys during the late 1970's by P.H. Smith (unpub. data) when daily captures of 56-167 toads were achieved. Factors responsible for the low captures appeared to be:

1. A recent increase in cover of *Ammophila arenaria* on the embryo dunes which interfered with searching (P.H. Smith pers. comm.).
2. A shortage of suitable objects such as driftwood for the toads to hide under compared to the late 1970's (P.H. Smith pers. comm.).

Mathias (1971) reported that during the day Natterjacks also shelter in tunnels at the base of the dunes. However, although tunnel entrances were found none were occupied. Capture data for the study period are summarised in Table 23.

Table 23. Summary of capture data, fore-dunes survey 1981-83

	1981		1982		1983	
	C	R	C	R	C	R
Males	12	1	42	4 (3)	15	2 (1)
Females	12	1	90	4 (4)	37	0
Immatures	3		0		7	
Total	27	2	132	8	59	2

C = captures

R = recaptures

Bracketed figures = number of individuals.

In 1982 and 1983 more females than males were caught. This contrasts with the breeding season when an excess of males was found. Thus, ♂:♀ ratios in the post breeding season were 1:1 (1981), 1:2.1 (1982), and 1:2.5 in 1983. (mean = 1:1.9). In all three years there were insufficient data for population estimation using Jolly's (1965) method. However, from the 1982 data it was possible to calculate an approximate index of population size using the weighted mean method described by Begon (1979). This is a simple method for estimating populations derived from the Lincoln Index (1930) and assumes a closed population (i.e. no immigration, emigration, births or deaths during the study period). Begon (1979) gives the expression:

$$N = \Sigma \frac{M_i n_i}{(\Sigma m_i) + 1}$$

where M_i = the number of marks released between day 1 and i.

n_i = sample size on day i.

m_i = the number of marks captured on day i.

with a standard error of:

$$SE_N = N \cdot \sqrt{\frac{1}{\Sigma m_i + 1} + \frac{2}{(\Sigma m_i + 1)^2} + \frac{6}{(\Sigma m_i + 1)^3}}$$

Capture data for 1982 and the computation of population estimates are given in Table 24. Using this method, the male and female populations were estimated as 171 ± 98 and 786 ± 450 respectively thus giving a sex ratio (♂:♀) of 1:4.6.

The estimated female population was greater than that estimated during the breeding season from spawn counts, although the standard error was large (57%) of the mean. Thus minimum and maximum estimates were 336 and 1236 respectively. However these estimates did not include 1st year toads therefore, as in the breeding season, the total female population is likely to be underestimated.

Summation of male breeding population estimates and female post-breeding season estimates suggested a population of 2 year old toads of approximately 1500-1900. Because some two year old males were not sampled in the breeding season, this was an underestimate. Also, first year toads were not included in this estimate. If the estimated number of toads metamorphosing in 1982 (2305-2823) is included (and no mortality assumed) the total population is estimated as approximately 4200-4700.

Table 24. Estimation of population size, 1982 Post-breeding season by the weighted mean method (Begon, 1979): see text for details

Total population

Date	12/7	13/7	14/7	19/7	26/7	3/8	4/8	11/8	12/8	13/8	19/8	27/8	3/9	7/9	10/9	17/9	
n_i	5	7	8	18	7	6	2	20	17	2	5	14	8	13	1	7	
m_i		0	0	0	1	3	0	0	1	0	0	0	0	2	0	1	$\Sigma = 8$
M_i		5	12	20	38	44	47	49	69	85	87	92	106	114	125	126	
$M_i n_i$		35	96	360	266	264	94	980	1173	170	435	1288	848	1482	125	82	$\Sigma = 8498$

$$\therefore N = \frac{8498}{9} = 944 \qquad SE_N = 944\sqrt{\frac{1}{10} + \frac{2}{11^2} + \frac{6}{12^3}} = 327$$

Table 24. (continued)

Female population

Date	12/7	13/7	14/7	19/7	26/7	3/8	4/8	11/8	12/8	13/8	19/8	27/8	3/9	7/9	10/9	17/9	
n_i	2	5	7	12	4	3	2	16	10	1	4	9	5	8	0	6	
m_i	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	1	$\Sigma = 4$
M_i		2	7	14	26	30	32	34	50	60	61	65	74	79	85	85	
$M_i n_i$		10	49	168	104	90	64	544	500	60	244	585	370	633	0	510	$\Sigma = 3931$

$$\therefore N = \frac{3931}{5} = 786 \qquad SE_N = 786\sqrt{\frac{1}{5} + \frac{2}{5^2} + \frac{6}{5^3}} = 450$$

Table 24. (continued)

Male population

Date	12/7	13/7	14/7	19/7	26/7	3/8	4/8	11/8	12/8	13/8	19/8	27/8	3/9	7/9	10/9	17/9	
n_i	4	2	1	6	3	3	0	4	7	1	1	5	3	5	1	1	
m_i		0	0	0	1	2	0	0	1	0	0	0	0	0	0	0	$\Sigma = 4$
M_i		3	5	6	12	14	15	15	19	25	26	27	32	35	40	41	
$M_i n_i$		6	5	36	36	42	0	60	133	25	26	135	96	175	40	41	$\Sigma = 856$

$\therefore N = \frac{856}{5} = 171$ $\qquad$ $SE_N = 171\sqrt{\frac{1}{5} + \frac{2}{5^2} + \frac{6}{5^3}} = 98$

4.3 Growth, population age structure and fecundity

4.3.1 Male and female body size

The length distributions of animals sampled during the 1981-83 breeding seasons are given in Fig. 10. Both sexes showed similar ranges of 41-73 mm although in 1981 and 1982 mean male length was lower than that of females (Table 25). Maximum recorded length for both sexes was 73 mm. This compares with Smith (1964) who recorded the largest British specimens as being Surrey males of 67-80 mm and an Irish female of 80 mm, although Cooke (1981) recorded male and female Natterjacks up to 80 mm at Saltfleetby. The weight distribution of animals sampled during the study are given in Fig. 11. Maximum recorded male weight was 35 g compared with 40 g for females. Mean lengths and weights (± 1 SD) for both sexes during the study years are given in Table 25. Length and weight data for all years were tested for equality (Table 26) and females found to be significantly larger ($p < 0.01$) and heavier ($p < 0.01$) than males.

Length and weight distributions for animals captured during the post-breeding season are given in Figs. 12 and 13. Data were pooled, and mean lengths and weights of animals during the post-breeding seasons (Table 27) tested for equality with breeding-season means (Table 28). Significant differences ($p < 0.01$) were found between means which suggested that although mean lengths of animals captured during the post-breeding seasons were signficantly lower than those during the breeding seasons, mean weights were significantly greater ($p < 0.01$).

The data for all years were pooled, and significant positive

Figure 10. Natterjack length distributions 1981-83, breeding season

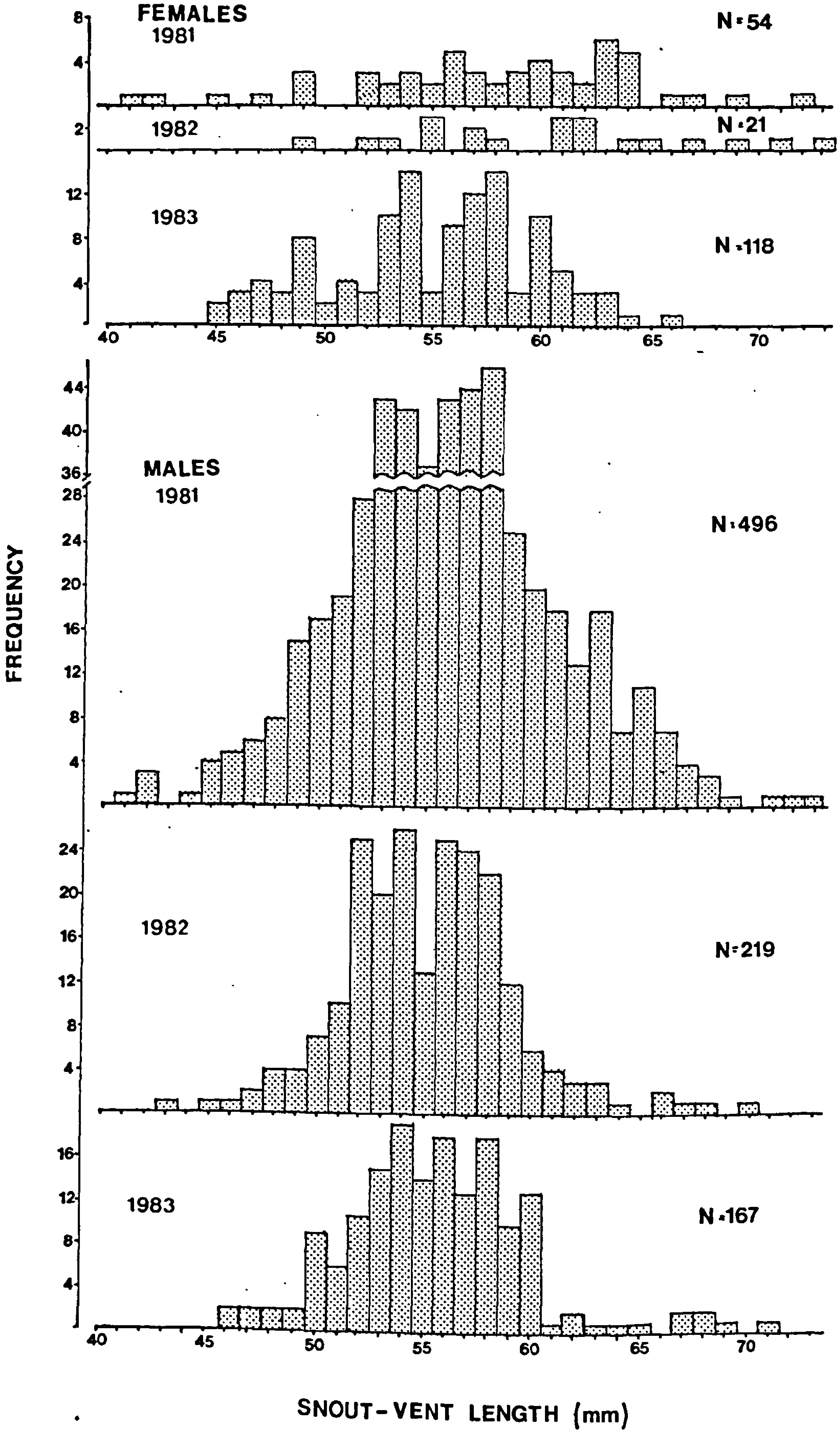

FEMALES
1981
N=54
1982
N=21
1983
N=118
MALES
1981
N=496
1982
N=219
1983
N=167
FREQUENCY
SNOUT-VENT LENGTH (mm)
40
45
50
55
60
65
70
8
4
2
12
8
4
44
40
36
28
24
20
16
12
8
4
24
20
16
12
8
4
16
12
8
4

Figure 11. Natterjack weight distributions 1981-83, breeding season.

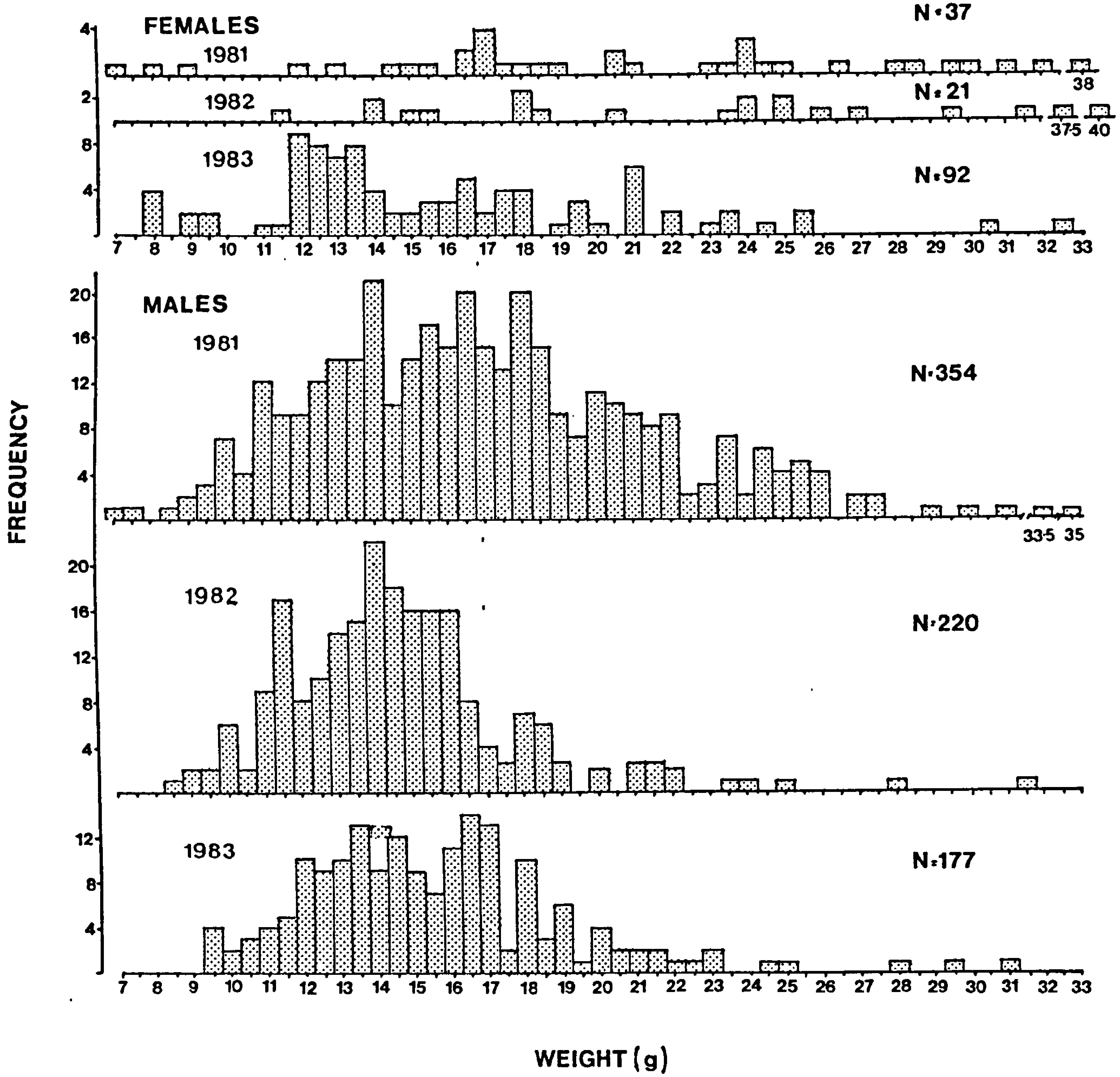

FEMALES
1981
N•37
38
1982
N•21
37·5
40
1983
N•92
MALES
1981
N•354
33·5
35
1982
N•220
1983
N•177
FREQUENCY
WEIGHT (g)
4
2
8
4
20
16
12
8
4
20
16
12
8
4
12
8
4
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33

Table 25. Mean weights and lengths of Natterjacks captured during the breeding season, 1981-83

		n	Mean weight ± 1 SD	n	Mean length ± 1 SD
Males:	1981	354	17.0 ± 4.5	496	56.1 ± 4.9
	1982	220	14.7 ± 3.2	219	55.2 ± 4.0
	1983	177	15.0 ± 3.4	167	56.6 ± 4.8
	Combined	751	15.9 ± 4.1	882	56.0 ± 4.7
Females:	1981	37	20.5 ± 7.3	54	57.8 ± 6.4
	1982	21	22.0 ± 6.4	21	60.4 ± 6.2
	1983	92	15.7 ± 4.7	118	55.2 ± 4.9
	Combined	150	15.9 ± 10.3	193	56.5 ± 5.7

Table 26. Anova for significant differences between male and female length and weight distributions

Males vs female weight

	Source of variation	df	SS	MS	F	p
1981	Among sexes	1	572.43	572.43	23.88	< 0.01
	Error	389	9323.11	23.97		
	Total	390	9895.54			
1982	Among sexes	1	1013.99	1013.99	77.25	< 0.01
	Error	239	3137.11	13.13		
	Total	240	4151.10			
1983	Among sexes	1	546.73	546.73	11.62	< 0.01
	Error	267	12562.36	47.05		
	Total	268	13109.09			

Males vs female length

	Source of variation	df	SS	MS	F	p
1981	Among sexes	1	127.51	127.51	4.94	< 0.05
	Error	548	14143.99	25.81		
	Total	549	14271.5			
1982	Among sexes	1	525.51	525.51	29.37	< 0.01
	Error	238	4259.09	17.90		
	Total	239	4784.60			
1983	Among sexes	1	136.96	136.96	5.90	< 0.05
	Error	283	6572.82	23.23		
	Total	284	6709.78			

Figure 12. Natterjack length distributions 1981-83, post-breeding season.

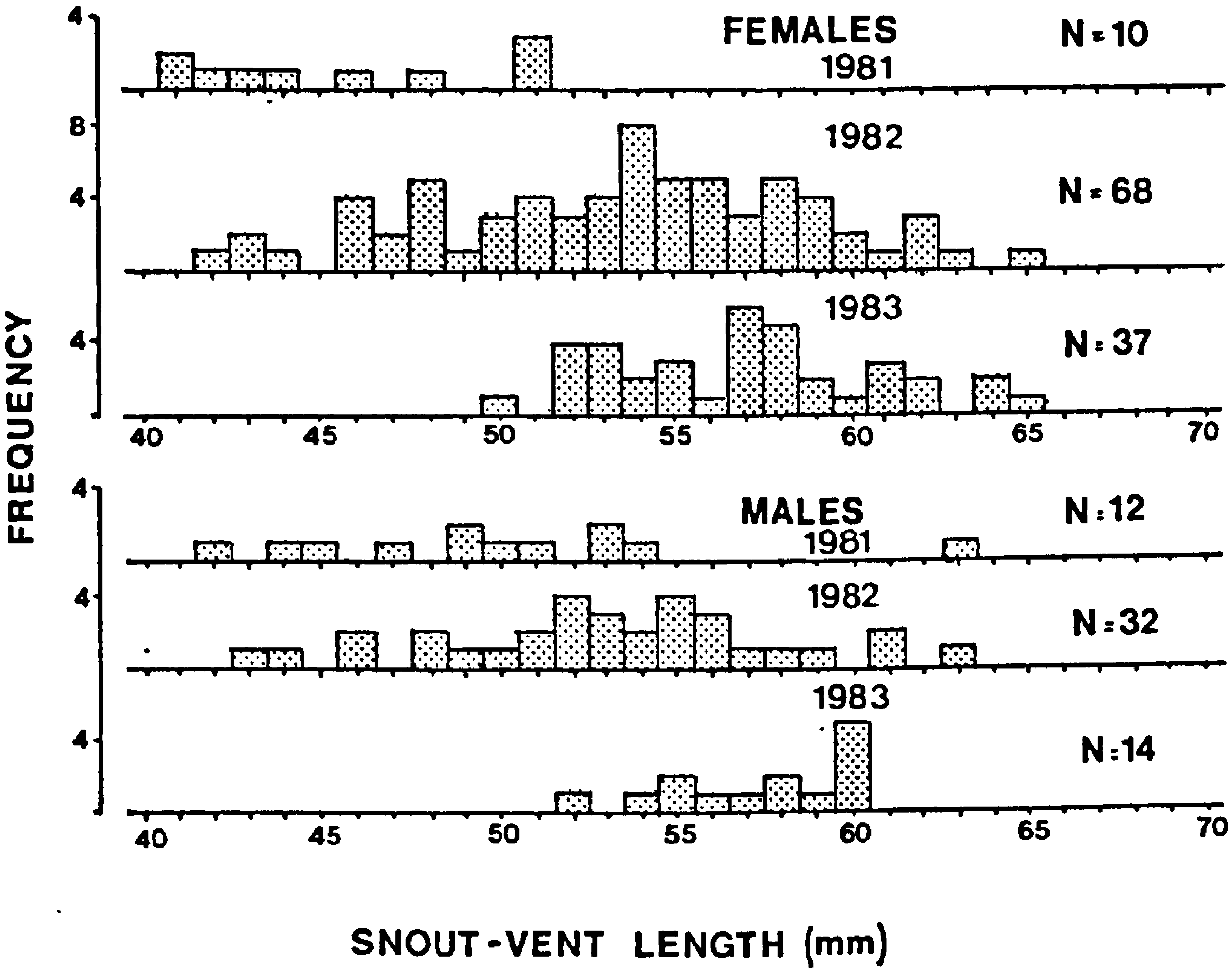

FREQUENCY
FEMALES
1981
N=10
1982
N=68
1983
N=37
MALES
1981
N=12
1982
N=32
1983
N=14
4
8
40
45
50
55
60
65
70
SNOUT-VENT LENGTH (mm)

Figure 13. Natterjack weight distributions 1981-83, post-breeding season.

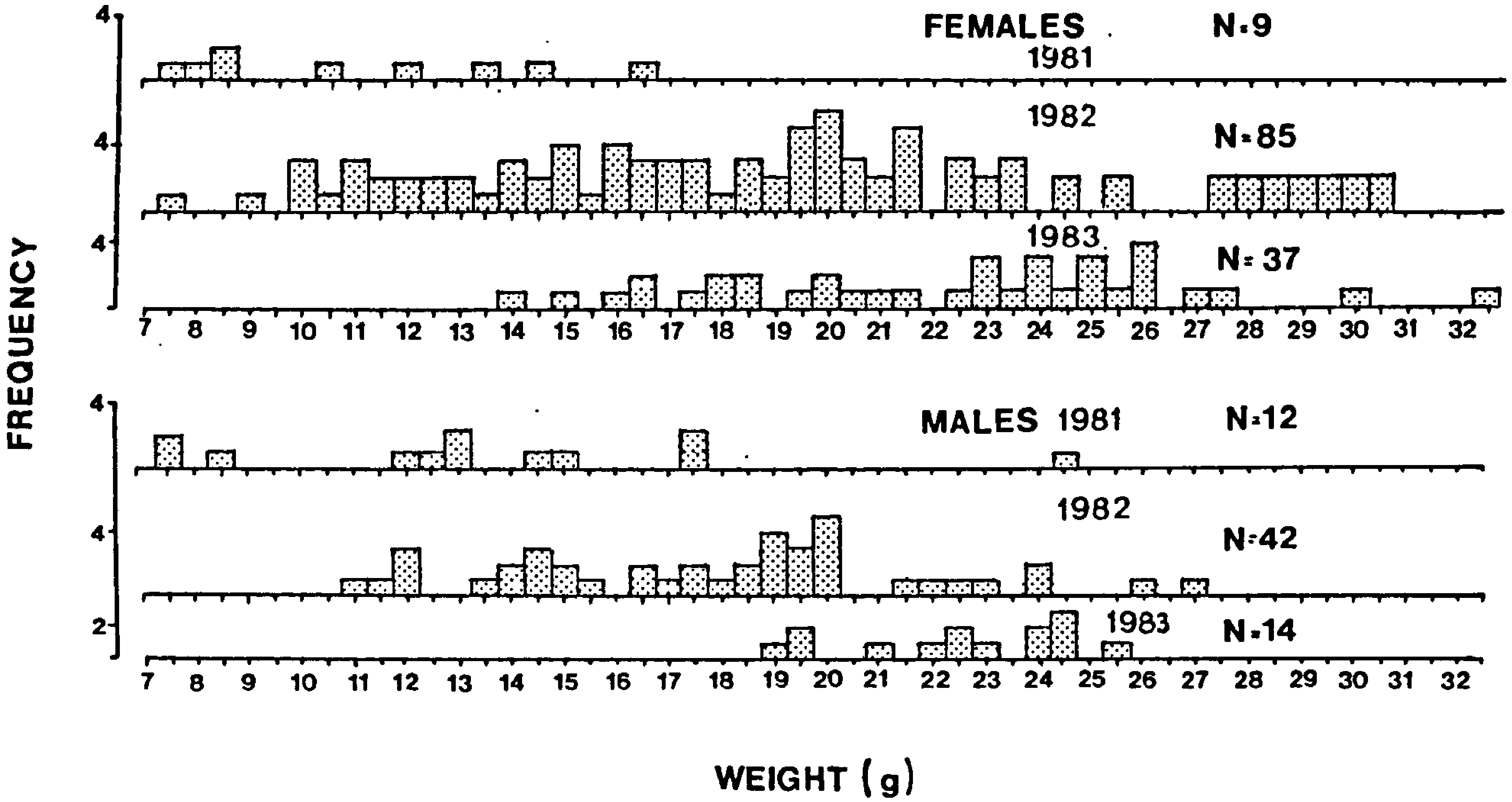

FEMALES
1981
N=9
1982
N=85
1983
N=37
MALES 1981
N=12
1982
N=42
1983
N=14
FREQUENCY
4
4
4
4
4
2
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
WEIGHT (g)

Table 27. Mean weights and lengths of Natterjacks captured during the post-breeding seasons, 1981-83

	n	Mean weight ± 1 SD	n	Mean length ± 1 SD
Males: 1981	12	13.6 ± 4.6	12	50.0 ± 5.3
1982	42	17.9 ± 3.9	32	53.1 ± 4.7
1983	14	22.6 ± 2.0	14	57.4 ± 2.6
Combined	68	18.1 ± 4.7	58	53.5 ± 5.1
Females: 1981	9	11.0 ± 3.0	10	45.8 ± 3.5
1982	85	18.5 ± 4.9	68	53.5 ± 5.3
1983	37	22.3 ± 4.2	37	57.0 ± 3.8
Combined	131	20.1 ± 5.4	115	54.0 ± 5.6

Table 28. Anova for significant differences between breeding and post-breeding season mean lengths and weights (Combined data for both sexes)

Male lengths

Source of variation	df	SS	'MS	F	p
Between seasons	1	343.29	343.29	15.39	< 0.01
Error	938	20925.45	22.31		
Total	939	21268.74			

Male weights

Source of variation	df	SS	MS	F	p
Between seasons	1	307.36	307.36	17.58	< 0.01
Error	817	14283.13	17.48		
Total	818	14590.49			

Female lengths

Source of variation	df	SS	MS	F	p
Between seasons	1	455.13	455.13	13.97	< 0.01
Error	306	9971.14	32.59		
Total	307	10426.27			

Female weights

Source of variation	df	SS	MS	F	p
Between seasons	1	714.43	714.43	10.18	< 0.01
Error	279	19585.08	70.20		
Total	280	20299.51			

correlations calculated between log. snout-vent length (SVL) and log. body weight (♀♀: $r = 0.957$, df = 108, $p < 0.001$; ♂♂: $r = 0.992$, df = 678, $p < 0.001$). Significant regressions (Table 29) were calculated using Sokal & Rohlf's (1969) method for multiple values of Y per X. These regressions (± 95% CL) are given in Fig. 14. Tests for equality revealed significant differences ($p < 0.001$) between regression coefficients (Table 30) and correlation coefficients (Table 31). Similar relationships between log. SVL and log. body weight were found for animals collected during the post-breeding season. Data were found to correlate significantly (♀♀: $r = 0.990$, df = 102, $p < 0.001$; ♂♂: $r = 0.994$, df = 55, $p < 0.001$), and significant regressions calculated (Table 29). These are given (± 95% CL) in Fig. 15. However there were no significant differences between regression coefficients (Table 30) or correlation coefficients (Table 31) suggesting that the relationships between log. SVL and log. body weight are the same for both sexes during the post-breeding season. This contrasts with the breeding season when female Natterjacks are significantly heavier than males of equivalent size. This is probably due to the presence of spawn in the females. Frazer (1982) suggests that in Common Toads the relationship between SVL and (dry) body weight is the same for both sexes although he does not specify whether this refers to the breeding or post-breeding season.

4.3.2 Age analysis of Natterjacks

Natterjack phalangeal sections have a similar appearance to that reported in other studies of bufonids (Hemelaar & Van Gelder, 1980; Hemelaar, 1981). Thus as Gittings *et al* (1982) describe, resting lines were seen as darkly stained bands alternating with light pink growth

Table 29. Anova of growth parameters (log. SVL vs. log. body weight) and significance of calculated regression lines

1. ♀♀: Breeding season (b = 3.0, a = -4.01)

Source of variation	df	SS	MS	F	p
Among groups (log. length)	26	1.902	0.073	21.02	< 0.001
Linear regression	1	1.744	1.744	276.78	< 0.001
Deviations from regression	25	0.158	0.006	1.80	> 0.05
Error	82	0.285	0.004		
Total	108	2.187			

2. ♂♂: Breeding season (b = 2.70, a = -3.52)

Source of variation	df	SS	MS	F	p
Among groups	30	6.238	0.208	75.15	< 0.001
Linear regression	1	6.140	6.140	1805.97	< 0.001
Deviations from regression	29	0.098	0.008	1.20	> 0.05
Error	648	1.793	0.002		
Total	678	8.031			

3. ♀♀: Post-breeding season (b = 3.02, a = -3.97)

Source of variation	df	SS	MS	F	p
Among groups	22	1.556	0.071	47.47	< 0.001
Linear regression	1	1.528	1.528	835.40	< 0.001
Deviations from regression	21	0.038	0.002	1.20	> 0.05
Error	80	0.122	0.001		
Total	102	1.688			

Table 29. (continued)

4. ♂♂: Post-breeding season (b = 2.91, a = -3.80)

Source of variation	df	SS	MS	F	p
Among groups	18	0.828	0.046	17.33	< 0.001
Linear regression	1	0.802	0.802	522.64	< 0.001
Deviations from regression	17	0.026	0.001	< 1	> 0.05
Error	37	0.098	0.002		
Total	55	0.916			

Figure 14. The relationship between SVL and body weight (logarithmic data) for male and female Natterjacks during the breeding season. Broken lines indicate ± 95% confidence limits to the regression.


MALES n =679
LOG. Y= 2·7 LOG. X − 3·52
FEMALES n=109
LOG.Y= 3LOG. X −4·01
WEIGHT (g) LOG. SCALE
SNOUT-VENT LENGTH (mm) LOG. SCALE
10
20
30
40
40
50
60
70
80

Table 30. F-test for difference between regression coefficients (log. SVL vs. log. body weight). From Sokal & Rohlf (1969)

$$F = \frac{(b_1 - b_2)^2}{\dfrac{\Sigma x_1^2 + \Sigma x_2^2}{(\Sigma x_1^2)(\Sigma x_2^2)} \cdot \bar{s}^2_{Y.X}}$$

$$\text{where } \bar{s}^2_{Y.X} = \frac{\Sigma y_1^2 - \dfrac{(\Sigma xy)_1^2}{\Sigma x_1^2} + \Sigma y_2^2 - \dfrac{(\Sigma xy)_2^2}{\Sigma x_2^2}}{n_1 + n_2 - 4}$$

∴ substitution gives:

1. ♀♀ Breeding season vs ♂♂ breeding season

$$F = \frac{(3.0 - 2.7)^2}{\dfrac{0.842 + 0.194}{0.842 \times 0.194} \times 0.001} = 10.81$$

$df = 1,784;\ p < 0.01$

2. ♀♀ Post-breeding season vs ♂♂ post-breeding season

$$F = \frac{(2.91 - 3.02)^2}{\dfrac{0.094 + 0.167}{0.094 \times 0.167} \times 0.0004} = 1.65$$

$df = 1,155;\ p > 0.05$

Table 31. t-test for differences between correlation coefficients (log. SVL vs. log. body weight)

♀♀ Breeding season: $r = 0.958$, $n = 109$

♂♂ Breeding season: $r = 0.843$, $n = 679$

♀♀ Post-breeding season: $r = 0.984$, $n = 56$

♂♂ Post-breeding season: $r = 0.988$, $n = 103$.

From Sokal and Rohlf (1969):

$$t = \frac{z_1 - z_2}{\sqrt{\frac{1}{n_1 - 3} + \frac{1}{n_2 - 3}}} \qquad \text{where } z = \frac{1}{2} \ln. \left(\frac{1 + r}{1 - r} \right)$$

(compare with $t_{\alpha[\infty]}$)

∴ substitution gives:

	♂♂ BS	♀♀ BS	♂♂ PBS	♀♀ PBS
♂♂ BS	-			
♀♀ BS	8.14***	-		
♂♂ PBS	2.46*	2.96**	-	
♀♀ PBS	2.08*	4.50***	0.76 NS	-

where *: $p < 0.05$

**: $p < 0.01$

***: $p < 0.001$

Figure 15. The relationship between SVL and body weight (logarithmic data) for male and female Natterjacks during the post-breeding season. Broken lines indicate ± 95% confidence limits to the regression.


MALES n=56
LOG.Y = 2·91 LOG.X − 3·8
FEMALES n=103
LOG.Y = 3·02 LOG.X − 3·97
WEIGHT (g) LOG. SCALE
SNOUT-VENT LENGTH (mm) LOG. SCALE
10
20
30
40
40
50
60
70
80

regions of periosteal bone. In some sections, partial resorption of the first (innermost) resting line was observed. Hemelaar (1981) showed that resorption could result in underestimation of age. She found that 85% of Common Toads showed no resorption, and although 9% showed partial resorption the lines were still discernible. A further 4% could be determined by considering the width and pattern of rings, the remaining toads being underestimated by not more than 1 year.

The age distributions of samples are given in Fig. 16. The oldest males and females sampled were 6 and 7 years respectively. However these results are based upon a small sample (33 ♂♂; 47 ♀♀) and it is possible that older individuals may be present in the population. For example, Smith (1964) records a Natterjack living 15½ years in captivity, and Smith & Flynn (1977) found toads apparently marked between 1968-70 by Mathias (1971).

Investigating *R. pretiosa*, Turner (1960) found that annual growth increments decreased yearly after metamorphosis. For example, during the first full year after metamorphosis, length increased by 10 mm compared to 3 mm during the fourth year. Thus in the present study, following Sokal & Rohlf (1969), a logarithmic transformation of the independent variable (age) was used. Both sexes showed significant correlations between SVL and log. age (♂♂: $r = 0.963$, $df = 33$, $p < 0.001$; ♀♀: $r = 0.985$, $df = 46$, $p < 0.001$) and significant regression equations (Table 32) were calculated. These are shown (± 95% CL) in Fig. 17. Tests for equality revealed significant differences ($p < 0.05$) between regression coefficients (Table 32) and correlation coefficients.

Similarly, significant correlations were found between weight and

Figure 16. Age distributions of male and female Natterjacks sampled at Cabin Hill.

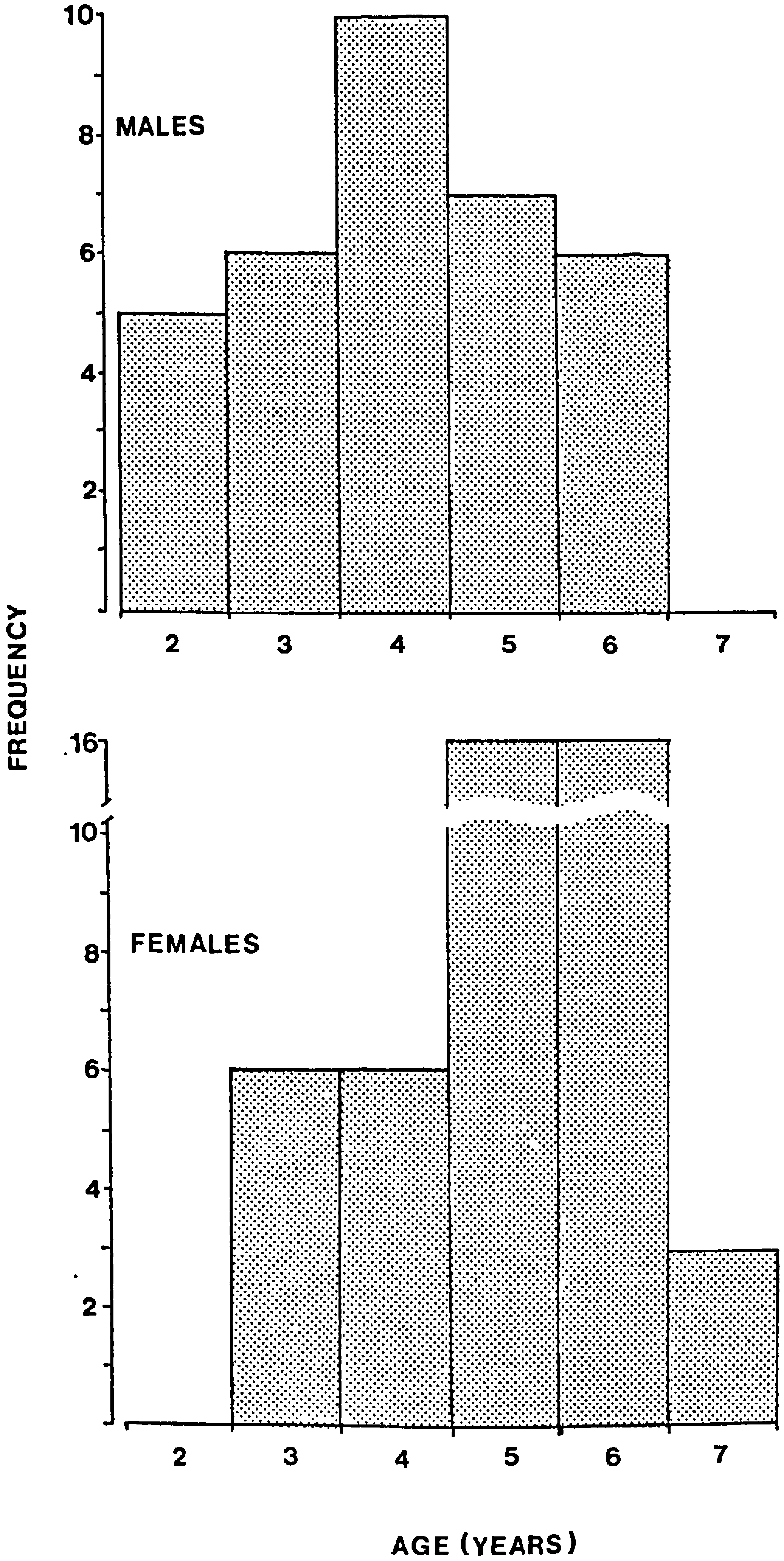

10
8
6
4
2
MALES
2
3
4
5
6
7
FREQUENCY
16
10
8
6
4
2
FEMALES
2
3
4
5
6
7
AGE (YEARS)

Figure 17. The relationship between age and length (semi-logarithmic data) for male and female Natterjacks. Broken lines indicate ± 95% confidence limits to the regression.

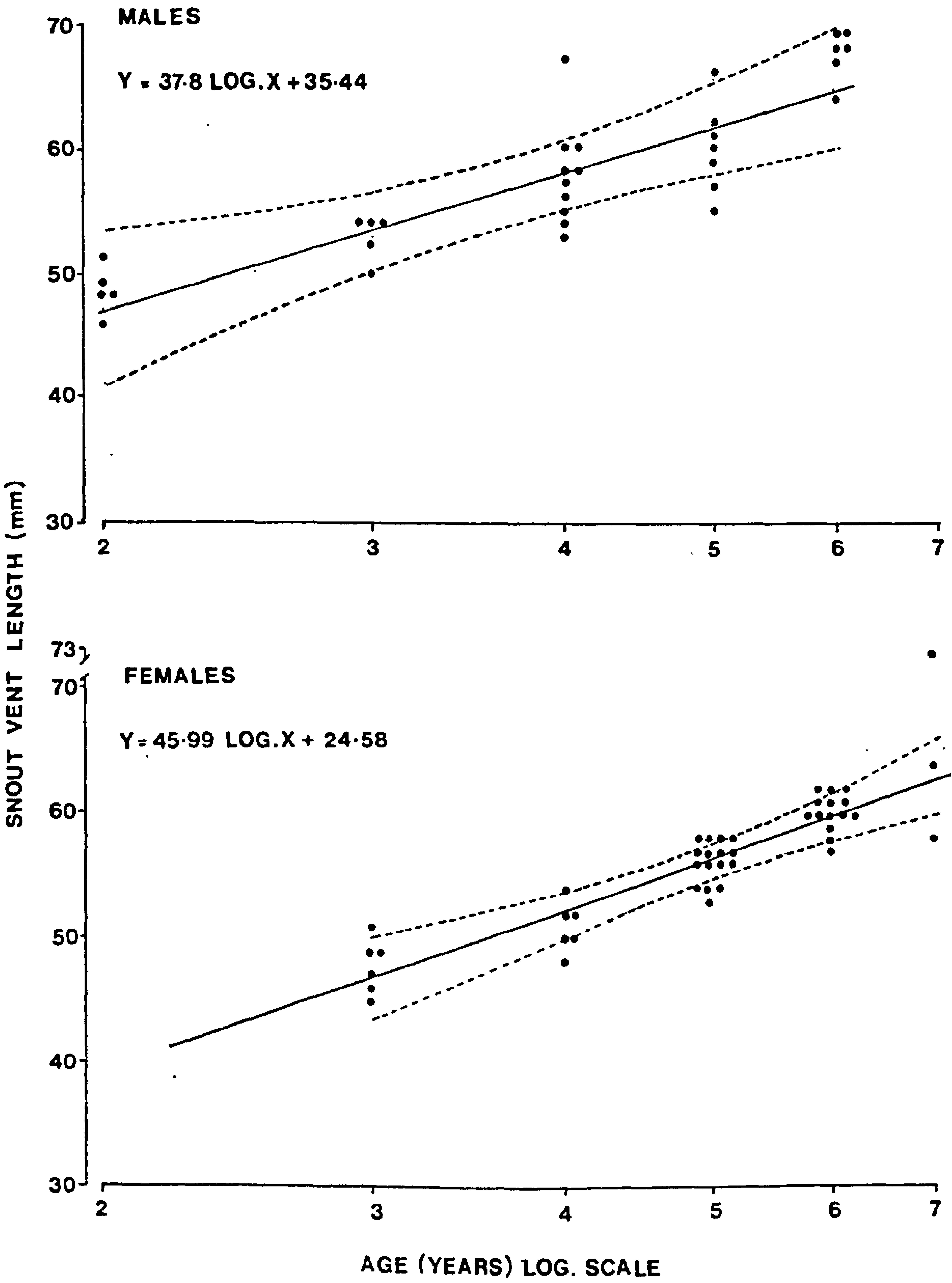

MALES
Y = 37·8 LOG.X + 35·44
70
60
50
40
30
2
3
4
5
6
7
FEMALES
Y = 45·99 LOG.X + 24·58
73
70
60
50
40
30
2
3
4
5
6
7
SNOUT VENT LENGTH (mm)
AGE (YEARS) LOG. SCALE

Table 32. F-test for significance of calculated regression lines (log. age vs. length) and comparison of regression coefficients; t-test for comparison of correlations

1. ♂♂: Log. age vs. length (b = 37.80, a = 35.44)

Source of variation	df	SS	MS	F	p
Among ages	4	1218.46	304.62	32.70	< 0.01
Linear regression	1	1130.22	1130.22	38.42	< 0.01
Deviations from regression	3	88.24	29.41		
Error	29	269.57	9.30		
Total	33	1488.03			

2. ♀♀: Log age vs length (b = 45.99, a = 24.58)

Source of variation	df	SS	MS	F	p
Among ages	4	1122.68	280.67	45.16	< 0.01
Linear regression	1	1089.86	1089.86	99.60	< 0.01
Deviations from regression	3	32.83	10.94	1.76	> 0.05
Error	42	261.02	6.31		
Total	46	1383.70			

Comparison of regression coefficients (method as in Table 30)

$$F = \frac{(45.99 - 37.80)^2}{\frac{0.791 + 0.515}{0.791 \times 0.515} \times 1.572} = 13.32$$

$df = 1,77, p < 0.01$

Comparison of correlation coefficients (method as in Table 31)

$$t = \frac{(2.41 - 1.94)^2}{\sqrt{\frac{1}{33} + \frac{1}{46}}} = 2.07 \quad p < 0.05$$

age (♂♂: $r = 0.987$, $df = 32$, $p < 0.001$); ♀♀: $r = 0.985$, $df = 26$, $p < 0.001$) and significant regressions (Table 33) calculated. These are shown (± 95% CL) in Fig. 18. Tests for equality revealed a significant difference between regression coefficients ($p < 0.001$, Table 33) but not between correlation coefficients ($p > 0.05$).

The results suggest that there are significant differences in growth patterns between male and female Natterjacks, with males both larger and heavier than females for a given age, although for any given length females are heavier than males (see above). By extrapolation, it is predicted that 1 year old males (during the 'breeding season') measure 35 mm and weigh 6.5 g, whereas females measure 24 mm and weigh 1.3 g. However, predictions of female weight are difficult, as female weight data used for regression analysis included spawn weight. The relationship between weight and age may alter markedly after spawning. Cooke (1981) suggested that Natterjacks entering hibernation for the first time measure 30 mm. The results from the present study seem to confirm this, suggesting that 1 year old toads measure 24-35 mm.

4.3.3 Population age structure

Difficulties were encountered in determining population age structure. In a stable population, the age distribution within a random sample reflects that of the population. The age distribution of samples taken from Cabin Hill (Fig. 16) suggest modal frequencies of 4, and 5 and 6 years for males and females respectively. However sample sizes were relatively small, and unconscious attempts to sample all ages/sizes of animals may have led to non-randomness of capture. Therefore

Figure 18. The relationship between age and weight for male and female Natterjacks. Broken lines indicate ± 95% confidence limits to the regression.

