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Studies on the ecology of Littorina Obtusata

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STUDIES ON THE ECOLOGY OF *LITTORINA OBTUSATA*

by

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ABSTRACT

The polymorphic, seaweed-dwelling intertidal prosobranch gastropo *Littorina obtusata* was studied at a sheltered shore in North Wales from March 1975 to October 1977. Shell shape changes with size, assists camouflage, and resists crab predation; there is no sexual dimorphism. Sex ratio rises with increasing size to a 20-30% excess of males in small adults, then declines below unity in the largest adults. Juvenile and adult shell colour morph ratios fluctuate with time and over short distance Morph proportions change substantially with age. There is no vertical migration.

Population size frequency structure is usually trimodal. Adults constitute a stable peak at c. 14 mm and account for 50-60% of the populati The rest consists of two actively-growing juvenile modes representing two year classes; recruitment is broadly continuous, with a winter peak. Probability-paper analysis suggests that juveniles grow steadily through winte then accelerate in spring to reach adult size in late summer or autumn approximately 18-24 months from hatching. Growth rate is approximately 0.12 mm/week.

Fifteen mark-and-recapture batch-tagging programmes using two or more 1-mm shell size cohorts provide size-specific and seasonal mean growth rates. Growth is fastest in early spring and slowest in late summer and autumn. Mean growth rate varies threefold with size, increasing from 6 mm to approximately 0.03 mm/day at 8.5 mm, then declining steadily through 14.5 mm. Differences between adult sexes are slight. Mean growth patter approximates to the von Bertalanffy equations. Survivorship is independen of size (and, in adults, sex) and unlike growth does not vary predictably with season.

Abstract

Two individual-numbering capture-recapture programmes reveal no differences between male and female growth patterns, growth rates, or survivorship. Individual growth is not always asymptotic, and may proceed in widely-separated steps. Size does not necessarily indicate age. Similar-sized snails growing concurrently and together may differ sevenfold in von Bertalanffy growth parameter k (c. 1×10^{-3} to 7×10^{-3} days^{-1}) and by more than an order of magnitude in growth rate (c. 2×10^{-3} to 3×10^{-2} day). Lifespan is three years or more.

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It is a pleasure to thank all these friends and colleagues.

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Faunists, as you observe, are too apt to acquiesce in bare descriptions, and a few synonyms: the reason is plain; because all that may be done at home in a man's study, but the investigation of the life and conversation of animals, is a concern of much more trouble and difficulty, and is not to be attained but by the active and inquisitive, and by those that reside much in the country.

Gilbert White
1 August 1771

for Anita and Jack

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SECTION 1

GENERAL INTRODUCTION

Littorina obtusata (L.) derives its name "blunt" from its very reduced spire. This small, rounded, inconspicuous prosobranch occurs in the mid- to upper intertidal fucoid algae belt, extending in general from Fucus spiralis (L.) at about MHW down through Ascophyllum nodosum (L.) Le Jol. and F. vesiculosus (L.) to F. serratus (L.) at about MLW.

The recent discovery that L. obtusata at Roscoff (Brittany, France) is composed of sibling species L. obtusata sensu stricto and L. mariae Sacchi et Rastelli 1966 was originally based on penis anatomy and population size frequency distributions, but has been confirmed elsewhere on many grounds including radular morphology, reproductive anatomy, enzyme polymorphisms, shell and body colour polymorphisms, shell shape, and vertical distribution (Sacchi 1969; Reimchen 1974; Goodwin & Fish 1977; Goodwin 1978; Wilkins & O'Regan 1980). Much previous work must therefore be disregarded, except where sampling details etc. permit confident species identification. Unfortunately some investigators - particularly in North America - still combine these species.

Consequently, L. obtusata's geographic distribution is not yet re-established. L. obtusata sensu lato, however, extends from the Mediterranean and Europe to New England via Norway, Britain, Iceland, Greenland and Labrador; it seems reasonable to expect little change for L. obtusata s.s.

The sexes are separate but cannot be distinguished by shell morphology. L. obtusata breeds throughout the year at many sites, normally depositing capsules containing more than 100 eggs directly onto the seaweed. *A. nodosum* fronds live from five to fifteen years, and holdfasts for decades (Schonbeck & Norton 1980b). Development time varies considerably with season (Guiterman 1971). Hatchlings are miniature crawling adults; there is no planktonic dispersal stage. Larval development and metamorphosis are fuelled by neutral lipids (Holland *et al*. 1975). Although hatchlings can feed on other algae such as *Chondrus crispus* Stackh. (Underwood 1973), they normally remain on the fucoids.

The fucoid algae provide *L. obtusata* with food, shelter, and the background for its remarkable camouflage. Fucoid distribution is affected by physical factors such as dry weather and wave action (Schonbeck & Norton 1978, 1979). *L. obtusata* is absent from shores lacking these plants. At high water, the flotation bladders of *A. nodosum* and *F. vesiculosus* lift the fronds free of the substratum. At low water, the fronds lie several layers deep, providing a damp refuge; the buffering role of fucoids was demonstrated by Daguzan (1976b). Any disturbance of the algae at low tide causes many *L. obtusata* to release their grip, falling deeper into the weed. This response may confer protection from bird predators but has not been studied experimentally.

Winkle distribution varies from shore to shore according to splash, wave exposure etc. *F. spiralis* dries out very rapidly when emersed (Schonbeck & Norton 1980a), so its *L. obtusata* populations tend to be greater where it remains damp at low tide. *L. obtusata* may overlap with *L. mariae* in the mid- to lower intertidal, for instance on *F. vesiculosus*, and over a wider vertical range where wave action dislodges and transports either species. *L. obtusata* tends to be sparse on *F. serratus* supporting dense *L. mariae* populations, but the mechanism setting the lower limit is unknown. Although food supply would appear to be unlimited, the possibility of competition with *L. mariae* cannot safely be ruled out until food requirements are studied closely (cf. Carter *et al*. 1979; Sacchi 1969). The siblings may differ in physiological tolerances (Sacchi 1969; Sacchi & Rastelli 1966).

L. obtusata may coexist on British beaches with *L. mariae*, *L. littorea* (L.), and members of the *L. saxatilis* Olivi species complex (Heller 1975a), especially *L. rudis* Maton. Penis morphology appears an important species isolating mechanism, particularly where food is believed to be similar (Heller 1975a), yet only *L. obtusata* and *L. mariae* occur in any number on the fucoid fronds.

L. obtusata is a reasonably convenient experimental subject. Although sampling is impeded by camouflage and algal structure, relatively few are concealed beneath stones, in deep rock crevices, inside barnacles etc., so mark-and-recapture studies are feasible. The absence of planktonic dispersal and of subtidal populations facilitates genetic studies and investigations of adaptation to local conditions. Several discrete shell and body colour varieties ("morphs") exist. *L. obtusata* remains active throughout the year and grows to shell diameter 10 to 20 mm depending on site. Adults may live for several years.

Brief informal taxonomic synopsis (see also Bequaert 1943; Knudsen 1949; Heppell 1974; Sacchi & Rastelli 1966)

Phylum Mollusca
  Class Gastropoda
    subcl. Prosobranchia
      Order Monotocardia
        subo. Mesogastropoda (= Taenioglossa)
          superf. Littorinaceae
            Family Littorinidae
              Littorina Férussac, 1822
              genotype: Turbo littoreus Linné, 1758
                L. obtusata (L.)
                types: Turbo obtusatus Linné, 1758
                  Nerita littoralis Linné, 1758
                  both at Linnaean Society, London
                synonyms include:
                  L. obtusata var. littoralis (L.)
                  L. littoralis (L.)
                  L. aestuarii Jeffreys
                  L. fabalis Turton
                  L. palliata Say
                split into:
                  L. obtusata sensu stricto, and
                  L. mariae Sacchi et Rastelli 1966

References before 1966, and often thereafter, may involve a mixture of these two species, especially if specimens were taken from F. vesiculosus or F. serratus. Shell morphology can become virtually indistinguishable in regions of substantial overlap on some shores: soft anatomy must be used.

Literature survey

L. obtusata s.s. literature is sparse. Appropriate references are discussed throughout the text. The following is a brief summary and evaluation of the more extensive contributions to date.

Sacchi and Rastelli recognised L. mariae, providing diagnoses in Latin and French (Sacchi & Rastelli 1966). Sacchi subsequently extended this work (e.g., Sacchi 1967, 1969); few of his papers are in English. Guiterman (1971) studied L. obtusata in North Wales. His strongest data concern fecundity, weight growth, and parasitic trematode infestation. Most of Bray's (1974) mobility experiments were brief and small-scale. Daguzan (1976a,c) investigated French L. obtusata but his papers are rather vague and it is difficult to accept many of his conclusions as published. Goodwin (1978, 1979; Goodwin & Fish 1977), working independently of the present author, described general population structure and thoroughly examined the reproductive biology of both sibling species at Aberystwyth (Wales), extending species diagnostic characteristics particularly for females.

The outstanding communication to date is the Ph.D. thesis of Reimchen (1974). A detailed study of colour polymorphism geographically, vertically within shores, and especially in relation to immediate (plant) background colour, together with brief breeding and predation experiments and a survey of shell shape which could vary astonishingly over very short distances, led him to conclude that each species' shell colour polymorphism is maintained by disruptive Natural Selection exerted through visual predation. Smith (1976), working independently with L. obtusata only, reached similar conclusions from less detailed evidence. Reimchen has so far published only his L. mariae results (Reimchen 1979), but many of the same concepts apply to L. obtusata.

Therefore the basic papers in English to date are those of Goodwin and Reimchen. Reimchen's thesis is recommended.

Aims

Although geographic surveys and brief comparisons between sites had established general population structure, less was known of its development with time, particularly with regard to relative frequencies of the sexes and shell colour varieties. Growth and survivorship were not reliably known.

One population was studied in detail. Intensive sampling from April 1975 to October 1977 was combined with mark-and-recapture programmes, allowing three growth measurement techniques to be evaluated: population size frequency analysis (the only method used hitherto), 1-mm cohort tagging, and number tagging. Survivorship was estimated from tagging results; number tagging revealed individual variation in adult growth patterns and rates.

Presentation

After a brief study site description and summary of methodology, shell shape is discussed in relation to predation, mimicry, and streamlining. Section 5 reports significant differences between juveniles and adults in shell colour morph frequencies and fluctuations with time at three sites.

Their importance is evaluated and colour polymorphism is considered in relation to camouflage, physiological adaptation, and pleiotropy. Population structure is then described, and growth is estimated from its changes with time. Section 7 concerns sex ratio over a wide size range but with particular emphasis on adults.

The subsequent chapter reports growth as determined by mark-and-recapture batch tagging using very narrow size ranges. A modified von Bertalanffy growth equation is used. Results are compared with those from size-frequency analysis. Growth rate is shown to vary seasonally and with size. Composite growth curves are constructed and are found to agree satisfactorily with field data.

Section 9 discusses the survivorship of these batches and evaluates dispersal, mobility and mortality factors. Between approximately 6 and 14 mm survivorship - unlike growth rate - is shown to be largely independent of size (and, in adults, sex) and not to vary predictably with season.

Section 10 presents results from mark-and-recapture individual tagging. Final size and life span are considered. The validity of using mean sizes in growth equations is discussed.

The final chapter is a general discussion.

Text tables generally summarise voluminous raw data. Fuller information and lengthy tables are presented as Appendix Tables. All queries should be sent to the author's permanent address: 935 - 47th Ave., Lachine, P.Q. H8T 2R4, Canada.

SECTION 2

SITES STUDIED

Littorina obtusata sensu stricto is the most numerous gastropod amongst Ascophyllum nodosum high in the midlittoral. Lower and on Fucus vesiculosus it co-occurs with Littorina mariae which it may locally resemble. To permit considerable repeated sampling without replacement, minimal confusion with L. mariae, and adequate searches for tagged animals, a site must support a large population, allow plenty of time between immersions, and ideally be close to the laboratory.

The Isle of Anglesey is separated from the Welsh mainland by the narrow, sheltered Menai Straits. The mainland shore near Bangor (map, Figure 1), although a brief walk from the University, is a rather unattractive beach frequented chiefly by strollers well above the strand line and by bait-digging fishermen who displace mid-shore rocks and small boulders and dig holes further down the shore. The beach is otherwise little disturbed as it is unsuitable for bathing.

A low wooded hill supported on layered sedimentary rocks, some very thin and weathering into small rubble, the others more solid and breaking into slabs and cobbles, gives way abruptly to the shore. Substratum and profile vary, but for about 100 m laterally the mid- to upper shore is a gentle slope, pebbled and cobbled over a firm silt. Surface silt comes and goes and may be locally plentiful (Appendix Table 1). Rocks and boulders support long thick fucoid algae: at midshore F. vesiculosus blends into A. nodosum which predominates higher, perhaps through successful competition (Dalby et al. 1978). Other algal species are also present in

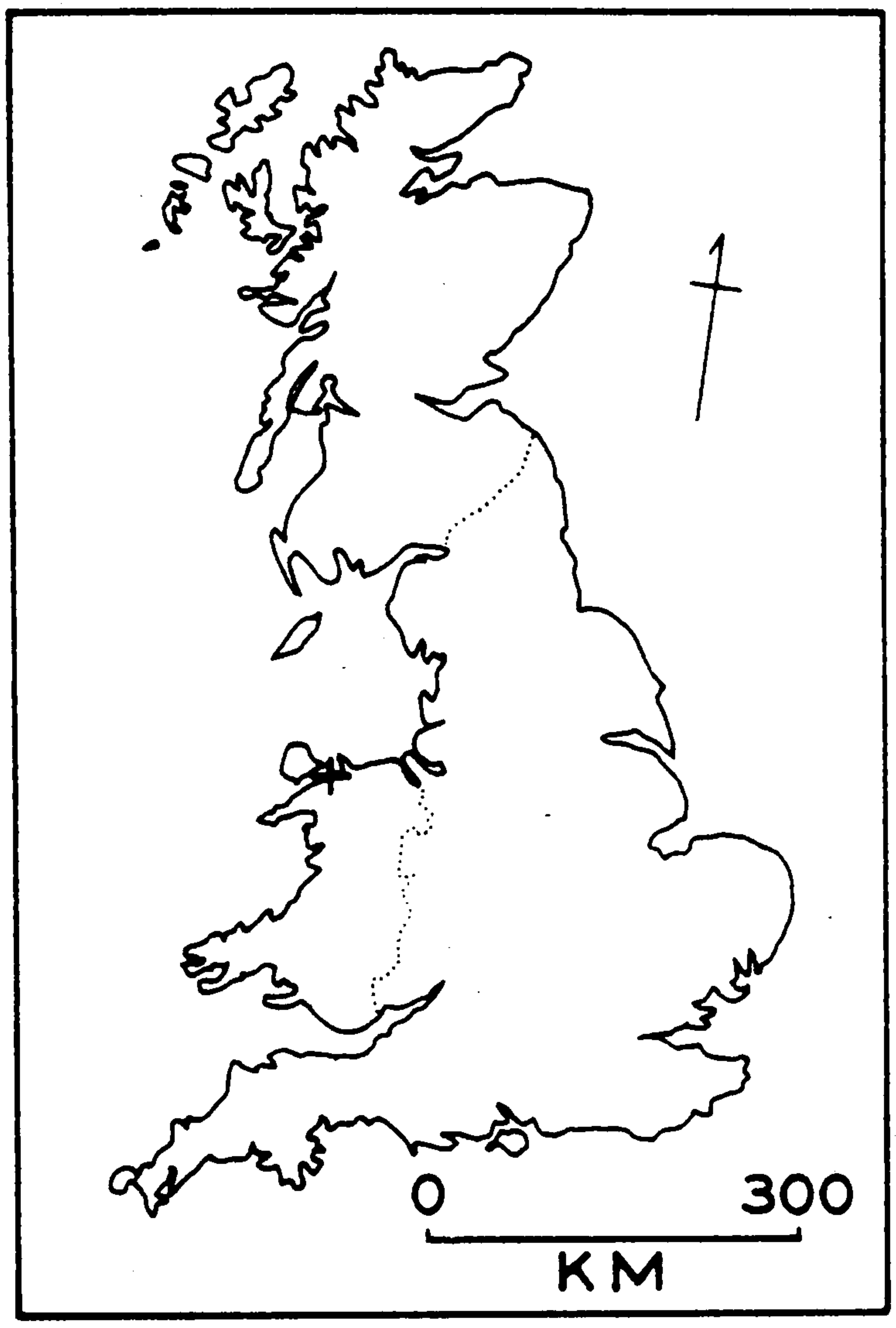


Figure 1. Sketch outline of Great Britain, omitting some Scottish islands. Cross indicates sampling location near Bangor, North Wales.

their usual tidal order. The shore faces generally westwards and receives full afternoon sun. A raised sand-and-gravel bar and wide flats moderate wave action except in gales, when weed-bearing rocks to about twice the size of a housing brick can be moved. The shore is stable and very sheltered, ranking 7 on Ballantine's (1961) exposure scale.

An irregular rock outcrop approximately 1.5 x 5 m covered exclusively in long, clean, healthy A. nodosum was designated site A: national grid reference SH 572 726. To either side stretched luxuriant A. nodosum, often more than 1.3 m long, supported on boulders and rocks interspersed with coarse grit. Downshore a similar substratum, although with increasing silt, anchored a large band of mixed A. nodosum and F. vesiculosus. These lateral and downshore weed bands were designated sites L and D respectively.

Site A became exposed approximately 4.5 hours before, and covered 3 hours after, predicted low tide using the Menai Bridge correction (e.g., Laver 1980), allowing 7.5 hours unbroken sampling on a calm day. Site D was surveyed at 15.5 m from site A, centre-to-centre, the vertical distance being 1.175 m and the slope7.60% (4° 21'). Preliminary surveys established that L. obtusata numbered from 200 to more than 500 per m^2 over more than 1000 m^2 of fucoid-covered substratum.

SECTION 3

SUMMARY OF METHODOLOGY

Sampling

The primary study site A was a small rocky outcrop covered with dense Ascophyllum nodosum, high in the intertidal of a very sheltered shore on the Menai Straits within walking distance of the laboratory (Section 2).

Outcrop A was systematically stripped of L. obtusata at approximately monthly intervals from April 1975 to October 1977 (dates and notes, Appendix Table 1). These winkles were not replaced. Except for the smallest, they were net immigrants from the nearby extensive weed bands D and L from which regular comparison samples were taken at similar intervals from September and November 1975 respectively (Appendix Table 1). Preliminary studies had established that replicable size frequency distribution, sex ratio and morph ratios required approximately 350 snails. Standard sample size was 500.

L. obtusata lives amongst tangled fucoid fronds. Sampling is tedious and inefficient when the weed is dry. Snails are mobile and more readily seen when the weed is damp and the light diffuse. Adults are readily shaken from wet fronds but juveniles tend to be found in branchings or inside damaged air bladders from which they may only be removed by hand. Hatchlings and very small juveniles are also held in place by surface tension. Consequently any sampling technique that seeks to avoid hand-picking will produce an unrepresentative sample. (The exception, lengthy immersion in fresh water, kills the snails and damages the habitat.)

Small snails are disproportionately overlooked even in hand-picked samples. Furthermore, colour polymorphism provides effective camouflage, especially when the weed bears yellow fruiting bodies: different morphs have the advantage against different backgrounds (discussion and photographs, Reimchen 1979).

Samples were begun immediately the tide retreated, by preference on still, humid overcast days. One frond at a time, starting at the holdfast, weed was examined by eye and by touch, then shaken, run through the fingers and laid aside. Snails were put into shaded containers with fresh damp A. nodosum. Sampling continued until a desired area had been cleared or a desired number had been caught, but always until the substratum originally beneath the fronds had been exposed and examined for dislodged snails.

When more alga had to be cleared than one tide would permit, cleared weed was weighted with flat rocks to reduce repopulation from nearby. Especially in silty areas, snails rarely crawled directly over the substratum, but moved from weed to weed at low tide. The next day the cleared weed was quickly checked, then sampling continued.

L. obtusata numbers are not meaningfully expressed per m^2 of shore. Even numbers per kilogram or per m^2 weed surface depend upon branching and weed reproductive state; snails of different ages and colours often inhabit different parts of the weed. Numbers collected in the first hour ranged from approximately 100 (November 1976, site L) to 750 (April 1976, site D): numbers per hour are strongly influenced by weed humidity and ambient temperature. Density is considered too unreliable to present usefully (data on request).

Sample analysis

Shell shape parameters were investigated and size was represented by shell length L (Section 4), the maximum diameter in the plane of the substratum, measured to the nearest 0.05 mm with dial vernier calipers. Snails were sorted into 1 mm size classes 3.0 - 3.95, 4.0 - 4.95 mm and so on. Snails smaller than about 5 mm were likely under-sampled. A typical sample had snails in classes 3 to 16. Classes 0, 1 and 2 were excluded from analysis. Separation of sample size-frequency distribution modes followed a modification of Cassie's (1954) probability-paper technique (details, Section 6).

Wetted shells were examined in transmitted and reflected light under a dissecting microscope and were sorted into colour morphs citrina (yellowish), olivacea (green), and light or dark reticulata (dark network on light or dark background), the only morphs occurring at Gorad (Section 5). Growing shells have fragile, chisel-edged lips which are yellow in plain morphs but may show reddish hatch-marks in reticulate snails.

The sexes are separate. Sex ratio is the positive decimal fraction obtained by dividing the number of males by that of females. Adults gripping some substratum could be sexed live by gently raising the shell to reveal the penis (Section 8). A male was defined by having a recognisable penis, in whatever state of development, although sexual differentiation is not necessarily complete in very small snails (Section 7). Four consequences affect methods. First, L. obtusata juveniles are most accurately sexed dead (see below). Second, juvenile sex ratios may be biased in favour of females. Third, any phenomenon such as penis shedding (reported for L. littorea, e.g. by Grahame 1969) or parasitic deformities would bias sex ratio likewise: the former has not been observed in L. obtusata; the latter was negligible at sites A, L and D. Fourth, some female L. obtusata and L. mariae may be confounded, especially when immature, unless shell shape or ribbing differs (Reimchen 1974); males are easily separated by penis anatomy.

Snails were killed in boiling water. As soon as they began to extrude, they were drained, quenched in cold water to limit "cooking", drained again, and preserved in 70% by volume industrial spirit/fresh water. When firm enough to handle with forceps and needle, they were partly extracted and the mantle was turned back. Within any sample, the smallest female size used in calculating sex ratio was the lower limit of that 1 mm class containing the smallest male - usually 3.0 mm.

Littorina mariae was scarce at sites A and L. Among males, L. mariae amounted to 1% or fewer, including those easily recognised by shell characteristics. At site D, this proportion increased to about 5%. Recently, Goodwin has advocated ovipositor pigmentation as a reliable guide for females (Goodwin & Fish 1977; Goodwin 1978, 1979).

Much routine sample analysis was performed on CDC 7600 computers maintained at the University of Manchester Regional Computer Centre and connected to the UCNW computer centre, using SPSS: "Statistical Package for the Social Sciences", marks 6.0, 6.5 and 7.0 (Nie et al. 1975; UMRCC 1980a,b). Briefly, SPSS is designed for survey result analysis, and embodies a wide range of sorting and analytic techniques using simple instructions. It is useful for performing standard statistical routines on large samples. Except where stated otherwise, any reference to sample statistics implies that they were computed from the entire sample by SPSS.

Tagging

Individual and group survivorship and growth were studied by mark-and-recapture techniques. Time away from shore was minimised. Snails were transported and kept on cool damp fresh A. nodosum.

Survivorship was expressed as a linear regression, of the natural logarithm of percent known to be alive vs. days elapsed from release. The remaining proportion were dispersed or dead. Dead snails or empty or broken shells were sometimes recovered. Because the date of death could not usually be established as reliably as date alive, emphasis was placed on living snails (details, Section 9).

1. cohort tagging

Snails within a 1 mm size class were given identical coded paint marks specifying group and release date (details, Section 8). Those smaller than 6 mm could not be tagged. Cohorts having mean size approximately 6.5 and 9.5 mm were released repeatedly between February 1976 and July 1977 to determine seasonal variations in growth from standard sizes. These were occasionally supplemented with other coded sizes, forming "extended cohorts" growing concurrently; adults were sexed live and coded separately. Shell lip thickness and profile identified growing snails (evaluation of technique, Section 10). Only they were used when calculating growth rates. A modified von Bertalanffy growth equation was used in comparisons. Field growth curves could be constructed from one cohort, or from the simultaneous growth of many sizes thereby removing seasonal fluctuations. Results were compared with estimates from the probability-paper analyses.

Mean-size growth rates may be criticised on mathematical grounds. Also, they may be distorted by size-specific mortality etc., and in adults by temporary or permanent cessation of growth. Accordingly, adult individual tagging supplemented cohort results.

2. resin tagging

In October 1975, tiny home-made flexible numbered plastic tags were affixed to adults larger than 13 mm with quick-setting translucent epoxy resin (details, Section 10). Individual records revealed individual growth rates and non-uniform growth patterns. Results could also be combined and treated as cohorts.

3. paint tagging

In February 1976, individual tagging was improved. Different paint colours represented digits 0 through 9. Three dots encoded serial numbers (details, Section 10). 12.0 to 12.95 mm adults judged to be growing were tagged. Individual records showing distinguishing marks were maintained and treated as before.

The scarcity of this size class resulted in an extended release period that complicated analysis. Certain dates were grouped. Standard sample dates were defined. Such recoding was only desirable when individual results were combined for treatment as cohorts, e.g. for survivorship curves.

Tag loss was slight. Such individuals were recognised by the sandpapered region to which the tag had been applied. Paint loss was seldom complete. Traces were evident under the microscope although care was needed to avoid confusing colours that in larger spots were quite distinct. Tags partially lost by shell damage were very rare and restricted to individually-numbered shells, which could be identified by a process of elimination.

SECTION 4

SHELL SHAPE

Introduction

Definition of shell shape depends as much on the investigator's needs as on shell form. Numerous angles, indices and ratios have been used (e.g., Crothers 1975; Goodwin & Fish 1977; Guiterman 1971; Heller 1975a and 1976; Hughes & Elner 1979; Kitching & Lockwood 1974; Kitching et al. 1966; Knudsen 1949; Miller 1974; Newkirk & Doyle 1975; Palmer 1980; Raffaelli 1978a; Reimchen 1974; Sacchi 1969; Spight 1973; Vermeij 1973a, b and 1974; Zipser & Vermeij 1978), including spire angle, length from apex to base of columella, body whorl diameter, and aperture dimensions.

The definition used here does not arise from attempts to describe the shell mathematically. Rather, its measurements may be taken rapidly and reliably with ordinary dial calipers: shell length L, height H, columellar length W, and lip thickness T (Figure 2).

Shell length is maximum shell diameter in the plane of the substratum, and shell height the bulge above it. Columellar length is a traditional parameter often called shell length or height. Lip thickness must not be confused with overall shell wall thickness.

Some appropriate combination of L and H would serve as an index of area exposed to shear forces exerted by water flowing over the substratum (normally a fucoid frond): especially in areas of rapid current, selection could be expected to favour shapes minimising the likelihood of a winkle being dislodged and swept away (cf. Miller 1974). Shell ridging

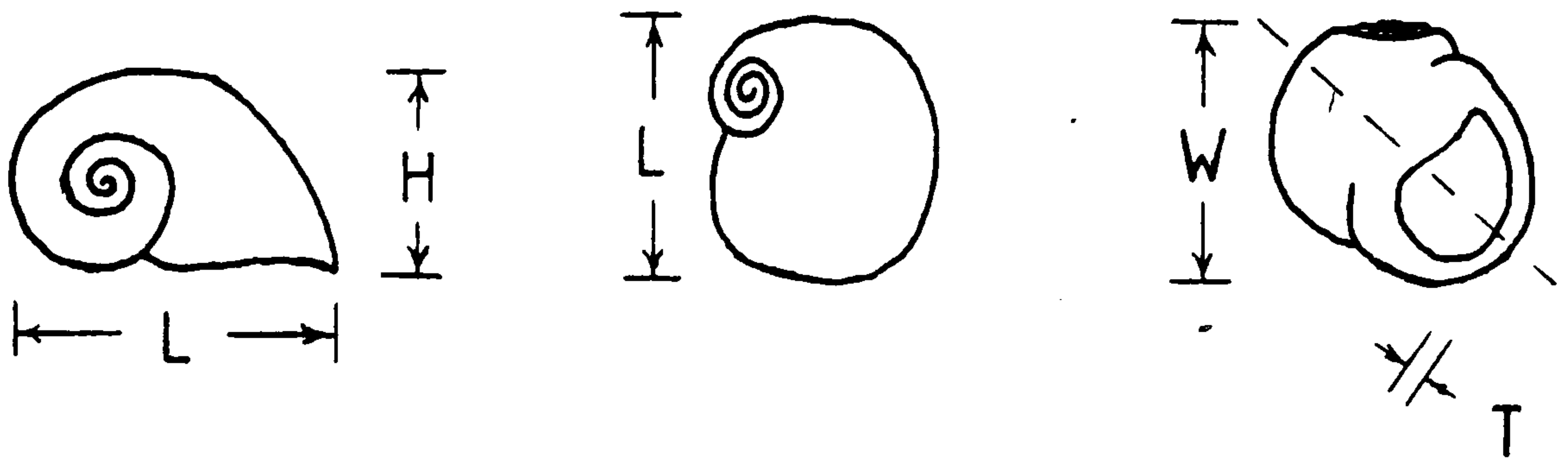


Figure 2. Shell measurements. Shell shape parameters described in text. Sketches, not to scale. Left sketch, lateral view; middle sketch, plan view; right sketch, aperture view. L, length. H, height. W, columellar length. T, lip thickness. Dashed line shows approximate axis of L.

and channelling (Reimchen 1974) may promote laminar flow over the shell, thus lessening impact or shear (Savage, pers. comm.), but thorough flume trials have not yet been conducted. Although Palmer (1980) considers estimated drag forces to be very weak, his calculations do not allow for currents or wave surges.

The role of foot size and shape is widely recognised, or rather postulated, but careful experimental evidence is still scanty (Kitching _et_ _al_. 1966; Miller 1974). Strong circumstantial evidence is found in the common observation that shell apertures differ in shape within species.

Those in exposed conditions tend to be broader than those in shelter, presumably to accommodate a larger foot, permitting a better grip: Kitching _et al_. (1966), in a brief set of trials, found grip to be proportional to foot area. This may not be the whole story, however. Miller, in her extensive review, remarked considerable intraspecific variation in foot shape depending on exposure.

Methods

Hatchlings (approximately 0.45 mm diameter) and tiny juveniles were measured under a binocular dissecting microscope fitted with an eyepiece graticule.

In shells larger than about 2.5 mm, all parameters were measured to the nearest 0.05 mm using dial vernier calipers. Length, height and columellar length were recorded only to the nearest 0.1 mm. Uncertain measurements were repeated three or five times and the mean was recorded. Because the rounded edge of the lip was considerably offset from the base of the columella, W was the least convenient measurement. Care was needed to avoid crushing the thinnest lips. T was measured at the centre or, if damaged, elsewhere if possible. Obvious irregularities were avoided. Some adults had a thickened "bead" at the edge of the lip, causing an overestimate.

Results

i. L. obtusata

Variation in replicated measurements of L, H and W was usually ± 0.1 mm, and ± 0.05 mm for T. Very many shells gave unvarying values of L, H and T.

To determine relationships among these parameters, measurements of 1623 snails ranging from 4 to 18 mm collected in July 1975 were analysed with SPSS (Nie et al. 1975; UMRCC 1980). L and H were very highly significantly correlated ($R^2 = 0.97$, $P < 0.0001$, Table 1), as were L and W ($R^2 = 0.98$). The scatter diagram (Figure 3) shows that the smallest shells had a higher profile than that maintained by larger snails - in effect, they were more globular - but the relationship between W and L was not curved.

Lip thickness did not increase as predictably with shell length ($R^2 = 0.64$). If mean lip thickness for each 1 mm length class is plotted against class midpoint (Figure 4), mean T initially increases, then levels-off from about 10 to 13 mm, then rises again. The male pattern is less regular than the female, but both are very similar. Consequently, a linear regression gives an unconvincing fit despite very high statistical significance (Appendix Table 14). Lip thicknesses were not necessarily normally distributed within shell length classes below about 9 mm, so the standard deviations quoted for small shells are approximations.

Irregularly-thick lips were common in "notched" shells, i.e. where a V-shaped piece had been broken away and replaced. Raffaelli (1978a) illustrates the same damage, similarly repaired, in L. rudis Maton.

Figure 3. Scatter diagrams of shell height H and columellar length W ("width") against shell length L. Parameters as shown in Figure 2. Data are 1623 L. obtusata ranging from 4.0 to 17.7 mm in shell length, collected in July 1975. Regression lines are shown with 95% confidence intervals: equations are given in Table 1, and are for combined sexes.

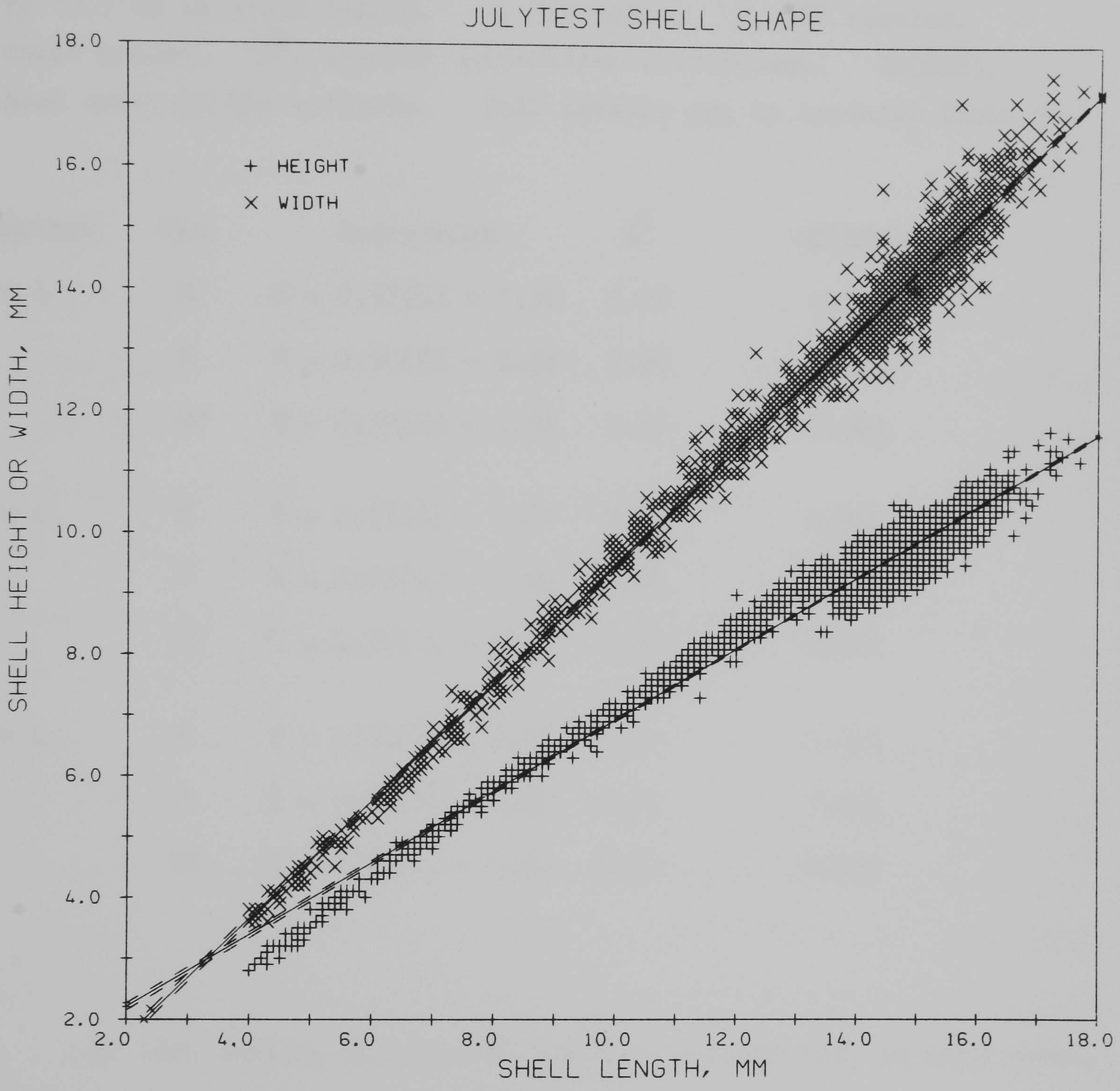

JULYTEST SHELL SHAPE
+ HEIGHT
× WIDTH
SHELL HEIGHT OR WIDTH, MM
SHELL LENGTH, MM
2.0
4.0
6.0
8.0
10.0
12.0
14.0
16.0
18.0

Table 1

Shell shape regressions

Table 1. Relationships of shell parameters illustrated in Figure 2, using July 1975 test sample containing 1623 snails ranging from 4.0 to 17.7 mm in shell length. M, 735 males. F, 888 females. MF, sexes pooled. R^2, squared correlation coefficient. SE(EST), standard error of the estimate. Full details are in Appendix Table 14.

Parameters	Sex	Regression	R^2	SE(EST)
H v L	M	H = 0.57(L) + 1.30	0.96	0.309
	F	H = 0.60(L) + 0.86	0.98	0.285
	MF	H = 0.59(L) + 1.03	0.97	0.302
W v L	M	W = 0.97(L) - 0.21	0.98	0.354
	F	W = 0.97(L) - 0.24	0.99	0.361
	MF	W = 0.97(L) - 0.23	0.98	0.361
T v L	M	T = 0.04(L) + 0.05	0.61	0.093
	F	T = 0.05(L) + 0.04	0.65	0.103
	MF	T = 0.05(L) + 0.04	0.63	0.099

Of 1629 snails, 503 (30.9%) had been notched and, in many cases, repaired. The sexes did not differ in the distribution of shell damage across length classes (250 males, 253 females in 14 length classes: raw Chi-square 20.8 with 13 degrees of freedom, P = 0.076). The similar total numbers of males and females damaged did however differ significantly from the ratio of sample totals, 737 males to 892 females (corrected Chi-square 5.58 with 1 degree of freedom, P = 0.018). (The lack of agreement in sample size with Table 1 and Figure 3 was caused by the necessary rejection therefrom of six misshapen shells.)

Shell lip thickness distributions did not differ significantly between the sexes in any 1 mm length class other than 7 and 12 mm, which were judged unimportant when the data were examined.

Comparable data pooled from 11 samples taken between 24 March and 22 April 1975 gave similar results (Figure 5). Shell lips of 9-15 mm males and females were thinner than in July, but standard deviations overlapped substantially. This difference between samples was most pronounced in length classes 11 and 12 (Appendix Tables 16 and 17). Mean lip thickness was unchanged from 10 to 13 mm. Differences between sexes were trifling. (Some arbitrary values had to be used in this data set. The summarised records grouped all measurements above 1.0 mm: these were assigned an arbitrary value of 1.1 mm as lips much thicker than this are exceedingly rare at this site. Similarly, measurements below 0.45 mm were set equal to 0.35 mm. Consequently, means in classes 3 to 6 are probably overestimates, and the narrow standard deviations inaccurate.)

During preliminary surveys (not otherwise presented), shell shape was also measured in the hatchling to 4 mm range. Individual samples were small. Two replicate samples taken on 2 July 1974 high in the <u>Ascophyllum</u> zone about 200 m NE of standard sampling site A (Section 2) (national grid SH 574 725), gave very similar results for snails up to 2 mm long. Corresponding graphs of H against L and of W against L were identical, and regression equations agreed closely (Table 2). These shells were much more globular than the larger ones in Table 1. The regressions of H on L from

Tables 1 and 2, when applied to a 10 mm long shell, yield heights of approximately 6.9 and 8.0 mm respectively. Large shells had a lower profile than post-hatchlings. In contrast, the relationship of W to L was unchanged. These results agree with the scatter diagram (Figure 3).

Table 2

Supplementary shell regressions

Table 2. Regression equations for some preliminary samples. Shell parameters as in Figure 2. N, number. Range, range of shell length (mm). R^2, squared correlation coefficient. SE(EST), standard error of the estimate. Full details appear in Appendix Table 15.

Sample	N	Range	Regression	R^2	SE(EST)
Gorad <u>obtusata</u>	71	0.53-1.95	$H = 0.80(L) - 0.03$	0.969	0.050
			$W = 0.98(L) - 0.18$	0.974	0.055
Gorad <u>obtusata</u>	74	0.48-1.93	$H = 0.83(L) - 0.05$	0.98	0.033
			$W = 0.91(L) - 0.11$	0.98	0.034
Llanddwyn <u>obtusata</u>	57	2.50-15.7	$H = 0.62(L) + 0.29$	0.99	0.249
			$W = 0.93(L) - 0.22$	0.99	0.361
Llanddwyn <u>mariae</u>	93	3.40-11.2	$H = 0.60(L) + 0.38$	0.97	0.197
			$W = 0.90(L) + 0.07$	0.97	0.276

ii. Comparison with L. mariae

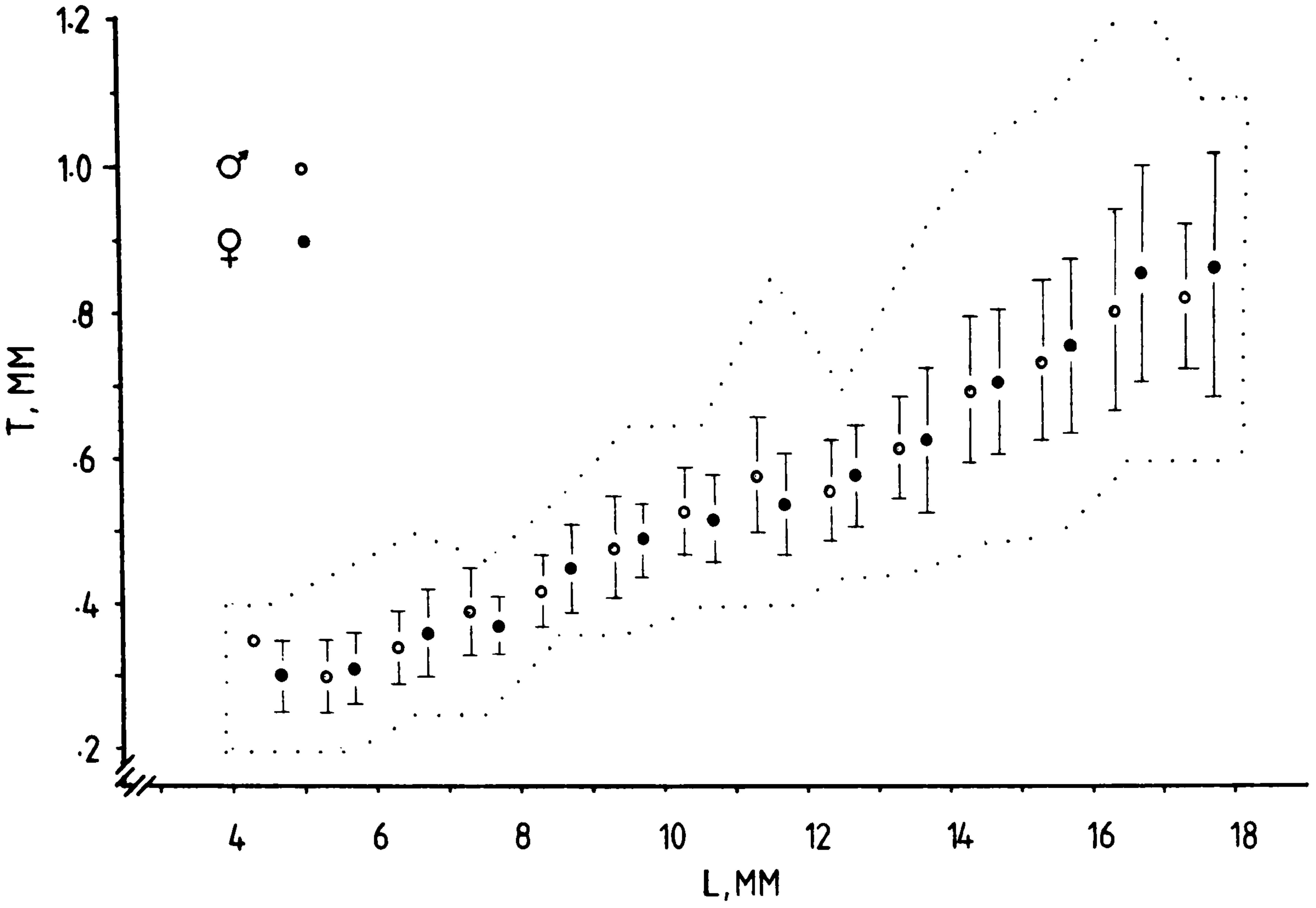
During another preliminary survey, L. obtusata and its sibling species L. mariae Sacchi & Rastelli were sampled close together at Llanddwyn Island, Anglesey (national grid SH 391 630). L. obtusata were taken from Ascophyllum nodosum draped on a steep rock promontory, and L. mariae from submerged Fucus serratus in the small bay it faced. Shells were separated according to the shape and ridging criteria of Reimchen (1974). Ambiguous shells were excluded from analysis.

The regressions of H on L agreed closely (Table 2), and those for W on L differed chiefly in the intercept: predicted values of W converged by about 10 mm shell length.

Shell lips of both species were remarkably thick (Figure 6, Appendix Table 18). Adult L. mariae averaged 0.9 mm, while L. obtusata of that size were about 0.75 mm and adults exceeded 1.2 mm. Such thick shell lips are extremely scarce at Gorad (Figures 4 and 5, Appendix Tables 16 and 17). When the ranges are compared, Llanddwyn Island snails not only grow much thicker lips, but abandon thickness below 0.4 mm at a much smaller size. At Llanddwyn, T may increase logarithmically with L, but low numbers forbid broad conclusions.

Figure 4 (upper). July 1975 shell lip thickness. Mean shell lip thickness in 1 mm length classes, shown plus or minus one standard deviation (data, Appendix Table 16). Symbols are displaced from class mid-point for clarity - males, circles; females, filled circles. Dotted polygon shows combined range of measurements (sexes similar).