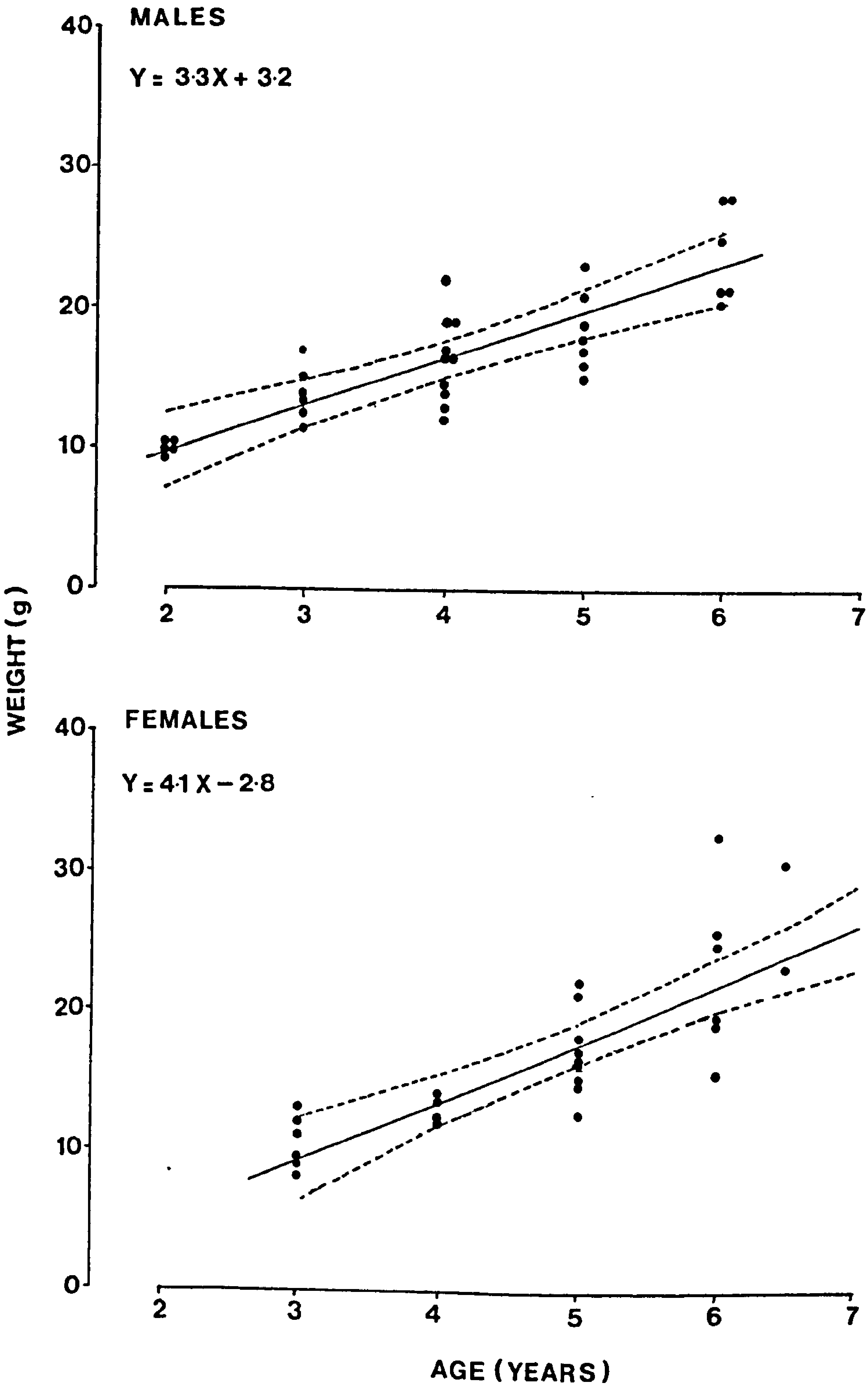

MALES
Y = 3·3X + 3·2
FEMALES
Y = 4·1X − 2·8
WEIGHT (g)
AGE (YEARS)
0
10
20
30
40
2
3
4
5
6
7

Table 33. F-test for significance of calculated regression lines (age vs. weight) and comparison of regression coefficients t-test for comparison of correlations

1. ♂♂: Age vs. weight (b = 3.30, a = 3.18)

Source of variation	df	SS	MS	F	p
Among ages	4	624.57	156.14	21.97	< 0.01
Linear regression	1	605.54	605.54	95.47	< 0.01
Deviations from regression	3	19.03	6.34	< 1	> 0.05
Error	28	198.95	7.10		
Total	32	823.52			

2. ♀♀: Age vs. weight (b = 4.13, a = -2.82)

Source of variation	df	SS	MS	F	p
Among ages	4	712.42	178.10	12.83	< 0.01
Linear regression	1	694.49	694.49	116.20	< 0.01
Deviations from regression	3	17.93	5.98	< 1	> 0.05
Error	22	305.43	13.88		
Total	26	1017.85			

Comparison of regression coefficients (method as in Table 30)

$$F = \frac{(4.13 - 3.30)^2}{\frac{40.66 + 55.51}{40.66 \times 55.51} \times 0.66} = 24.48$$

df = 1,56, p < 0.01

Comparison of correlation coefficients (method as in Table 31)

$$t = \frac{(2.44 - 2.36)^2}{\sqrt{\frac{1}{26} + \frac{1}{32}}}$$

size frequency data (Fig. 10) were re-analysed using MacDonald & Pitcher's (1979) method for separating age-distribution mixtures. Initial attempts to separate age groups graphically (Cassie, 1954) proved unsuccessful as the size distributions were not distinctly polymodal. However, MacDonald & Pitcher (1979) suggest that their method is 'more powerful' than graphical techniques, particularly if actual values from an aged sub-sample are known. A copy of the program was obtained from Dr. T.J. Pitcher, Bangor University, and run on a DEC-20 computer.

The program is interactive and consists of approximately 900 FORTRAN statements. The user enters initial estimates of mean lengths (± 1 SD) and the proportions present in the population of each age group. The program then uses alternate proportion estimations and Nelder-Mead (1965) calculations for optimisation of means and standard deviations. Final values are estimated by maximum likelihood iteration. Chi-square values are generated to test the model against observed frequency data. The results of this analysis are given in Table 34, together with estimated lengths from histological studies (see above). The analysis of male Natterjacks will be considered first.

Significant mixture fittings ($p > 0.05$) (Table 34) were obtained for all data and there appears to be close agreement with predicted mean lengths calculated from histological studies. For all years there seems to be an increase in the proportion of 3 and 4 year old toads relative to 2 year olds. For example, analysis of the 1981 data indicates that the breeding population contained 43% of 3 year olds compared with only 2% of 2 year olds (Table 34) suggesting that males enter the breeding population over 2 years. This compares with studies

Table 34. Summary of results from MacDonald & Pitcher (1979) mixture analysis, male and female Natterjacks 1981-83 (" means value fixed as above)

Sample	n	Proportions ± 1 SE					Means					Standard deviation ± 1 SE					χ^2	df	p
		π_1	π_2	π_3	π_4	π_5	μ_1	μ_2	μ_3	μ_4	μ_5	σ_1	σ_2	σ_3	σ_4	σ_5			
Males 1981	496	0.02	0.43	0.47	0.06	0.01	50	54	58	63	69	8	4	4	3	6	22.45	23	p>0.5
		0.01	0.08	0.11	0.11	0.46	"	"	"	"	"	9	2	7	3	10			
Males 1982	219	0.14	0.37	0.37	0.09	0.03	51	53	58	61	67	3	1	1	2	2	12.87	18	p>0.5
		0.04	0.07	0.05	0.03	0.01	"	"	"	"	"	1	1	1	1	1			
Males 1983	167	0.18	0.40	0.33	0.03	0.03	50	54	58	61	67	3	2	2	2	2	14.64	16	p>0.5
		0.12	0.08	0.07	0.06	0.03	"	"	"	"	"	1	1	1	1	1			
'True' values							47	54	58	62	65								
Females (combined)	203	0.12	0.13	0.40	0.22	0.13	48	53	58	59	62	2	1	2	8	1			
		0.03	0.06	0.12	0.10	0.07	"	"	"	"	"	1	1	1	2	1	22.76	19	p>0.5
'True' values							48	52	56	60	65								

π_1 - π_5 : Estimated proportions of age groups present in the population. μ_1 - μ_5 : Estimated mean lengths (mm) of toads in year groups.

σ_1 - σ_5 : Standard deviations of estimated mean lengths for toad year groups. Standard errors of estimates shown below given values.

of Common Toads by Gittings *et al* (in press) who found an increase in males entering the breeding population between 2 and 3 years of age. They suggested that the observed distribution is due to a combination of mortality and maturation, with age of maturation affecting younger individuals most, whereas older individuals are most affected by mortality. They found a 50% mortality rate in the declining phase of the age distribution which agreed with a mortality rate of 48% calculated for the same population using mark-recapture data (Gittings, 1983).

Natterjack mortality was estimated using static life tables (Table 35) constructed by multiplying estimates of population size (Table 20) by the proportions of age groups present. Population mortality may also be investigated using 'Cohort' or 'Parallel' life tables (Krebs, 1978) however this method did not seem appropriate due to the 'lower precision' of 1981 population estimates. Although static life tables may prove useful in determing age-specific mortality rates, mortality will be underestimated where age-groups are not fully represented (Krebs, 1978). Thus, mortality rates of 2 year old Natterjacks (Table 35) should be ignored as unrepresentative of the true mortality in this age group. Similarly, mortality of 1 year olds can not be calculated. Furthermore, this method assumes that, after maturation, all individuals attempt to breed, whereas the age distribution may represent different reproductive strategies operating within the population. For example, if individuals are active breeders for a few years only, rather than sustaining breeding throughout their lives, their apparent mortality would be overestimated. Age-specific mortality rates calculated for Cabin Hill Natterjacks are shown graphically in Fig. 19.

Table 35. Estimated life tables for male Natterjacks, 1981-83

1981

Age_x	n_x	a_x	$l_x 1000$	d_x	q_x
1	0	1588	1000	0	0
2	32	1588	1000	1	0.001
3	690	1556	999	454	0.45
4	754	866	545	474	0.87
5	96	112	71	61	0.85
6	16	16	10	10	(1)
7 (6+)	0				

1982

Age_x	n_x	a_x	$l_x 1000$	d_x	q_x
1	0	757	1000	0	0
2	106	757	1000	140	0.14
3	280	651	860	370	0.43
4	280	371	490	370	0.76
5	68	91	120	90	0.75
6	23	23	30	30	(1)
7 (6+)	0				

1983

Age_x	n_x	a_x	$l_x 1000$	d_x	q_x
1	0	919	1000	0	0
2	164	919	1000	178	0.18
3	364	755	822	397	0.48
4	328	391	425	356	0.84
5	27	63	69	30	0.43
6	36	36	39	39	(1)
7 (6+)	0				

Table 35. (continued)

where n_x = Estimated number of individuals in the population

a_x = Estimated number alive each year

$l_{x_{1000}}$ = Standardised number surviving at the start of age interval x

d_x = Standardised number dying between x and x + 1

q_x = Mortality rate

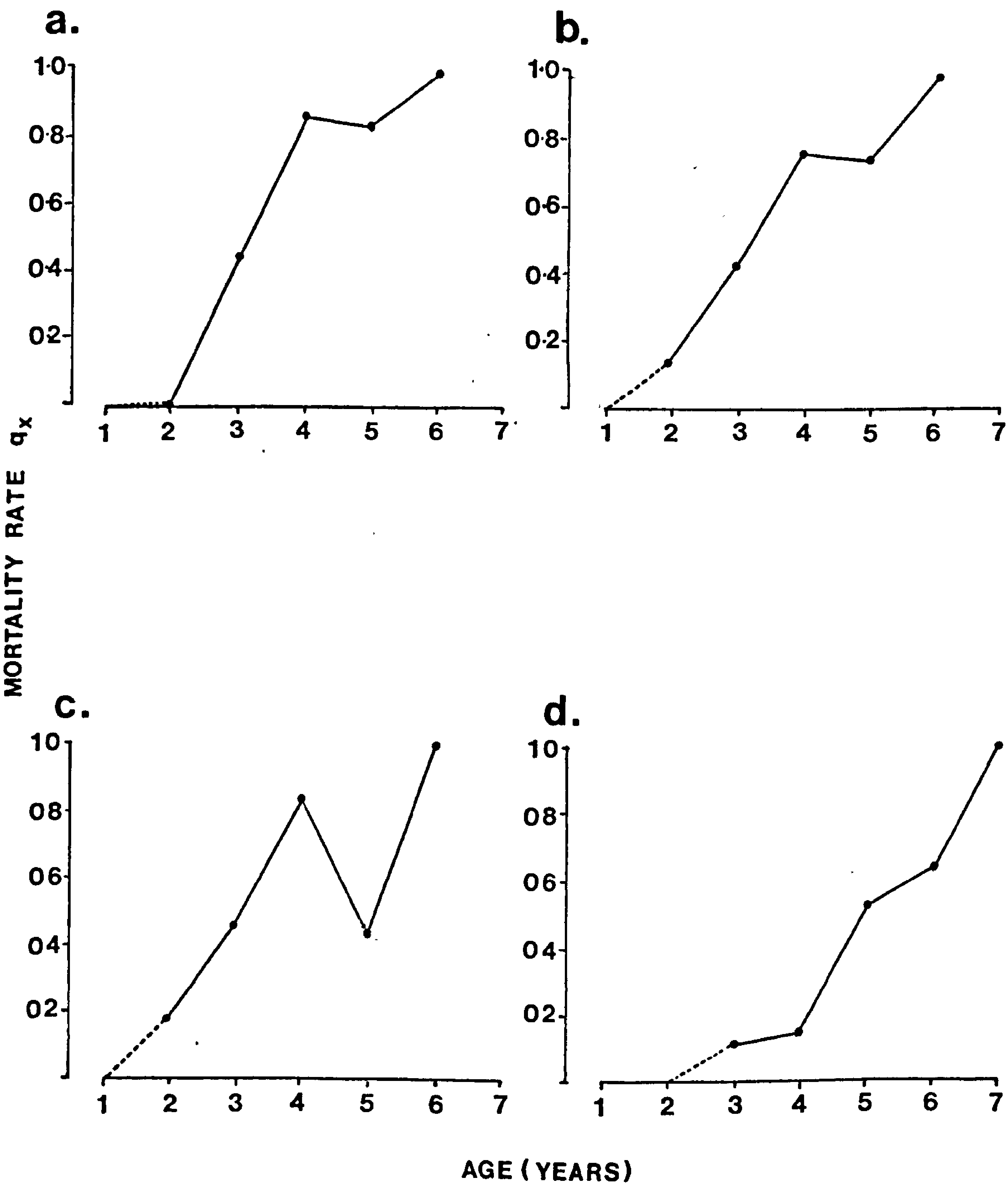
Figure 19. Age specific mortality rates (q_x) for male and female Natterjacks.

a. Males, 1981

b. Males, 1982

c. Males, 1983

d. Females, 1983


a.
b.
c.
d.
1·0
0·8
0·6
0·4
0·2
1
2
3
4
5
6
7
MORTALITY RATE q_x
AGE (YEARS)

In the 'descending arm' of the age distribution (i.e. > 3 years) mortality apparently increases from 43-48% in 3 year olds to 75-87% in 4 and 5 year olds. The 1983 results (Fig. 19c) suggest that mortality decreases to 43% in 5 year old toads. However this seems likely to be due to data error - the age distribution (Table 34) suggests that the number of 5 year old toads (n_5) is less than 6 year old toads (n_6). This is the opposite of trends in 1981 and 1982 (i.e. $n_5 > n_6$). The results suggest that there is no increase in mortality for 4 and 5 year old toads. Caution must be used in assuming 100% mortality of 6 year old toads (Table 35). These results are based upon MacDonald & Pitcher (1979) mixture fittings for 5 age groups (i.e. maximum male age = 6 years) and does not take account of animals living beyond this.

The high mortality rates of 4 and 5 year old Natterjacks relative to Common Toads (Gittings, 1983) compare with previous estimates for Natterjacks. Using published data for a Zurich population (Heusser & Meisterhans, 1969), Hemmer & Kadel (1971) suggested that these animals showed an annual mortality rate of 90%, and that the mean maximum age was 4 years. However, Hemmer & Kadel (*op. cit.*) found that a population near Bauseheim, containing individuals up to 12 years old, had an annual mortality rate of 28%. High mortality rates have been reported for other anuran species. For example, Green (1957) found that *Pseudacrys brachyphona* showed a constant age-specific mortality of 70%. Similarly Blair (1968), investigating *B. valliceps*, reported annual mortalities of 88, 59, and 89% (mean=79%) for male toads during the first three years after metamorphosis. He also found mortality rates of 94, 18 and 67% (mean = 60%) for female toads. Clarke (1977) studying *B. woodhousei fowleri* found an estimated annual mortality rate of 70%, and Kelleher & Tester (1969) reported annual mortalities of 59-70% for *B. hemiophrys*.

If age-specific mortality is constant in Cabin Hill Natterjacks (at 75-87%), as has been reported for other anurans (Green, 1957; Clarke, 1970), the results imply that there is a large number of 3 year old males which are not represented in the breeding population, and which which do not enter until they are 4 years old. This may be due to an extended maturation period, compared to Common Toads which are fully mature after 3 years (Gittings *et al*, in press). There is, however, an alternative explanation. Smith & Flynn (1977) showed that the number of toads present at a breeding pool is positively correlated with length of shoreline. Arak (1983) attributes this to territoriality, larger males being more strongly teritorial than smaller males. Thus there may be a 'carrying capacity', i.e. a limit to the number of calling sites. Older males will be able to exploit these more successfully than younger ones, although 'satellite' behaviour (Arak, 1983) of younger individuals may modify this pattern. Thus a proportion of the total 3 year old population may be forced to wait a year until calling sites become available due to mortality of "incumbent" toads. A combination of high mortality (75-87%) and the arrival of unmarked 3 and 4 year old toads could explain the low number of recaptures experienced between years during this study.

However, if it is assumed that all male Natterjacks have completed maturation and entered the breeding population after 3 years, as has been observed in Common Toads (Hemelaar & Van Gelder, 1980; Gittings *et al*, in press) it appears that there is an approximate doubling of mortality between 3 year old (40-43%) and 4 and 5 year old toads (75-87%) (Fig. 19). It is possible that this increase in mortality may be related to some form of stress causing differential mortality effects between age classes (Tester & Breckenridge, 1964). For example, the extended breeding seasons and high levels of vocal activity may result in large expenditures of energy by males, contrasting with Common Toads which have a relatively short ('explosive') breeding season and do not vocalise to attract females (Smith, 1964). Energy expenditure by Natterjacks may be particularly important if feeding is reduced during the breeding season (Mathias, 1971). Older, possibly more active toads may find it increasingly difficult to make up this energy loss during the post-breeding season, thus experiencing heavier mortality during hibernation. Although a literature review does not reveal any studies on anuran energy expenditure during breeding which might confirm this, there is some supporting evidence from Arak (1983) who found that males experienced up to 20% weight loss during breeding, larger males showing relatively greater weight loss than smaller males. If mortality in Natterjacks is related to 'reproductive stress' this would result in increased longevity when adverse conditions reduce annual breeding activity. It is difficult to confirm this as previous reports of population size and recruitment as Cabin Hill tend to be qualitative, however possible evidence for this hypothesis is an observation by Smith (1977) that 500-1000 males took part in breeding that year. This represented an apparent population increase which was observed throughout the Sefton coast (P.H. Smith, pers. comm.) despite the fact that breeding and recruitment in the late 1960's and early 1970's had been very poor (Smith *et al*, 1974). These were apparently old toads which had survived this period and were thus able to take advantage of a suitably high water-table in 1977 to breed.

A life table was constructed for female Natterjacks (Table 36) by

Table 36. Estimated Life table for female Natterjacks, 1981-83 (combined data)

Age	n_x	a_x	l_x1000	d_x	q_x
3	35	291	1000	120	0.12
4	38	256	880	131	0.15
5	116	218	749	398	0.53
6	64	102	351	220	0.63
7	38	38	131	131	(1)
8 (7+)	0				

For explanation of symbols see Table 35.

combining data for mean population size/spawn numbers (Table 21) and the proportions of age groups present in the population (Table 34). Age-specific mortalities are shown graphically in Fig. 19d.

The MacDonald & Pitcher (1979) mix-fittings (Table 34) suggest that the maximum numbers of females do not appear within the population until they are 5 years old. This contrasts with studies of Common Toads by Gittings *et al* (in press) who found that females matured between 3 and 6 years, although 4 year old females represented the largest proportion of the breeding population. If female Natterjacks do tend to forgo breeding until they are 5 years old, this may be due to an extended maturation period, or a 'choice' to undertake a low frequency of reproduction. Bull & Shine (1979) have described iteroparous anurans (*B. americanus*, *B. woodhousei*, *R. pretiosa*) that 'skip' opportunties for reproduction , thus increasing average fecundity and reducing mortality associated with reproduction.

Study of Fig. 19d suggests that mortality of 5 and 6 year old females (53-63%, mean = 58%) is lower than males (75-87%). These estimates compare with 60% mortality in female Common Toads based upon mark-recapture data (Gittings, 1983), although studies of age distribution in the same population suggest an annual mortality rate of 70-75% (Gittings *et al*, in press). If mortality in Natterjacks is related to 'reproductive stress' the apparently lower rate in females could be due to shorter periods of breeding activity compared to males (Smith, 1964) or to missing breeding opportunities. Of course, females may still encounter reproductive stress through egg production.

Natterjack mortality seems unlikely to be due to sustained predation of the species. Smith (1964) and Frazer (1983) describe predation of Natterjacks by Grey Herons (*Ardea cinerea*), Wigeon (*Anas penelope*), Blackheaded Gulls (*Larus ridibundus*) and Brown Rats (*Rattus norvegicus*), but both authors state that predation mainly occurs in the breeding season. In 1981, 30 male Natterjacks were found around pools, 1, 3 and 18 which had been killed and disemboweled, apparently by Greater Black-Backed Gulls (*L. marinus*). However, these were isolated incidents and no sustained predation was observed, indeed low predation rates of adult Natterjacks seem likely due to the production of toxic bufonins within the skin (Beebee, 1983a) which deter predators.

Smith (1964) describes mortality in Common Toads due to myiasis by the Greenbottle (*Bufolucilia bufonivora*), however there is apparently no infection of Natterjacks. Smith notes that the eggs of this fly have been found on Common Frogs, but there are no records of subsequent mortality. Frazer (1983) describes parasites (*Nematotaenia dispar*, *Plistophora* sp.) which may kill Common Toads but gives no indication whether these affect Natterjacks.

4.3.4 Female age and fecundity

Eleven spawning females were measured and their eggs counted. Following Hemmer & Kadel (1971) log. egg number was significantly correlated with log. SVL ($r = 0.699$, $df = 10$, $p < 0.05$) and a significant regression (Table 37) calculated. The regression (± 95% CL) is shown in Fig. 20.

Similarly, log. egg number was found to be significantly correlated with log. body weight ($r = 0.768$, $df = 10$, $p < 0.01$), and a significant regression (Table 37) calculated. The regression (± 95% CL) is shown in Fig. 20.

Table 37. F-test for significance of the regressions log. egg no.vs. log. SVL and log. egg no. vs log. body wt

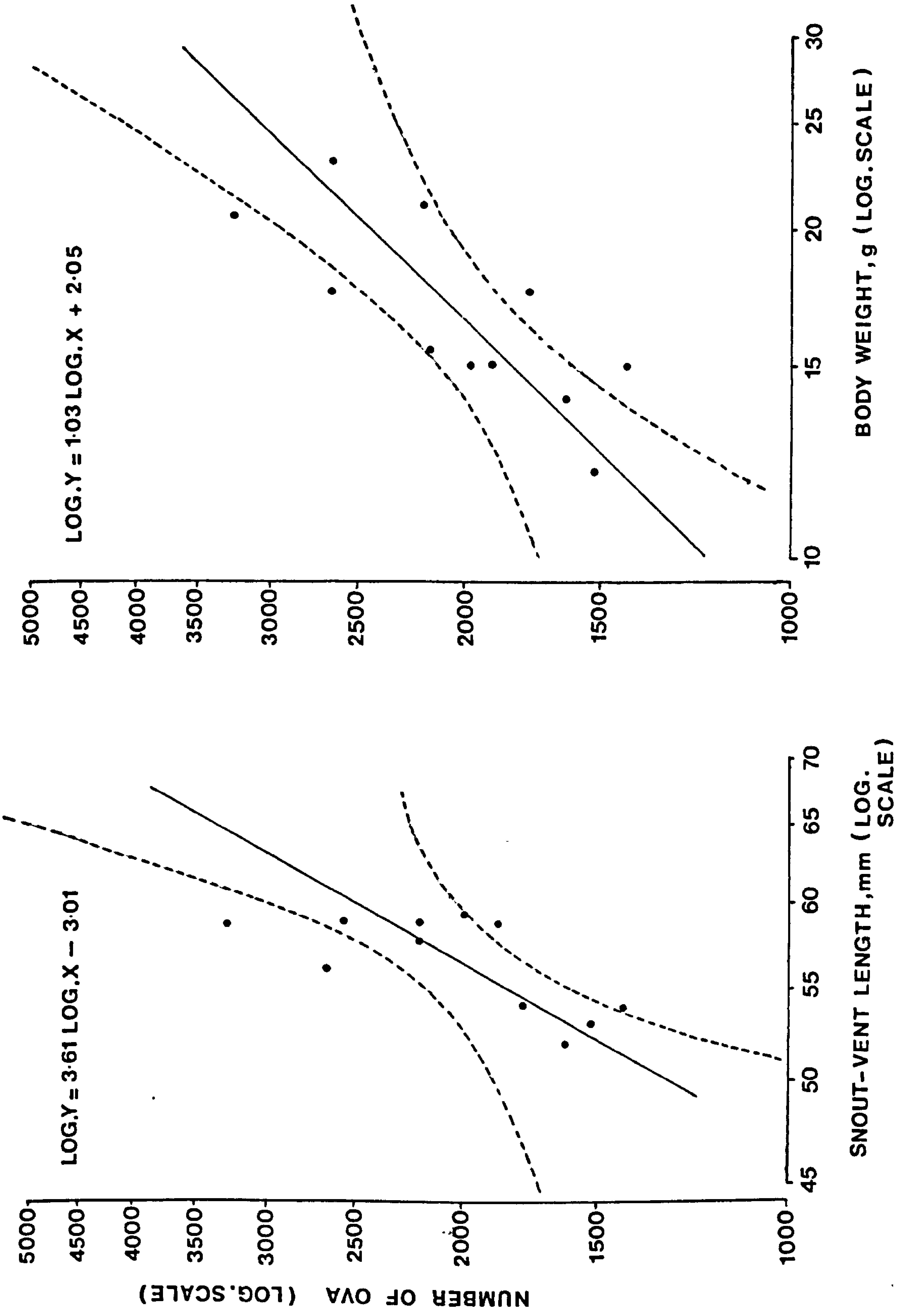
1. Log. egg number vs. log SVL $b = 3.61$ $a = -3.02$

Source of variation	df	SS	MS	F	p
Linear regression	1	0.062	0.062	8.63	< 0.05
Residuals	9	0.065	0.07		
Total	10	0.127			

2. Log. egg number vs. log body weight $b = 1.03$ $a = 2.05$

Source of variation	df	SS	MS	F	p
Linear regression	1	0.074	0.074	12.98	< 0.01
Residuals	9	0.052	0.005		
Totals	10	0.126			

Figure 20. The relationship between fecundity and body length (logarithmic data) and fecundity and body weight (logarithmic data) for Natterjacks. Broken lines indicate ± 95% confidence limits.



LOG.Y = 1·03 LOG.X + 2·05
BODY WEIGHT, g (LOG. SCALE)
10
15
20
25
30
LOG.Y = 3·61 LOG.X − 3·01
SNOUT-VENT LENGTH, mm (LOG. SCALE)
45
50
55
60
65
70
NUMBER OF OVA (LOG. SCALE)
1000
1500
2000
2500
3000
3500
4000
4500
5000

Previous workers gave estimates of egg production (e.g. Mertens, 1964; Kowalewski, 1967; Curry-Lindahl, 1974; Kadel, 1975) however, these were mean number of eggs per spawn string at their respective sites. Hemmer & Kadel (1971) showed that egg production was directly proportional to female body size, therefore mean spawn size at a site would depend upon the population age and size composition.

My results are similar to those of Hemmer & Kadel (1971) although their predicted egg numbers are slightly higher. For example they estimate a 60 mm female lays 2800 eggs whereas my results predict 2500. At Cabin Hill, female body length ranged from 45-73 mm, thus expected minimum and maximum egg numbers are approximately 950 and 5000. The actual range for the study period was 400 to 5800. However this study disagrees with Hemmer & Kadel's predictions of age dependent fecundity. For example they predict a 3 year old female lays approximately 2400 eggs whereas a Formby Natterjack is estimated to lay approximately 1000 eggs. This difference appears to be related to their predictions of age and growth which are higher than mine. For example they suggest that a 3 year old female has a mean length of approximately 57 mm whereas I would predict 47 mm. Also, Hemmer & Kadel suggest that females start to spawn as 2 year-olds, measuring 50-55 mm (compared with 38 mm for Formby females at this age). The present study suggests that females do not begin spawning until 3 years.

The dependence of egg number upon female body size has been demonstrated in several amphibian species. Howard (1978) found a significant relationship between snout-ischium length and egg number in *R. catesbeiana*. He showed that larger females produced larger clutches (6000 - > 20000) than smaller females, although the largest females produced fewer eggs in second than first clutches within each year. Rose (1966) and Lotter (1978) demonstrated an increase in reproductive potential with increasing body size in *Amphiuna means* and *Plethodon cinereus*, although Rose (1966) found that extreme variations could occur. Davies & Halliday (1977) and Gittings *et al* (1984) showed a relationship between length and fecundity in Common Toads, although Gittings *et al* (1984) suggest there is a minimum fecundity of approximately 450 eggs in this species. They also suggest that there may be a maximum fecundity for any given body length. My results suggest that female Natterjacks produce about 2½ times as many eggs as Common Toads of equivalent size. (Table 38).

Table 38. Comparative fecundities of Common Toads and Natterjacks (Common Toad data from Gittings *et al*, 1984)

Size (mm)	Natterjacks	Common Toads
60	2500	1000
70	4400	1900
80	7100	2800

4.4 Assembly and spawning

4.4.1 The 1981 spawning

The first Natterjack observed was a solitary individual in pool 19 on March 8 which escaped before its sex could be determined. On March 13 the first chorus was heard. The weather that night was calm and clear, and so it was difficult to approach the pools undetected by the toads. However it was estimated that no more than 30 individuals were involved. No calling was heard subsequently until the night of March 24. All pools were visited and a total of 168 toads was counted. Two nights later 264 toads were counted. Early in the season calling began between 18.30 and 20.00 hrs. Later it began around 21.00 hrs.

It was possible to divide the season into early and late spawnings. Fig. 21 shows daily spawn deposition throughout the breeding season. Spawn deposition ceased around April 19 and did not begin again until 13 days later. Spawning then continued until June 5. There was a reduction in calling between April 19-May 1, after which it increased. This change in behaviour appeared to be influenced by the weather, in particular a decrease in air temperature. Mean daily temperatures decreased from 9.6 between April 1-18, to 6.3 between April 19-May 1. During May, mean daily temperature rose to 11.7°C.

The first spawn was found on March 28 in pool 18. A total of 240 spawn strings were counted (Table 39), the three most important pools being numbers 1, 3 and 18 which held 52, 38 and 29 strings respectively. Comparison with observations made previously at Cabin Hill (Table 40) shows that in 1981 there was a marked reduction in the relative importance of pool 1. For example, in 1978 69% of all spawn was laid in pool 1 compared with 22% in 1981. Many new areas flooded in 1981 due to the high water table. For example, flooding of pool 18 produced a shallow, bare sandy margin on the western edge. This seemed particularly attractive to toads, 19 of the 29 strings (Table 39) being deposited there.

During late May and early June calling diminished, the last breeding chorus being recorded on June 5, although solitary individuals were occasionally heard until June 15.

Figure. 21. Spawn deposition at Cabin Hill, 1981-83.

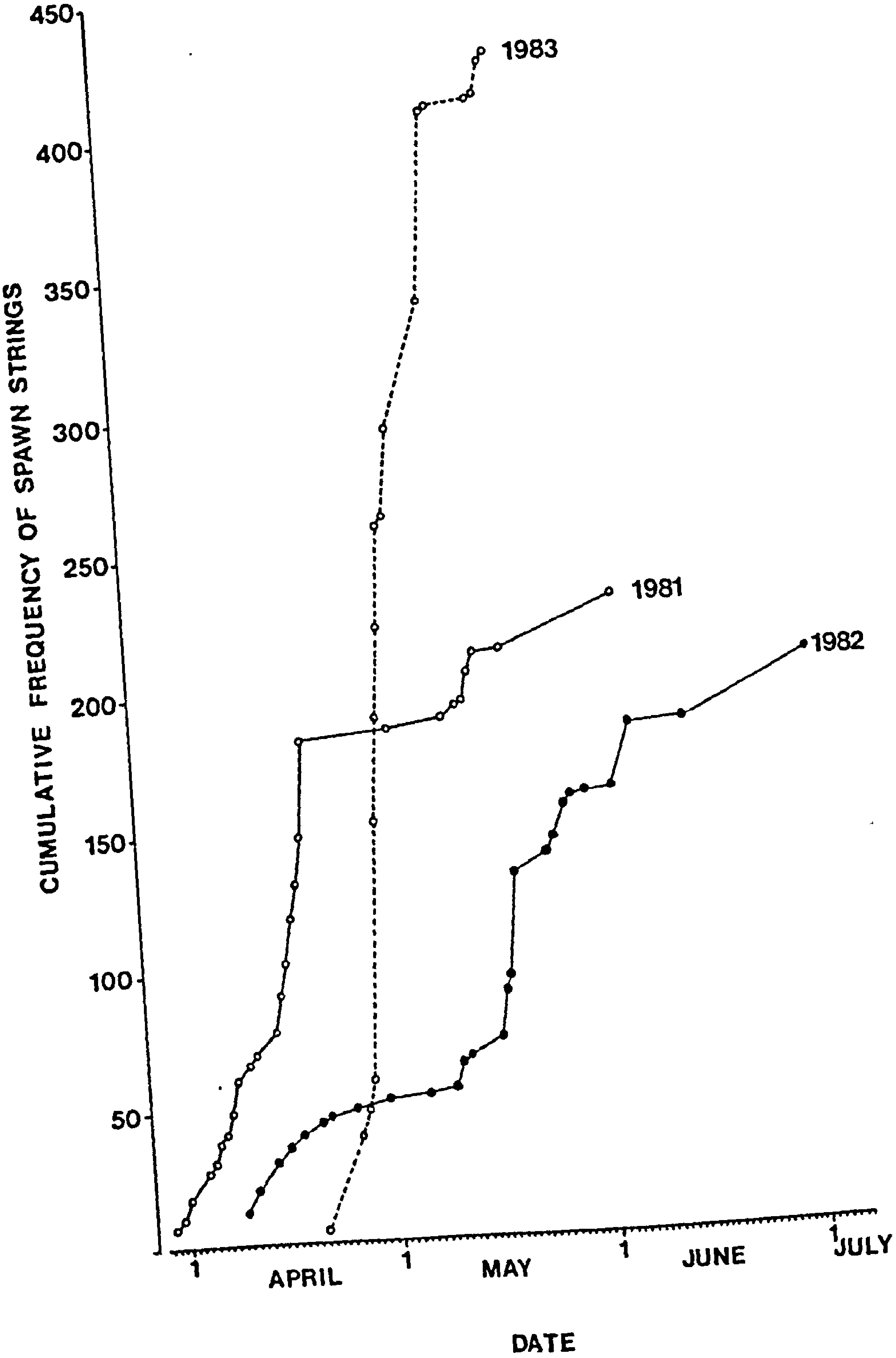

450
400
350
300
250
200
150
100
50
CUMULATIVE FREQUENCY OF SPAWN STRINGS
1983
1981
1982
1
APRIL
1
MAY
1
JUNE
1
JULY
DATE

Table 39. Spawn deposition at Cabin Hill 1981-83

Pool No.	1981	1982	1983
1	52	91	137
2	2	*	0
3	38	10	13
4	2	1	1
5	15	7	15
6	5	0	41
7	1	0	
8	9	16	
9	18	0	4
10	6	14	21
11	1	3	8
12	0	*	*
13	6	*	*
14	7	10	12
15	8	13	44
16	16	37	31
P	10	2	8
17	14	0	0
18	29	3	46
19	0	0	0
20	0	0	0
21	1	0	46
TOTAL	240	207	427

*unrecorded

Table 40. Spawn distribution at Cabin Hill, 1977-1980 (Data from Smith, 1977-80)

Pool No.	1977	1978	1979	1980
1	70 (64)	252 (69)	136 (61)	194 (87)
2	4 (4)	1 (0.5)		
3	1 (1)	2 (0.5)	3 (1)	
4				
5			4 (2)	
6			1 (0.5)	
7	1 (1)		19 (8)	4 (2)
8	11 (10)	48 (13)		4 (2)
9				
10	2 (2)	23 (6)	13 (6)	
11	8 (7)	15 (4)		10 (4)
12	4 (4)			
13	3 (3)	9 (3)		
14		4 (1)	8 (4)	3 (3)
15	2 (2)	6 (2)	6 (3)	
16		6 (2)	22 (10)	3 (1)
17	3 (3)			1 (0.5)
18				
19				
20			12 (5)	1 (0.5)
21				2 (1)
TOTAL	109	366	224	222

Bracketed figures = percentages

4.4.2 The 1982 spawning

Possibly because of the lower water table, the first Natterjacks did not appear as early as in 1981. The first chorus of about 20 males was recorded on April 4, starting at 20.30 hrs. Spawning also began later than in 1981, the first strings being found on April 7. As before there were two main spawning periods (Fig. 21), the first between April 7-29 and the second between May 9-June 6. During the intervening period, although 2 strings were laid, calling ceased coinciding with a spell of colder, windy weather, A third, shorter spawning period occurred at the end of June, 14 fresh strings being found on July 1.

A total of 207 spawn strings was counted in 12 of the 21 pools (Table 39). The majority (44%) were laid in pool 1. No spawn was detected in pool 2 although tadpoles were seen later in the season. Pool 16 was used to a greater extent than in 1981. 37 strings (18%) being laid here. Other pools much used were 3, 8, 10 and 15.

4.4.3 The 1983 spawning

Calling and spawning were delayed due to high winds and low temperatures. Mean daily temperatures for March and April were 6.6 and 6.8°C respectively. Mathias (1971) found that Natterjacks emerged from hibernation when daytime temperatures reached 15°C and night temperatures 8°C. The first breeding chorus was heard on April 16 and, unlike previous years when relatively small numbers were counted early on, a large adult assemblage was present from the start of the breeding season. Thus on April 18, 105 toads were counted and on the following night 171. This was possibly due to the delayed onset in breeding caused by the adverse weather conditions.

A larger number of spawn strings was laid - 427 in 14 sites (Table 29). As in previous years pool 1 was the most important, containing 137 strings. Pools 15, 18 and 21 were also heavily used containing 44, 44 and 46 strings respectively. The delay in breeding may also have been responsible for the quantity of spawn laid in a relatively short time. Fig. 21 shows that the first spawn was found on April 19 and 15 days later 293 strings had been laid. Between May 4-10 calling declined during colder, windy weather after which spawning resumed. By the completion of spawning on May 22, 427 strings had been laid. The break in spawning between May 4-10 allowed the season to be divided into an early spawning between April 10-May 4 (293 strings) and a later spawning from May 10-22 (134 strings).

4.4.4 Environmental factors and choice of spawn site

Environmental data for spawn sites are given in Fig. 32 as frequency histograms, while water quality data for Cabin Hill are shown in Table 41.

Table 41. Water quality of Cabin Hill pools (concentrations in mg.l^{-1})

Physical variable	No. samples	Range	Mean ± 1 SD
K^+ conc.	15	0.04-5.5	1.8 ± 1.2
Na^+ conc.	15	18.1-33.1	22.1 ± 3.6
Ca^+ conc.	15	11.5-45	29.2 ± 13.6
pH	25	7.7-10.8	8.6 ± 0.4

Concentrations of the cations K^+, Ca^{2+} and Na^+ were determined using an EEL flame photometer and standard methodology described by

Figure 22. Environmental factors at Cabin Hill spawn sites, 1983.

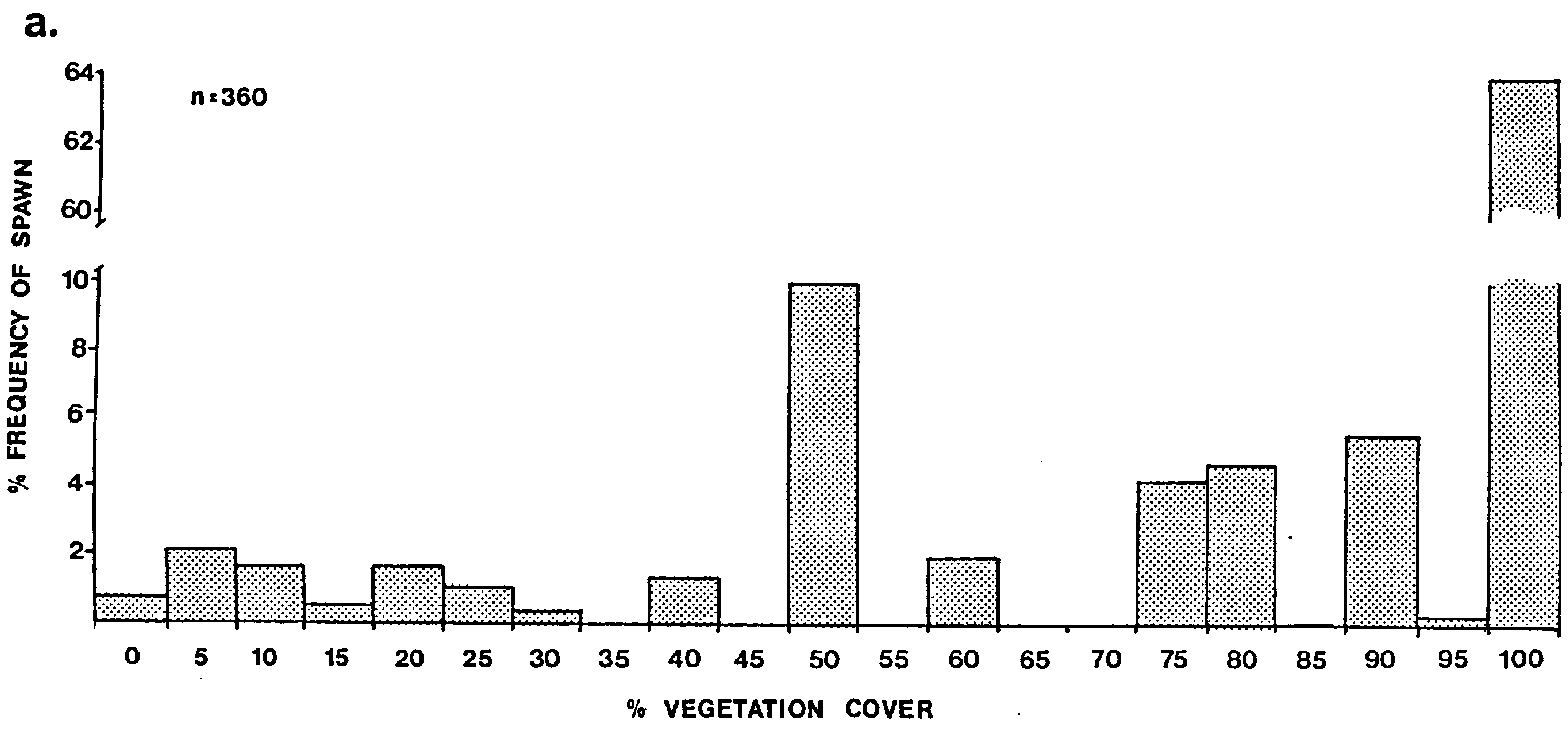
a. Vegetation cover

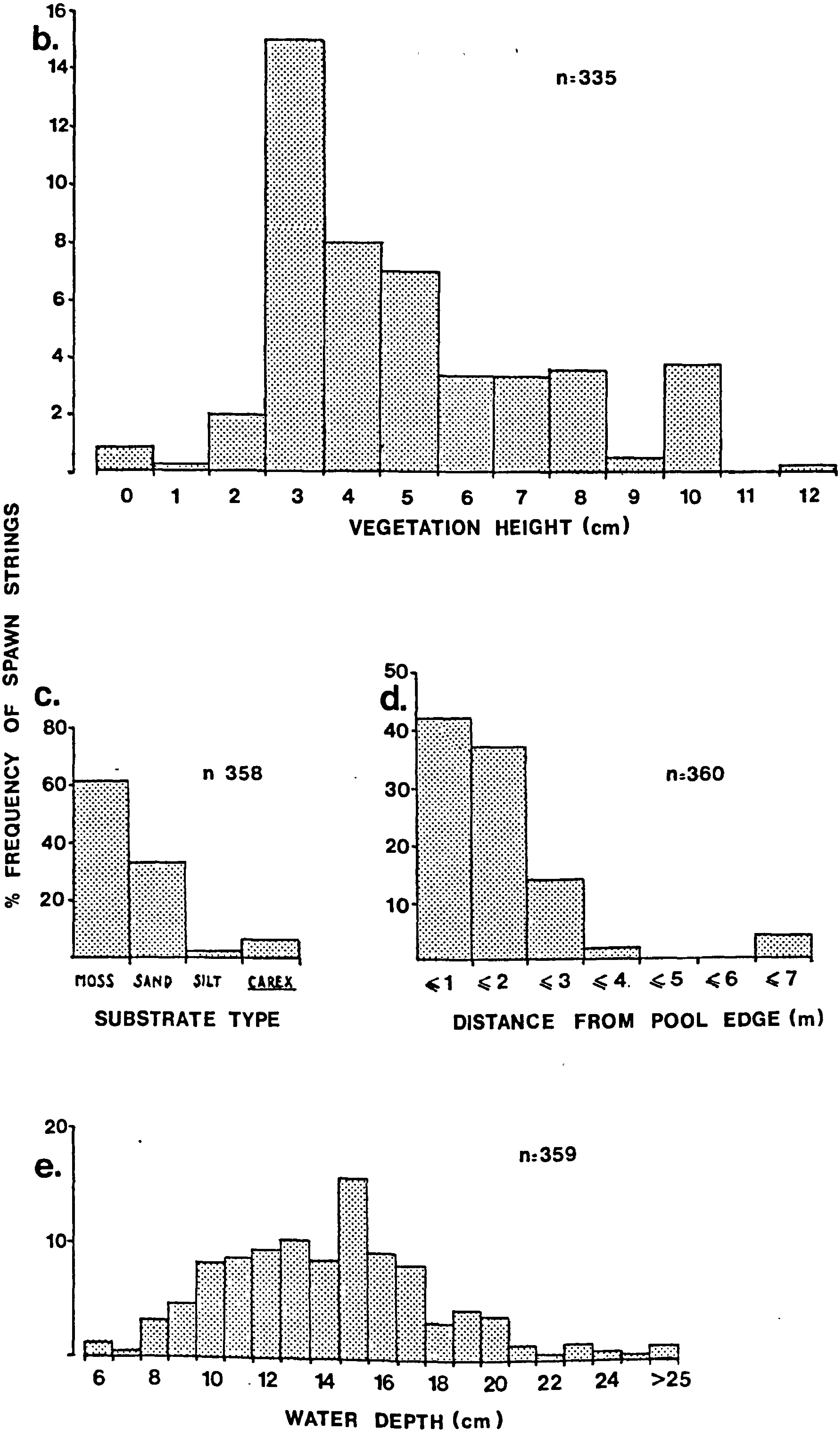
b. Vegetation height

c. Substrate type

d. Distance of spawn from shoreline

e. Water depth


a.
n=360
% FREQUENCY OF SPAWN
64
62
60
10
8
6
4
2
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
% VEGETATION COVER


% FREQUENCY OF SPAWN STRINGS
b.
n:335
16
14
12
10
8
6
4
2
0
1
2
3
4
5
6
7
8
9
10
11
12
VEGETATION HEIGHT (cm)
c.
n 358
80
60
40
20
MOSS
SAND
SILT
CAREX
SUBSTRATE TYPE
d.
n:360
50
40
30
20
10
≤1
≤2
≤3
≤4
≤5
≤6
≤7
DISTANCE FROM POOL EDGE (m)
e.
n:359
20
10
6
8
10
12
14
16
18
20
22
24
>25
WATER DEPTH (cm)

Mathias (1971). He gives mean values of 30.3 mg l^{-1} Ca^{2+} and 2.4 mg l^{-1} K^{+} for Ainsdale sites. Similar concentrations of 29.2 mg l^{-1} and 1.8 mg l^{-1} respectively were found at Cabin Hill. The mean Na^{+} concentration of Cabin Hill pools (22.1 mg l^{-1}) is lower than Mathias' (1971) figure (49.2 mg l^{-1}) however all ionic concentrations reported seem typical of British dune systems (Ranwell, 1972).

The mean pH of Cabin Hill pools was 8.6 with a range of 7.7-10.8 reflecting the high lime content of the dune sand. Beebee & Griffin (1977) state that there is no significant selection of dune pools by Natterjacks on the basis of pH, although acidic pools (pH 4-5) were avoided. They found that the majority of dune pools used by Natterjacks had pH values of 6-9 which are typical of calcareous sand dunes (Ranwell, 1972).

Vegetation cover and height at spawning sites are represented in Fig. 22a and b. Modal values are given as 100% cover (64%) and 3 cm height (31%). However the former may represent a compromise the toads are forced to make due to a lack of preferred sites. Smith (1964) states that breeding pools often have little or no aquatic vegetation. However the majority of Cabin Hill sites are 'mature slacks' with 100% vegetation cover although there is a second modal value of 50% vegetation cover (Fig. 22a). Some slacks (e.g. 1, 2 and 3) are grazed by cattle and this may account in part for the low vegetation height (Fig. 22b) however if the data for slacks 1 and 3 are excluded from analysis, the modal value for vegetation height remains 3 cm (45%).

Substrate type is shown in Fig. 22c but the above arguments also apply. The majority of spawning sites (61%) had a moss substrate, reflecting the 'maturity' of the pools, many of which have been colonised by the moss *Acrocladium cuspidatum*. Fig. 22c shows that sites with sandy substrates comprised 33% of all observations, whereas silt and *Carex* substrates comprised only 2 and 6% respectively.

Distance of spawn from bank and water depth at spawn site are given in Figs. 22d and e. The majority of spawn (41%) was laid within 1 m of the bank (mean = 0.8 ± 0.3 m) although a further 36% occurred between 1-2 m. Spawn was found between 6-7 m from the bank in pool 1, however the water in these areas was only about 10 cm deep. Spawn was mainly found at water depths of 6-20 cm, although 4% was found in deeper water (Fig. 22e) with a maximum of 27 cm. Modal and mean values were 15 and 14.2 ± 3.7 cm respectively. These results agree with those of Mathias (1971). He found that mean spawn depth was 15 cm and that deposition occurred close to the bank. His maps for spawn distribution indicate that deposition occurred within 4 m of the shoreline at maximum water levels.

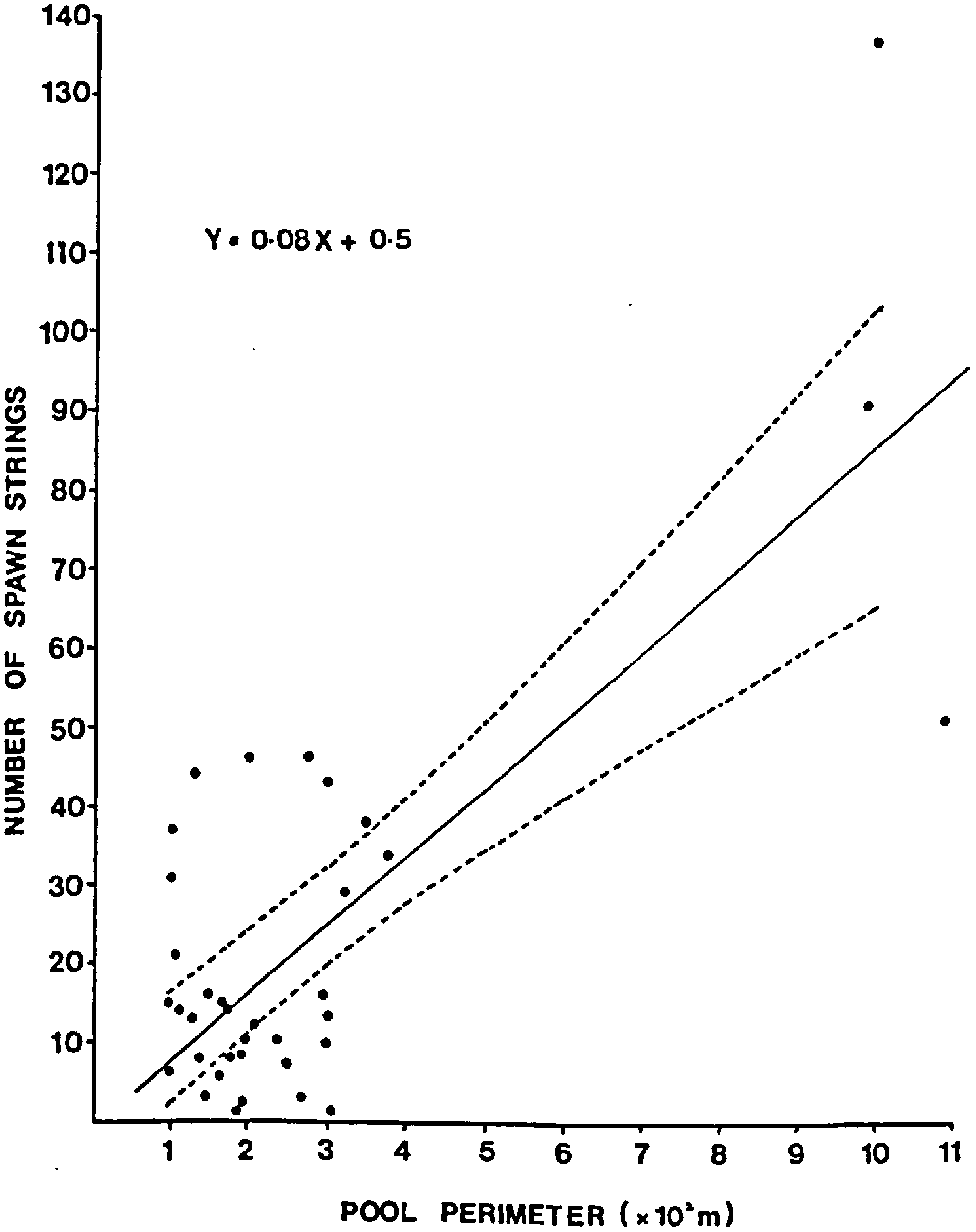
Using data for all study years, a positive correlation was calculated betwen pool perimeter and numbers of spawn deposited ($r = 0.758$, $df = 35$, $p < 0.001$). It should be noted that pool perimeter refers to the maximum recorded distance during the spawning period i.e. at the onset of breeding. A significant regression (Table 42) was computed and is shown (± 95% CL) in Fig. 23. There is a wide scatter of points around the computed regression, however this is probably due to the dependence of spawn deposition upon factors other than pool size. As might be expected, Fig. 23 shows that increased spawn deposition occurs in larger pools. This is probably due to more females being attracted to the larger number of calling

Table 42. F-test for the significance of the regression: Pool perimeter vs. spawn number

$b = 0.08$ $a = 0.50$

Source of variation	df	SS	MS	F	p
Linear regression	1	15040.3	15040.3	47.3	< 0.001
Residuals	35	11128.6	317.95		
Total	36	26168.9			

Figure 23. The relationship between numbers of spawn deposited and length of pool perimeter. Broken lines indicate ± 95% confidence limits to the regression


Y = 0·08X + 0·5
NUMBER OF SPAWN STRINGS
140
130
120
110
100
90
80
70
60
50
40
30
20
10
1
2
3
4
5
6
7
8
9
10
11
POOL PERIMETER (× 10² m)

males at these pools (Arak, 1983), Smith & Flynn (1977) having previously demonstrated a positive relationship between male numbers and pool size (perimeter).

4.5 Estimation of larval survival

4.5.1 Data treatment

Survival analysis between developmental stages was carried out using key factor analysis (*k*-analysis) as described by Southwood (1978). This permits recognition of the major mortality factors (Burns, 1984), although ideally several years' data are required (Manly, 1978). Population estimates were obtained as follows.

1. Eggs

For each year, the daily and total mortalities were calculated from the spawn strings sampled. The total length of viable strings in each developmental stage was multiplied by the mean number of eggs cm^{-1} to give an estimate of the total number of viable embryos. Using the same method, mortalities were estimated and simultaneously classified as to their cause. Before *k*-analysis between hatching and free swimming larvae could be undertaken, it was necessary to estimate the total number of hatched embryos for the site thus:

$$T = N \times S \times m$$

where T = total number of eggs hatching.

N = total number of spawn strings

S = mean number of eggs $string^{-1}$

m = % mortality within each stage.

2. Tadpoles

Estimates of tadpole numbers and stage survival were obtained using Southwood's (1978) graphical method. This simple method of integration gives estimates of numbers surviving to the mid-point of the developmental stage. Successive population estimates were plotted against day number and the points joined by straight lines. The calculated area enclosed by the plot (the number of 'tadpole days') was then divided by the mean developmental time under field conditions. However two problems were encountered with the method. First, sampling could not start immediately free swimming tadpoles appeared. This was partly because other sampling programmes were in progress, and also because the young tadpoles were easily killed during sampling. Thus there were periods before the first sampling for which survival could not be calculated, thus leading to underestimates. To compensate for this, the first population estimate was joined to the total number of eggs first hatching. The area enclosed by this plot was then included in survival analysis. This method is suspect as both under and overestimates for this early period of larval life are possible. However it seemed preferable to include an estimate for this period rather than ignore it.

The second problem associated with the method was determining the mean duration of the tadpole stage. Beebee & Beebee (1978) studied metamorphosis in Natterjacks. They found that the developmental period of individuals spawned within 24 hours of each other could vary by a factor of two (i.e. between 9-18 weeks) and that metamorphosis began approximately 54 days after the first spawn hatched. This represents the minimum possible stage duration for the tadpoles. From observations at Cabin Hill during the present and previous studies (Smith, 1977,1978b,1979) metamorphosis occurred approximately 50-60 days after the first spawn hatched. The published value of 54 days (Beebee & Beebee, 1978) was therefore used to calculate tadpole survival. However, by assuming all tadpoles metamorphose at 62 days, over-estimates are possible if the majority of tadpoles are long lived.

3. Metamorphosis

The graphical method (Southwood, 1978) was also used to estimate metamorphic success. From previous observations (P.H. Smith, in litt.) the mean period between formation of the fourth leg and toadlets leaving the water is approximately 3-4 days. This value was used to calculate stage survival.

However there is an alternative method of estimating numbers metamorphosing. Where the duration between successive sampling days approximately 3-4 days, it could be assumed that all metamorphosing tadpoles had left the pools before the next sample. Summation of the numbers metamorphosing on each sampling day would thus give an index of total metamorphosis. In view of this a second set of k-analyses were made using these values.

4.5.2 Larval survival, 1981

1. Eggs

The calculations and estimation of survival for egg stages are given in Table 43. The first spawning consisted of 191 strings of which 163 were monitored. Forty-one out of 49 strings in the second spawning were studied. The mean number of eggs cm^{-1} was 4.8 ± 0.3, while the

Table 43. Estimation of spawn mortality, 1981

Mean No. eggs cm^{-1} (± 95% CL) = 4.8 ± 0.3 = n.

Mean No. eggs $string^{-1}$ (± 95% CL) = 1262.6 ± 108.3

1st spawning (Strings 1-191)

Stage	Total length spawn (cm), L	Est. No. eggs N = L x n	% Apparent mortality	% Real mortality	Σ Real mortality	Survival rate	log N	*k*
Blastula	42615	204552 ± 12785					5.311	
k. Saprolegnia mortality	5306	25489 ± 1592	12.45	12.45	12.45	87.55		0.058
Tailed	37309	179083 ± 11193					5.253	
k. Saprolegnia mortality	3692	17722 ± 1108	9.90	8.66	21.11	78,89		0.045
Hatched	33617	161362 ± 10085					5.208	

Table 43 (continued)

2nd spawning (Strings 192-240)

Stage	Total length spawn (cm),L	Est. No. eggs N = L x n	% Apparent mortality	% Real mortality	Σ Real mortality	Survival rate	log N	k
Blastula	13162	63178 ± 4251					4.801	
k. *Saprolegnia mortality*	681	3269 ± 204	5.17	5.17	5.17	94.83		0.024
Tailed	12481	59909 ± 3744					4.777	
k. *Saprolegnia mortality*	63	302 ± 19	0.50	0.48	5.65	94.35		0.002
Hatched	12418	59607 ± 3725					4.775	

Combined spawnings (Strings 1-240)

Stage	Total length spawn (cm),L	Est. No. eggs N = L x n	% Apparent mortality	% Real mortality	Σ Real mortality	Survival rate	log N	k
Blastula	55777	267730 ± 16733					5.428	
k. *Saprolegnia mortality*	5987	28738 ± 1796	10.73	10.73	10.73	89.27		0.05
Tailed	49790	238992 ± 14937					5.378	
k. *Saprolegnia mortality*	3755	18024 ± 1127	7.54	6.73	17.46	82.54		0.034
Hatched	46035	220968 ± 13811					5.344	

Table 43 (continued)

Estimation for strings 1-240

Total estimated no. eggs = 240 x 1262.6 ± 108.3 = 303024 ± 25992

∴ Estimated no. tailed stage = 303024 ± 25992 x 89.27% = 270510 ± 23374

∴ Estimated no. hatched = 303024 ± 25992 x 82.54% = 250116 ± 21454 mean number of eggs per string was 1263 ± 108 (Table 43). Due to the high spring watertable there was no desiccation of strings this year, however there was a high incidence of fungal infection especially in the early part of the season (Table 43). Thus 21.1% of eggs from the first spawning were infected compared with 5.7% in the second spawning. Table 43 shows that throughout the season there was a heavier mortality of the early egg stages due to *Saprolegnia*. During the first spawning 12.4% of the blastula stage was infected ($k = 0.06$), whereas during the tailed stages only 9.9% ($k = 0.05$) was infected. The percentage mortalities and k-values were greatly reduced during the second spawning. Only 5.2% ($k = 0.02$) of blastula stages were affected by fungus, and this decreased to 0.5% infestation during the tailed stages ($k = .002$).

Overall, *Saprolegnia* appeared to cause 10.7% mortality ($k = 0.05$) of all eggs in the blastula stage (Table 43) and a further 7.5% mortality of tailed stages ($k = 0.03$). Thus 82.5% of spawn laid in 1981 was estimated to have survived to hatching.

Table 43 shows the estimated numbers surviving to hatching for the site. A total of 240 strings was laid, with a mean number of 1263 ± 108 eggs per string. Thus, approximately 303,000 ± 26,000 eggs were laid in 1981, of which 250,000 ± 21,500 survived to hatching. There was no post-hatch mortality due to desiccation. The newly hatched larvae remained attached to the jelly strings for approximately 5 days, after which they dropped off and were found lying or resting on the pool floors. During this period the tadpoles exhibited brief swimming movements and began to disperse.

2. Tadpoles

Fig. 24 shows the estimated numbers (± 95% CL) of tadpoles per

Figure 24. Estimated sizes of tadpole populations ± 95% confidence limits within Cabin Hill breeding pools, 1981. Initial value = number of eggs first observed hatching. N = the area enclosed by each plot (the number of 'tadpole days').

a. Pool 1

b. Pool 3

c. Pool 4

d. Pool 5

e. Pool 6

f. Pool 7/8

g. Pool 9

h. Pool 10

i. Pool 11

j. Pool 13

k. Pool 14

l. Pool 15

m. Pool 16

n. Pool 17

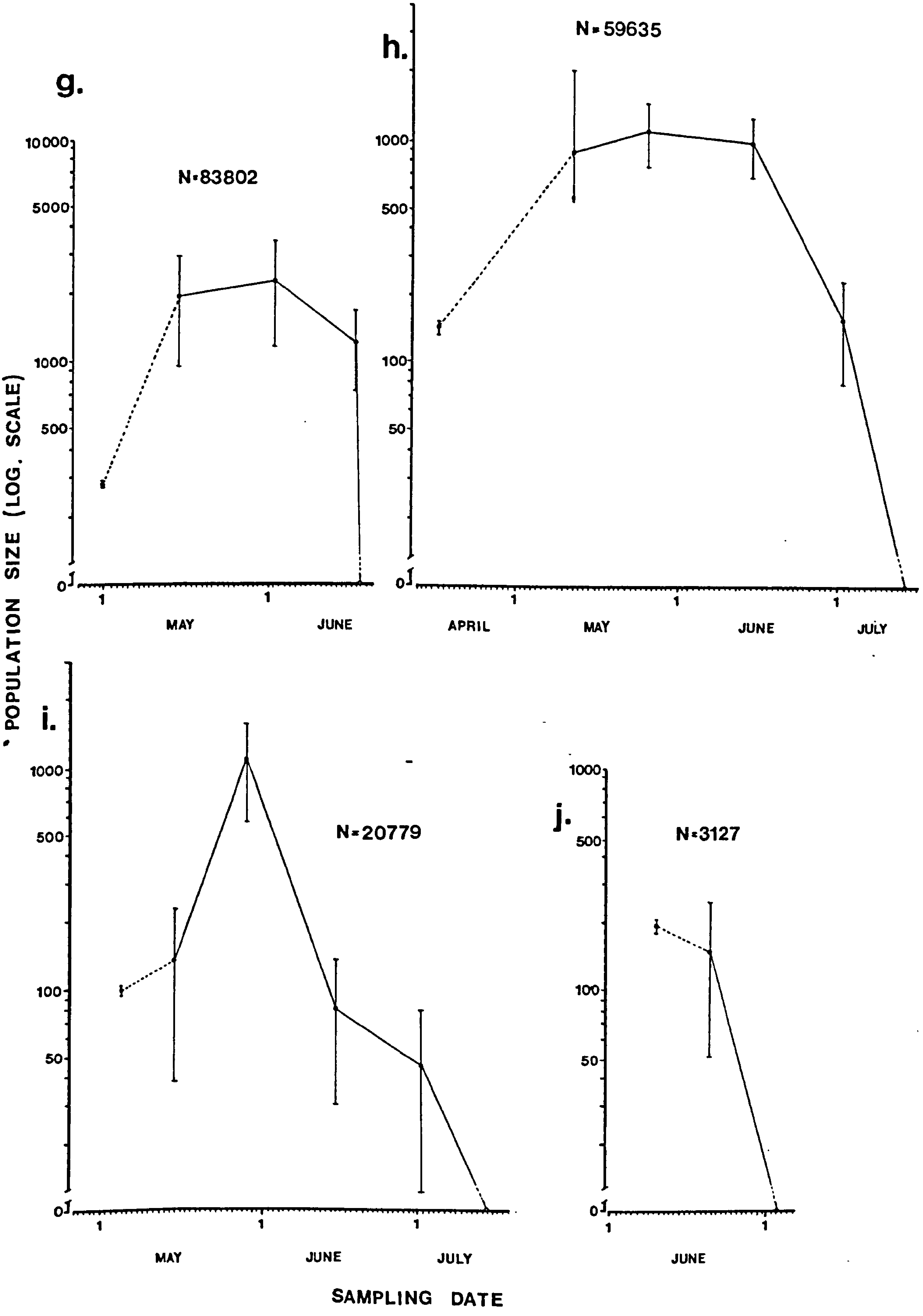
o. Pool P

p. Pool 18

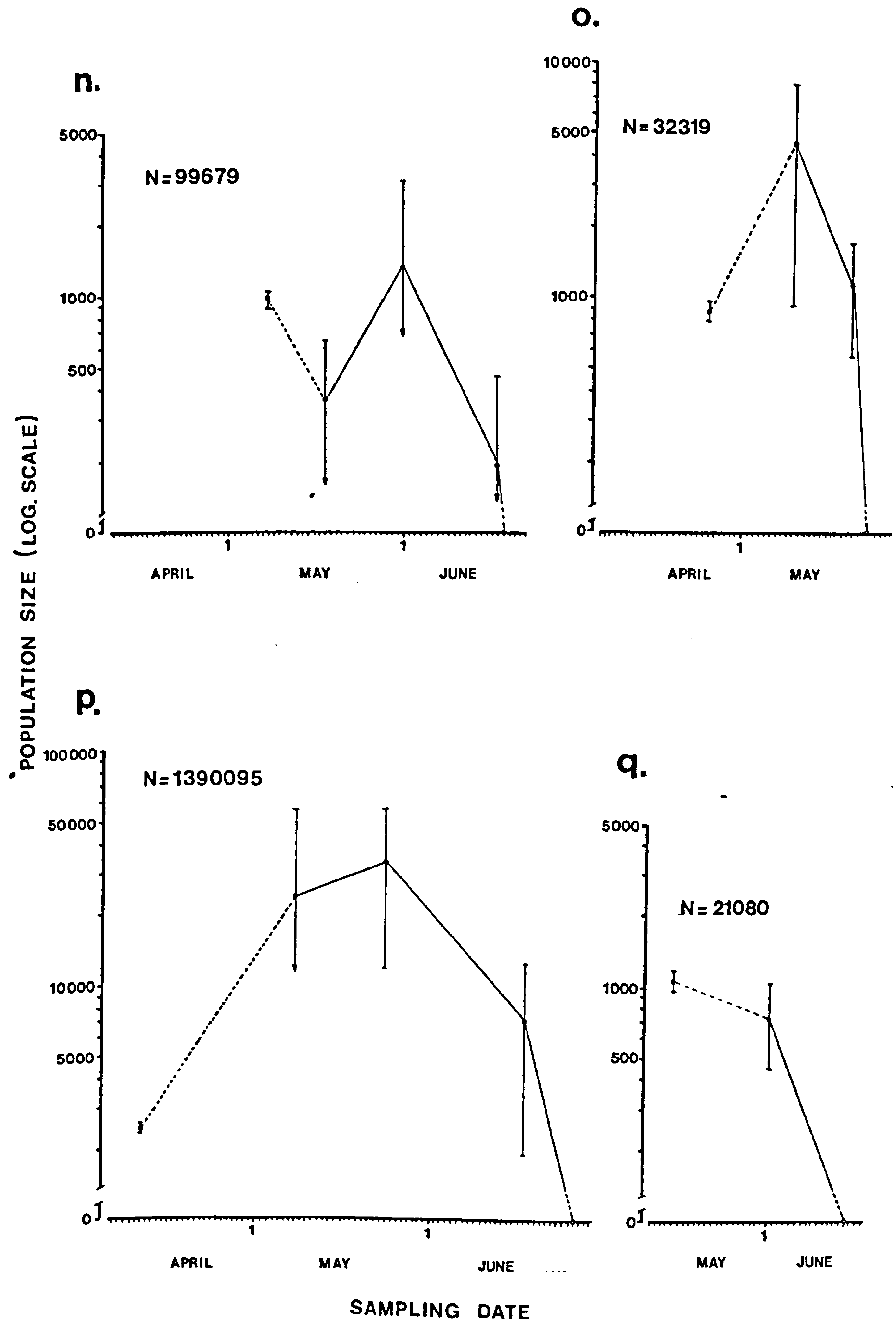
q. Pool 21


a.
130000
50000
10000
5000
1000
500
0
APRIL
1
MAY
1
JUNE
N=1198475
b.
10000
5000
1000
0
1
MAY
1
JUNE
1
JULY
N=953409
POPULATION SIZE (LOG. SCALE)
SAMPLING DATE


c.
50000
10000
5000
1000
500
0
N=84034
MAY
1
JUNE
1
d.
10000
5000
1000
500
0
N=541800
MAY
1
JUNE
1
JULY
POPULATION SIZE (LOG SCALE)
e.
10000
5000
1000
500
0
N=64979
1
MAY
f.
10000
5000
1000
500
100
50
0
N=149521
APRIL
1
MAY
1
JUNE
1
JULY
SAMPLING DATE


g.
N=83802
10000
5000
1000
500
0
1
1
MAY
JUNE
h.
N=59635
1000
500
100
50
0
1
1
1
APRIL
MAY
JUNE
JULY
POPULATION SIZE (LOG. SCALE)
i.
N=20779
1000
500
100
50
0
1
1
1
MAY
JUNE
JULY
j.
N=3127
1000
500
100
50
0
1
1
JUNE
SAMPLING DATE


k.
N= 5628
1000
500
100
50
0
1
1
APRIL
MAY
l.
N= 519695
50000
10000
5000
1000
500
0
1
1
1
APRIL
MAY
JUNE
JULY
m.
N=143618
50000
10000
5000
1000
500
0
1
1
1
APRIL
MAY
JUNE
POPULATION SIZE (LOG. SCALE)
SAMPLING DATE


n.
N=99679
5000
1000
500
0
1
1
APRIL
MAY
JUNE
o.
N=32319
10000
5000
1000
0
1
APRIL
MAY
p.
N=1390095
100000
50000
10000
5000
0
1
1
APRIL
MAY
JUNE
q.
N=21080
5000
1000
500
0
1
MAY
JUNE
POPULATION SIZE (LOG. SCALE)
SAMPLING DATE

pool on successive sampling occasions. Table 44 gives the estimation of tadpole mortality between hatching and the stage mid-point.

These data show that tadpole numbers are highly variable (Fig. 24) probably because there is no single impulse of recruitment, and tadpoles enter the population from successive spawnings. The large confidence intervals are due to the aggregated distribution of the tadpoles within the pools. An initial sampling programme showed significant agreement with a negative binomial distribution at the 95% probability level (Table 45). Schooling or clumping of tadpoles appears to be common to many amphibian species e.g. *Scaphiopus holbrooki* (Richmond, 1947).

Integration of Fig. 24 gave an estimate of approximately 99,500 tadpoles surviving from hatching (Table 44). This represents 60.2% mortality of hatched larvae (k = 0.4) and is equivalent to 32.8% survival of all eggs laid.

3. Metamorphosis

The first metamorphosis was observed on June 22 in pools 5 and 18 (Table 46) and was confirmed by observation of toadlets at six pools (3, 4, 5, 15, 16 and 18). No metamorphosis was observed at pool 1. The most important pools appeared to be numbers 3, 4 and 15. The toadlets dispersed rapidly, although individuals could be found under pieces of wood as late as the end of July. The last metamorphosing toadlets were found on July 20.

As mentioned previously (section 3.3.1) problems were encountered with the trapping techniques employed in 1981. Table 46 lists these trappings (116 individuals) which represent a minimum metamorphic success

Table 44. Estimation of tadpole mortality 1981

Estimation of tadpole numbers:

1. Σ Areas under population curves ("tadpole days") = 5371675
2. Life of tadpole under field conditions = 54 days.

Estimated No. tadpoles surviving to stage mid-point = $\frac{5371675}{54}$ = 99475

Stage	Estimated No.	% Apparent mortality	% Real mortality	Σ Real mortality	Survival rate	log N	*k*
Blastula	303024 ± 25992	10.73	10.73	10.73	89.27	5.482	0.05
Tailed	270510 ± 23374	7.54	6.73	17.46	82.54	5.432	0.034
Hatched	250116 ± 21454					5.398	
k. early tadpole mortality	150641	60.23	49.72	67.18	32.82		0.4
Tadpoles	99475					4.998	
k. late tadpole mortality	99359	99.88	32.78	99.96	0.04		2.934
*Metamorphosis (Σ absolute estimates)	116					2.064	

*See Table 46.

Table 45. Preliminary tadpole sampling at Cabin Hill, 1981: χ^2-test for agreement with a negative binomial distribution (Method in Elliot, 1971)

Count	Observed frequency	Expected frequency	χ^2
0	6	7.29	0.23
1	9	5.17	2.84
2	5	3.89	0.32
3	3	2.98	0.0001
4	3	2.31	0.21
5	0	1.79	1.79
6	0	1.40	1.40
7	0	1.10	1.10
8	0		
9	0		
10	1		
11	1 } 4	} 4.98	0.14
12	0		
13	0		
14	1		
⋮			
29	1		

Mean sample size ± 1 SD = 3.84 ± 5.83

$\Sigma \chi^2 = 8.05$, df = 9 - 3 = 6, $p > 0.05$

∴ Distribution shows no significant departure from the negative binomial.

Table 46. Numbers of metamorphosing toadlets trapped 1981

Pool	Number of toadlets	1st trapping date	Final trapping date
3	35	6-7	20-7
4	13	7-7	19-7
5	5	22-6	26-6
15	36	6-7	19-7
16	2	2-7	7-7
18	25	22-6	25-6
	116	22-6	20-7

in 1981, thus giving an apparent mortality of 99.9% (*k* = 2.93) from the mid point of the tadpole stage. This is equivalent to 0.04% survival of all eggs laid in 1981. However, because the trapping method was unreliable, the actual survival to metamorphosis was probably higher.

4.5.3 Larval survival, 1982

1. Eggs

Estimated egg mortalities are given in Table 47. The first spawning consisted of 53 strings, all of which were monitored. A total of 154 strings was laid in the second spawning of which 131 were monitored. The mean number of eggs per string was 1504 ± 189, and the mean number of eggs cm^{-1} was 6.3 ± 0.4.

Saprolegnia infestation was lower than in 1981, and desiccation became a major mortality factor. Blastula mortality from fungal infection was 1.1% (*k* = 0.005) while 2.5% (*k* = 0.01) of tailed stages were affected. However, desiccation resulted in a further 24.1% mortality (*k* = 0.12) of monitored strings during the tailed stages. Thus there was 73.1% survival to hatching of ova laid in the first spawning. However, the decline in water levels caused a further 61% mortality, thus reducing the overall survival rate for strings 1-53 to 28.5% (Table 47). These strings were estimated to contain 80,000 ± 10,000 eggs of which 23000 ± 2900 were estimated to have survived as free-swimming tadpoles.

Mortality of strings 54-207 was lower (8.8%) although desiccation was still a major factor. *Saprolegnia* infestation caused 0.8%

Table 47. Estimation of spawn mortality, 1982

Mean no. eggs cm^{-1} (± 95% CL) = 6.3 ± 0.4

Mean no. eggs $string^{-1}$ (± 95% CL) = 1504.4 ± 189.5

1st spawning (Strings 1-53)

Stage	Total length spawn (cm).L	Est. No. eggs N = L x n	% apparent mortality	% Real mortality	Σ Real mortality	Survival rate	log N	*k*
Blastula	10052	63328 ± 4021					4.802	
k. Saprolegnia mortality	109	687 ± 44	1.08	1.08	1.08	98.82		0.005
Tailed	9943	62641 ± 3977					4.797	
k. Saprolegnia mortality	252	1588 ± 101	2.54	2.51	3.59	96.41		0.011
"Survivors"	9691	61053 ± 3876					4.786	
k. Desiccation mortality	2339	14736 ± 936	24.14	23.27	26.86	73.14		0.12
Hatched	7352	46318 ± 2941					4.666	
k. Desiccation mortality	4488	28274 ± 1795	61.04	44.65	71.51	28.49		0.410
"Survivors"	2864	18043 ± 1146					4.256	

Table 47. (continued)

Estimation for strings 1-53

Total estimated no. eggs = 53 x 1504.4 ± 189.5 = 79733 ± 10044

∴ Estimated no. tailed stage = 79733 ± 10044 x 98.82% = 78792 ± 9925

∴ Estimated no. hatch = 79733 ± 10044 x 73.14% = 58317 ± 7346

∴ Estimated survivors = 79733 ± 10044 x 28.49% = 22716 ± 2861

Table 47. (continued)

2nd spawning (Strings 54-207)

Stage	Total length spawn (cm).L	Est. No. eggs N = L x n	% Apparent mortality	% Real mortality	Σ Real mortality	Survival rate	log N	k
Blastula	9782	61627 ± 3913					4.790	
k. Saprolegnia mortality	74	466 ± 30	0.76	0.76	0.76	99.24		0.004
"Survivors"	9708	61160 ± 3883					4.786	
k. Desiccation mortality	647	4076 ± 259	6.66	6.61	7.37	92.63		0.029
Tailed	9061	57084 ± 3624					4.757	
k. Saprolegnia mortality	8	50 ± 3	0.09	0.08	7.45	92.55		0.001
Hatched	9053	57034 ± 3621					4.756	
k. Desiccation mortality	131	825 ± 52	1.45	1.34	8.79	91.21		0.006
"Survivors"	8922	56209 ± 3569					4.750	

Table 47. (continued)

Estimates for Strings 54-207

Total estimated no. eggs = 154 x 1504.4 ± 189.5 = 231678 ± 29183

∴ Estimated no. tailed stages = 231678 ± 29183 x 92.63% = 214603 ± 27032

∴ Estimated no. hatched = 231678 ± 29183 x 92.55% = 214418 ± 27009

∴ Estimated no. survivors = 231678 ± 29183 x 91.21% = 211313 ± 26618

Table 47. (continued)

Combined spawning (Strings 1-207)

Stage	Total length spawn (cm).L	Est. no. eggs N = L x n	% Apparent mortality	% Real mortality	Σ Real mortality	Survival rate	log N	*k*
Blastula	19834	124954 ± 7934					5.097	
k. Saprolegnia mortality	183	1153 ± 73	0.92	0.92	0.92	99.08		0.004
"Survivors"	19651	123801 ± 7860					5.093	
k. Desiccation mortality	647	4076 ± 259	3.29	3.26	4.18	95.82		0.015
Tailed	19004	119725 ± 7602					5.078	
k. Saprolegnia mortality	260	1638 ± 104	1.37	1.31	5.49	94.51		0.006
"Survivors"	18744	118087 ± 7498					5.072	
k. Desiccation mortality	2339	14736 ± 936	12.48	11.79	17.28	82.72		0.058
Hatched	16405	103352 ± 6562					5.014	
k. Desiccation mortality	4619	29100 ± 1848	28.16	23.29	40.57	59.43		0.143
"Survivors"	11786	74252 ± 4714					4.871	

Table 47. (continued)

Estimates for string 1-207

Total estimated no. eggs = 207 x 1504.4 ± 189.5 = 311411 ± 39227

∴ Estimated no. tailed stages = 311411 ± 39227 x 95.82% = 298394 ± 37587

∴ Estimated no. hatch = 311411 ± 39227 x 82.72% = 257599 ±31092

∴ Estimated no. survivors = 311411 ± 39227 x 59.43% = 185071 ± 23312 mortality during the blastula stages ($k = 0.004$); however desiccation caused 6.7% mortality ($k = 0.03$). Apparent mortality of tailed stages due to fungal infection was reduced to 0.09% ($k = 0.001$) and mortality of newly hatched tadpoles was also reduced, with only 1.4% affected ($k = 0.006$) desiccation. Thus overall survival of strings 54-207 was estimated to be 91.2%.

Variations in mortalities from desiccation between spawnings are attributable to differences in spawn deposition. Early in the season spawn was laid in shallow, marginal areas which dried rapidly Later, spawning was confined to the main pool bodies which were not prone to such rapid desiccation.

Combined data for 1982 (Table 47) suggest an overall real mortality of 40.6% of which 2.2% was due to *Saprolegnia*, and 38.4% due to desiccation. The survival rate to hatching was similar to 1981 with 82.7% of eggs surviving. However, post-hatch mortality reduced this to 59.4%. Thus it is estimated that in 1982, of 311000 ± 39200 eggs laid, 257600 ± 31000 survived to hatching. (Table 47) although post-hatch mortality from desiccation resulted in 185000 ± 23000 free swimming tadpoles surviving.

2. Tadpoles

Tadpoles were identified at 8 pools (1, 2, 3, 8, 10, 14, 15, and 16). However pools 3 and 15 dried rapidly being totally dry by June 3, thus no larvae survived. Table 48 gives the estimated survival to the mid-point of this stage. When sampling began larvae were only present in pools 1, 8, 10, 14, and 16. The population estimates on successive days are given in Fig. 25. Integration of these plots gave an estimate

Figure 25. Estimated sizes of tadpole populations ± 95% confidence limits within Cabin Hill breeding pools, 1982. Initial value = number of eggs first observed hatching. N = the area enclosed by each plot (the number of 'tadpole days').

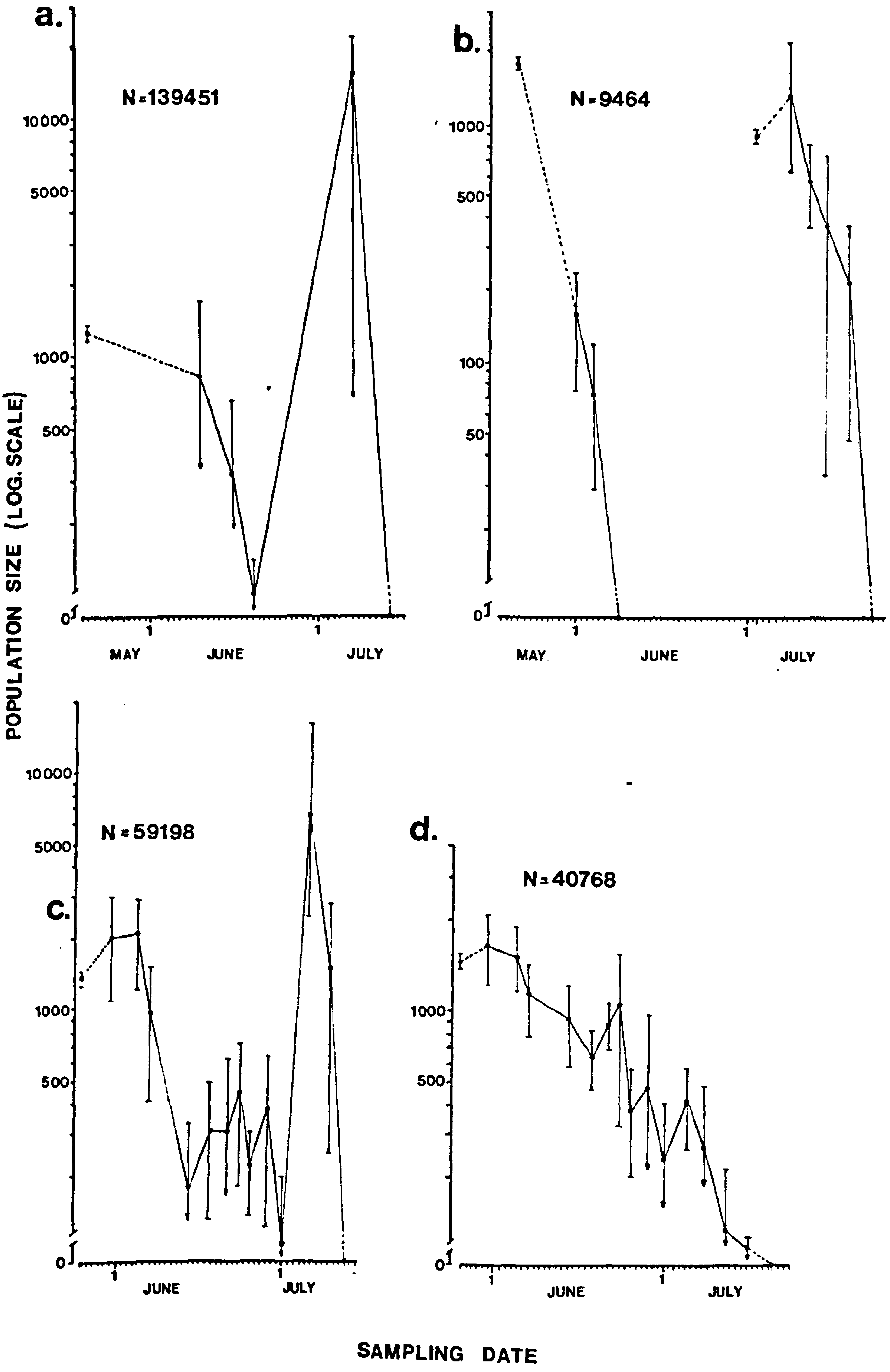
a. Pool 1

b. Pool 8

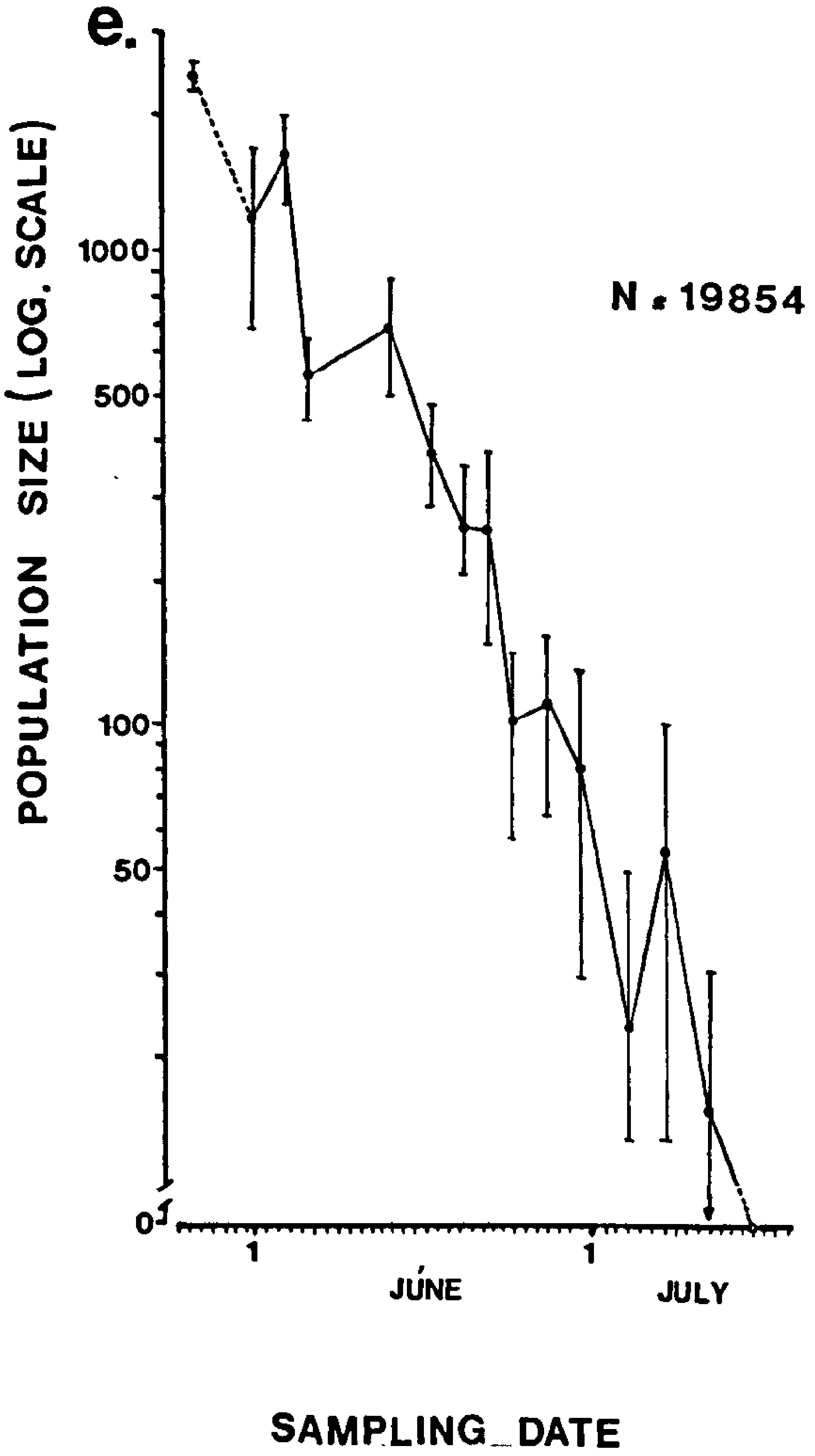
c. Pool 10

d. Pool 14

e. Pool 16



a.
N=139451
10000
5000
1000
500
0
1
1
MAY
JUNE
JULY
b.
N=9464
1000
500
100
50
0
1
1
MAY
JUNE
JULY
c.
N=59198
10000
5000
1000
500
0
1
1
JUNE
JULY
d.
N=40768
1000
500
0
1
1
JUNE
JULY
POPULATION SIZE (LOG. SCALE)
SAMPLING DATE


e.
POPULATION SIZE (LOG. SCALE)
1000
500
100
50
0
N = 19854
1
JUNE
1
JULY
SAMPLING DATE

of 5000 tadpoles surviving to 27 days. This represents an apparent mortality of 97% from hatching (k = 1.57) equivalent to 57.8% real mortality of 1982 ova. Thus estimated survival to the stage mid-point was 1.6% (Table 48).

3. Metamorphosis

Metamorphosis was observed at 4 pools (8, 10, 14 and 16) but after a period of restricted access to pool 8 no tadpoles were found when sampling resumed. Toadlets were only found at pools 14 and 16, the numbers found (July 5) being 21 and 76 respectively. As different methodologies were used to estimate population numbers in 1981 and 1981 the results are not directly comparable, although the results suggest an increased metamorphic success in 1982. Population estimates of metamorphosing tadpoles are given in Fig. 26 and estimated survival is given in Table 4.8.

Using the Graphical method (Southwood, 1978) an estimated 2300 individuals survived to the stage mid-point, suggesting an apparent mortality of 53.7% (k = 0.33), equivalent to 0.7% survival to metamorphosis.

Summation of daily estimates suggested that 2600 individuals metamorphosed in 1982. Thus using this method the overall survival to metamorphosis was estimated to be 0.9% (Table 48).

4.5.4 Larval survival, 1983

1. Eggs

No mortality from desiccation was observed this year. *Saprolegnia* infestation appeared to be the sole mortality cause, levels being the highest recorded for the study. The first spawning (Table 49) was

Table 48. Estimation of tadpole mortality 1982

1. Estimation of tadpole numbers

(i) Σ Areas under population curves = 268825

(ii) Life of tadpoles under field conditions = 54 days

$\therefore$ Estimated No. tadpoles surviving to stage mid-point:

$$\frac{268825}{54} = 4978$$

2. Estimation of metamorphosis:

(i) Σ Areas under population curves = 9217

(ii) Stage duration = 4 days

$\therefore$ Estimated No. surviving to stage mid-point:

$$\frac{9217}{4} = 2305$$

(iii) Σ Daily totals = 2622.

Table 48. (continued)

Estimation of mortality

Stage	Estimated No.	% Apparent mortality	% Real mortality	Σ Real mortality	Survival Rate	log N	*k*
Blastula	311411 ± 39227	4.18	4.18	4.18	95.82	5.493	0.019
Tailed	298394 ± 37587	13.67	13.10	17.28	82.72	4.475	0.064
Hatched	257599 ± 31092	28.16	23.29	40.57	59.43	5.411	0.144
"Survivors"	185071 ± 23312					5.267	
k. early tadpole mortality	180093	97.31	57.83	98.40	1.60		1.57
Tadpoles	4978					3.697	
k. late tadpole mortality	2673	53.70	0.86	99.26	0.74		0.334
Metamorphosis	2305					3.363	
(Estimated survival to mid-pt.)							
k. late tadpole mortality	2356	47.33	0.76	99.16	0.84		0.278
Metamorphosis	2622					3.419	
(Σ daily totals)							

Figure 26. Estimated sizes of metamorphosing tadpole populations ± 95% confidence limits within Cabin Hill breeding pools, 1982. N = the area enclosed by each plot (the number of 'tadpole days').

a. Pool 10

b. Pool 14

c. Pool 16

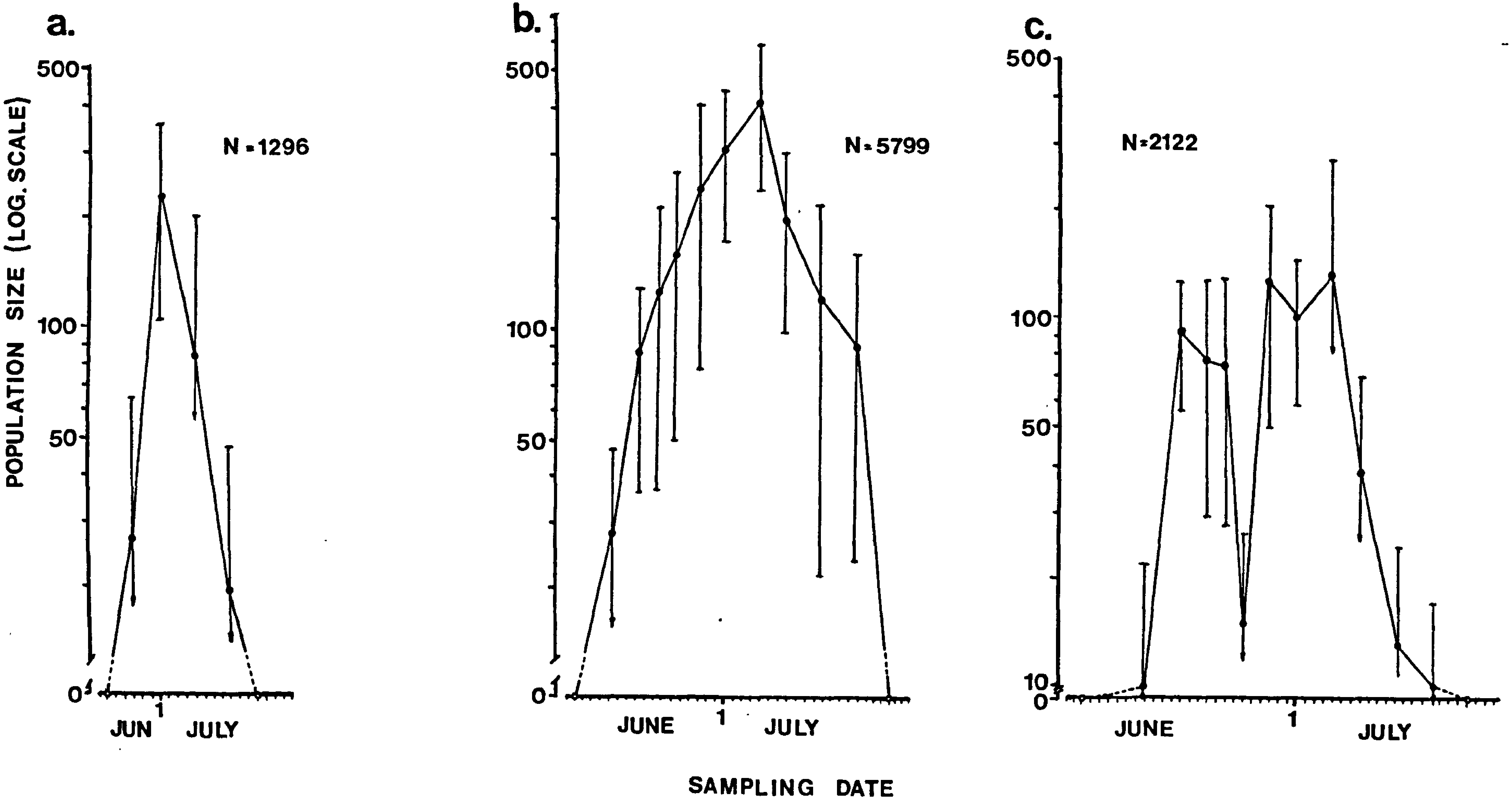

a.
b.
c.
POPULATION SIZE (LOG. SCALE)
500
100
50
10
0
N=1296
N=5799
N=2122
JUN
JUNE
1
JULY
SAMPLING DATE

Table 49. Estimation of spawn mortality 1983

Mean no. eggs cm^{-1} (± 95% CL) = 7.8 ± 0.3 = n

Mean no. eggs $string^{-1}$ (± 95% CL) = 1788.9 ± 145.5

1st spawning (strings 1-293)

Stage	Total length spawn (cm) L	Est. No. eggs N = L x n	% Apparent mortality	% Real mortality	Σ Real mortality	Survival rate	log N	*k*
Blastula	15118	117920 ± 4535					5.072	
k. Saprolegnia mortality	2723	21239 ± 817	18.01	18.01	18.01	81.99		0.087
Tailed	12395	96681 ± 3719					4.985	
k. Saprolegnia mortality	337	2629 ± 101	2.72	2.23	20.24	79.76		0.011
Hatched	12058	94263 ± 3617					4.974	

Table 49. (continued)

2nd spawning (strings 294-427)

Stage	Total length spawn (cm) L	Est. No. eggs N = 1 x n	% Apparent mortality	% Real mortality	Σ Real mortality	Survival Rate	log N	*k*
Blastula	6962	54304 ± 2089					4.735	
k. Saprolegnia mortality	2197	17137 ± 659	31.56	31.56	31.56	68.44		0.165
Tailed	4765	37167 ± 1430					4.570	
Hatched	4765	37167 ± 1430					4.570	

Table 49. (continued)

Combined spawnings (strings 1-427)

Stage	Total length spawn (cm) L	Est. No. eggs $N = L \times n$	% Apparent mortality	% Real mortality	Σ Real mortality	Survival Rate	log N	k
Blastula	22080	177224 ± 6624					5.236	
k. *Saprolegnia mortality*	4920	38276 ± 1476	22.28	22.28	22.28	77.72		0.109
Tailed	17160	133848 ± 5148					5.127	
k. *Saprolegnia mortality*	337	2629 ± 101	1.96	1.53	23.81	76.19		0.009
Hatched	16823	131219 ± 5047					5.118	

Estimates for strings 1-427

Total estimated no. eggs = 427 x 1788.9 ± 145.5 = 763860 ± 62129

∴ Estimated no. tailed stages = 763860 ± 62129 x 77.72% = 593672 ± 48287

∴ Estimated no. hatched = 763860 ± 62129 x 76.19% = 581985 ± 47336 subject to 18% fungal infection of blastula stages (k = 0.09) although infestation of tailed stages was lower, with an apparent mortality of 2.7% (k = 0.01). Total real mortality of eggs was estimated to be 20.2%, equivalent to 79.8% survival. Fungal infection of the second spawning was higher, with 31.6% of all eggs killed (k = 0.16) during the blastula stages. Nearly all the affected strings were laid in pool 21, where 33 out of 46 suffered 100% mortality.