Figure 5 (lower). March/April 1975 shell lip thickness. Mean shell lip thickness displayed as in Figure 4 (data, Appendix Table 17). Upper and lower range limits marked * are arbitrary: see text.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L, MM
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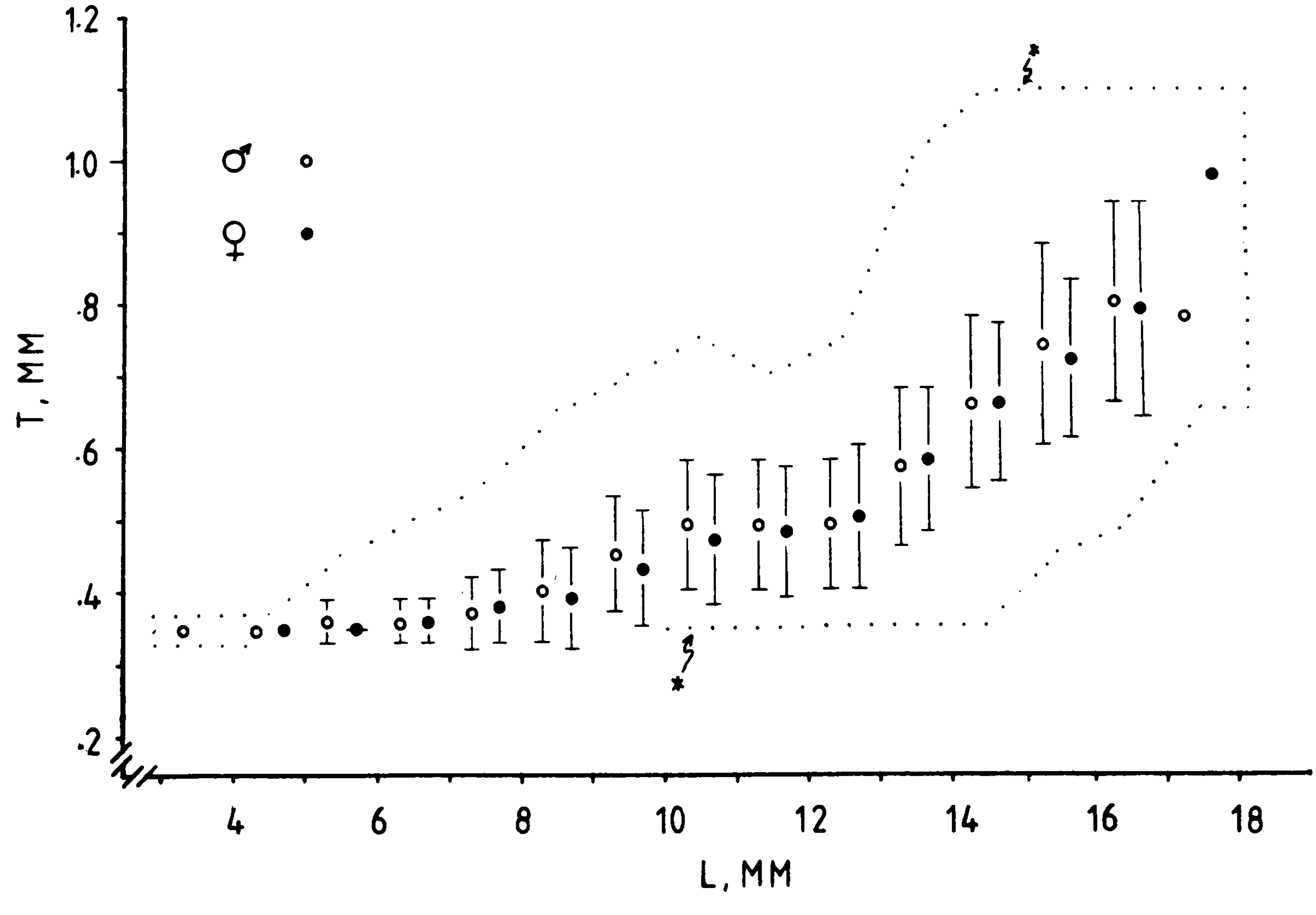
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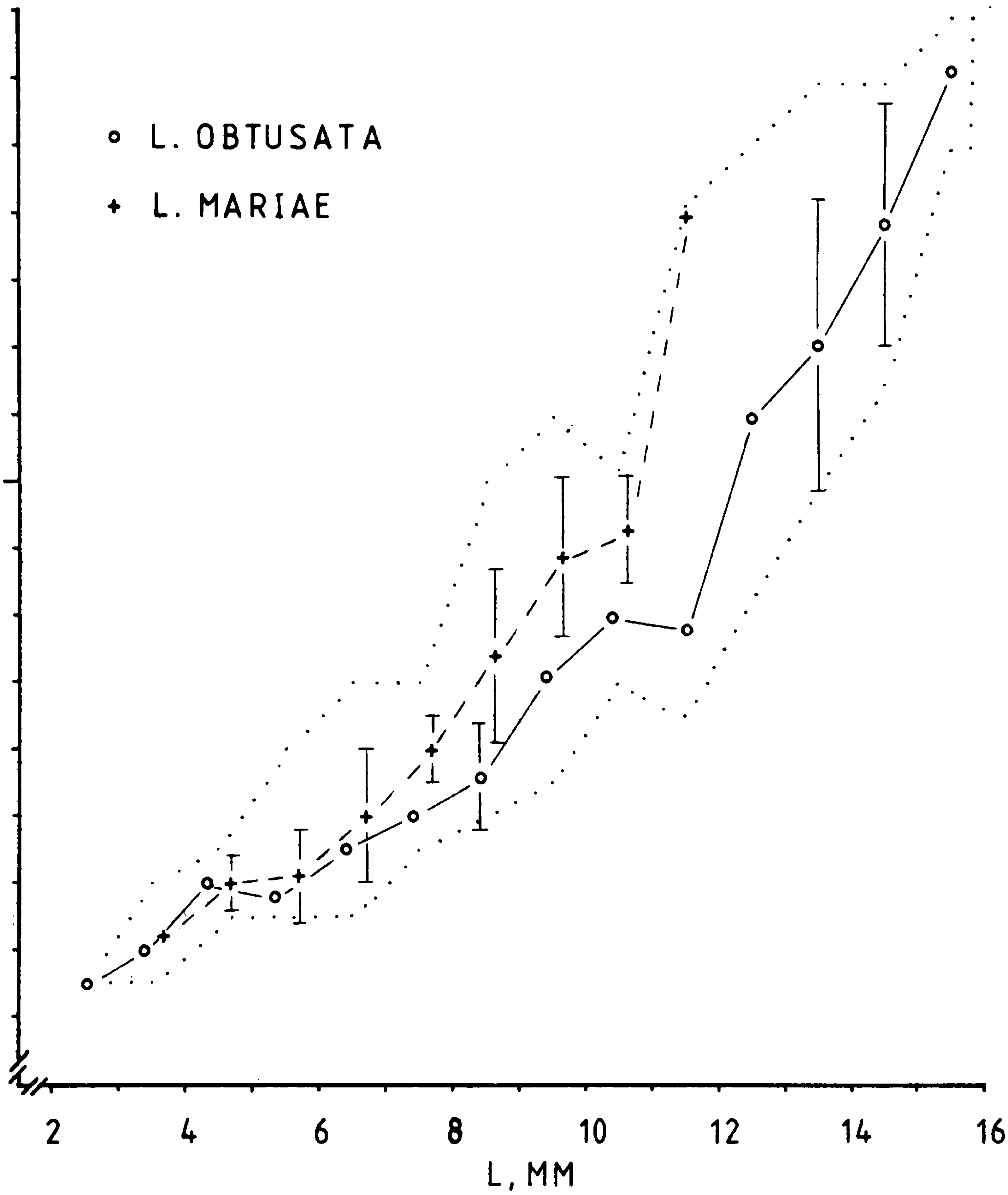
Figure 6. Llanddwyn shell lip thickness. Mean shell lip thickness in 1 mm length classes, shown plus or minus one standard deviation when available (data, Appendix Table 18). Some symbols are displaced from class mid-point for clarity. Solid line, *L. obtusata*; dashes, *L. mariae*. Dotted polygon shows combined range of measurements. Compare Figures 4 and 5.


1·6
1·4
1·2
1·0
·8
·6
·4
·2
T, MM
o L. OBTUSATA
+ L. MARIAE
2
4
6
8
10
12
14
16
L, MM

iii. summary of results

1. Shell shape was defined by length L (maximum diameter in plane of substratum), height H (protrusion above substratum), columellar length W (apex to base of shell lip), and aperture lip thickness T.
2. In a test sample of 1623 snails over the juvenile to adult length range 4 to 18 mm, H and W were very highly significantly correlated with L. Although T was also significantly correlated with L, the relationship was in fact sigmoid: lip thickness increased to length about 10 mm, and again from about 13 mm. Different regressions applied to the more globular hatchlings.
3. Males and females did not differ markedly in shape.
4. Males and females did not differ in pattern of shell damage with size. A higher proportion of males were damaged.
5. In a small sample from Llanddwyn Island, a more exposed site, L. obtusata was shaped similarly to L. mariae, and both species displayed remarkably high values of T. Although L. obtusata appeared more depressed (regression of H on L) at Llanddwyn than at Gorad, the small sample did not justify a detailed comparison.

Discussion

Shell length L was so closely correlated with H and W that these latter parameters were not routinely measured in the bulk of the field work. This relationship was particularly useful because W, while traditional, was so inconvenient to measure. The constancy of shell proportions, once changed from the globular hatchling shape, may imply streamlining, but this needs to be tested properly. Published comments on streamlining tend to be inferential, and the few experimental studies using littorinids (e.g., Guiterman 1971; Struhsaker 1968) are difficult to relate to field conditions and confound streamlining with tenacity. Jones & Demetropoulos (1968) discuss drag and its importance to fucoids and littorinids; *Ascophyllum nodosum* could not tolerate as little as 5 pounds or 2 kg as measured by a dynamometer. Kitching *et al.* (1966) determined that *Nucella lapillus* from more exposed shores clung better because they had big feet: grip per mm^2 foot area remained unchanged. Miller (1974) provides a good review of foot form and tenacity in approximately 300 species from 52 families, but regrettably she has no data on *L. obtusata* or *L. mariae* and has never seen either (pers. comm.). Palmer (1980) distinguishes drag from tenacity and discusses shell shape hydrodynamics clearly, if briefly, restricting himself to standing water. Drag and tenacity would probably be more finely balanced at water speeds experienced by *L. obtusata*.

Littorina obtusata and *L. mariae* of certain colour morphs (Section 5) are splendidly camouflaged, closely resembling the flotation vesicles of *A. nodosum* and *Fucus vesiculosus*. Restrictions on shell shape imposed by this mimicry should be investigated. It might prove difficult to eliminate confounding effects of vesicle streamlining.

Sexual dimorphism was negligible and insufficient for separating sexes. Sacchi (1969) similarly found no difference between the sexes in *L. obtusata*, although *L. mariae* females were larger than males. Goodwin & Fish (1977) confirmed this, although with very small samples, and state that sexual dimorphism in *L. mariae* increases with increasing shelter.

A semantic problem vitiates most published comments, probably including those. Sexual dimorphism, strictly speaking, is a difference in shape between male and female. The careless application of this term to a difference in mean size is confusing, as it can encompass any process affecting the sexes differently (and hence their representation in a sample). Guiterman (1971) found that females outnumbered males in unparasitised "large adults", while males outnumbered females in "small adults"; his results would be much more convincing had he sexed the snails first and then reported the size-frequency distributions. See Section 7 for a more complete discussion of sex ratio.

A size difference is nevertheless meaningful when certain conditions are satisfied. For instance, sampling must be unbiased with respect to sex and size, and where appropriate, samples must be corrected for differential predation or delayed differentiation. These and similar criteria are not likely to be met in a field population, but much can be learned from tagging and culture.

Mollusc shell shape, although broadly genetically determined, may display considerable local variation. The dogwhelk Nucella (Thais) lapillus Gmelin is a classic example of morphological plasticity. Kitching and his colleagues (e.g., Kitching et al. 1966) demonstrated that shells from sheltered sites are more slender, with smaller apertures and stouter walls, than shells from exposed shores. These differences are related to foot size and crab predation. Similar predictable differences have since been described over a wider geographic range (e.g., Crothers 1975; Kitching & Lockwood 1974). Seed (1978) offers the interesting speculation that the tall narrow shells from sheltered sites may not be adaptive as such, but a consequence of growing while maintaining an adaptive small aperture, or that this shape might permit a higher proportion of digestive and reproductive organs, thereby allowing faster growth and greater fecundity than the squat shape characteristic of more exposed shores. Spight (1973) compared several local races of T. lamellosa and concluded that differences in shape of similar-sized animals from different sites were indeed due to environmental effects, and not merely to diet; within sites, shape could also change with age.

Environmental stresses are believed to affect the shape of many intertidal molluscs. Struhsaker (1968) found a balanced polymorphism for extent of shell sculpture in the Hawaiian L. picta, and interpreted this in terms of locally varying substratum and of seasonal weather extremes favouring sculpture extremes (possibly indirectly through genetic linkage to physiological tolerances). Heller (1976) considered between-shore shell shape and size differences in L. rudis and L. nigrolineata to be responses to exposure and crab predation. Newkirk & Doyle (1975) discuss the effects of waves on shell shape in L. "saxatilis" (they did not separate the several species in the complex - see Heller 1975a). Knudsen (1949) examined museum specimens, asserted that L. obtusata's relative spire height increases northwards, and attributed this effect to decreasing temperature, but provides insufficient information on sampling or shell size to ensure that he was not also examining L. mariae. Sacchi & Rastelli (1966), who first separated these species, state that maximum shell diameter decreases southwards in both species as a result of air temperature and from shelter to exposure because of turbulence. Sacchi (1969) confirmed these observations, often with very large samples, although some of his analyses are unclear. Reimchen (1974) found suggestions of two forms within L. mariae differing in shell sculpture and other characters in a manner predictable from microhabitat, but was unable to determine their significance. Finally, Vermeij has embarked on a long series of reviews (e.g., 1973a,b, 1974, 1979) analysing shell shape and attempting to interpret zonation and geographic variation in the light of physiological demands and, latterly, predation.

Goodwin & Fish (1977) extend the diagnostic characters for *L. mariae* originally provided by Sacchi & Rastelli (1966). Columellar length W greatly influences their ratios. The last body whorl is relatively larger in *L. mariae* than in *L. obtusata*, producing the characteristic "stretched" shape of the adult in plan view. Goodwin & Fish further state that mean adult size increases with increasing shelter in *L. obtusata*, and with increasing exposure in *L. mariae*, an issue considered at length by Sacchi (1969).

L. mariae and *L. obtusata* were not compared in detail in the present study. At Llanddwyn Island, shell sculpture criteria (Reimchen 1974) helped to sort a small mixed sample, but ambiguous shells still remained. At Gorad, in preliminary transect surveys (not presented), shell shape was so closely similar, especially in the zone of overlap low in the *Fucus vesiculosus* belt, that separation was only reliable for adult males which have greatly different penis shapes (Sacchi & Rastelli 1966; Reimchen 1974). Regardless of shell size, it is important to preserve the bodies if sorting is by shell characters alone.

Adult snails that have stopped growth have thicker shell lips than those that are still growing. This range extension helps to account for the sigmoid relationship between lip thickness and shell length. The levelling between roughly 10 and 13 mm might relate to metabolic demands at maturity (approximately 12 mm: Sections 6, 7). Alternatively, the cause might be mechanical and/or a matter of growth rate. Perhaps T initially increases with L because low values cannot support the large growing edge or withstand normal wear and tear, while appreciably-higher values would impede growth, but once growth stops a thicker lip is possible. Individual tagging (Section 10) shows that large snails may grow sporadically, so that a thickened lip does not infallibly indicate final size as supposed by Goodwin & Fish (1977) and others. Lip thickness is an indication of growth activity and not necessarily of shell thickness, density, weight or age. In L. rudis however, shell lip thickness is a linear function of columellar length from 5 to 15 mm (Raffaelli 1978a).

Shell lip damage caused by crabs and by impact can be difficult or impossible to separate (Reimchen 1974; Raffaelli 1978a; Hughes 1980). It is hard to say whether the significantly higher damage to males in the test sample is meaningful. Given the similarity between males and females in pattern of damage, this seems unlikely.

Sacchi (1969) associates thick shells with exposure, the opposite pattern to that in Nucella. Shell lips at Llanddwyn, rather more exposed than Gorad, were remarkably thick, and in particular the minima were increased at quite small sizes. In a series of samples at Strangford Lough, Northern Ireland, shells from Carnan Point on the rocky open coast were substantially stouter than those from five sites within the Lough. (Data summaries available on request. Strangford Lough is the large cucumber-shaped inlet at the NE.) The simplest explanation is that rough seas batter the algal fronds against the rock to the detriment of any fragile individuals attached. Physiological considerations cannot be ruled out, however: in colour morph reticulata (Section 5), where presence of the network is governed by a single dominant gene (Reimchen 1974), snails at the most exposed sites have unusually heavily pigmented shells and bodies

(Sacchi 1969).

It seems increasingly likely, however, that shell thickness is greatly influenced by predation. Much recent work has been directed towards predation, foraging strategies, and anti-predator responses. In brief, intertidal snails are particularly vulnerable to attack by certain fish and especially crabs. The fish (Blennius spp.) tend to crush small snails, whose best strategy is crypsis or camouflage; Reimchen (1974, 1979) provides elegant work and a thorough discussion. Camouflage is considered further in Section 5. Crabs Carcinus maenas (L.) may attack shells by (a) crushing them outright, (b) crushing the whorls just below the apex, often removing the apex, (c) inserting the large chela into the aperture and crushing the columella, (d) inserting a chela into the aperture and chipping away the lip progressively, the method depending on crab strength and shell shape (Elner & Raffaelli 1980; Hughes & Elner 1979; Reimchen 1974). Defensive shell features include depressed spires, strong or elaborate sculpture, narrow or elongate apertures, aperture-edge obstructions such as "teeth" or folds, a thick rigid operculum, or thick shell walls (Gibson 1970; Hamilton 1976; Vermeij 1974, 1979; Zipser & Vermeij 1978). Because Carcinus maenas is not a visual predator and will test any shell it encounters, robust shells will be beneficial (Elner & Hughes 1978). Vermeij (1979) discounted Currey's idea that certain types of shell microstructure resist breakage or drilling better than others, but modified his opinion after collaborating (Vermeij & Currey 1980). He pointed out (1979) that concealment and fast juvenile growth might be equally valid responses to intense predation.

It is not clear to what extent the shape of L. obtusata reflects predation by crabs, although the depressed spire seems to cause handling difficulties (Elner, pers. comm.), as opposed to streamlining. Although shell lip notches cannot with certainty be attributed to attack, the frequent V-shaped opercular notches are unlikely to have been caused by blows from stones. At Gorad at least, damaged opercula are sometimes left unrepaired for months, seemingly without effect (pers. obs. from individual tagging).

It is important to remember that field samples necessarily contain survivors, and may reveal little about population variability if selection is intense. For instance, adult shells from a sheltered shore abounding in crabs would misrepresent the true range of shell thickness. Ideally, before any explanation for locally-varying shell shape is accepted, controlled reciprocal transplants (e.g., Kitching _et al_. 1966) or some other appropriate manipulation should be attempted.

SECTION 5

COLOUR MORPHS

Introduction

Littorina obtusata displays a stable shell colour polymorphism. Early workers recognised numerous varieties now known to be stages in a continuum (Reimchen 1974). Some morphs have restricted geographic distributions, discussed in detail in Reimchen's thesis (1974) and by Smith (1976). Of the remaining discrete morphs, four are found at sites A, L and D. Reimchen (1974) describes each at length and provides colour plates. His terminology is simplified for use here.

Citrina: yellow, ranging from very pale straw to rich orange. No markings. (Formerly, extreme examples were considered to be two other morphs, the whitish albescens and the orange aurantia.)

Olivacea: greenish, ranging from light olive to very dark olive green or on some shores dark olive brown. No markings. Light specimens may be confused with citrina bearing greenish epiphytes.

Light reticulata: dark reticulation, sometimes broken into check-marks or zig-zags, on citrina background. This morph is vanishingly rare at sites A, L and D and has therefore been combined with dark reticulata.

Dark reticulata: dark reticulation, sometimes broken, on olivacea or dark brown background. Care must be taken to distinguish this morph from very dark olivacea, especially in thick shells, as the colour contrast between reticulation and background can be slight. Reimchen (1974) suggests that background colour can infuse into the reticulation. Growing shells have lips with fine chisel edges coloured yellow in plain morphs but often showing reddish "hatch marks" in reticulate specimens. (The almost black variety fusca may be an extreme form, but Smith (1976) considers it distinct.)

Very rarely shells showed faint evidence of light or pigmented bands, as found elsewhere in morphs alternata, inversicolour, or zonata (Smith 1976), but none was distinct enough to be so classified. Tagged shells that sustained lip damage occasionally developed a permanent pale band (pers. obs.).

Before L. obtusata and L. mariae were distinguished (Sacchi & Rastelli 1966), investigators confused these species, sometimes calling the former "var. olivacea" and the latter "var. citrina". For this reason the work of Bakker (1960), Barkman (1955), Van Dongen (1956) and others is now best disregarded. Such papers are specially marked in the bibliography.

Reimchen (1974) concluded from laboratory breeding experiments that reticulation was genetically controlled independently of background colour. He also demonstrated that some morphs are reached through intermediate stages in early growth, and cautioned that the scoring of very small individuals may therefore be unreliable. While citrina may change to olivacea and conceivably thence to reticulata, he never observed the reverse. Morph ratios in very small juveniles may exaggerate citrina or underestimate dark reticulata. The degree to which this happens, and the pathways, evidently vary from population to population and thus should ideally be established in each population by rearing large numbers in the laboratory. In the field, the possibility of differential survival forbids inferences from ratios in successive size classes.

Any change in morph ratios with age, however caused, undermines work based on samples including a wide size range. Similarly ratios based solely on adults may be of limited value. At present there is no information on morph-specific fecundity: Smith's (1976) assertion that citrina are more fecund is unfortunately a supposition without experimental basis (pers. comm. 22 June 1976), as is his view that morphs spawn with regard to background colour.

Reimchen (1974, 1979) argues persuasively that colour morphs are adaptive, that - especially among juveniles - cryptic colouration confers protection from visual predation by fish (blennies Blennius spp.), crabs Carcinus maenas (L.), and various shore birds (review, Pettitt 1975).

If so, one expects to find different morph ratios on different backgrounds and at different tidal heights. Reimchen's geographic survey (1974) produced abundant evidence of this, and he found remarkable changes over very short distances where conditions differed. Smith (1976) found changes in proportions with tidal height on transects, and argues that these changes were caused largely by changes among the juveniles. His results are as one would predict from Reimchen's work. They are also as expected if - particularly where passive dispersal by wave action is important - juveniles are more sedentary than adults. Juveniles may not be able to cling to weed as firmly as adults, but seem to compensate for this by gathering in the safer parts of the weed, such as damaged air bladders, multiple branchings, etc.

Morph frequencies were recorded at all three sites nine times between August 1976 and October 1977; these samples were selected for analysis (see Sections 3 and 6 for details of full sampling programme).

Methods

Preliminary studies (not presented) showed that samples large enough to yield repeatable size-frequency distributions also gave satisfactory morph ratios, so replicate samples were unnecessary.

Many older shells are covered with epiphytes. Some bear barnacles (invariably Elminius modestus Darwin). Boiling in alkali is advocated by Reimchen (1974), Smith (1976) and others, but is inconvenient and damages the soft parts. The following method proved adequate for non-genetic purposes.

Snails were wetted and examined individually under a Wild M4 binocular dissecting microscope fitted with x10 eyepieces and a strong narrow spotlight. The beam passed obliquely across a white ceramic plate so as to strike the outside of the lip when the aperture faced directly into the objective. This transmitted light revealed any reticulation in all but the thickest shells, which required a powerful lamp. Doubtful cases (usually very dark olivacea thought to have reticulations) were reconsidered after all unambiguous ones had been seen. Living snails were protected from overheating.

For comparison of juveniles and adults, 1 mm size classes were selected which were common to all 27 samples. Juveniles were represented only by the totals of classes 3, 4 and 5 mm because classes 6, 7, 8 or 9 mm were sometimes used in tagging experiments (Section 8). Adults were represented by the totals of classes 13, 14 and 15 mm. Three adjoining classes were combined to give workable numbers of minority morphs.

Three tests of significance were used: Chi-square for raw frequencies; Kendall's tau for similarity in patterns of percentages (Sokal &

Rohlf 1969 p. 533); and t for differences between mean percentages (t-test for samples with unequal variances, Ferguson 1966).

Results

i. total proportions

14,761 snails were classified from 27 samples containing from 192 to 1,016 individuals. The data are summarised in Appendix Table 19.

No morph was missing from any sample. At each site, olivacea greatly outnumbered reticulata and citrina combined.

Month-to-month variation in relative proportions of morphs was examined with Chi-square. Chi-square values for each within-site set of nine samples in Appendix Table 19 are shown in Table 3. There would seem to be very highly significant ($P < 0.001$) fluctuations in morph frequencies with time at each site.

Table 3

Morph frequency tests

Table 3. Chi-square tests for the three 9 x 3 segments of Appendix Table 19. Entries have 16 degrees of freedom.

Site	Chi-square	Significance
A	89.08	P <0.001 ***
L	51.00	P <0.001 ***
D	59.96	P <0.001 ***

Chi-square is highly sensitive to large sample size and as with many tests of independence, very weak relationships between large groups may be considered significant (Nie et al. 1975). Furthermore, changes in the size-frequency distribution (Section 6) limit the value of tests based on whole samples. Accordingly, subsequent analysis is confined to the representative juveniles and adults, of 3.0 to 5.99 and 13.0 to 15.99 mm respectively.

ii. representative juveniles

Data of 3,133 representative juveniles are summarised in Appendix Table 20. Numbers ranged from 24 to 343. Numbers of individual morphs were often low, but only twice was a morph missing. Olivacea was less dominant than in the whole samples.

Chi-square tests performed as for the whole samples are summarised in Table 4. As before, there appear to be significant fluctuations with time in morph ratios, but less so downshore at site D.

If these fluctuations are meaningful, they may be synchronous at two or three sites. A quick check for synchrony is to rank the nine percentages of each morph at each site independently, then use a non-parametric rank correlation test such as Kendall's tau to make pairwise site comparisons one morph at a time (Table 5). Significant synchrony occurred only in morph reticulata between sites L and D.

Another approach is to convert raw frequencies to percent proportions, in effect to standardise sample size at 100. Means and variances may be computed and compared. Appendix Table 22 summarises such a conversion. Means are invariably based on n = 9; 0% is treated as a valid

Table 4

Juvenile morph frequency tests

Table 4. Chi-square tests for the three 9 x 3 segments of Appendix Table 20. Entries have 16 degrees of freedom.

Site	Chi-square	Significance
A	49.82	P <0.001 ***
L	44.99	P <0.001 ***
D	31.83	P <0.02 *

Table 5

Juvenile morph synchrony tests

Table 5. Results of pairwise Kendall's tau tests for synchronous fluctuations of juvenile morph proportions. Entries are values of tau computed as discussed in text. *, $P < 0.05$; others non-significant.

Sites		Morph	
	Reticulata	Citrina	Olivacea
A v L	0.17	0.50	0.28
A v D	0.17	0.33	0.22
L v D	0.67 *	0.06	-0.06

Table 6

Comparisons of juvenile morph percentages

Table 6. Data of Appendix Table 22 compared pairwise by two-tailed t-test. Entries are t values. Critical value of t at $P = 0.05$ is 2.31. All tests non-significant.

Sites		Morph	
	Reticulata	Citrina	Olivacea
A v L	0.25	0.51	0.42
A v D	0.25	0.59	0.51
L v D	0.41	0.87	0.68

entry. Except for olivacea at sites A and D, variances exceed their corresponding means, often substantially.

On the assumption that values contributing to each mean are normally distributed, means may be compared with a t-test. It is however prudent to assume that corresponding variances are not necessarily equal, and to apply a special t-test (e.g. Ferguson 1966, p. 171). This involves dividing the difference between the means by the standard error of this difference. (When the means have differing degrees of freedom, a new critical value of t must also be computed.)

Table 6 summarises the results of nine pairwise between-site comparisons. Tests were two-tailed, i.e. they merely assumed equality of means. All tests were non-significant at the 5% level. Overall, corresponding morphs were comparably abundant (as % of sample) at each site.

Combining dates in this way to compare the resulting means detects overall differences, especially if morph proportions are invariant with time. However, the large variances suggest that - notwithstanding the lack of synchrony between sites - comparisons should be made one month at a time. Of chief interest is the relationship between sites L and D, large weed belts at different tidal heights. The raw frequency data (Appendix Table 20) may be used to construct nine monthly 3 x 2 contingency tables, for which Chi-square is computed as usual with two degrees of freedom (Appendix Table 24).

Although Chi-square for September 1976 is not significant regardless of whether reticulata is eliminated from the calculations, this month is left out of subsequent analysis.

In only three months of eight do proportions differ significantly between sites L and D. To determine whether the eight months may be pooled, heterogeneity Chi-square is computed by subtracting from the sum of the individual Chi-squares the value for a 3 x 2 table using total frequencies. Because heterogeneity Chi-square is non-significant ($P > 0.30$), the months may be pooled. The resulting pooled Chi-square is very highly significant ($P < 0.001$). Juvenile morph frequencies at sites L and D differ overall.

It is important to recall that each morph was comparably abundant overall at each site (Table 6). That is, averaged over samples extending from August 1976 to October 1977, morphs when considered individually were equally abundant overall at sites L and D, but the relative proportions of all three morph groups (olivacea, citrina, the reticulatas) were not the same at sites L and D month by month.

iii. representative adults

Data of 7,061 snails from 13.0 to 15.99 mm shell length are summarised in Appendix Table 21. Numbers ranged from 74 to 450. Morph citrina was generally scarce, but was only absent once (July 1977, downshore). Olivacea dominated all samples.

These data were analysed as in the previous part.

As before, morph ratios fluctuated significantly with time within sites, and less so at Site D (Table 7, corresponding to Table 4). (No correction was made for small expected frequencies as there was more than one degree of freedom.)

As with the juveniles, sites did not generally fluctuate synchronously, although olivacea was just significant ($P = 0.05$) high on shore (Table 8, corresponding to Table 5).

Table 7

Adult morph frequency tests

Table 7. Chi-square tests for the three 9 x 3 segments of Appendix Table 21. Entries have 16 degrees of freedom.

Site	Chi-square	Significance
A	47.68	P <0.001 ***
L	46.97	P <0.001 ***
D	37.90	P <0.01 **

Table 8

Adult morph synchrony tests

Table 8. Results of pairwise Kendall's tau tests for synchronous fluctuations of adult morph proportions. Entries are values of tau. *, P = 0.05; others non-significant.

Sites		Morph	
	Reticulata	Citrina	Olivacea
A v L	0.39	0.28	0.56 *
A v D	0.39	0.06	0.28
L v D	0.44	-0.11	0.28

Table 9

Comparisons of adult morph percentages

Table 9. Data of Appendix Table 23 compared pairwise by two-tailed t-test. Conventions as in Table 6. All tests non-significant.

Sites		Morph	
	Reticulata	Citrina	Olivacea
A v L	0.24	0.07	0.18
A v D	0.39	0.65	0.24
L v D	0.72	0.54	0.50

Appendix Table 23, corresponding to Appendix Table 22, shows percentages with means, variances and standard deviations. As before, zero was considered valid. Adult variances were closer to their corresponding means than were those of juveniles.

Table 9, corresponding to Table 6, summarises the results of two-tailed pairwise comparisons between sites of those means. As for the juveniles, all tests were non-significant ($P > 0.05$): overall, corresponding morphs were comparably abundant at each site.

Month-by-month comparisons of relative proportions of morphs at sites L and D are summarised in Appendix Table 25, corresponding to Appendix Table 24. Proportions differ between sites in four months of nine, only two of which co-occur with such differences among juveniles. The highly significant heterogeneity Chi-square ($P < 0.01$) forbids pooling of dates as was done for juveniles.

As with juveniles, it is important to distinguish between relationships of average percentages over time and relationships of morph ratios on particular occasions.

At first glance, adults may seem to behave as juveniles. A closer examination of the data reveals important differences.

iv. comparison of juveniles and adults

If different morphs confer camouflage on different backgrounds, and if this effect is more important to juveniles, which are thought to be more vulnerable to predation than adults, then the relative proportions of these morphs may differ between juveniles and adults. Similarly, differences between morphs in physiological tolerances etc. might also lead to changing morph ratios with age.

If juvenile and adult morph total raw frequencies are compared by three Chi-square tests having two degrees of freedom (Appendix Table 26), Chi-square values at each site are huge and very highly significant ($P < 0.001$). The minority morphs citrina and reticulata reverse position. Citrina is the more abundant among juveniles, but reticulata the more common among adults, regardless of site.

The expectations used in preparing Appendix Table 26 are as usual based on the assumption of independence, i.e. that morph ratios are independent of age. If these are compared with the observed data, then at every site the juveniles have more citrina and fewer reticulata than expected. The converse is true for adults. Olivacea is as expected throughout. Appendix Table 26 contains a worked example: olivacea contributes negligibly to the very large Chi-square values.

The scarcity of some morphs in some samples makes a month-by-month comparison between juveniles and adults of little value. The means from Appendix Tables 22 and 23 may however be compared. Table 10 shows more detail but otherwise corresponds to Tables 6 and 9.

Tables 6 and 9 were based on two-tailed tests, i.e. on the null hypothesis that means are identical. If there is cause to believe _a priori_ that one ought to be the greater, then a one-tailed test is appropriate, the null hypothesis being that it is less than or equal to the other mean. Although t is computed unchanged, new critical values apply.

In the two-tailed test (Table 10), the proportion of olivacea is invariant with age within each site. Citrina changes highly significantly at site A. Reticulata changes significantly at sites A and D, and highly significantly at site L.

Table 10

Comparisons of juvenile and adult morph percentages

Table 10. One- and two-tailed t-tests of the difference between juvenile and adult mean percentages for each morph at each site. Diff., juveniles minus adults, %. SE, standard error of this difference. t, Diff./SE (with 8 degrees of freedom). n.a., test not applied.

Morph	Site	Diff.	SE	t	Significance	
					2 tails	1 tail
R	A	-18.05	5.90	3.06	P <0.02 *	P <0.01 **
	L	-17.78	5.06	3.51	P <0.01 **	P <0.005 **
	D	-19.41	7.13	2.72	P <0.05 *	P <0.025 *
C	A	18.51	5.28	3.51	P <0.01 **	P <0.005 **
	L	24.54	11.06	2.22	P <0.1 NS	P <0.05 *
	D	14.36	7.13	2.01	P <0.1 NS	P <0.05 *
O	A	- 0.46	7.06	0.07	P >0.9 NS	n.a.
	L	- 6.78	11.98	0.57	P >0.5 NS	n.a.
	D	5.05	7.72	0.65	P >0.5 NS	n.a.

It is interesting to apply a one-tailed test to the following hypotheses. (a) The proportion of citrina will decrease with size (age). (b) The proportion of reticulata will increase with size.

One-tailed tests (Table 10) support both hypotheses. At each site, reticulata increases with age. The level of significance is improved at site A. Citrina decreases with age at each site; sites L and D are now significant (compared with the two-tailed tests).

v. summary of results

1. 14,761 L. obtusata in three concurrent sets of nine monthly samples from standard sites A, L and D were scored for colour morph: 3,133 representative juveniles and 7,061 representative adults of shell length 3.0 to 5.99 and 13.0 to 15.99 mm respectively were used in analysis to avoid complications caused by changing size-frequency distributions.
2. The olive-green morph olivacea was dominant in every sample. Two other morphs were usually present, the yellow citrina and the dark-gridded reticulata.
3. Morph ratios fluctuated with time in juveniles and adults, though less so at site D.
4. Whether in juveniles or adults, they did not do so synchronously at any two sites.
5. When dates were summed within sites, the mean abundance of a given morph was similar at each site.
6. The variances associated with these mean percentages were much higher for juveniles than for adults.
7. When month-by-month comparisons between sites L and D were pooled, juvenile morph frequencies were highly significantly different between sites. Adult values could not be pooled, but in four months differences were significant or highly significant.
8. Although a given morph had the same average abundance in all samples, the relative proportions of the different morphs were not necessarily the same from sample to sample.
9. Morph frequencies were compared between juveniles and adults within sites. Citrina and reticulata differed highly significantly. Citrina

became relatively less abundant with age, reticulata relatively more abundant, and olivacea remained unchanged.

10. One-tailed t-tests for citrina and reticulata percentages gave variously significant differences between juveniles and adults at each site.

Discussion

Sites L and D were originally sampled as comparisons for site A, partly to check for size-specific immigration to that outcrop. There was no reason to expect site A to display markedly different morph ratios from those at L which is at the same tidal height, except that while A is a pure stand of *Ascophyllum nodosum*, L contains a sprinkling of other algae such as *Fucus spiralis* and has a more particulate substratum. On the other hand, D was sufficiently below L to differ in tidal immersion time (Section 2). The substratum at D seemed darker overall than at L, and *F. vesiculosus* was present.

It is always possible to rationalise good cause for practically any morph to be more (or less) abundant than expected at any particular site in retrospect. A better test would involve selecting habitats for sampling according to predominant background colour: chiefly some portion of the fucoid (Reimchen 1979). Colours change from hour to hour, for instance *F. spiralis* fronds darken rapidly as they dry out at low tide, so the seeming precision gained from sampling very exactly must be set against a careful consideration of conditions at that same spot when sampling is inconvenient.

Given the very sheltered and little-changing conditions at sites A, L and D, with attendant domination by Ascophyllum, the preponderance of olivacea was to be expected (Reimchen 1974; Sacchi 1969; Smith 1976).

Likewise the low frequency of citrina amongst adults is normal. Reasons for the hypotheses to which one-tailed t-tests were applied - that proportions of citrina and reticulata will respectively decrease and increase with size - are various. Citrina is by no means as cryptic on Ascophyllum as on F. vesiculosus further downshore. Citrina adults are the most conspicuous when the tide is out and birds are foraging. Citrina juveniles may change to olivacea in time, although the extent to which this happens in the Gorad population is uncertain. Similarly, some olivacea may become reticulata. Reticulata is more cryptic on dark backgrounds such as shaded crannies, old holdfasts, and small dark pebbles at sites L and D. The proportion of citrina drops considerably with age. Suppose that the number of reticulata and olivacea remains unchanged. An adult sample should therefore contain higher proportions of reticulata and of olivacea. However, the olivacea fraction is unchanged - i.e. the absolute number has in fact gone down - so the reticulata fraction rises. This implies that olivacea becomes subject to some limiting mechanism that does not affect reticulata. Smith (1976) contends that olivacea is influenced by tidal level per se, independently of fucoid species and of exposure, but that reticulata and citrina are not.

Although corresponding morphs were equally abundant overall at each site, ratios among morphs differed significantly between sites L and D. This is not the paradox it may seem to be at first glance. The first result smooths out the sample-to-sample variation incorporated in the second. A large invariable difference between sites so close would be much more remarkable.

Synchronous changes in morph proportions at two nearby sites might indicate the action of abiotic factors, especially if they involved snails large enough and thick enough to escape predation. No such changes were detected. Some evidence for the influence of abiotic factors is presented in Section 9 (survivorship), where numbers in different tagged cohorts dropped synchronously - whether by mortality or passive dispersal is uncertain. The extent to which morphs are differentially susceptible to abiotic factors is not reliably known. Many early experiments on "var. citrina" and "var. olivacea" must be disregarded because of contamination with L. mariae, while Sacchi (1969) found no good evidence for differences in physiological tolerances between morphs comparable to those he found between L. obtusata and L. mariae. In the field, behavioural adaptations such as taking refuge deep among fucoid fronds on sunny days are likely to be at least as important - especially in the short term - as subtle differences in physiological tolerances. It is assumed for the sake of argument that no such differential susceptibilities, if they exist, affect the present results materially.

Juveniles exhibited higher variances in monthly percentages of each morph than did adults. Before this can be attributed, for instance, to differential survival, it is necessary to know the proportions hatching or developing recognisable colours for selection to affect.

A possible flaw in the differential predation argument presents itself. The present investigation confirmed Reimchen's (1974) observation that many infants and juveniles are found in damaged air bladders, and that when these structures are not gashed but perforated, the snails inside may exceed the entry hole in diameter. Their colour morphs seem properly developed and do not appear to differ markedly from the usual juvenile ratios, but regrettably no rigorous comparison has been made. Predators cannot select snails they cannot find. Observed morph ratios are based chiefly on exposed survivors. The ratios in hidden and exposed juveniles could profitably be compared.

Studies based only on adults (e.g. geographic survey in Reimchen 1979) may lead to serious misinterpretations, as may those based on whole samples. Morph proportions differ substantially between juveniles and adults (see also Smith 1976). Size-frequency histograms (Section 6) show that such adults are more than a year older than the juveniles. Individual tagging of 12 mm snails - nearly or actually adult - proved them capable of living a further 1½ years or more: some were still being recaptured more than 500 days from release (Section 10). Such a lifespan allows plenty of opportunity for differential survival. Thus ratios among adults could conceivably reflect conditions long before the investigator makes his field notes.

The rest of this discussion touches briefly on several topics pertinent to mollusc polymorphism in general as well as that of L. obtusata.

"A population in which two or more distinct inherited varieties coexist at frequencies too great to be attributed to mutation is said to exhibit genetic polymorphism." (Clarke 1975) Widespread genetic polymorphism revealed by enzyme electrophoresis has received much attention. Theoreticians as well as field workers have attempted to establish whether it is selectively advantageous, and if so the forces maintaining it. Because spatial and temporal environmental change and diversity seem associated with enzyme polymorphism, it is thought likely to be important (e.g., Bryant 1976; Clarke 1979; Johnson 1971; McDonald & Ayala 1974). Mechanisms maintaining genetic polymorphisms include disruptive or frequency-dependent selection favouring extreme or rare genotypes (Gromko 1977; Maynard Smith 1962, 1966), heterozygous advantage (Clarke 1975; Wilkins & O'Regan 1980), and migration (Gillespie 1975). Clarke (1979) provides a good review stressing frequency-dependent selection.

Littorina obtusata's resemblance of fucoid flotation vesicles and fruiting bodies has long been remarked (e.g., Walton 1915). Green-brown colour polymorphisms are not unusual (Smith 1976) and are frequently taken as camouflage against visual predation (review of vision, Pettitt 1975). Although many such interpretations are inferential, colour polymorphisms are held to be maintained by visual predators in many gastropods including *Crepidula convexa* (Hoagland 1977), winkles *Littorina* spp. (Heller 1975b; Pettitt 1975; Reimchen 1979; Smith 1976), beach clams *Donax faba* (Smith 1975), dogwhelks *Nucella (Thais) lamellosa* (Spight 1976), and limpets *Acmaea digitalis* (Giesel 1970).

Undoubtedly predators take large numbers of snails - particularly the more vulnerable juveniles - but solid field or experimental predation rate data are often lacking. Elner & Raffaelli (1980) provide mean daily predation rates for shore crabs *Carcinus maenas* (L.) eating three size groups of *Littorina rudis* Maton and *L. nigrolineata* Gray. Polymorphism can be shown on theoretical grounds to reduce predation rates, especially when prey are clumped, when predators form short-term preferences (Thompson & Vertinsky 1975).

Land snails *Cepaea nemoralis* (L.) and *C. hortensis* (Müll.) and their song thrush predator *Turdus ericetorum* (Turton) provide classic evidence for visual predation maintaining colour polymorphism by disruptive selection for crypsis on dissimilar backgrounds (e.g., Cain & Sheppard 1950; Clarke 1962, 1979; Harvey *et al.* 1975). However, Bengtson *et al.*

(1976) consider <u>C. hortensis</u> morph ratios in Iceland to be affected by temperature, while Heath (1975) showed that dark morphs of <u>C. nemoralis</u> become measurably hotter in natural sunshine than lighter morphs. Murray & Clarke (1978) attribute allele frequency changes in a <u>C. nemoralis</u> population carefully studied since 1926 to habitat changes. Because <u>Cepaea</u> genetics are well understood, differing effects of climate and visual selection may eventually allow the relative importance of these mechanisms to be evaluated.

In littorinids, Sacchi & Rastelli (1966) assert that pale morphs of <u>L. mariae</u> and <u>L. obtusata</u> move more in bright light than dark morphs, but present no data. Heller (1975b) rejects the idea that temperature influences colour morph ratios in <u>L. rudis</u> and <u>L. nigrolineata</u>, and Raffaelli (1979) suggests that <u>L. rudis</u> polymorphism is maintained by selection acting on pleiotropic characters. Berger (1977) looked for pleiotropy in <u>L. obtusata</u> (and, inadvertently, <u>L. mariae</u>) but found no association between shell colour and esterase allele frequencies. Goodhart (1977) contends rather surprisingly that visible littorinid polymorphism is probably selectively neutral, and certainly not all gastropod shell patterns are entirely genetically controlled (Berry & Crothers 1974; Creese & Underwood 1976; Grüneberg 1979; Underwood & Creese 1976).

Nevertheless, Reimchen's thorough study of shell colour polymorphism in <u>L. obtusata</u> and <u>L. mariae</u> (Reimchen 1974, 1979) leaves little doubt that this visible variation is selectively important in a visually diverse and varying habitat. He first drew attention to crypsis in light transmitted through algal fronds, thus plausibly accounting for high frequencies of morphs very conspicuous in reflected light. His findings imply subtle and close local adaptations of shell colour to background, algae, and light regime. It seems quite unnecessary to postulate pleiotropy in these species. Genetic and predation experiments following Reimchen's lead are desirable.

SECTION 6

POPULATION STRUCTURE AND GROWTH

Introduction

Although mark-and-recapture methods provide the most satisfactory measure of growth rate, they are laborious. Growth may be estimated by repeated sampling. If juveniles are produced in occasional pulses rather than in a steady trickle, a pulse will appear as a peak in the size-frequency histograms. As the snails in the pulse grow, the peak moves, and growth rates are estimated from this movement. The best results are obtained when batches of juveniles are well separated in time and when members of a batch grow at similar rates: the narrow peaks are easily tracked.

Peaks that spread or overlap may nevertheless be disentangled. The experimenter's judgement plays a larger role as peaks become more ambiguous. A particular problem arises when one mode merges with another, as when large juveniles join a stable adult peak. Different workers may "lump" or "split" overlapping peaks differently. For this reason, the method used here is elaborated.

This analysis was undertaken to study population structure over a period thought likely to encompass two generations, and to provide growth estimates to set against measurements from cohort tagging (Section 8).

Method

i. general outline

Site A was systematically cleared of L. obtusata at approximately monthly intervals from April 1975 to October 1977. Comparison samples of about 500 winkles were taken at sites D and L from September 1975 and November 1975 respectively. Sites are described in Section 2, and sample dates and code names are given in Appendix Table 1. Except when required for tagging, snails were promptly killed and preserved.

Shell length L was selected for growth analysis. Shell shape measurements are explained in Section 4. Length correlates very closely with the more traditional columellar height, and is much easier to measure in L. obtusata. Dial calipers were used to measure size to the nearest 0.05 mm. Measurements were grouped into 1 mm size classes: 3.0 to 3.95 mm in class 3, and so forth. Snails larger than 17.95 mm were vanishingly rare - fewer than one in ten thousand - and were scored as 17.

Size-frequency histograms were prepared showing classes 3 to 17. Corresponding cumulative frequency distributions were analysed following the method of Cassie (1954), modified as explained later, to yield estimates of numbers in, and mean shell sizes of, modes in the histograms. Changes in means between samples were taken to represent growth. All snails in a mode were considered to be growing uniformly except as noted. Means were plotted against month, and crude average growth rates within modes were computed. Results for sites A, L and D were compared.

ii. polymodal analysis: modification of Cassie's method

Cumulative percent frequency at different sizes is plotted on arithmetic probability paper (Cassie 1954). A normal curve is thereby transformed into a straight line having intercepts that give its mean and standard deviation. Two overlapping normal curves generate an S-shaped cumulative frequency line which is then split at the inflection - the point of steepest slope - to yield, after transformation, two straight lines, each of which is then interpreted in the usual way. The inflection also permits an estimate of numbers in each mode: if at 50%, the modes contain equal numbers of individuals, and so on. Three or more modes are dissected similarly, provided that numbers are large enough to yield convincing results.

Although designed to work with normal distributions, the method can be adapted. Cassie (1954) provides a procedure to correct for truncation occasioned for instance by biased sampling. This correction works well for distributions that end suddenly with extreme classes missing. When extreme classes merely have freakishly low numbers however, the calculations can produce absurd values which must then be adjusted to meet extrapolations from more central classes (tests with artificial data, Appendix 1).

<u>L. obtusata</u> were deemed to be uniformly distributed within each 1 mm size class, and were plotted at its upper limit. That is, all snails in size class 3 were plotted at 3.99 mm, but if an estimated mean fell within size class 3 it was taken as read and not arbitrarily assigned to 3.5 mm.

Calculations for the smallest shells were adjusted when necessary to predict a minimum size greater than 0.0 mm. This usually resulted in an arbitrarily small standard deviation without greatly affecting the mean.

Supposed adult truncations were generally ignored, especially when they predicted unrealistic mean sizes (e.g., 18.5 mm when snails that large are extremely rare at Gorad) or extreme sizes well outside the known range.

Cassie's method works progressively through the distribution from one end to the other. The second mode is corrected for any overlap by the first, and not vice-versa. When intermediates (large juveniles) begin to blend with adults, the usual calculations can produce a joint mean smaller than the true adult value. To avoid this misleading effect, emphasis was often placed on the adult mode. Rather than being fitted last and corrected for overlap by intermediates, it was fitted from the upper end of the distribution just as the first mode was fitted from the lower end. A fit was then obtained for the remainder, overlapped from each end by juveniles and adults.

Because results can be strongly influenced by decisions whether to combine or split supposed modes, the rationale used here is summarised now. Further comments are in the discussion. The samples were treated as series rather than in isolation. Preference was given to clarifying the progress of modes from sample to sample. Modes that were unclear on the probability paper plots, or on the histograms, were treated whenever possible so as to fit logically between those in previous and subsequent samples. Interpretations that implied growth rates known from tagging experiments to be unlikely were not favoured.

Results

i. site A

21,190 L. obtusata were measured in 25 samples. Sample size ranged from 192 to 2,045 (Appendix Table 2), and population structure was generally trimodal (Figure 7).

Adults presented a stable peak with a mean size of about 14 mm (range 13.4 to 14.9 mm, Figure 8). There was no evidence of massive seasonal mortality, and adults constituted 50.2 ± 12.8% of the population (range 22 to 70%, Appendix Table 27).

The 1974 hatchlings, approximately 9.5 mm in April 1975, merged with the adults by about September 1975.

In 1975, 3 mm juveniles appeared by early July and grew steadily to reach approximately 8.5 mm by April 1976. They then grew faster, and their peak merged with that of the adults by August or September. Perhaps a few late 1974 or early 1975 juveniles grew quickly enough from about 8 mm in July or August 1975 to merge with the adults by the new year.

In 1976, early juveniles grew rapidly to about 7.5 mm in June, then merged with stragglers from 1975. Subsequent 1976 juveniles followed the pattern seen in 1975, growing steadily until spring 1977 and then more rapidly to merge with the adults between June and August 1977.

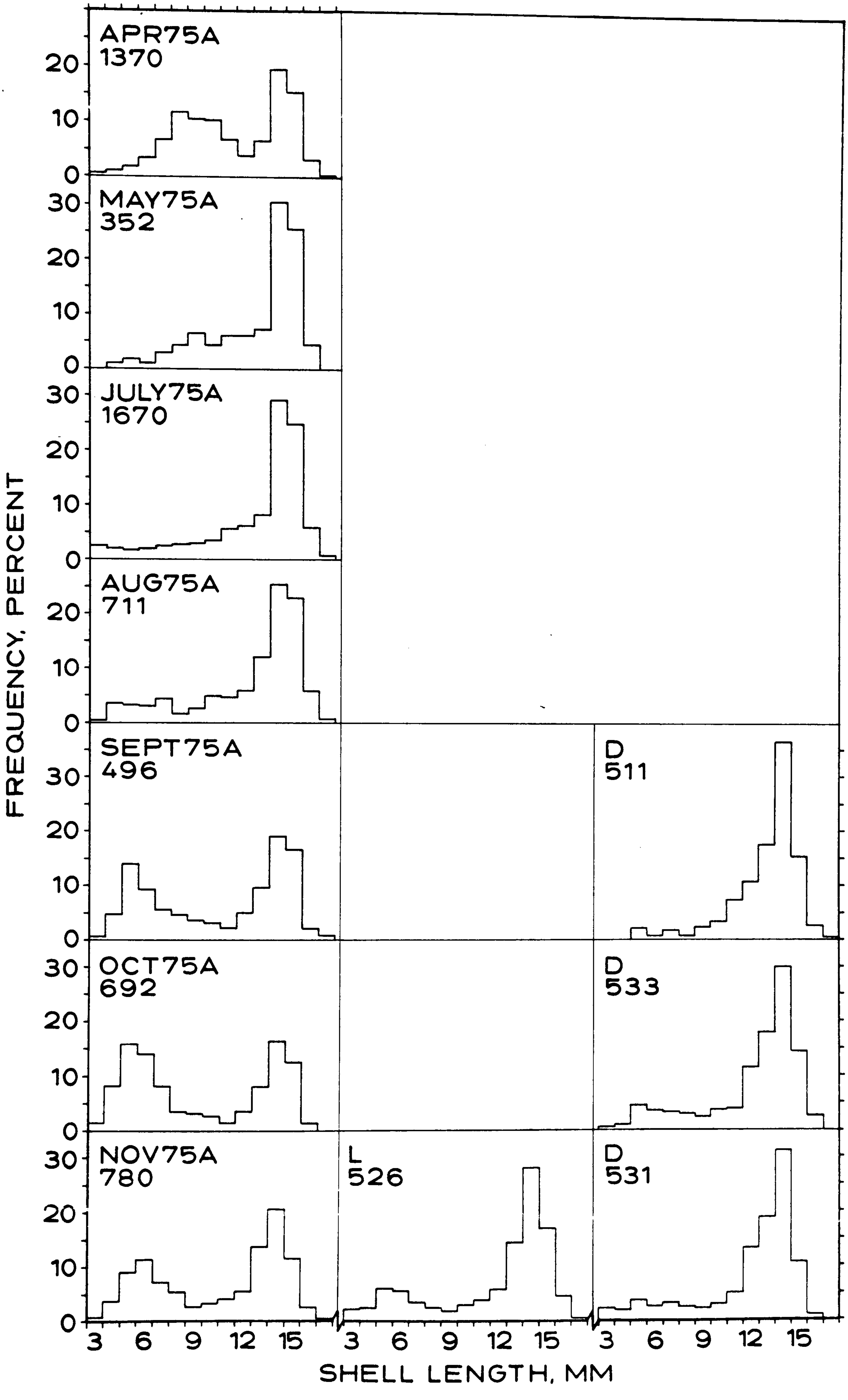
The 1977 juveniles appeared to be following the same pattern but were very much more numerous than in 1975 or 1976.

The difference between positions of a mode before and after some period of steady growth may be taken as a very approximate juvenile growth rate. Growth was 0.11 mm per week for 1975 juveniles and 0.12 mm/week for 1976 juveniles (Table 11).

Figure 7

Population structure at sites A, L and D

Figure 7. Size-frequency histograms for site A (left column), site L (centre column), and site D (right column). Vertical axis, percentage frequency. Horizontal axis, shell length in 1 mm classes. Sizes below 3.0 mm are omitted. Sample code names as in Appendix Table 1, with sample size. Figure 7 extends over 4 pages.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JULY75A
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AUG75A
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D
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OCT75A
692
D
533
NOV75A
780
L
526
D
531
FREQUENCY, PERCENT
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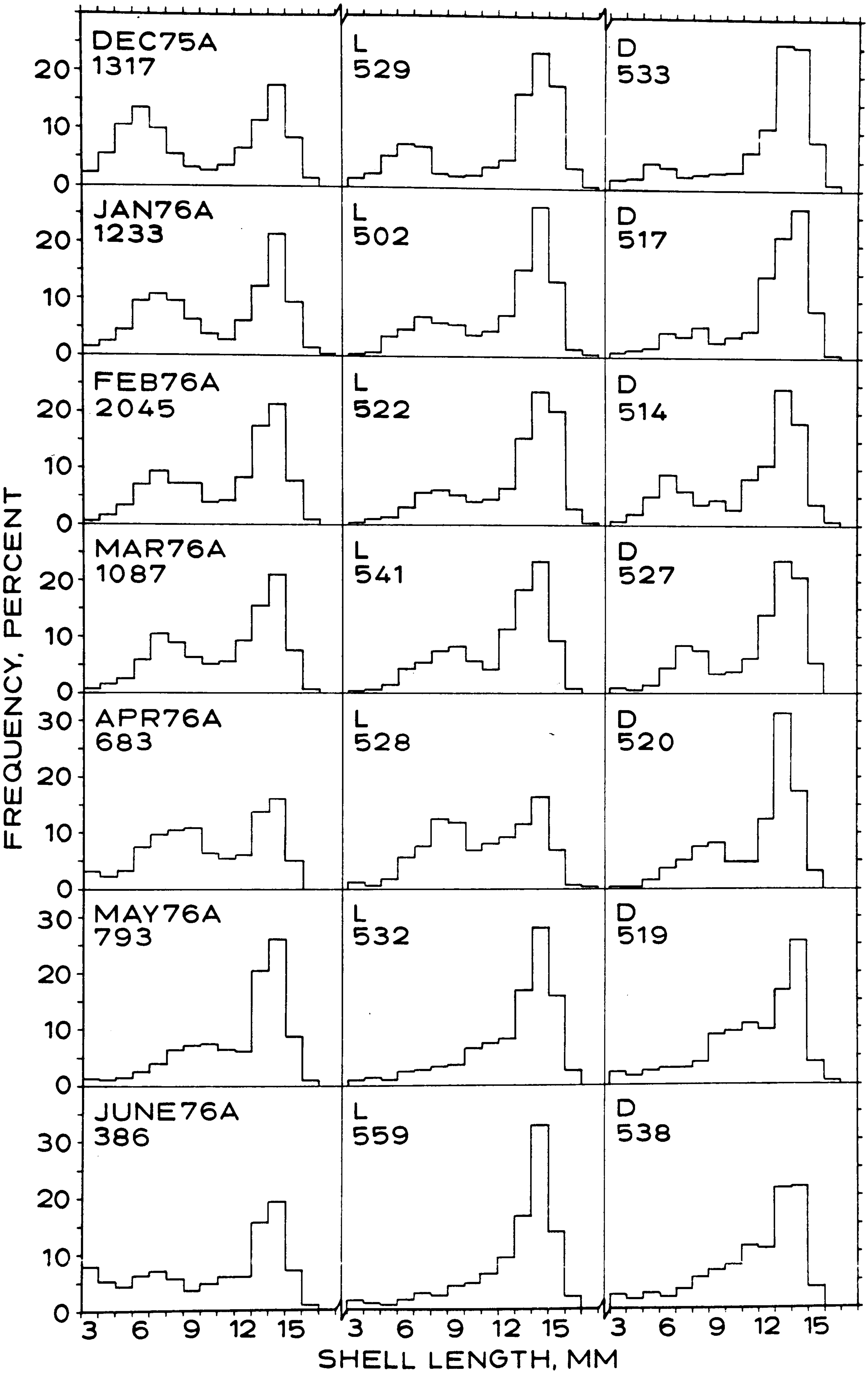
20
30
3
6
9
12
15
SHELL LENGTH, MM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D
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JAN76A
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D
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FEB76A
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MAR76A
1087
L
541
D
527
APR76A
683
L
528
D
520
MAY76A
793
L
532
D
519
JUNE76A
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D
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12
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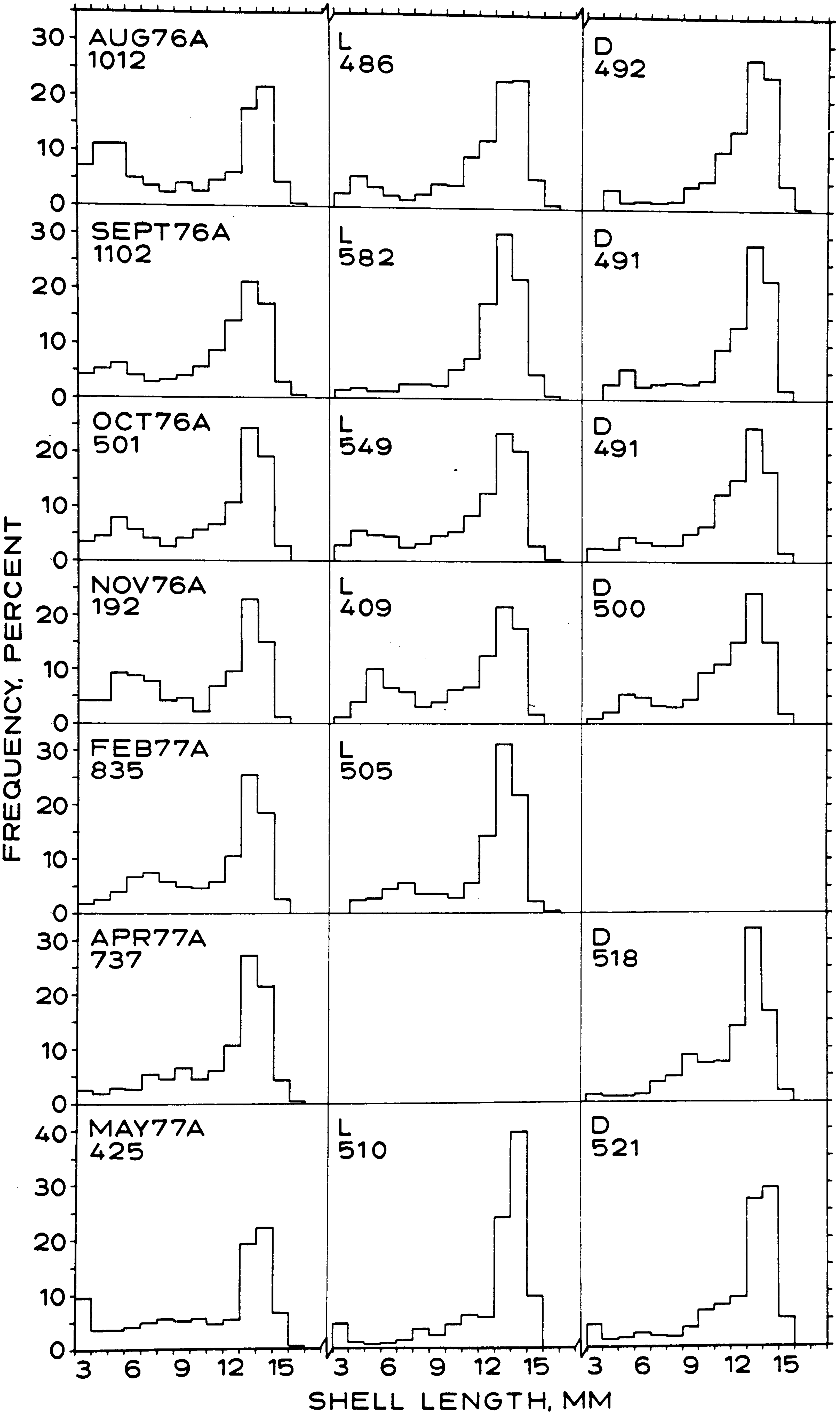
SHELL LENGTH, MM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NOV76A
192
L
409
D
500
FEB77A
835
L
505
APR77A
737
D
518
MAY77A
425
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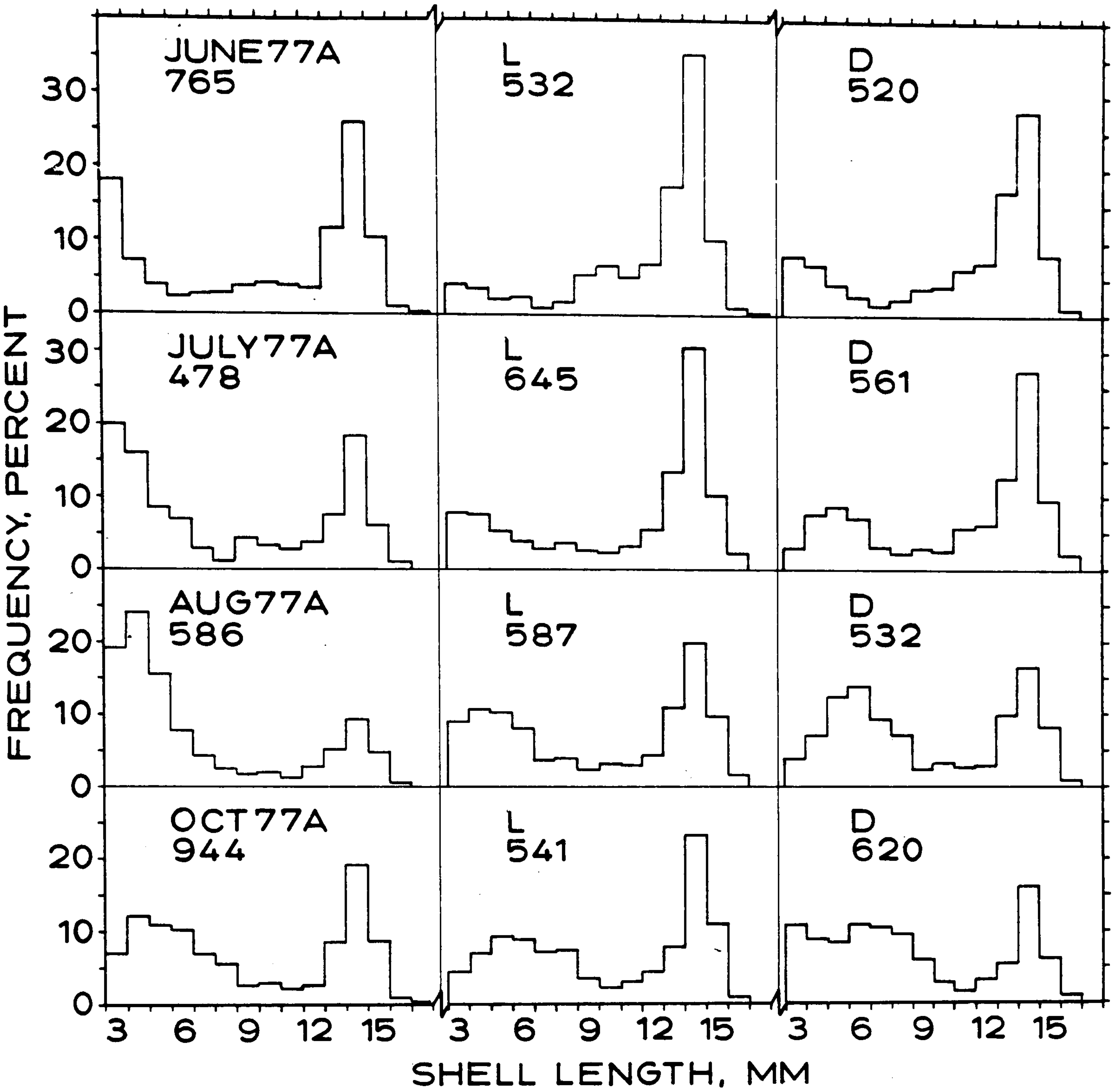
FREQUENCY, PERCENT
SHELL LENGTH, MM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D
520
JULY77A
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L
645
D
561
AUG77A
586
L
587
D
532
OCT77A
944
L
541
D
620
FREQUENCY, PERCENT
0
10
20
30
3
6
9
12
15
SHELL LENGTH, MM

Table 11

Estimated juvenile growth rates

Table 11. Overall growth rate for juvenile L. obtusata, estimated from mean sizes in Appendix Tables 27 to 29. M, mean shell length (mm). G, growth (mm). T, time interval (weeks). Rate, overall growth rate (mm/week). Intervals were chosen to encompass periods of steady growth.

Site	Date	M	G	T	Rate
A	3 July 75	4.5			
	24 May 76	9.4	4.9	46.6	0.105
A	23 June 76	4.2			
	14 Feb. 77	7.3	3.1	25.0	0.124
L	4 Nov. 75	6.2			
	10 Feb. 76	8.0	1.8	14.0	0.129
L	22 Sep. 76	4.6			
	16 Feb. 77	7.1	2.5	21.0	0.119
D	8 Dec. 75	6.0			
	15 Apr. 76	8.8	2.8	18.4	0.152
D	21 Sep. 76	5.1			
	7 Apr. 77	9.7	4.6	28.3	0.163

ii. site L

9,585 L. obtusata were measured in 18 samples (Appendix Tables 3 and 28, Figure 7).

Adults constituted a stable peak with a mean size of about 14 mm (range 13.5 to 14.7 mm, Figure 9), and made up 60.0 ± 11.7% of the population (range 39 to 80%).

Juveniles grew steadily from 6.2 mm in November 1975 until February (8.0 mm), then more rapidly to merge with adults by September 1976 (Figure 9). The few early spring 1976 juveniles reached adult size by May 1977. Later 1976 young grew steadily through the winter and faster from spring, to merge with adults by about July 1977. Early 1977 juveniles again grew rapidly, while later ones proceeded steadily until sampling ended in October. Juveniles were much more abundant in 1977 than in 1976.

Crude growth rates were 0.13 mm/week for 1975 juveniles and 0.12 mm/week for the 1976 juveniles (Table 11).

iii. site D

10,489 winkles were measured in 20 samples (Appendix Tables 4 and 29, Figure 7).

Adults had a mean size of approximately 14 mm (range, 13.4 to 14.5 mm, Figure 10) and accounted for 58.9 ± 10.3% of the population (range, 32 to 72%).

Although juvenile peaks were "split" in analysis more often at site D than at A or L, the pattern was still clear (Figure 10). 1975 snails grew steadily through the winter and more rapidly from spring, to merge with adults by September 1976. The best fits to the Cassie plots suggested that a few grew more rapidly from December to reach adult size by about April 1976.

Recruitment was low in 1976. Some early juveniles seemed to grow rapidly and combine with stragglers from 1975 to blend with the adults before April 1977 (no samples were available between December and March). Later 1976 juveniles grew steadily until April 1977, then more quickly to reach adult size by August 1977.

A similar pattern appeared in 1977, except that recruitment was much increased. Early juveniles again grew quickly to reach adult size by October, while later young appeared to be growing steadily when routine sampling ended.

Crude juvenile growth rates were 0.15 mm/week in 1975 and 0.16 mm/week in 1976 (Table 11).

iv. comparison of sites

When the growth trajectories for each site (Figures 8 to 10) were superimposed pairwise, no differences not already mentioned were found. Patterns of juvenile growth corresponded closely, and statistical analyses were not applied to estimated juvenile growth rates (Table 11).

The 17 months in which samples were taken from all three sites were selected for further comparisons (Appendix Tables 27 to 29, months not marked x).

Adults made up 47.3 ± 12.3% of the population at site A, 60.2 ± 12.0% at site L, and 56.7 ± 9.6% at site D. Mean proportions at sites A and L differed significantly ($t = 3.09$, 32 degrees of freedom, 2 tails, $P < 0.01$) as did those at sites A and D ($t = 2.49$, $P < 0.05$), but not L and D ($t = 0.94$, $P > 0.20$).

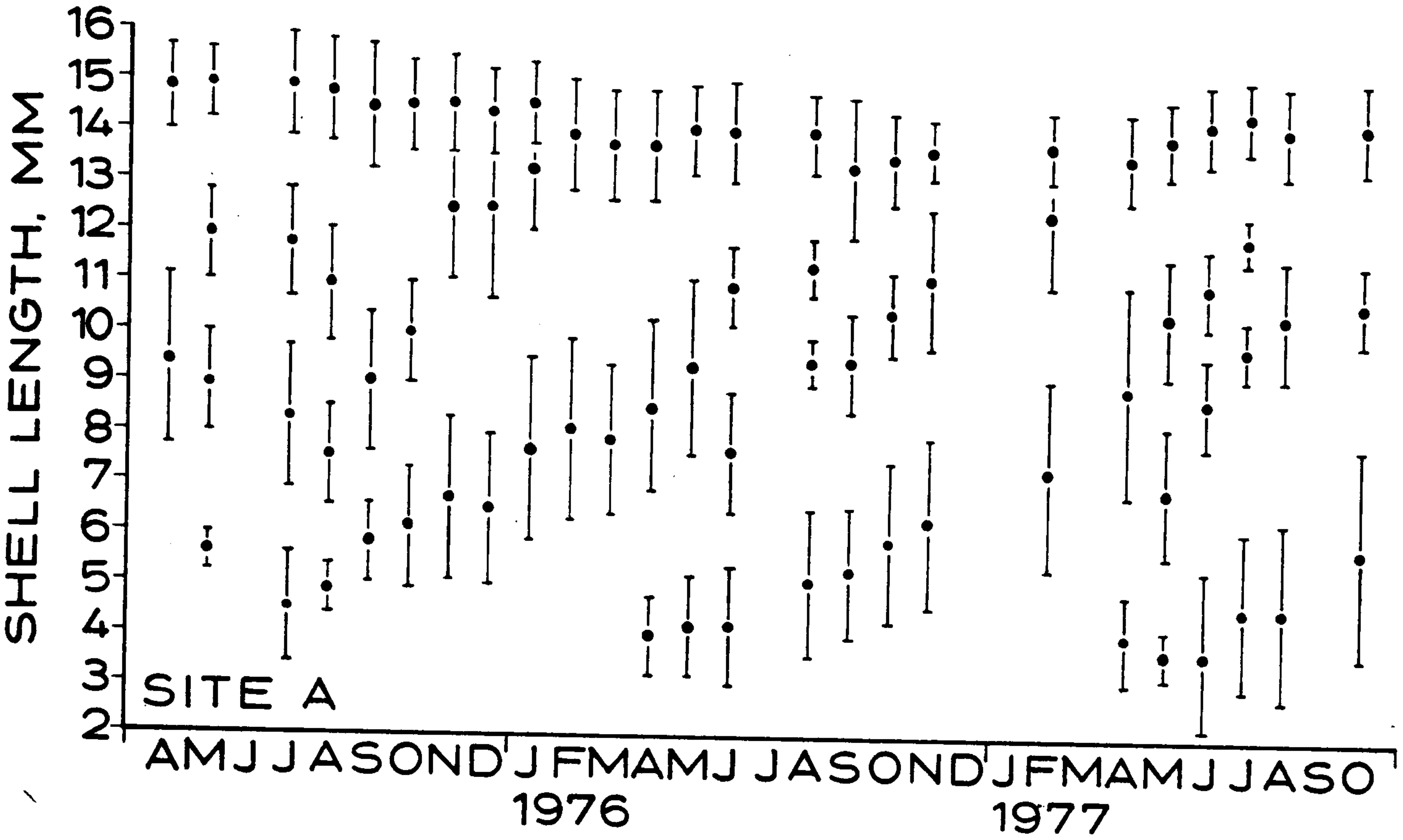
Figures 8 to 10

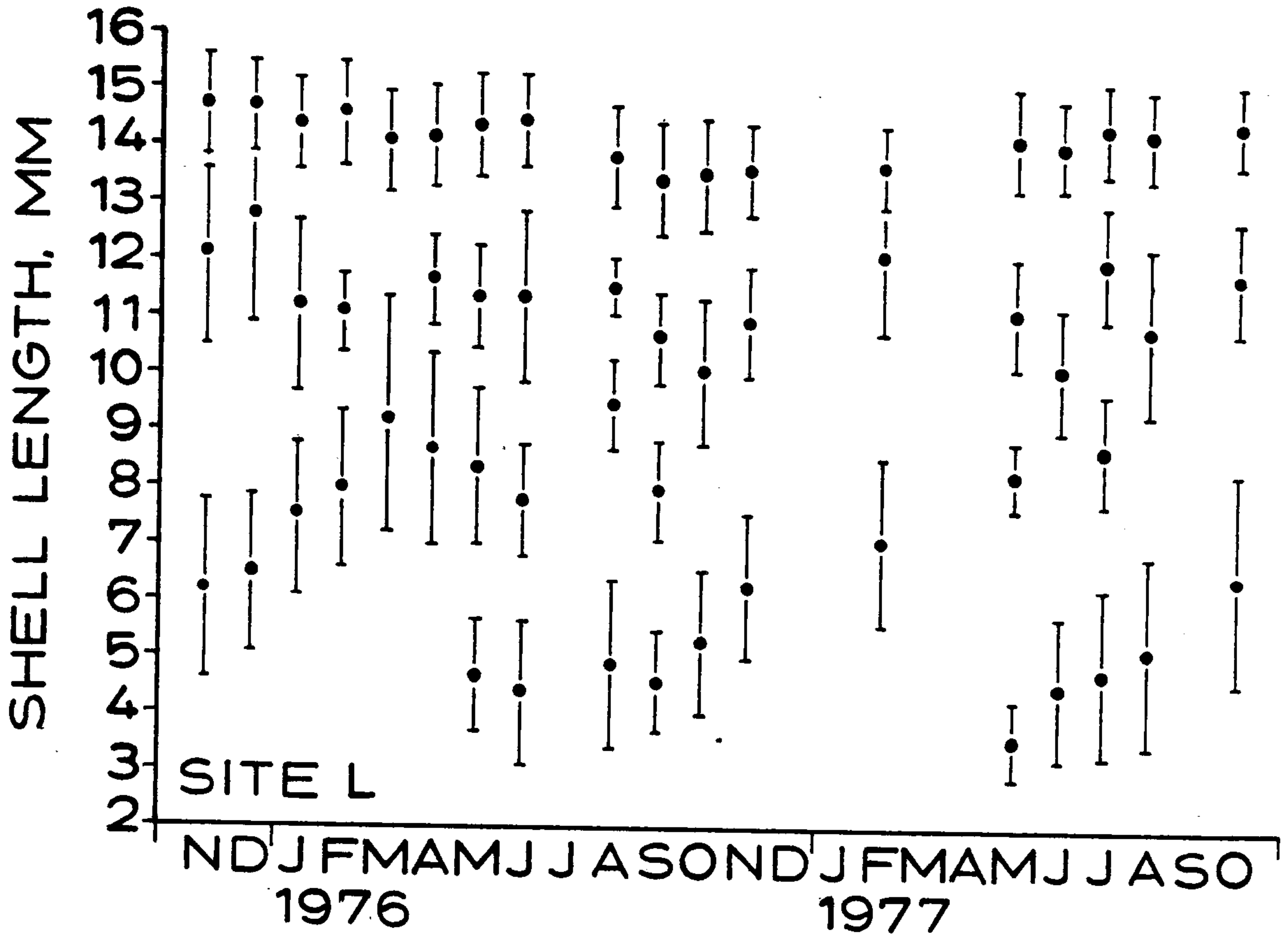
Population growth curves

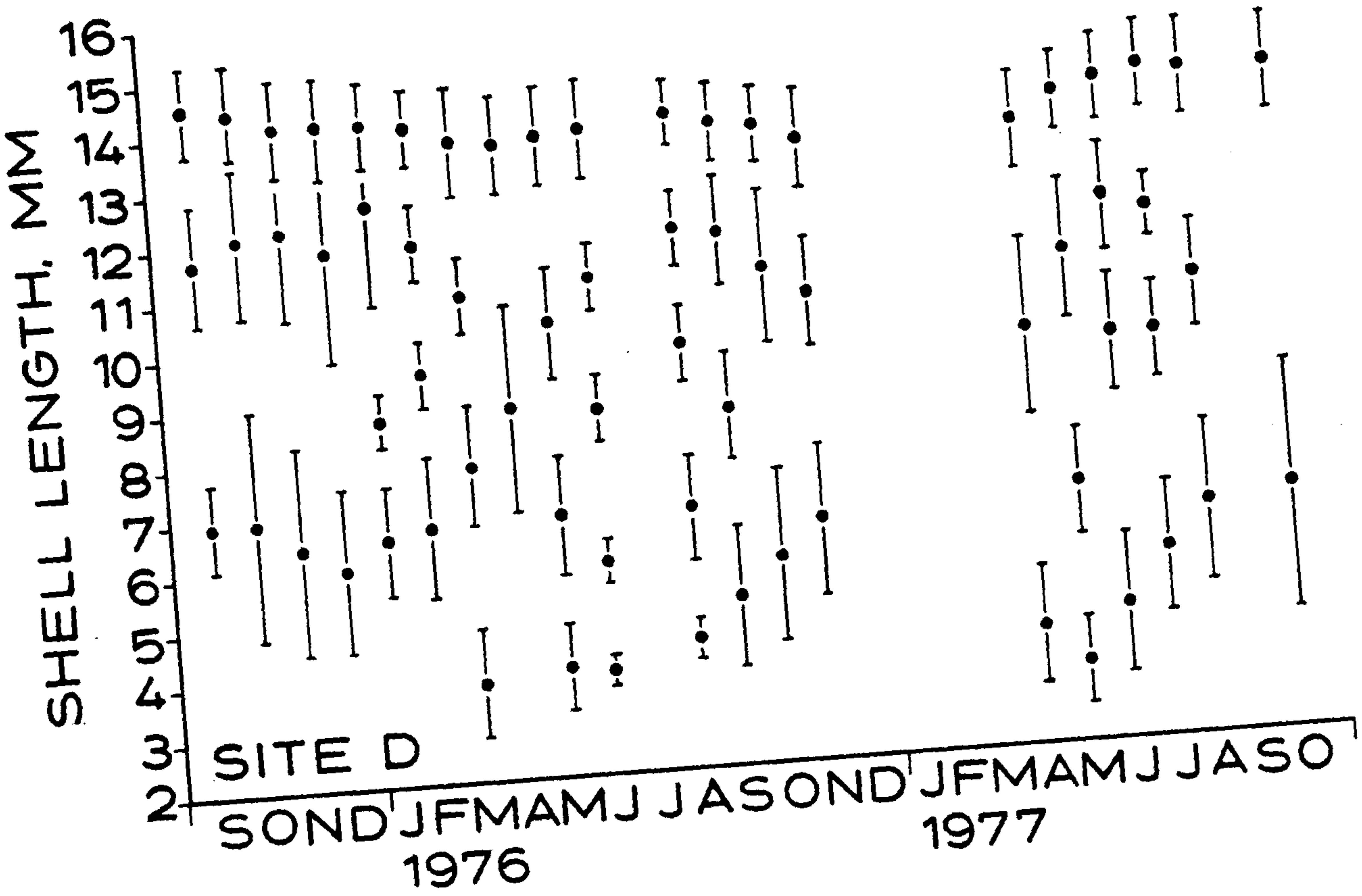
Figure 8. Progression of modes at site A. Vertical axis, mean shell length, mm. Horizontal axis, sampling month: see Appendix Table 1 for exact dates. Means are shown ± standard deviation (data from Appendix Table 27). Fusion of upper modes does not necessarily indicate rapid growth to adult size: see text.

Figure 9. Progression of modes at site L. Data from Appendix Table 28. Conventions as in Figure 8.

Figure 10. Progression of modes at site D. Data from Appendix Table 29. Conventions as in Figure 8.


SHELL LENGTH, MM
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
SITE A
A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O
1976
1977


SHELL LENGTH, MM
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
SITE L
N D J F M A M J J A S O N D J F M A M J J A S O
1976
1977


SHELL LENGTH, MM
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
SITE D
SOND
JFMAMJ
JASOND
1976
JFMAMJ
JASO
1977

The patterns of changes from month to month in proportion of adults at sites A and D were not correlated (Kendall's tau, P = 0.37), but the similarity between sites A and L was very highly significant (P = 0.0008). Graphs showing percent adults against date (not presented) revealed no evidence of large rises or falls at one shore level being accompanied by complementary changes at another.

v. summary of results

1. 41,264 L. obtusata larger than 3.0 mm were measured in 63 samples. Site A was sampled in 23 months between April 1975 and October 1977. Comparison samples were available from both sites L and D on 17 of these months between November 1975 and October 1977.
2. A size-frequency histogram was constructed for each sample. Corresponding cumulative percentage frequency plots were dissected into component modes - thought to represent age groups - with a modification of Cassie's (1954) probability paper method. Most histograms were trimodal, containing two actively-growing juvenile groups and an adult peak.
3. Recruitment, as indicated by numbers surviving to 3 mm or larger, was light in 1976 and much higher in 1977.
4. Juvenile growth was monitored by movement of peaks in the size-frequency histograms. The same general pattern was observed at each site for juveniles hatched early in 1975 and early in 1976: juveniles grew steadily - as expressed per unit time in mm, not % body size - until spring the following year, when they tended to grow faster. Adult size was reached by late summer or autumn. There was some evidence that fast-growing juveniles could achieve adult size rather earlier than this, but their peaks

were unclear and their numbers low.

5. Crude juvenile growth rates, estimated from periods of steady increase in mean size, were of the order of 0.12 mm per week at sites A and L, and 0.15 mm per week at site D.

6. At each site, adults constituted a stable proportion of the population. Over the 17 common months this proportion was similar at sites L and D, but site A differed significantly from each.

7. Patterns of changes, from month to month, in the proportion of adults were very highly significantly similar at sites A and L, which were at the same tidal height. Concurrently, there was no significant correlation between patterns at sites A and D, nor was there evidence of changes at one tidal height being matched by complementary changes at the other.

8. Mean adult size was similar at all sites, approximately 14 mm.

Discussion

The notion that movement of peaks accurately measures growth (e.g., Daguzan 1976a) is fallacious. Modes shift as members of adjoining size classes grow, immigrate, disperse, reproduce (Section 7), or die. In addition, because the modes are on percentage histograms, sudden large changes in absolute numbers in one section may conceal important changes among less numerous classes. The limitations of probability paper analysis are considered further after results are discussed.

Nonetheless, it is convenient to regard changes in means as growth with all snails in a mode growing uniformly. Growth in this sense, mm per unit time rather than percent body size per unit time, may be misleading.

Accordingly, growth estimates derived from juvenile peak movement were termed "crude". Crude growth rates from about 4-6 mm to about 7-10 mm (Table 11) were approximately 0.12 mm per week at sites A and L. Similar calculations by Goodwin (1978) yielded crude growth rates of approximately 0.09 mm per week for L. obtusata growing from 0.5 to 5 mm; he probably estimated date of hatching from egg mass abundance.

Although crude growth rate at site D seemed a bit higher than at sites A and L, this growth estimate is not judged sufficiently accurate to merit tests of significance. Crude growth rate is considered similar at all sites. Goodwin (1978) also found that crude growth rate did not vary with tidal level. This is not surprising because, at least on sheltered shores like those studied here and by Goodwin, winkles are able to feed whether the tide is in or out. One might expect those feeding on scattered Fucus spiralis high on shore to experience difficulty when the weed became dry. Goodwin was unable to determine growth there as juveniles were very scarce.

The evidence for a few early juveniles reaching adult size well before the rest is tenuous but suggestive. Hatching continues throughout the year (Goodwin 1978; Guiterman 1971; Sacchi 1969; pers. obs.), and tagging studies (Section 8) demonstrate that 6 mm snails grow faster in spring than do snails of the same size in the summer or autumn. Regrettably smaller snails could not practicably be tagged.

A more likely artefact is the supposedly rapid merger with adults (~~Figures~~ 8 to 10). Rapid growth may continue to 10 or 11 mm, but growth slows as adult size is reached, much as recorded by Goodwin (1978) and Goodwin & Fish (1977). The data did not always resolve tidily into two closely-similar modes as in sample Jan76A (~~Figures~~ 7, 8), so no special effort was made to split near-adults from adults. (The adult mode was often dissected before nearby modes, however. This would tend to separate them, because numbers in the largest classes generally fell steeply, effectively creating a narrow peak when the method constructed a mirror image of these larger classes to subtract from the region of overlap.) Any estimates of near-adult growth rate or of the exact date of fusion with adults were considered too subject to error to be useful. Growth above 10.0 mm is discussed in considerable detail in Section 8.

Snails smaller than about 3 mm were severely under-sampled and are omitted. A seemingly tiny 3 mm peak may in fact be the tail of a large peak of post-hatchlings (hatchlings at sites A, L and D measure approximately 0.45 mm in diameter). Size classes 3, 4 and 5 mm were also affected to different extents by sampling inefficiency, chiefly in cold weather when many normally detected by touch were overlooked. Preliminary studies (not presented) showed that enough small snails were captured to indicate their presence and approximate numbers. In warm weather sampling was accurate.

Notwithstanding these reservations, the pattern of changes in population structure was clear and comparable at all sites. Although L. obtusata hatch all year, there is evidently a peak in winter: these hatchlings are large enough to appear on the histograms by June or July, by which time the previous year's batch is well clear at approximately 9 mm. Juveniles grow steadily until the following spring when their growth accelerates. Adult size is reached by late summer or autumn; a conservative estimate of minimum adult age would therefore be 18 to 24 months. Goodwin (1978) obtained a similar estimate from a sheltered shore in Cardigan Bay. Guiterman (1971) believed that maturity was reached in only 10 months at his Anglesey sites, as an adaptation against early mortality owing to wave action.

Lifespan is shown in Section 10 to be as long as three years, possibly longer. The histograms show no sign of massive adult mortality at any season. Survivorship is considered in Section 9. The high number of adults relative to big juveniles also indicates that large winkles in a sample are the accumulation of several years. Daguzan (1976c) states that L. "littoralis" lifespan is approximately four years but provides no evidence. Goodwin (1978) deduces that few L. obtusata sensu stricto survive beyond three years because few shells are badly damaged by epifauna.

Neither the histograms, nor plots of adult abundance against time at each site, nor tau tests for synchrony, display evidence of vertical migration as has been reported for L. littorea (Gendron 1977; Williams & Ellis 1975), for L. obtusata sensu lato avoiding winter ice (Bequaert 1943; Pohley 1976), or for other intertidal molluscs (e.g., Bertness 1977; Feare 1970; Vermeij 1972). The same conclusion was reached from detailed study of sex ratios (Section 7), and by Goodwin (1978), Guiterman (1971), and Sacchi (1969). This is not surprising. Eggs are deposited in capsules of about 200 (Goodwin 1979) directly onto the weed on which juveniles and adults live. Repeated egg mass deposition in areas suitable to adults might outweigh the risks entailed in spawning migrations, such as increased exposure, loss of camouflage, or suffocation by silt.

Population structure for most of the year is thus trimodal: the peaks represent small actively-growing juveniles of one year, large actively-growing juveniles of the previous year, and a stable adult fraction some members of which may still grow (Sections 8 & 10). In mid-winter, before the new hatchlings appear in any number, and in particular high on shore, the distributions are generally bimodal.

Reimchen (1974) provides suitable information for L. obtusata only, on Fucus spiralis at Sandy Bay, Anglesey, sampled approximately quarterly between November 1971 and August 1973 (his Appendix E and Appendix Figure E). His figure includes very small snails, and the pattern is much the same as at Gorad. The stable adult peak is at 13-14 mm. Recruits exceed 3 mm by August, and their mode progresses steadily, blending with adults by late autumn the following year.

Guiterman (1971), working at various sites on Anglesey, obtained polymodal size frequency distributions which he was unable satisfactorily to analyse. He believed his populations to have two stable components, adults and tiny juveniles, and a moving component of juveniles in between. This would imply much more steady recruitment than at Gorad. Guiterman provides much information on fecundity. He found eggs throughout the year at all sites studied, calculated that at one very sheltered site a mature unparasitised female lays approximately 8,000 eggs between August and May (fecundity varied significantly between shores), and observed that hatching time in the field varied from 18 to 80 days (July and January respectively). Egg mass abundance was therefore an inexact indicator of reproductive activity.

By contrast Goodwin (1978), working on a sheltered shore near Aberystwyth, found clear-cut pulses rather like those in the present study. Goodwin examined egg mass abundance and gonad condition. He found both sexes reproductively capable throughout the year, with a spring peak in proportion of oviducts containing mature eggs. There was little evidence of cyclic reproduction involving gonadal regression. Goodwin (1979) found no significant seasonal trend in number of eggs per egg mass, but masses from higher shore levels were bigger and contained more eggs; egg size was unrelated to egg number. L. obtusata and L. mariae egg masses could not be distinguished by comparative histochemistry, but differed somewhat in mean egg diameter, shape, and deposition substratum (Goodwin & Fish 1977).

Underwood (1973) found a long breeding season with a late summer - early autumn resting period in L. "littoralis" near Plymouth. Hatchlings were most common in spring and autumn. Winter storms reduced fucoid cover and hence winkle populations, and the main hatching coincided with algal cover increase. Guiterman (1971) also suggested that egg masses act as a population reserve against adult storm mortality, and remarked that the Torrey Canyon oil spill killed all adult and young L. obtusata at Chapel Porth, Cornwall, but not the eggs, which may have re-established the population although immigration could not be ruled out.

Adults constituted a stable component of the present population, averaging 14 mm in shell length. Goodwin's (1978) stable adult component averaged approximately 13 mm. Mean adult size varies locally to at least 17.7 mm (Milkhaven, Ireland: Reimchen 1974). The Gorad adult population fluctuated with time. Changes in proportion are caused by growth, mortality, immigration, dispersal, and by changes in the absolute numbers of other size classes. These changes in proportion were highly significantly synchronous at sites A and L, although A (and hence presumably L) was not correlated with D.

Site A is a small rocky outcrop slightly isolated from weed band L by about 1 m of coarse sand and fine gravel, although loose weed and weed-bearing cobbles often come to rest there. Snails at A are - theoretically - net immigrants (active or passive) since the previous clearance of the same individual plants. Big differences between sites A and L could indicate non-random, or size-specific, dispersal. Although the pattern of change in adult numbers was the same at these two sites, the mean proportion of adults in the population at A differed significantly from those at L and at D, which did not differ from each other.

It is unnecessary to suppose that juveniles actively dispersed into site A more efficiently than adults, or that spawn numbers were higher at A, or that site A is unsuitable for adults: tagged adults persisted for over 18 months (Section 10). Large shells are easily dislodged and are often rolled about by waves. The conservative explanation for the lower mean adult proportion at site A is that there was insufficient time between samples for the more vagile adults to accumulate, as samples were taken without replacement (cf. Falk 1974; Underwood 1973). Mobility is discussed further in Section 9.

The general pattern of population structure in L. obtusata is much like that in other littorinids. Daguzan (1976b) found that French L. neritoides and L. "saxatilis" (? L. rudis) bred all year; his remarks on growth and mortality cannot be assessed as they are unsupported by data - in particular from the mark-and-recapture study mentioned in Daguzan (1976a). In that paper, concerning these species and L. littorea and L. "littoralis", he fit Von Bertalanffy growth equations (Section 8) to results of probability paper analysis, then reconstructed early growth and computed longevity and mortality. This technique lacks rigour. His other contribution on L. littorea and L. "littoralis" (1976c) is greatly weakened by ambiguous presentation. These disappointing papers may of course be largely the fault of lax editing and reviewing: unfortunately Daguzan's results and conclusions cannot confidently be accepted as presented.

Hughes and his students have studied most Welsh Littorina species.

The minute, barnacle-dwelling *L. neglecta* Bean displays a shore-level size gradient influenced by that of suitable refuge crevices (Raffaelli 1978b); a similar effect has been demonstrated for *L. rudis* and *L. neritoides* (Raffaelli & Hughes 1978; Hughes & Roberts 1981).

L. neritoides (L.) maintained in the laboratory spawned only in the early part of the year (Hughes & Roberts 1980). Field populations had constantly unimodal size-frequency distributions caused by low recruitment and slow adult growth (Hughes & Roberts 1981).

L. nigrolineata Gray had indistinct size-frequency distributions for most of the year, but increased summer oviposition produced a separate, short-lived mode the following spring (Hughes 1980).

A summer spawning burst in saltmarsh *L. rudis* Maton produced a clear travelling mode that merged with older age classes by spring, but the timing and overall patterns were different in boulder shore and cliff populations (Hughes & Roberts 1981).

In general, then, these *Littorina* size-frequency distributions contain one broad peak representing several age classes, and may have others corresponding to recruitment pulses. The same is true of *L. littorea* (e.g., Smith & Newell 1955 - table 2), although vertical migration may confuse results taken only at one tidal level. Accurate information on growth and mortality, especially in the larger snails, will have to come from tagging (Sections 8 & 10).

The great limitation of polymodal size-frequency analysis (e.g., Cassie 1954) lies in the arbitrary treatment of obscure or doubtful inflections. Modes may be "split" or "lumped". A small curve may be thought to overlap a larger one which is just skewed. Sometimes there will be good reason to reject a supposed mode or to assign an inflection arbitrarily, for instance to isolate an obscure mode present in previous and subsequent samples. Because cumulative percentages are used, small samples may produce spurious small modes. Grouping of very large sample data produces a "coarse-grained" curve.

Macdonald & Pitcher (1979), in a clear discussion of methods of analysing size-frequency data, stress the preferability of histograms to cumulative frequency plots in evaluating apparent modes. (Unfortunately their automated analysis presupposes both knowledge of the number of component modes and accurate starting estimates of their means and standard deviations.)

Approximately-normal distributions were found more regularly among the young and adults. Any intermediate mode was often less symmetrical. This was partly a consequence of numbers, for the adults were much more numerous than those large juveniles. The data must be approximated to, or treated as though they are, normal distributions. Every effort was made to obtain the best such fit, sometimes by trial and error. This was usually done by adjusting the inflection, hence some of the odd values for proportions in different modes (e.g., sample Jan76A, 16.6% intermediates). Some interpretations in Appendix Tables 27 to 29 look odd when compared with Figure 7. For instance, the two small bulges in sample June 76D classes 3 and 5 were treated as valid separate modes. In view of the small numbers of young being produced in the summer of 1976, and the ability of L. obtusata to reproduce throughout the year, it was thought best to treat them as real hatching pulses.

In effect then, "lumping" was generally avoided, especially as snails had already been grouped into size classes. Although the data are open to different interpretations on points of detail, the general results are unaffected.

Truncation corrections must be used sparingly, if at all. Since they reconstruct the missing classes from those present, any departure from normality in the latter will distort the former, often substantially (see also Appendix 1). There may be no valid biological reason to believe the "missing" classes ever occur. For instance, in the present study, the sharp drop in numbers beyond 15 mm is meaningful, is not caused by sampling bias, and should not be "corrected". The reconstructed normal curve may have unreasonable mean or extreme sizes. Reconstruction should not be attempted without prior knowledge of the naturally-occurring distributions in the population under study.

SECTION 7

SEX RATIO

Introduction

Although males and females may differ in longevity, behaviour, size, etc., sex ratio is seldom reported in much detail. Even in extensive field studies, it may be disregarded altogether (e.g., Smith 1976) or merely expressed as a single figure combining many sizes and sample sites (e.g., Guiterman 1971). Pooling is particularly unfortunate if sex ratio changes with size because of differential growth or development, parasitism, etc.