The overall survival rate of eggs in 1983 was 76.2% (Table 49). Major mortalities occurred during the blastula stages, with 22.3% (k = 0.11) killed by *Saprolegnia* . Reduced mortality (2%) was observed in tailed stages, and no post hatch mortality due to desiccation was recorded. It was estimated that of 764000 ± 62000 eggs laid in 1983, 582000 ± 47000 survived to hatching (Table 49).

2. Tadpoles

Tadpoles were monitored in 12 pools used by the adults (Table 39) and population estimates on successive sampling occasions are given in Fig. 27. It was estimated that 22000 tadpoles survived to the stage mid-point (Table 50), equivalent to 2.9% survival of all eggs laid.

3. Metamorphosis

Metamorphosing tadpoles were found at 8 sites, although this was only confirmed for pools 1, 11, and 16. On sunny days in particular, toadlets were readily observed in the vegetation surrounding the pools. At pool 1, during approximately 1 hour searches of a 45 m stretch of southern shoreline on June 19, 24, and August 3, totals of 68, 55, and 108 toadlets were found. Toadlets remained in the pool vicinities until August 17, after which none were located despite careful searches.

Figure 27. Estimates sizes of tadpole populations ± 95% confidence limits within Cabin Hill breeding pools, 1983. Initial value = number of eggs first observed hatching. N = the area enclosed by each plot (the number of 'tadpole days').

a. Pool 1

b. Pool 3

c. Pool 5

d. Pool 6

e. Pool 8

f. Pool 10

g. Pool 11

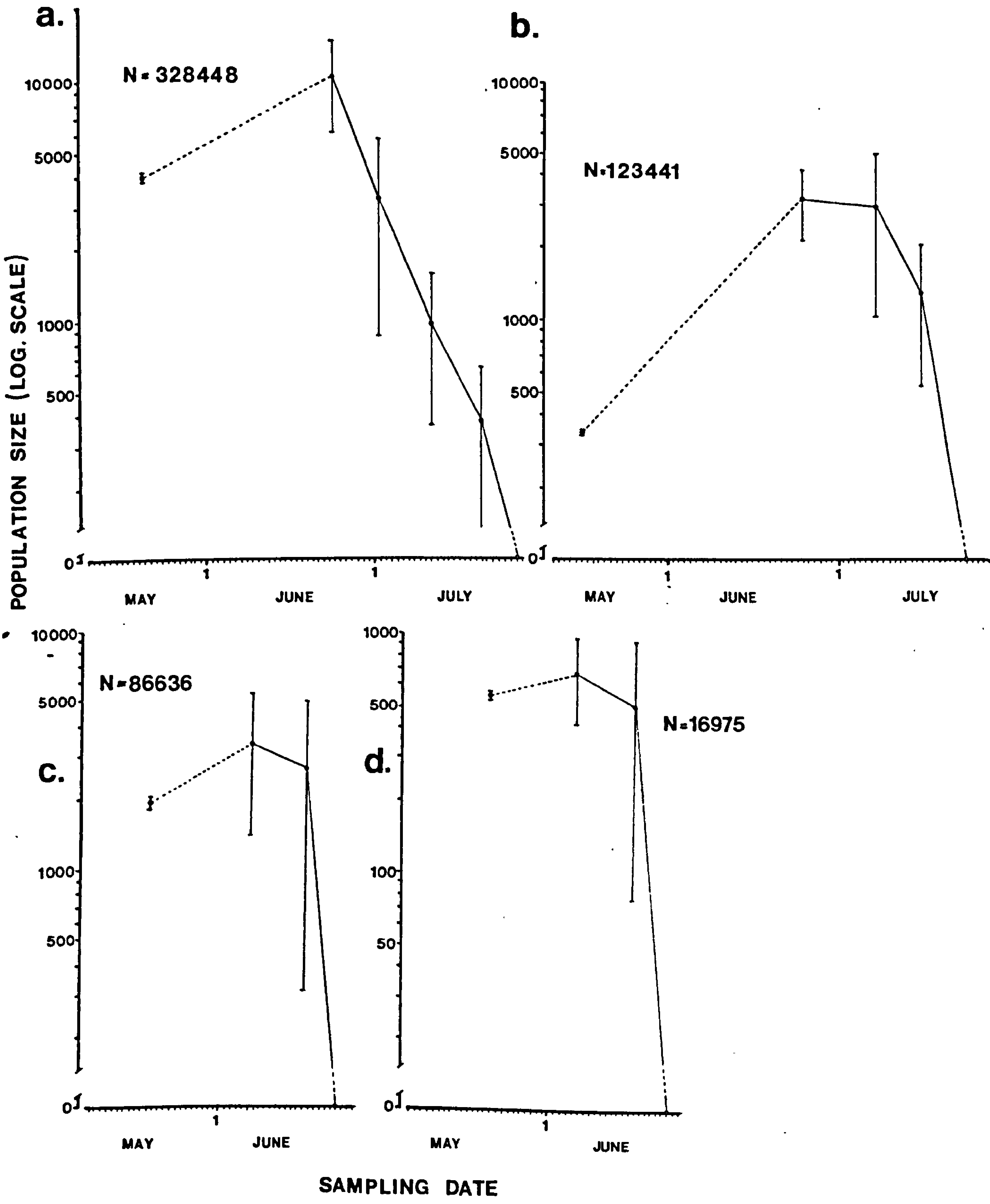
h. Pool 14

i. Pool 15

j. Pool 16

k. Pool P

l. Pool 18


a.
N=328448
10000
5000
1000
500
0
1
1
MAY
JUNE
JULY
b.
N=123441
10000
5000
1000
500
0
1
1
MAY
JUNE
JULY
POPULATION SIZE (LOG. SCALE)
c.
N=86636
10000
5000
1000
500
0
1
MAY
JUNE
d.
N=16975
1000
500
100
50
0
1
MAY
JUNE
SAMPLING DATE


POPULATION SIZE (LOG. SCALE)
e.
N=60073
5000
1000
500
100
50
0
1
1
MAY
JUNE
JULY
f.
N=29461
1000
500
100
50
0
1
1
MAY
JUNE
JULY
g.
N=14355
1000
500
100
50
0
1
1
MAY
JUNE
JULY
h.
N=581
100
50
10
5
0
1
MAY
JUNE
SAMPLING DATE

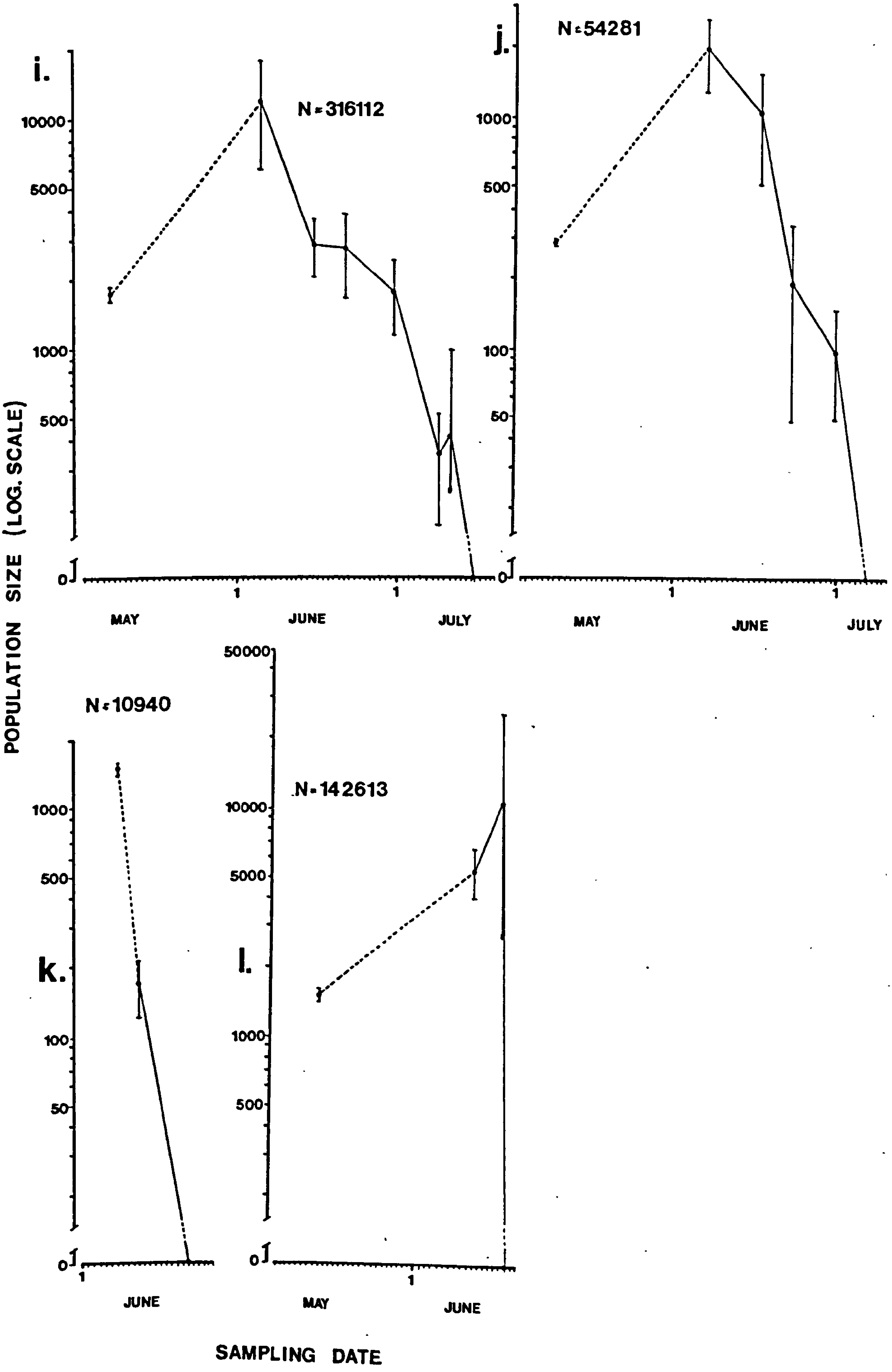

i.
N=316112
10000
5000
1000
500
0
1
1
MAY
JUNE
JULY
j.
N=54281
1000
500
100
50
0
1
1
MAY
JUNE
JULY
POPULATION SIZE (LOG. SCALE)
k.
N=10940
1000
500
100
50
0
1
JUNE
l.
N=142613
50000
10000
5000
1000
500
0
1
MAY
JUNE
SAMPLING DATE

Table 50. Estimation of tadpole mortality, 1983

i. Estimation of tadpole numbers

1. Σ Areas under population curves = 1183916
2. Life of tadpoles under field conditions = 54 days

∴ Estimated no. tadpoles surviving to stage mid-point = $\frac{1183916}{54}$ = 21924

ii. Estimations of survival

Stage	Estimated No.	% Apparent mortality	% Real mortality	Σ Real mortality	Survival rate	log N	k
Blastula	763860 ± 62129	22.28	22.28	22.28	77.72	5.883	0.109
Tailed	593672 ± 48287	1.96	1.53	23.81	76.19	5.774	0.009
Hatch.	581985 ± 47336					5.765	
k. early tadpole mortality	560061	96.23	73.32	97.13	2.87		1.424
Tadpoles	21924					4.341	

Table 50. (continued)

Stage	Estimated No.	% Apparent mortality	% Real mortality	Σ Real mortality	Survival rate	log N	*k*
k. late tadpole mortality	6654	30.35	0.87	99.00	2.00		0.157
Metamorphosis	15270					4.184	
(Estimated survival to mid-pt.)							
k. late tadpole mortality	11754	53.61	1.54	98.67	1.33		0.334
Metamorphosis	10170					4.007	
(Σ daily totals)							

Estimated numbers of metamorphosing tadpoles are shown in Fig. 28, and survival estimates are given in Table 50.

Comparison with Table 47 suggests that metamorphic success was greater in 1983 than 1982. Summation of daily totals suggested 10,200 individuals metamorphosed, equivalent to 1.3% of all eggs laid (Table 50). Integration of Fig. 30 gave an estimate of 15200 individuals surviving, equivalent to 2% survival of all eggs laid.

4.5.5 Summary of estimated larval survival, 1981-83

The estimated survival rates of larval Natterjacks are summarised in Fig. 29 and follow Pearl's (1928) Type 3 survival curve. Metamorphic survivals represent calculated minima for the study.

in 1981 and 1982 survival to hatching was approximately 83% but was lower (76.2%) in 1983 . The mean survival to hatching during the study was 80.5%, however there were marked difference in embryonic mortalities. Thus in 1981 and 1983, there was greater mortality of blastula stages than later, tailed stages, while in 1982 the reverse occurred (Fig. 29).

Greater variation was found for post-hatch survival. In 1981, survival to the tadpole stage mid-point was 32.8% compared to 1.6 and 2.9% (mean = 2.3%) in 1982 and 1983 respectively. Due to sampling problems and the different methodologies, comparison of metamorphic survival during the study are difficult. In 1981, minimum survival was estimated as 0.04% compared to 0.7 and 1.3% in 1982 and 1983 respectively. The mean survival rate for the study was 0.7%, but due to the unreliability of the 1981 result it seems more appropriate to

Figure 28. Estimated sizes of metamorphosing tadpole populations ± 95% confidence limits within Cabin Hill breeding pools, 1983. N = the area enclosed by each plot (the number of 'tadpole days').

a. Pool 1

b. Pool 3

c. Pool 7/8

d. Pool 10

e. Pool 11

f. Pool 15

g. Pool 16

h. Pool 18

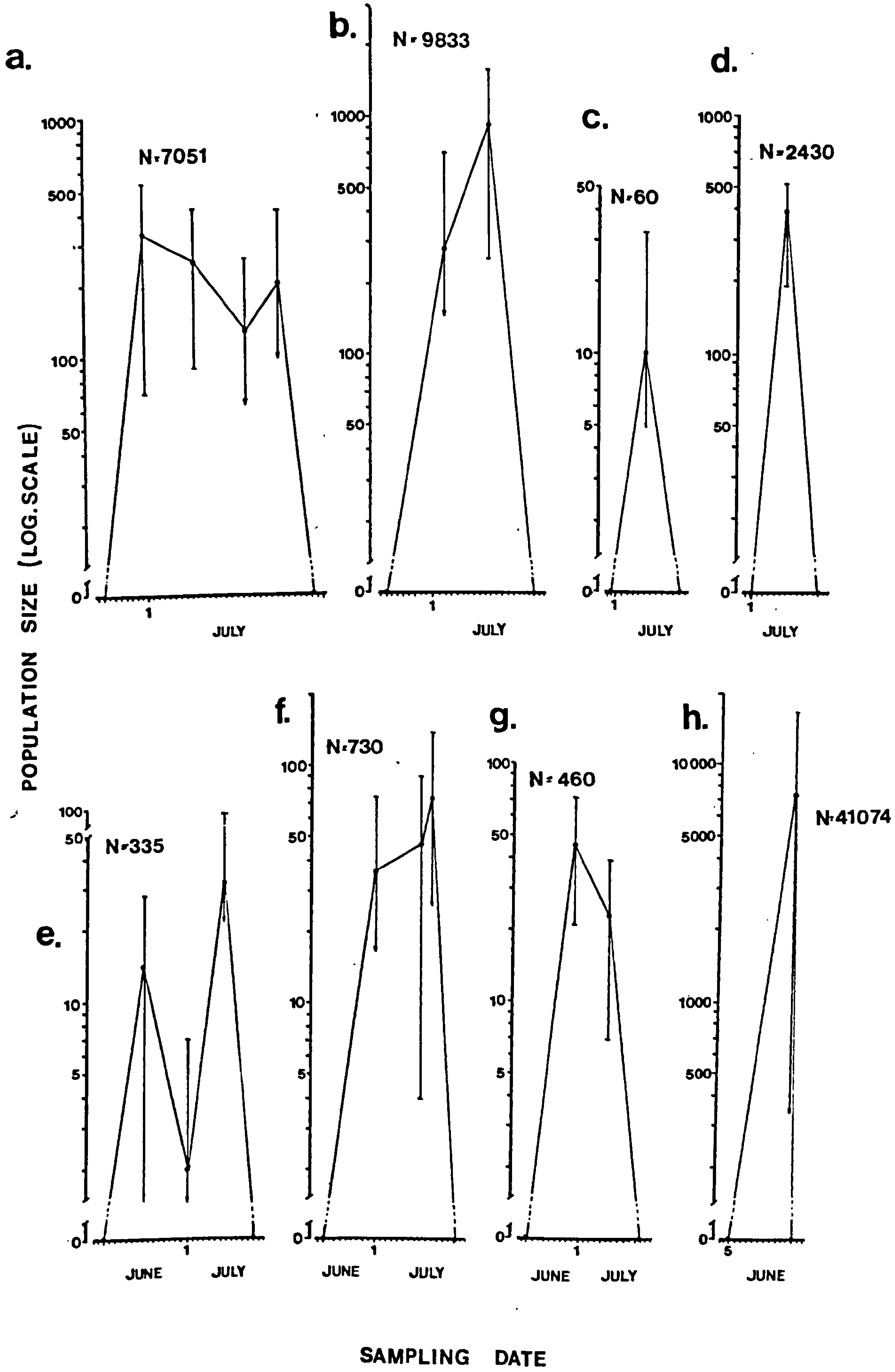
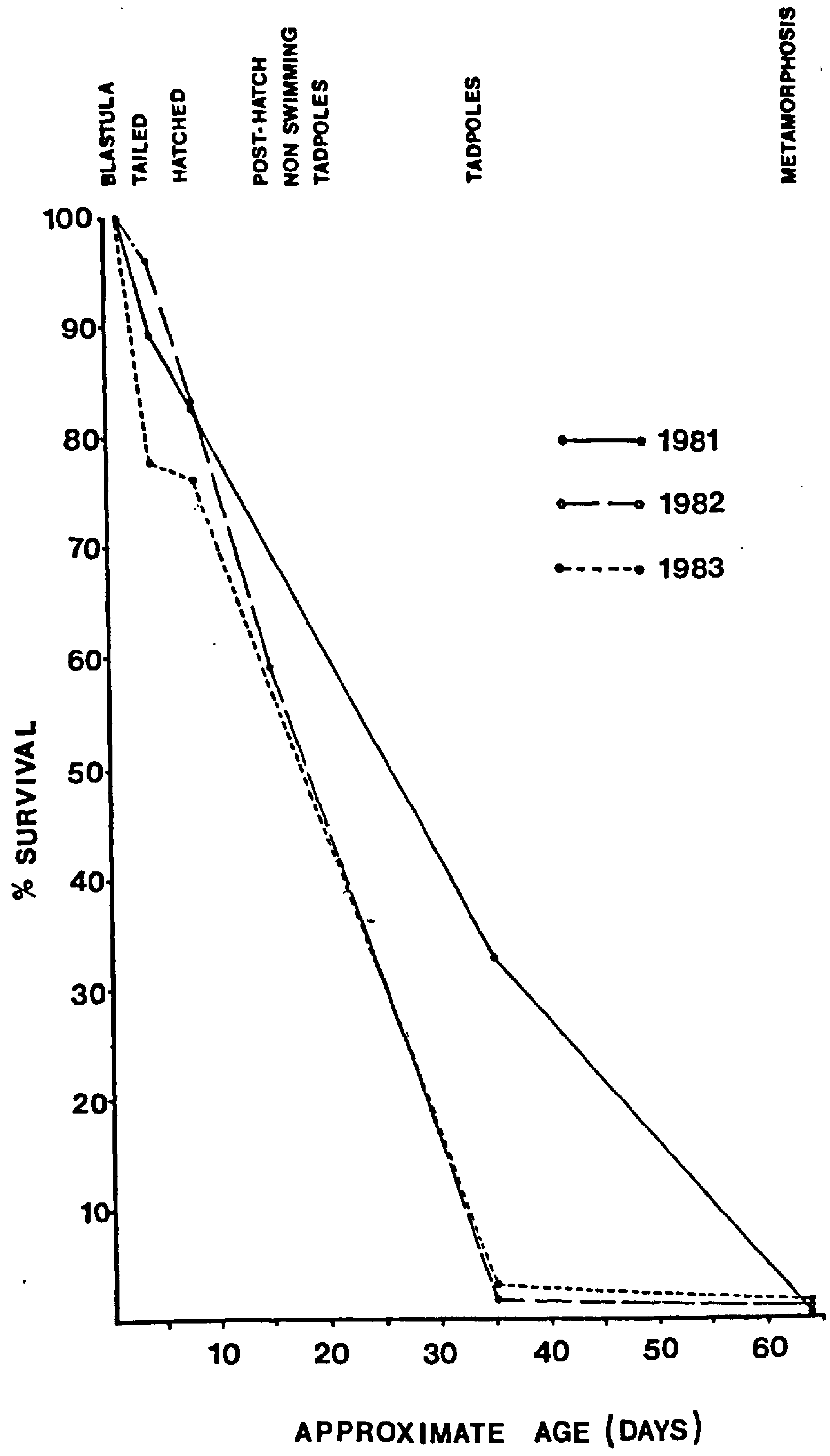

a.
N=7051
1000
500
100
50
0
1
JULY
b.
N=9833
1000
500
100
50
0
1
JULY
c.
N=60
50
10
5
0
1
JULY
d.
N=2430
1000
500
100
50
0
1
JULY
POPULATION SIZE (LOG. SCALE)
e.
N=335
100
50
10
5
0
1
JUNE
JULY
f.
N=730
100
50
10
5
0
1
JUNE
JULY
g.
N=460
100
50
10
5
0
1
JUNE
JULY
h.
N=41074
10 000
5000
1000
500
0
5
JUNE
SAMPLING DATE

Figure 29. Summary of larval survival rates, 1981-83.


BLASTULA
TAILED
HATCHED
POST-HATCH NON SWIMMING TADPOLES
TADPOLES
METAMORPHOSIS
% SURVIVAL
100
90
80
70
60
50
40
30
20
10
10
20
30
40
50
60
APPROXIMATE AGE (DAYS)
1981
1982
1983

consider 1982 and 1983 only (mean survival = 1%).

The results of the k-analysis are summarised in Fig. 30. Figure 30a shows stage specific mortality of embryonic stages. None of the generation mortalities appeared to follow total generation mortality suggesting inconsistency of mortality factors between years. Thus in 1981 and 1983 embryonic fungal infection (k_1 and k_3) were major factors, while in 1982 embryonic desiccation (k_2 and k_4) were more important. It is noticeable that fungal mortality and desiccation appear to show complementary patterns, however a longer study is required to establish whether this is a consistent trend.

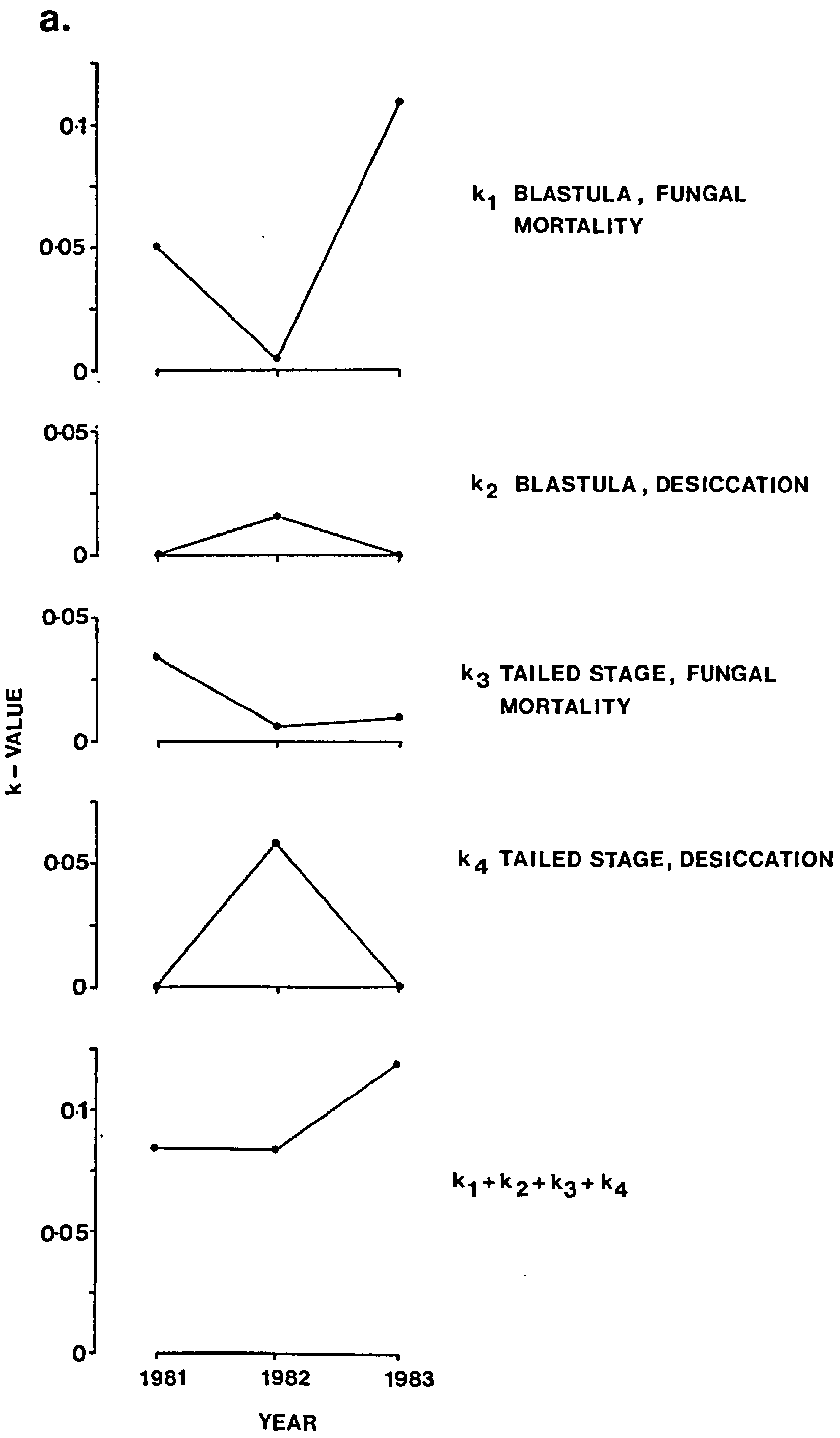
Figure 30b shows generation mortalities for pre- and post-hatched larvae. Late tadpole mortality (k_7) appeared to show the closest similarity to total mortality, however in terms of numerical size, k_7 did not appear to contribute greatly to total mortality in 1982 or 1983. Instead, early tadpole mortality (k_6) was the major mortality factor for these two years. It is apparent from Fig.30b that total embryonic mortality is not a major factor, indeed in 1982 post-hatch desiccation (k_5) was greater than total embryonic mortality.

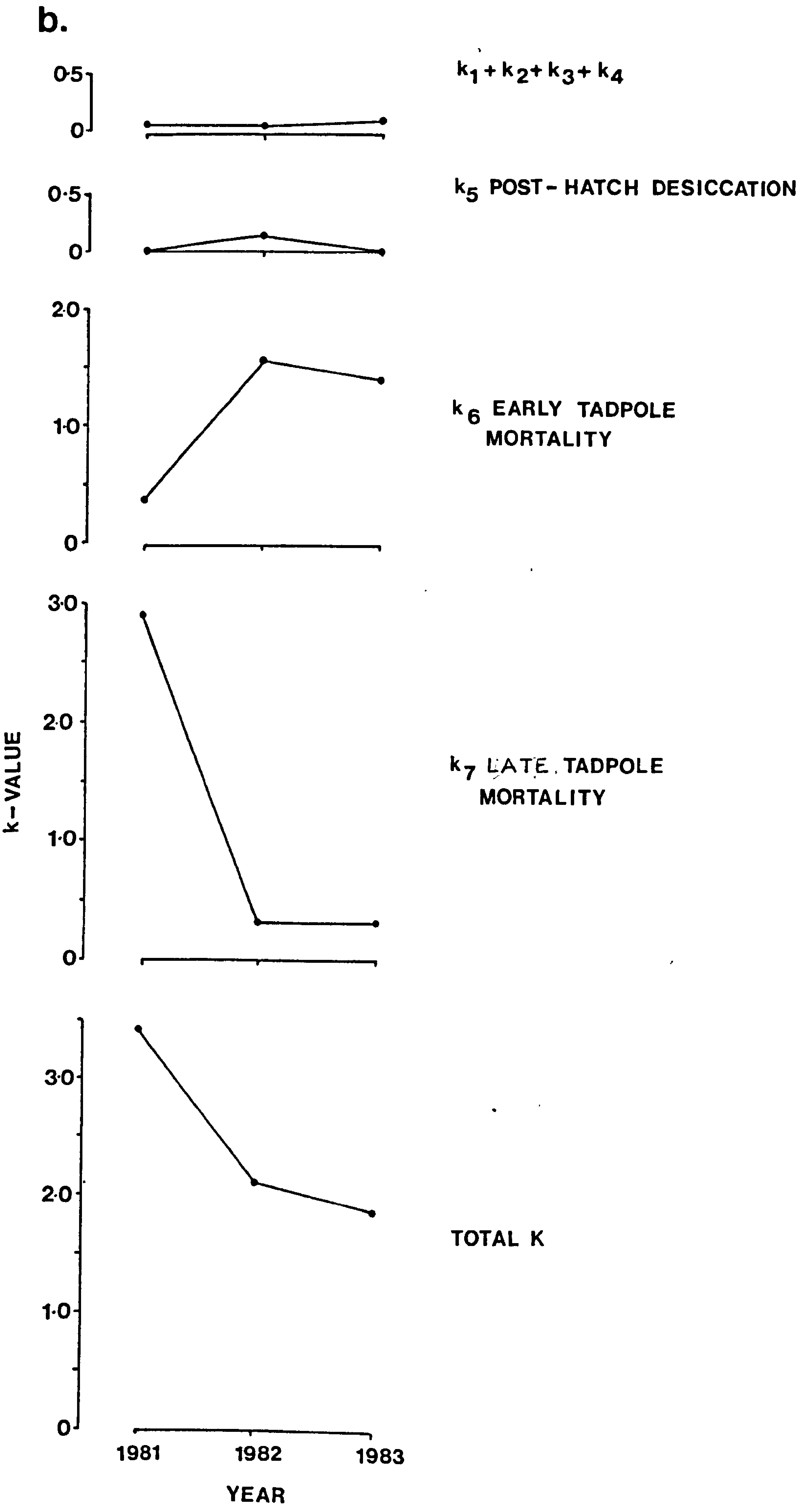
Embryonic mortality from fungal infection and desiccation has been observed by previous workers (Smith, 1974; Kadel, 1975; Beebee, 1979a). Frazer (1983) states that *Saprolegnia* rapidly covers infertile, but not fertile, eggs. However, although *Saprolegnia* is generally considered a secondary infective agent, it can become a primary agent when established (Deverall, 1981). Beebee (1979a) states that fungal infection seems more widespread during cold periods such as unusually cool springs. He suggests that this could be associated with

Figure 30. Summary of *k*-analysis, 1981-83.

a. Stage-specific mortalities of embryonic stages.

b. Stage-specific mortalities of all developmental stages.


a.
0·1
0·05
0
k_1 BLASTULA, FUNGAL MORTALITY
0·05
0
k_2 BLASTULA, DESICCATION
0·05
0
k_3 TAILED STAGE, FUNGAL MORTALITY
0·05
0
k_4 TAILED STAGE, DESICCATION
0·1
0·05
0
$k_1+k_2+k_3+k_4$
k – VALUE
1981
1982
1983
YEAR


b.
0·5
0
$k_1 + k_2 + k_3 + k_4$
0·5
0
k_5 POST-HATCH DESICCATION
2·0
1·0
0
k_6 EARLY TADPOLE MORTALITY
3·0
2·0
1·0
0
k_7 LATE TADPOLE MORTALITY
k-VALUE
3·0
2·0
1·0
0
TOTAL K
1981
1982
1983
YEAR

decreased embryonic viability at lower temperature (Mathias, 1971) which might encourage fungal infection, although he notes that length of exposure to low temperatures is important.

During this study mortality of tadpoles due to pool desiccation was observed every year. Beebee (1979a) states that catastrophic mortalities can occur in this manner, and there appeared to be evidence for this at Cabin Hill. Thus in 1982, desiccation resulted in 100% mortality of the first spawning (mortality to hatching = 26.9%). Previously, Smith (1977,1978b,1979,1980b) reported catastrophic mortality of spawn and tadpoles at Cabin Hill, although he carried out licensed rescue operations which resulted in metamorphosis each year. If is difficult to determine quantitatively the relative importance of desiccating mortality during this period as other factors e.g. predation are also operating. Also desiccation may act insidiously upon the population. For example, in 1981 temporary, shallow offshoots from the mainwater bodies formed during periods of rain into which tadpoles could enter, only to become stranded as the water levels dropped again. Also wind induced waves caused tadpoles clustering around pool margins to be stranded. An index of mortality was obtained by assuming that when pools dried between subsequent sampling dates, all apparent mortality was due to desiccation. As this represents 'catastrophic' mortality, it is probably an underestimate of the total desiccatory mortality occurring during this period. This analysis is given in Table 51. It was estimated that desiccation resulted in 4.3, 12.8 and 2.9% of tadpole mortalities during the respective study years. Although desiccation caused relatively low percentage mortalities, these occurred late in the season (Table 51) from mid June onwards.

Table 51. Estimation of desiccatory mortality during tadpole development

1981:

Pool number	Date dried	Estimated tadpole mortality
6	26-5	348
P	26-5	1152
5	16-6	599
17	17-6	197
18	18-6	7162
13	19-6	1182
		10640

∴ Estimated apparent mortality $= \frac{10640}{250079*}\% = 4.3\%$

Estimated real mortality $= \frac{10640}{303024*}\% = 3.5\%$

(Estimated predation = 100 - 4.3 = 95.7%)

1982:

Pool number	Date dried	Estimated tadpole mortality
3	3-6	22713 (strings 1-53)
1	3-6	
15	3-6	
10	9-7	765
		23478

∴ Estimated apparent mortality $= \frac{23478}{182766**}\% = 12.8\%$

Estimated real mortality $= \frac{23478}{311411**}\% = 7.5\%$

Estimated predation = 100 - 12.8 = 87.2%)

Table 51. (continued)

1983:

Pool number	Date dried	Estimated tadpole mortality
P	15-6	1683
18	16-6	10986
5	21-6	2702
6	21-6	504
15	15-7	419
		16314

∴ Estimated apparent mortality $= \frac{16314}{571815^{***}}\% = 2.9\%$

Estimated real mortality $= \frac{16314}{763860^{***}}\% = 2.1\%$

(Estimated predation = 100 - 2.9 = 97.1%)

* From Table 43

** From Table 47

*** From Table 49

Thus these tadpoles were individuals close to metamorphosis which had survived previous mortality factors.

Between 1981-83, predation was estimated to have caused 95.7, 87.2 and 97.1% of mortality of tadpoles, although the 1981 figure is probably an overestimate. Heusser (1970) reports that Common Frog tadpoles feed upon Natterjack spawn, and Beebee (1977) suggests that predation of newly hatched tadpoles by Common Toad larvae is important. However, although larvae of these species were recorded in the same pools as Natterjacks throughout the study (Table 52) no direct predation of the latter was observed. Smooth Newts (*T. vulgaris*) were present at Cabin Hill but Mathias (1971) reports that they find Natterjack tadpoles unpalatable. However, predation by invertebrate species may constitute a major mortality factor. Mathias (1971) reports that captive *Dytiscus marginalis* larvae can eat up to 20 tadpoles per day. He also lists *Colymbetes fuscus* and *Notonecta* sp. as important predators. Kadel (1975) observed Odonata larvae ate 2-4 tadpoles per day. Table 53 summarises population estimates of potential invertebrate predators at Cabin Hill during summer 1983, together with estimated Natterjack and Common Toad populations. During this period most Common Toad tadpoles had already metamorphosed and left the pools, as had Common Frog larvae approximately one month earlier. Thus, during this period, mainly Natterjack tadpoles were available to invertebrate predators. Although it is difficult to apply laboratory based rates of predation to wild populations where increased vegetation cover etc. may increase larval survival (Severtzov & Surova, 1979), Mathias (1971) and Kadel's (1975) estimates suggest that invertebrate populations at Cabin Hill (Table 53) were potentially able to account for all Natterjacks present. It is unclear at which stage of tadpole

Table 52. Presence of Common Toads and Frogs in Cabin Hill breeding pools, 1981-83

	Common Toad									Common Frog								
Pool	1981			1982			1983			1981			1982			1983		
	S	T	M	S	T	M	S	T	M	S	T	M	S	T	M	S	T	M
1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2				+	+								+	+	+			
3	+	+	+	+	+		+	+	+	+	+	+	+	+		+	+	+
4				+	+	+				+	+	+	+	+	+	+	+	+
5	+	+	+	+	+					+	+	+	+	+				
6				+	+								+	+		+	+	
7				+	+	+	+	+	+									
8	+	+		+	+		+	+		+	+	+				+	+	+
9													+	+	+			
10	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
11	+	+	+	+	+	+	+	+	+	+	+	+				+	+	+
12																		
13							+	+										
14	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
15	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
16	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
P																		
17	+	+		+	+					+	+	+	+	+		+	+	+
18	+	+		+	+		+	+					+	+				
19																		
20										+	+							
21																		

+ denotes presence; S = spawn, T = tadpoles, M = metamorphosis

Table 53. Estimated population sizes (± 95% CL) of invertebrates, Common Toad, and Natterjack larvae (0-10 cm depth), June 1983

Date	Pool	*Dytiscus*	Odonata	Hemiptera	Ephemeroptera	Common Toad	Natterjack
5.6	5	21 ± 13					3131 ± 2039
	7/8		58 ± 66	64 ± 114	12 ± 91		2573 ± 1422
6.6	16	91 ± 73	378 ± 247	186 ± 170	18 ± 29	423 ± 245	2067 ± 732
10.6	15					374 ± 191	12107 ± 6022
	14					1748 ± 1503	26 ± 32
	18					536 ± 296	5349 ± 1328
16.6	16	44 ± 89	792 ± 307	321 ± 255	28 ± 41		1013 ± 562
	15	391 ± 76				267 ± 140	2882 ± 806
22.6	11		9 ± 11	12 ± 14			57 ± 42
	16	11 ± 4	117 ± 31	78 ± 29	11 ± 9	50 ± 37	197 ± 202
30.6	16		32 ± 23	43 ± 30			101 ± 49

development invertebrate predation might be most important, although Arnold & Wassersug (1978) report increased predation of *B. boreas* and *Hyla regilis* during metamorphosis. They relate this to limb formation reducing swimming and thus escape ability.

Other mortality during tadpole development may have been due to predation by birds. Lapwings (*Vanellus vanellus*) were seen feeding around pool margins at Cabin Hill, and Smith (1981) observed Blackbirds (*Turdus merula*) feeding on Natterjack tadpoles at Formby Point. Bridson (1978) reports that trampling and pollution of water by cattle can cause large mortalities of Natterjack larvae. However, although approximately 20 cattle were grazed in areas adjoining pools 1 and 3, trampling did not seem to be a major problem at Cabin Hill, although it may have had a greater effect when water areas were restricted in midsummer. Disturbance by children and dogs was a problem which increased after 1982 when the Rifle Range boundary was fenced, although I was able to prevent children taking spawn/tadpoles during the breeding season.

The results show similarities with previous studies of survival in Natterjacks and other anurans. Kadel (1975) found 90% survival of Natterjack ova which compares with my mean estimate of 80.5%. Voris & Bacon (1966) estimated 95% embryonic survival of *B. americanus*, and Licht (1974) observed >90% survival in *R. aurora* and 70% survival in *R. pretiosa* embryos. Published values of metamorphic survival are summarised in Table 54.

Table 54. Summary of published annuran survival rates to metamorphosis

Species	Study	Estimated survival (%)
Bombina bombina	Bannikov (1950)	5
R. catesbeiana	Cecil & Just (1979)	14.2 (Mean)
R. sylvatica, R. pipiens	De Benedictis (1974)	13.2
R. temporaria, R. arvalis	Wijnands (1972)	< 10
R. aurora, R. pretiosa	Licht (1974)	< 5 (< 1 for pond populations)
R. aurora	Calef (1973)	5
R. sylvatica	Herreid & Kinney (1966)	3.7 (Mean)
B. calamita	Present study	1 (mean for 1982 and 1983)
B. calamita	Kadel (1975)	0.3

Metamorphic survival rates in other anuran species range from 3.7% in *R. sylvatica* (Herreid & Kinney, 1966) to 54% in *Bombina bombina* (Bannikov, 1950). By comparison Natterjack survival rates are very low. Kadel (1975) found 0.3% survival to metamorphosis whereas I estimated mean survival in 1982 and 1983 to be 1%. Beebee (1979a) states that mortality rates in Natterjacks are especially high, however catastrophic mortalities have been reported for other anurans. For example, Licht (1974) reports < 1% survival in pond populations of *R. aurora* and *R. pretiosa*. He found that *R. pretiosa* was particularly subject to extensive or complete mortality. As with Natterjacks, the adults deposit their eggs in shallow water close to pool/river margins, thus in dry weather spawn may become stranded. Richmond (1947) reports 100% mortality of *Scaphiopus holbrooki* eggs when water temperature fall below 40°F. Reports by Cooke (1980,1981) suggest Natterjack survival is highly variable. Thus there may be no spawn survival at some sites for several years in succession. At Cabin Hill, survival to metamorphosis varied from 0.7% in 1982 to 1.3% in 1983, and there were indications that 1981 survival was lower than either of these estimates.

4.6 Thermal relations in Natterjack and Common Toad larvae

4.6.1 Terms used during analysis of results

The metabolic rate of an organism is not fixed but may vary, within limits appropriate to the species, in response to the thermal history of the individual concerned. Several terms are used to describe the effect of environmental history on the physiology of an organism, and although there is some plurality of meaning within the literature, the definitions as used in this study are as follows:

Acclimation: the phenotypic adjustment of an animal to changes in a specific environmental variable induced under controlled conditions.
Acclimatization: the phenotypic adjustment of an animal to changes in environmental variables experienced under natural conditions.
Adaptation: the genetic adjustment of a species to differences in environmental conditions which occurs by natural selection over many generations.

These definitions follow those given by Rose (1967).

Precht *et al* (1973) describe five types of acclimatory response exhibited by an animal transferred from an acclimatory temperature T_1 to a second temperature T_2. In practice, these responses may be determined by comparing the metabolic rate-temperature curves of an organism at two or more acclimatory temperatures. If an animal is moved to a lower environmental temperature, metabolic rate is found to decrease to a lower level (Fig. 31). If after prolonged exposure to T_2 metabolic rate remains at this reduced level, then no compensatory acclimation has occurred. This is termed a type 4 acclimatory response (Precht *et al*, 1973). However, metabolic rate may gradually be restored towards the rate measured at T_1, in which case compensation may be partial (type 3) or ideal (type 2) whereby the original rate is fully restored. It is possible to express the extent of partial compensation occurring as a percentage. For example, 50% compensation occurs if metabolic rate of an animal acclimated and measured at T_1 returns halfway to the original level when acclimated and measured at T_2. In some cases compensation may be greater than 100% (ideal or type 2) and become supra-optimal (type 1). The final possibility is that a further decrease in metabolic rate may occur, which is termed inverse compensation (type 5).

4.6.2 Preferred body temperature (PBT)

The results of this experiment are given in Fig. 32 as frequency histograms of temperature choice. All thermal preferenda are shown, but recordings below 10°C were not included in analysis as tadpoles became immobilised at these temperatures and were therefore unable to move back to more moderate temperatures. Thus inclusion of these data would introduce an erroneous bias in favour of a lower mean PBT. Modal values for Natterjack tadpoles acclimated to 10 and 20°C were both 27°C, while mean thermal preferenda (± 1 SD) were 25 ± 5°C and 24 ± 5°C respectively. Similarly, modes of 26°C and means of 26 ± 4°C and 25 ± 4°C were recorded for Common Toads. Comparison of

Figure 31. The influence of environmental temperature on the standard metabolic rate of a bradymetabolic organism acclimated to two different environmental temperatures, T_1 and T_2. (see text 4.6.1 for explanation).