The large regular samples in the present study allowed several interrelated questions to be addressed. Is sex ratio different from unity, and under what circumstances? Does sex ratio change with time? Do adults of either sex migrate up or down the shore to spawn? Is sex ratio more stable lower on the shore at site D?

Methods

Any snail possessing a recognisable penis was considered male. All others were termed female. The validity of this approach is discussed later.

Sex ratio is defined as the ratio of males to females, and is expressed as a decimal fraction: 1.0 represents equality, any larger value a surplus of males. Sex ratio was not computed when only one sex was present.

Adults were defined as snails equal to or larger than 12.0 mm in shell length L (Section 4). While adults may be smaller, size-frequency analysis (Section 6) showed that size classes 10 and 11 mm usually fell within juvenile peaks.

Sex ratio was examined in different shell size classes and different samples. Certain sizes were extracted for special attention. Frequencies were compared by Chi-square. Means were compared by t-tests. For clarity, details of particular tests are presented with the results.

Some snails used in tagging (Section 8) were not available for analysis.

Results

Results are presented in this order: first, sex ratio in different size classes; next, adult sex ratio at individual sites; then, comparisons between sites; last, a summary.

i. sex ratio in different size classes

Small numbers in some 1 mm size classes in some samples could produce unrepresentative sex ratios. For instance, October 1976 8 mm sex ratio 5.0 was derived from 10 males and two females (site A raw data: Appendix Table 30). Sex ratios based on totals summed over many samples (Appendix Table 30, "SRT") could obscure variation among samples. Accordingly, mean sex ratios were computed with standard deviations (Appendix Table 31).

A general trend is evident. At first sex ratio rises with size. Males are in excess from approximately 11 to 13 mm, then decline below unity in the largest adults.

The rest of this section is devoted to adults.

ii. adult sex ratio: individual sites

In each of 25 samples from site A, male and female frequencies in shell length classes 12 to 16^+ mm were analysed by Chi-square in 5 x 2 contingency tables (4 x 2 tables when 16^+ mm snails were lacking). Five tests were statistically significant (Appendix Table 32). In April 1975 the 16^+ mm class was largely responsible for the total Chi-square, although no single cell Chi-square (not presented) was significant. In February 1976, the 12 mm class made the chief contribution to Chi-square, but again no cell was significant on its own. October 1976 was only just significant, and once again the 12 mm class contributed most. The highly significant result in April 1977 was caused by a surplus of 12 mm males and of 15 mm females. (Fusing the 15 and 16^+ mm classes to form a 4 x 2 table made no difference: Chi-square 14.1, 3 d.f., $P < 0.01$.) In June 1977 the major contributors to Chi-square were the largest snails, but fusing the two uppermost classes again made no difference (Chi-square 8.37, $P < 0.05$).

Results for sites L and D are presented before month-to-month variation is evaluated. In all, nearly 24,000 adults were scored from the three sites.

At site L, only two tests of 18 were significant (Appendix Table 33). In August 1976 the significant Chi-square was eliminated by pooling the three 16^+ mm females with the 15 mm class (Chi-square 3.91, P >0.2). November 1976 had more than twice as many 12 mm males as females (35 to 16), the reverse among 14 mm (26 : 45), and only one 15 mm male compared with six females, so the highly significant total Chi-square was appropriate. Cell Chi-square values (not presented) showed both 12 mm cells to be significant (males 4.00, females 3.85, one d.f. each, P <0.05 each).

Further downshore at site D, only two tests of 20 were significant (Appendix Table 34). In February 1976, combining the three 16^+ mm females with the 15's did not appreciably alter Chi-square (9.24, 3 d.f., P <0.05). The surplus 12 mm males were its major contributors, but no single cell was significant. In April 1977, the 15 mm class (one male, nine females) was chiefly responsible; when it was merged with the 14's, Chi-square was no longer significant (2.09, 2 d.f., P >0.3).

iii. adult sex ratio: comparison of sites

Samples were available from all three sites on 17 months. Mean sex ratios for each site (Table 12) did not differ significantly from one another (Table 13). (The same was true if all samples were used (Appendix Tables 35, 36) - a less rigorous test, however.)

The total frequencies of males and females did not differ significantly at each site (Table 14), nor between sites (Table 15). That is, total sex ratio did not depart from unity at any site.

Because of the frequent contribution of 12 mm sex ratio to significant adult Chi-square (Part ii), the sex ratios in 12 mm adults were compared between sites. No significant differences were found (Table 16).

To check for seasonal differences between sites, raw frequencies (Appendix Tables 32 to 34, months not marked x) were compared in seventeen 3 x 2 tables, and those for sites L and D were compared in 2 x 2 tables. All tests proved non-significant (Appendix Table 37). In each set, non-significant heterogeneity Chi-square permitted pooling of all 17 months. Total proportions at each site - in effect, the sex ratio for all adult size classes combined - did not differ from site to site in any month. In particular, sites L and D never differed from each other.

Each test so far in part (iii) has combined size classes 12 to 16^+ mm. Proportions of males and females were similar at all three sites overall and from month to month. Likewise, the proportions of adult colour morphs (Section 5), when considered separately, appeared neither to change with time nor to differ between sites. Nevertheless, when morphs were considered in relation to each other, within sites, one month at a time, their ratios proved to fluctuate significantly from month to month. Accordingly, the proportions of adult size classes in each sex were investigated within sites. That is, part (ii) results were reanalysed for heterogeneity.

Chi-square values for the 17 common months were obtained from the 5 x 2 contingency tables used to prepare Appendix Table 32 to 34. One adjustment was performed. Tables to be pooled to test for heterogeneity should have similar degrees of freedom. In some months, only 4 x 2 tables were available: these were expanded to 5 x 2 tables by adding two zero cells representing the missing 16^+ mm snails. This procedure left Chi-square unaltered but, by "inflating" the number of degrees of freedom in the analysis, caused a higher critical value of Chi-square to apply and so erred on the side of caution before indicating a significant result.

At site A, heterogeneity was non-significant, so dates could be pooled, yielding very highly significant differences in size-frequency distribution between males and females (Table 17). The only significant cell Chi-square values were for 12 mm males and females (4.80 and 4.64, one d.f. each, $P < 0.05$ each).

At site L, significant heterogeneity disallowed pooling and invalidated the highly significant total Chi-square. At site D, in contrast to A, pooled Chi-square was non-significant.

Table 12

Mean adult sex ratios, common months only

Table 12. Sex ratios for the 17 months having samples from all three sites, expressed as means (data: Appendix Tables 32 to 34). MSR, mean sex ratio. S, standard deviation. Appendix Table 35 gives similar data using all available samples.

Site	MSR	S	Range
A	0.96	0.11	0.79 - 1.12
L	1.02	0.15	0.82 - 1.36
D	0.95	0.10	0.77 - 1.13

Table 13

t-tests for Table 12

Table 13. Mean sex ratios shown in Table 12 compared pairwise by t-tests (equal variances assumed, 32 degrees of freedom). Significance, result of test with probability (2 tails). Appendix Table 36 gives similar data using all available samples.

Sites	t	Significance
A v L	1.33	A = L P >0.1
A v D	0.25	A = D P >0.2
L v D	1.56	L = D P >0.1

Table 14

Total adult frequencies, common months, tested within sites

Table 14. Frequencies within each site of adult males and females, summed over the 17 common months, tested for departure from equality. Obs, observed frequency. Exp, expected frequency. Test, Chi-square (1 d.f.), with significance.

Site	Sex	Obs	Exp	Test	
A	Male	3,485	3,548.5		
	Female	3,612	3,548.5		
	Sum	7,097		2.28	P >0.1
L	Male	2,880	2,871.5		
	Female	2,863	2,871.5		
	Sum	5,743		0.06	P >0.8
D	Male	2,611	2,677		
	Female	2,743	2,677		
	Sum	5,354		3.26	P >0.05

Table 15

Total adult frequencies, common months, compared between sites

Table 15. Adult male and female total frequencies from Table 14 ("Obs") compared between and among sites.

Sites	Chi-square (d.f.)	Significance
A v L	1.37 (1)	P >0.2
A v D	0.14 (1)	P >0.7
L v D	2.09 (1)	P >0.1
A v L v D	2.39 (2)	P >0.3

Table 16

12 mm Size class totals, common months, compared between sites

Table 16. 12 mm male and female totals for the 17 common months, for each site, with the results of Chi-square comparisons.

Site	Males	Females	Total
A	528	449	977
L	405	349	754
D	487	457	944

Sites	Chi-square (d.f.)	Significance
A v L	0.01 (1)	P >0.9
A v D	1.20 (1)	P >0.2
L v D	0.77 (1)	P >0.3
A v L v D	1.30 (2)	P >0.5

Table 17

Within-site tests for stability of adult sex ratios

Table 17. Results of tests for heterogeneity within sites, during the 17 common months, of adult male and female size-frequency distributions. See text regarding degrees of freedom.

Site A			
Total Chi-square (68 d.f.)	89.85	P < 0.05	*
Pooled Chi-square (4 d.f.)	21.25	P < 0.001	***
Heterogeneity Chi-square (64 d.f.)	68.60	P >0.1	
Site L			
Total Chi-square (68 d.f.)	100.29	P <0.01	**
Pooled Chi-square (4 d.f.)	9.83	inappropriate	
Heterogeneity Chi-square (64 d.f.)	90.46	P <0.05	*
Site D			
Total Chi-square (68 d.f.)	55.43	P >0.5	
Pooled Chi-square (4 d.f.)	5.51	P >0.2	
Heterogeneity Chi-square (64 d.f.)	49.92	P >0.9	

iv. summary of results

1. Sex ratios were computed within 1 mm size classes in 63 samples from sites A, L and D. Penis presence or absence was the scoring criterion. Adults were defined as those equal to or larger than 12.0 mm; 23,879 adults were examined.
2. At site A, the ratio of males to females rose with size until about 11 mm. Males were in excess until approximately 13 mm, then declined.
3. At each site, total numbers of adult males and females did not depart significantly from equality.
4. In most months, the relative proportions of adult size classes 12 to 16^+ mm were the same in males and females. Significant differences between sexes were caused by excess 12 mm males or large females.
5. The sex ratio in 12 mm adults did not differ significantly among sites.
6. Mean adult sex ratios did not differ significantly among sites.
7. Grand total proportions of adult males and females did not differ significantly among sites, nor did monthly totals. In particular, sites L and D never differed.
8. The data for result (4) were reanalysed for heterogeneity among months. At site A, adult males and females had significantly different size-class frequency distributions. This difference was constant with time, and was attributable largely to males having a much higher proportion of the 12 mm size class. At site L, there were significant month to month fluctuations in adult size-frequency distributions, but at site D these did not differ between sexes nor with time.

Discussion

Any supposed shortage of males among juveniles may be an artefact of delayed penis development. Although some males differentiated well before 7 mm, sex ratio only approached unity by about 10 mm. The 11 mm and particularly 12 mm classes had a clear surplus of males. Large adults tended to be female although males were common in all adult sizes. According to Goodwin & Fish (1977), Littorina obtusata at College Rocks, Aberystwyth (Dyfed, Wales) differentiate from about 7 mm and especially just before the adult size of 10 to 12 mm is reached. Goodwin (1978, fig. 5) shows adult mean size at his site to be approximately 12 mm plus or minus 1.5 mm. (His measurement "shell height" underestimates length used in the present study, and corresponds to columellar length W; length and W are closely correlated at all sizes (Section 4).) Goodwin & Fish (1977) also found that at a particular shell size - they do not give limits - males were slightly more developed than females. Thus, well-developed males tended to be smaller than equivalent females. Results from the present study confirm these observations.

The 15 samples at site A having more than forty 12 mm snails had a mean 12 mm sex ratio of 1.29 ± 0.31. Such a high sex ratio, although not quite statistically significant, is believed to be biologically meaningful. This excess of males could theoretically be caused in several ways. For example, males might rarely grow any larger. They might grow very slowly at that stage, or females might grow rather more rapidly. Many females might die at about 12 mm, while more males might persist to 13 mm.

Most such explanations may be discounted, at least as sole causes. Grahame (1969) and Alifierakis & Berry (1980) reported penis shedding in adult Littorina littorea, but as this does not occur in L. obtusata (Goodwin 1978; pers. obs.) any low adult sex ratio would require another explanation. Rare growth past 13 mm would require larger males to be accumulated from many generations. Appendix Table 30 might suggest that the many 16^+ mm specimens collected in early samples were indeed such remnants, but the size-frequency distributions (Section 6) show regular recruitment to a stable adult population centered on approximately 14 mm. Certainly the largest snails - excluding rare specimens distorted by parasitism - may represent at least two year classes, and preliminary studies with individual tagging of 14 mm snails suggest that they may easily be four years old. There is no good evidence for large-scale mortality in either sex just after attaining adulthood, as for instance if exhausted by spawning. There is no reason to suppose that wave action preferentially transports one sex.

One plausible explanation must remain unaddressed. Unfortunately the sex ratio at hatching cannot conveniently be determined, and so it is not possible to say whether males are produced in excess. If this were so, it would only become evident when all males were visibly differentiated from females, at adulthood. Goodwin & Fish (1977) and Goodwin (1978) give no detailed breakdown of sex ratio.

In the absence of data on chromosomal sex ratios, the conservative explanation for the high proportion of males in the 12 mm class lies in relative growth patterns of the sexes: males of that size, being more developed than the females (Goodwin & Fish 1977), would put less energy into growth and so take longer to pass from 11.9 to 13.0 mm. If males and females were equally numerous at 11 mm, a sample would contain more 12 mm males than females. Goodwin (1978) recorded slow growth as

L. obtusata approached maturity; his data are based on inferences from analysis of polymodal size-frequency distributions. Growth rates at different sizes were determined by tagging in the present study (Section 8). In particular, Section 10 treats of individual tagging of 12 mm males and females, and of their subsequent growth and mortality.

Another possibility, considered remote, is that females of about 12 mm might migrate downshore to spawn. Sex ratio in 12 mm adults did not differ significantly between sites, and the likelihood of active migrations even further downshore is low. L. obtusata is a sedentary species, and extensive locomotion over fine substrata frequently proves lethal. Snails attempting to crawl any great distance over silt rapidly suffocate: tracks across silt commonly end in freshly-dead winkles, their mantle cavities packed full of silt. (See Section 9 for a more detailed discussion of mobility and dispersal.) Spawning migrations are known for example in Nucella (Thais) lamellosa (Bertness 1977) but do not seem common in littorinids. In L. obtusata, Goodwin (1978) found no sign of such migration in any size class, nor did Sacchi (1969). Guiterman (1971) found no evidence in size-frequency distributions at different shore levels, although he claimed a general upward movement on the shore. (His concept of snails inexorably driven up the shore to die on the strand line, martyrs to assorted and frequently-shifting positive and negative taxes, is unhelpful. Descriptions of actions are not reasons for them.)

Several tests were made to determine whether the samples from sites A, L and D could be treated as coming from a single population, as would be expected if site microhabitat differences were negligible, or if there was extensive passive dispersal by wave action as on more exposed shores. These tests would be expected to reveal any large-scale active vertical migration whether within the range studied or to lower levels. Similar migrations in particular size classes would also be detected.

There were no differences between sites in adult sex ratio, whether from month to month or on average or taken as grand totals over the 17 common months.. It appeared therefore that the sites could indeed be regarded as replicates, and that adult sex ratio remained uniform with time as well as site. This conclusion was, however, based on totals. Closer examination revealed rather different results.

At site A, the male size-frequency distribution was highly significantly different from that of females. The direction of this difference was constant from month to month. The major contributor to Chi-square was the 12 mm class, in which males outnumbered females by 18% overall. At site L there was significant heterogeneity among samples, so they could not be pooled and no broad trend could be seen. The sex ratios fluctuated from month to month but these changes could not be attributed to spawning migrations. No pattern was evident in the raw data, and no corresponding changes were observed further downshore. At site D, meanwhile, the male and female patterns were constantly similar to each other.

Parasitism was not examined. Trematode parasites may affect sex ratio for instance by castrating males (e.g., Baudoin 1975), killing hosts (e.g., Pohley 1976), or affecting host growth rate (e.g., Feare 1970; Kuris 1974). The influence on host population dynamics may be substantial (Hughes & Roberts 1981). Guiterman (1971), in an extensive study of trematode infection of L. obtusata, determined that males and females were equally infested, saw no evidence of sex reversal, and in particular found that even heavily-parasitised males retained at least a vestigial penis.

The results in the present Section, therefore, are unaffected by unknown infection rates. Parasitism is discussed further in Section 9.

Daguzan (1976b) found that L. neritoides sex ratio decreased with increasing size from 1 in young adults (2.5 mm), so that the largest specimens (>5.5 mm) were all female. L. "saxatilis" sex ratio, on the other hand, was generally about unity but varied seasonally and increased with age. These results he attributed respectively to differential longevity and growth rate, but presented no supporting data.

There are few published reports of L. obtusata sex ratio to compare with Gorad. Guiterman (1971) scored 5,288 males and 5,605 females in various samples: sex ratio 0.943 differs highly significantly from unity (Chi-square 9.23, 1 d.f., $P < 0.005$). (His appendix D results are unsatisfactory as explained in Section 4.) Daguzan's (1976c) data are invalidated by confusion with L. mariae.

Sacchi & Rastelli (1966) argue that L. obtusata adult sex ratio is invariably just less than unity, while that of L. mariae is a bit higher. Their data do not support these generalisations when reanalysed by Chi-square. Sex ratio departed significantly from unity only in L. obtusata in two sites of five. Sex ratio differed significantly between sites in each species, but sex ratio differed significantly between species at only one site, Concarneau (L. obtusata 0.79, N = 3,645; L. mariae 1.06, N = 797), although the raw value for L. mariae was the higher at four sites of five. Sacchi later (1967) discussed seasonal variations at Roscoff and Bindic; total sex ratios were recalculated here as Roscoff, 0.91 (N = 17,097) and Bindic, 0.86 (N = 2,722). Both these ratios depart significantly from unity, but seasonal values did not necessarily do so. These results were later extended (Sacchi 1969, table D-1). As before, conclusions were based on large samples but were not supported statistically. Although Sacchi (1967, 1969) found no good relationship between sex ratio and exposure, he perceived some differences between colour morphs. It is difficult to interpret all these findings because the size range is not stated. It seems likely that Prof. Sacchi's extensive samples will yield much valuable information when analysed.

Reimchen (1974) does not discuss sex ratio in detail. His appendix B indirectly gives adult values for very many sites, but most samples are very small. Pooled data of repeated samples from the upper shore at Sandy Bay, Anglesey, yield 582 males to 592 females - adult sex ratio 0.98. Concurrent values for L. mariae are 325 males to 305 females - adult sex ratio 1.07. These values do not differ significantly (Chi-square 0.66, 1 d.f., P >0.1). (Interestingly, L. obtusata values for the lower shore region of overlap with L. mariae are 245 males to 232 females - adult sex ratio 1.06.)

Conclusions

Four interrelated questions were posed in the introduction. First, is sex ratio different from unity, and under what circumstances? Mean sex ratio - defined by external morphology - changes as snails grow and develop. Adult males and females are equally abundant in the population as a whole. On the grand scale, therefore, adult sex ratio could be taken as unity. However, in the absence of information on relative fecundity at different sizes, this simplification is dangerous. Goodwin (1978) reports that the presence in the oviduct of mature eggs shows a seasonal peak in mature females (defined as those with thickened shell lips). Regrettably, he does not state the proportions of gravid females of various sizes during that peak.

The second question was, does sex ratio change with time? Among adults as a whole it does not, but when individual adult size classes are considered, sex ratio only remains constant at sites A and D. Site L displays fluctuations showing no clear pattern. It is not obvious why two sites A and L at the same tidal height, separated by only a few metres, should differ in this way. The idea that greater microhabitat uniformity at A than at L was responsible does not seem tenable. Snails from site A were removed each month from the same plants but those at site D were not, yet A and D behaved similarly.

The third question was whether adult spawning migrations occurred in either sex. No evidence was found to support this hypothesis. Furthermore, size-frequency distributicns (Section 6) showed juveniles consistently to be less abundant at site D, where the risk of predation is also thought to be greater (Section 5). Juveniles high on the shore compensate for stressful conditions by taking refuge inside damaged air bladders and other damp crannies. Reimchen's (1974) breeding experiments showed that females could retain sperm for at least a week before spawning, so perhaps the males need not move. Especially where plants are widely scattered over a silty substratum, migrations would be risky. Mobility is also discussed in Sections 6 and 9.

Finally, is sex ratio more stable lower on the shore where conditions are less variable? This appears to be so. Site D is an extensive weed band supporting a large winkle population. Except when silt becomes abundant, conditions are very suitable there. Site D is less exposed to the weather, and while predatory crabs and fish have more time to exert heavy selection pressure on different colour morphs (Reimchen 1974, 1979; present study, Section 5), there is no reason to suppose that either sex is attacked preferentially.

SECTION 8

GROWTH

Introduction

Growing snails must be distinguished from those that are not, lest growth rates be underestimated. This is particularly important in large adults; some stop growing at a smaller size than others - although sometimes temporarily (Section 10). A growing snail has a delicate, chisel-edged aperture lip. One that has long since ceased growing has a thick lip with a glossy rounded edge. Snails falling between these extremes may be growing or thickening. With experience the condition of the edge provides a satisfactory guide to growing state (see also Section 10).

Shell measurements are closely correlated, allowing shell length L to serve as a convenient size index (Section 4). Length is maximum diameter from the lip. Growth is defined as increase in length.

Littorina obtusata hatches at about 0.45 mm, but age at subsequent sizes is not known, so length is not an absolute measure of age.

Growth rates may vary with size or with season. No single technique easily distinguishes these effects. Growth rates may be inferred from sample size-frequency distributions. Measured snails of similar size may be tagged identically, released, and measured on recapture. Individually numbered winkles may be measured whenever caught.

Growth estimation from size-frequency data is treated in Section 6. Juvenile snails at sites A and L grew at about 0.12 mm per week, and at approximately 0.15 mm per week at site D. Growth was steady in winter and faster in early spring.

A cohort is a group, identically code-marked, having a total size range at release of 1 mm. Changes in survivors' mean size may be taken to represent growth while numbers remain adequate. However, the effects of size and season are not separated. This may be done by releasing several cohorts of different sizes concurrently, and ideally in different seasons: an extended cohort is a set of cohorts released concurrently, each having a different size and distinguishing mark. Limitations on frequent extended cohorts include availability of scarce sizes, the numerous markings which may be misidentified, and "the law of diminishing returns". If mortality or dispersal is heavy, only short-term growth rates are obtained, but these may be pieced together to form a composite growth curve.

The main objection to growth curves based on mean sizes is that individual variability is obscured (Sainsbury 1980). Because L. obtusata is fairly sedentary, individual tagging was feasible, but it was necessary to restrict this to the adults, 12 mm and larger (Section 10).

This section is concerned chiefly with growth as determined from cohort tagging. Such growth estimates can be affected by dispersal and mortality (see also Section 9). Size-specific dispersal is disregarded for two reasons. First, monthly size-frequency histograms of untagged winkles (Section 6) indicated no size-specific vertical migration. Second, tagged snails that had dispersed from site A were occasionally retrieved at sites L and D, but no particular sizes were encountered out of proportion to numbers released.

Methods

i. tagging

Cohorts having mean sizes of approximately 6.5 and 9.5 mm were released together on twelve occasions representing ten months of the year, and were supplemented occasionally with other sizes. For individual tagging, see Section 10.

Snails for cohort tagging were extracted from the regular samples (Section 6) or were specially collected from site L. Shell length was measured as usual (Section 4), snails of the desired 1 mm interval were selected, and shell lip thickness was recorded. Only snails judged to be growing were tagged. Snails larger than 12.0 mm were sexed live as explained below. Snails were tagged and released as promptly after collection as possible.

Living adults firmly gripping some substratum may, if taken by surprise, permit the shell to be raised enough to reveal the penis (pers. obs., Reimchen 1974). This technique demands a nice touch and much time. No relaxant drug was found suitable or deemed appropriate.

Shells (but not bodies or apertures) were blotted and small areas of the flattened spire were gently cleaned with fine sandpaper: "3M Wetordry Tri-M-ite" P180 grit waterproof silicon carbide coated abrasive (Minnesota Mining and Manufacturing Corporation, 3M United Kingdom Ltd., 3M House, 28 Great Jackson St., Manchester M15 4PA). Care was taken not to break the shells, especially when sanding near the apex. Small shells were thin and fragile, and all were delicate near the apex, so snails smaller than about 6.0 mm could not be tagged. Tags consisted of one or two small dots of "Humbrol non-poisonous" enamel model paint (Humbrol Ltd., Hull, England). Each cohort was assigned a unique code based on colour and location (whorl). Adult sexes were coded separately. To inhibit movement and contact with wet paint, snails were placed on trays of sandpaper in a cool constant-temperature room.

Snails were then refreshed in ambient sea water with recently-collected <u>Ascophyllum nodosum</u>. Normal winkles rapidly extended the foot, clambered onto the seaweed, and began to feed. Any snail failing to do so was discarded - such individuals were rare.

Tagged snails were released at site A at the next available low tide, preferably shortly after the water had receded so the seaweed was cool and damp. Part of the dense <u>A. nodosum</u> was lifted aside, the winkles were sprinkled over the rest, and the weed was replaced. Winkles attached to each other were separated, except when copulating, to increase the likelihood of attaching to the alga before the tide returned.

Marked snails were recaptured during normal sampling at site A, and occasionally at L and D. Snails were taken to the laboratory on fresh <u>A. nodosum</u> and were sorted at once. Tagged shells were measured, judged to be growing or not, and kept on cool damp fresh weed in the constant-temperature room until release, usually at the next low tide.

Missing or badly damaged paint spots were replaced. Missing spots were easily detected from the sanded patches and from paint traces. Tag loss was of the order of one or two percent - that is, of all the tagged winkles recaptured on a given occasion, regardless of cohort, one or two in a hundred would require retagging. Tag loss was lowest when paint was applied sparingly.

Some empty shells, whole or broken, were recovered at site A or occasionally at L or D. Others were found by sieving the fine sediment that occasionally accumulated in clefts and depressions in outcrop A. Owing to dense weed cover it was not practicable to search widely for missing snails (Section 9).

ii. analysis

Mean sizes and standard deviations were calculated; when some members of a cohort were judged not to be growing, these statistics were calculated separately for the growing component and the complete sample. Means were plotted against date, although means based on five or fewer snails were considered unhelpful. Comparisons were facilitated by standardising dates to days elapsed from release.

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At this point a brief exposition of measures of growth is needed.

Consider an immortal snail. Measure its length at fixed time intervals. Denote the growth increment, i.e. the difference between lengths on any two occasions T_1 and T_2, as $(L_2 - L_1)$. If final size is unconstrained, if growth is unaffected by fluctuations in weather or food supply etc., and if growth increment is a fixed amount regardless of starting length L_1, then growth may be expressed in some absolute measure such as mm per day.

Otherwise a more elaborate description is needed: in *Littorina obtusata* growth increment is not fixed (this Section). The well-known growth equations of von Bertalanffy (e.g., 1960) were considered likely to provide an adequate approximation to winkle growth; see Hughes (1980) for an evaluation in *L. nigrolineata*.

The equation appropriate to length growth in L. obtusata is

$$L_T = l^\infty - (l^\infty - l_o)e^{-kT} \qquad (1)$$

and if $l_o = 0$, $$L_T = l^\infty(1 - e^{-kT}) \qquad (2)$$

where L_T is length at age T, l_o is hatching size, e is 2.71828 the base of natural logarithms, k is a growth parameter, and l^∞ (called L infinity) is the limited final size approached asymptotically with time. Growth begins for the present purposes at hatching size 0.45 mm, and successive sizes 1.5, 2.5, 3.5 mm etc. are achieved increasingly slowly.

These equations use age from hatching. This is unknown in field specimens. Because size at tagging cannot be used as l_o for mathematical reasons, it is necessary to employ a modified equation based on two lengths L_1 and L_2 measured at times T_1 and T_2 respectively. The derivation is given in Hughes (mimeo) and the equation is

$$\frac{l^\infty - L_1}{l^\infty - L_2} = e^{k(T_2 - T_1)} \qquad (3)$$

from which $$k = \frac{1}{T_2 - T_1} \cdot \log_e \frac{l^\infty - L_1}{l^\infty - L_2} \qquad (4)$$

Now l^∞ may differ between populations or individuals. The computed estimate of k depends on the chosen l^∞. k has units of inverse time (e.g., days^{-1}) and is constant throughout life.

The growth rate that varies with length (and, by implication, age) is dl/dt. That is, for some uniform time interval, the curve of $(L_2 - L_1)$ against L_1 is expected to be a straight line with slope -k.

If k appears to vary during life, or if dl/dt is not linear, the model may appear to be violated. This may not be so (Hughes 1980; Sainsbury 1980): the model assumes for instance that assimilation and metabolic rates are respectively proportional to the square and cube of some standard linear measure, but these assumptions are not necessarily valid. Changes in shape with increasing size will also introduce non-linearities. L. obtusata becomes increasingly vertically compressed during the first few mm of growth after hatching (Section 4), in contrast to the relatively constant shell shape in L. nigrolineata (Hughes 1980, who discusses this issue in more detail). Seasonal effects are considered in the discussion.

For the purposes of this Section, variables L_1 and L_2 are cohort mean lengths. The rigour of using means in equations devised for individuals is considered in the discussion.

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l^{∞} calculated using as test data the March 1977 extended cohort was approximately 21 mm. Because fewer than one L. obtusata in ten thousand grows to 18 mm at site A, this value was unreasonably high (and predicted unreasonable longevity), and so would yield unrealistically low k values. Accordingly, l^{∞} was set at 18.0 mm in all calculations.

k was computed for suitable intervals, generally of the order of four months. Only snails considered growing were used. Estimates of k were not subjected to pairwise statistical tests, but graphical comparisons and rank correlations (Kendall's tau) were used to identify relationships between k values and time of year or snail size. For clarity, details of rank correlation tests are furnished with the results.

"Negative growth" was disallowed. L. obtusata is not subject to shrinkage by abrasion, and broken lips are readily recognised, so an apparent decrease in mean size of shells judged to be growing reflects mortality, dispersal, or cessation of growth by the larger winkles. If k values had to be computed for comparative purposes, then size at the end of the interval was set to some appropriate previous value, provided that numbers had not dropped drastically. For example, if mean lengths at times T_1 to T_5 were 11.0, 12.0, 12.5, 12.9 and 12.6 mm, where the decrease from T_4 to T_5 was caused by some large snails growing at T_4 but not at T_5, and if k had to be computed for T_2 to T_5, then length at T_5 would be set to 12.9 mm. (For some purposes it was more informative to use mean lengths based on all available snails rather than only those growing.) Any such cases are clearly identified in the results.

Results

Results are presented in the following sequence. First, the 6.5 and 9.5 mm cohorts. In part (ii), they are compared. Parts (iii) to (vi) report the extended cohorts of September 1976, March 1977, April 1977, and July 1977 respectively. These are compared in part (vii). Results are summarised in the next subsection.

i. 6.5 and 9.5 mm cohorts

Cohorts with mean sizes of approximately 6.5 and 9.5 mm were released during 1976 in February, March, April, May, August, September, October and November, and during 1977 in April, May, June and July. These sizes were also included in the four extended cohorts (parts iii to vi).

Growth curves extended until a cohort went extinct or until the last sample, 8 October 1977. Figures 11 to 22 are simplified. Entries based on one or two measurements are generally omitted. Entries based on three to five snails are shown with special symbols and without standard deviations. The cut-off number 5 is arbitrary.

Gales in September 1976 caused a sharp decline in numbers and a temporary halt or reduction in growth. The 6.5 mm line in Figure 13 (April 1976) shows this effect particularly clearly. "Negative growth" as in the corresponding 9.5 mm line is an artefact (see methods).

Inspection of early portions of these curves suggests that in general growth proceeds at similar rates from 6.5 and 9.5 mm, and that cohorts released in springtime grow faster than those released in summer or autumn.

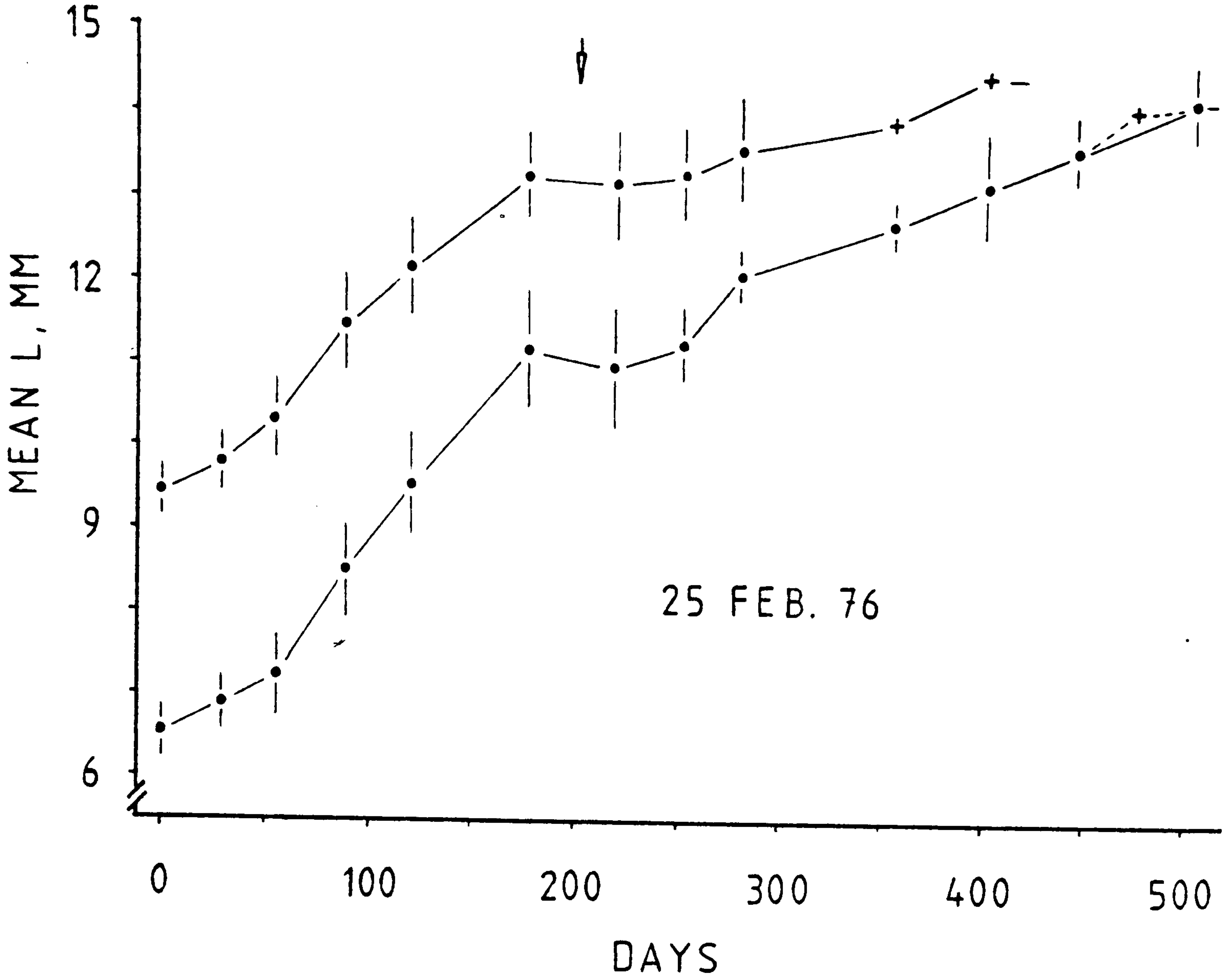
k varied seasonally, with the highest values for cohorts released in spring and the lowest in late summer or autumn (Tables 18 and 19). k was sometimes computed for different segments of the same curve to allow comparisons between cohorts growing concurrently. k values in Table 18 are from release except as follows. (1) 6.99 mm, 123 days from April 1976: March cohort days 24-147. (2) 7.23 mm, 123 days from April 1976: February cohort days 53-176. (3) 6.59 mm, 62 days from September 1976: August cohort days 45-107. (4) 7.68 mm, 119 days from November 1976: September cohort days 62-181. k values in Table 19 are from release except as follows. (5) 10.09 mm, 123 days from April 1976: as (1). (6) 10.33 mm, 123 days from April 1976: as (2). (7) 10.20 mm, 119 days from November 1976: October cohort days 40-159. (8) 10.42 mm, 119 days from November 1976: as (4).

Figures 11 to 22

Cohort growth curves

Figures 11 to 22. Cohort mean sizes plotted against elapsed time, shown plus or minus one standard deviation. Crosses represent 5 or fewer growing snails (data, Appendix Table 5). Some curves are simplified as explained in text. Arrow denotes September gales: location is inexact. Extra cohorts in Figure 19 are discussed in part (v).

Figure 11. Cohorts released 25 February 1976
Figure 12. Cohorts released 25 March 1976
Figure 13. Cohorts released 21 April 1976
Figure 14. Cohorts released 31 May 1976
Figure 15. Cohorts released 16 August 1976
Figure 16. Cohorts released 30 September 1976
Figure 17. Cohorts released 22 October 1976
Figure 18. Cohorts released 19 November 1976
Figure 19. Cohorts released 9 April 1977
Figure 20. Cohorts released 15 May 1977
Figure 21. Cohorts released 18 June 1977
Figure 22. Cohorts released 18 July 1977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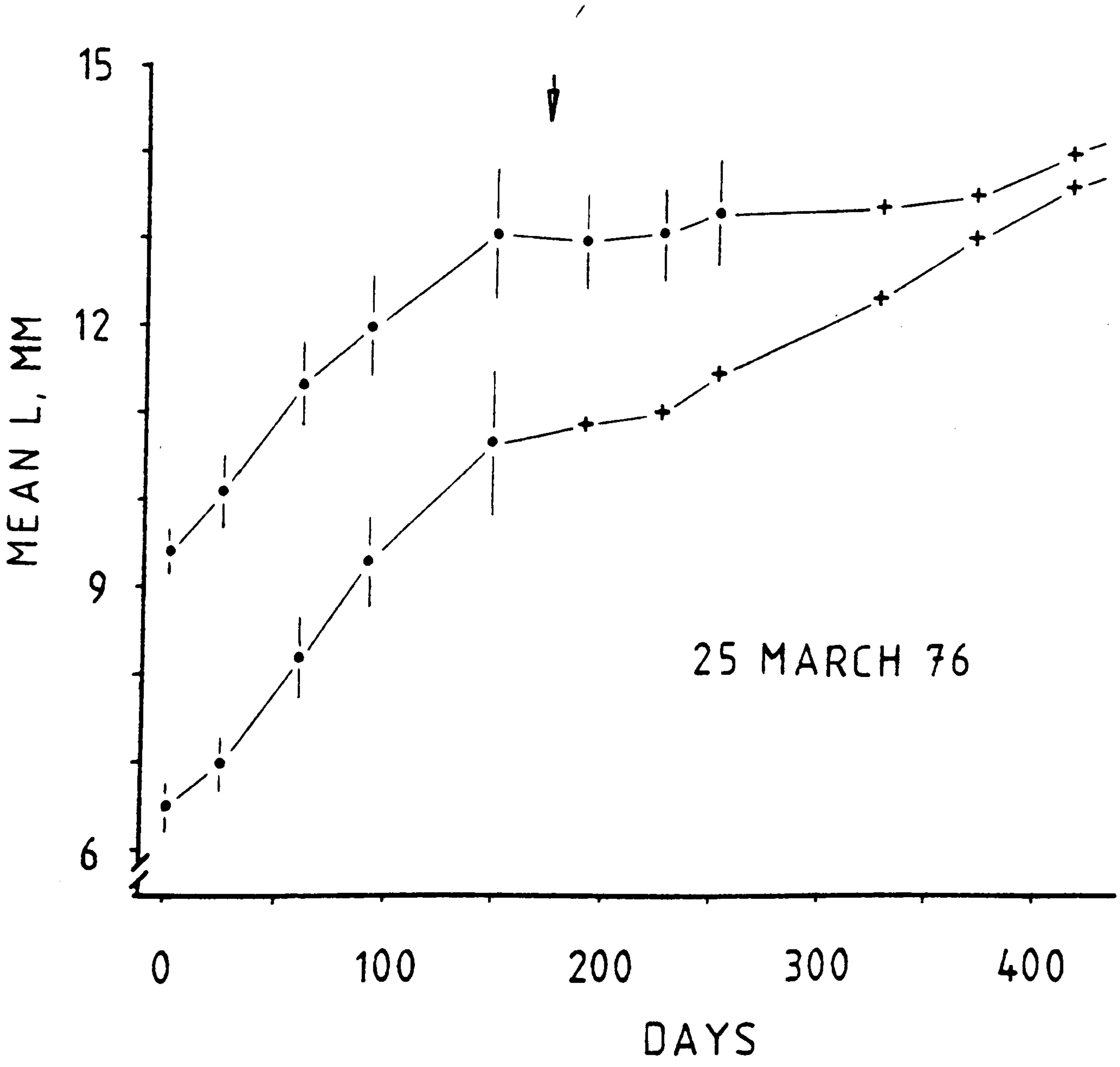
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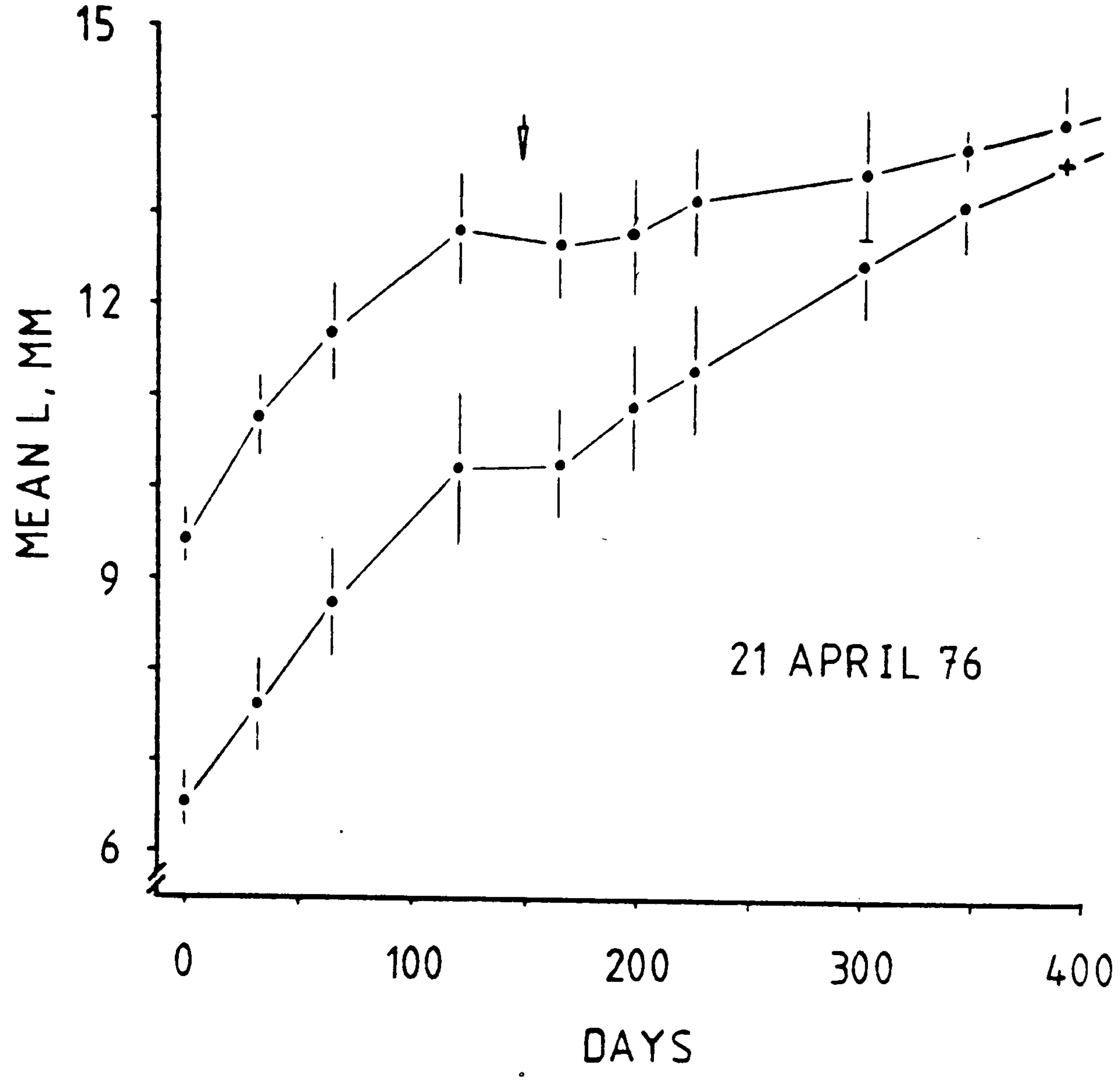
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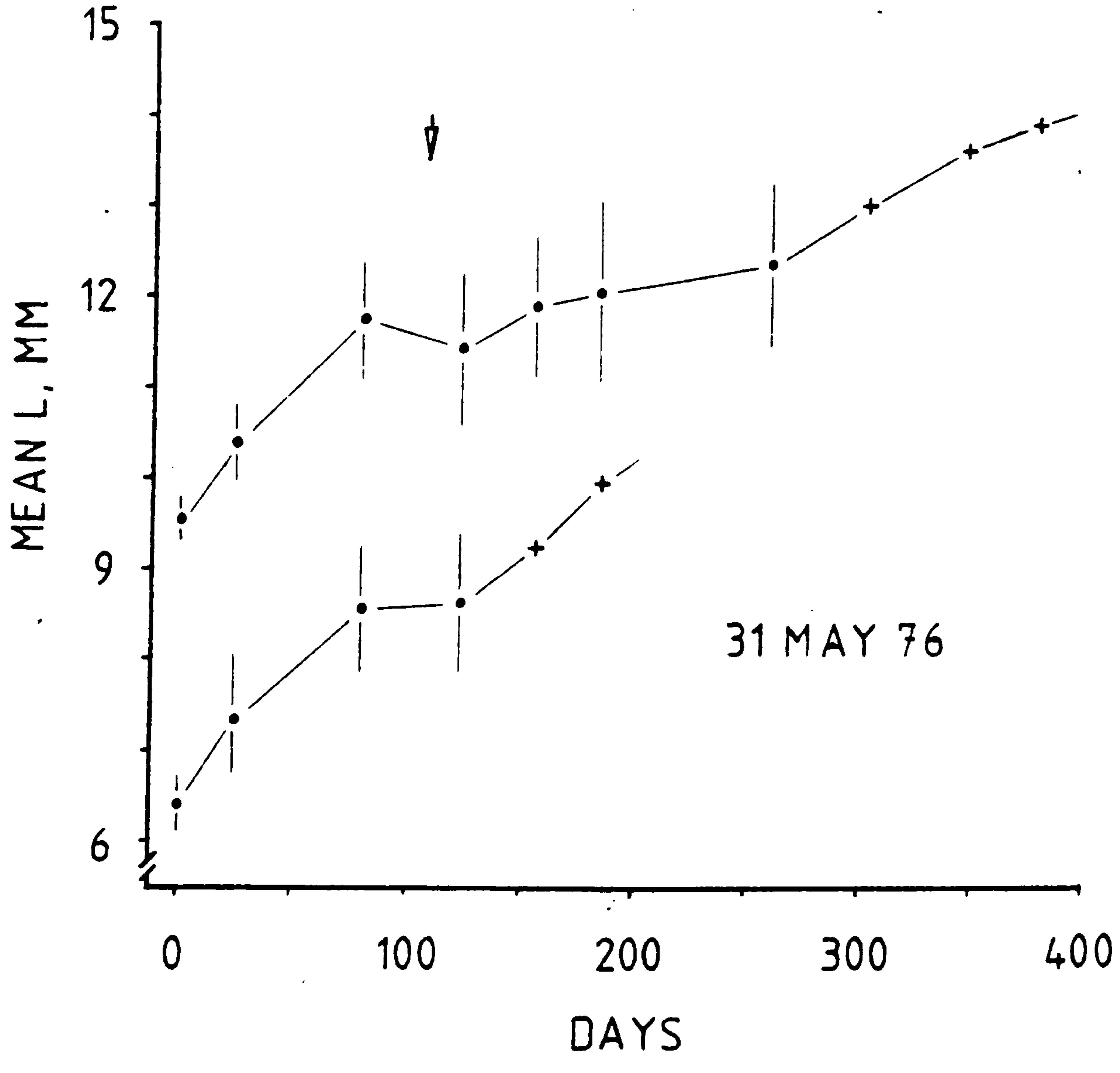
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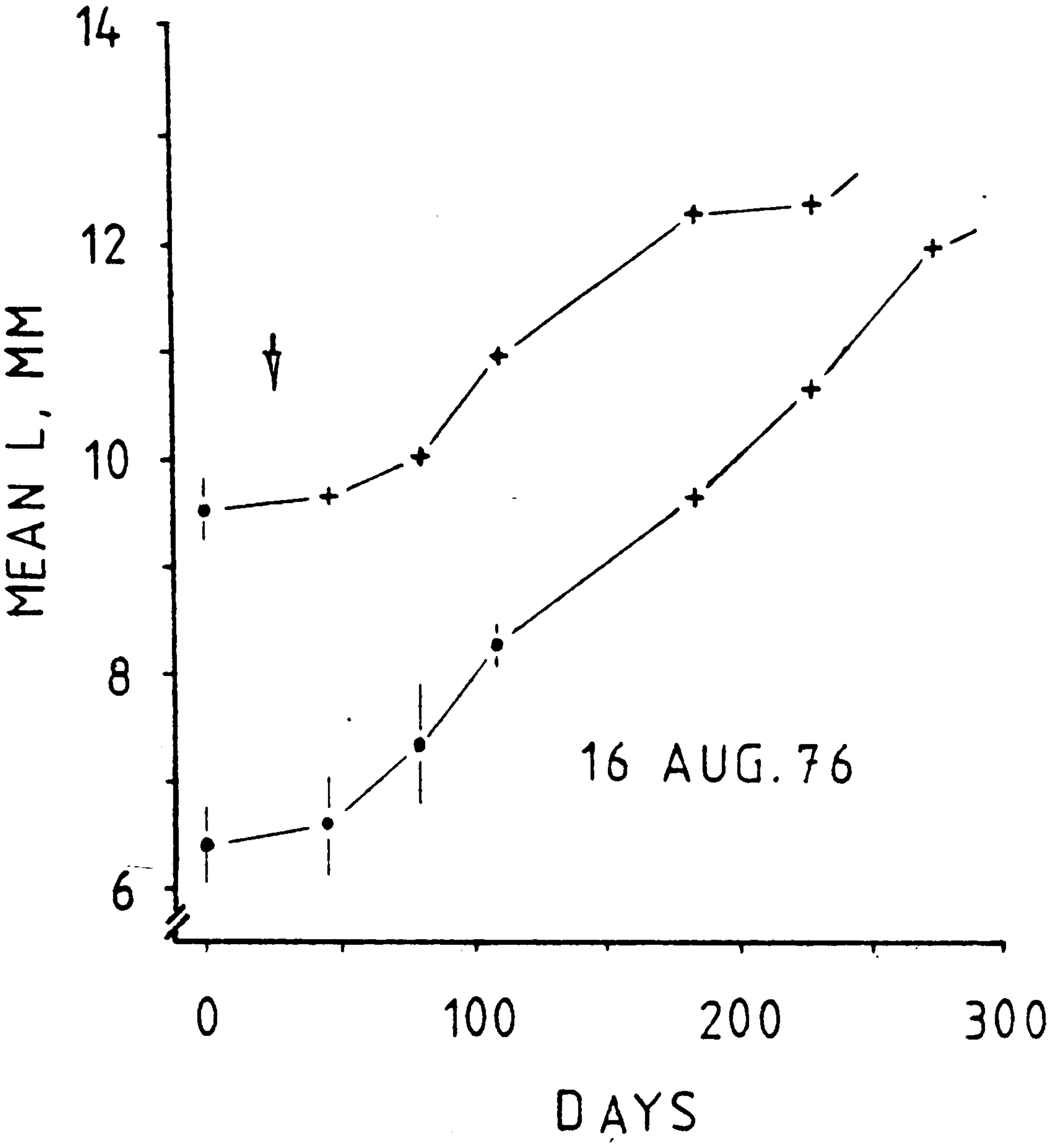