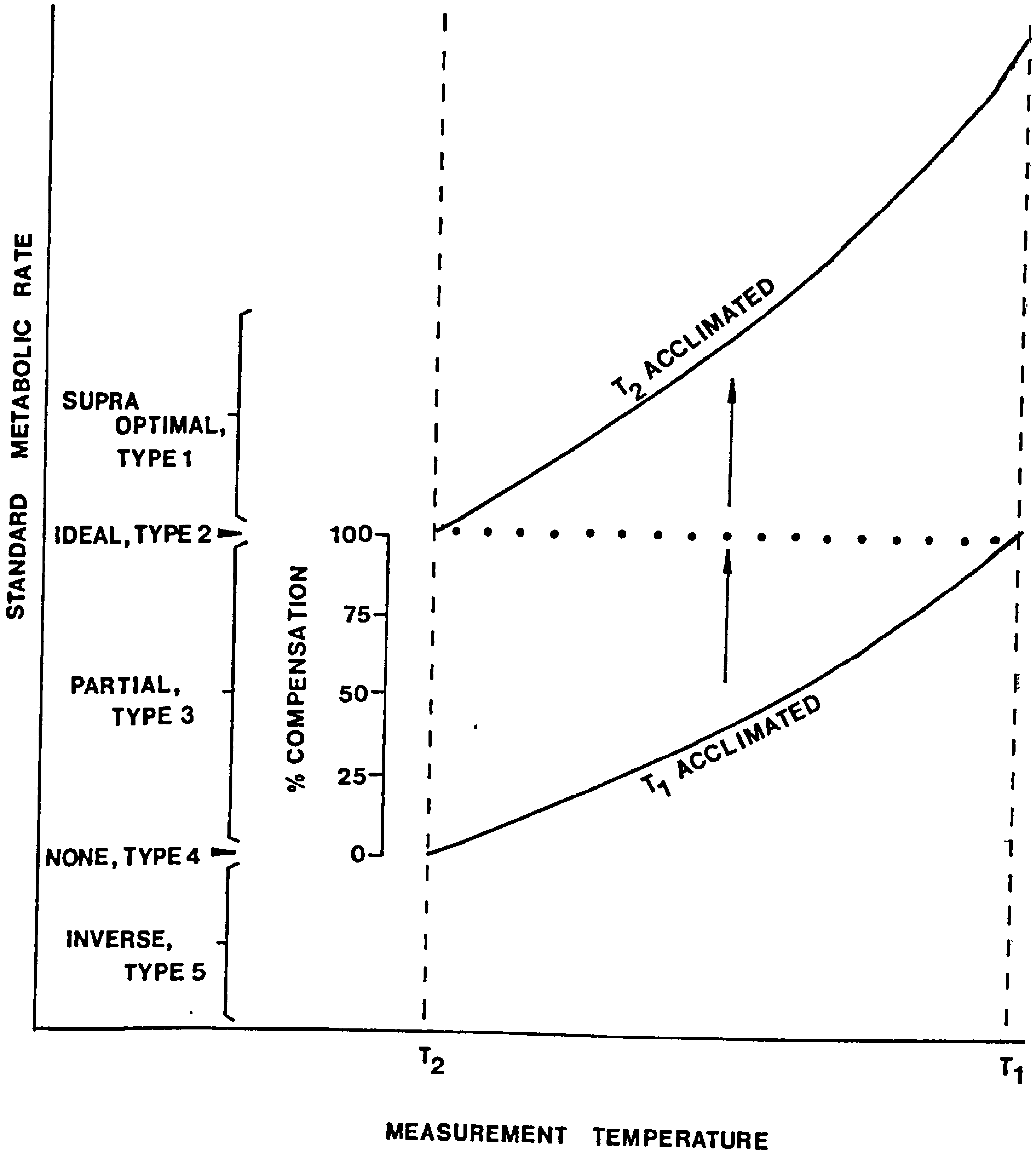
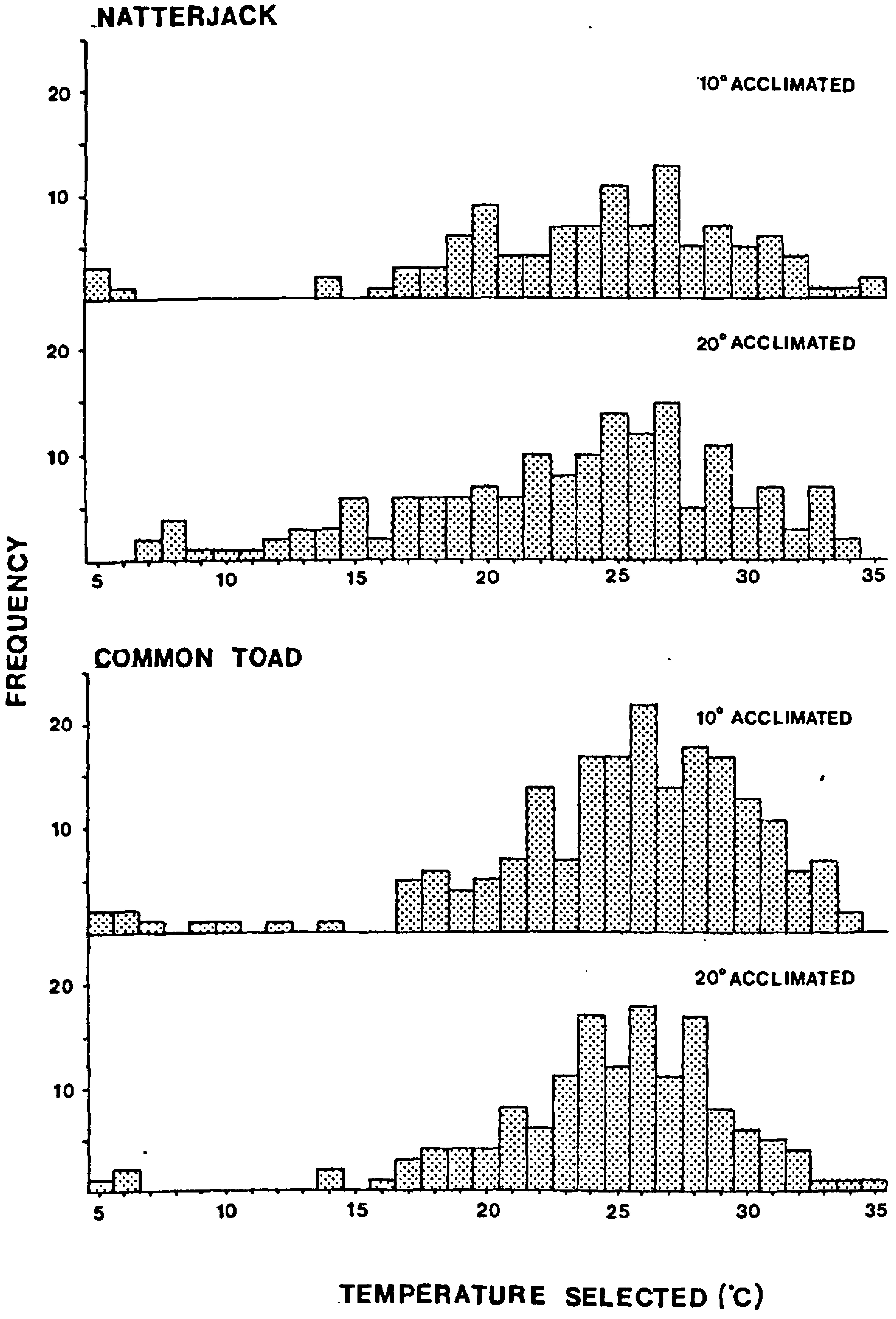

STANDARD METABOLIC RATE
SUPRA OPTIMAL, TYPE 1
IDEAL, TYPE 2
PARTIAL, TYPE 3
NONE, TYPE 4
INVERSE, TYPE 5
% COMPENSATION
100
75
50
25
0
T2 ACCLIMATED
T1 ACCLIMATED
T2
T1
MEASUREMENT TEMPERATURE

Figure 32. Thermal preferenda of Natterjack and Common Toad larvae acclimated at 10 and 20°C.



NATTERJACK
10° ACCLIMATED
20
10
20° ACCLIMATED
20
10
5
10
15
20
25
30
35
FREQUENCY
COMMON TOAD
10° ACCLIMATED
20
10
20° ACCLIMATED
20
10
5
10
15
20
25
30
35
TEMPERATURE SELECTED (°C)

mean thermal preferenda revealed no significant differences ($p > 0.05$) between species or acclimation temperatures (Table 55).

Figure 32 suggests that both species regulate body temperature, although the wide range of temperature choice (mean span.24°C) suggests that neither species regulates particularly well. Other anuran species show 'loose' thermal regulation. Lucas & Reynolds (1967) found that larval *R. pipiens* and *R. clamitans* acclimated to 20°C both displayed modal thermal preferenda of 23°C, however tadpoles were found between 10-39°C and 12-33°C respectively. Similarly, DeVlaming & Bury (1970) found that second year *Ascaphus truei* acclimated at 5, 10, and 16°C (photoperiod = 16L/8D) showed modal preferenda of 16°C, however the larvae ranged between 0-22°C. The low thermal choice of this species appeared to be an adaptation to its low temperature habitat of mountain streams (De Vlaming & Bury (1970). . Workers studying other groups of lower vertebrates have found that PBT's are usually conservative within genera. For example Bogert (1949a,b) studying behavioural thermoregulation of lizards found that members of the same genus from different climatic regions of North America had similar PBT's. More recent studies (Licht *et al*, 1966; Spellerberg, 1972a,b; Huey & Slatkin, 1976) have supported conservatism of PBT's within Saurian genera. The results from the present study indicate that PBT may be conservative within the genus *Bufo*. This appears to be confirmed by Beiswenger (1978) who found that *B. boreas* and *B. americanus* tadpoles acclimated to 22°C aggregated between 28-34°C and 27.5-37°C respectively.

The results show that PBT in these two species do not appear to

Table 55. Anova of temperature choice by Natterjack and Common Toad larvae

	Natterjacks 10° C	Natterjacks 20° C	Common Toad 10° C	Common Toad 20° C
n	108	157	184	147
mean	25	24	26	25
± 1 SD	5	5	4	4

Source of variation	df	SS	MS	F	p
Among groups	3	259.21	86.40	3.99	> 0.05
Error	592	12791.71	21.60		
Total	595	13050.92			

be influenced by acclimation temperature. This agrees with previous studies of amphibia and other groups of lower vertebrates (Stebbins, 1963; Licht, 1968). For example, Lucas & Reynolds (1967) working with *R. pipiens* found that tadpoles acclimated to 13°C and 25-27°C selected 20°C, although a control group acclimated to 20°C had a PBT of 27°C. Hutchison & Hill (1978) studying *R. catesbeiana* larvae at four acclimation temperatures of 4.4, 15.5, 26.7, and 35°C, found mean PBT's of 16.9, 20.7, 22.2, and 22.2°C respectively (overall mean = 20.7°C). The lower PBT of 4.4°C acclimated tadpoles appears to be due to a group of stage 35-36 tadpoles which displayed modal temperatures of 5°C, although Hutchison & Hill do not give any information which might explain this. Brattstrom (1970a) states that, while amphibians do display species specific preferred temperatures, acclimation temperatures rarely induce changes. It was found in the present study that some tadpoles were unable to avoid lethal temperatures (e.g. 40°C) and some chose temperatures (e.g. 35°C) that would have been lethal within 24 hours. Other tadpoles chose low temperatures (< 10°C) that were also effectively lethal. However these may be atypical individuals less able to respond to temperature changes. In the wild these individuals might not survive to metamorphosis, being likely to inhabit areas of pools where temperatures are lethal.

The mean PBT's (24-26°C) in the present study are higher than mean water temperarures which may be normally encountered in the field. Table 56 shows mean water temperarures recorded at Cabin Hill during 1982. Thermal maxima and minima are also given. The May figure in parenthesis represents the maximum temperature recorded on two days (May 30 and 31).

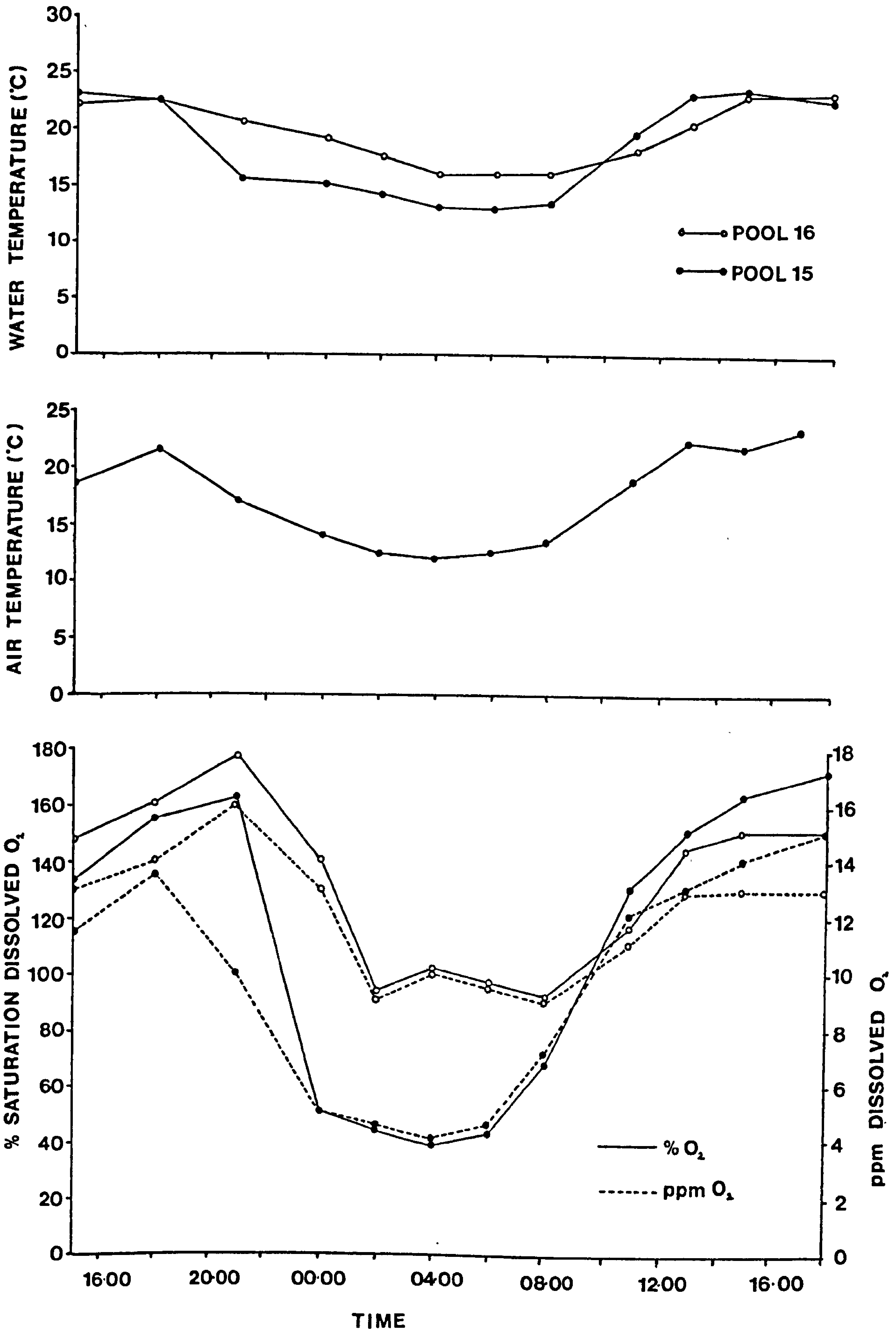
Table 56. Mean water temperature recorded at Cabin Hill, 1982 (10 cm deep, pool 14)

Month	n	Min. temp.	Max. temp.	Mean ± 1 SD
March	6	2.5	12	7.6 ± 4.0
April	18	3.5	26	12.8 ± 7.6
May	10	5.0	25.5 (29)	18.4 ± 8.2
June	10	11	26	18.5 ± 6.6
July	6	13	26	19.1 ± 5.6

Table 56 shows that mean water temperatures are below mean preferenda, in particular during April when Common Toads are already hatched and actively swimming. Apart from the two values recorded at the end of May, maximum water temperatures were 25.5-26°C, equivalent to mean PBT's of both species. However, in shallow, incipient slacks within the mobile dunes, maximum summer water temperatures may regularly approach 30°C during hot weather (P.H. Smith, pers. comm.). Figure 33 shows physical variables (air and water temperatures, oxygen concentrations) recorded over 24 hours at two pools in Summer 1983. This shows that water temperatures may fluctuate by 10°C although recordings in early April showed fluctuations of 20.5°C.

Difficulties arise in relating laboratory studies of PBT to tadpole behaviour under natural conditions. First, other factors may override temperature choice in the wild, e.g. foraging or escape behaviour. In the laboratory there would have been a slight oxygen gradient concommitant with the thermal gradient which may have modified temperature choice. However, in the field there are probably greater variations in oxygen concentration, for example between areas of bare sand and vegetation, which could have an important effect on overriding temperature choice. Second, the dark pigmentation of tadpoles may absorb solar radiation, thus raising their temperature above that of their surroundings, particularly where large aggregations occur (Brattstrom & Warren, 1955; Bragg, 1965). Brattstrom (1962) observed *H. regilla* oriented with their tails pointing towards the sun, thus exposing their dorsal surfaces to solar radiation. He concluded that this was a behavioural adaptation to increase body temperature. Thus it is possible that mean body temperatures in the field differ from PBT as the animals are forced to compromise with environmental

Figure 33. Physical variables (air and water temperature, dissolved oxygen) measured over 24 hours at Cabin Hill, June 7-8 1983.


WATER TEMPERATURE (°C)
0
5
10
15
20
25
30
POOL 16
POOL 15
AIR TEMPERATURE (°C)
0
5
10
15
20
25
% SATURATION DISSOLVED O₂
0
20
40
60
80
100
120
140
160
180
ppm DISSOLVED O₂
0
2
4
6
8
10
12
14
16
18
% O₂
ppm O₂
16·00
20·00
00·00
04·00
08·00
12·00
16·00
TIME

temperatures and other variables encountered in the field. This has been shown by workers studying lizards (Mayhew, 1963; Stebbins, 1963; McGinnis, 1966) who reported seasonal differences between body temperatures of wild *Sceloporus* spp. whereas PBT's measured in laboratory gradients remained fixed within species.

4.6.3 Metabolic rates of Natterjack and Common Toad tadpoles

Figure 34 shows the relationship between log. metabolic rate and temperature for the two species measured in week 5. For all sets of experimental animals significant correlations and regressions were calculated between log. metabolic rate and temperature. The computed correlation coefficients and regression equations are given in Figs. 34a and b.

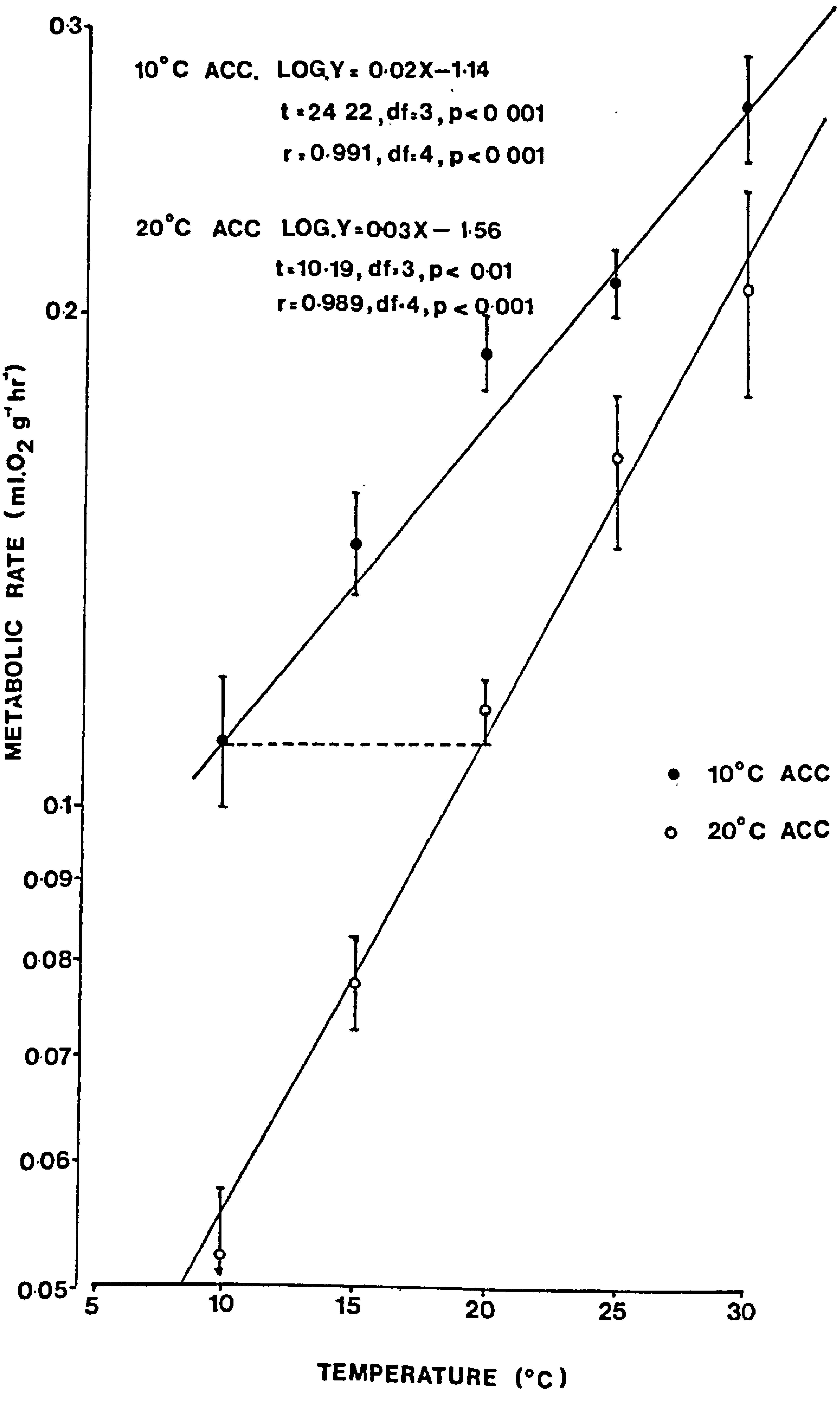
Figure 34a shows that after 5 weeks the metabolic rates of Common Toad tadpoles acclimated to 10°C were higher than those acclimated to 20°C. However, the increase in metabolic rate with increasing temperature was relatively greater in the 20°C acclimated tadpoles. Thus, the latter were found to have a Q_{10} value of 2.0 compared to 1.6 in the 10°C acclimated group. Using the method described previously (section 4.5.1), Common Toads were found to exhibit 100% acclimation of metabolism i.e. ideal or type 2 compensation (Precht *et al*, 1973), Natterjack larvae acclimated at 10°C also showed higher metabolic rates than those at 20°C (Fig. 34b). In both groups metabolic rates were greater than those of the comparable group of Common Toads. The Q_{10} values of Natterjack tadpoles were similar to those of Common Toads. (10°C acc: $Q_{10} = 1.7$; 20°C acc: $Q_{10} = 2.0$) however only 75% acclimation of metabolism was exhibited.

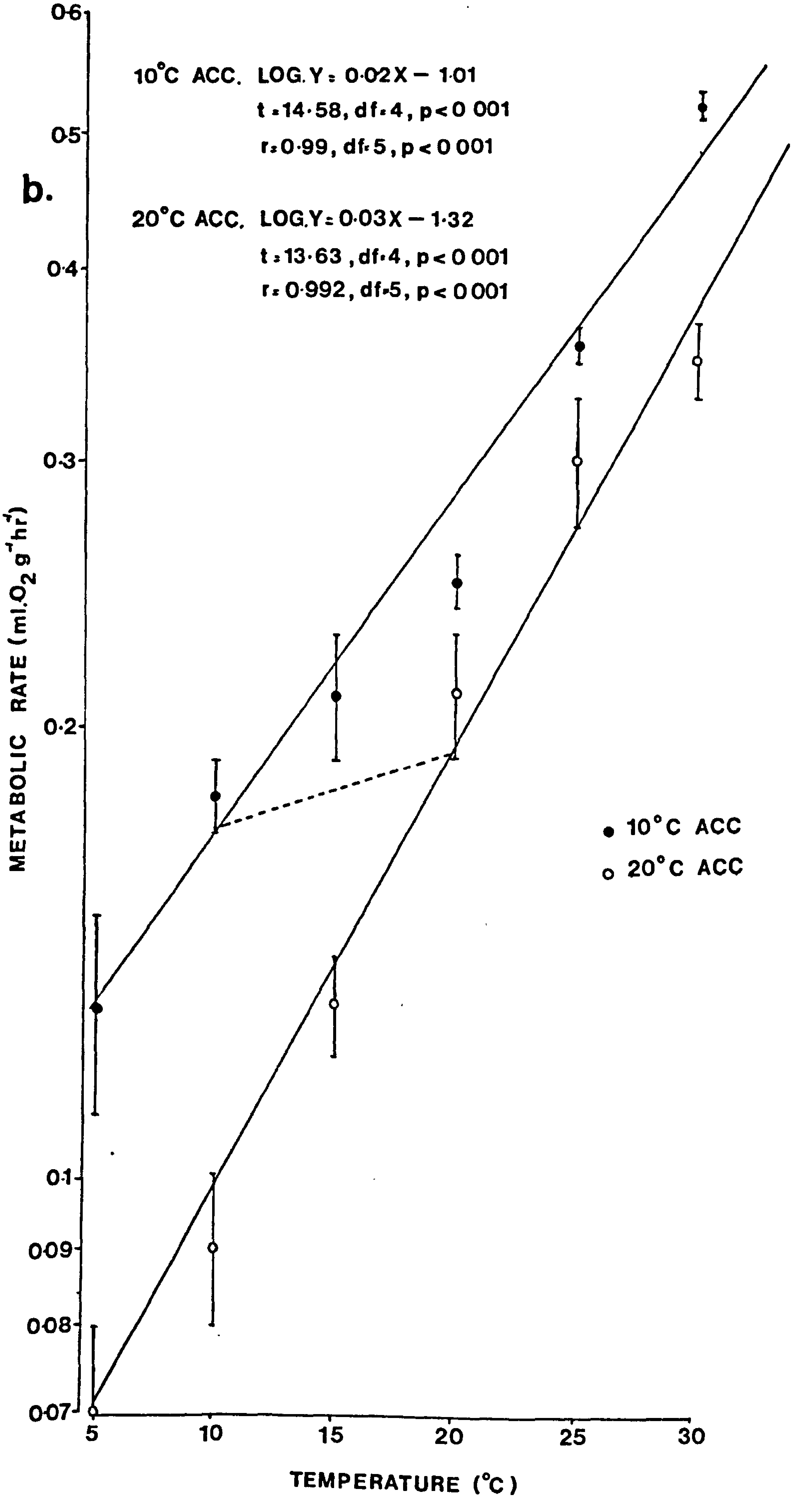
Figure 34. The relationship between metabolic rate and temperature (±.1 SE) in 10 and 20°C acclimated larvae, measured after 5 weeks acclimation. Broken line indicates acclimation response (see text 4.6.1).

a. Common Toads

b. Natterjacks.

a.


10°C ACC. LOG.Y = 0·02X−1·14
t = 24 22, df = 3, p < 0 001
r = 0·991, df = 4, p < 0 001
20°C ACC LOG.Y = 0·03X − 1·56
t = 10·19, df = 3, p < 0·01
r = 0·989, df = 4, p < 0·001
● 10°C ACC
○ 20°C ACC
METABOLIC RATE (ml.O$_2$ g^{-1} hr^{-1})
0·3
0·2
0·1
0·09
0·08
0·07
0·06
0·05
5
10
15
20
25
30
TEMPERATURE (°C)


b.
10°C ACC. LOG.Y = 0·02X − 1·01
t = 14·58, df = 4, p < 0 001
r = 0·99, df = 5, p < 0 001
20°C ACC. LOG.Y = 0·03X − 1·32
t = 13·63 , df = 4, p < 0 001
r = 0·992, df = 5, p < 0 001
● 10°C ACC
○ 20°C ACC
METABOLIC RATE (ml.O2 g⁻¹hr⁻¹)
0·6
0·5
0·4
0·3
0·2
0·1
0·09
0·08
0·07
5
10
15
20
25
30
TEMPERATURE (°C)

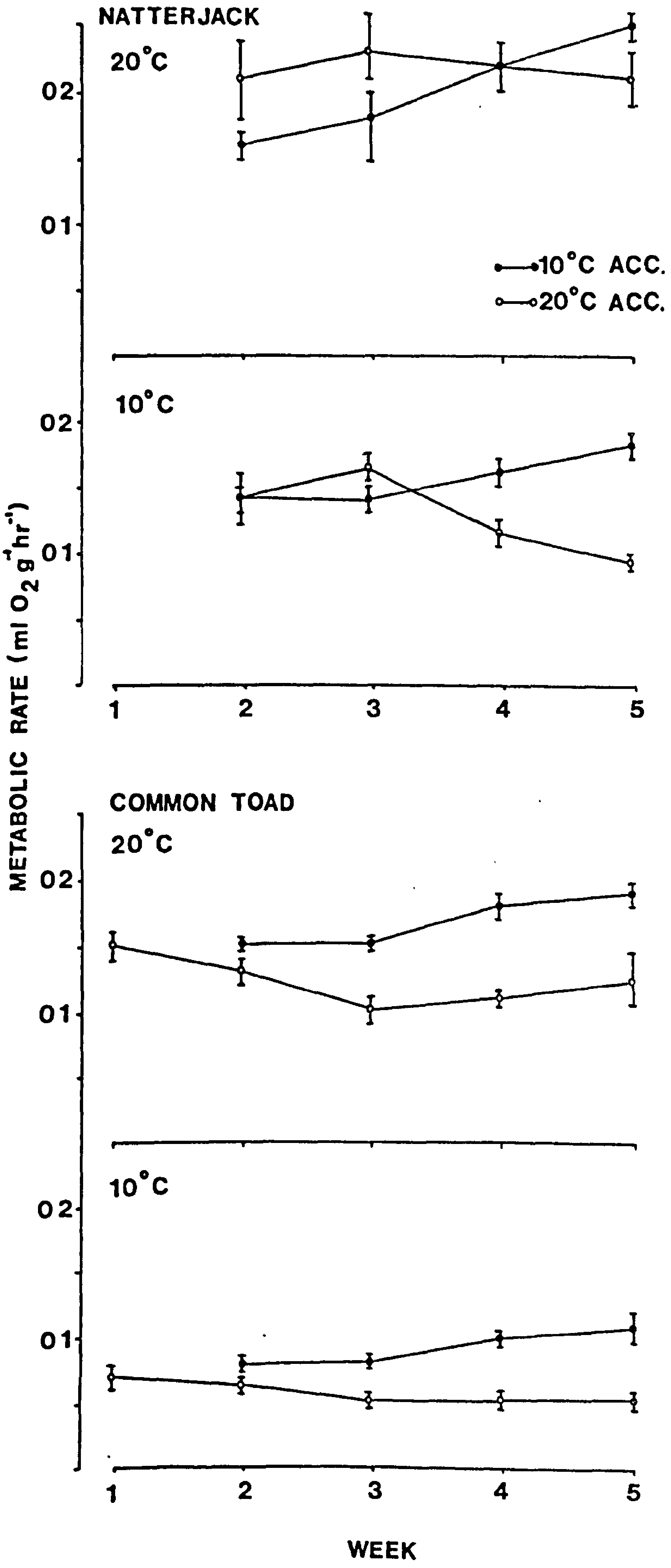
Thus, over 5 weeks, Natterjacks were found to be partial (type 3) compensators.

The Q_{10} values for these two species are similar to those reported for other anurans. Burggren *et al* (1983) reported that oxygen consumption by *R. catesbeiana* and *R. berlandieri* increased significantly with increasing temperature. They found that both species exhibited Q_{10} values of 1.8-2.4. Similarly, Noland & Ultsch (1981) found that *R. pipiens* and *B. terrestris* had Q_{10} values of 1.2-1.9. The close similarity in Q_{10} values between the present study (1.6-2.0) and other studies is not unexpected. Feder (1982) states that the ability to undergo acclimation of oxygen consumption does not appear to result in major changes in Q_{10} values for amphibians, which was reflected by the results of the present study. Furthermore, he reports that there are no marked differences in Q_{10} values between temperate and tropical species.

The mass-specific metabolic rates measured throughout the study period are given in Fig. 35. The metabolic rates of both species acclimated to 10°C increased during this period. There are two possible explanations for this. First the increase may have been a normal acclimatory response, although it is unclear whether this was completed by week 5. Alternatively it could be attributed to physiological and anatomical changes during tadpole growth and development.

Common Toad tadpoles acclimated to 20°C showed an immediate reduction of metabolic rate, indicating that type 2 acclimation had begun in week 1. This was completed by week 3 after which the rates began to rise, comparable to those acclimated to 10°C. This parallel increase therefore suggests that the increasing metabolic rates of 10°C

Figure 35. The mass-specific metabolic rates (± 1 SE) of Natterjack and Common Toad tadpoles maintained at 10 and 20°C (weeks 1-5).


NATTERJACK
20°C
0·2
0·1
10°C ACC.
20°C ACC.
10°C
0·2
0·1
1
2
3
4
5
METABOLIC RATE (ml O2 g-1 hr-1)
COMMON TOAD
20°C
0·2
0·1
10°C
0·2
0·1
1
2
3
4
5
WEEK

acclimated larvae was due to physiological changes associated with development rather than acclimatory responses. The metabolic rates of Natterjacks held at 20°C (Fig. 35) increased between weeks 2 and 3 after which they began to decrease, suggesting a delay before acclimation began. However it is uncertain whether acclimation was completed by week 5.

The results show that both species are able to acclimate, although the onset occurs more rapidly in Common Toads than Natterjacks. The latter appeared to exhibit a delay of approximately 3 weeks before detectable acclimation began. It is uncertain whether the duration of the acclimatory period was the same for both species, with only Common Toad known to have completed acclimation after 14 days. After 5 weeks, there was a 25% difference in acclimation levels, Common Toads showing greater acclimation than Natterjacks. Feder (1982) states that no acclimation of metabolism with a duration greater than 7 days has been reported for any amphibian species, although it is unclear whether he is referring to adults or larvae. A consequence of the differing acclimatory abilities is that Common Toads should be able to compensate for changes in temperature under field conditions more rapidly than Natterjacks. This could occur during hot or cold spells of weather when conditions in the breeding pools might vary markedly. Beebee (1983b) suggests that Natterjack development will be more successful in years with cool springs and warmer summers rather than the converse. However, in terms of their ability to acclimate, neither situation will particularly favour Natterjacks, more constant conditions having a less perturbing effect upon metabolic rate.

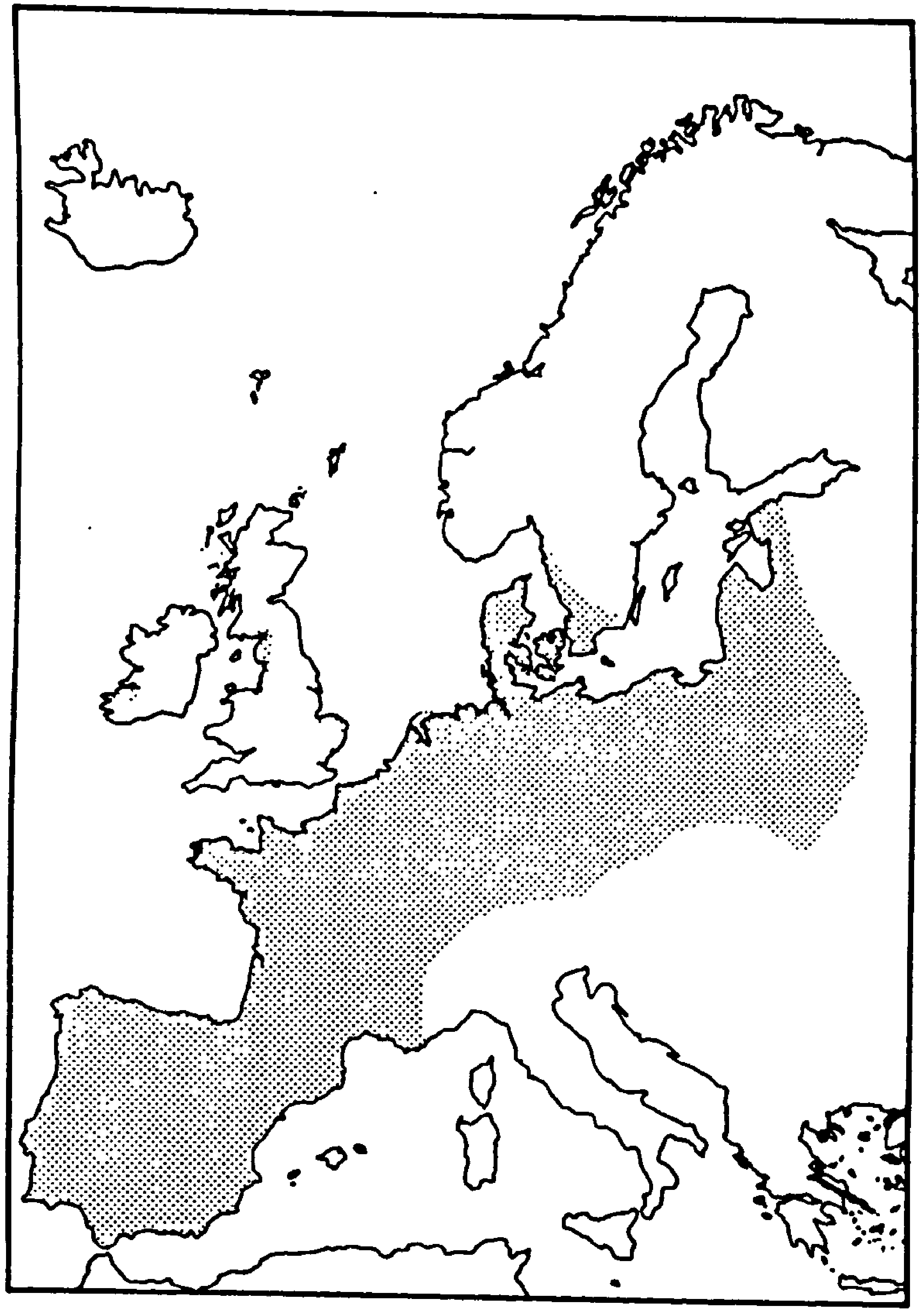
The differing abilities of the species to acclimate may also have consequences for microhabitat selection. The results suggest that Common Toad larvae should be able to select more widely than Natterjacks between areas of differing temperature, and thus be able to exploit more areas of the pool bodies e.g. deeper, cooler water. Observations at Cabin Hill tend to confirm this - Natterjacks were found mainly in the pool margins (0-10 cm deep) whereas Common Toad larvae were found as deep as 30-40 cm.

Earlier workers (Janzen, 1967; Feder, 1978; Huey, 1978) have suggested that species with limited acclimatory ability might only be able to live and reproduce in a narrow climatic, and hence geographic, range. This is supported by studies such as Brattstrom (1968,1970b) who found that species with limited geographical ranges showed lesser acclimation to critical thermal maxima (CTM) than more widely ranging species. The present study suggests that because Natterjacks are poor, or limited acclimators compared to Common Toads they may be more restricted in their geographic range. A comparison of the distributions of the two species (Fig. 36) confirms this, Natterjacks being limited to a relatively narrow latitudinal zone within Europe, while Common Toads extend their range north and south. Mathias (1971) suggested that geographical variation may be attributable to adult and larval temperature tolerances. He found larval Natterjacks had CTM of 29-33°C compared with 25-28°C for Common Toads. Similarly, he found that adult Natterjacks had CTM of 41°C compared with 37.7°C for Common Toads. However these results do not account for the more southerly distribution of Common Toads relative to Natterjacks. Also, thermal requirements and acclimatory ability are likely to be more important in larvae than adults. The larval developmental period is

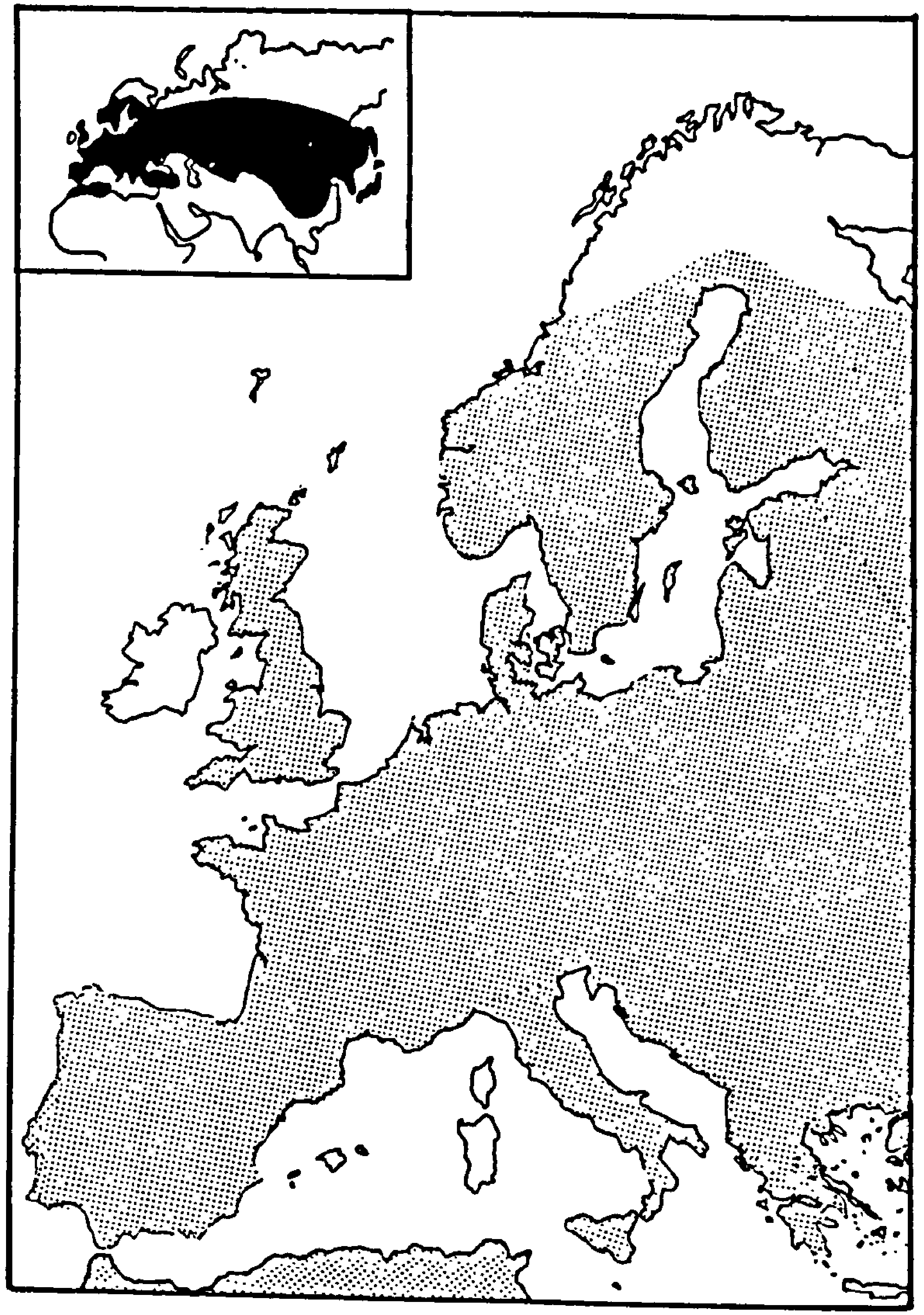
Figure 36. European distributions of the Natterjack and Common Toad.

Inset World distribution of the Common Toad.

NATTERJACK



COMMON TOAD



relatively short, and failure to compensate for changes in temperature may have a more adverse effect upon growth and survival than in adults which have to compensate for seasonal changes.

4.6.4 Larval growth rates

Mean tadpole weights during the study period are given in Fig. 37. Natterjacks acclimated to 10°C showed no growth, however Common Toads showed some increase in mass (27 mg) by day 17 after which no further increase was observed. Fluctuations in growth rates of larvae held at 10°C were due to tadpole mortality during this period. Figure 37a also shows the sample ranges of tadpole weight and it is seen that Natterjack larvae held at 10°C did not appear to increase in weight beyond approximately 30 mg.

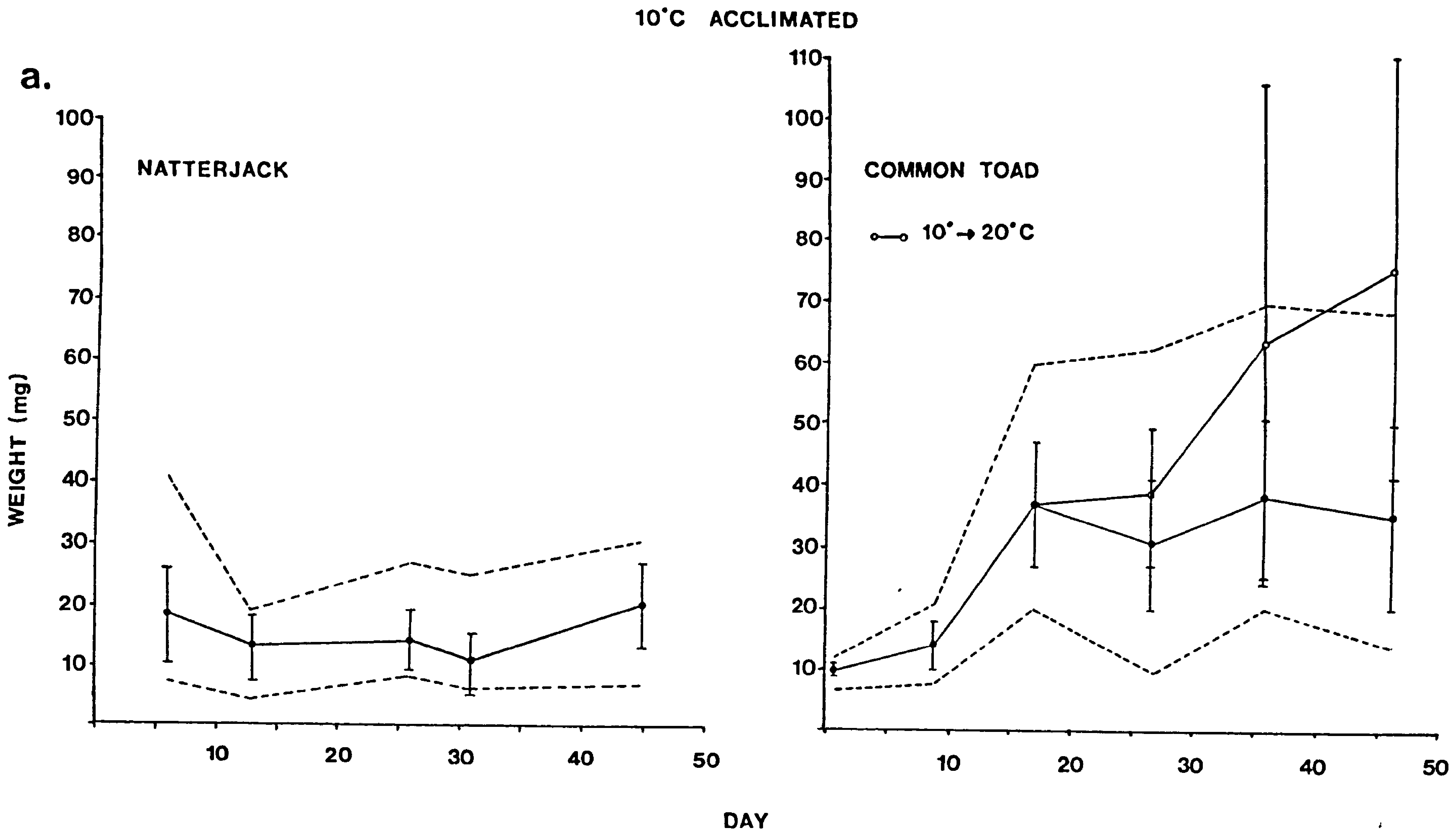
Common Toad larvae held at 20°C increased in weight throughout the study, except for an apparent decline between days 27 and 36 due to mortality of the largest tadpoles depressing the mean (Fig. 37b). Mean weight after 39 days was 89 mg. A group of 10°C acclimated tadpoles which were transferred to 20°C after day 17 increased their growth rate in the same way as 20°C acclimated larvae (Fig. 37b). Natterjack tadpoles held at 20°C did not increase in weight until day 26 after which their mean weight increased by 50 mg over 19 days.

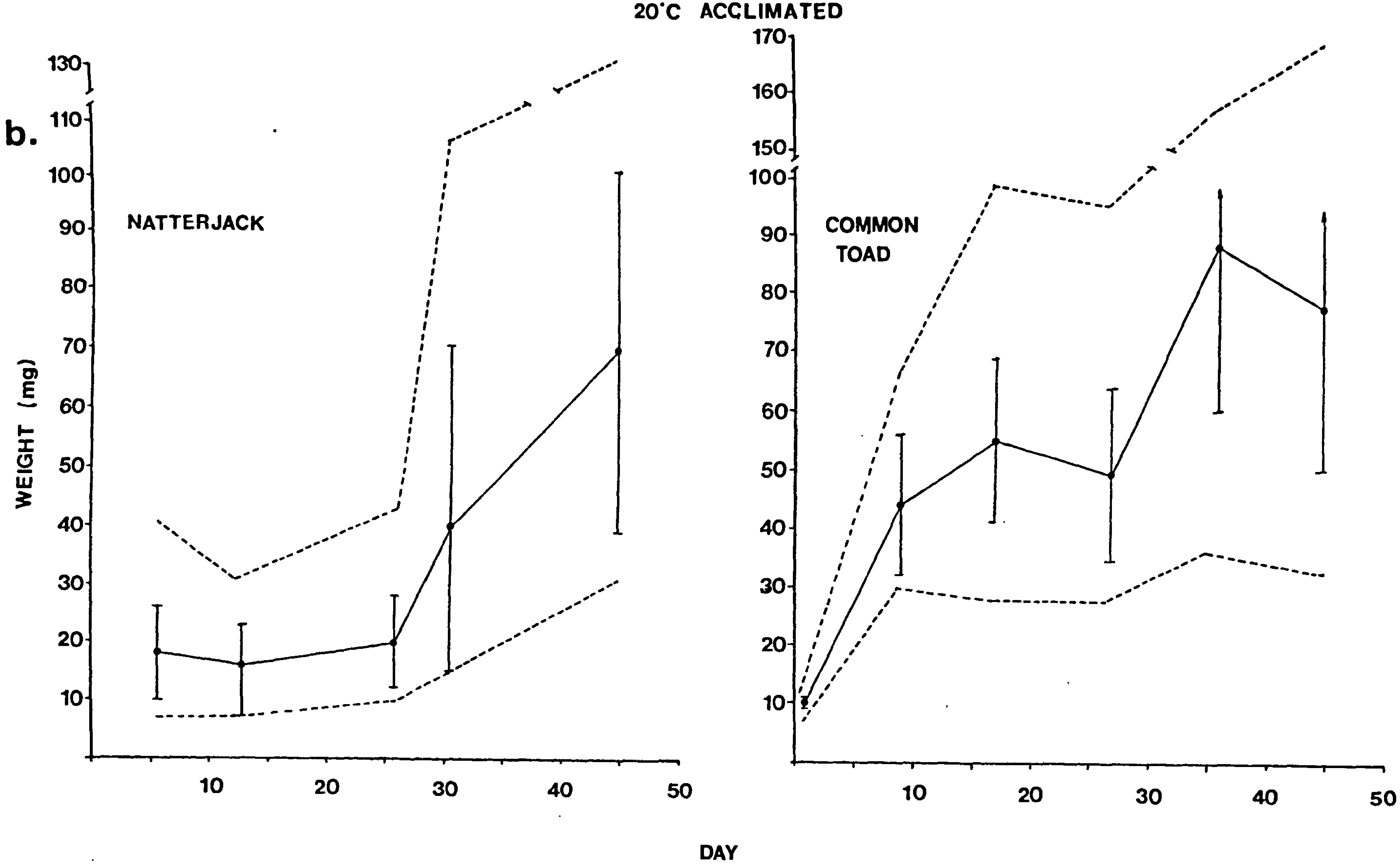
If growth rates are compared with metabolic rates for the experimental period, there appears to be a close relationship. Natterjacks held at 20°C did not begin to grow until acclimation began after day 21. This contrasts with Common Toads which acclimated and gained weight concurrently from week 1.

Figure 37. Mean weights (± 1 SD) of Natterjack and Common Toad larvae maintained at 10 and 20°C. Broken lines indicate range of weights.

a. 10°C acclimated

b. 20°C acclimated.


10°C ACCLIMATED
a.
NATTERJACK
COMMON TOAD
10° → 20°C
WEIGHT (mg)
10
20
30
40
50
60
70
80
90
100
110
DAY
10
20
30
40
50


b.
20°C ACCLIMATED
NATTERJACK
COMMON TOAD
WEIGHT (mg)
10
20
30
40
50
60
70
80
90
100
110
130
150
160
170
DAY
10
20
30
40
50

Beebee (1983b) studied growth rates of Natterjack larvae at temperature regimes between 14-25°C. However, his results are not directly comparable with the present study as he measured increase in length rather than weight. His results suggested constant growth of tadpoles at 14 and 25°C throughout the study, however his experimental procedure meant that acclimation occurred before growth was measured. Comparison with the present study is also difficult since change in length may not measure growth as sensitively as weight.

In the present study, the correspondence between acclimation and weight gain is not marked in larvae held at 10°C although there is some growth of Common Toad larvae which corresponds to an increase, and possible acclimation of metabolic rate. However, the results are unclear and it is possible that both species were approaching, or had reached, their lower limiting temperatures thereby disrupting physiological processes.

The lower metabolic rates of Common Toad larvae relative to Natterjacks probably allowed some growth at 10°C. In other animals with a lower metabolic rate more energy can be partitioned for growth (Petersen & Luxton, 1982). Therefore Common Toad larvae should be able to grow more successfully than Natterjacks earlier in the year when food and/or oxygen levels may be relatively lower than in summer. Thus Common Toads appear better adapted physiologically for breeding earlier than Natterjacks.

4.7 Post-breeding season movements of Natterjacks

Figure 38 shows the relative positions of the breeding pools and post-breeding season 'quadrats' (i.e. search areas), and Fig. 39 shows

Figure 38. Positions of 'quadrats' used during the post-breeding season study. (key as in Figure 4).

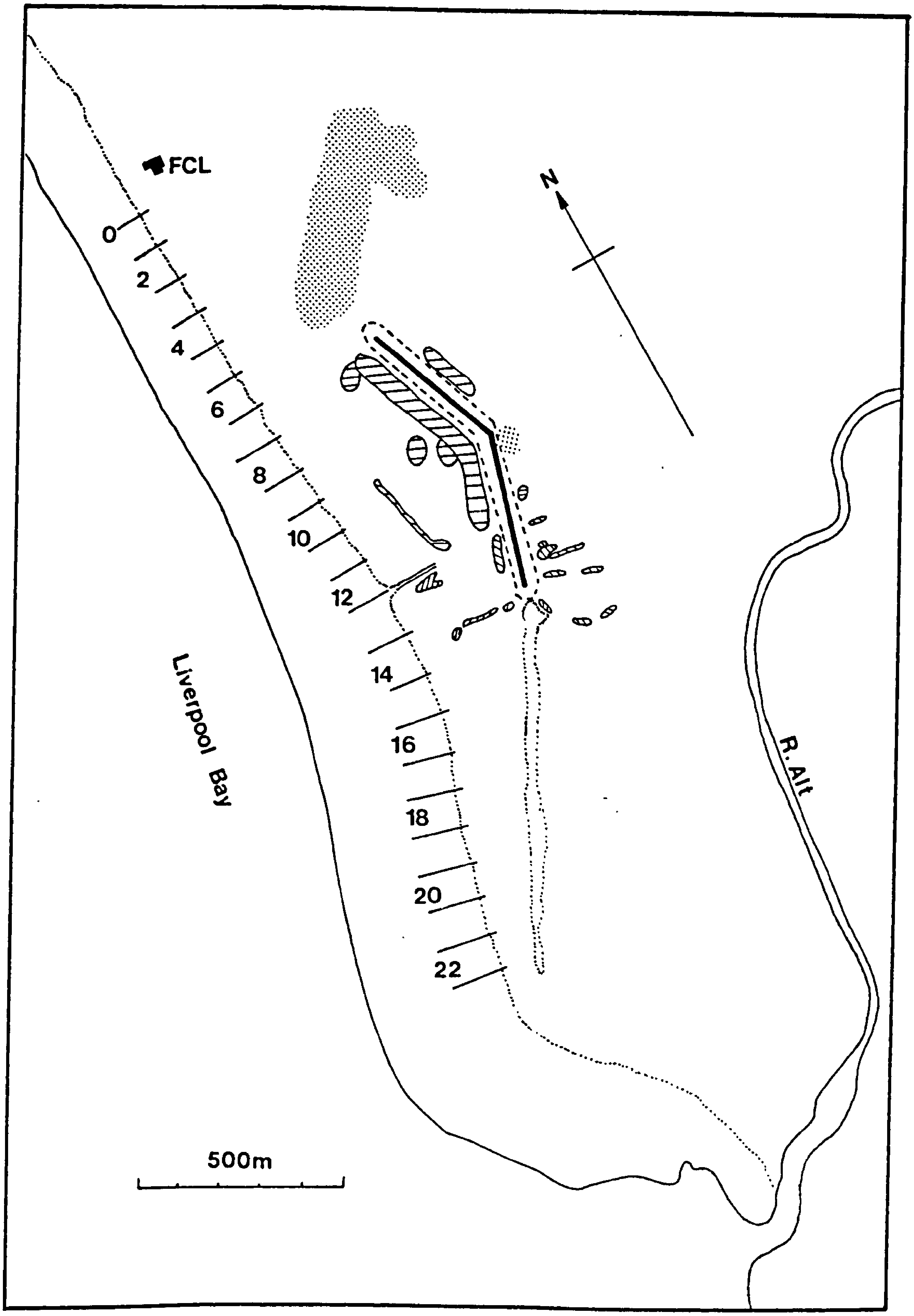
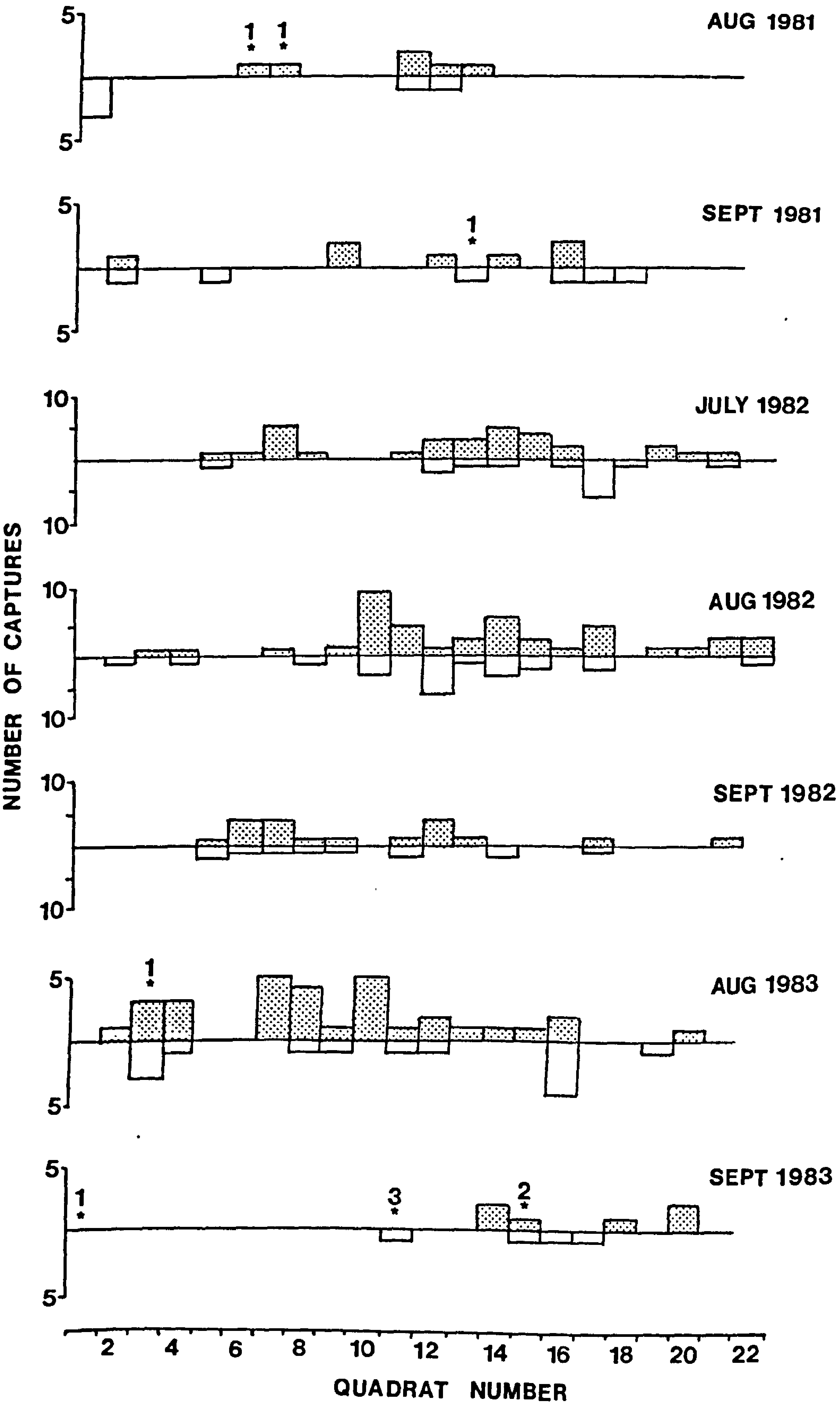

FCL
N
0
2
4
6
8
10
12
14
16
18
20
22
Liverpool Bay
R. Alt
500m

Figure 39. Distribution of toads captured during the post-breeding season, 1981-83. Shaded bars = females, open bars = males. Asterisks indicate captures of immature (newly metamorphosed toads) together with the number of captures.



5
5
AUG 1981
1
1
5
5
SEPT 1981
1
10
10
JULY 1982
10
10
AUG 1982
10
10
SEPT 1982
5
5
AUG 1983
1
5
5
SEPT 1983
1
3
2
NUMBER OF CAPTURES
2
4
6
8
10
12
14
16
18
20
22
QUADRAT NUMBER

the distributions of individuals found during the study period. These numbers are given on a monthly basis. In all years, individuals were found within 2 km.of Formby Coastguard Lookout by August. However, the 1982 captures (Fig. 39) suggested that there was a general displacement north along the dunes. Mean positions ± 1 SD (i.e. quadrat number) of toads captured along the beach were 13 ± 4, 13 ± 5, and 10 ± 4 respectively for July to September. Analysis of variance (Table 57) showed that the 1982 distributions (Fig. 39) differed significantly ($p < 0.01$).

Table 58 summarises data for all marked toads recaptured during the post-breeding season. In 1982, of 7 toads marked during the post-breeding season, 4 were found at the same position up to 30 days later. However, 3 had moved a maximum of 200 m. north between captures. Three toads were recaptured in 1982 which had previously been marked at the breeding pools (Table 58). In 1983, one toad marked at the pools was recaptured during this period. These animals were found approximately 500-600 m from the original capture area. The maximum movement shown by an adult animal within the post-breeding season was a male marked in 1981 which had moved approximately 500 m in 21 days between captures.

Smith & Bownes (1978), investigating the use of artificial scrapes by Natterjacks, report that toads were captured up to 2.2 km from their original location, although the majority moved less than 100 m. Similarly, Mathias (1971) found that most toads moved 100 m or less, except for 3 individuals which had travelled 300 m. He found that although some animals moved large distances between post-breeding sites, the majority (58%) remained in the vicinity of their original capture

Table 57. Anova of Natterjack distributions along Formby beach, 1982 post-breeding season

	July	August	September
n	45	66	29
Mean distance along beach (Quadrat number)	13	13	10
± 1 SD	4	5	4

Source of variation	df	SS	MS	F	p
Among months	2	322.80	161.40	8.42	< 0.01
Error	137	2628.19	19.18		
Total	139	2950.99			

Table 58. Summary of recaptures of marked toads, post-breeding season, 1982 and 1983

Year	Sex	Date 1st captured	Quadrat or Area 1st captured	Date recaptured	Area recaptured	Movement
1982	M	12/7	17	26/7	17	-
	F	13/7	11	3/8	11	-
	M	13/7	12	3/8,12/8	12	-
	F	14/7	7	7/9	6	100 m
	M	14/7	5	3/8	4	100 m
	F	3/9	11	17/9	9	200 m
	F	3/9	12	7/9	12	
	M	11/5	Pool 1	12/7	12	500 m
	M	23/4	Pool 15	3/9	17	600 m
	F	4/4/81	Pool 6	7/9	12	
1983	M	4/8	18	12/8	18	-
	M	11/5	Pool 1	10/8	15	500 m

site. However, 68% of his marked toads were not recaptured. He suggests that these were either "passing through" when first caught, or migrated to foraging sites some distance away. He also suggests that toads recaptured in the same areas either remained in a limited area all the time, or had a pattern of movement within a fairly large home range. The results from the present study tend to agree with previous observations. The majority of recaptured toads had moved 100 m or less (70%) with a smaller proportion (30%) exhibiting greater mobility. The apparent movement along the beach in 1982 may represent migration to foraging areas, as suggested by Mathias (1971).

Only 10 first-year toads were captured during the post-breeding study, 3 in 1981 and 7 in 1983. Mean weights (± 1 SD) of juveniles captured in August and September were 2 ± 0.5 g (n = 3) and 3.2 ± 0.5 g (n = 7) respectively. Six animals, found in areas 11-14 (Fig. 39), appeared to have moved approximately 400 m since metamorphosing. In 1981, two individuals were found in areas 6 and 7, approximately 800 m from the breeding pools, while in 1983 two animals were found in areas 1 and 3 which had probably travelled minimum distances of 1 and 1.2 km.

CHAPTER 5

DISCUSSION

5.1 Population dynamics of the Natterjack

5.1.1 The adult population

Since the 1940's the Natterjack has undergone a large national decline in numbers (Beebee, 1973), and the Merseyside population is now one of the largest in Britain (Cooke, 1981), although there are few reliable population estimates. Prestt *et al* (1974) gave an estimate of 10,000 individuals in 1970, while Corbett & Beebee (1975) state that the Merseyside population in 1974 was less than 5000, although they do not describe the methods used to obtain this estimate. Using mark-recapture, Mathias (1971) estimated the number of Natterjacks in Ainsdale NNR at between 516-2265. Smith & Flynn (1977) and Smith & Bownes (1978) attempted to census adult Natterjacks at newly dug scrapes in the NNR. Although 880 toads were marked during the two seasons, such low recapture rates were experienced the resulting estimates were subject to large error terms. However it was thought that over 2000 toads used these scrapes, and the total could have been greater than 3000 (Smith & Payne, 1980).

Between 1981 and 1983, the population estimates at Cabin Hill indicate that the male breeding population remained stable at approximately 1100 (Table 20). Female breeding numbers also remained relatively stable during 1981 and 1982 at approximately 207-240, although numbers appeared to increase to 427 in 1983 (Table 21). It is not clear whether this was due to immigration from other populations or to the entry of a successful cohort. Summation of male breeding season estimates and female post-breeding season estimates in 1982 suggested a minimum adult population (i.e. ⩾ 2 years old) of 1500-1900.

Sex ratios during the breeding season showed an excess of males (mean.3.2-4:1) although this bias was reduced during the post-breeding season (mean 1:1.9). The male bias during the breeding season was due to behavioural differences favouring male capture and also to more rapid male maturation allowing earlier entry to the breeding population. Age studies suggested that males begin breeding as 2 year olds, although they are not fully active until 3. Females do not begin to breed until 3, and possibly do not spawn until 5 years.

Mathias (1971) suggested that Natterjacks show sexual dimorphism, with females larger than males. His females had a mean weight of 20.6 g compared with 18.1 g for males, suggesting that females grew more rapidly than males. However, the present study shows that this size difference is related to population age-structure. In fact, males grew more rapidly than females reaching an estimated length of 45 mm after 2 years, compared with females which take 3 years to attain this size. Similarly, 2 year old male and female Natterjacks weigh approximately 6.5 and 5 g respectively.

Estimated mortality rates of 4 year old toads were 75-87% in males, and 15% in females (Tables 35,36). It is unclear whether high mortality rates are sustained throughout male life, or are associated with breeding activity. If mortality is associated with reproduction, the death rate may be reduced in years with adverse breeding conditions, thereby increasing population longevity. If high male mortality rates are sustained throughout life, they may be counter-balanced by high female fecundity. Natterjacks show fecundities approximately 2½ times greater than Common Toads of equivalent size (Table 38). Lower Common Toad fecundity may be associated with relatively lower male mortality (50%) in this species (Gittings, 1983). High Natterjack fecundity may be important in maintaining population levels during periods with adverse breeding conditions. Thus in 'poor' years Natterjacks may experience little or no recruitment, but may take advantage of a particularly successful cohort to maintain or increase the population, although a longer period of study would be necessary to confirm this trend. However, the present study and previous work (Smith, 1977,1978b,1979,1980b) have shown that Natterjack recruitment is highly variable (see below).

Opportunistic breeding has been observed in other anuran species, for example Tevis's (1966) study of *B. punctatus*. He found that although successful reproduction (i.e. survival of larvae to metamorphosis) was apparently very rare a viable population was still maintained. The species was opportunistic, being able to take advantage of any available water during warm weather. Also, only a small proportion of the population bred at any one time, thus a reservoir of breeders was maintained for repeated attempts at reproduction, with the likelihood of many juveniles eventually being produced in favourable periods. That the Natterjack may be an opportunistic breeder is supported by the 'explosive breeding' seen at Cabin Hill (Smith, 1977) and other Merseyside sites (P.H. Smith, pers. comm.) after several years of low rainfall, and apparently low metamorphic success (Smith *et al*, 1974).

Finally, high fecundity may be important for exploitation of new sites, allowing the animal to establish itself rapidly, particularly in environmentally precarious sites (Begon & Mortimer, 1981). In the case of the Natterjack, many new breeding pools appear to be subject to rapid desiccation (Smith & Payne, 1980).

5.1.2 Colonisation and site choice

Adult vagility is important for colonisation of new breeding sites (Begon & Mortimer, 1981) and there is much evidence from the present and previous studies supporting the Natterjack's colonising ability.

Direct evidence for Natterjack colonisation was observed during the present study when spawning (4.6% of all spawn) occurred in two new sites in 1981 - the flooded footpath connecting sites 16 and 17, and site 21, although some spawning (0.2%) had occured for the first time in site 21 the previous year (Smith, 1980). In 1981 4.2 and 0.4% of spawn strings were deposited in these sites respectively. In 1983, 10.8% of spawn was laid in pool 21. Other workers have provided evidence of the Natterjack's colonising ability. Smith & Bownes (1978) recaptured 83 individuals marked previously by Smith & Flynn (1977) at breeding sites on Ainsdale NNR. Only 42% were recovered at the pools where they were originally marked, and although the majority had moved less than 100 m some animals were found up to 2.2 km from their original location. In the present study, adults were found to move 500-600 m between the breeding and post-breeding seasons, while newly metamorphosed juveniles were found which had apparently moved up to 1.2 km from the breeding pools.

The species' mating strategy is likely to assist colonisation. Arak (1983) notes that the characteristic loud calling by the males is audible up to 2 km distant. He also observed females moving towards chorussing males 1 km away, and found that females were attracted to the loudest calling males. This seems likely to ensure that wandering males which locate a new site will be able to attract females from a considerable distance. Indeed, scrapes dug for conservation purposes in the Merseyside dunes have often been colonised immediately (Smith & Bownes, 1978).

In contrast, Common Toads have been shown to be particularly site faithful (Heusser, 1969; Haapanen, 1974), and the males do not call to attract females but intercept them as they assemble at the breeding site (Davies & Halliday, 1977). This system is unlikely to result in rapid colonisation of new breeding sites and in Merseyside, colonisation of new scrapes by Common Toads does not usually occur until 3-4 years after Natterjacks (P.H. Smith, unpub. data). During the present study, no colonisation of the flooded footpath or pool 21 by Common Toads was observed, although both these sites were used regularly by Natterjacks.

The most productive natural Natterjack breeding sites in the Merseyside dunes are newly-formed incipient slacks in wind-eroded blow-outs (Smith & Payne, 1980). These flood as the water table rises during the winter, and dry out progressively in summer. Such slacks form in the mobile dunes, and a characteristic feature is that they are sparsely vegetated. Newman (1869) described the Natterjack breeding habitat as shallow pools on open, sandy areas while Greening (1888) showed that spawning sites were usually devoid of water plants. The results from the present study disagreed with the latter observation, the majority of Cabin Hill spawning sites being characterised by 100% vegetation cover (64% of observations) and mossy substrate (61%). However, most sites at Cabin Hill (e.g. pools 1, 2, 3, 4, and 15) are 'mature' slacks with 100% vegetation cover. Thus there are few open, sandy sites available, and the results may represent a compromise the toads are forced to make due to a lack of preferred sites. It is likely that if other, less vegetated sites were available the toads would choose these. This is supported by the increased use of site 18 in 1981 when the unusually high water table created shallow, sandy margins on the seaward side. Nineteen (66%) out of 29 strings laid in pool 18 were deposited in this area.

More spawn strings were found in pools with longer perimeters. This confirms Smith & Flynn's (1977) findings that numbers of calling males were positively correlated with pool perimeter. This is explained by Arak's findings that male Natterjacks defend calling sites during the breeding season.

Smith & Payne (1980) and Payne (1983) provide further evidence that Natterjacks tend to colonise newly formed slacks and may abandon older, more mature slacks. Incipient slacks can be artificially mimicked by shallow excavations in dry slacks which breach the water table, and in the mid-1970's 34 such scrapes were dug in response to a depleted water table following several years of reduced effective rainfall. In 1978, all these scrapes were used for spawning (Smith & Payne, 1980), and 80% of sites where metamorphosis occurred were newly excavated pools. However, most of these pools had been dug in old slack basins within the fixed dunes and were progressively abandoned by Natterjacks until, by 1983, they were hardly used at all (Payne, 1983). Payne's data show that between 1978 and 1983 there was an increased trend for Natterjacks to use slacks on the seaward side of the Ainsdale reserve, 45% of spawn being laid in incipient slacks in 1983. These data are summarised in Fig. 40. The reasons for site abandonment appear to be a substantial rise in the water table which made the water in the scrapes too deep and/or cold to attract Natterjacks, and rapid revegetation of the water bodies and their surrounds which also created a less attractive habitat for the toads. There may also have been adverse competitive interaction with colonising Common Toads and Common Frogs.

5.1.3 The larval population

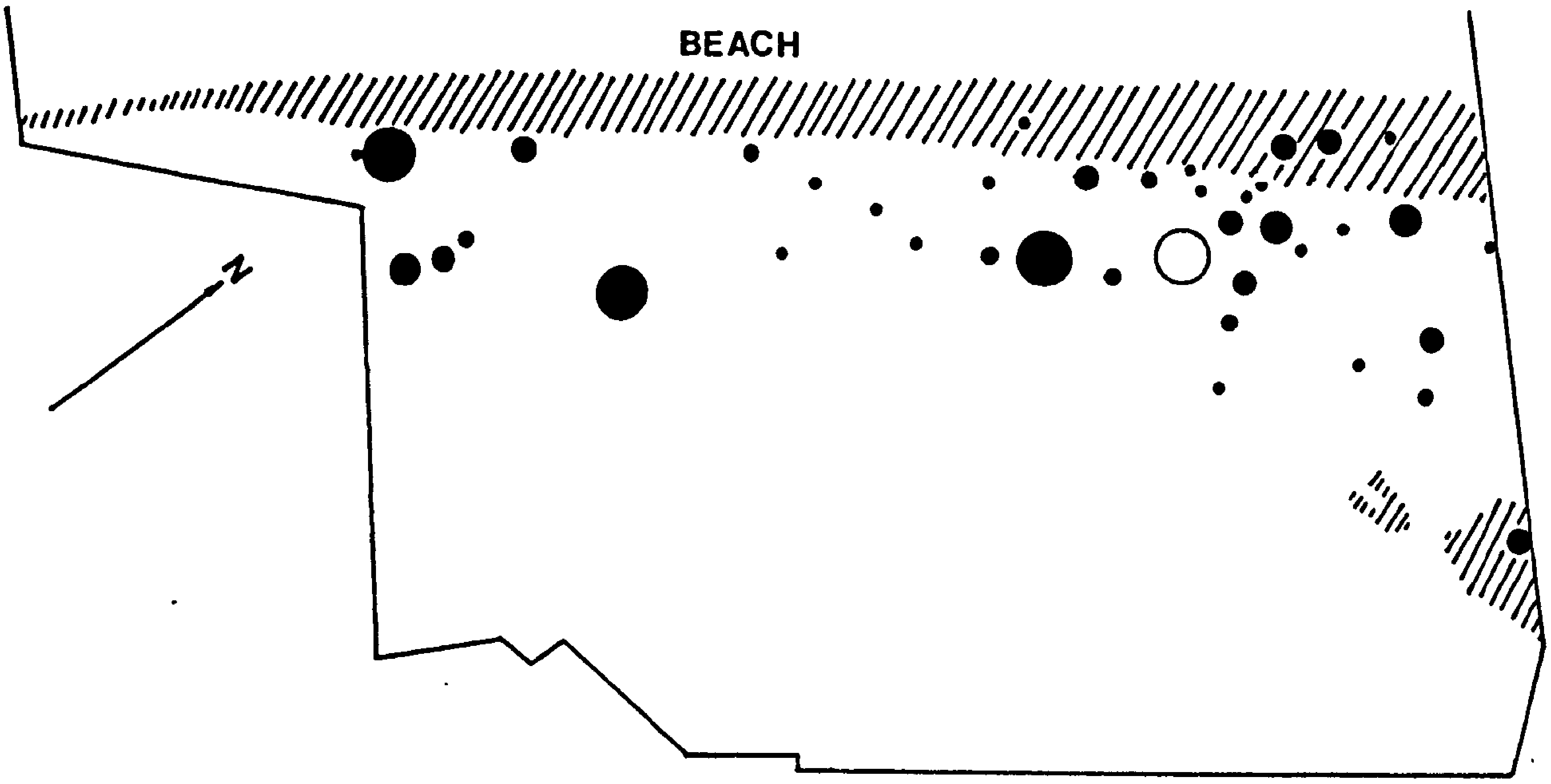
Female Natterjacks spawn in water approximately 10-15 cm deep in late spring when the water table is already falling. Spawn and tadpoles develop rapidly (Smith, 1964) nevertheless many sites are subject to desiccation before metamorphosis can occur. In the present study, mortality factors were investigated using key-factor analysis, a method which does not appear to have been applied to previous anuran studies.

The two major causes of spawn mortality, desiccation and *Saprolegnia* infestation were found to vary in their relative importance, desiccation being most important in 1982. In this year 26.9% of all ova laid in the first spawning (April 7-29), and 6.6% of ova from the second spawning (May 9-June 6) dried before hatching. Further drying of pools resulted in 100% mortality of the first spawning. Smith (1982) reported heavy mortality of ova from desiccation at other sites in the

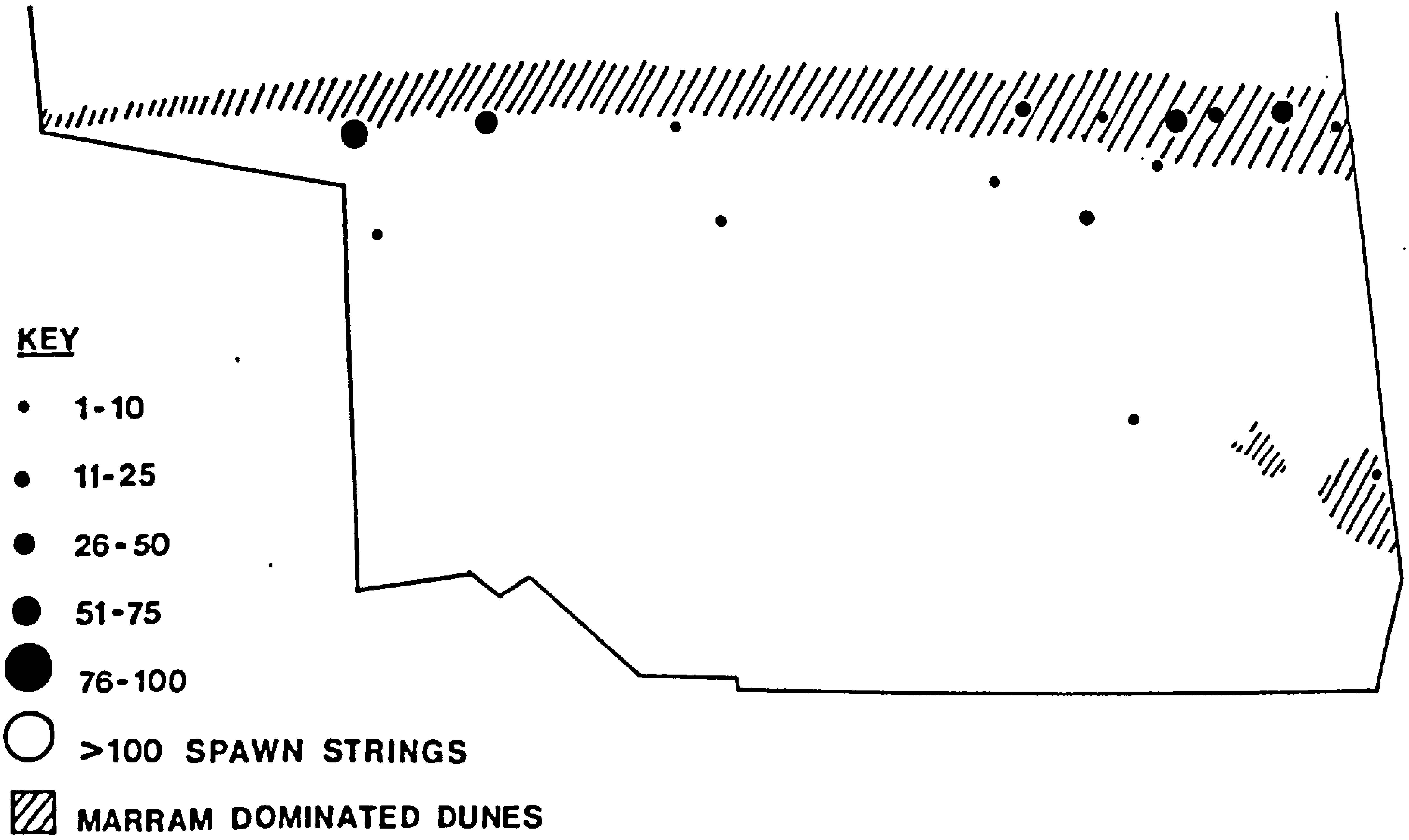
Figure 40. Changes in spawn deposition within Ainsdale NNR, 1978-83.

(Summarised from Payne, 1983).

1978


BEACH
N

1983


KEY
● 1-10
● 11-25
● 26-50
● 51-75
● 76-100
○ >100 SPAWN STRINGS
▨ MARRAM DOMINATED DUNES

Merseyside dunes. *Saprolegnia* infestation was most important in 1981 and 1983. Beebee (1979a) suggested that low temperatures are responsible for fungal attack and that the earliest spawn is most susceptible, although Smith (1981) suggests that a site-specific factor may be involved. For example, heavily vegetated sites seem to suffer more *Saprolegnia* infection than open, sandy pools. During the present study, *Saprolegnia* infection was greater at Cabin Hill than 'less mature' sites along the Sefton coast (Smith, 1981,1982).

At Cabin Hill in 1981 and 1982 there appeared to be some difference in levels of fungal attack between 'early' and 'late' spawnings. In 1981 21.1% of the first spawn (March 28-April 19) was killed by fungus, compared with only 5.7% of the second spawning (May 1-June 5). In 1982, 3.6% of the first spawning was infested by *Saprolegnia*, compared with 0.8% of the second spawning. In 1983, *Saprolegnia* infestation of the first (April 10-May 4) and second (May 10-22) spawnings was high, 20.2 and 31.6% respectively. However, in this year, spawning occurred during a relatively short period (34 days) and so the time intervals between the two spawnings was short (Fig. 21). *Saprolegnia* infection of spawn may be related to water depth. At Cabin Hill, where pools are relatively deep and well vegetated, fungal infestation was observed throughout the study period. However, elsewhere in the dune system e.g. Formby Point, Raven Meols, and Ainsdale NNR, where slacks are generally shallower and more open, fungal infestation was low (Smith, 1982,1983a; Payne, 1983). Interestingly, levels of fungal mortality increased in 1981, when the highest recorded water table in the dune system caused extensive flooding and deeper water in slacks. Smith (1981) recorded 25% of spawn killed by fungus at Raven Meols. He notes that this problem had not been previously recorded to any significant extent in Merseyside.

Another important factor which seems to preclude early spawning by the Natterjack is the relatively poor metabolic performance of tadpoles in colder water. Comparisons of thermal preferenda and oxygen uptake of Natterjack and Common Toad tadpoles acclimated to 10 and 20°C showed that although there is no significant difference in preferred body temperatures, both species regulating loosely around 25°C, Natterjacks have a higher metabolic rate than Common Toad tadpoles when acclimation state and measurement temperature are similar.

Although Natterjacks can acclimate they only exhibit 75% metabolic compensation after 5 weeks, compared to Common Toads which show 100% compensation. Also Natterjacks, unlike Common Toads, are unable to begin acclimation immediately, showing a delay of approximately 3 weeks. These results suggest that Natterjacks are likely to develop more rapidly than Common Toads when food and oxygen are not limiting, although this was not tested. It also seems that under varying environmental conditions the growth rates of Common Toad larvae are less likely to be perturbed than Natterjacks. Common Toads are also likely to be less restricted than Natterjacks to a particular temperature range, and can probably develop successfully across a wider range of temperatures.

These findings probably account for field observations that Natterjack tadpoles develop best in shallow, unshaded water warmed by insolation, and also cluster at the extreme edges of pools where water temperatures are highest and oxygen concentrations high (Mathias, 1971).

The results also accord with the geographical distributions of the two species (Fig. 36), Common Toads extending their range into hotter, southern and colder, northern regions than Natterjacks which have a more restricted distribution in west Europe.

Common Toad tadpoles are also better adapted physiologically for growth and development earlier in the year than Natterjacks. This may also have consequences upon growth of Natterjack tadpoles. Previous workers (Lynn & Edelman, 1936; Rose & Rose, 1961; Licht, 1967) have shown that crowding of tadpoles can cause growth inhibition, both intra- and interspecifically. Beebee (1979a) states that 'conditioning' of water by Common Toads and Common Frogs results in growth inhibition of Natterjacks during the first 2-3 weeks of life. This may reduce the Natterjacks' ability to compete for food (Wilbur, 1977; Steinwascher, 1978) which could result in delayed metamorphosis (Collins, 1979; Hota & Dash, 1981). This in turn could result in increased mortality of tadpoles from predation or desiccation.

Studies at Cabin Hill suggested that between 1981-83 desiccation was responsible for 4.3, 12.8,and 2.9% respectively of all tadpole mortality during this period (real mortalities = 3.5, 7.5, and 2.1%). However, it is important to note that these represent 'catastrophic' mortalities. Desiccation is an insidious process which was seen to occur throughout the survey periods, thus it is likely that actual mortalities were higher than those estimated. Also, the mortalities occurred late in the year, mainly June, and thus represent losses of tadpoles close to metamorphosis which had escaped other forms of mortality. Field observations at Cabin Hill suggested that the development of Common Toad tadpoles early in the season generally resulted in their avoiding this type of catastrophic mortality from desiccation. Indeed the tendency of Common Toads to use deep pools for spawning (Smith, 1964) seems to preclude desiccation as a major mortality factor in this species.

Mortality apparently due to invertebrate predation seemed to be the most important factor operating at Cabin Hill. Estimates for 1981-83 suggested that this was responsible for 95.7, 87.2, and 97.1% respectively of tadpole mortalities. These results agree with Kadel (1975) who found that 84% of Natterjack larvae were predated. Similarly, Common Toads may be subject to up to 94% predation (Gittings *et al*, 1984, citing unpub. data), however Common Toads, being better adapted physiologically to develop earlier in the year, may be able to complete metamorphosis before the majority of invertebrate predators appear.

Field observations indicate that the more ephemeral slacks support fewer potentially predatory invertebrates, and Griffiths (1979) has shown a positive relationship between the age of excavated pools at Ainsdale and the diversity of aquatic organisms as measured by the Shannon-Wiener index. Tadpoles in older, mature pools could thus be exposed to higher predation pressure, especially in cool summers when development is retarded. Therefore colonisation of incipient slacks (Smith & Payne, 1980; Payne, 1983) may be a method of avoiding high predation mortality. Beebee (1977,1979b) reports that Common Toad tadpoles feed on newly hatched Natterjacks, and suggests that colonisation by Common Toads may be an important reason for declines in Natterjack colonies (Beebee, 1979b). Thus it could be advantageous for the Natterjack to avoid the Common Toad by colonising new sites.

During the present study levels of Natterjack recruitment were highly variable. In 1982 and 1983 minimum survivals to metamorphosis were 0.7 and 1.3% respectively. This was equivalent to approximately 2600 and 10,200 individuals metamorphosing. Other Merseyside surveys (Smith 1983b) suggest that 1983 was an "exceptional year". Smith estimated that > 2000 toads metamorphosed at 3 sites in the Birkdale hills. Previous workers have shown variability in levels of Natterjack recruitment. In 1977 metamorphosis was high, being confirmed at 37 Merseyside sites (Smith & Payne, 1980). However, this contrasts with poor breeding success in 1972 (Smith *et al*, 1974) when metamorphosis was only confirmed at 11 sites. Other poor years were 1975 and 1976 (P.H. Smith, pers. comm.), 1978 (Smith & Payne, 1980) and 1979 (Smith, 1979) when Merseyside sites were affected by low rainfall and/or rapid desiccation during Natterjack development. This variability in recruitment contrasts with the Common Toad which seems to be characterised by constant annual recruitment (Gittings, 1983). Field observations at Cabin Hill since the late 1970's (Smith, 1977) indicate that many thousands of Common Toads regularly metamorphose at this site.

5.1.4 Life history strategy of the Natterjack Toad

Descriptions of species' life history strategies have often used the r and k concept (Pianka, 1970). Although this concept is useful, 'r-ness' and 'k-ness' are only one aspect of the environment (Begon & Mortimer, 1981), thus an organism's life history strategy is an adaptive response to its whole environment. Adaptations relating to r and k strategists are summarised in Table 59. Begon & Mortimer (1981)

Table 59. Characteristic features of *r* and *k* strategists (after Begon & Mortimer, 1981)

r	*k*
Small size	Large size
Short generation time	Long lifespan
High reproductive effort	Low reproductive effort
Early maturity	Late maturity
Many, small young	Few, large young
No parental care	Parental care
Adult mortality rates density-independent and uncertain	
Juvenile mortality rates density-independent and uncertain	
Population fluctuates: opportunities for colonisation	Steady, crowded population

state that comparisons of species can only show which are 'more *r*' or 'more *k*'. Thus, although Gittings *et al* (1984) have described the Common Toad as a typical *r*-strategist with high egg numbers and no parental care, the present study suggests that Natterjacks are more highly adapted *r*-specialists. Based upon the present work and previous studies in Merseyside the following life history strategy of the Natterjack is proposed.

The Natterjack shows typical *r*-characteristics of rapid maturation and high mortality, possibly associated with large reproductive effort, although this may be counterbalanced by reduced mortality during years of adverse breeding conditions, thus maintaining the population for later resumption of breeding. It is a rapid coloniser which exploits ephemeral or newly formed water bodies, thus experiencing environmental conditions more favourable for the development of juvenile stages, avoiding competition from more slowly colonising amphibians, and experiencing lower predation of larvae than in older established pools. However, by spawning late in shallow water the animal risks catastrophic mortality of young stages by desiccation. This seems to be offset by opportunistic, large recruitment under favourable conditions.

Interestingly, the presence of Natterjacks in Ireland may reflect aspects of their ecology discussed above. Yalden (1980) has pointed out that the rapid climatic amelioration which occurred between 10,000 and 9,000 years ago would have allowed open habitat species like the Natterjack to invade the British Isles before the rising sea-level severed the land bridges between England and France, and between south-west Scotland and Ireland, and also before afforestation occurred. Possibly the colonising ability of the Natterjack enabled it to reach

Ireland before the landbridge flooded, while the 'slower' Common Toad did not arrive in time. The Natterjack is now restricted to the mild south-west corner of Ireland with other 'Lusitanian' fauna and flora.

5.2 Conservation management of the Natterjack

Current knowledge of the national status, biology, and cause of declines of Natterjacks and other rare herptiles has been summarised by the NCC (1983). This recommends a strategy for practical measures designed to "reinforce success of management" based upon three main elements:

1. Consolidation of the species within its known range.
2. Management of site ecosystems in order to maintain population levels whereby natural fluctuations can be accommodated without risk of local extinction.
3. Avoidance of concentrating efforts upon a few major sites so that the total British population will not be at risk from catastrophic mortalities.

This strategy is defined by fifteen operational objectives grouped under the headings: site protection and management; translocation; advice and information; research; review.

In reponse to this document, Smith (1984) described a conservation strategy for Natterjacks in north Merseyside giving details of previous managerial measures, and defining future objectives. Conservation measures implemented in Merseyside may be summarised thus:

1. Surveys of Natterjack breeding sites.
2. Creation of new sites by digging scrapes.
3. Rescue of spawn and/or tadpoles at sites facing desiccation.

4. Formation of SSSI's and NNR's, and cooperative management with local land owners.
5. Advice and information designed to increase public awareness of the Natterjack and its conservation.

Since 1972 (Smith *et al*, 1974) surveys of Natterjack distribution and breeding success have been made throughout the north Merseyside sand-dune system. At Cabin Hill there have been regular surveys since 1977 (Smith, 1977). These monitored yearly breeding activity and identified factors limiting Natterjack recruitment. Although spawn counts were made to confirm whether or not breeding occurred, quantitative estimates of toadlet production were not attempted. Nevertheless a general indication of breeding success may be obtained from the survey data.

During the early to mid-1970's low water-tables prevailed with the result that successful breeding occurred only in man-made sites (Smith *et al*, 1974). Although it was felt that the dune water-table was likely to recover, it was decided to excavate a number of scrapes, thereby increasing availability of breeding sites. The first experimental excavations, dug by hand at Birkdale and Ainsdale in 1972 and 1973, were immediately colonised by Natterjacks, and this success prompted an extensive programme of mechanical excavation at various sites, especially since 1976. These include excavations at Cabin Hill (8 sites), Formby Point (2), Ainsdale and Birkdale Hills LNR's (14) and Ainsdale NNR (25). Smith (1984) details the relative success of these sites and their present status. It has been shown that scrapes are quickly colonised by Natterjacks after construction (Smith & Flynn, 1977; Smith & Bownes, 1978) and are successfully used for breeding (Smith & Payne, 1980). However, in recent years many sites have been abandoned (Payne, 1983; Smith, 1984). The reasons for this appear to be:

1. Sand accretion and infilling of slacks.
2. A rise of approximately 80 cm in the water table since 1974 (Clarke, 1980) rendering many sites too deep and/or cold for Natterjack breeding.
3. An increase in predator populations in what have become permanent ponds in many instances.
4. Encroachment of vegetation making sites less attractive to Natterjacks.
5. Colonisation by other, competitive anuran species.