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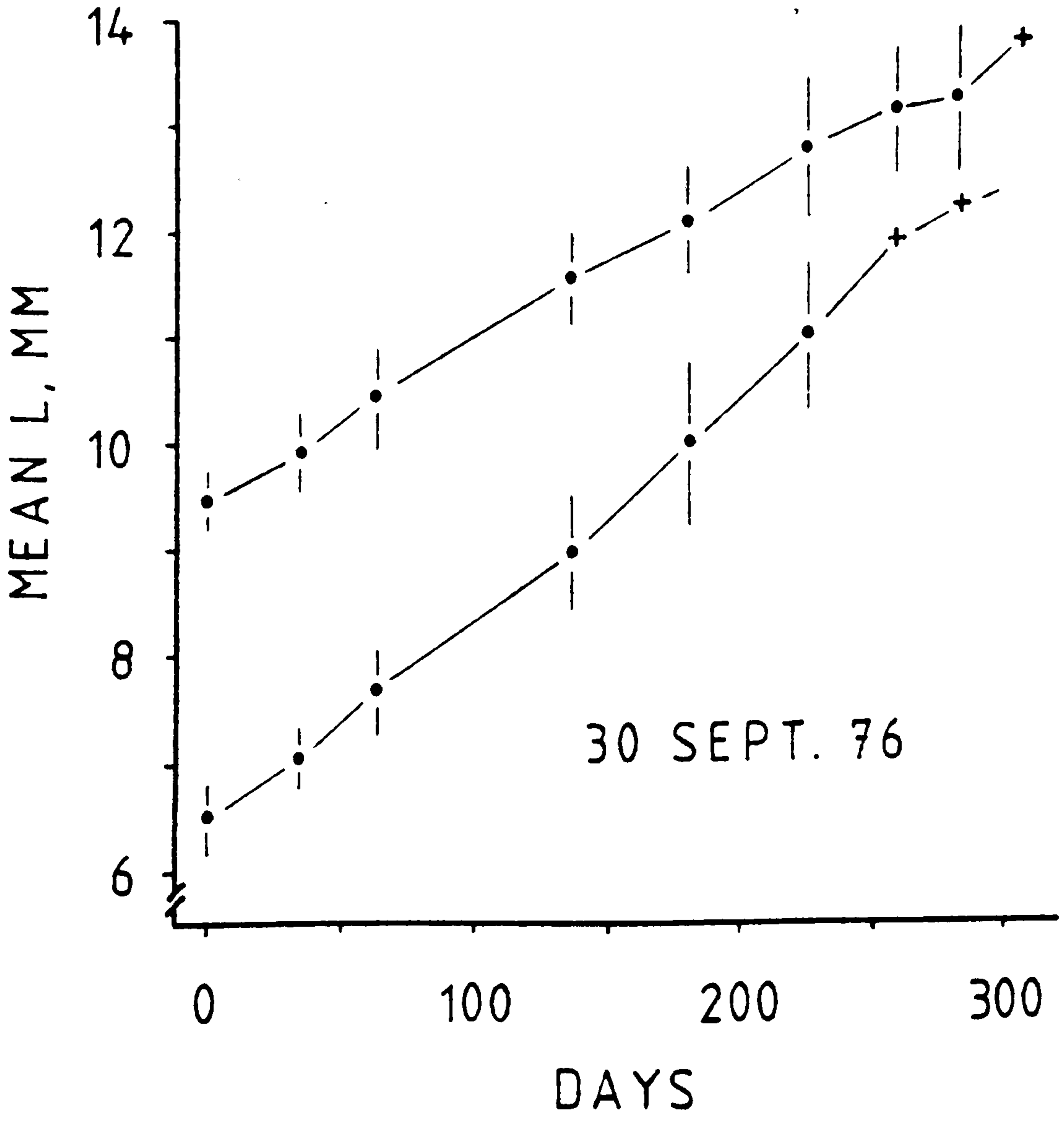

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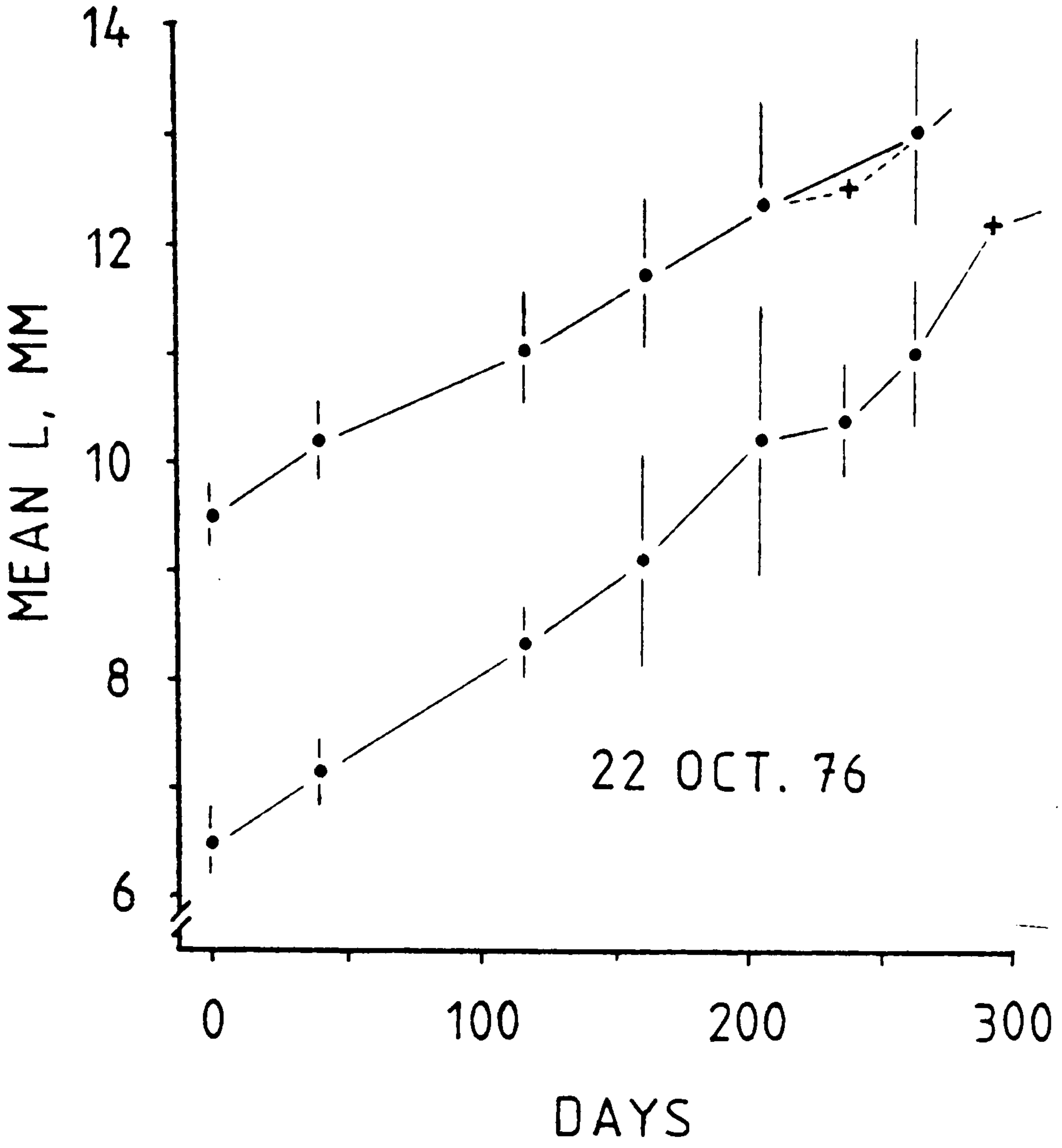
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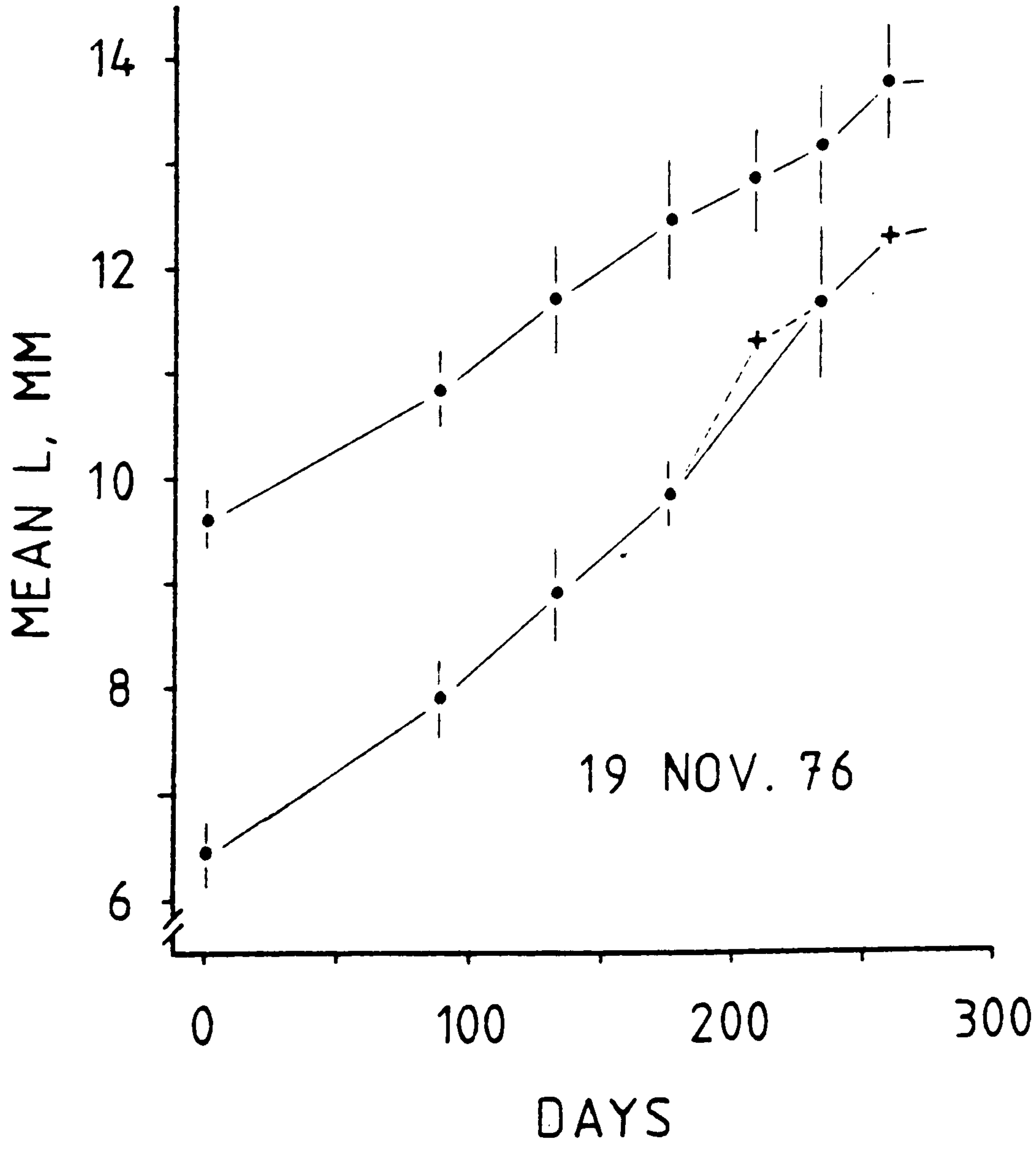
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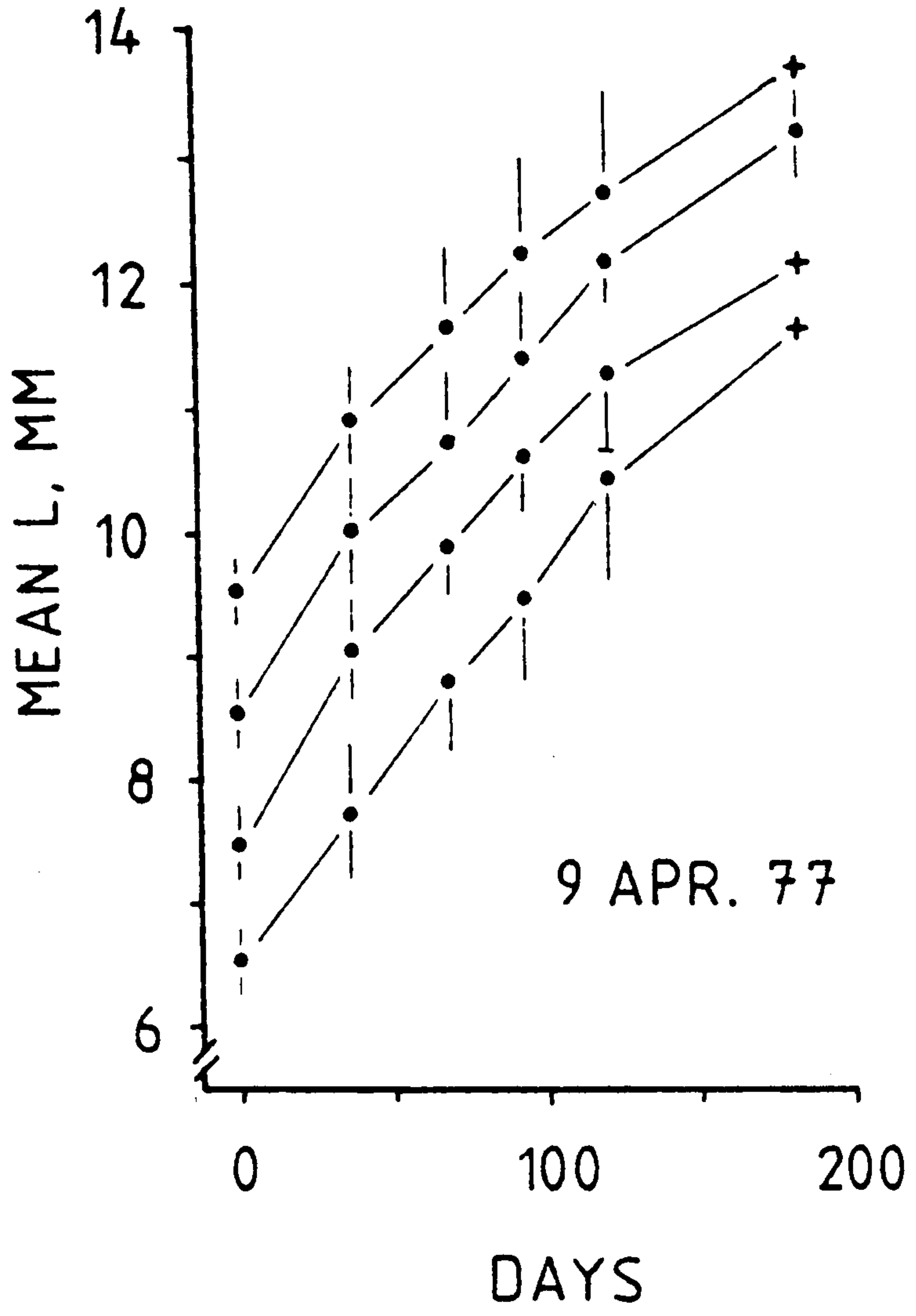
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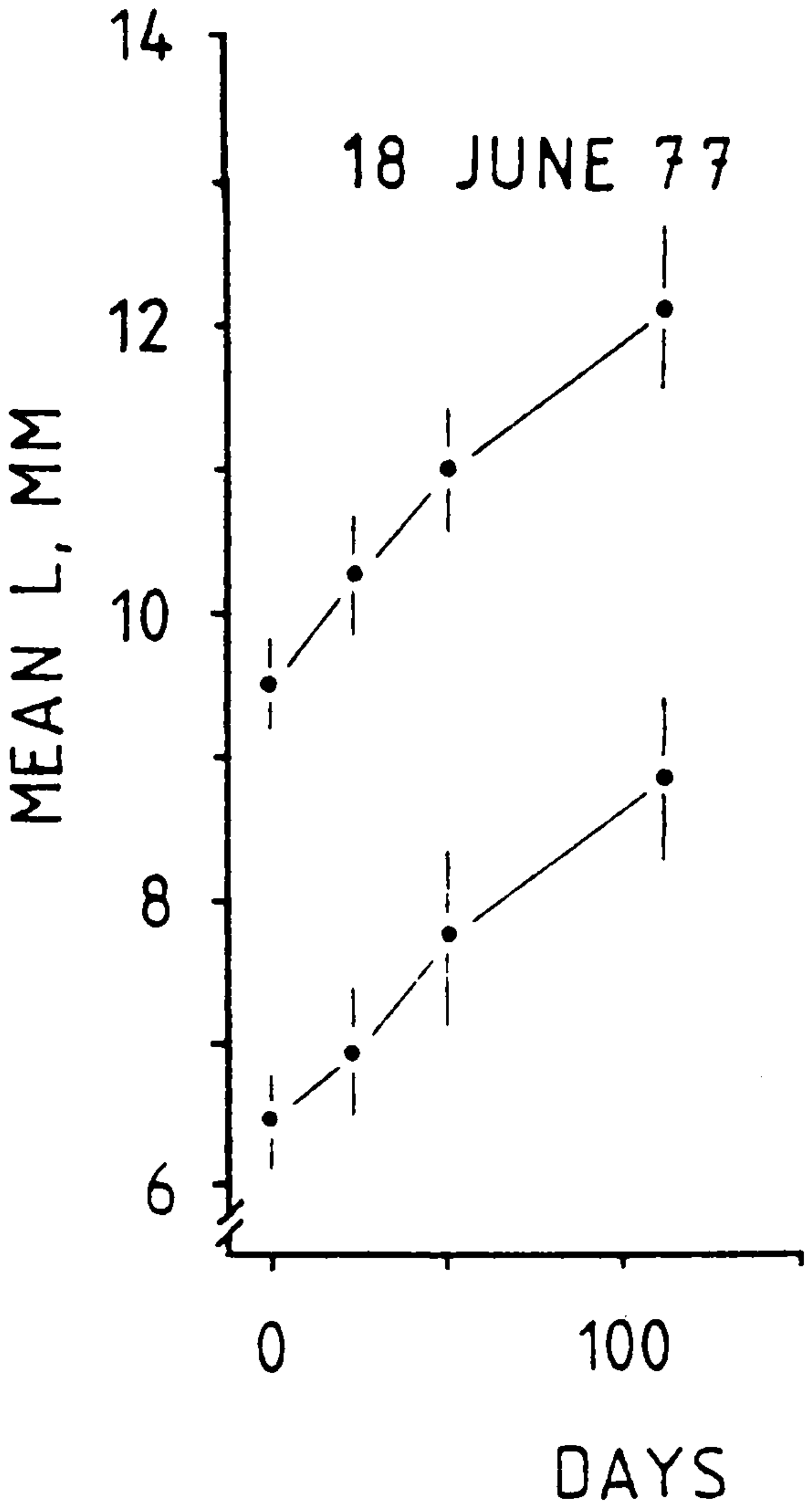
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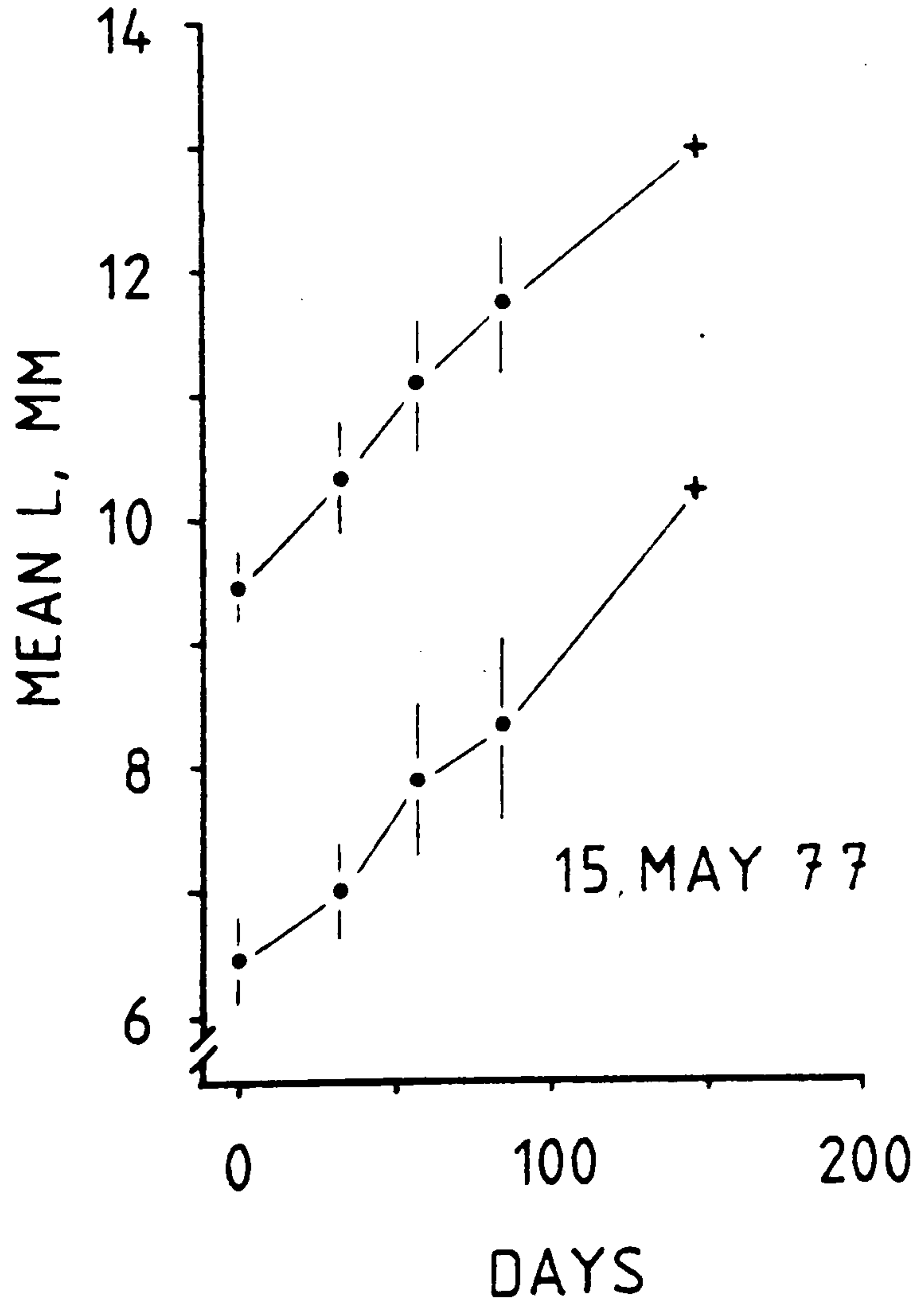
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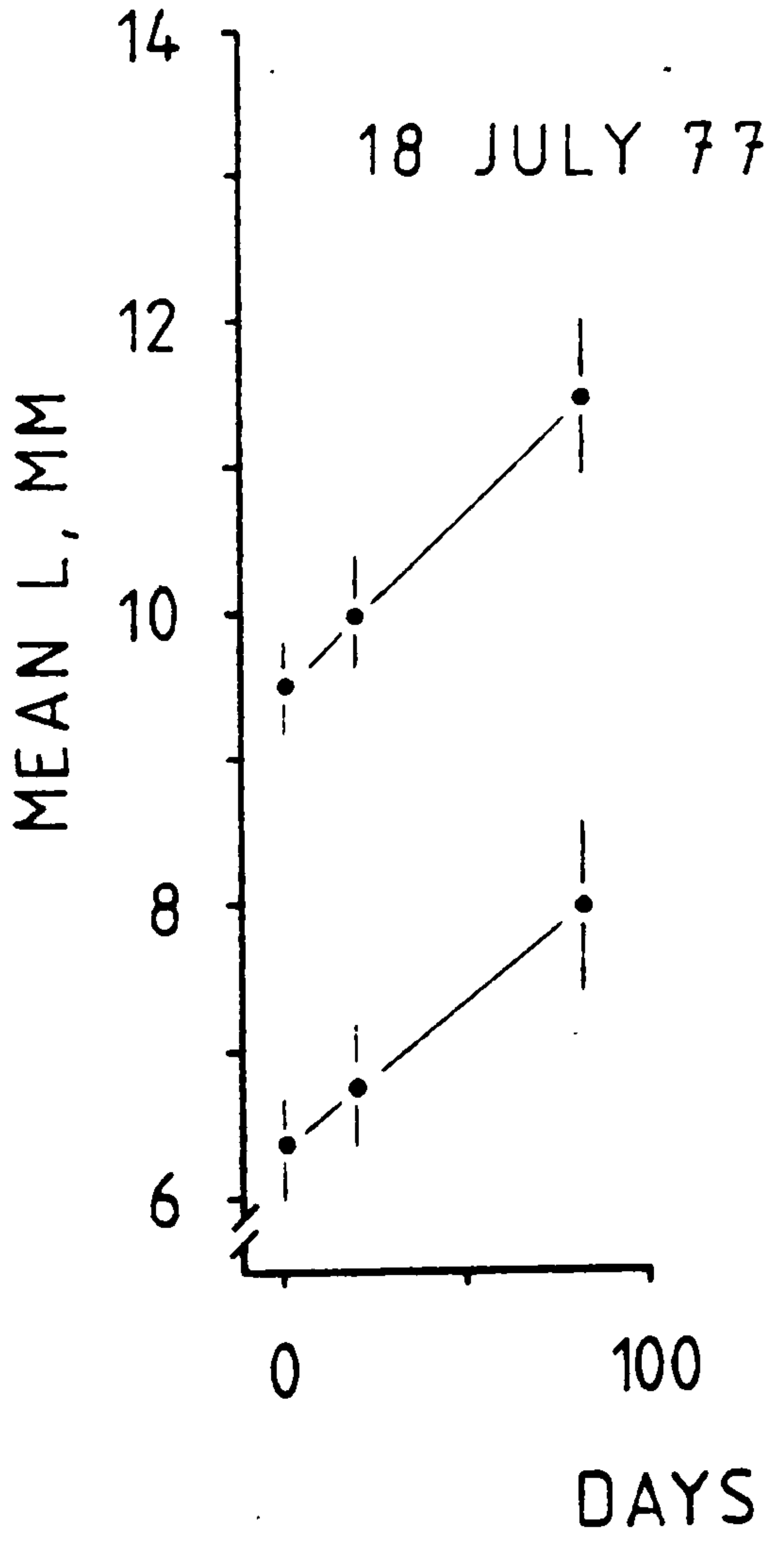
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MEAN L, MM
18 JULY 77
0
100
DAYS

Table 18

6.5 mm cohort k values

Table 18. k calculated from mean lengths given in Appendix Table 5. Values in parentheses are extracted from extended cohorts. Values marked x are extracted from previous 6.5 mm cohorts: see text. k, growth parameter. L_1, initial shell length, mm. T, interval over which k was computed, days. Only growing snails were used.

Month	1976			1977		
	L_1	T	k	L_1	T	k
F	6.53	176	0.0030	-	-	-
M	6.50	147	0.0031	(6.40	129	0.0026)
A	6.56	120	0.0032	6.53	120	0.0035
	x 6.99	123	0.0033			
	x 7.23	123	0.0038			
M	6.41	80	0.0025	6.46	84	0.0021
J	-	-	-	6.42	112	0.0021
J	-	-	-	6.32	82	0.0019
A	6.40	107	0.0016			
S	6.48	137	0.0018			
	(6.59	137	0.0015)			
	x 6.59	62	0.0026			
O	6.48	159	0.0016			
N	6.43	131	0.0018			
	x 7.68	119	0.0021			

Table 19

9.5 mm cohort k values

Table 19. k calculated from mean lengths given in Appendix Table 5. Conventions as in Table 18.

Month		1976			1977	
	L_1	T	k	L_1	T	k
F	9.43	176	0.0034	-	-	-
M	9.40	147	0.0038	(9.51	129	0.0036)
A	9.45	120	0.0042	9.51	120	0.0040
	x 10.09	123	0.0039			
	x 10.33	123	0.0040			
M	9.52	80	0.0038	9.47	84	0.0037
J	-	-	-	9.50	112	0.0033
J	-	-	-	9.48	82	0.0032
A	9.52	-[a]	-[a]			
S	9.47	137	0.0021			
	(9.41	137	0.0018)			
O	9.51	159	0.0019			
N	9.62	131	0.0022			
	x 10.20	119	0.0019			
	x 10.42	119	0.0021			

Note: a. Heavy mortality in the first interval makes k unreliable - see long-term value in Table 20.

Case 1, 2, 5 and 6 allow comparisons within two sets of three cohorts growing from April to August 1976. Compared to the April 1976 cohort, March and February cohorts have increasingly large starting sizes in April, but k increases correspondingly only in the 6.5 mm set.

Case 3 was calculated because the first segment of the August 1976 cohort was much shallower than the two subsequent segments. The interval is, however, only 62 days.

Cases 4, 7 and 8 allow comparisons within two sets of three cohorts growing from November to April; October 6.5 mm k was not recalculated. September, October and November k values are similar within each set.

k values calculated for much longer intervals when numbers permit (Table 20) assume a more narrow range. When an extended interval now includes autumn, k is lower than before, but when it now includes winter and spring, k is higher. It is not possible to say how much of the decrease may be attributable to the September 1976 gales.

Table 20

6.5 and 9.5 mm cohort long-term k values

Table 20. k calculated from mean lengths given in Appendix Table 5. Conventions as in Table 18. All cohorts begin in 1976. Interval extends from release to decay of number below 6. Cohorts before September may have been affected by gales: see text.

Month	6.5 mm			9.5 mm		
	L_1	T	k	L_1	T	k
F	6.53	444	0.0022	9.43	280	0.0024
M	-	-	-	9.40	251	0.0024
A	6.56	344	0.0025	9.45	389	0.0021
M	6.41	122	0.0017	9.52	259	0.0016
A	-	-	-	9.52	226	0.0018[a]
S	6.48	226	0.0022	9.47	284	0.0021
	x 6.59	181	0.0025[b]			
O	6.48	262	0.0019	9.51	262	0.0021
N	6.43	176	0.0020	9.62	261	0.0026

Notes: a. N reduced to 5 in the first interval; this value based on N = 3 and not regarded as comparable to the others.

b. August N reduced in first interval but growth curve is regular until April; this value is for days 45 to 226.

ii. comparison of 6.5 and 9.5 mm cohorts

To test for association between k values for 6.5 and 9.5 mm cohorts, Kendall's rank correlation coefficient tau was calculated (Sokal & Rohlf 1969, pp. 533 ff, method 3a). Thirteen pairs of values from Tables 18 and 19 were used: eleven for growth from day 0 of monthly cohorts excluding August 1976, and two for growth from day 0 of the September 1976 and March 1977 extended cohorts. Ties were split using unrounded k. Tau was 0.846 which, when a normal approximation is applied, corresponds to 4.03 standard deviation units: $P < 0.0001$. The null hypothesis, that there is no correlation between ranks for corresponding 6.5 and 9.5 mm cohorts, was rejected. A good month for one size was a good month for the other.

iii. September 1976 extended cohort

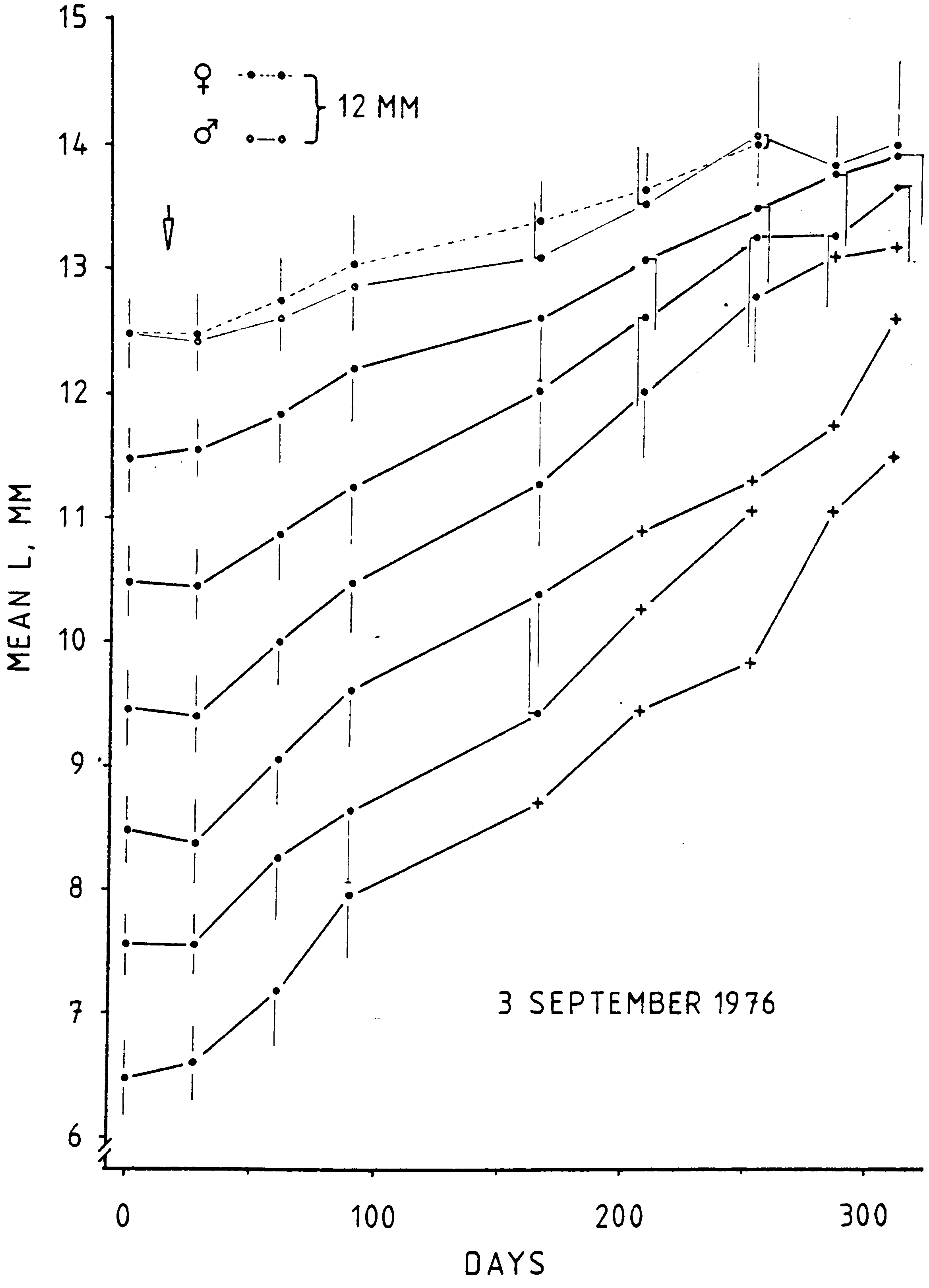
Numbers in all eight component cohorts of the first extended cohort, released 3 September 1976, were reduced substantially after the gales mentioned previously (data, Appendix Table 6), but fortunately large numbers had been released. Cohort starting sizes were 6 through 11 mm, and 12 mm males and females.

All sizes grew briskly after 30 September (Figure 23). Growth in some cohorts slackened after 1 December (day 89), and increased again after 14 February (day 164), but by then few of the 6.5, 7.5 and 8.5 mm cohorts remained.

<u>Figure 23</u>

September 1976 extended cohort growth curves

Figure 23. Growth curves for component cohorts of extended cohort released 3 September 1976. Adult males and females are combined from day 253. Some curves are truncated (data, Appendix Table 6). Each vertical bar is one standard deviation. Conventions are otherwise as in Figures 11 to 22.



♀ •····•
♂ ∘—∘
12 MM
3 SEPTEMBER 1976
MEAN L, MM
DAYS
15
14
13
12
11
10
9
8
7
6
0
100
200
300

Table 21

September 1976 extended cohort growth increments

Table 21. Growth increments and associated ratios for growing snails only (data, Appendix Table 6). L_1, initial length, mm. T, time interval from 30 September. Inc, increase in mean length, mm. Inc/L_1, proportional growth, mm per mm. Inc/T, growth rate, mm per day. Adult data are shown for males (M), females (F), and totals (MF): note that sex ratio may bias totals.

L_1	T					
	34			62		
	Inc	Inc/L_1	Inc/T	Inc	Inc/L_1	Inc/T
6.59	0.58	0.0880	0.0171	1.36	0.2064	0.0219
7.56	0.68	0.0899	0.0200	1.08	0.1429	0.0174
8.38	0.65	0.0776	0.0191	1.22	0.1456	0.0197
9.41	0.60	0.0638	0.0176	1.07	0.1137	0.0173
10.46	0.42	0.0402	0.0124	0.79	0.0755	0.0127
11.54	0.30	0.0260	0.0088	0.67	0.0581	0.0108
12.43 M	0.20	0.0161	0.0059	0.44	0.0354	0.0071
12.48 F	0.26	0.0208	0.0076	0.56	0.0449	0.0090
12.45 MF	0.23	0.0185	0.0068	0.50	0.0402	0.0081

Growth increments were calculated for two intervals, each beginning at 30 September: 34 days, to 3 November, and 62 days, to 1 December. In the first month growth increment declined steadily with increasing size except for the 6.5 mm cohort (Table 21). Females grew slightly more than males. After two months, the pattern in the smaller sizes was more erratic, but overall larger snails grew less. Females outgrew males as before. Irregular size intervals contributed to these eccentricities. When increments were divided by starting size, proportional growth displayed a somewhat smoother pattern, generally declining with increasing starting size (Table 21, "Inc/L_1"); as before, females outgrew males. Growth rates, increments divided by time interval, are compared in part (vii).

Table 22

September 1976 extended cohort k values

Table 22. k calculated from mean lengths of growing snails only (data, Appendix Table 6). L_1, initial length, mm. Adult data are shown for males (M), females (F), and totals (MF): note that sex ratio may bias totals. Both intervals begin on 30 September: see text.

L_1	k, 137 days	k, 226 days
6.59	0.0015	-
7.56	0.0014	-
8.38	0.0017	-
9.41	0.0018	0.0023
10.46	0.0017	0.0021
11.54	0.0014	0.0017
12.43 M	0.0010	0.0016
12.48 F	0.0014	0.0015
12.45 MF	0.0011	0.0016

k values were calculated for two intervals, both beginning at 30 September: 137 days (to 14 February) and, where numbers permitted, 226 days (to 14 May). In the shorter term there was no clear trend with starting size (Table 22); 12.5 mm females had higher k than males. After 226 days, k declined with increasing starting size, and adult sexes performed very similarly.

Only three cohorts survived in numbers to day 338 (7 August), and none maintained numbers to day 400 (8 October) when sampling ended. The 10.5, 11.5 and 12.5 mm cohorts were all about 14 mm in mean size, but numbers of each had stopped growing by day 286 (16 June).

iv. March 1977 extended cohort

The second extended cohort was released on 4 March 1977. A particular effort was made to tag large numbers of adults (12.5, 13.5 and 14.5 mm) so that workable numbers of growing adults might supplement or replace September large survivors in the summer. The smallest size, 6.5 mm as usual, was disappointingly scarce (Appendix Table 7).

All cohorts began to grow steadily (Figure 24). Some cohorts showed a slackening between May and June, but others did not; meanwhile, numbers dropped sharply in several (see also Section 9). Adult cohorts 13.5 and 14.5 mm still had members growing in August.

Growth increments and associated ratios for the first month followed a clear pattern, increasing with size to the 8.5 mm cohort and declining smoothly in larger sizes (Table 23). Males outperformed females slightly in the 12.5 and 13.5 mm cohorts, but the largest females outgrew them.

Figure 24

March 1977 extended cohort growth curves

Figure 24. Growth curves for component cohorts of extended cohort released 4 March 1977. Adult males and females are combined. Upper set ("all") include snails not necessarily growing (data, Appendix Table 7). Conventions are otherwise as in Figure 23.

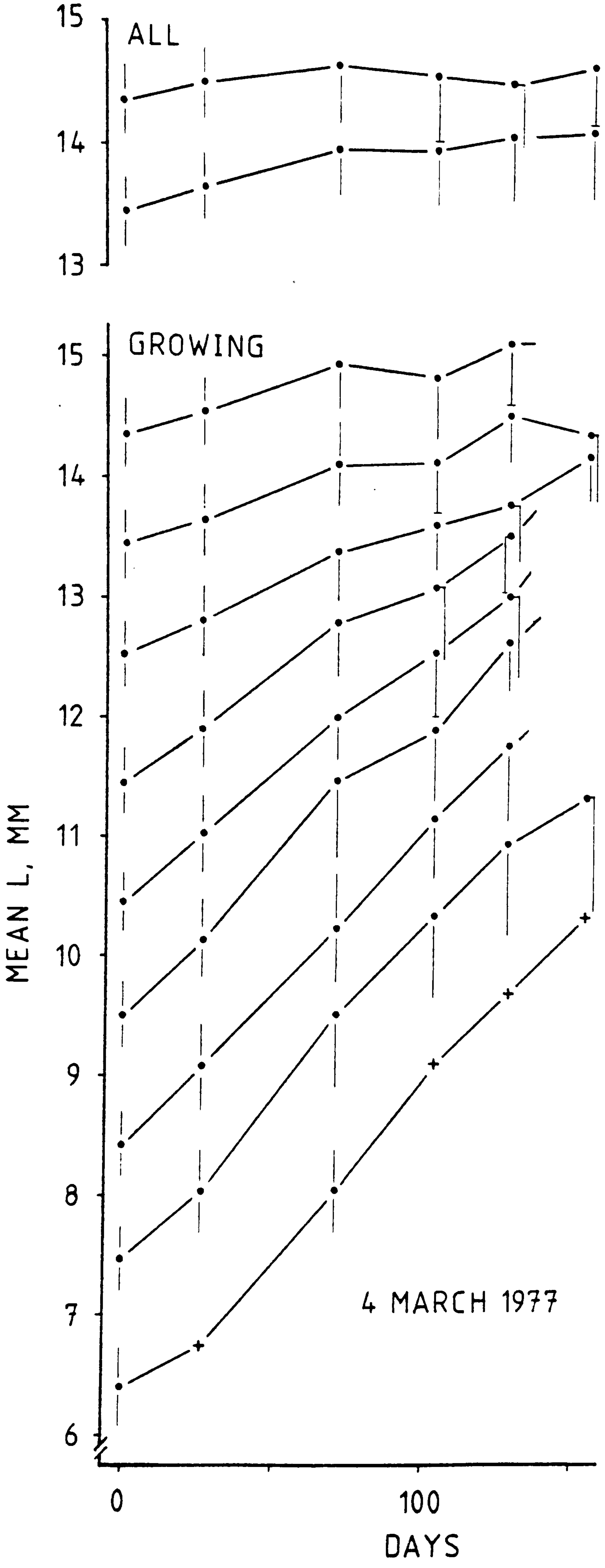

15
ALL
14
13
GROWING
15
14
13
12
11
10
9
8
7
6
MEAN L, MM
4 MARCH 1977
0
100
DAYS

Table 23

March 1977 extended cohort growth increments

Table 23. Growth increments and associated ratios for growing snails only (data, Appendix Table 7). Intervals are from release; other conventions as in Table 21.

L_1	T					
	26			71		
	Inc	Inc/L_1	Inc/T	Inc	Inc/L_1	Inc/T
6.40	0.32	0.0500	0.0123	1.62	0.2531	0.0228
7.47	0.55	0.0736	0.0212	2.02	0.2704	0.0285
8.42	0.65	0.0772	0.0250	1.81	0.2150	0.0255
9.51	0.62	0.0652	0.0238	1.96	0.2061	0.0276
10.45	0.57	0.0545	0.0219	1.55	0.1483	0.0218
11.46	0.44	0.0384	0.0169	1.33	0.1161	0.0187
12.52 M	0.29	0.0232	0.0112	0.94	0.0751	0.0132
12.54 F	0.26	0.0207	0.0100	0.79	0.0630	0.0111
12.53 MF	0.28	0.0223	0.0108	0.87	0.0694	0.0123
13.40 M	0.24	0.0179	0.0092	0.74	0.0552	0.0104
13.47 F	0.18	0.0134	0.0069	0.66	0.0490	0.0093
13.44 MF	0.20	0.0149	0.0077	0.69	0.0513	0.0097
14.33 M	0.13	0.0091	0.0050	0.47	0.0328	0.0066
14.39 F	0.17	0.0118	0.0065	0.62	0.0431	0.0087
14.36 MF	0.18	0.0125	0.0069	0.59	0.0411	0.0083

After two months, the increment pattern in the small sizes was less regular, but proportional growth declined from the 7.5 mm cohort to the largest adults. The relative performance of males and females was unchanged.