Sand accretion does not appear to be a major problem at Cabin Hill, although Smith (1984) describes sites on Birkdale frontal dunes which have been filled with blown sand and recommends re-excavation. The increased water-table since the 1970's also does not appear to have affected Cabin Hill as greatly as other Merseyside sites, e.g. Ainsdale NNR (Payne, 1983) where pools have been abandoned in favour of shallower, incipient slacks. However, the present study suggests that such conditions are likely to favour Common Toad development compared with Natterjacks. Thus, the excavation of new, shallow sites for Natterjacks at Cabin Hill would probably enhance recruitment to this population. Similarly, clearance of encroaching willow (*Salix*) scrub from Cabin Hill sites should provide more suitable conditions for Natterjack breeding. Smith (1984) reports that many Merseyside sites are becoming overgrown, and this is particularly noticeable at Cabin Hill where invasion of *Salix* scrub has occurred. Re-vegetation of sites may reduce suitable areas in pool surrounds for toads to dig daytime retreats, and decrease suitability of spawn sites (Beebee, 1979a). Also there is a possible relationship between levels of fungal infection of spawn and the extent of vegetation cover in pools. This merits further investigation. The creation of new, open, shallow slacks, and selective vegetation clearance may also reduce potential invertebrate predation during larval development. The present study suggests that this is a major mortality factor at Cabin Hill.

Smith (1984) reports that there appears to be reduced Natterjack breeding success at sites which have been colonised by other anuran species. The present study suggests that Common Toads are better adapted physiologically than Natterjacks for early breeding and may develop more successfully at the expense of Natterjacks. Removal of Common Toad and Frog spawn from Natterjack breeding sites will eliminate possible competition during development and increase the chance of successful Natterjack metamorphosis.

Rescues of spawn and tadpoles have been carried out regularly at Cabin Hill and other sites since the early 1970's and these appeared to have ensured some metamorphosis took place in most years, although increased availability of breeding sites now means that rescue operations are less important. Hopefully, improved site management and slack maintenance may reduce the need for these operations further still, although large variations in the water table are not amenable to regulation, except where surface water drains outfall into potentially suitable breeding sites, as at Birkdale (Smith, 1983b).

Inclusion of Natterjack breeding pools into SSSI's and NNR's (Smith, 1984) has assited Natterjack conservation, allowing concerned bodies such as NCC and Lancashire Trust for Nature Conservation (LTNC) greater control of site management. Implementation of the Sefton Coast Management Scheme (SCMS) in 1978 has also promoted nature conservation as a major land-use within the entire dune system and has provided funds for further scrape excavation.

Finally there is a need to increase public awareness about the Natterjack and its conservation (Smith, 1984). Many sites are situated in areas to which the public has access for informal recreation. Although illegal, collection of larval and adult Natterjacks has been reported, while trampling of toadlets by pedestrians walking around pools is an annual problem. Mass strandings of spawn and/or tadpoles also occur from the activity of uncontrolled dogs. At Ainsdale and Birkdale Hills LNR, illegal motor cycle scrambling has occurred in some of the slacks. The use of appropriately worded notices, and fencing of smaller sites, coupled with wardening may reduce this type of damage. At the time of writing, several voluntary wardening schemes are being implemented in conjunction with an expanded Ranger Service operated by SCMS. Smith (1984) has also recommended a programme of public information which might include a booklet similar to that already published by NCC, but modified to take account of the special circumstances prevailing on the Sefton coast.

CHAPTER 6

SUMMARY

1. Estimates of male breeding populations were undertaken using Jolly's (1965) stochastic model. Mark-recapture data were tested mathematically to confirm the suitability of this method. No major violations of the method's assumptions were found.
2. During the study years the male breeding populations were estimated to comprise 1605 ± 884, 757 ± 212, and 910 ± 156 toads respectively. Additional estimates based upon summation of male ingress gave values of 1112 ± 208 and 1064 ± 177 for 1982 and 1983. Female population estimates based upon spawn counts were 240, 207, and 427 respectively.
3. During the breeding season sex ratios based upon direct counts suggested a mean male:female ratio of 9.1:1. Comparison of male population estimates and spawn counts gave mean sex ratios of 3.2:1 and 4:1.
4. Low recapture rates during the post-breeding seasons were apparently related to a shortage of driftwood etc. which provided many retreats for toads in the late 1970's when preliminary surveys were undertaken, and an increase in *Ammophila* growth along the frontal dunes which hampered searching. Using the 1982 data,estimates based upon the Lincoln (1930) index suggested male and female population sizes of 171 ± 98 and 786 ± 450, thus giving a sex ratio of 1:4.6. Based upon direct counts during study, the mean sex ratio during this period was estimated to be 1:1.9 .
5. Age and growth studies based upon phalangeal sections gave higher male than female growth rates, although females were significantly heavier ($p < 0.01$) than males of equivalent length.

6. Males enter the breeding population as 2 year olds, but do not take part fully until the following year. Females begin to enter the breeding population at 3 years, but possibly do not breed until 5 years. Maximum male and female ages were 6 and 7 years respectively.

7. Estimated mortality rates of 4-6 year old males were 75-87% compared with 43-45% for 3 year olds. It is unclear whether the apparent increase in mortality was associated with reproduction, or whether early mortality was underestimated due to the absence of males from the breeding population. The mortality of 4-6 year old females was estimated to be 15-63%.

8. Fecundity was positively correlated with female length and weight. Estimated fecundities were approximately 2½ times greater than for Common Toads of equivalent size (Gittings *et al*, 1984), but were less than those estimated for Swiss Natterjacks (Hemmer & Kadel, 1971).

9. During the study years 240, 207, and 427 spawn strings were laid at Cabin Hill. Spawn deposition occurred mainly in sites with 100% vegetation cover (64%), 3 cm vegetation height (31%) and a mossy substrate (61%), however these results probably represent a compromise in site selection due to a lack of preferred sandy substrates. Mean water depth at spawning sites was 14 cm and 41% of spawn was laid within 1 m of the pool margin. The number of spawn strings deposited was positively correlated with the length of pool perimeter.

10. Between 1981-83 estimated survival rates of spawn to hatching were 76.2, 82.5 and 82.7% respectively. Mortality factors were fungal infection and desiccation. During the study,total estimated mortalities due to *Saprolegnia* were 17.5, 2.2 and 23.8% respec-

tively. In 1982, desiccation caused 15.1% mortality.

11. Within years there appeared to be differences in levels of fungal mortality between spawnings. In 1981, 21.1% mortality of the first spawn (March 28-April 19) was estimated compared with 5.7% of the second spawning (May 1-June 5). In 1982, 3.6% mortality of the first spawning (April 7-29) was recorded, compared with 0.8% mortality for the second spawning (May 9-June 6). However, in 1983 fungal mortalities of both the first (April 10 -May 4) and second (May 10-22) spawnings were high, 20.2 and 31.6% respectively. This may reflect the relatively short time interval between spawnings compared with previous years. A site-specific factor may be involved in fungal infection, in particular the level of vegetation cover. Throughout the study there was higher fungal mortality at Cabin Hill than at other, less vegetated Merseyside sites.

12. Key factor analysis suggests inconsistency of mortality factors between years. For ova, fungal infection was a major factor in 1981 and 1983, while in 1982 desiccation was more important. In the case of tadpoles, mortality in the late stage of development contributed most to total k in 1981, while early tadpole mortality was more significant in 1982 and 1983. A longer study would be needed to elucidate these trends.

13. Minimum yearly metamorphic survival rates were estimated to be 0.04, 0.7, and 1.3% respectively, although sampling difficulties suggest that the 1981 result is unreliable. Desiccation was estimated to have caused 4.3, 12.8, and 2.9% of tadpole mortalities during the study years. Although desiccation caused relatively low mortalities, these occurred from mid-June onwards and thus affected individuals close to metamorphosis which had

survived previous mortality factors. Between 1981-83, predation of tadpoles by invertebrates species was estimated to have caused 95.7, 87.2, and 97.1% mortality respectively. The high levels of predation are probably due to the 'maturity' of Cabin Hill sites.

14. Comparison of thermal preferenda of Natterjack and Common Toad larvae acclimated to 10 and 20°c revealed no significant difference between species or acclimation temperature. Mean PBT (± 1 SD) of Natterjacks acclimated to 10 and 20°C were 25 ± 5 and 24 ± 5°C respectively. Similarly mean PBT's of 26 ± 4 and 25 ± 4°C were recorded for Common Toads.

15. Metabolic rates of Natterjacks were higher than Common Toads at the same acclimation temperature. Natterjacks had Q_{10} values of 1.7 (10°C acclimated) and 2.0 (20°C) and showed 75% metabolic compensation after 5 weeks. Common Toads had Q_{10} values of 2.0 and 1.6 respectively, and exhibited 100% metabolic compensation.

16. The mass-specific metabolic rates of both species acclimated to 10°C increased between weeks 1-5. This was probably due to physiological changes associated with development rather than an acclimatory response. Common Toads held at 20°C began acclimating in week 1, and had completed acclimation by week 3. Natterjacks exhibited a delay of approximately 3 weeks before beginning acclimation. It is uncertain whether this response was completed by week 5.

17. Larval growth was related to acclimatory response. Thus, although Common Toads held at 20°C increased in weight throughout the study, Natterjacks did not begin growth until acclimation began after day 21. Natterjacks held at 10°C showed no growth, although Common Toad larvae showed a 27 mg increase in weight by day 17, after which no further increase was observed. It is possible that both

species were approaching or had reached their lower limiting temperatures with consequent sub-lethal physiological effects.

18. The results show that Common Toads are physiologically better adapted than Natterjacks to compensate for changes in temperature under field conditions. Common Toads should be able to select more widely than Natterjacks between areas of differing temperature in pool bodies and are better adapted for development earlier in the year. The results accord with the geographical ranges of the two species.

19. Captures of toads during the 1982 post-breeding season suggested a significant ($p < 0.01$) movement of animals northwards along Formby dunes. Of 7 marked toads which were subsequently recaptured, 4 were found at the same position up to 30 days later. However, 3 had moved up to 200 m between captures. Two toads marked initially during the breeding season were found 500-600 m from the original capture area.

20. Only 10 first-year toads were captured during the study, 3 in 1981 and 7 in 1983. Six were found 400 m from the breeding pools and in 1981 two were found 800 m distant. In 1983, two individuals travelled at least 1 km from the breeding pools.

21. A life history strategy is proposed which suggests that the Natterjack is a highly adapted *r*-specialist. It displays rapid colonisation of newly formed, shallow, ephemeral water bodies thus experiencing more favourable conditions for larval development; avoiding competition from slower colonising anurans and experiencing lower predation of larvae than in deeper, older established pools. Although it risks catastrophic mortality from desiccation this seems to be counter-balanced by large, opportunistic recruitment when conditions are favourable.

22. Future conservation measures should include selective vegetation clearance; removal of Common Toad and Frog spawn to reduce inter-species competition; excavation of new sites in suitable mobile dune habitat, and liaison to increase public awareness of the Natterjack and its conservation.

REFERENCES

Arak, A. (1983) *Male-male competition and mate choice in frogs and toads*. Unpublished Ph.D. thesis, University of Cambridge.

Arnold, S.J. & Wassersug, R.J. (1978) Differential predation on metamorphic anurans by Garter Snakes (*Thamnophis*): social behaviour as a possible defence. *Ecology*, *59*: 1014-1022.

Babiker, M.M. & Ibrahim, H. (1979) Studies on the biology of reproduction in the cichlid *Tilapia nilotica* (L): gonadal maturation and fecundity. *J. Fish Biol.*, *14*: 437-448.

Bannikov, A.G. (1950) Age distribution of a population and its dynamics in *Bombina bombina* L. *Trans. Acad. Sci. USSR.*, *70*: 101-103.

Barbault, R., Castanet, J., Francillon, H. & de Ricqles, A. (1979) Determination de l'age chez un anoure desertricole *Bufo pentoni* Anderson 1893. *Terre Vie, Rev. Ecol.*, *33*: 129-141.

Beebee, T.J.C. (1973) Observations concerning the decline of the British amphibia. *Biol. Conserv.*, *5*: 20-24.

-------------- (1976) The Natterjack Toad in the British Isles - a study of past and present status. *Br. J. Herpet.*, *5*: 515-521.

-------------- (1977) Environmental change as a cause of Natterjack Toad (*Bufo calamita*) declines in Britain. *Biol. Conserv.*, *11*: 87-102.

-------------- (1978) An attempt to explain the distributions of the rare herptiles *Bufo calamita*, *Lacerta agilis* and *Coronella austriaca* in Britain. *Br. J. Herpet.*, *5*: 763-770.

-------------- (1979a) A review of scientific information pertaining to the Natterjack Toad (*Bufo calamita*) throughout its geographical range. *Biol. Conserv.*, *16*: 107-134.

Beebee, T.J.C. (1979b) Population interactions between the toads *Bufo bufo* (Linnaeus) and *Bufo calamita* (Laurenti): some theoretical considerations and consequences. *Br. J. Herpet., 6*: 1-5.

-------------- (1983a) *The Natterjack Toad*, Oxford University Press, Oxford.

-------------- (1983b) Factors influencing the growth and survival of Natterjack Toad (*Bufo calamita*) tadpoles in captivity. *Br. J. Herpet., 6*: 294-299.

Beebee, T.J.C. & Beebee, M.L. (1978) A quantitative study of metamorphosis in the Natterjack Toad, *Bufo calamita*. *Br. J. Herpet., 5*: 689-693.

Beebee, T.J.C., Bolwell, S., Buckley, J., Corbett, K., Griffin, J., Preston, M. & Webster, J. (1982) Observation and conservation of a relict population of the Natterjack Toad *Bufo calamita* (Laurenti) in Southern England over the period 1972-1981. *Amphibia-Reptilia, 3*: 33-52.

Beebee, T.J.C. & Griffin, J.R. (1977) A preliminary investigation into Natterjack toad (*B. calamita*) breeding site characteristics in Britain. *J. Zool., Lond., 181*: 341-350.

Begon, M. (1979) *Investigating animal abundance - mark recapture for biologists*. Edward Arnold, London.

Begon, M. & Mortimer, M. (1981) *Population Ecology: A unified study of animals and plants*. Blackwell Scientific Publications, Oxford.

Beiswenger, R.E. (1978) Responses of *Bufo* tadpoles (Amphibia, Anura, Bufonidae) to laboratory gradients of temperature. *J. Herpetol. 12*: 499-504.

Bishop, J.A. & Sheppard, P.H. (1973) An evaluation of two capture-recapture models using the technique of computer simulation. In: *The mathematical theory of the dynamics of biological populations.* Eds. Bartlett, M.S. & Hiorns, R.W. Academic Press, London and New York.

Blair, W.F. (1960) A breeding population of the Mexican Toad (*Bufo valliceps*) in relation to its environment. *Ecology, 41*: 165-174.

Blankenhorn, H.J. (1972) Meteorological variables affecting onset and duration of calling in *Hyla arborea* L. and *Bufo bufo* Laur. *Oecologia, (Berl.), 9*: 223-234.

Blankenhorn, H.J., Burla, H., Muller-Meyre, P. & Villiger, M. (1969) Die baestarde an amphibien zur Laichzeit in drei gewässern des Kantons Zürich. *Vjschr. naturf. Ges. Zürich, 114*: 255-267. Cited in Beebee (1979a).

Bogert, C.M. (1949a) Thermoregulation in reptiles, a factor in evolution. *Evolution, 3*: 195-211.

------------ (1949b) Thermoregulation and eccritic body temperatures in Mexican lizards of the genus *Sceloporus*. *Ann. Inst. Biol. Mex., 20*: 415-426.

Boulenger, G.A. (1898) *The tailless Batrachians of Europe (vol. II).* Ray Society, London.

Bragg, A.N. (1965) *Gnomes of the night: The Spadefoot Toads.* Univ. of Pennsylvania Press, Philadelphia.

Brattstrom, B.H. (1962) Thermal control of aggregation behaviour of tadpoles. *Herpetologica, 18*: 38-46.

---------------- (1968) Thermal acclimation in anuran amphibians as a function of latitude and altitude. *Comp. Biochem. Physiol., 24*: 93-111.

Brattstrom, B.H. (1970a) Amphibia. In: *Comparative Physiology of Thermoregulation Vol. I: Invertebrates and Nonmammalian Vertebrates.* Ed. Whittow, G.C. Academic Press, New York and London.

---------------- (1970b) Thermal Acclimation in Australian amphibians. *Comp. Biochem. Physiol.*, *35*: 69-103.

Brattstrom, B.H. & Warren, J.H. (1955) Observations on the ecology and behaviour of the Pacific treefrog, *Hyla regilla. Copeia*, *1955*: 181-191.

Breder, C.M., Breder, R.B. & Redmond, A.C. (1927) Frog tagging: A method of studying anuran life habits. *Zoologica*, *9*: 201-229.

Bridson, R.H. (1978) *Natterjacks at Caerlaverock, 1978.* Unpublished report to Nature Conservancy Council, South Scotland Region.

Bull, J.T. & Shine, R. (1079) Iteroparous animals that skip opportunities for reproduction. *Am. Nat.*, *114*: 296-303.

Burggren, W.W., Feder, M.E. & Pinder, A.W. (1983) Temperature and the balance between aerial and aquatic respirationin larvae of *Rana berlandieri* and *Rana catesbeiana. Physiol. Zool.*, *56*: 263-273.

Burn, A.J. (1984) Life tables for the Carrot Fly, *Psila rosae. J. appl. Ecol.*, *21*: 891-902.

Byerley, I. (1856) *The fauna of Liverpool.* London and Liverpool.

Calef, G.W. (1973) Natural mortality of tadpoles in a population of *Rana aurora. Ecology*, *54*: 741-758.

Campbell, J.E. (1978) *An investigation into fluctuations in water-table within Ainsdale National Nature Reserve.* North West Water Authority, Rivers Division.

Carleton, H.M. & Short, R.H.D. (1954) *Schafer's essentials of histology. 16th Edition.* Longmans, London.

Cassie, R.M. (1954) Some uses of probability paper in the analysis of size frequency distributions. *Aust. J. Freshwat. Res.*, *5*: 513-522.

Caughley, G. (1980) *Analysis of Vertebrate Populations.*' *2nd Edition.* Wiley, Chichester.

Cecil, S.G. & Just, J.J. (1979) Survival rate, population density and development of a naturally occurring Anuran larvae (*Rana catesbeiana*). *Copeia, 1979*: 447-453.

Clarke, D. (1980) *The groundwater balance of a coastal sand-dune system. A study of the water table conditions in Ainsdale Sand Dune National Nature Reserve, Merseyside.* Unpublished Ph.D. thesis, University of Liverpool.

Clarke, R.D. (1972) The effect of toe clipping on survival in Fowler's Toad (*Bufo woodhousei fowleri*). *Copeia, 1972*: 182-185.

------------ (1977) Postmetamorphic survivorship of Fowler's Toad, *Bufo woodhousei fowleri*. *Copeia, 3*: 594-597.

Collier, R.V. (1970) Notes on the toad (*Bufo bufo*) at Castor Hanglands. *Br. J. Herpet.*, *4*: 144-151.

Collins, J.P. (1979) Intrapopulation variation in the body size at metamorphosis and timing of metamorphosis in the Bullfrog, *Rana catesbeiana*. *Ecology, 60*: 738-749.

Cook, M.A. (1976) *The Natterjack Toad (Bufo calamita) in North Merseyside.* Unpublished B.Sc. Dissertation, Liverpool Polytechnic.

Cooke, A.S. (1978) Neutral red dye as a marker for tadpoles. *Br. J. Herpet.*, *5*: 701-705.

----------- (1980) *Natterjacks in Britain, 1979.* Nature Conservancy Council Report.

----------- (1981) *Natterjacks in Britain, 1980.* Nature Conservancy Council Report.

Cooke, A.S. (1982) *Natterjacks in Britain, 1981.* Nature Conservancy Council Report.

Cooke, A.S. & Banks, B. (1983) *Natterjacks in Britain, 1982.* Nature Conservancy Council Report.

Corbett, K.F. & Beebee, T.J.C. (1975) The disappearing Natterjack. *Oryx, 13*: 47-49.

Coward, T.A. (1910) (Ed.) *The vertebrate fauna of Cheshire and Liverpool Bay. Vol. 2.* Witherby & Co., London.

------------ (1917) Notes on the vertebrate fauna of Cheshire and South Lancashire. *Lancs. & Ches. Fauna Comm. 4th Ann. Rep.* 185-282.

Curry-Lindahl, K. (1975) *Groddjur och Kräldjur i farg. Almqvist & Wiksell Forlad AB, Stockholm.* Cited in Beebee (1979a).

Davies, N.B. & Halliday, T.R. (1977) Optimal mate selection in the toad *Bufo bufo. Nature, 269*: 56-58.

----------------------------- (1978) Deep croaks and fighting assessment in toads, *Bufo bufo. Nature, 274*: 683-

----------------------------- (1979) Competitive mate searching in male Common Toads, *Bufo bufo. Anim. Behav., 27*: 1253-1267.

Davis, C.A. (1979) *Reproductive biology of Minnows (Phoxinus phoxinus* L.). Unpublished M.Sc. Thesis, Plymouth Polytechnic.

DeBenedictis, P.A. (1974) Interspecific competition between tadpoles of *Rana pipiens* and *Rana sylvatica*: an experimental field study. *Ecol. Monogr., 44*: 129-151.

Deverall, B.J. (1981) *Institute of Biology studies in biology No. 17: Fungal Parasitism. 2nd edition.* Edward Arnold, London.

DeVlaming, V.L. & Bury, R.B. (1970) Thermal selection in tadpoles of the Tailed-Frog, *Ascaphus truei. J. Herpetol., 4*: 179-189.

Elliot, J.M. (1971) *Some methods for the statistical analysis of samples of benthic invertebrates.* F.B.A. Scientific Publication No. 25.

Ellison, N.F. (1959) Vertebrate fauna of Lancashire and Cheshire. *Lancs. & Ches. Fauna Comm. 31st Ann. Rep.*, 1-35.

Feder, M.E. (1978) Environmental variability and thermal acclimation in neotropical and temperate-zone salamanders. *Physiol. Zool.*, *51*: 7-16.

----------- (1982) Environmental variability and thermal acclimation of metabolism in tropical anurans. *J. Therm. Biol.*, *7*: 23-28.

Fisher, R.A. & Ford, E.B. (1947) The spread of a gene in natural conditions in a colony of the moth.*Panaxia dominula.* *Heredity*, *1*: 143-174.

Flindt, R. & Hemmer, H. (1967) Die Parameter für das Einsetzen der Paarungsrufe bei *Bufo calamita* und *Bufo viridis.* *Salamandra*, *3*: 98-100.

---------------------- (1968) Beobachtungen zur Dynamik einer Population von *Bufo bufo* und *Bufo calamita.* *Zool. Jb. (Syst)*, *95*: 469-476.

Frazer, J.F.D. (1966) A breeding colony of toads (*Bufo bufo* L.) in Kent. *Br. J. Herpet.*, *3*: 236-252.

Frazer, D. (1983) *Reptiles and Amphibians in Britain.* Collins, London.

George, W. (1962) *Animal Geography.* Heinemann, London.

Gittings, S.P. (1983) Population dynamics of the Common Toad (*Bufo bufo*) at a lake in mid-Wales. *J. Anim. Ecol.*, *52*: 981-988.

Gittings, S.P., Kennedy, R.I. & Williams, R. (1984) Fecundity of the Common Toad (*Bufo bufo*) at a lake in mid-Wales. *Br. J. Herpet.*, *6*: 378-380.

Gittings, S.P., Kennedy, R.I. & Williams, R. (in press) Aspects of population age structure of the Common Toad (*Bufo bufo*) at Llandrindod Wells lake, mid-Wales.

Gittings, S.P., Parker, A.G. & Slater, F.M. (1980) Population characteristics of the Common Toad *Bufo bufo* visiting a breeding site in mid-Wales. *J. Anim. Ecol.*, *49*: 161-174.

Gittings, S.P., Steeds, J.E. & Williams, R. (1982) Population age structure of the Common Toad (*Bufo bufo*) at a lake in mid-Wales determined from annual growth rings in the phalanges. *Br. J. Herpet.*, *6*: 249-252.

Green, N.B. (1957) A study of the life history of *Pseudacris brachyphona* (Cope) in West Virginia with special reference to behaviour and growth of marked individuals. *Dissertation Abstr.* *17*: 23692.

Greening, L. (1888) British frogs and toads: *Bufo calamita* (Natterjack Toad). *The Young Naturalist*, *9*: 214-217.

Gresson, R.A.R. & O'Dubhda, S. (1974) The distribution of the Natterjack Toad, *Bufo calamita* Laur., in county Kerry. *Irish Naturalists J.*, *18*: 97-103.

Griffiths, B.S. (1979) *A study of the colonisation of some freshwater ponds*. Unpublished B.Sc. project report, Liverpool Polytechnic.

Guttman, S.I. & Creasey, W. (1973) Staining as a technique for marking tadpoles. *J. Herpetol.*, *7*: 388.

Haapanen, A. (1974) Site tenacity of the Common Toad, *Bufo bufo*. *Ann. Zool. Fennici*, *11*: 251-388.

Hagström, T. (1977) Growth studies and ageing methods for adult *Triturus vulgaris* L. and*T. cristatus* Laurenti (Urodela, Salamandridae). *Zool. Scripta.*, *6*: 61-68.

Hall, B.R. & Folland, C.J. (1967) *Soils of south-west Lancashire coastal plain.* Agricultural Research Council, Harpenden.

------------------------- (1970) *Soils of Lancashire.* Agricultural Research Council, Harpenden.

Hamilton, W.J. (1934) The rate of growth of the toad (*Bufo americanus americanus* Holbrook) under natural conditions. *Copeia, 1934*: 88-90.

Harding, J.P. (1949) The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. Mar. Biol. Assoc., 28*: 141-153.

Hardy, E. (1939) A rare toad (Natterjack). *The Field, 174*: 415.

Hart, P.J.B. & Pitcher, T.J. (1969) Field trials of fish marking using a jet inoculator. *J. Fish Biol.,1*: 383-385.

Hemelaar, A.S.M. (1981) Age determination of male *Bufo bufo* from the Netherlands based on year rings in phalanges. *Amphibia - Reptilia, 1*: 223-233.

Hemelaar, A.S.M. & Van Gelder, J.J. (1980) Annual growth rings in phalanges of *Bufo bufo* (Anura, Amphibia) from the Netherlands and their use for age determination. *Neth. J. Zool., 30*: 129-135.

Hemmer, H. & Kadel, K. (1971) Untersuchungen zur Laichgrösse nebst Bernerkungen zur Populationsdynamik der Kreuzkröte (*Bufo calamita* Laur.) und der Wechselkröte (*Bufo viridis* Laur.). *Zool. Beitr. NS., 17*: 327-336.

Herreid, C.F. & Kinney, S. (1966) Survival of Alaskan Woodfrog (*Rana sylvatica*) larvae. *Ecology, 47*: 1039-1041.

Heusser, H. (1969) Unkreaktion mit Befreiungsruf beim Weibchen der Kreuzkröte, *Bufo calamita*. *Experientia, 25*: 121-123.

Heusser, H. (1970) Laichfressen durch Kualquappen als mögliche Ursache spezifischer Biotoppräferenzen und kurzer Laichzeiten bei europäischen Froschlurchen (Amphibia, Anura). *Oecologia (Berl.) 4*: 83-88.

----------- (1971) Laich-Räubern und Kannibalismus bei sympatrischen Anuren-Kaulquappen. *Experientia, 27*: 474.

Heusser, H. & Meisterhans, K. (1969) Zur Populationsdynamik der Kreuzekröte, *Bufo calamita* L. *Vjschr. naturf. Ges. Zürich, 114*: 269-277.

Hota, A.K. & Dash, M.C. (1981) Growth and metamorphosis of *Rana tigrina* larvae: effects of food level and larval density. *Oikos, 37*, 349-352.

Howard, R.D. (1978) The influence of male-defended oviposition on early embryo mortality in Bullfrogs. *Ecology, 59*: 789-798.

Huey, R.B. (1978) Latitudinal pattern of between-altitude faunal overlap: Mountains might be "higher" in the tropics. *Am. Nat., 112*, 225-229.

Huey, R.B. & Slatkin, M. (1976) Cost and benefits of lizard thermoregulation. *Quart. Rev. Biol., 5*: 363-384.

Hutchison, V.H. (1961) Critical thermal maxima in salamanders. *Physiol. Zool., 34*: 91-125.

Hutchison, V.H. & Hill, L. (1978) Thermal selection of Bullfrog tadpoles (*Rana catesbeiana*) at different stages of development and acclimation temperatures. *J. Therm. Biol., 3*: 57-60.

Jameson, D.L. (1955) The population dynamics of the Cliff Frog, *Syrrhophus marnocki*. *Amer. Midl. Nat., 54*: 342-381.

Janzen, D.H. (1835) Why mountain passes are higher in the tropics. *Am. Nat., 101*: 233-249.

Jenyns, L. (1835) *A manual of British vertebrate animals.* Cambridge.

Jolly, G.M. (1965) Explicit estimates from capture-recapture data with both death and immigration - Stochastic model. *Biometrika, 52*: 225-247.

Kadel, K. (1975) Freilandstudien zur Uberlebensrate Kreuzkrötenlarven (*Bufo calamita* Laur.). *Revue Suisse Zool., 82*: 237-244.

Kelleher, K.E. & Tester, J.R. (1969) Homing and survival in the Manitoba Toad, *Bufo hemiophrys*, in Minnesota. *Ecology, 50*: 1040-1048.

Kelly, W.H. (1967) Marking freshwater and a marine fish by injected dye. *Trans. Am. Fish Soc., 96*: 163-175.

Kowalewski, L. (1967) Nowe stanowiska ropuchy paskowki *Bufo calamita* Laur. *Przegl. zool. 11*: 310-312. Cited in Beebee (1979a).

Krebs, C.J. (1978) *Ecology: The experimental analysis of distribution and abundance. 2nd edition.* Harper and Row, New York.

Leslie, P.H. (1958) Statistical appendix. *J. Anim. Ecol., 27*: 84-86.

Licht, L.E. (1967) Growth inhibition in crowded tadpoles: intra-specific and interspecific effects. *Ecology, 48*: 736-745.

---------- (1974) Survival of embryos, tadpoles, and adults of the frogs *Rana aurora aurora* and *Rana pretiosa pretiosa* sympatric in southwestern British Columbia. *Can. J. Zool., 52*: 613-627.

Licht, P. (1968) Response of the thermal preferendum and heat resistance to thermal acclimation under different photoperiods in the lizard *Anolis carolinensis*. *Am. Midl. Nat., 79*: 149-158.

Licht, P., Dawson, W.R., Shoemaker, V.H. & Main, A.R. (1966) Observations on the thermal relations of Western Australian Lizards. *Copeia, 1966*: 97-110.

Lincoln, F.C. (1930) Calculating waterfowl abundance on the basis of banding returns. *U.S. Dept. Agric. Circ., 118*: 1-4.

Lotter, F. (1978) Reproductive ecology of the salamander *Plethodon cinereus* (Amphibia, Urodela, Plethodontidae in Conneticut. *J. Herpetol.*, *12*: 231-236.

Lucas, E.A. & Reynolds, W.A. (1967) Temperature selection by amphibian larvae. *Physiol. Zool.*, *40*: 159-171.

Lynn, W.G. & Edelman, A. (1936) Crowding and metamorphosis in the tadpole. *Ecology*, *17*: 104-109.

Macan, T.T. (1979) *A guide to freshwater invertebrate animals. 11th edition.* Longmans, London.

Macdonald, P.D.M. & Pitcher, T.J. (1979) Age groups from size-frequency data: a versatile and efficient method for analysing distribution mixtures. *J. Fish Res. Bd. Can.*, *36*: 987-1001.

Macer, C.T. (1974) The reproductive biology of the Horse Mackerel *Trachurus trachurus* (L.) in the North Sea and English Channel. *J. Fish Biol.*, *6*: 415-438.

Manly, B.F.J. (1978) Some examples of a method for determining key factors from life table data. *Oecologia (Berl.)*, *35*: 119-122.

Manly, B.F.J. & Parr, M.J. (1968) A new method of estimating population size, survivorship, and birth rate from capture-recapture data. *Trans. Soc. Br. Ent.*, *18*: 81-89.

Mathias, J.H. (1971) *The comparative ecologies of two species of amphibian (Bufo bufo and Bufo calamita) on the Ainsdale Sand Dunes National Nature Reserve.* Unpublished Ph.D. thesis, Manchester University.

Mayhew, W.W. (1963) Temperature preference of *Sceloporus orcutti*. *Herpetologica*, *18*: 217-233.

McGinnis, S.M. (1966) *Sceloporus occidentalis*: Preferred body temperature of the Western Fence lizard. *Science*, *152*: 1090-1091.

McIlwain, T.D. & Christmas, J.Y. (1975) A new batch marking technique for fingerling striped bass. *Progve. Fish. Cult.*, *37*: 123-125.

Mertens, R. (1964) *Kreichtiere und Lurche*. Kosmos, Stuttgart. Cited in Beebee (1979a).

Moore, H.J. (1954) Some observations on the migration of the toad (*Bufo bufo bufo*). *Br. J. Herpet.*, *1*: 194-224.

Nature Conservancy Council (1983). *The ecology and conservation of amphibian and reptile species endangered in Britain*. London, Nature Conservancy Council.

Nelder, J.A. & Mead, R. (1965) A simplex method for function minimisation. *Comput. J.*, *7*: 308-313.

Newman, E. (1869) Collected observations on British reptiles: Subclass 2, metamorphic reptiles. *Zoologist*, *Ser. 3*, *4*: 1707-1719.

Noland, R. & Ultsch, G.R. (1981) The roles of temperature and dissolved oxygen in microhabitat selection by the tadpoles of a frog (*Rana pipiens*) and a toad (*Bufo terrestris*). *Copeia*, *1981*, 645-652.

Oldham, R.S. (1967) Orienting mechanisms of the Green Frog, *Rana clamitans*. *Ecology*, *48*: 477-491.

Payne, K.R. (1983) *Amphibian breeding survey report 1983*, *Ainsdale Sand Dunes NNR*. Unpublished report to Nature Conservancy Council, North West Region, Blackwell, Bowness-on-Windermere, Cumbria.

Peabody, F.E. (1961) Annual growth zones in living and fossil vertebrates. *J. Morph.*, *108*: 11-62.

Pearl, R. (1928) *The rate of living*. Knopf, New York.

Pearson, P.G. (1955) Population ecology of the Spadefoot Toad, *Scaphiopus h. holbrooki* (Harlan). *Ecol. Monogr.*, *25*: 233-267.

Perry, R.K. (1934) *Lancs. & Ches. Fauna Comm. 20th Ann. Rep.*: p 13.

----------- (1945) Report on mammals, reptiles and amphibians, 1939-42. *Lancs. & Ches. Fauna Comm. 26th Ann. Rep.*: p 42.

Petersen, H. & Luxton, M. (1982) A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos*, *39*: 288-388.

Pianka, E.R. (1970) On *r*- and *k*-selection. *Am. Nat.*, *104*: 592-597.

Pollister, A.W. & Moore, J.A. (1937) Tables for the normal development of *Rana sylvatica*. *Anat. Rec.*, *68*: 480-496.

Precht, H., Christophersen, J., Hensel, J. & Larcher, W. (1973) *Temperature and life*. Springer-Verlag, Berlin.

Prestt, I., Cooke, A.S. & Corbett, K.F. (1974) British Amphibians and Reptiles. In: *The changing flora and fauna of Britain*. Ed. Hawksworth, D.L., 229-254. Academic Press, London and New York.

Pyburn, W.F. (1958) Size and movements of a local population of cricket frogs (*Acris crepitans*). *Tex. J. Sci.*, *10*: 325-342.

Raney, E.C. (1940) Summer movements of the Bullfrog, *Rana catesbeiana* Shaw, as determined by the jaw-tag method. *Am. Midl. Nat.*, *23*: 733-745.

Raney, E.C. & Ingram, W.M. (1941) Growth of tagged frogs (*Rana catesbeiana* Shaw and *Rana clamitans* Daudin) under natural conditions. *Am. Midl. Nat.*, *26*: 201-206.

Ranwell, D.S. (1972) *Ecology of salt marshes and sand dunes*. Chapman & Hall, London.

Ratcliffe, D.A. (Ed.) (1977) *A Nature Conservation Review*. Cambridge University Press, Cambridge.

Richmond, N.D. (1947) Life history of *Scaphiopus holbrooki*: 1. Larval development and behaviour. *Ecology*, *28*: 53-67).

Riley, J.D. (1966) Liquid latex marking technique for small fish. *J. Cons. perm. int. Explor. Mer.*, *30*: 354-357.

Roberts, J.M. (1981) *A study of the Natterjack Toad at an atypical but productive breeding site - Formby Point denatured tobacco waste dump in Lancashire.* Unpublished B.Sc. Project Report, Liverpool Polytechnic.

Robson, D.S. & Regier, H.A. (1964) Sample size in Petersen mark recapture experiments. *Trans. Amer. Fish. Soc.*, *93*: 215-226.

Rose, A.H. (1967) *Thermobiology.* Academic Press, London and New York.

Rose, F.L. (1966) Reproductive potential of *Amphiuna means*. *Copeia*, *1966*: 598-599.

Rose, S.M. & Rose, C.F. (1961) Growth controlling exudates of tadpoles. *Symp. Soc. Exp. Biol.*, *15*: 207-218.

Savage, R.M. (1934) The breeding behaviour of the Common Frog, *Rana temporaria temporaria* Linn., and the Common Toad, *Bufo bufo bufo* Linn. *Proc. Zool. Soc. London*, *1934*: 55-70.

Savidge, J.P., Heywood, V.H. & Gordon, V. (Eds.) (1963) *Travis's Flora of South Lancashire.* Liverpool Botanical Society, Liverpool.

Schaub, D.L. & Larsen, J.H. (1978) The reproductive ecology of the Pacific Treefrog (*Hyla regilla*). *Herpetologica*, *34*: 409-416.

Schroeder, E.E. & Baskett, T.S. (1968) Age estimation, growth rates, and population structure in Missouri Bullfrogs. *Copeia*, *3*: 583-592.

Severtzov, A.S. & Surova, G.S. (1979) Effects of predators on the population of *Rana temporaria* tadpoles. *Zool. Zh.*, *58*: 1374-1379.

Simms, C. (1966) The status of amphibians and reptiles in the dunes of southwest Lancashire, 1961-64. *Lancs. & Ches. Fauna Soc. 51st Ann. Rep.*, 7-10.

Smirna, E.M. & Roček, Z. (1969) On the possibility of using annual bone layers of alpine newts, *Triturus alpestris* (Amphibia: Urodela), for their age determination. *Věst. čsl. Spol. zool.*, *40*: 232-237.

Smith, M.A. (1964) *The British Amphibians and Reptiles. 3rd edition.* Collins, London.

Smith, P.H. (1977) *Natterjack Toad report - Cabin Hill and Altcar Rifle Range, 1977.* Unpublished report to Nature Conservancy Council, North West Region, Blackwell, Bowness-on-Windermere, Cumbria.

----------- (1978a) *The ecological evaluation of weland habitats in the north west Merseyside sand dune system.* Merseyside County Council.

----------- (1978b) *Natterjack Toad report - Cabin Hill and Altcar Rifle Range, 1978.* Unpublished report to Nature Conservancy, Council, North West Region, Blackwell, Bowness-on-Windermere, Cumbria.

----------- (1979) *Natterjack Toad report - Cabin Hill and Altcar Rifle Range, 1979.* Unpublished report to Nature Conservancy Council, North West Region, Blackwell, Bowness-on-Windermere, Cumbria.

----------- (1980a) *An ecological survey of Raven Meols sandhills and foreshore, Formby Point.* Merseyside County Council.

----------- (1980b) *Natterjack Toad report - Cabin Hill and Altcar Rifle Range, 1980.* Unpublished report to Nature Conservancy Council, North West Region, Blackwell, Bowness-on-Windermere, Cumbria.

Smith, P.H. (1981) *Natterjack Toad report - Raven Meols and Formby Point, 1981.* Unpublished report to Nature Conservancy Council, North West Region, Blackwell, Bowness-on-Windermere, Cumbria.

----------- (1982) *Natterjack Toad report - Raven Meols and Formby Point, 1982.* Unpublished report to Nature Conservancy Council, North West Region, Blackwell, Bowness-on-Windermere, Cumbria.

----------- (1983a) *Natterjack Toad report - Raven Meols and Formby Point, 1983.* Unpublished report to Nature Conservancy Council, North West Region, Blackwell, Bowness-on-Windermere, Cumbria.

----------- (1983b) *Ecology and management of Birkdale frontal dunes, Merseyside.* Unpublished report to Sefton Metropolitan Borough Council, by the Lancashire Trust for Nature Conservation.

----------- (1984) *A strategy for the conservation of the Natterjack Toad in the north Merseyside sand-dune system.* Unpublished report to Nature Conservancy Council, North West Region, Blackwell, Bowness-on-Windermere, Cumbria.

Smith, P.H. & Bownes, C.F. (1978) *The use of artificial breeding pools by adult Natterjack Toads in Ainsdale Sand Dunes Nature Reserve in 1978.* Unpublished report to Nature Conservancy Council, North West Region, Blackwell, Bowness-on-Windermere, Cumbria.

Smith, P.H. & Flynn, D.H. (1977) *A population census of adult Natterjack Toads (Bufo calamita) at excavated breeding sites on Ainsdale Sand Dunes National Nature Reserve, Merseyside.* Unpublished report to the Nature Conservancy Council, North West Region, Blackwell, Bowness-on-Windermere, Cumbria.

Smith, P.H., Harris, J.I. & Hancock, E.G. (1974) The Natterjack Toad in south-west Lancashire - 1972. *Nature. Lancs., 4*: 44-48.

Smith, P.H. & Payne, K.R. (1980) A survey of Natterjack Toad *Bufo calamita* distribution and breeding success in the north Merseyside sand-dune system, England. *Biol. Conserv., 19*: 27-39.

Smith, R.J.F. (1970) A technique for marking small fish with injected fluorescent dyes. *J. Fish. Res. Bd. Can., 27*: 1889-1891.

Smith, S.H. (1974) *Hybridisation in the two species of amphibia (Bufo bufo and Bufo calamita) in controlled conditions and in the wild at Ainsdale, south west Lancashire.* Unpublished M.Sc. thesis, Manchester University.

Sokal, R.R. & Rohlf, F.J. (1969) *Biometry.* W.H. Feeeman and Co., San Francisco.

Southwood, T.R.E. (1978) *Ecological Methods, with particular reference to the study of insect populations. 2nd edition.* Chapman & Hall, London and New York.

Spellerberg, I.F. (1972a) Thermal ecology of allopatric lizards (*Sphenomorphus*) in Southeast Australia. II. Physiological aspects of thermoregulation. *Oecologia, 9*: 385-398.

----------------- (1972b) Thermal ecology of allopatric lizards (*Sphenomorphus*) in Southeast Australia. III. Behavioural aspects of thermoregulation. *Oecologia, 11*: 1-16.

----------------- (1975) Conservation and management of Britain's reptiles based on their ecological and behavioural requirements: a progress report. *Biol. Conserv., 7*: 289-300.

Standen, R. (1914) The Natterjack (*Bufo calamita* Laur.) on the Wirral coast, Cheshire. *Lancs. and Ches. Nat., 7*: 177-180.

Stebbins, R.C. (1963) Activity changes in the Striped Plateau lizard with evidence on influence of the parietal eye. *Copeia, 4*: 681-691.

Steinwascher, K. (1978) Interference and exploitation competition among tadpoles of *Rana utricularia. Ecology, 59*: 1039-1046.

Storm, R.M. & Pimentel, R.A. (1954) A method for studying amphibian breeding populations. *Herpetologica, 10*: 161-166.

Tester, J.R. & Breckenridge, W.J. (1964) Population dynamics of the Manitoba Toad, *Bufo hemiophrys*, in northwestern Minnesota. *Ecology*, *45*: 592-601.

Tevis, L. (1966) Unsuccessful breeding by Desert Toads (*Bufo punctatus*) at the limit of their ecological tolerance. *Ecology*, *47*: 766-775.

Turner, F.B. (1960) Population structure and dynamics of the Western Spotted Frog, *Rana p. pretiosa* Baird & Girard, in Yellowstone Park, Wyoming. *Ecol. Monogr.*, *30*: 251-178.

Voris, H.K. & Bacon, J.P. (1966) Differential predation on tadpoles. *Copeia*, *1966*: 594-598.

Warburg, M.R., Degani, G. & Warburg, I. (1979) Growth and population structure of *Salamandra salamandra* (L.) larvae in different limnological conditions. *Hydrobiologica*, *64*: 147-155.

Warner, W.H. (1884) The Natterjack Toad (*Bufo calamita*). *The Young Nat.*, *5*: 125-128.

Whitaker, J.O. (1971) A study of the Western Chorus Frog, *Pseudacris triseriata*, in Virgo County, Indiana. *J. Herpetol.*, *5*: 127-150.

Wijnands, H.E.J. (1972) Mortality of *Rana temporaria* and *Rana arvalis* larvae. *Neth. J. Zool.*, *22*: 224-225.

Wilbur, H.M. (1977) Interactions of food level and population density in *Rana sylvatica*. *Ecology*, *58*: 206-209.

Wilkinson, D.R. & Jones, J.W. (1977) The fecundity of Dace, *Leuciscus leuciscus* (L.) in Ernral Brook, Clwyd, North Wales. *Freshwat. Biol.*, *7*: 135-147.

Wisniewski, P.J., Paull, L.M., Merry, D.G. & Slater, F.M. (1980) Studies on the breeding migration and intramigratory movements of the Common Toad (*Bufo bufo*) using panjet dye-marking techniques. *Br. J. Herpet.*, *6*: 171-174.

Yalden, W.D. (1980) An alternative explanation of the distributions of the rare herptiles in Britain. *Br. J. Herpet.*, *6*: 37-40.

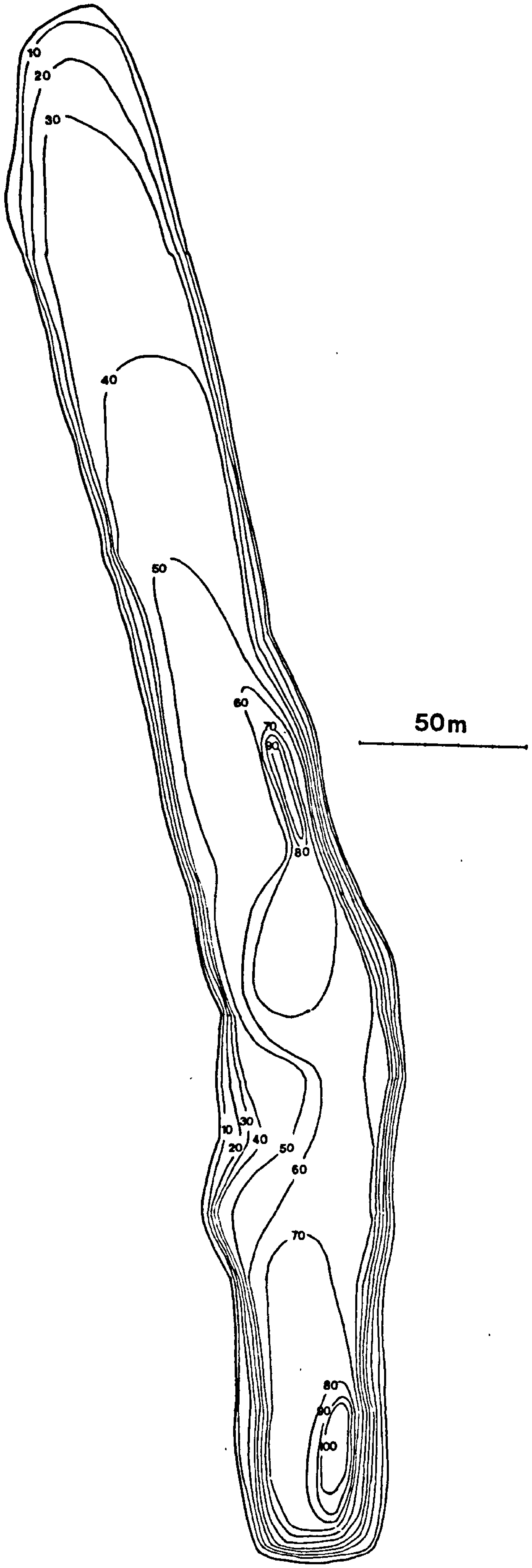
Zweiffel (1968) Reproductive biology of anurans of the arid southwest with emphasis on adaptation of embryos to temperature. *Bull. Am. Mus. Nat. Hist.*, *140*: 1-64.