Table 24

March 1977 extended cohort k values

Table 24. k calculated from mean lengths of growing snails only (data, Appendix Table 7). Conventions as in Table 22. Interval is 129 days. Value for 14.33 mm males is underestimate, obtained by setting length at day 129 equal to that of days 71 and 104, 14.80 mm. n.a., not applicable (no males). 71 day value for 14.36 mm totals is heavily influenced by sex ratio (13M/34F).

L_1	k	L_1	k
6.40	0.0026	12.52 M	0.0022
7.47	0.0031	12.54 F	0.0019
8.42	0.0033	12.53 MF	0.0020
9.51	0.0036	13.40 M	0.0023
10.45	0.0032	13.47 F	0.0021
11.46	0.0030	13.44 MF	0.0022
14.33 M	0.0011 (71 days, 0.0019)		
14.39 F	0.0019 (71 days, 0.0027)		
14.36 MF	n.a. (71 days, 0.0025)		

k was calculated for an interval of 129 days from release (Table 24); numbers in several cohorts declined thereafter. Adult k was calculated separately for each sex to avoid any bias caused by sex ratio (Section 7). From 6.5 to 11.5 mm, 129-day k shows a gently peaked pattern with starting size, similar to that of one-month growth rates. k drops suddenly between the 11.5 and 12.5 mm cohorts, from about 0.0032 to about 0.0021 days^{-1}. The relationship between the sexes is as in the increment measures, but the only interval over which numbers of 14.5 mm males permit a fair comparison, 71 days, is rather short. Size at sexual maturity is considered in Section 7.

6.5 to 11.5 mm cohort survival to 8 October was too low to permit computation of a longer-term k. Most surviving adults were no larger than on 7 August, approximately 14 mm (Appendix Table 7).

v. April 1977 extended cohort

The modest third extended cohort consisted of 7.5 and 8.5 mm cohorts released with the regular 6.5 and 9.5 mm cohorts on 9 April 1977 (Appendix Table 8), to supplement the low numbers released in March and to permit more comparisons during the spring growth spurt.

Both cohorts grew steadily and similarly to their companions; all four growth curves are shown in Figure 19.

Growth increments and ratios rose from 6.5 to 7.5 mm and declined to 9.5 mm (Table 25). After two months, growth increment behaved similarly, but proportional growth declined with increasing size.

Table 25

April 1977 extended cohort growth increments

Table 25. Growth increments and associated ratios for growing snails only (data, Appendix Tables 5 and 8). Intervals are from release. Conventions as in Table 21.

L_1	T					
	35			68		
	Inc	Inc/L_1	Inc/T	Inc	Inc/L_1	Inc/T
6.53	1.21	0.1853	0.0346	2.31	0.3538	0.0340
7.50	1.56	0.2080	0.0446	2.38	0.3173	0.0350
8.52	1.49	0.1749	0.0426	2.19	0.2570	0.0322
9.51	1.41	0.1483	0.0403	2.15	0.2261	0.0316

120-day k values (Table 26), when compared with some from other cohorts (chosen largely by survival for more than 100 days after a suitable mean size), support the hypothesis that k varies seasonally, with highest values in spring, as in the corresponding 6.5 and 9.5 mm cohorts (Tables 18 and 19).

As in March, 6.5 mm k appears slightly lower than in the next larger sizes. k for the 6.5 to 9.5 mm cohorts are respectively 0.0035, 0.0037, 0.0041 and 0.0040 days^{-1}. Each is higher than the corresponding March value.

Table 26

April 1977 extended cohort k values

Table 26. k for 7.5 and 8.5 mm cohorts released 9 April 1977, supplementing the usual 6.5 and 9.5 mm cohorts (Tables 18 and 19). Comparative results are from other cohorts: E, extended cohort; X, extracted from a routine 6.5 mm cohort identified at right. L_1, initial length, mm. T, interval, days. Go, starting date.

L_1	T	Go		k	
7.50	120	9 April 1977		0.0037	
7.56	137	3 Sept. 1976	E	0.0014	
7.68	119	1 Dec. 1976	X	0.0021	(Source: Sept. 1976)
7.47	129	4 March 1977	E	0.0031	
7.23	123	18 April 1976	X	0.0038	(Source: Feb. 1976)
8.52	120	9 April 1977		0.0041	
8.38	137	3 Sept. 1976	E	0.0017	
8.36	147	14 Feb. 1977	X	0.0022	(Source: Oct. 1976)
8.42	129	4 March 1977	E	0.0033	

vi. July 1977 extended cohort

The fourth and final extended cohort released on 11 July 1977 contained cohorts from 6.5 to 15.5 mm, with adults separated as usual (Appendix Table 9). The release date corresponded to day 129 of the March extended cohort. The modest numbers dropped sharply during the first month, especially in the largest adults. Few cohorts retained workable numbers of growing snails by 8 October, after only 89 days.

Winkles grew steadily, except the 13.5 mm snails which levelled out (Figure 25).

Growth increments and ratios were erratic (Table 27). In the first month a trend was evident only in proportional growth: excluding the 9.5 mm cohort which grew much faster than the others, growth decreased with increasing initial size. Differences between the sexes were large. The rapid decline in numbers permitted no generalisations after three months.

Only three k values (Table 28) are based on steady growth and enough snails to be useful for comparisons. The 8.5 mm cohort grew a bit faster than its September 1976 counterpart (Table 22), but much more slowly than those in March and April (Table 26). The 11.5 mm cohort grew faster than its September equivalent and a bit more slowly than that of March. The combined male and female 12.5 mm k is twice that of September 1976, and similar to that of March. That is, in these three sizes at least, July 1977 snails grew faster than their September 1976 counterparts, but a bit more slowly than those of March 1977.

Figure 25

July 1977 extended cohort growth curves

Figure 25. Growth curves for component cohorts of extended cohort released 11 July 1977. Adult males and females are combined (data, Appendix Table 9). Conventions are as in Figure 24. Note that release date is day 129 of Figure 24.

15
ALL
14
13
GROWING
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9
8
7
6
MEAN L, MM
11 JULY 1977
0
100
DAYS

Table 27

July 1977 extended cohort growth increments

Table 27. Growth increments and associated ratios for growing snails only (data, Appendix Table 9). Conventions as in Table 21. Parentheses enclose values based on only 5 or 4 individuals; n.a., not applicable, number below 4.

L_1	T					
	27			89		
	Inc	Inc/L_1	Inc/T	Inc	Inc/L_1	Inc/T
6.36	0.56	0.0881	0.0207	(1.52)	(0.2390)	(0.0171)
7.44	0.63	0.0847	0.0233	(1.89)	(0.2540)	(0.0212)
8.46	0.52	0.0615	0.0193	1.70	0.2009	0.0191
9.43	0.87	0.0923	0.0322	n.a.	n.a.	n.a.
10.36	0.57	0.0550	0.0211	(1.19)	(0.1149)	(0.0134)
11.42	0.35	0.0306	0.0130	1.29	0.1130	0.0145
12.40 M	0.40	0.0323	0.0148	(1.14)	(0.0919)	(0.0128)
12.43 F	0.26	0.0209	0.0096	(0.82)	(0.0660)	(0.0092)
12.41 MF	0.34	0.0274	0.0126	1.00	0.0806	0.0112
13.50 M	0.04	0.0030	0.0015	n.a.	n.a.	n.a.
13.54 F	0.34	0.0251	0.0126	(0.21)	(0.0155)	(0.0024)
13.52 MF	0.18	0.0133	0.0067	0.23	0.0170	0.0026
14.46 M	n.a.	n.a.	n.a.			
14.52 F	0.25	0.0172	0.0093	n.a.	n.a.	n.a.
14.49 MF	(0.09)	(0.0062)	(0.0033)			
15.31 M	n.a.	n.a.	n.a.			
15.36 F	n.a.	n.a.	n.a.			
15.34 MF	n.a.	n.a.	n.a.			

Table 28

July 1977 extended cohort k values

Table 28. k calculated from mean lengths in Appendix Table 9. Conventions as in Table 22. Interval is 89 days. n.a., not applicable. All 14 and 15 mm values not applicable.

L_1	k	L_1	k
6.36	0.0016 x	12.40 M	0.0026 x
7.44	0.0022 x	12.43 F	0.0018 x
8.46	0.0022	12.41 MF	0.0022
9.43	n.a.	13.50 M	n.a.
10.36	0.0019 x	13.54 F	0.0009 x
11.42	0.0025	13.52 MF	n.a.

vii. comparison of extended cohorts

The September 1976 and March 1977 extended cohorts were released exactly six months (182 days) apart, but owing to gales September 30 was the starting date for calculations. Thus growth increments are for late autumn to early winter, and early to mid-spring. k values correspond to growth during late autumn and winter (the 137-day values), and during spring and early summer.

The September and March patterns of four-month k values with size (Table 29) are not significantly different: the highest k is found in intermediate sizes 8.5, 9.5 and 10.5 mm, with lower values in either direction (Kendall's tau for association 0.714, $P < 0.05$). With one exception, k is substantially higher in March than in September; in several cases, k is doubled. In the exceptional 12.5 mm females, k is nonetheless higher in March.

k values for the four April cohorts are higher than those of March and follow a similar pattern, increasing from 6.5 mm. The dates for these estimates overlap. July 1977 survivorship does not permit reliable comparisons.

Growth increments for corresponding cohorts are not strictly comparable unless corrected for starting size and time interval. When growth rate is plotted against starting size (Figure 26), a pattern is revealed notwithstanding within-season irregularities and between-season

Table 29

Comparison of September 1976 and March 1977 extended cohort k values

Table 29. k values for September 1976 and March 1977 extended cohorts arranged for comparison by Kendall's tau rank correlation coefficient. Cohorts are arranged in increasing order of September k. March 13.5 and 14.5 mm cohorts are omitted. Ties were broken using unrounded k as shown. Significance table: Sokal & Rohlf (1969), p. 537.

Cohort, mm	September 1976		March 1977	
	k	rank	k	rank
12.5 M	0.0010	1	0.0022	2
12.5 F	0.00136	2	0.0019	1
11.5	0.00138	3	0.0030	4
7.5	0.00143	4	0.0031	5
6.5	0.0015	5	0.0026	3
8.5	0.00172	6	0.0033	7
10.5	0.00173	7	0.0032	6
9.5	0.0018	8	0.0036	8

tau = 40/56 = 0.714 Null hypothesis: tau = 0

$P < 0.05$

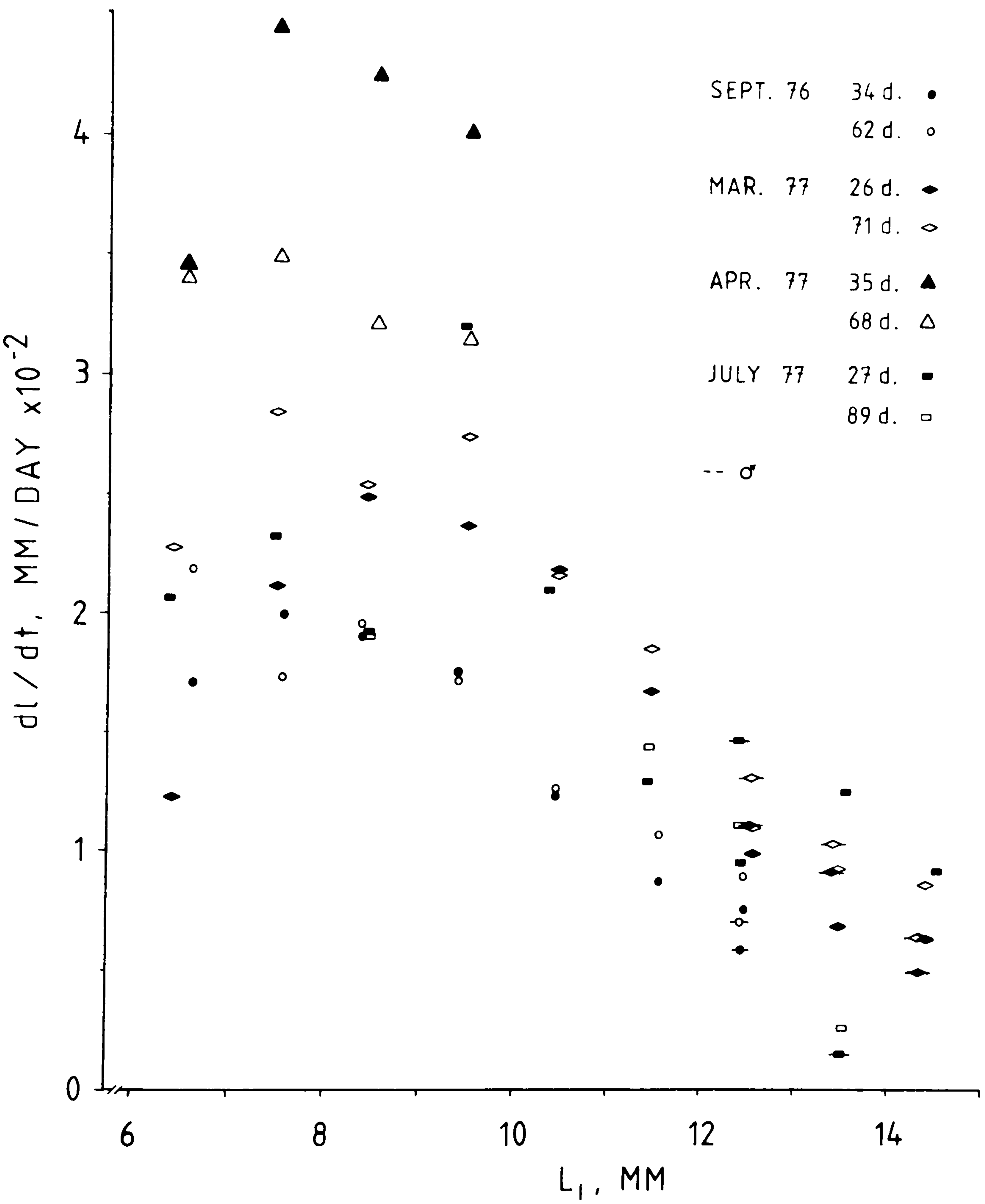
differences. Growth rate in mm per day tends to rise from 6.5 mm to approximately 8 mm and to decline thereafter. The difference between corresponding 6.5 and 7.5 mm cohorts decreases as the time interval increases. Snails at the peak grow about three times as fast as adults (non-growing adults were excluded from calculations).

Growth rates differed seasonally in all size classes. Disregarding the April extended cohort which was restricted to the four small classes, the spread of values is very similar over the common range 6.5 to 12.5 mm: about 0.01 mm per day. 12.5 mm males outgrew females in March and July but not in September. 13.5 mm males outgrew females in March but not July. 14.5 mm females outgrew males in March; July males all vanished. The differences between sexes were slight compared to among-size differences. The reversal in growth rates in March 14.5 mm snails, if meaningful, might show a tendency for males to stop growing at a smaller size than females. Sex ratio declines from a surplus of males at about 12 mm to an increasing excess of females through 15, 16 and 17 mm (Section 7). Adult growth was investigated using individually-tagged snails (Section 10).

Figure 26

Extended cohort growth rates

Figure 26. Relationship between growth rate ("Inc/T" in tables) and starting size. Data are given in Tables 21, 23, 25 and 27. Where sexes are shown separately, male symbols are winged. July 89 days 13.5 mm not shown because curve levelled out. Other July symbols are only shown when numbers exceeded 5.


SEPT. 76 34 d. ●
62 d. ○
MAR. 77 26 d. ◆
71 d. ◇
APR. 77 35 d. ▲
68 d. △
JULY 77 27 d. ■
89 d. □
-- ♂
dl / dt, MM / DAY x10^{-2}
0
1
2
3
4
6
8
10
12
14
L$_I$, MM

viii. summary of results

1. Cohorts consisting of 1 mm shell size classes coded with paint dots were released at site A on fifteen occasions between February 1976 and July 1977. Tags identified date of release and original size class, but not individuals.

2. Eleven of these occasions had cohort mean sizes of approximately 6.5 and 9.5 mm. On another, these two cohorts were supplemented by 7.5 and 8.5 mm cohorts. On the other three occasions, termed extended cohorts, all classes from 6.5 to 11.5 mm were released, with various adult classes separately coded according to sex. In all, 3,962 tagged snails were released.

3. Tagged snails were recaptured, dead or alive, during normal sampling at site A, and occasionally at sites L and D. Tag loss was slight and readily recognised. It was not possible to search widely for missing snails. Increase in mean size of survivors deemed to be growing was taken as growth; means were considered reliable if based on six or more snails. Shell lip condition and thickness served to indicate whether a shell was growing.

4. Growth curves showed mean size against elapsed time. When numbers and time interval permitted, the von Bertalanffy growth parameter k was calculated from a modified formula. A maximum shell length of 18.0 mm was used in all calculations in accordance with observed population size frequency distributions; the value obtained by the usual method, 21 mm, was unreasonably large. Curves and k values were compared by inspection and rank correlation.

5. Cohorts released in springtime grew faster than corresponding sizes released in summer or autumn. k values for the 6.5 and 9.5 mm cohorts

varied seasonally, with the highest values (k approximately 0.0035 to 0.0040 days^{-1}) in early spring, and the lowest (k approximately 0.0015 to 0.0020 days^{-1}) in late summer or autumn. The same pattern was observed in other classes similarly compared, for instance 7.5 and 8.5 mm. These k values were calculated over the first few months of growth after release: longer-term values were less varied.

6. k values of corresponding 6.5 and 9.5 mm cohorts were very highly significantly associated. A favourable period for one size was similarly favourable for the other.

7. The September 1976 extended cohort (mean sizes 6.5 to 12.5 mm) showed some evidence of reduced growth between December and February. Growth rate in mm per day determined before then declined with increasing size, although the smallest snails behaved erratically depending on the time interval considered. 12.5 mm females outgrew males slightly. k showed no clear trend with starting size when computed from October to February, but declined with increasing starting size when computed over the longer interval October to May. Adult females had higher k than males in the short interval, but results were similar after seven months. By June, some members of the 10.5, 11.5 and both 12.5 mm cohorts had stopped growing, and mean size of each of these cohorts was about 14 mm.

8. The March 1977 extended cohort (mean sizes 6.5 to 14.5 mm) grew steadily. Growth rate increased with size to about 8.5 mm, then declined steadily through 14.5 mm. 12.5 and 13.5 mm males outgrew females, but 14.5 mm females outgrew males. Differences between sexes were small compared with differences between sizes. k values computed for March to July showed no steady trend with size. They were however substantially higher than (often double) the corresponding September figures. k dropped abruptly

from the 11.5 to the 12.5 mm cohorts. Adult males and females had comparable k; many stopped growing by August, at about 14 mm.

9. The small April 1977 extended cohort (mean sizes 7.5 and 8.5 mm, released concurrently with the usual 6.5 and 9.5 mm) grew measurably faster than corresponding sizes released only a month earlier. Growth rate peaked at 7.5 mm. The two larger sizes had higher k values than the two smaller.

10. The July 1977 extended cohort (mean sizes 6.5 to 15.5 mm) was badly depleted after only 27 days. As far as could be judged, growth rate (in mm per day) displayed no clear trend with size; proportional growth (in mm per mm) declined with increasing size. After 89 days, the few reliable k values agreed with earlier findings: k was lower than in March but higher than in September (1976).

11. September and March k values followed a similar pattern, high in intermediate sizes 8.5, 9.5 and 10.5 mm, and lower in either direction ($P < 0.05$). Corresponding k values were much greater in March than in September. April values were higher still, although the time interval used in the calculations overlapped substantially with that of March. Poor July survivorship discouraged detailed comparisons.

12. When plotted together, growth rates (mm per day) generally rose from 6.5 to about 8.5 mm, and declined thereafter. Snails at the peak grew about three times as fast as adults. Increasing the time interval decreased the difference between 6.5 and 7.5 mm cohorts. All size classes displayed seasonal differences, with a spread of about 0.01 mm per day, roughly one third of peak rates. There was a suggestion that males might stop growing at a smaller size than females, but confirmatory data from larger size classes were unavailable.

13. Mortality is discussed in Section 9.

14. Results presented here are for snails judged to be growing, when enough remain on a particular date. The full data are given in Appendix Tables 5 to 9.

Discussion

Growth rate from hatching (at about 0.45 mm) to 5 or 6 mm is not known. Daguzan (1976a) obtained his post-hatching growth rates by extending backwards von Bertalanffy curves constructed from probability paper analysis: this technique can lead to grossly misleading conclusions. Egg masses are laid throughout the year, but are particularly abundant early in the year. The field notes (extracts in Appendix Table 1) mention high numbers in March and April 1976, and in February and April 1977, and low or negligible numbers from August to November 1976 and in 1977 from May to the end of field work in October. (No data are available for December 1976 or January and March 1977.) Guiterman (1971) and Goodwin (1978) caution, however, that time to hatching is greatly reduced in summer, so egg mass abundance may be an unreliable guide to supposed age of the many 3 mm juveniles that appear in summer samples (Section 6). If these juveniles do indeed hatch in spring, their initial growth must be very rapid.

Mean size of juvenile modes in population size-frequency histograms increases by about 0.12 to 0.15 mm per week (Section 6), with steady winter growth and a spurt in spring. The chief limitations to this sort of estimate are that a mode includes a wide size range and so its movement may be affected by size-specific growth mortality or dispersal rates, and that size-specific and environmental effects are not distinguished.

Repeated cohort tagging overcomes these difficulties, at least for suitably abundant or large snails. The lower size limit for L. obtusata was 6 mm, but smaller rock-dwelling littorinids have been tagged successfully by Hughes (1980), Hughes & Roberts (1980, 1981; Roberts & Hughes 1980), and others.

If handling induces a "growth check" - i.e., a shell mark caused by temporary cessation of growth - then on recapture individual growth increments are available to calibrate increments calculated from group means. Hughes (1980) found this phenomenon in 30% of L. nigrolineata at a moderately sheltered boulder shore; in his study, snails were retagged on every recapture. Growth checks were only observed in L. obtusata in the large adults, which may grow intermittently (Section 10).

It is difficult to assess the effects of tagging on growth. Enamel model paint weighs little. It was put on the spire so that if repugnant to the snail, it would not interfere with the next body whorl, nor become hidden.

Tagging stress will most readily be detected if mortality in the interval after release is consistently abnormally high. Mortality is treated in Section 9. There is little evidence for substantial tagging mortality - see e.g. the survivorship curves for the March 1977 extended cohort - and time away from the shore was minimised. The four most likely causes of tagging stress are poisoning, heat, desiccation and shell damage when sanding. The long survival of many tagged snails is evidence against the first. A cool constant-temperature room and tests for normal behaviour were intended to help guard against the second and third. The fourth was eliminated. Snails were released in a manner intended to maximise the likelihood that they would attach normally to the weed. Of course a drop in numbers does not necessarily indicate death; sound evidence consists of empty shells.

Large numbers of recently-tagged snails were found dead on one occasion. The catastrophic depletion of 14.5 and 15.5 mm adults in the July 1977 extended cohort was likely due largely to mortality rather than to dispersal. The mortality agent is unknown but may have been environmental, for similar losses were observed concurrently in part of the March 1977 extended cohort, especially the 12.5, 13.5 and 14.5 mm classes. Adult vertical migration is unlikely (Sections 6 & 7).

Questions addressed by cohort tagging are: (1) how variable are growth rates of similar-sized individuals growing concurrently?; (2) do snails of a given (mean) size grow at the same rate throughout the year, and if not, is there a seasonal trend?; and (3) do snails of different (mean) sizes growing concurrently have a uniform growth rate, and if not, do the growth rates show a trend with size?

1. individual variability

Individual variability is best judged by individual tagging (adults, Section 10), but may be inferred in the short term from changes in standard deviation of size, given a small initial standard deviation and high survivorship. Every cohort had a standard deviation of 0.35 mm or less when released. After about four months, the standard deviations of suitable cohorts were approximately 0.6 mm, although many were lower (Appendix Tables 5 to 9). The raw data (not presented) sometimes show a few unusually large or small individuals, but measurements are usually bunched within a range of about 2 mm.

Such differences in growth after four months are unremarkable; differences in the very short term were negligible. It must be acknowledged, furthermore, that owing to seasonal variations in growth rate, snails of a given size will not necessarily be the same age. Ideally, members of a cohort would hatch synchronously.

In a stimulating contribution, Sainsbury (1980) questions the rigour of applying to means equations devised for individuals. He shows for instance that if l^{∞} varies among individuals, then mean length at a given age or mean growth increment for a given starting length are largely unaffected. If on the other hand k varies among individuals, then the variance of mean length at a given age and of mean growth increment will be affected. The assumption in the present analysis is that l^{∞} is fixed at 18.0 mm. Sainsbury examines the implications of this and other assumptions, and remarks that "in molluscs a high degree of variability in k seems to be common." Data on individual l^{∞} and k are presented in Section 10, in which final size and lifespan are discussed.

2. seasonal effects

Growth curves and k values for repeated 6.5 and 9.5 mm cohorts show a clear seasonal trend, with highest values in spring declining to late summer and autumn and then rising. The monthly patterns of growth rates in these two size classes, considered broadly representative of growing juveniles, are very similar. Other sizes, when available, support this evidence, and untagged sample size-frequency histograms (Section 6) also suggest that juveniles in spring grow faster than later ones.

The cause of this seasonal cycle in growth rates in all sizes is uncertain. Food seems unlikely to be limiting, for the plants were not heavily grazed. Temperature seems a possible factor. Several sizes appeared to slacken growth between December and February. The field notes mention snow and bitter cold in part of January. The reduction in growth of September 1976 extended cohort adults (Figure 23, where adults are those larger than 12.0 mm on December 1) might plausibly be attributed to reproductive effort, but there is no evidence that the many egg masses found in February were laid by tagged snails, and immature snails as small as 9.5 mm showed a similar slackening.

Interestingly, <u>L. nigrolineata</u> grows significantly slower in winter than in other seasons (Hughes 1980). This species lives at much the same level as <u>L. obtusata</u> (e.g., Roberts & Hughes 1980) but can also tolerate greater exposure. <u>L. rudis</u>, which overlaps substantially with <u>L. obtusata</u>, displayed a uniform pattern in populations from a salt marsh, a boulder beach, and an exposed cliff: monthly k rose in spring or summer and fell in autumn or winter (Roberts & Hughes 1980). Values of k (recalculated from monthly means in their Figure 2) ranged from 0.0003 to 0.0023 days^{-1} - i.e., their maxima corresponded approximately to the upper range of <u>L. obtusata</u> minima. The comparative metabolic studies of McMahon and Russell-Hunter (McMahon & Russell-Hunter 1974, 1977; Russell-Hunter & McMahon 1974) are greatly weakened by their confusion of similar species. Borkowski (1974) asserts that five littorinids in southern Florida showed accelerated spring growth. Spawn production could account for 65-85% of secondary productivity: adult growth slowed during summer spawning.

Cloern & Nichols (1978) advocate adding a coefficient to the von Bertalanffy equations to simulate seasonal effects, and claim that this can help to identify factors affecting mean size, such as size-specific mortality or episodic recruitment. This technique could be of value when working with untagged animals.

3. relationship between size and growth rate

According to the von Bertalanffy model, for a standard time interval, $(L_2 - L_1)$ decreases linearly with increasing L_1. It is assumed that growth rate does not vary with season. Seasonal variations (Tables 18 & 19) will cause brief changes of slope in the increment vs. size curve for any individual snail, or for a cohort if individual variation is not excessive. For instance, the 6.5 mm cohort growth curve in Figure 11 (February 1976) shows a steep spring rise that need not be attributed to dramatically-increased growth rate at 7 mm and hence to non-Bertalanffy growth. Other sources of non-linearity (i.e., of varying slope) are mentioned in the methods: departures from basic assumptions regarding assimilation and metabolic rates, and change in shape with increasing size.

Correcting for season by using extended cohorts does not necessarily assure linear decrease (Tables 21, 23, 25 & 27), especially over short time intervals (Figure 26). Growth rate apparently rises from 6.5 mm to about 8 mm and only then declines approximately linearly. The curve may be symmetrical but data for classes 0 to 5 mm are unavailable. Hughes (1980) obtained a similar result for <u>L. nigrolineata</u>: his 4 to 14 mm snails peaked at 6 to 9 mm, at rates of about 0.017 mm per day. As in the present study, the pattern of growth in the smaller sizes is not known. Hughes discusses possible physiological causes for such departures from the von Bertalanffy model, and implications for interpretations of presumed size-age relationships.

Sainsbury (1980) attributes the domed shape to individual variability in k and 1^{∞}, and to the age structure of the cohort. His use of "cohort" does not seem to involve any initial constraint on size, but just a uniform release date. Therefore some of his reservations will not apply to any great degree in the winkle studies, except where extended cohorts are considered. It must be remembered when using extended cohorts, that however finely the component cohorts are divided, the age distribution prior to tagging is unknown. In Figure 13 at about 300 days, a sample of 12.0 to 13.0 mm snails would include members of cohorts of very different ages and growth rates despite their similar sizes.

Knight (1968) warns that inappropriate curve-fitting may produce nonsensical l^{∞} estimates. In his discussion of sources of non-linearity in the growth increment vs. starting size plot, Sainsbury (1980) points out that if size at tagging overlaps with the distribution of l^{∞} (assuming that l^{∞} varies among individuals), then the slope of that portion of the line will become less negative (shallower), causing an overestimate of mean l^{∞} and hence an underestimate of mean k. In the present study, where only growing snails were tagged, this is a real possibility. On the other hand, the arbitrary l^{∞} of 18.0 mm was lower than that predicted (21 mm). Calculations using 16.0 and 17.0 mm gave poor fits, so these values may not be substantially more realistic than 18.0 mm, which approximates maximum observed size at the study area. Roberts & Hughes (1980) discuss other reasons for preferring maximum observed size to calculated values.

Growth rates for the largest snails are complicated by the fact that many stop growing. The proportion growing decreases with size, the sexes can behave differently, and furthermore growth may become intermittent (Section 10).

An idealised composite growth curve may be concocted from the simultaneous growth curves of extended cohorts, using the times taken by each component cohort to reach the starting size of the next (Table 30, Figure 27). Such a curve for September begins at 6.6 mm and reaches 10.0 mm by day 182, 12.0 mm by day 360, and 13.5 mm by day 570. A similar curve for March begins at 6.4 mm, reaches the same sizes by days 156, 250 and 364, and 15.0 mm by day 590 (19½ months, or 17½ months allowing for the kinks in the 13.5 and 14.5 mm curves, Figure 24).

Table 30

Composite growth data

Table 30. Times to grow from cohort mean starting size to that of the next larger cohort. Data are read directly from Figures 23 and 24; data in parentheses are based on extrapolation to correct for sharp drops. Go, starting size, mm. Stop, final size, mm. T, time intervals, days. Tcum, cumulative days. M, males; F, females; MF, sexes pooled. Starting days are 30 September 1976 and 4 March 1977. Note well that starting date is constant within each extended cohort. See text.

SEPTEMBER				MARCH			
Go	Stop	T	Tcum	Go	Stop	T	Tcum
6.6	7.55	48	48	6.4	7.57	53	53
7.55	8.4	45	93	7.57	8.42	38	91
8.4	9.4	52	145	8.42	9.51	43	134
9.4	10.45	62	207	9.51	10.45	38	172
10.45	11.55	92	299	10.45	11.46	47	219
11.55	12.43 M	105	404	11.46	12.53 MF	58	277
11.55	12.48 F	110	409				
12.43 M	13.5	175	579	12.53 MF	13.45 MF	80	357
12.48 F	13.5	152	561	13.45 MF	14.36 MF	118 (96)	475 (453)
				14.36 MF	15.0	115 (76)	590 (529)

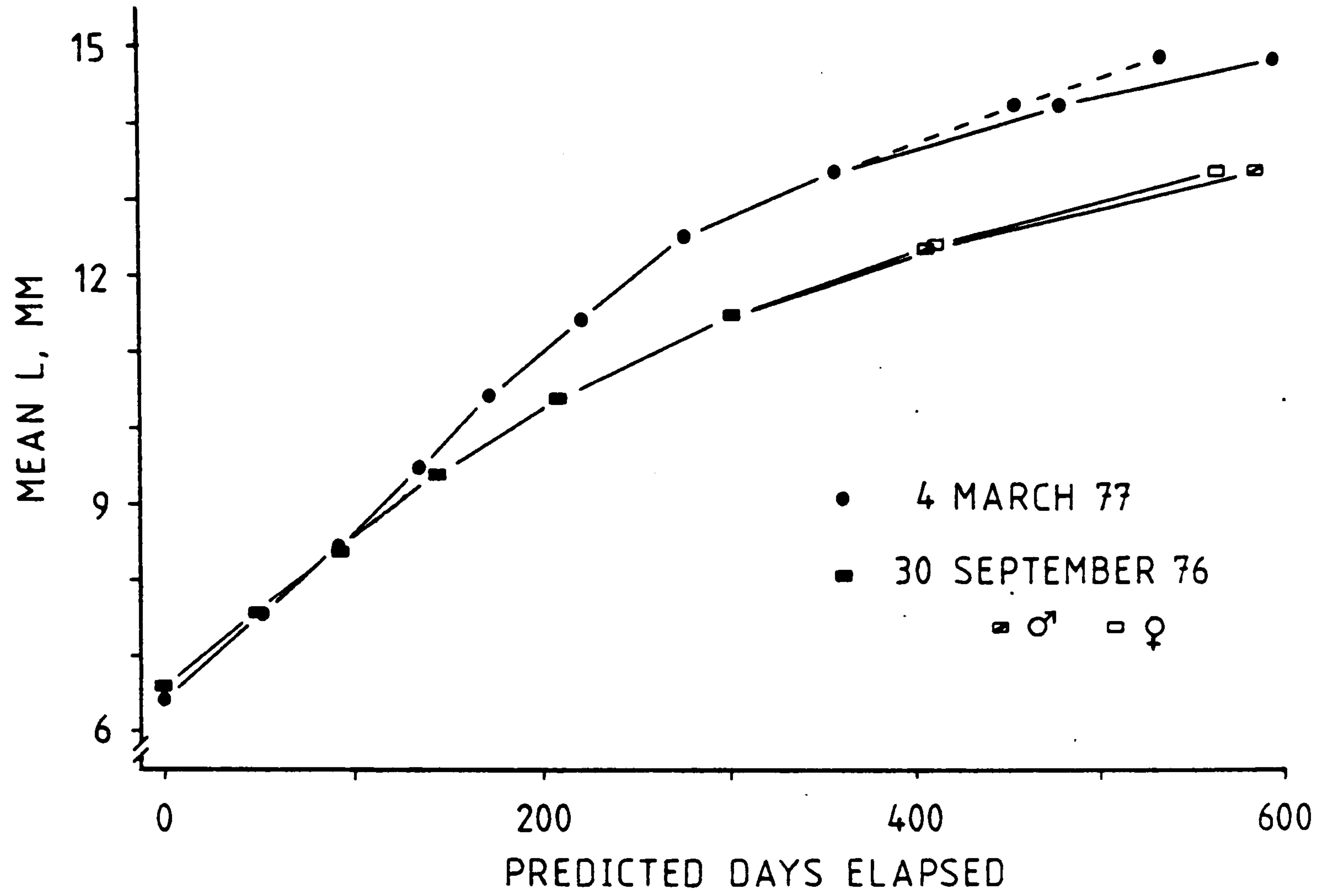


Figure 27. Composite growth curves for hypothetical 6.5 mm snails growing in constant environments and instantaneously changing their growth rates at approximately 1 mm intervals (data, Table 30). Upper curve, endless springtime (March data): solid line makes no allowance for kinks, short dashes from 13.5 mm do so - see text. Adult sexes combined. Lower curve, constant autumn (September data): line does not distinguish sexes until 11.5 mm. Overlapping points are slightly displaced for clarity. Curves cross at 8.4 mm.

These curves are unrealistic insofar as growth rates at given sizes are not invariant, but change seasonally. However, if the March and September rates fairly represent the normal range (the four available April rates were higher), then a real growth curve for a 6.5 mm snail starting at any time of the year should fall somewhere between these curves, and be shaped according to the season in which the snail reaches different sizes. k values (using l^{∞} = 18.0 mm as usual) calculated from these curves for intervals of 125, 250 and 500 days are respectively: for the slow curve, 0.0019, 0.0019 and 0.0016 days^{-1}; for the fast curve, 0.0024, 0.0026 and 0.0024 (or 0.0025 if allowing for slackening as before) days^{-1}. k values for the 6.5 mm component cohorts of the September and March extended cohorts were 0.0015 (137 days) and 0.0026 (129 days) days^{-1} respectively. Hughes (1980) found similar satisfactory agreement between actual growth curves and von Bertalanffy curves fitted to the data, although his curves were constructed differently. For certain mark-and-recapture data the Richards function (e.g., Ebert 1980) may prove useful; in the present examples it reduces to a von Bertalanffy equation.

Finally, to return to the polymodal size frequency analysis mentioned in the second paragraph, it was concluded (Section 6) that snails of about 6.5 mm in early winter would reach adult size by late summer or autumn the following year. This is in broad agreement with the results presented here assuming growth at the higher rate, but suggests that the polymodal technique overestimates individual growth for reasons already discussed (e.g., size-specific mortality at the lower end of the mode). Although the polymodal technique is much less labour-intensive, cohort tagging yields a higher grade of result and is to be preferred when practicable.

SECTION 9

SURVIVORSHIP

Introduction

Survivorship must not be confused with longevity. Survivorship is a measure of that proportion remaining alive after a given elapsed time.

Nevertheless, age might influence survivorship: hatchlings might suffer drastic mortality, or full-grown snails might be preferred by foraging French epicures. Consequently, field investigations ought ideally to use snails of similar size and to take into account other factors such as season.

Section 8 described the 6 and 9 mm tagged cohorts released between February 1976 and July 1977, the extended cohorts having a wider set of sizes, and their recaptures through October 1977. This material is also used here.

Living tagged snails are the minimum surviving, while empty or broken tagged shells are the minimum dead. Because emigration could not readily be distinguished from mortality, it is only possible to state that true survivorship lies somewhere between these estimates. Because time of death cannot be fixed as precisely as observations of living snails, and for reasons of numbers found, this section deals with numbers alive. Numbers and elapsed times are shown in Appendix Tables 5 to 9.

Data treatment

Illustrative data for the April 1976 6 mm cohort appear in Table 31. Parentheses indicate days on which the number recaptured is known to be less than the number alive because more snails were found in a later recapture. In all figures, such underestimates are raised to the later value.

Table 31

Survivorship example

Table 31. Survivorship data for 6 mm cohort released 21 April 1976. T, days elapsed from release. N, number found alive (see Figure 28, A). %, percentage of original 91 snails. Log, natural logarithm of percent frequency (see Figure 28, B). Parentheses enclose known underestimates as explained in text.

T	N	%	Log
0	91	100.0	4.605
33	(30)	(33.0)	(3.496)
63	51	56.0	4.026
120	37	40.7	3.705
162	(7)	(7.7)	(2.040)
196	(12)	(13.2)	(2.579)
225	13	14.3	2.659
300	8	8.8	2.174
344	6	6.6	1.886
389	4	4.4	1.481
422	(1)	(1.1)	(0.094)
447	2	2.2	0.787
474	1	1.1	0.094
536	1	1.1	0.094

The plot of frequency against elapsed time follows a curved path; a linear regression does not fit the data adequately (Figure 28, A). The percent frequency plot has the same shape.

Semilog transformation allows a much better fit, but comparisons among samples are easier if the Y-axis is scaled instead as the natural logarithm of percent frequency (Figure 28, B). All plots then begin at 4.605, and most end by 0 (1%).

Certain points must be discarded. For unknown reasons, numbers may drop so disproportionately in the first interval that the day 0 value is best rejected. Sometimes this seems unnecessary (Figure 28, B), but it was thought best to treat cohorts consistently. Occasionally day 0 had to be retained; such cases are explained where appropriate. The known underestimates contribute nothing and like day 0 were left out of the final regression. It was considered inappropriate to reconstruct intermediate values to replace them. Finally, small numbers persisting for long periods may bias survivorship estimates. Any dates having fewer than four snails were arbitrarily eliminated except as noted.

The remaining records were used to determine the regression of log percent frequency with elapsed days. In Figure 28, C this regression with its 95% confidence intervals is fitted through the hollow symbols, and the rejected values are shown as crosses. The regression is:

$$\begin{aligned} \log_e\% &= 4.553 \quad -0.00790\ (\text{days}) \\ &\pm 0.077 \quad \pm 0.00029 \end{aligned}$$

standard error of the estimate = 0.082 $\quad R^2 = 0.995$

F (1, 4 d.f.) = 762.488, $P < 0.001$ ***

Figure 28

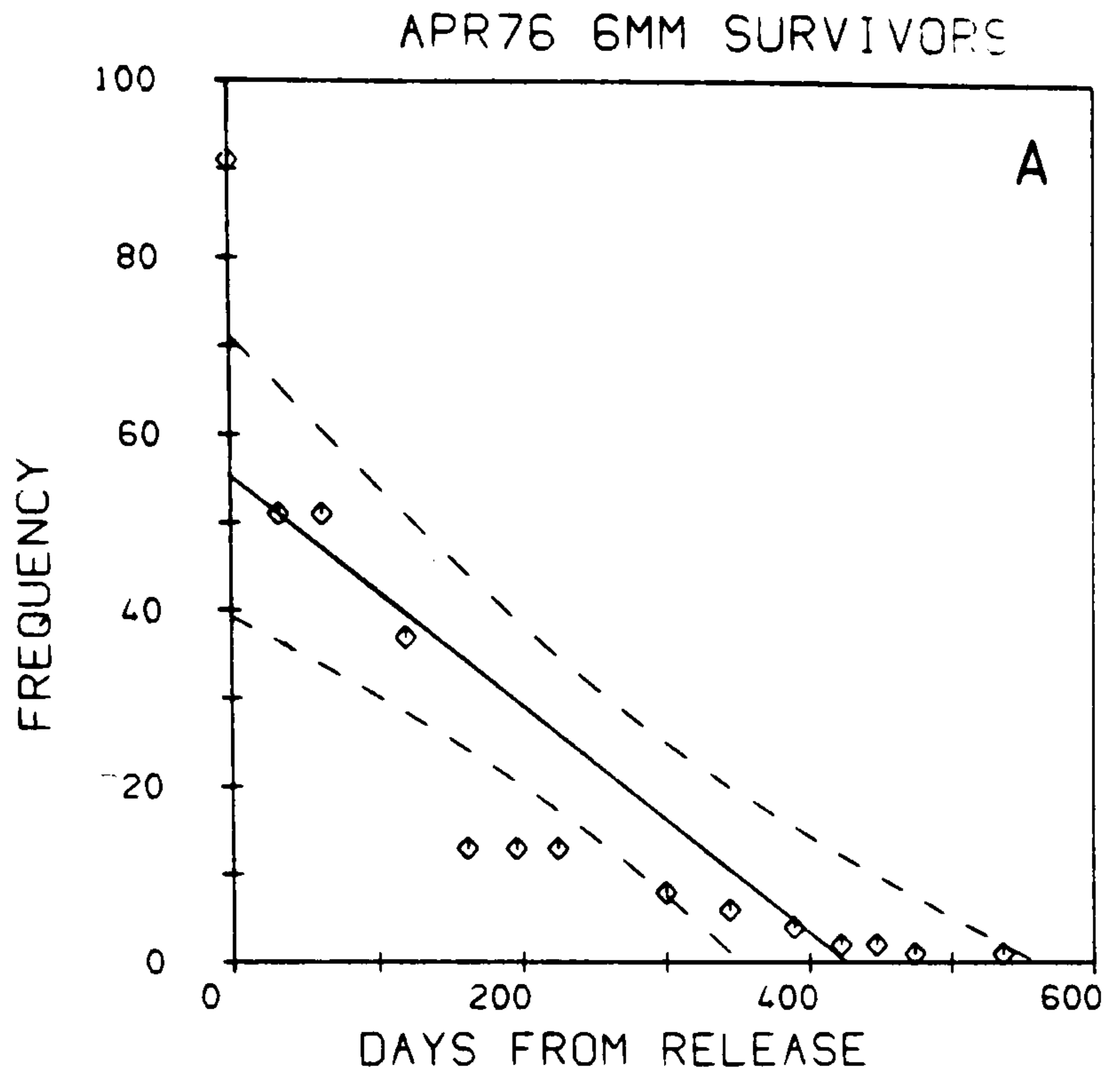
Example survivorship curves

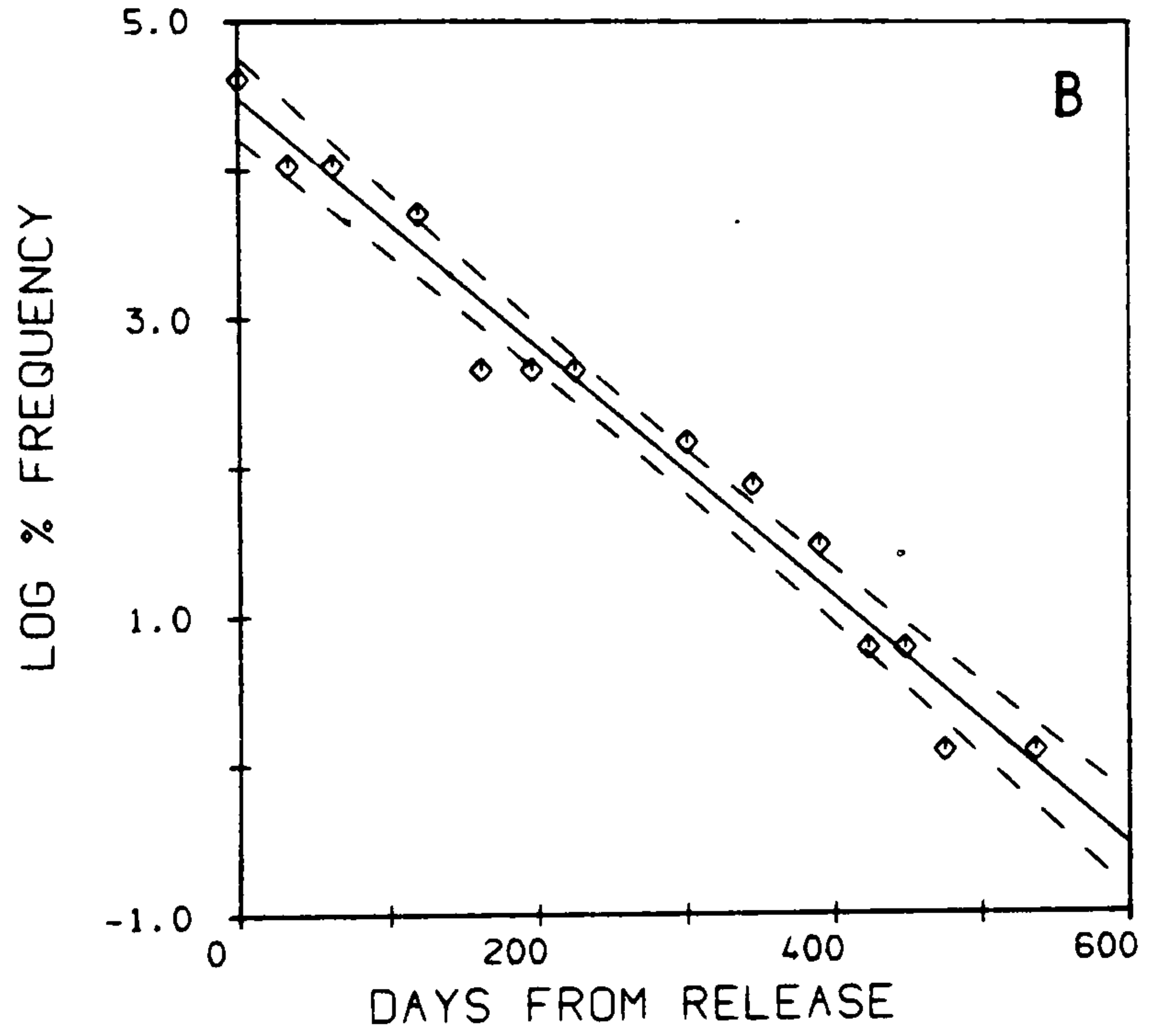
Figure 28. Illustrative survivorship curves. Data from Table 31. Known underestimates are increased to true later values as explained in text.

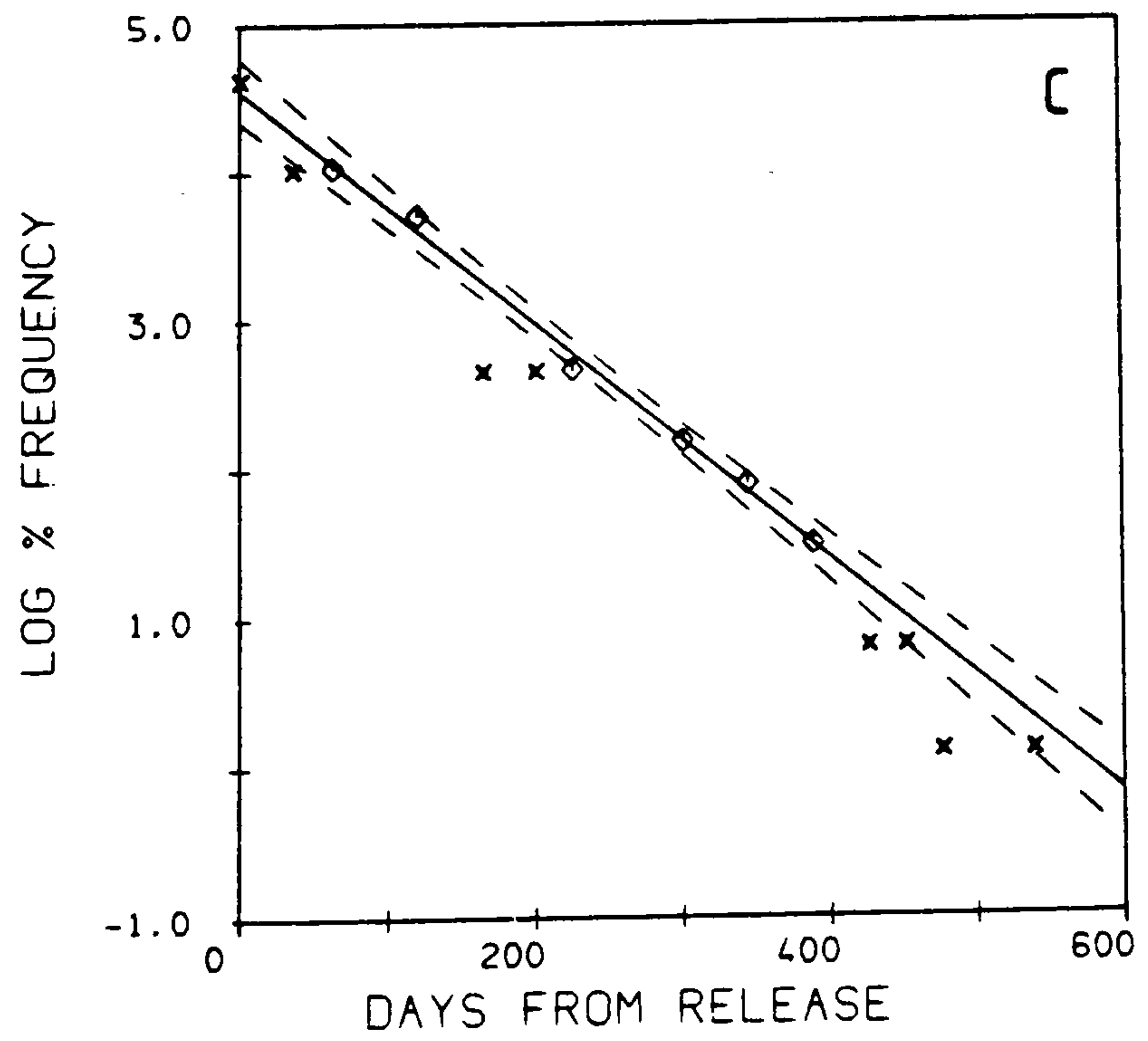
(A) Number of survivors vs. time. All points are used to compute the regression line, shown with its 95% confidence limits. Plot produced on digital plotter - location of symbols is accurate.

(B) Log_e percent surviving vs. time. Regression uses all points.

(C) Log_e percent surviving vs. time. Crosses (added by hand) represent points rejected from regression as explained in text. All subsequent survivorship curves adopt this format.


APR76 6MM SURVIVORS
A
FREQUENCY
100
80
60
40
20
0
0
200
400
600
DAYS FROM RELEASE


B
LOG % FREQUENCY
5.0
3.0
1.0
-1.0
0
200
400
600
DAYS FROM RELEASE


C
LOG % FREQUENCY
5.0
3.0
1.0
-1.0
0
200
400
600
DAYS FROM RELEASE

Data interpretation

In the foregoing example, the regression is evidently a close description of the reliable data, accounting for 99.5% of the variance. It seems reasonable to postulate logarithmic decline.

The Y-intercept is meaningful in so far as a gross deviation from 4.605 would indicate that numbers had not declined steadily from the outset. A disproportionate early drop would produce a low intercept, a late drop a high one. To force the regression through 4.605 is to overlook this convenient guide. The X-intercept is unhelpful because the natural logarithm of 0% is minus infinity.

The slope is a decay rate. This is not strictly the death rate, as death and dispersal are confounded. Slopes may be compared usefully without regard to the Y-intercept; the values are the same for log frequency and log percent frequency. When dealing with percentages it is worthwhile to keep in mind the starting numbers, which differ according to size class availability for tagging.

The standard error of the estimate measures the variation of the residuals - i.e., the differences between observed and predicted values - and so may be compared among cohorts as an indication of closeness of scatter to the line. The squared correlation coefficient R^2 measures the goodness of fit, and P(F) the significance of R - effectively the same as the significance of the slope (Nie *et al*. 1975, UMRCC 1980b).

Results

Results are presented as follows. First the 6 and 9 mm cohorts are described. In part (ii), they are compared. Parts (iii) to (v) concern the September 1976, March 1977 and July 1977 extended cohorts respectively; comparisons among them are made within these sections. Results are summarised in part (vi).

i. 6 and 9 mm cohorts

Figures 29 to 40 are grouped at the end of this chapter. All results are expressed in elapsed days. Calendars are in Appendix Tables 1, 5 and 8. Details of regressions are in Appendix Table 10. Slopes for all cohorts are given in part (ii), Table 32.

1. 25 February 1976 (Figure 29)

The 6 and 9 mm snails persisted in satisfactory numbers for approximately 500 and 400 days respectively. Numbers caught dropped steeply on the seventh observation - the sixth recapture - but this date (30 September) was not excluded from analysis. Similar drops occurred concurrently in other cohorts: part (ii). Regressions were respectively significant and very highly significant.

2. 25 March 1976 (Figure 30)

Each cohort lasted approximately 400 days. Numbers dropped sharply on the fifth recapture. Few 6 mm snails then remained. Nevertheless, regressions were respectively highly and very highly significant.

3. 21 April 1976 (Figure 31)

Both cohorts survived for about 400 days. Numbers were abruptly reduced on the fourth recapture. Regressions were respectively very highly significant and significant. Slopes were quite similar. (Figure 31, top, is the same as Figure 28, C.)

4. 31 May 1976 (Figure 32)

The 9 mm cohort survived at least a year. Numbers dropped on the third recapture, but the regression was highly significant.

The 6 mm snails also declined sharply on the third recapture. Normal data selection left only days 80 and 122. A rough equation could be obtained by reinstating the next eligible point (day 184, 3 snails), day 0, or both. The regression based on adding day 184 was not significant. The further addition of day 0, while not affecting the slope or intercept markedly, led to lower standard errors and an improved fit. This regression based on four points is significant, represents the data scatter tolerably well ($R^2 = 0.973$), and is adequate for comparative purposes.

5. 16 August 1976 (Figure 33)

Many members of each cohort vanished in the first interval, corresponding to the big drops mentioned previously.

A highly significant regression could be obtained from the second to sixth 6 mm points, but the fit was much improved ($R^2 = 0.966$) by considering also days 271 and 332 (3 and 2 snails respectively).

Only five 9 mm snails of 64 remained after the first interval.

Each regression was drawn from the central group of eligible dates; day 0 and end zeros were ignored. That for the 6 mm cohort was robust, but the 9 mm regression, although statistically significant, was based on too few snails to be useful.

6. 30 September 1976 (Figure 34)

Each cohort lasted at least 250 days. The 6 mm snails dropped abruptly on the sixth recapture (16 June 1977) but no comparable reduction struck the 9 mm cohort.

Only three suitable dates could be used for a 6 mm regression. Although it was not statistically significant, the scatter was very tight.

The larger winkles persisted in workable numbers for approximately ten months; the regression was very highly significant.

These sizes were also represented in the September 1976 extended cohort released at the start of the month: part (iii).

7. 22 October 1976 (Figure 35)

Both cohorts maintained adequate numbers for at least 250 days. 6 mm numbers declined steadily without sharing the sudden 9 mm drop on the seventh recapture (7 August 1977). Regressions were respectively highly and very highly significant.

8. 19 November 1976 (Figure 36)

Once again, each cohort had a useful life of at least 250 days. Although the 6 mm snails disappeared steadily, the others seemed to change slope after the third recapture (14 May 1977). Nonetheless, the regressions were respectively highly significant and significant.

9. 9 April 1977 (Figure 37)

7 and 8 mm cohorts were also released.

The 6 mm cohort began with only 27 members and maintained useful numbers for four months. Normal data treatment left only two points (days 93, 120) so day 0 was reinstated to allow a regression to be calculated; it was not significant. Day 182 was not added because only two snails were recaptured - the day 0 value was known with certainty.

The other three cohorts had larger starting numbers, persisted at least six months, and yielded regressions significant (8 mm) or highly so. Indeed, standard errors of the intercept and of the slope were uniform, as were R^2 and standard errors of the estimate (Appendix Table 10). The 8 mm cohort had a shallower slope than the others.

10. 15 May 1977 (Figure 38)

Customary data treatment left only 6 mm days 57 and 84. Rather than day 146 (3 snails), day 0 was used as the third point, producing the more conservative survivorship estimate. The regression was not significant.

The 9 mm snails declined steadily at least until sampling ended in October. The regression was significant. (The inclusion of day 0, not presented, made virtually no change to the slope or Y-intercept.)

11. 18 June 1977 (Figure 39)

As in May, normal data selection left only two 6 mm points, days 50 and 112. As before, day 0 was added: it lay well in line with the others but the regression was not significant. The 9 mm regression also was not significant despite narrow scatter. (As in May, adding day 0 made little difference.)

Each line's close fit reflected in the very low standard errors of the estimate (Appendix Table 10) permits each to represent the data despite non-significant F values, at least for comparative purposes.

12. 18 July 1977 (Figure 40)

Only three dates were available, so day 0 was not rejected.

In contrast to June, the 6 mm cohort did not decline steadily. The regression was not significant, with a large standard error of the estimate. The 9 mm snails declined more regularly: the regression was significant and the fit close.

These sizes were also represented in the July 1977 extended cohort released a week earlier: part (v).

ii. 6 and 9 mm cohorts compared

Figures 41 and 42 display the survivorship traces for the 6 and 9 mm cohorts respectively, from release of the first on 25 February 1976 until field work ended on 8 October 1977. Each line connects all points before data selection (compare Figure 28, B).

Cohorts released from February to September 1976 showed concurrent steep drops which are attributed to September gales. No attempt was made to adjust the data.

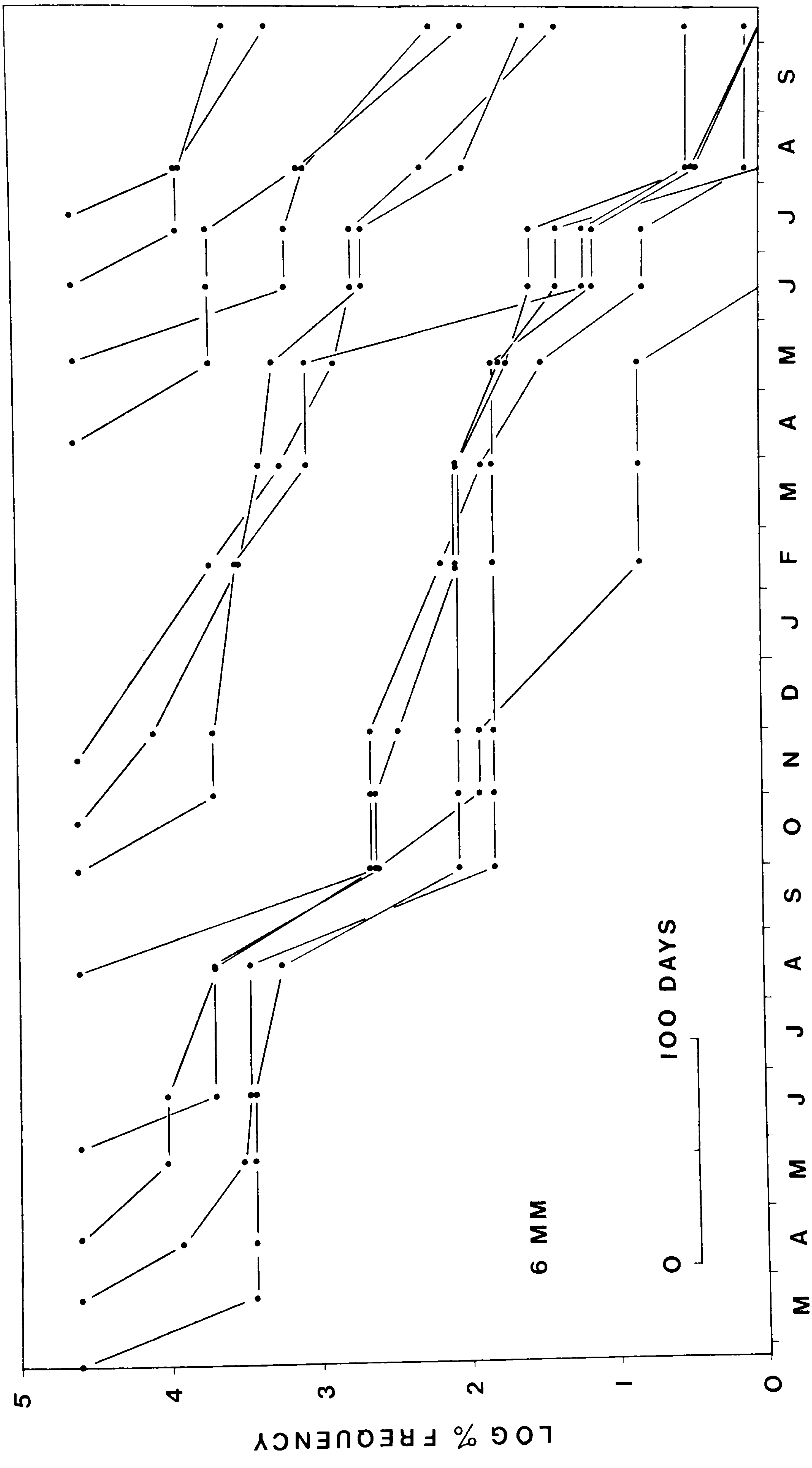
Six 6 mm regressions were based on non-standard date selection - usually day 0 had to be reinstated to provide the third point needed to evaluate fit. The 9 mm cohorts provided more useful results, with one non-standard month and one deemed useless (July 1977 and August 1976 respectively).

Figures 41 and 42

Survivorship traces

Figure 41. Survivorship patterns of 6 mm cohorts, expressed as natural logarithm of percent surviving vs. calendar date. Known underestimates are raised to true later values. Data are unselected, as in Figure 28, B.

Figure 42. 9 mm survivorship patterns. Format as in Figure 41. April 1976 day 536 (8 October) value, off-scale, is -0.482.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6 MM
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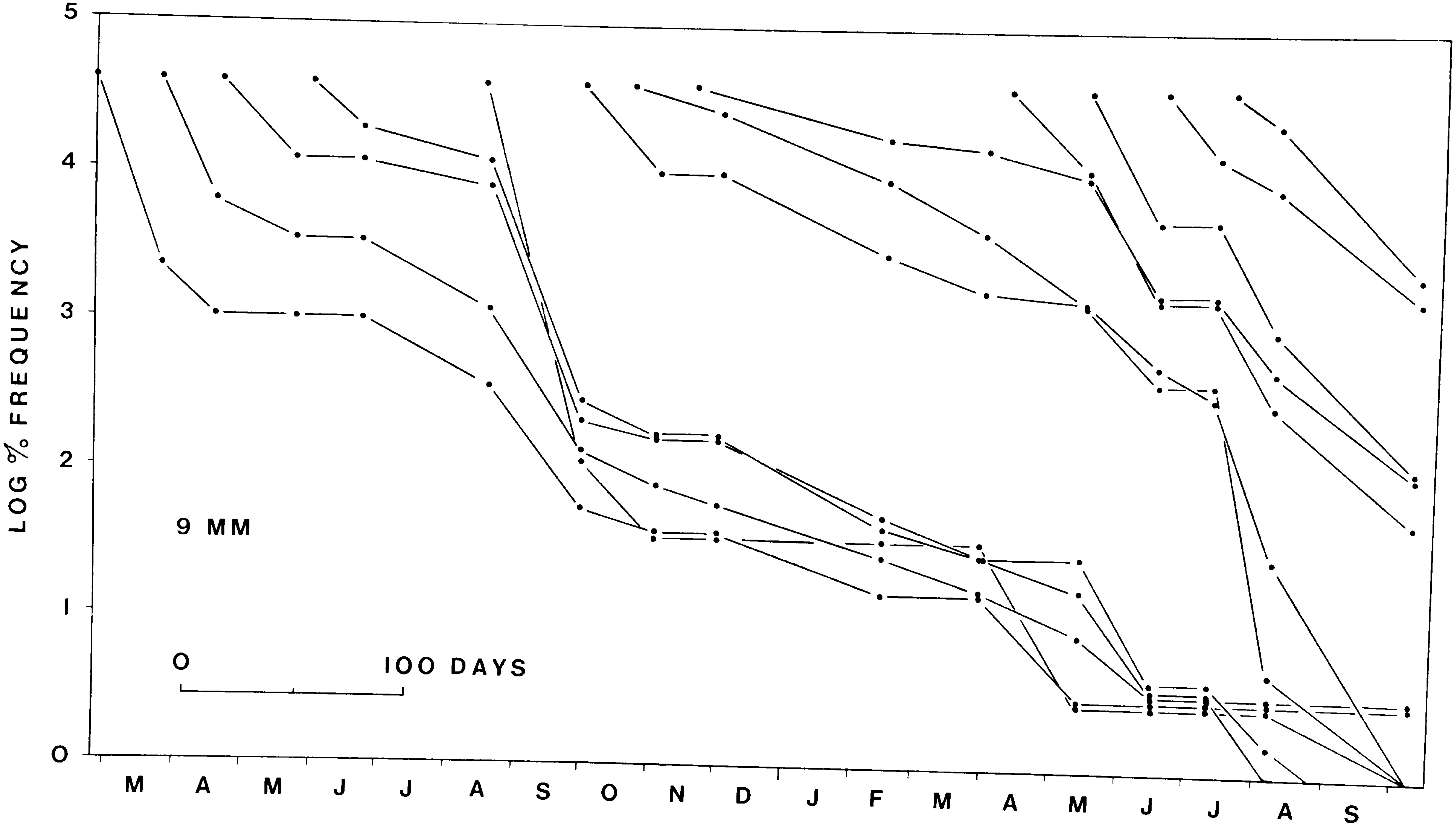
100 DAYS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J
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Table 32

Slope comparison

Table 32. Slopes extracted from Appendix Table 10. Standard errors in parentheses. All slopes are negative and should be multiplied by 10^{-3} (e.g., 4.54 represents -0.00454). X denotes non-standard date selection explained in text. NA, not applicable: regression judged unsuitable for comparison - these months were excluded from Kendall test.

Released		Slope (± SE)	
		6 mm	9 mm
1976	February	4.54 (1.15)	6.50 (0.62)
	March	5.88 (1.28)	8.21 (0.88)
	April	7.90 (0.29)	8.50 (1.88)
	May	X 15.15 (1.78)	9.77 (1.49)
	August	X 4.34 (0.37)	NA
	September	4.03 (0.88)	6.23 (0.60)
	October	6.36 (0.81)	8.17 (0.56)
	November	7.29 (1.06)	8.88 (1.87)
1977	April	X 11.79 (2.34)	16.36 (1.32)
	May	X 19.45 (4.81)	15.69 (2.46)
	June	X 11.45 (1.20)	10.88 (1.04)
	July	NA	X 15.23 (1.04)

The 9 mm slopes were generally the steeper (Table 32), but the difference varied from month to month. Kendall's rank correlation test was performed on the ten valid pairs of slopes: tau = 0.78, $P < 0.01$ ** (Sokal & Rohlf 1969). There was a highly significant association between the 6 mm and 9 mm patterns of slope with initial release date.

Although slopes increased remarkably in cohorts released in 1977, no overall seasonal trend was evident. None was clear in Figures 41 and 42, either: decline in numbers followed a reasonably uniform pattern.

iii. September 1976 extended cohort

Figure 43, comprising eight survivorship plots, is at the end of this chapter. All results are expressed in elapsed days. Calendars are in Appendix Table 6. Details of regressions are in Appendix Table 11.

Sizes released were 6 to 11 mm and 12 mm males and females - eight cohorts in all. In each cohort, numbers dropped abruptly in the first interval. Many then seemed to level off for one or two months before declining. The sudden drop is attributed to the September gales mentioned previously. The apparent levelling might have resulted from return to the study area of snails dispersed by the gales, but in the absence of proof from individual tagging these values were not excluded unless known underestimates.

Only four valid 6 mm points remained after normal date selection, extending approximately seven months from release (Figure 43). The regression was however significant (Appendix Table 11).

The 7 mm cohort also left only four suitable dates although it maintained satisfactory numbers for roughly 250 days. The curved scatter produced a non-significant regression.

The 8 mm snails lasted about 300 days and declined steadily. The regression was very highly significant. Numbers initially released were similar to those of 6 and 7 mm. Snails 9 mm and larger were much more abundant.

The 9 mm cohort persisted for at least 300 days. The regression was highly significant despite a sudden drop on the seventh recapture (day 286, 16 June 1977). A similar drop, usually involving undersampling, occurred in all larger cohorts. Concurrent sudden decreases were also evident in some ordinary cohorts such as November 1976 9 mm (Figure 36, day 209), and in the March 1977 extended cohort (part (iv), day 104).

A very highly significant regression was obtained for the 10 mm cohort, which survived in adequate numbers for approximately eleven months.

The 11 mm snails declined steadily for over a year; the regression was again very highly significant.

12 mm adults were live-sexed and separately coded. Pooled data of both cohorts (not illustrated) gave numbers lasting at least 400 days. The regression was very highly significant, but the slope was steeper than for either sex and the standard errors were greater - especially that of the estimate. Both effects were largely caused by two final dates omitted from the individual-sex regressions.

12 mm males persisted for about ten months, as did the females. The latter declined the more steeply but otherwise the sexes performed similarly.

A figure and regression for pooled totals (6 to 12 mm) is inappropriate because the separate cohorts did not contribute equally.

Table 33

September 1976 extended cohort slopes

Table 33. Slopes (with standard errors) extracted from Appendix Table 11. 12 mm entry pools separate-sex data (M, males; F, females).

Cohort, mm	Slope, x 10^{-3}	Cohort, mm	Slope, x 10^{-3}
6	8.37 (1.23)	11	7.30 (0.62)
7	6.02 (1.77)	12	8.07 (0.72)
8	3.91 (0.34)	M 12	5.92 (0.59)
9	6.95 (0.86)	F 12	7.42 (0.61)
10	6.22 (0.92)		

There was no clear trend of slope with starting size (Table 33) but the 6 and 7 mm cohorts failed to maintain adequate numbers as long as the others: decay rates typically were computed over at least nine months.

When comparing the 6 and 9 mm components with the September 1976 ordinary cohorts (Appendix Table 10, Figure 34), it is necessary to remember that because the extended cohorts were released much earlier, the second point on the extended cohort plot corresponds to the first on the ordinary, and so on. The 6 mm cohorts cannot confidently be compared but the 9 mm cohorts behaved similarly to each other.

iv. March 1977 extended cohort

Figures 44 and 45 are at the end of this chapter. Calendars are in Appendix Table 7. Details of regressions are in Appendix Table 12.

As in September, 6 to 11 mm cohorts were released along with sexed 12 mm adults. Sexed 13 and 14 mm adults were also used. Six recaptures were possible before field work ended in October. Many cohorts were undersampled on day 104 (16 June), when numbers generally dropped abruptly. (This was day 286 for the September 1976 extended cohort.) Such known underestimates, day 0, and end dates with low numbers were eliminated as usual before regressions were calculated. However, this left too few 6 mm points and the non-significant 7 to 10 mm regressions were based on only four points. Accordingly, alternative regressions reinstating certain dates are presented where the main effect is to increase the confidence with which they may be compared with others. That is, if including a point does not alter the slope but improves P(F), then this new equation is more useful for comparisons: it is a more sound description of observed decline in numbers, and may apply to a wider time span.

Only eighteen 6 mm snails were available for tagging. Too few survived the first interval to permit a regression to be presented confidently.

The 7 mm cohort fared rather better, maintaining numbers for at least five months (Figure 44). A more satisfactory regression resulted from retaining days 0 and 218 than from normal data selection (Table 34, Appendix Table 12).

Table 34

March 1977 extended cohort slopes

Table 34. Slopes (with standard errors) extracted from Appendix Table 12. OR, alternative regression explained in text. Conventions otherwise as in Table 33.

Cohort, mm		Slope, x 10^{-3}	Cohort, mm	Slope, x 10^{-3}
7		9.02 (2.69)	12	13.89 (1.04)
	OR	10.29 (1.22)	13	16.58 (2.39)
8		11.20 (2.73)	14	17.88 (1.99)
	OR	10.18 (0.89)	M 12	12.92 (1.25)
9		16.30 (4.36)	F 12	15.12 (1.13)
	OR	14.80 (2.73)	M 13	15.02 (1.99)
10		18.41 (4.71)	F 13	16.29 (1.43)
	OR	18.89 (2.94)	M 14	16.59 (2.49)
11		14.35 (1.66)	F 14	17.08 (2.05)

Likewise, adding days 0 and 218 had little effect on the 8 mm slope and intercept, but greatly improved the standard errors and significance. Otherwise the cohort lasted at least four months.

In the 9 mm cohort, replacing day 0 made a small improvement without changing the slope and intercept much. Numbers dropped abruptly in the third interval and were too low after approximately four months.

A similar decline in the 10 mm cohort caused a slightly kinked distribution if day 0 was reinstated, but day 156 lay close to the regression line and its inclusion produced a more satisfactory equation. (If day 0 was then also included, the Y-intercept and slope became 4.768 and -0.01734 respectively, and the regression remained highly significant.)

The 11 mm snails declined more regularly for about five months. The standard regression was highly significant; the day 0 point lay close to this line.

Adult 12 mm males and females declined steadily. The regressions were respectively highly and very highly significant (Appendix Table 12). Numbers remained adequate after seven months. Females declined somewhat faster than males. Neither cohort dropped markedly in the first interval.

While 13 mm males seemed to decline abruptly after four months, the females did not. Accordingly, their respective regressions were significant and highly significant. Numbers were maintained for at least seven months, and the females had the steeper slope. Neither sex dropped disproportionately just after tagging.

Fewer 14 mm snails were available to tag, but adequate numbers remained for at least five months. As usual, there was no great drop in the first interval. Males declined only slightly more slowly than females. Regressions were significant and highly significant.

Adult slopes increased gently with increasing size within sexes (Table 34), but standard errors overlapped considerably. If adults are pooled within sexes - remembering that numbers are unequal - it becomes clear that males and females perform similarly (Table 35, Figure 45). The only noteworthy difference is the greater male drop to day 156 (7 August).

As with the previous extended cohort, it was considered inappropriate to pool all size classes.

Extra 7 and 8 mm cohorts were released in April 1977 and were treated in parts (i) and (ii).

Table 35

March 1977 extended cohort survivorship: pooled adults

Table 35. Adult data summed across sizes within sexes. Conventions as in Appendix Table 12.

Sex	N	A	Slope, x 10^{-3}	SE(EST)
M	345	4.786 (0.381)	15.99 (2.77)	0.413
F	405	4.976 (0.201)	16.24 (1.46)	0.218

	R^2	F (d.f.)	P(F)	
M	0.917	33.249 (1,3)	0.020	*
F	0.976	123.529 (1,3)	0.002	**

v. July 1977 extended cohort

Calendars are in Appendix Table 9. Details of regressions are in Appendix Table 13.

The same size classes were released as in March, along with 15 mm males and females. Numbers were rather low to begin with and generally dropped sharply in the first four weeks. Because only two recaptures were possible, day 0 was included in regressions to allow significance tests as usual. Although some had moderate standard errors or high R^2 values, none was significant (Appendix Table 13). Regressions could not be calculated for 14 and 15 mm males: none were found on the second recapture.

There was no clear pattern of decay rate with shell length (Table 36); Y-intercepts differed very little.

Table 36

July 1977 extended cohort slopes

Table 36. Slopes (with standard errors) extracted from Appendix Table 13. Conventions as in Table 33. NA, not applicable.

Cohort, mm	Slope, x 10^{-3}	Cohort, mm	Slope, x 10^{-3}
6	18.86 (11.41)	M 13	21.54 (4.84)
7	22.67 (4.58)	F 13	14.82 (8.39)
8	13.63 (4.70)	M 14	NA
9	20.44 (8.57)	F 14	26.15 (16.58)
10	19.85 (3.27)	M 15	NA
11	12.64 (4.35)	F 15	31.45 (18.76)
M 12	14.60 (1.75)		
F 12	18.58 (6.85)		

Individual cohorts are not illustrated. The following have a sufficiently narrow scatter with enough survivors on day 89 to permit comparisons of slope: 7, 8, 10, 11 mm, 12 mm males, 13 mm males.

Males and females could not usefully be pooled over size classes as in March, nor within cohorts.

The July 1977 regular 6 and 9 mm cohorts were released a week later. The 6 mm snails performed similarly to, but the 9 mm snails declined much more regularly than, their extended cohort counterparts.

vi. summary of results

1. Survivorship is reported for repeated 6 and 9 mm and extended tagged cohorts, released from February 1976 to July 1977 and recaptured until October 1977.

2. Wherever possible, to eliminate bias, initial and low late values were eliminated from regressions of $\log_e$ percent surviving vs. elapsed days. Known underestimates were also rejected. Fit was evaluated with R^2 and its significance with an F-test.

3. Regression slopes estimated maximum mortality rate because active or passive emigration could not be discounted.

4. Patterns of 6 and 9 mm slope with release date were highly significantly correlated. Slopes increased in 1977 but no overall seasonal trend was found. The 9 mm cohorts generally declined the faster.

5. The September 1976 extended cohort had component cohorts 6 to 11 mm and 12 mm males and females. Slope did not depend on starting size. Adult females declined slightly faster than males.

6. The March 1977 extended cohort had components 6 to 11 mm and 12, 13, and 14 mm males and females. Slopes were greater (steeper) than in September and did not depend on starting size. Adult males and females performed alike.

7. The July 1977 extended cohort had similar components to March, as well as 15 mm males and females. Many cohorts crashed in the first interval. Little confidence could be placed in the results.

8. Occasionally exceptional drops in numbers were seen concurrently in many cohorts. One such event in September 1976 was attributed to gales.

Discussion

i. emigration and mobility

> "Until recently migration has often been regarded as an idiosyncrasy to be included with unaccountable mortality in life tables based on census information from a restricted area. Yet migration is not synonymous with mortality." (Taylor & Taylor 1977)

It is regrettable that death could not thoroughly be distinguished from emigration. The effort of hand-searching large areas of tangled seaweed is prohibitive. A proposal to use portable scintillation counters to sweep a Ministry of Defence restricted-access beach for snails tagged with a feeble gamma-emitting scandium isotope was not accepted. Hilborn & Krebs (1976) put tantalum-182 wire on fish tags attached to vole ears. Some such experiment is desirable to establish the distance and rate of dispersal, the fate of dispersed snails, and to determine to what extent passive dispersal by waves and currents affects dislodged living animals as well as the empty shells so abundant and mobile on some beaches.

The importance of dispersal to gene flow in this oviparous species is poorly understood. Berger (1973, 1977) probably confounded <u>L. mariae</u> with <u>L. obtusata</u>. Scudder (1974) points out that gene flow may not be as important in the field as was formerly thought. Wilkins & O'Regan (1980) studied six <u>Littorina</u> species (including <u>obtusata</u> and <u>mariae</u>) electrophoretically, and found that genetic variability was not necessarily correlated with dispersal ability.

<u>L. obtusata</u>, although generally sedentary, does move from weed to weed. From a series of limited experiments and a few large transplant trials using file-marked snails, Guiterman (1971) concluded that wave action

promoted a state of flux and caused most mortality. Some of his results must be erroneous: he did not explain how a population can maintain itself in the face of daily loss rates of 10% or more. In a series of brief mobility experiments using snails tagged with very conspicuous pale blue epoxy resin, Bray (1974) likewise attributed a high turnover on revisited boulders to wave action. Active locomotion over fine mobile substrata was difficult and sometimes led to death by suffocation, but firm damp surfaces such as seaweed, fine gravel or rock presented few difficulties; these observations were confirmed in the present study. Reimchen (1974) remarked that at his collecting sites in the Bristol Channel, "any snail that was dislodged from plant to the substrate disappeared into 0.5 m of mud" and suffocated.

Various workers have attempted to investigate *L. obtusata*'s preference for fucoids and to account for its abundance on them in terms of chemical gradients, geotaxis, rheotaxis, phototaxis, etc. (e.g., Bakker 1960; Barkman 1955; Janssen 1960; Underwood 1972, 1973; Van Dongen 1956). Confusion with *L. mariae*, improper experimental design, or failure to consider alternative factors such as predation greatly reduce their value.

At first glance it would seem prudent for *L. obtusata* to stay put: one might expect Natural Selection to favour sedentary individuals less likely to be dislodged, particularly on silty shores or those where weed cover is patchy. In the present study, no evidence was found for vertical migrations, and cohort tagged animals were recovered where released after 591 days: one resin-tagged female was still present when sampling ended 723 days after her release, having been found at site A throughout (Section 10). Hughes (1980) reported that fewer than 1% of tagged *L. nigrolineata* Gray thought to be dead could be accounted for by emigration, at least over short distances, but L. obtusata is more mobile. Fucoid algae are also its food: it appears fastidious, leaving decaying parts promptly (Janssen 1960; pers. obs.). It seems reasonable to expect mobility to differ from site to site according to weed cover and condition, wave action, substratum etc. Accordingly, "death rates" obtained by tagging must be interpreted with care.

ii. causes of mortality

It is conventional to regard the - necessarily negative - slopes of survivorship curves as death rates. Where replicates are available and agree, the mean may be taken as the instantaneous death rate μ, where the proportion surviving per time t is given by $e^{-\mu t}$ (Hughes & Roberts 1981). Where emigration is important these rates will be overestimated unless, as in the well-documented predation of the land snail Cepaea nemoralis L. by the song thrush Turdus ericetorum Turton, the number dead can be determined independently (e.g., Richardson 1975; Williamson et al. 1977).

The slope may change strongly, for instance should high juvenile mortality give way to lower adult mortality. Such curves must be split at some appropriate age not chosen from the shape of the curve (Pinder et al. 1978; good illustration in Hughes & Roberts 1981, Fig. 6, L. rudis). This problem does not arise in the present study, where very young animals could not be tagged.

Whole-life survivorship data may be compared statistically if expressed as a Weibull distribution, provided that lifespan is long enough to avoid unrepresentative death rates caused by brief events such as unpredictable weather (Pinder et al. 1978). The application of this technique to winkles is uncertain. Although Hughes (1980) found no marked effect of equinoxial gales on tagged *L. nigrolineata*, those of September 1976 depressed several *L. obtusata* cohorts in the present study. Both species live for several years, but *L. obtusata* may be more susceptible to wave action.

Tag loss was slight and readily identified. Other causes of disproportionate first-interval losses might include tagging shock if tagging stressed animals more than recapture handling. Manly (1971) provides a test for mortality induced by tagging. This requires individual tagging and furthermore assumes that the effect occurs promptly, that subsequent handling has no effect, that emigration is permanent, and that each animal is equally likely to be captured during a particular sample. The third condition in particular (permanent emigration) is not likely to hold for *L. obtusata*. In addition, it is risky to attribute increased mortality at the time of tagging to the tagging process, unless the effect can be repeated and shown to be independent of weather etc. (This matter is considered further in part (iii).) Cameron & Williamson (1977) stress that mere handling considerably affected dispersal and hence survivorship estimates in a six-year study of adult *Cepaea nemoralis*, and provide a technique to allow for such effects. Their results must call into question Manly's (1971) supposition that handling *per se* has no effect. Hughes & Roberts (1981) feared that handling might increase mortality of cliff-dwelling *L. rudis* and *L. neritoides* by increasing the chances of being washed from crevices, and report good accuracy in measuring their species *in situ* against a set of "standard winkles", confirming Emson & Faller-Fritsch (1976). In the present study it was not possible to measure snails *in situ* without dislodging them.

Predation on winkles has been reviewed elsewhere (Pettitt 1975) and is considered in Section 5. Parasitic infection (e.g., Hughes & Roberts 1981; Kuris 1974; Raffaelli 1979; Thomas 1974; Williams & Ellis 1975) was not investigated but Guiterman (1971) examined more than ten thousand *L. obtusata* from beaches in the vicinity. *Microphallus similis* amounted to between 78 and 99% of trematode parasites found in samples taken from five shores over a year. Mixed infections were rare. Pohley (1976) found eight species of larval trematodes in littorinids at three New England shores over a year. All eight were found in combined *L. obtusata* and *L. mariae*; *M. pygmaeus* was the most abundant. Like Guiterman, he found that infestation varied seasonally, presumably in part because of different frequencies of encounter between winkles and bird droppings. Pohley's remarks on snail size are largely conjectural; Baudoin (1975) has provided six explanations for any correlation between parasitic castration and host size. Regardless of whether or not trematodes do increase their host's size, they might affect its survivorship either by killing it or, by reducing its reproductive effort, extending its lifespan. The latter seems likely to be important in species that become weakened by occasional massive reproduction, while Borkowski (1974) found that spawn amounted to as much as 85% of total somatic and spawn production in his species.

Effects of unsuitable weather are difficult to demonstrate in the field without catastrophic mortality. Guiterman (1971) argues for a behavioural adaptation to wave exposure consisting of moving from *Fucus* to rock in winter, but gives no data from an interesting mass transplant to a Cornish beach then newly recovered from the 1966 "Torrey Canyon" oil spill. He does not consider the alternative, that something keeps the snails off the rock in summer. Shore crab *Carcinus maenas* foraging varies seasonally:

feeding rate is highest in summer to support rapid growth and breeding, while in winter the crabs eat little or nothing and do not much migrate vertically with the tides (Elner 1980). Guiterman also attempted to show that snails from an extremely sheltered site were physiologically better adapted to conditions there than were snails from a moderately sheltered site. His experiments are difficult to relate to field conditions. For example, he did not measure temperature or oxygen tension at his experimental subjects' source sites.

Food is not believed to be limiting at Gorad. Guiterman (1971) reported overgrazing of Fucus vesiculosus in Trearddur Bay, Anglesey (Wales). Fucoids were severely grazed in some parts of Strangford Lough, County Down, Northern Ireland (P.J.S. Boaden, pers. comm.; pers. obs.) although it is uncertain that L. obtusata was solely responsible.

Crevices or other damp refuges influence size-specific survivorship of other littorinids (Emson & Faller-Fritsch 1976; Raffaelli 1978b; Raffaelli & Hughes 1978 extended in Hughes & Roberts 1981). Hatchling and juvenile L. obtusata commonly aggregate in perforated Ascophyllum nodosum and Fucus vesiculosus air bladders and at branchings (pers. obs.; Goodwin 1978; Guiterman 1971; Reimchen 1974), but no experimental manipulations seem to have been published; Guiterman's remarks on rock crevices are conjectural.

iii. L. obtusata survivorship at Gorad

Repeated 6 and 9 mm cohorts showed little evidence of seasonal effects *per se* but the highly significant association between 6 and 9 mm patterns of decay rate with initial release date suggests some environmental influence on survivorship. Although 1977 cohort slopes were steeper, this may be partly a truncation artefact of sampling ending in October, and partly attributable to the occasional inclusion of day 0 in the regressions. The survivorship trajectories (Figures 41 and 42) follow much the same pattern throughout the year, declining at a uniform rate except when dislocated e.g. by weather in September 1976 or by undersampling in June 1977. The same applies to L. rudis and L. neritoides (Hughes & Roberts 1981, Fig. 3).

The generally more rapid decline of the larger snails was unexpected. 9 mm snails are by no means senile (Section 8) and have more robust shells (Section 4). Ordinarily one might expect mortality to decrease with age, perhaps becoming constant after maturity, much as shown for L. rudis and L. neritoides by Hughes & Roberts (1981) and for L. nigrolineata by Hughes (1980).

When comparing survivorship of synchronous cohorts having different shell sizes it is important to remember firstly, that their ages and hence early life histories are different, and secondly that snails available for tagging are necessarily survivors. That is, barring size-specific predation etc., the larger snails may well begin with a lower proportion of the physiologically unfit or behaviourally foolhardy. Furthermore, such forces as visual predation according to colour morph may complicate results unless either great care is taken to standardise tagged snails, or results come from individual tagging where accurate descriptions are taken. The overall pattern revealed by cohort tagging may mask much important detail.

The September 1976 extended cohort showed no strong trend of decay rate with starting size but did not include small juveniles or adults larger than 13 mm. All sizes fared similarly and most dropped in June along with some 6 and 9 mm cohorts and many components of the March 1977 extended cohort, supporting the supposition that post-juveniles normally decline steadily but are vulnerable to stressful weather. This is interesting because the dense weed should moderate conditions appreciably and because L. obtusata moves deep into the damp weed when confronted with heavy rain, strong direct sunshine, high ambient temperature, sleet, or snow (pers. obs.). The one condition it seems unable to outrun - apart from wave action - is strong wind, which rapidly dries the weed. L. obtusata prefers not to crawl over dry surfaces; winkles placed on a dry wooden laboratory bench rarely venture more than one to two cm.

Decay rates in the March 1977 extended cohort, incorporating a wider range of adults, are typically about twice those of corresponding September cohorts. (Because the intercepts are higher than in September, predicted proportions surviving after a given interval do not necessarily differ so much. For instance, after 100 days 26.84% of September 11 mm snails will remain compared with 25.79% of the March 11 mm snails. This discussion is confined to the slopes, but the full regressions are provided.) This is in keeping with the increased slopes of 1977 routine cohorts. The occasional inclusion of day 0 did not affect the March slopes, and standard truncation generally kept them shallower, so some other explanation must be sought. While many conjectures are possible - for instance, predator immigration (cf. Elner 1980) - none is convincing.

It is interesting that Hughes (1980, Fig. 4), working at a jetty approximately 2 km NE of Gorad on the same shore of the Menai Straits, found that one-mm cohorts of tagged L. nigrolineata larger than 6 mm survived much better from December 1977 to March 1978 than from then to June; results for the previous and succeeding quarters were intermediate. Unfortunately, his cohorts were not fully independent, survivors being supplemented each quarter and the whole re-tagged as a new cohort of a new size. That is, the March 8 mm cohort might consist in whole or in part of snails also shown in his Figure 4 as the December 7 mm cohort. This complicates detailed comparisons, and Hughes presents none. In fairness, the method used in the present study is not above reproach. As a cohort ages, its size range may increase (Section 8), and so comparisons from month to month within cohorts would be open to question if sizes differed markedly in survivorship. This does not appear to be the case. Long-lived cohorts with good starting numbers such as February 1976 9 mm, March 1976 9 mm, or April 1976 6 mm can decline steadily for a year or more despite increases in mean size from 9.43, 9.40, and 6.56 mm to 14.30, 13.60, and 13.65 mm respectively (data from Appendix Table 5, each to last day included in regression).

Although there is again no striking trend in slope with starting size in the March 1977 extended cohort, the largest snails declined rather swiftly. This would be expected if adults quickly became senile, but individual tagging (Section 10) showed that adults may live for several years.

Hughes (1980) obtained fairly constant slopes for L. nigrolineata on a moderately sheltered boulder shore on Anglesey from September 1976 to September 1979. While each quarterly cohort contained snails ranging from 5 to 18 mm (approximate data from his Figure 2, confirmed pers. comm.), his other work showed no trend in mortality over roughly this size range. L. nigrolineata lays benthic egg masses like L. obtusata, and likewise can live in the Ascophyllum zone of moderately sheltered shores, although it can also tolerate exposure (Hughes 1980; Hughes & Roberts 1981). L. nigrolineata does not occur at Gorad.

Relatively few adults were tagged in July 1977; their disappointing performance makes comparisons unhelpful. Many of the largest were found dead but undamaged within a couple of days from release, often with much silt around the body and within the mantle, and more empty shells were later discovered, filled with silt, near to the release site. Guiterman (1971) claims that many large adults die during warm weather, an inference from weight-frequency distributions subjected to probability-paper analysis. He suggests that one summer mortality agent might be lowered oxygen tension beneath the algal fronds: on hot cloudy days silt would release hydrogen sulphide, or organic sediment would take up large amounts of oxygen.

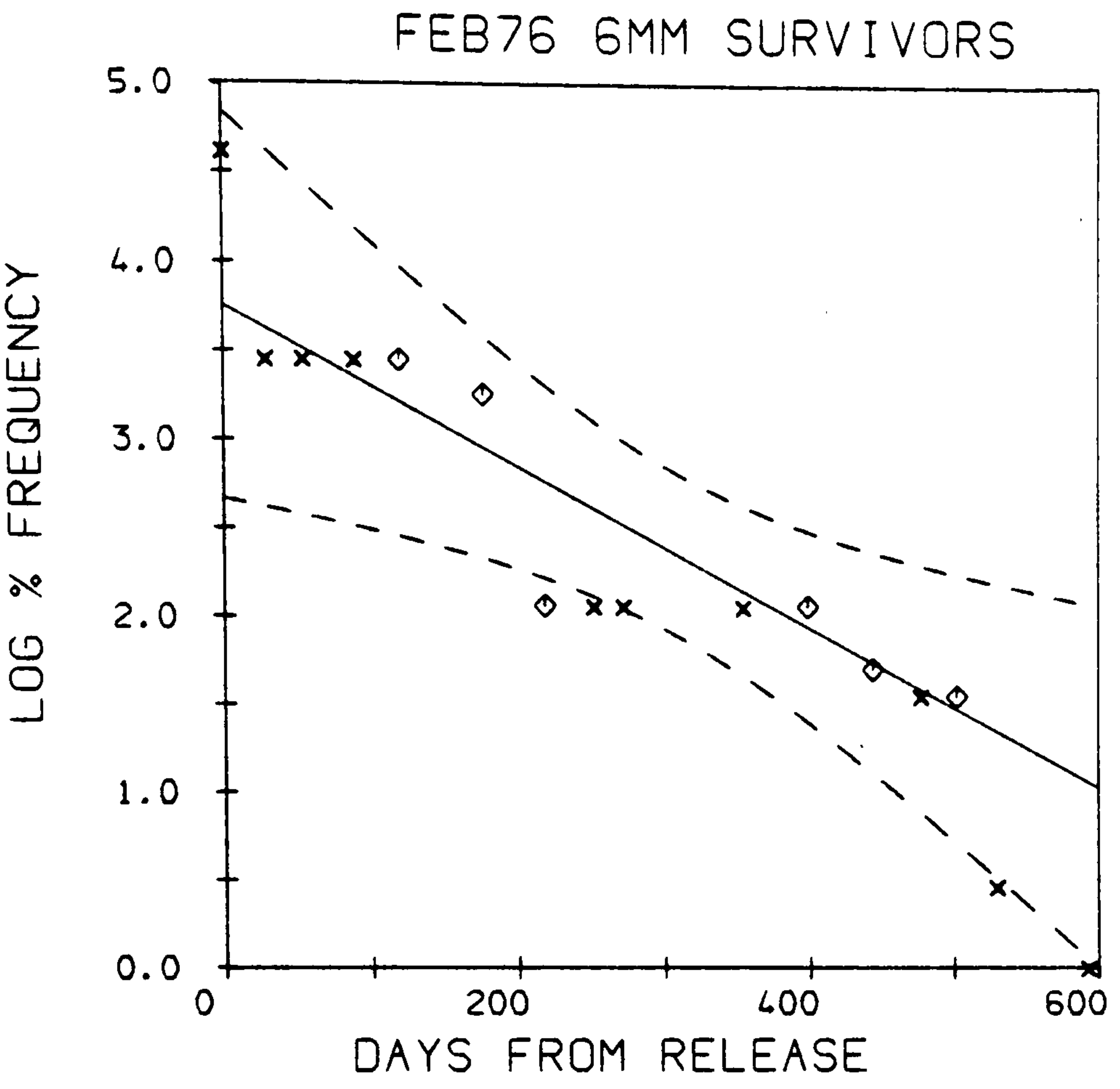
The large number of dead tagged snails found on 22 July 1977 raised the unpalatable question of handling or tagging shock. To determine whether this might be responsible, the proportions of those known to be alive on 11 and 14 July found dead on 22 July were compared between two groups: the July extended cohort released 11 July, and all other tagged snails. These groups had not been kept in the laboratory concurrently. The field notes showed that much fine sediment had appeared in recent days. If the mortality agent was environmental, both groups should have lost similar proportions by 22 July. 411 July extended cohort snails were alive on 11 July and 69 were found dead: 16.79%. 571 other tagged snails were alive on 14 July, and those found dead were 1 individually-numbered, 33 regular cohorts (10.4% of 318), 11 September 1976 extended cohort (25% of 44), and 51 March 1977 extended cohort (23.5% of 217), 96 in all: 16.81%. The astonishing agreement strongly suggests that the snails were killed by some field agent and not by tagging shock.