APPENDIX 1

DEPTH CONTOUR MAPS OF CABIN HILL POOLS

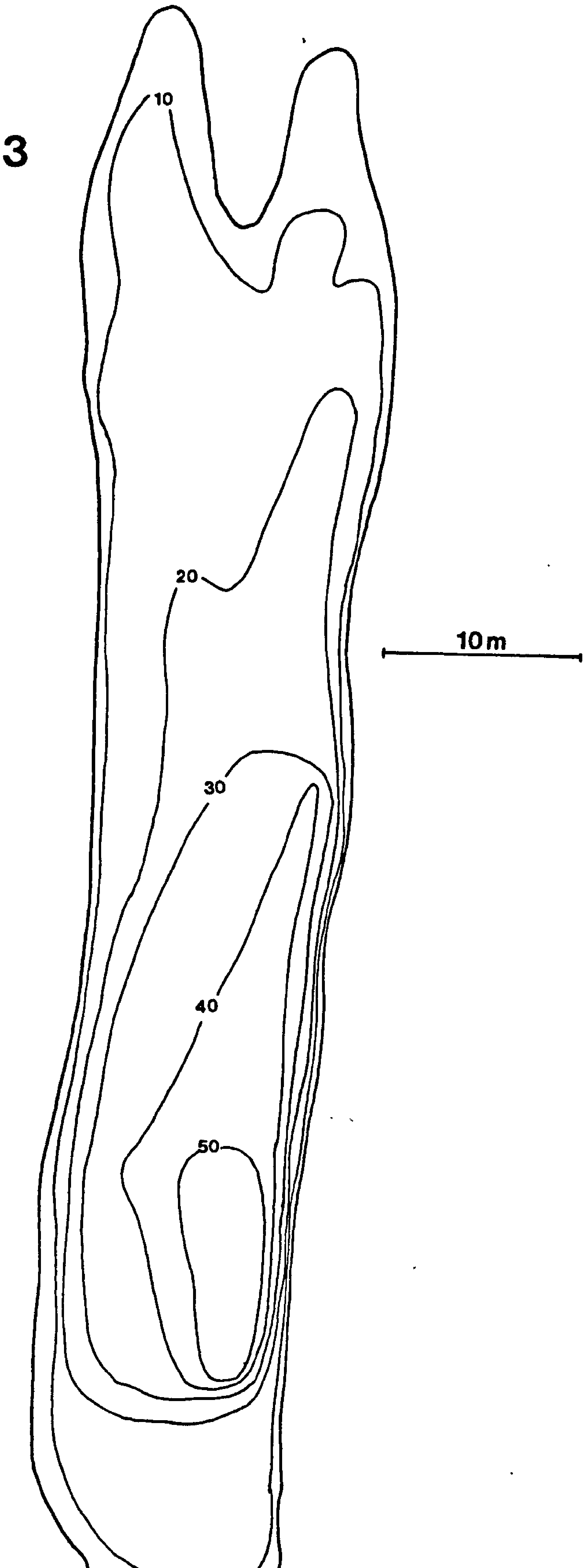
Contour lines given in 10 cm intervals. NB. Pools 2, P and 19 excluded.

1

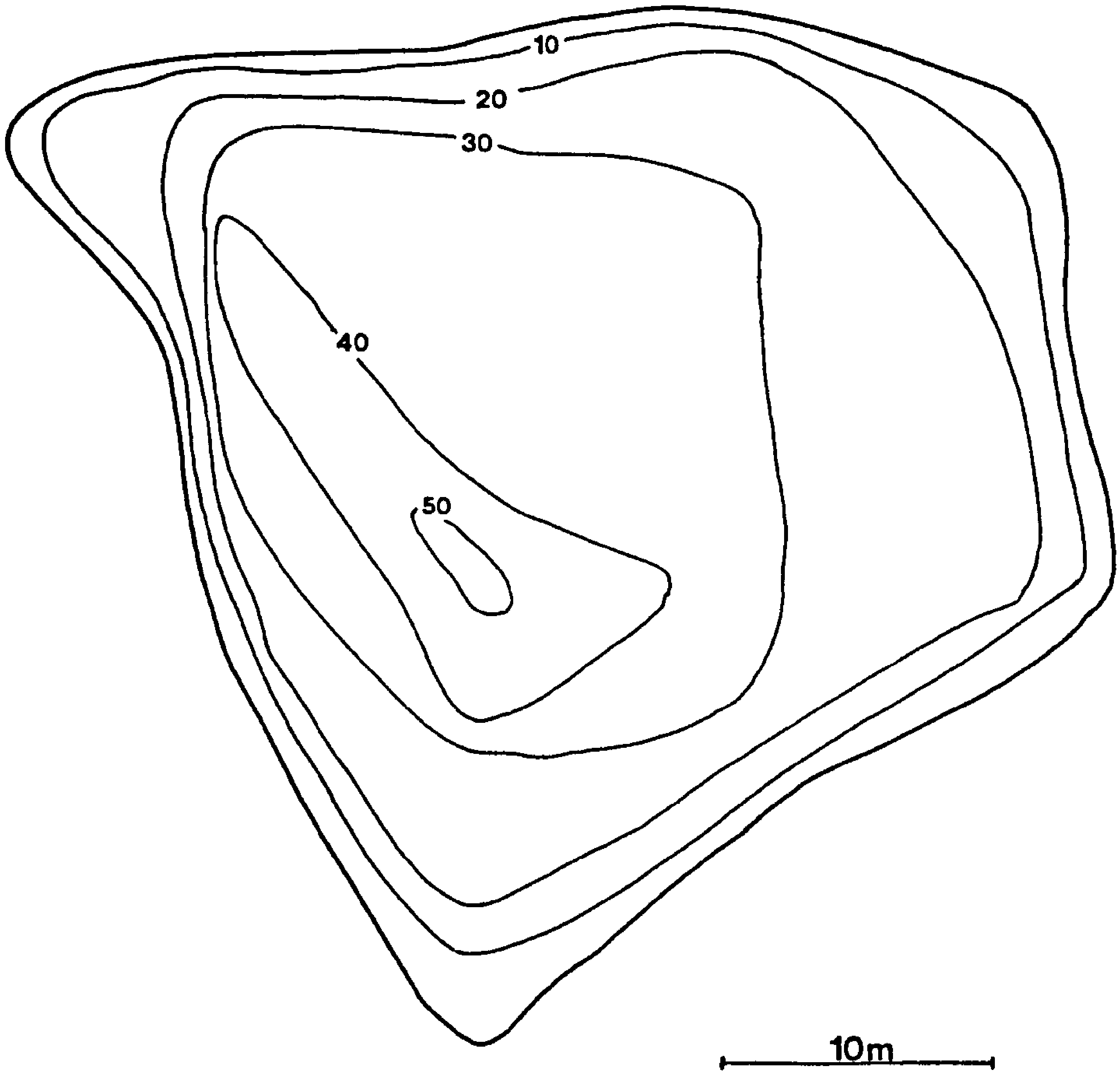


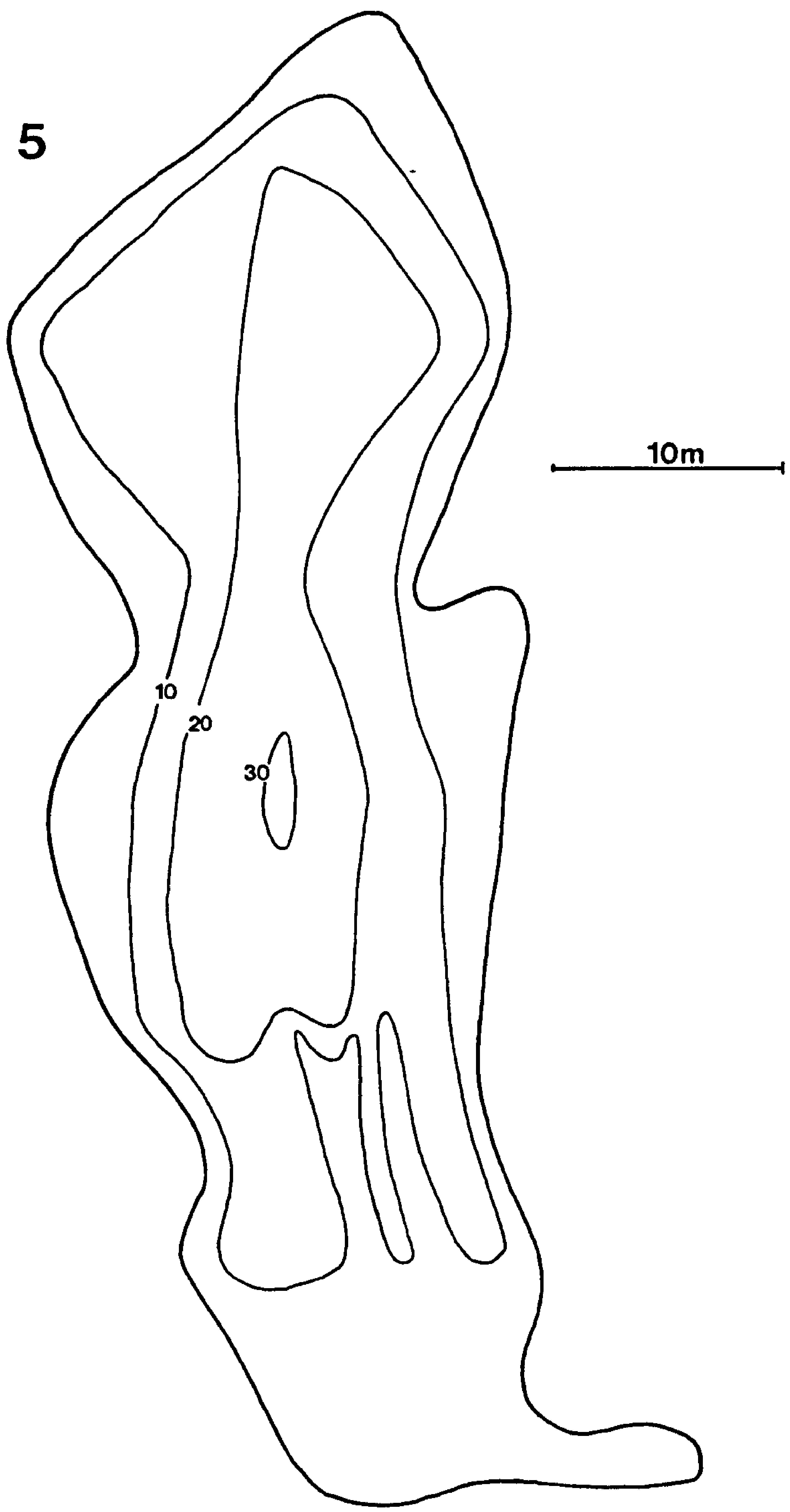
A1.1

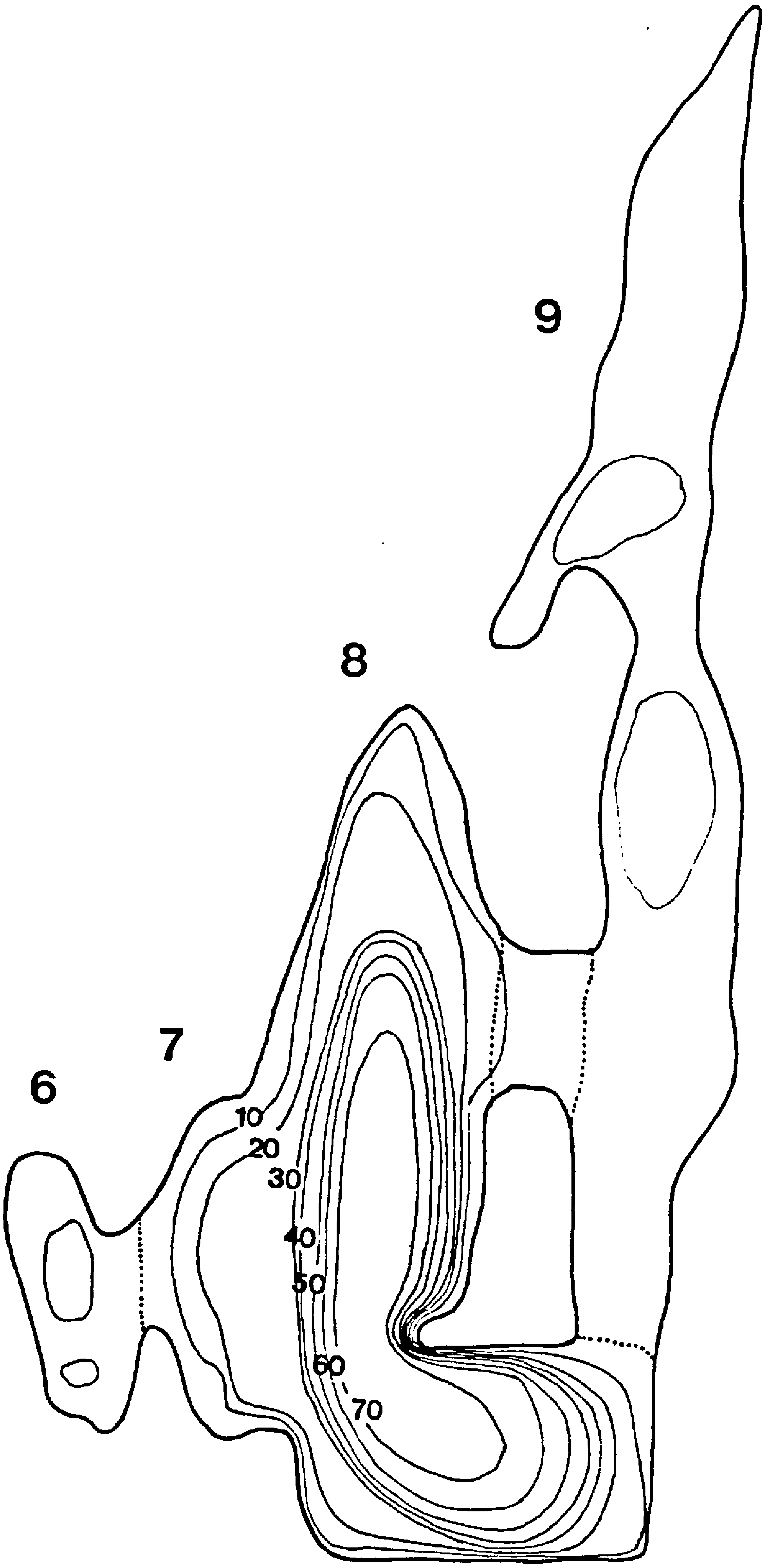
3



4

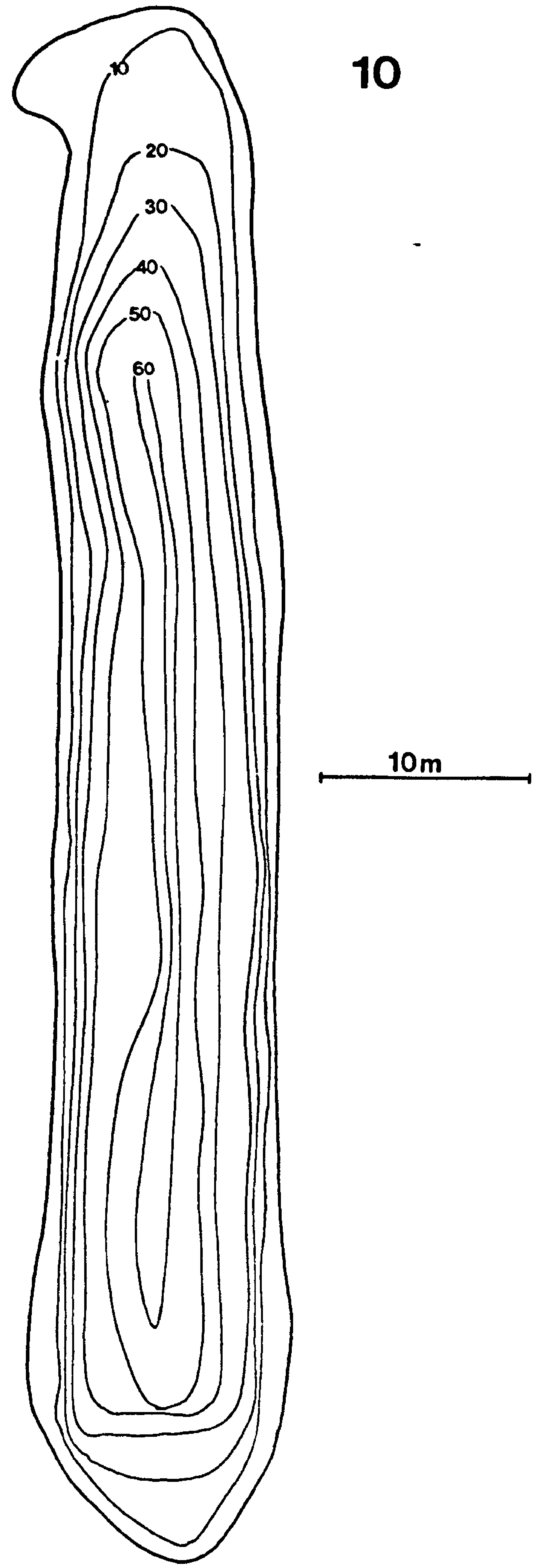



5
10m
10
20
30

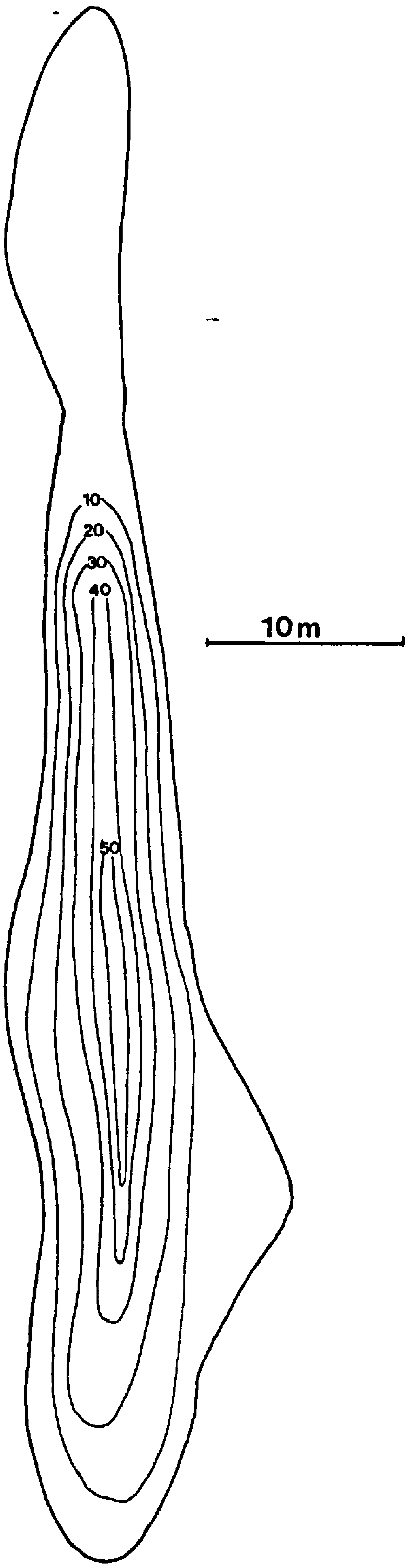


A1.5

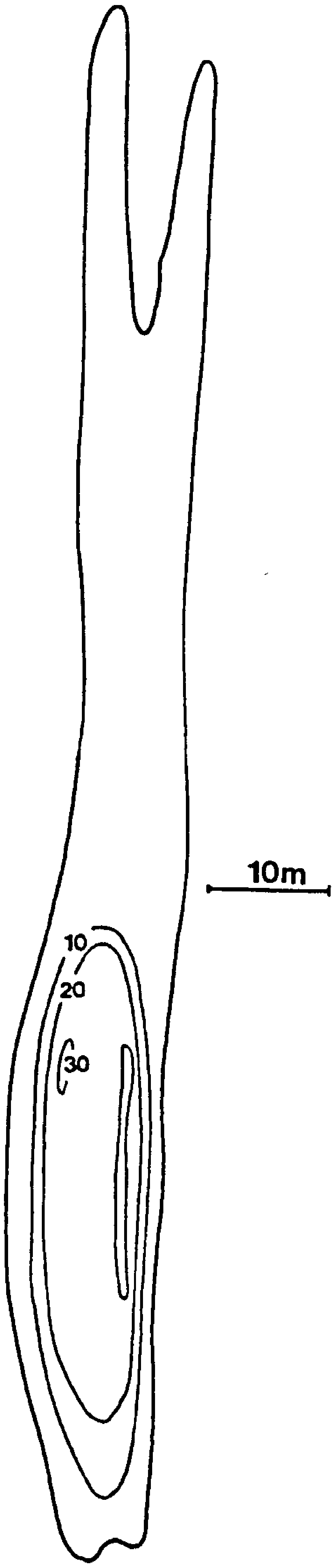
10



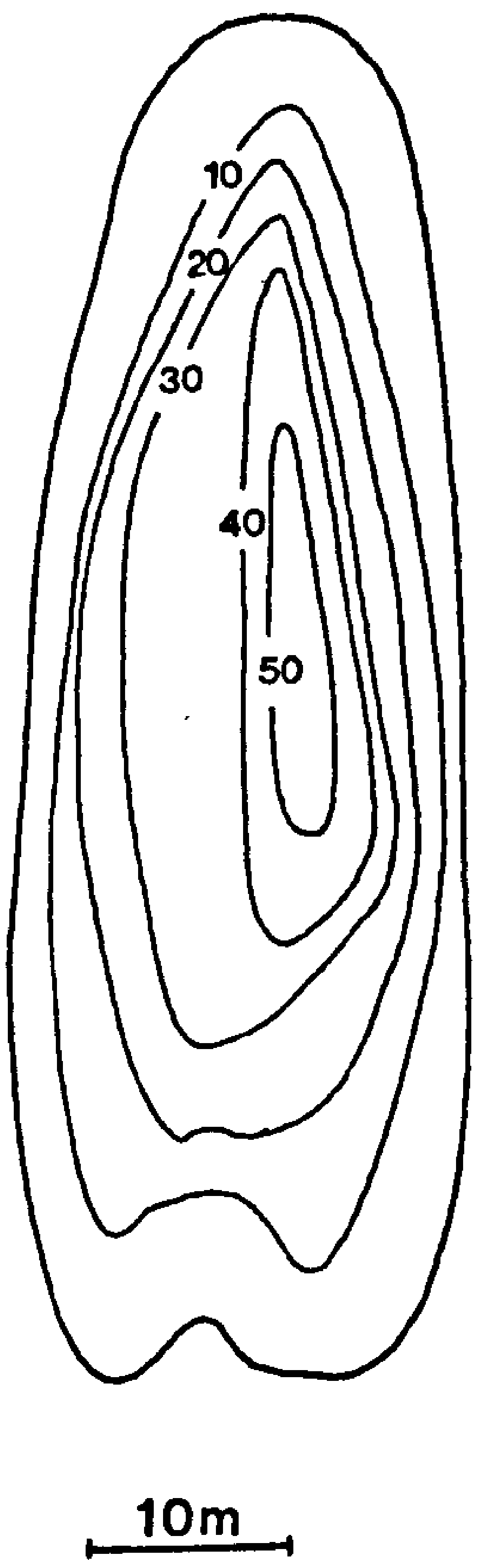
11



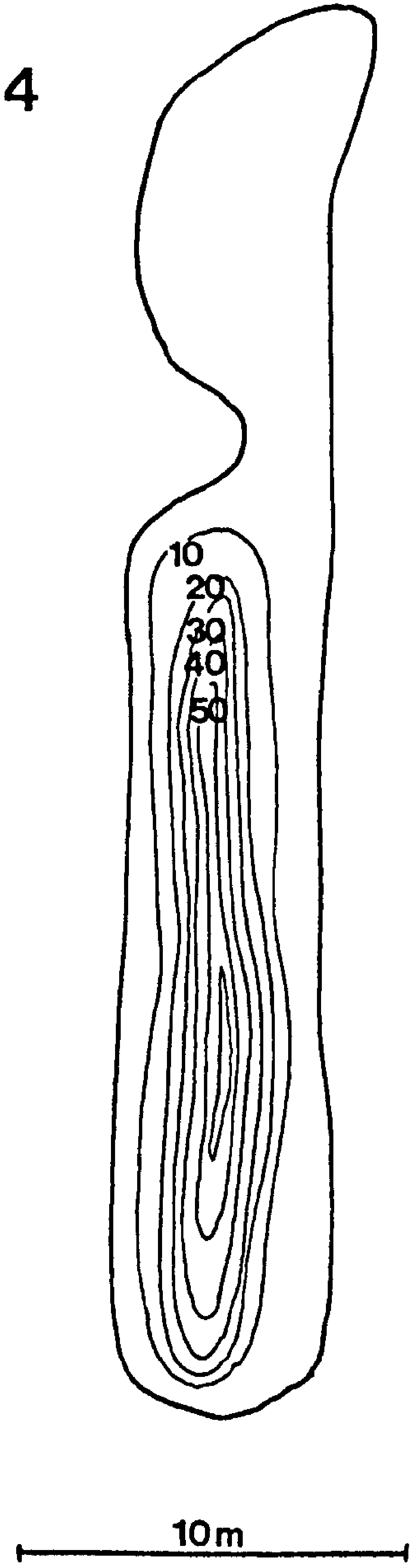
12



13

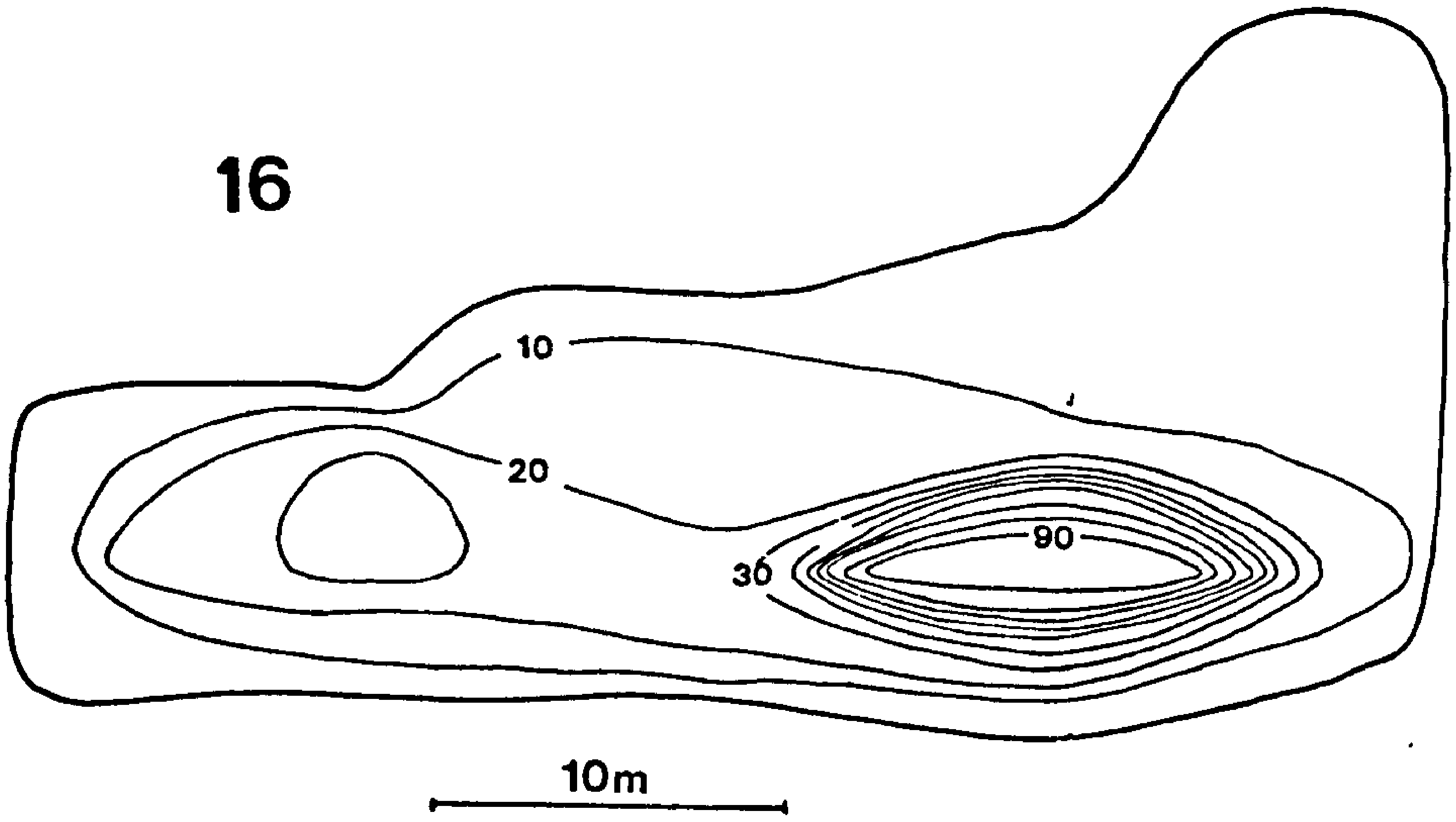


14

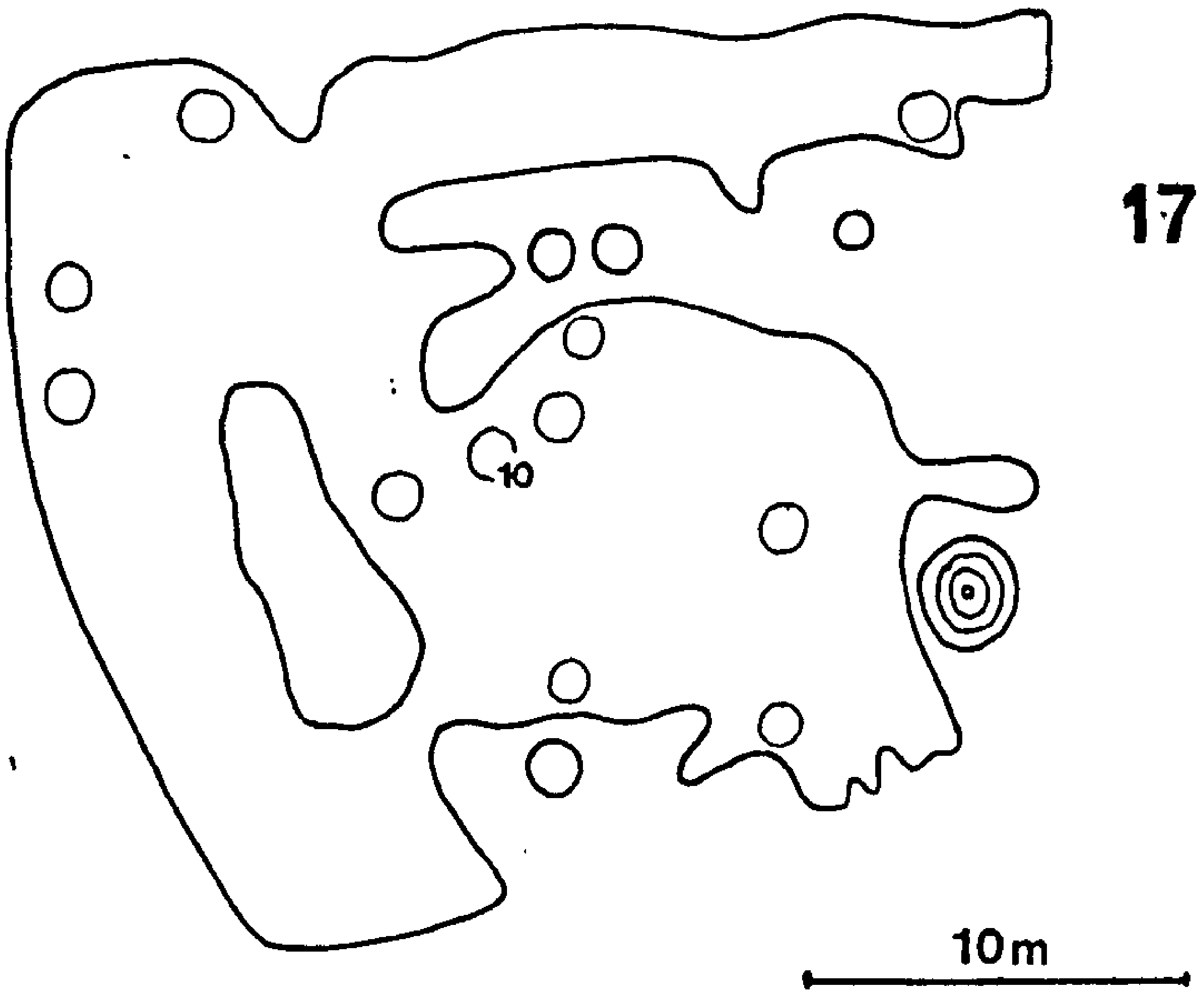


15

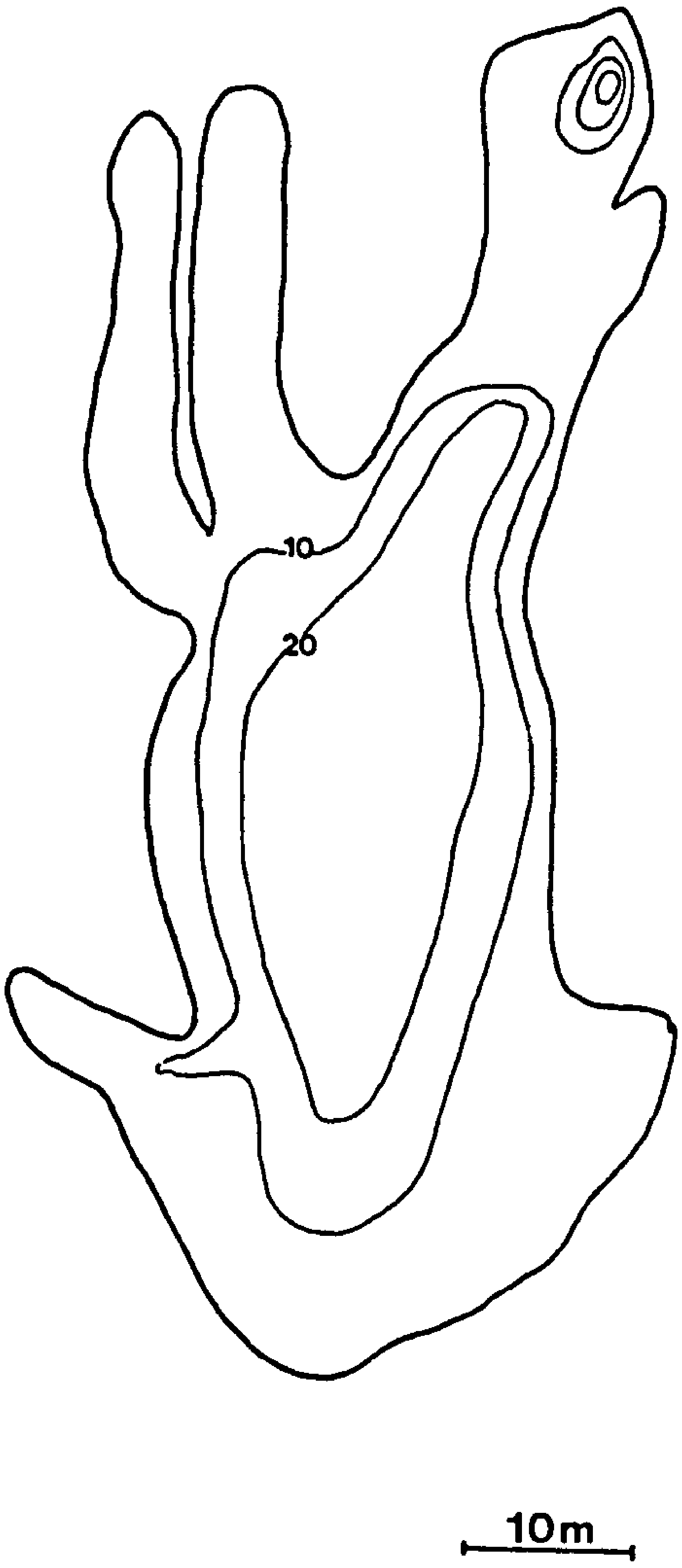
16



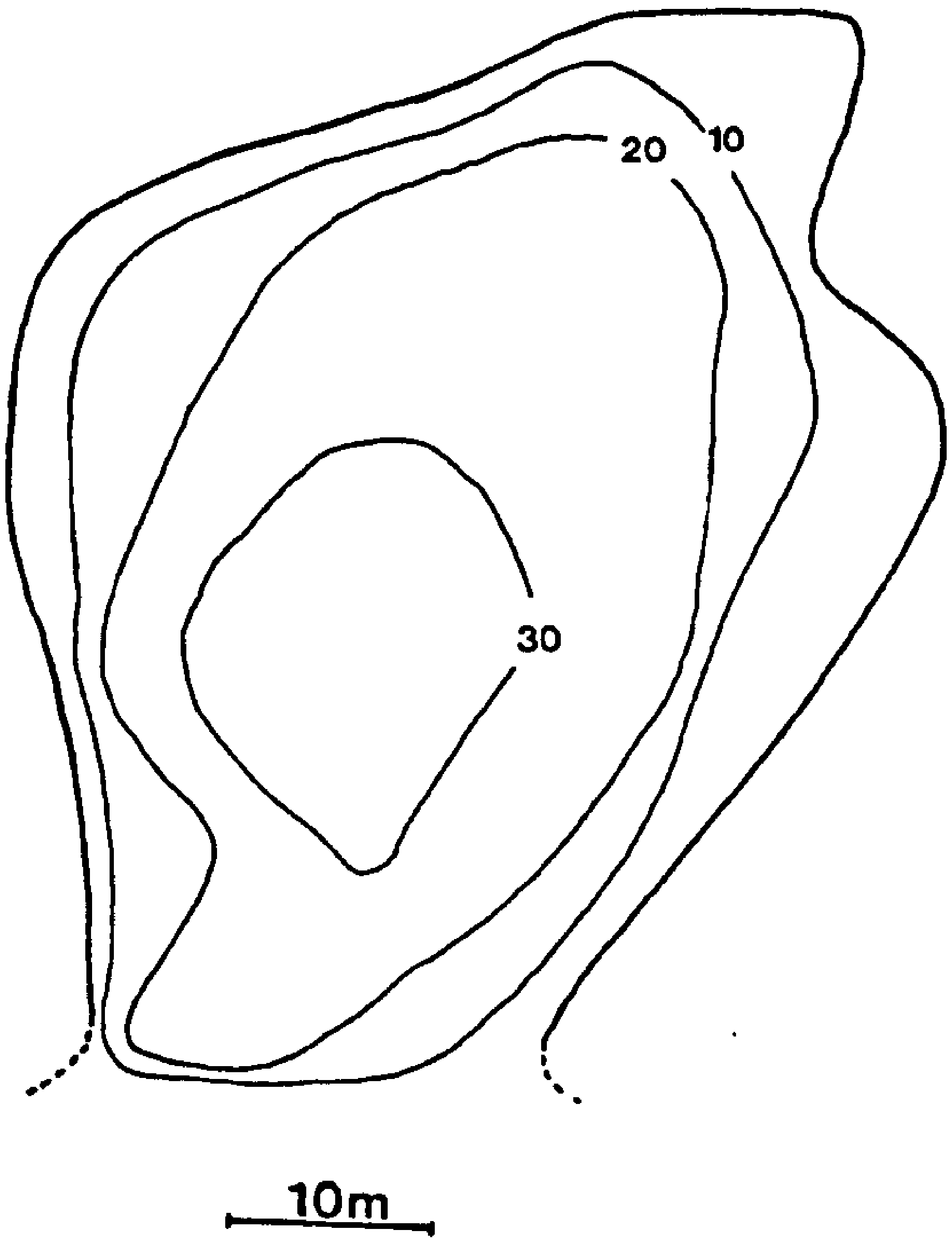
17



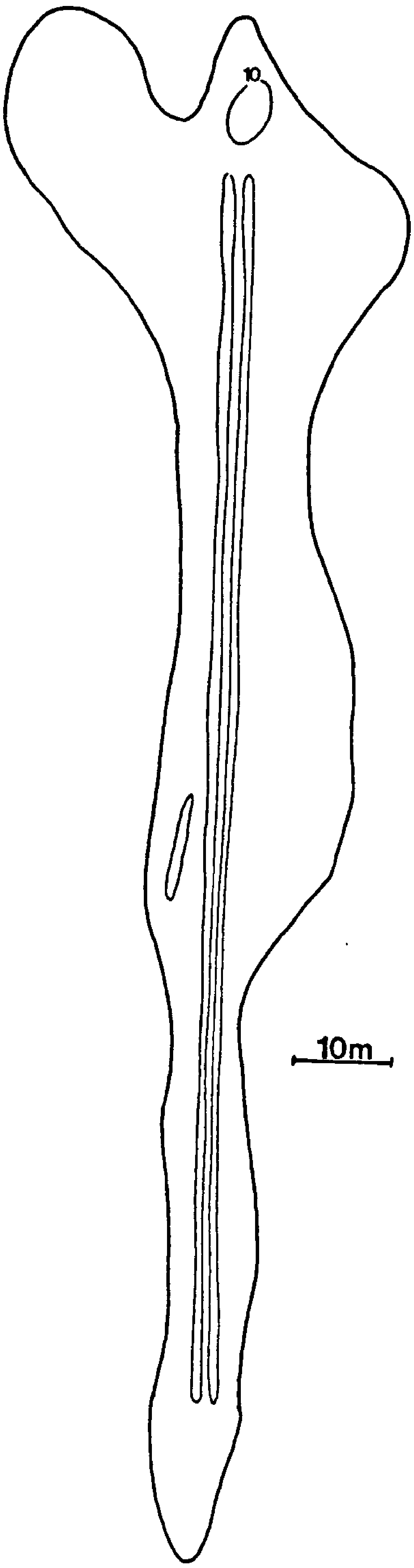
18



20



21



APPENDIX 2

VEGETATION IN CABIN HILL POOLS

Species	Pool No.																				
	1	2	3	4	5	6	7/8	9	10	11	12	13	14	15	16	17	18	19	20	21	P
Agropyron repens	VLF		LF	F	O	O	O	F						VLF	R	O			O		
Agrostis stolonifera	LA	LA	A	LA	C	A	F	C	F	C			C	A	A	C	C	A	A		O
Alopecurus geniculatus			VLC																		
Anagallis tenella															VLA						
Apium nodiflorum	VLA																				
Blysmus compressus																			LA		
Carex arenaria						LF		O					F	LF	O	F				C	
C. flacca	LC				F	F	O		O	F			LC		LC	C	C	VLF			
C. hirta	LC		O	O				O		R								O	F		
C. nigra	O	F		A	VLA													LC	LC		
C. otrubae				R	R			R											R		
C. serotina	VLC				C	O	F	O	F	F			O	R	C	O	C				
Centaurium erythraea																	R				
C. littorale																	R				
C. pulchellum																	R				
Cirsium arvense	VLF		O				R		R					O			R		O		
Dactylis glomerata														R							
Dactylorhiza incarnata	R		R		O	O	F	R	VLF	O			F	O	O	F	F	O	LC		
Eleocharis palustris	A	C	LA	F	VLC	O	LA	O	C	LA					R	LC		F			
Epilobium hirsutum	VLC		O											R					O		
E. palustre	O			R														O	VLF		
E. parviflorum	O			R																	
Epipactis palustris														LC		O					
Equisetum arvense	F	O	F	C	VLF	O	O	O	O	O			O	F	R		VLF	O	O		
E. fluviatile	VLF	LF																	R		
E. palustris	LF	F	LC	A															F		
E. variegatum	LA				VLC										F		VLF	LF			
Euphrasia nemorosa	VLO					R			O	O			O			O	O				
Festuca rubra																					LC
Galium palustre	LA	A	LC	F										F					LC		
Glaux maritima															R						
Gnaphalium uliginosum			R																LO		
Holcus lanatus	VLF		LF																		
Hydrocotyle vulgaris	C	A	F	LA	O	O	C	F						LA	F	A	C	LA			
Juncus acutiflorus		LA	F	VLA																	
J. articulatus	LF	LC		O	F	O	F	O	F	F			F	F	F	F	F	F	F		O
J. bufonius					VLO																
J. effusus		O																			
J. inflexus	O	O	O	O	R	R		O	O	F			R	O	R	O	O	O	O	LC	
Lathyrus pratensis	VLO		O				R		VLF					O	VLF		VLF	F	O		
Leontodon autumnalis	LF		F	O	F	F	F	O	O	O			O	O	F	R	O	O	O	F	O
L. taraxacoides	VLO				O	O	O	O	F	O			F	O	F	O	F			F	F
Linum catharticum																					F
Littorella uniflora	VLA																				

	1	2	3	4	5	6	7/8	9	10	11	12	13	14	15	16	17	18	19	20	21	P
Lolium perenne	VLO																				
Lotus corniculatus	VLC				O	O	O		O	LF			O		O	F	O	F		F	O
Lycopus europeus	R																				
Lythrum salicaria		F	O															O			
Medicago lupulina			R	R										O							
Mentha aquatica	A	C	LA	O	F	C	F	C	C	C			F	C	F		O	F	C	F	
Myosotis caespitosa	LA	O	LF	R			R		R	VLF									O		
Odontites verna	VLO		O																		
Parnassia palustris	R				O	O	O		R	O			O		LF	C	F	O		O	R
Phalaris arundinacea					R						LA										
Phleum pratense	VLO														R			R			
Phragmites australis	O	R	R																		
Plantago lanceolata	R		VLF		R			O								O				O	
P. major	LF		O		R												VLF			O	
Poa pratensis	VLF																		LO		
Prunella vulgaris																		O			
Polygonum persicaria			R	R						R											
Potentilla anserina	F	LF	O	A	F	O	LC	F	F	F	C		F	LC	O	F	F			A	O
P. reptans	O		O	O	R			LF													
Pulicaria dysinterica	O		O			R	O		C	C			LF		R		R				R
Ranunculus acris	R																				
R. flammula	O	O	O	O	R		O		O	O				O			R	O	O		
R. repens	LF	VLC	F	LF	O	O		O	O	O				O	O	O			O		
R. sp.	O	LF																			
Rhinathus minor	LO		LO					O	VLO									O	VLO		
Rubus caesius	LF	O	R	O	R		R	O			C			O	R			O	O	O	
Rumex crispus	O	O	O	O	R									O			VLO	O	O		
Sagina nodosa	LO																LC			R	
Salix alba		R																			
S. cinerea	LF	LA	O	R		R	R	R			R			O			R	O	O		
S. fragilis							R							R							
S. x friesiana	LF	F		VLA			O											O	O		
S. purpurea		R																			
S. repens	C	C	O	LC	O	C	F	C	O		A		LC	O	F	C	C	A	C	A	O
Samolus valerandi	F				LC	LC	C		O	F			O		O						
Scirpus maritimus	VLF	LF					VLF							VLC	R						
Senecia jacobaea	VLO								R												
Trifolium dubium	VLO																				
T. pratense	VLO																		VLO	VLC	
T. repens	VLC	LC	LF		O		R		O	O			O		VLA		O	LC	LF	R	O
Tripleurospermum maritimum																	R				
Veronica anagallis-aquatica			O																		
Vicia cracca	LF	O	LF	F	O	O	F	F					O	F	R			F	O		