From the information in this chapter, it appears that L. obtusata survivorship is reasonably constant from 6 to 14 mm, that adult males and females do not differ from each other, and that while there is no clear seasonal trend in survivorship of comparably-sized snails, survivorship at any size from 6 mm may vary from year to year.

Individual tagging results can be pooled and treated as cohorts, yielding more information on adult males and females: Section 10.

Survivorship figures

Figures 29 to 40	6 and 9 mm cohorts
Figure 43	September 1976 extended cohort
Figures 44, 45	March 1977 extended cohort



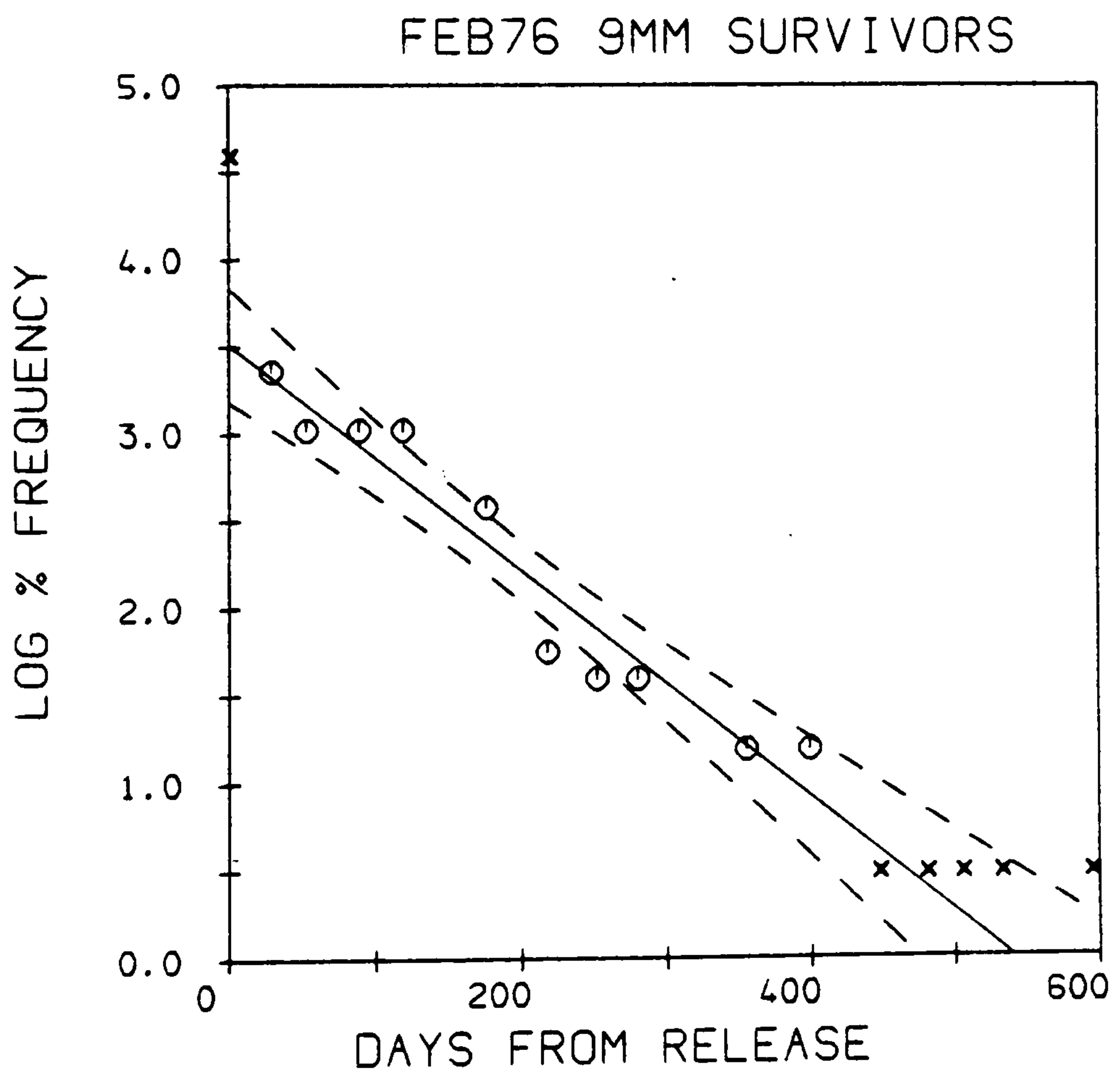
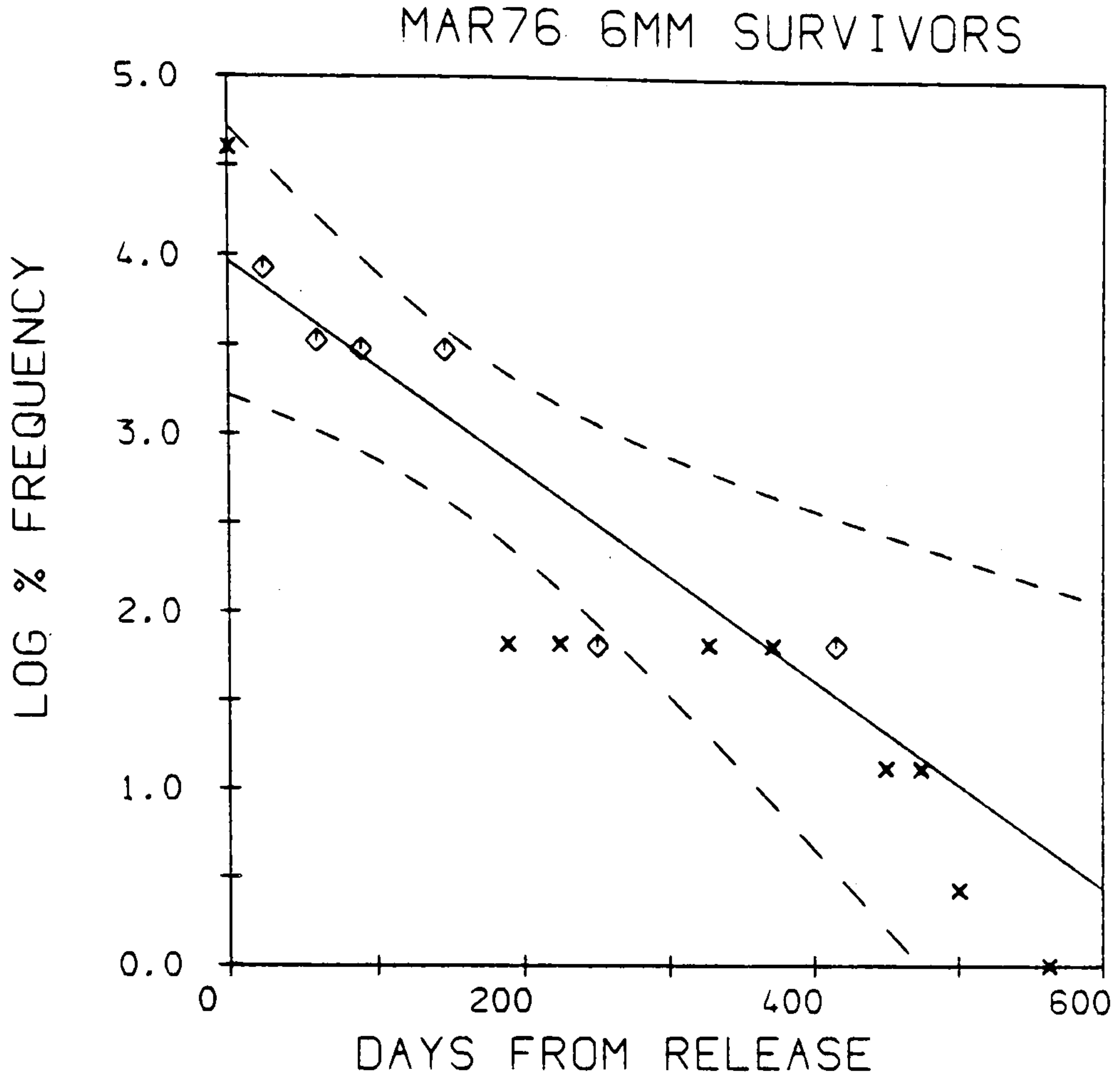


Figure 29. Survivorship of 6 mm (upper) and 9 mm (lower) cohorts released 25 February 1976. Format as in Figure 28, C. Dates, starting numbers and regressions are in Appendix Tables 5, 8 and 10.



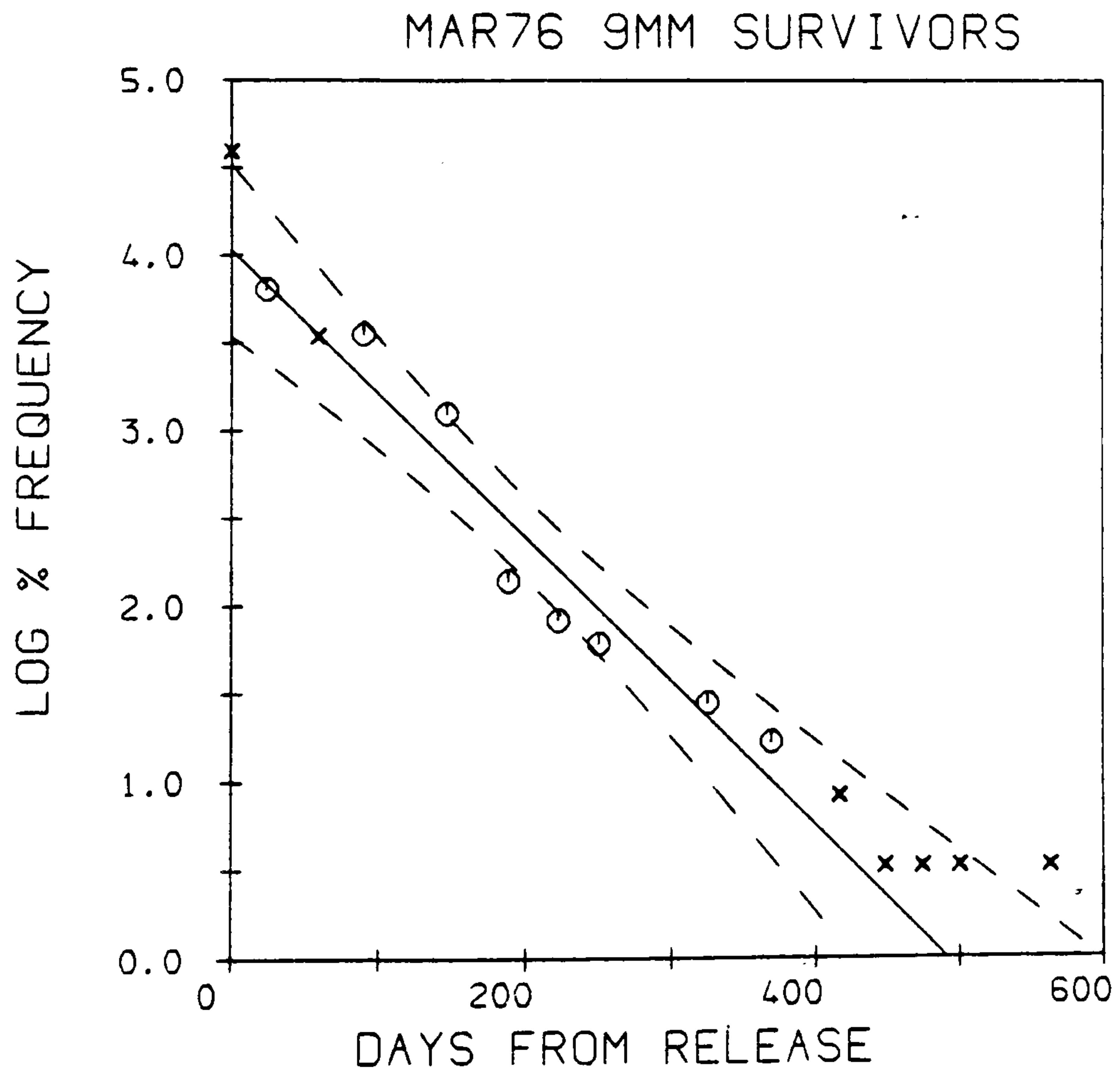
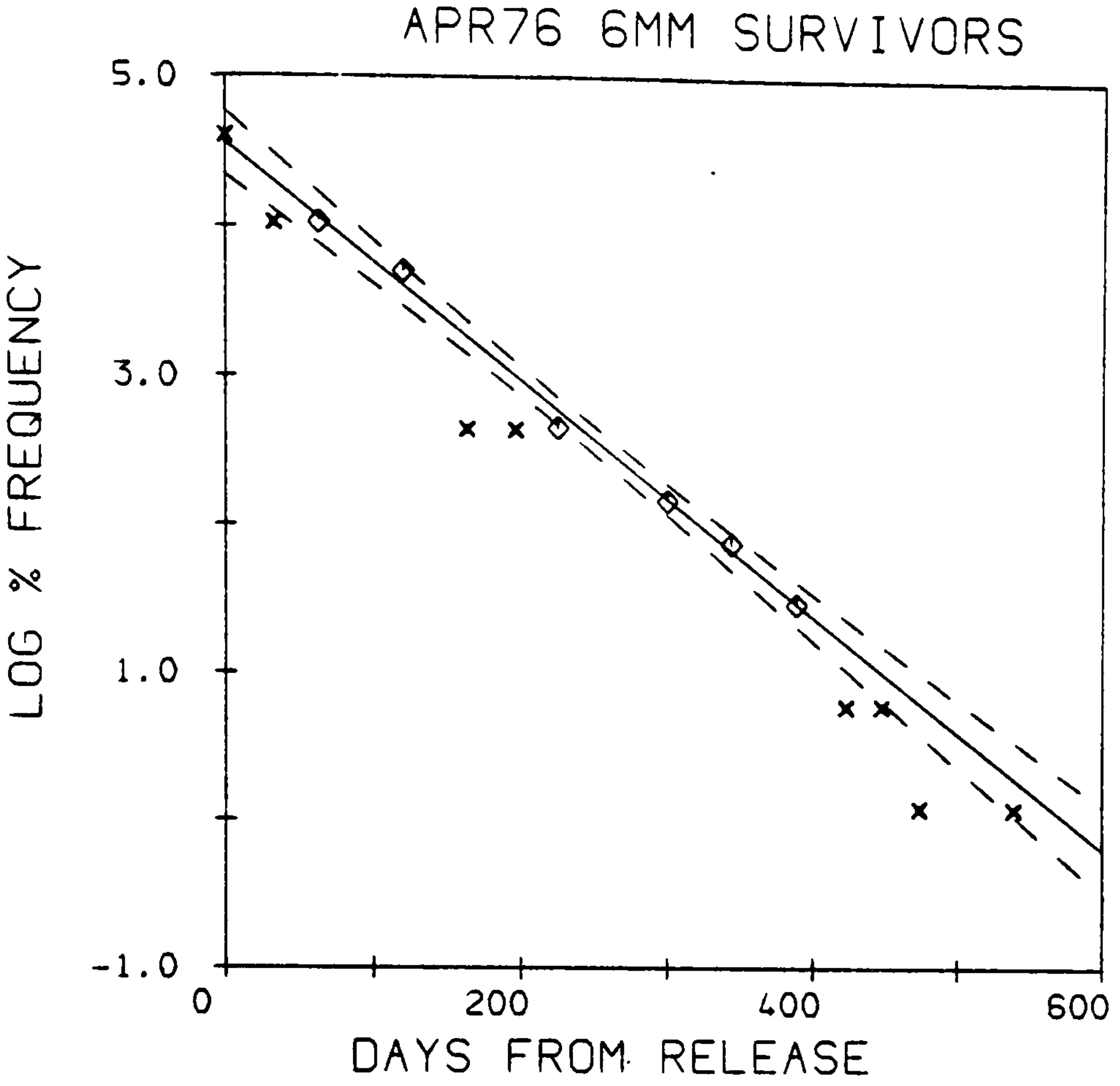


Figure 30. Survivorship of 6 mm and 9 mm cohorts released 25 March 1976. Conventions as in Figure 29.



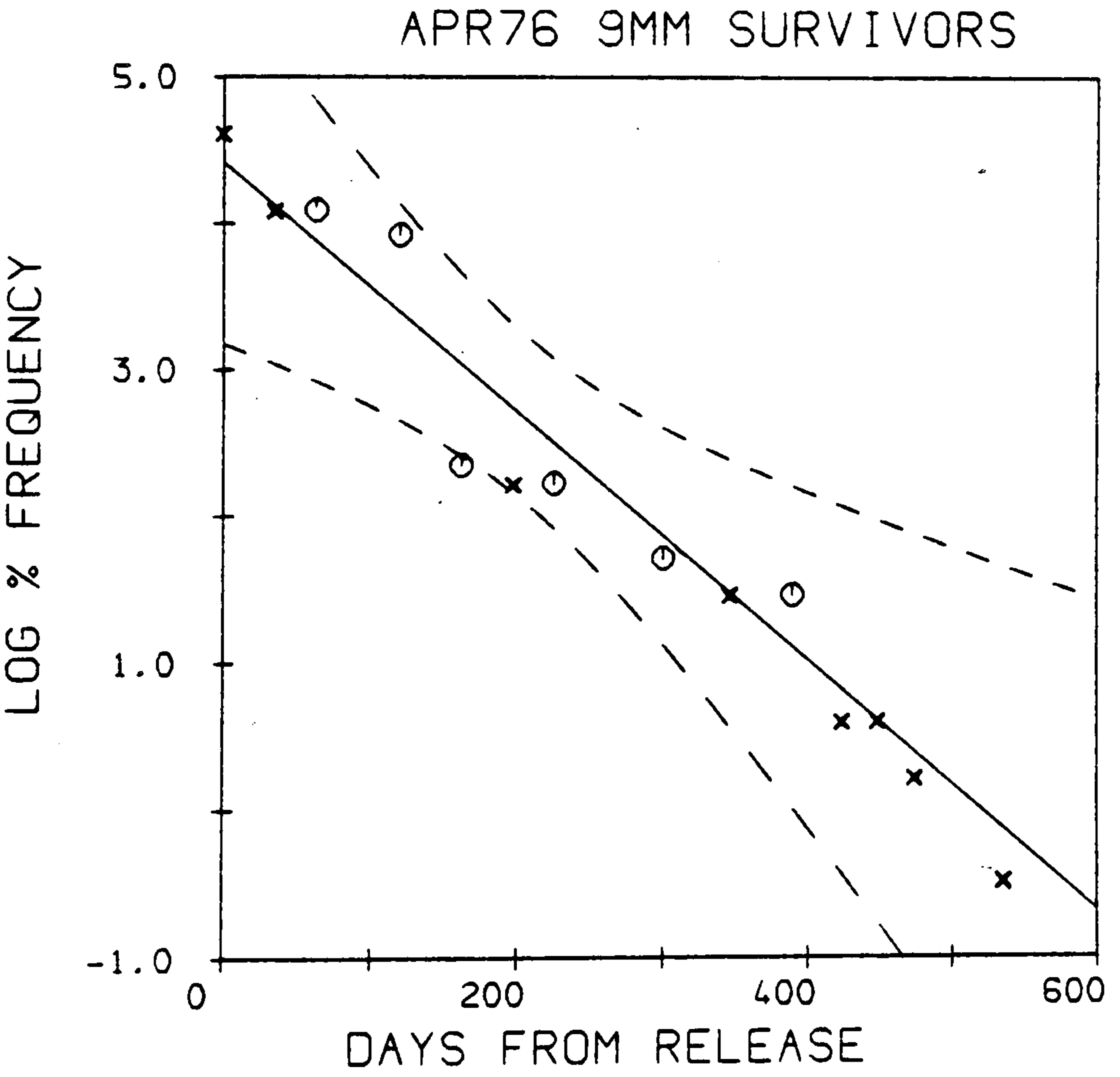
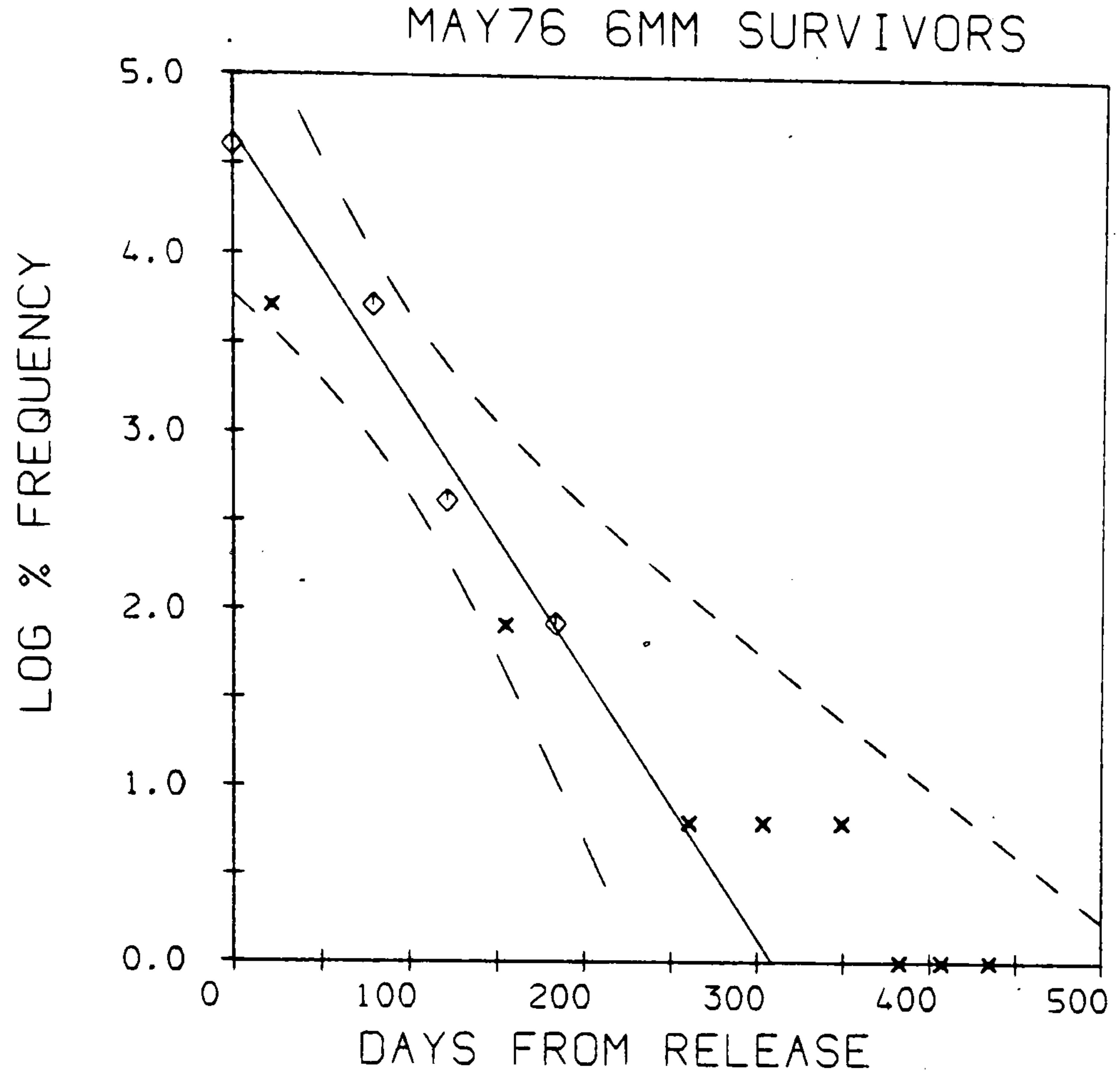


Figure 31. Survivorship of 6 mm and 9 mm cohorts released 21 April 1976. Conventions as in Figure 29. Note Y-axis scale.



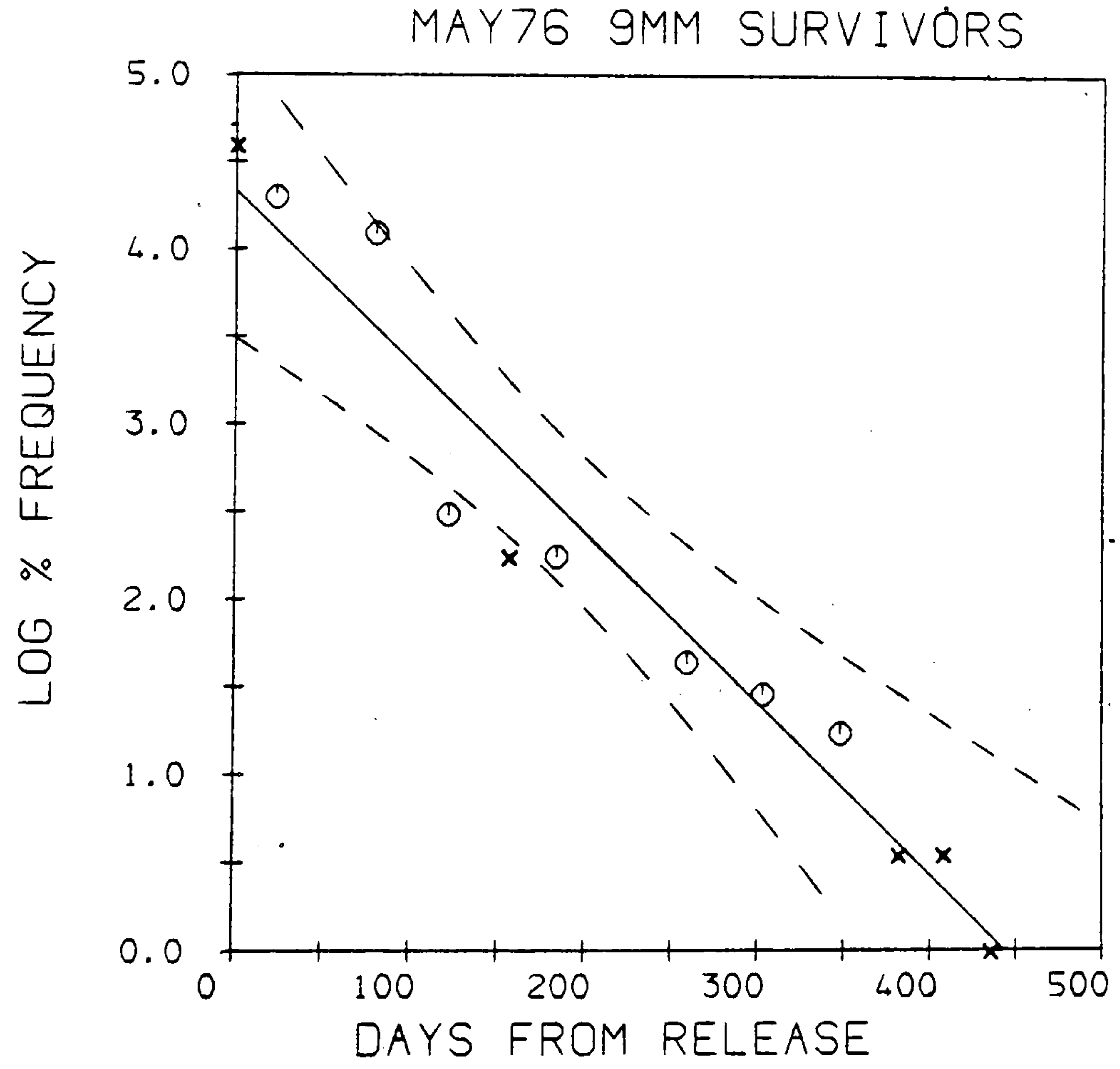
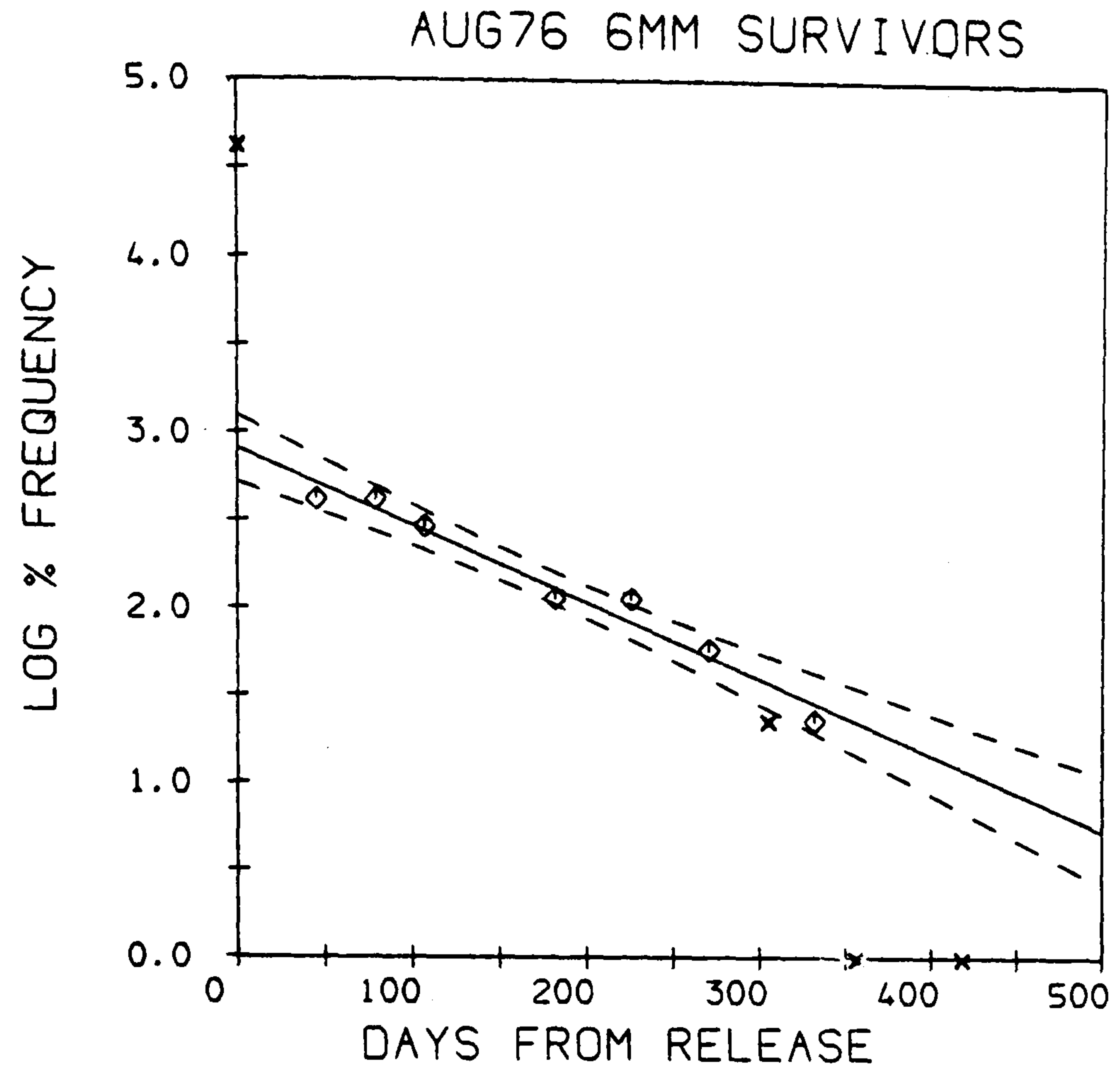


Figure 32. Survivorship of 6 mm and 9 mm cohorts released 31 May 1976. Conventions as in Figure 29. 6 mm regression as explained in text.



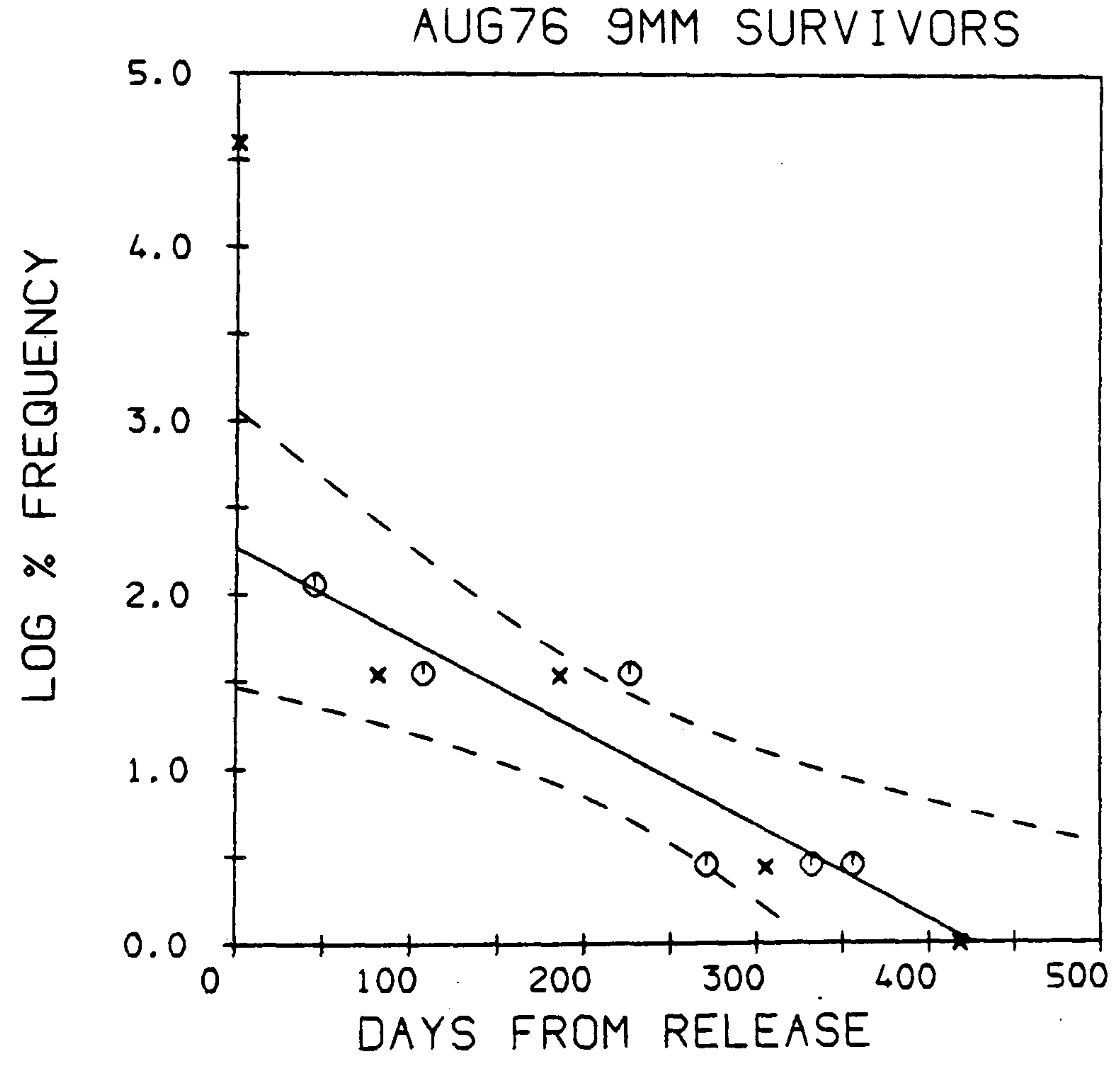
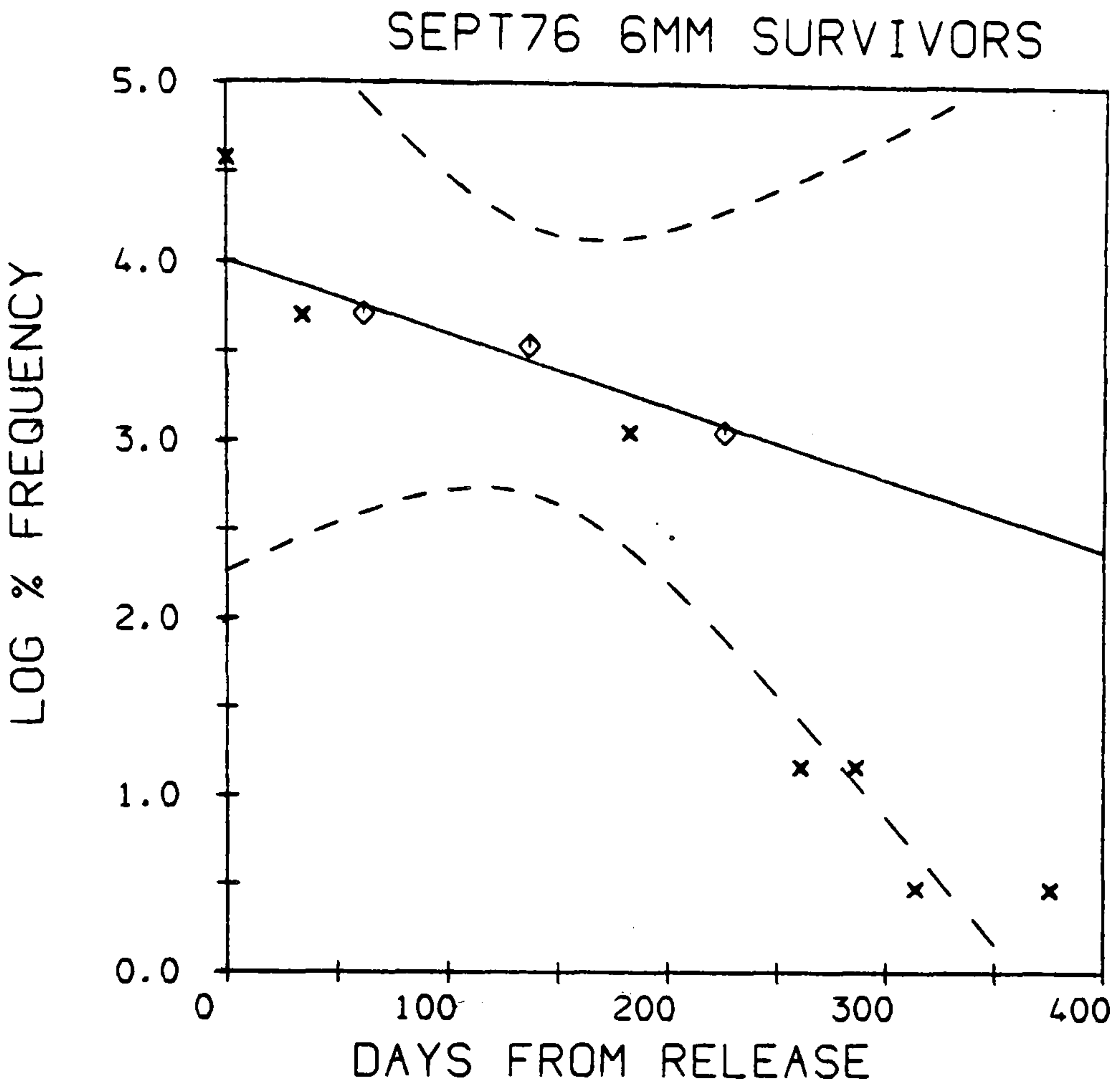


Figure 33. Survivorship of 6 mm and 9 mm cohorts released 16 August 1976. See text for explanation of dates chosen for regression.



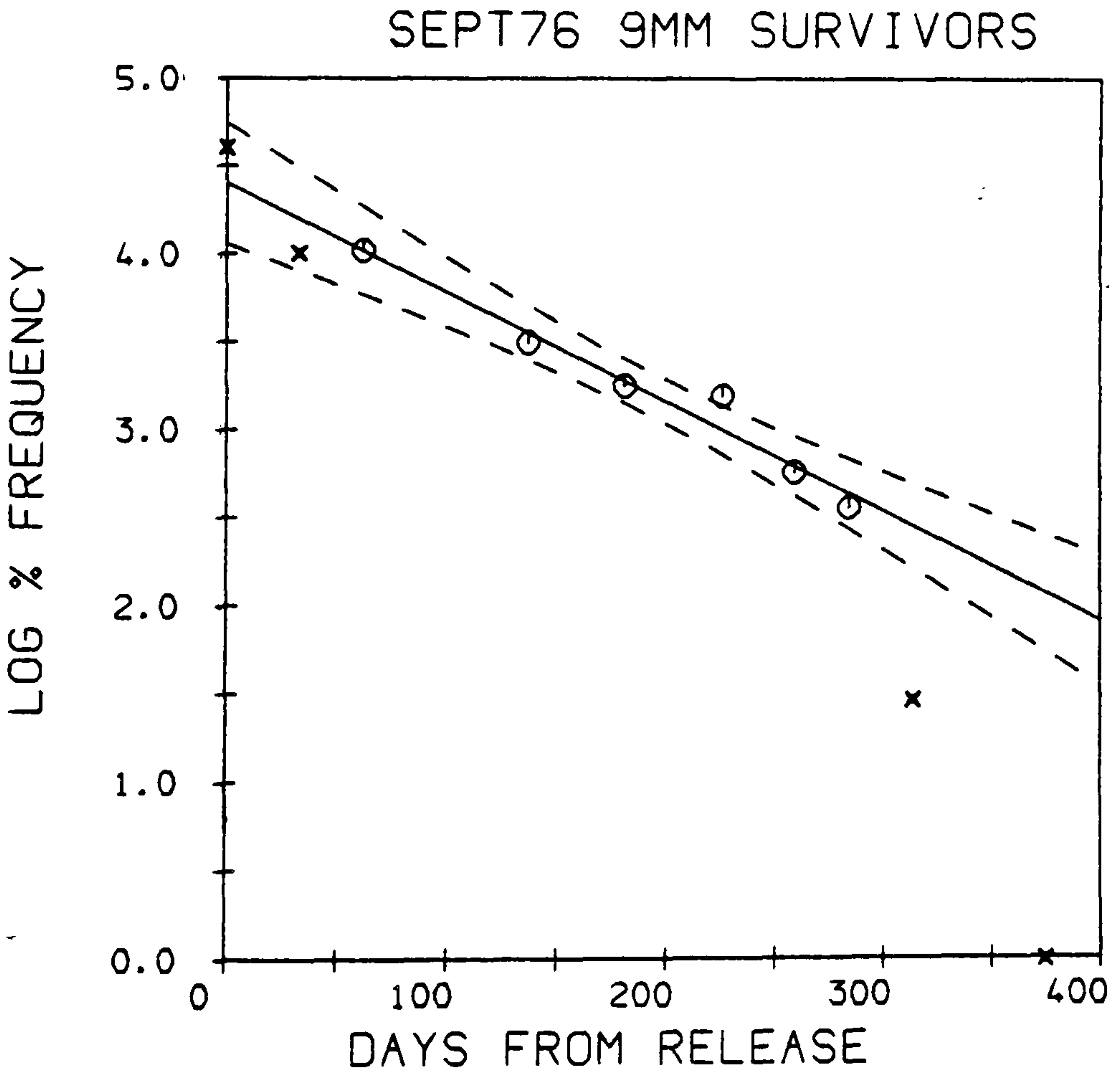
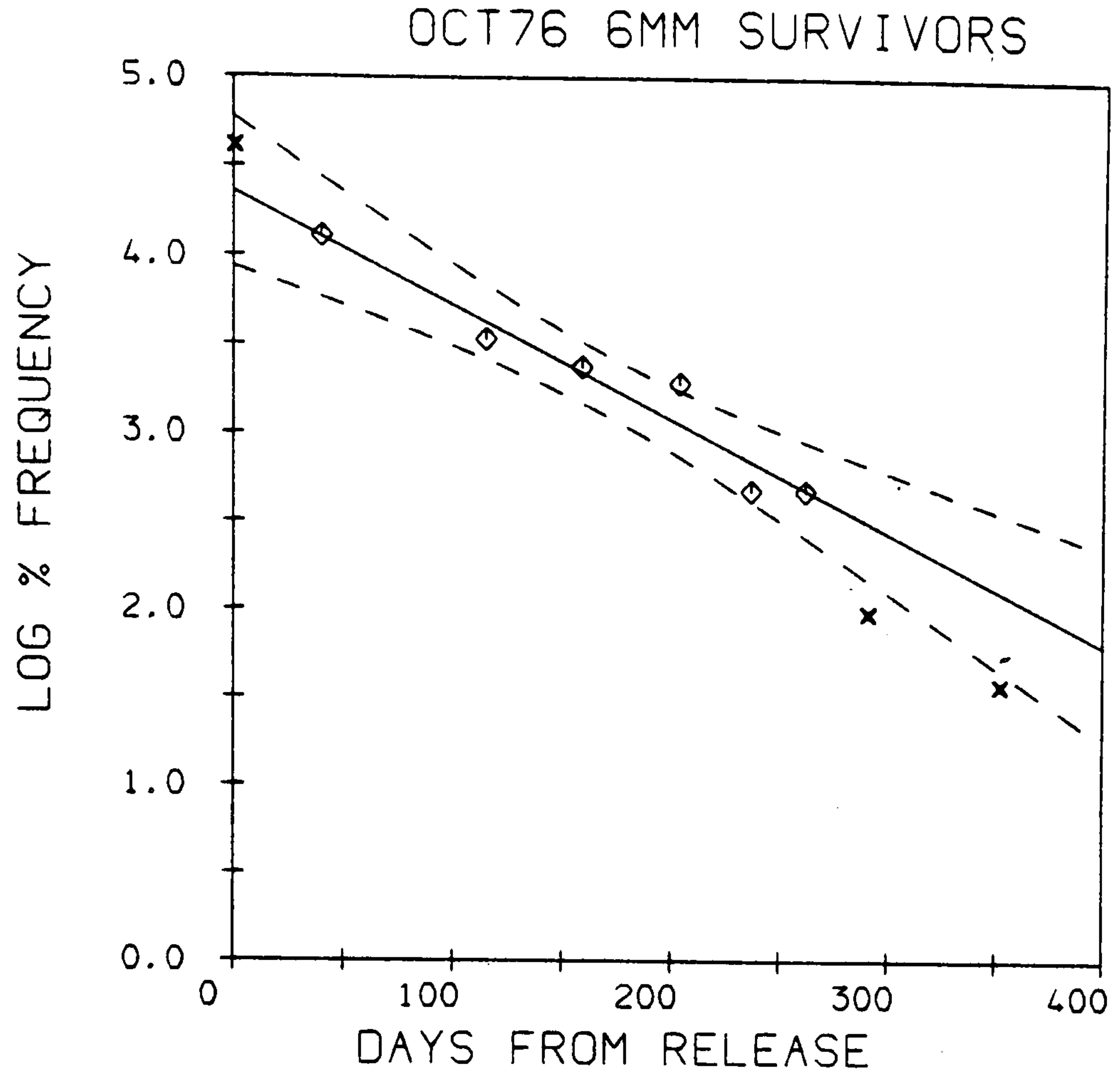


Figure 34. Survivorship of 6 mm and 9 mm cohorts released 30 September 1976. Conventions as in Figure 29.



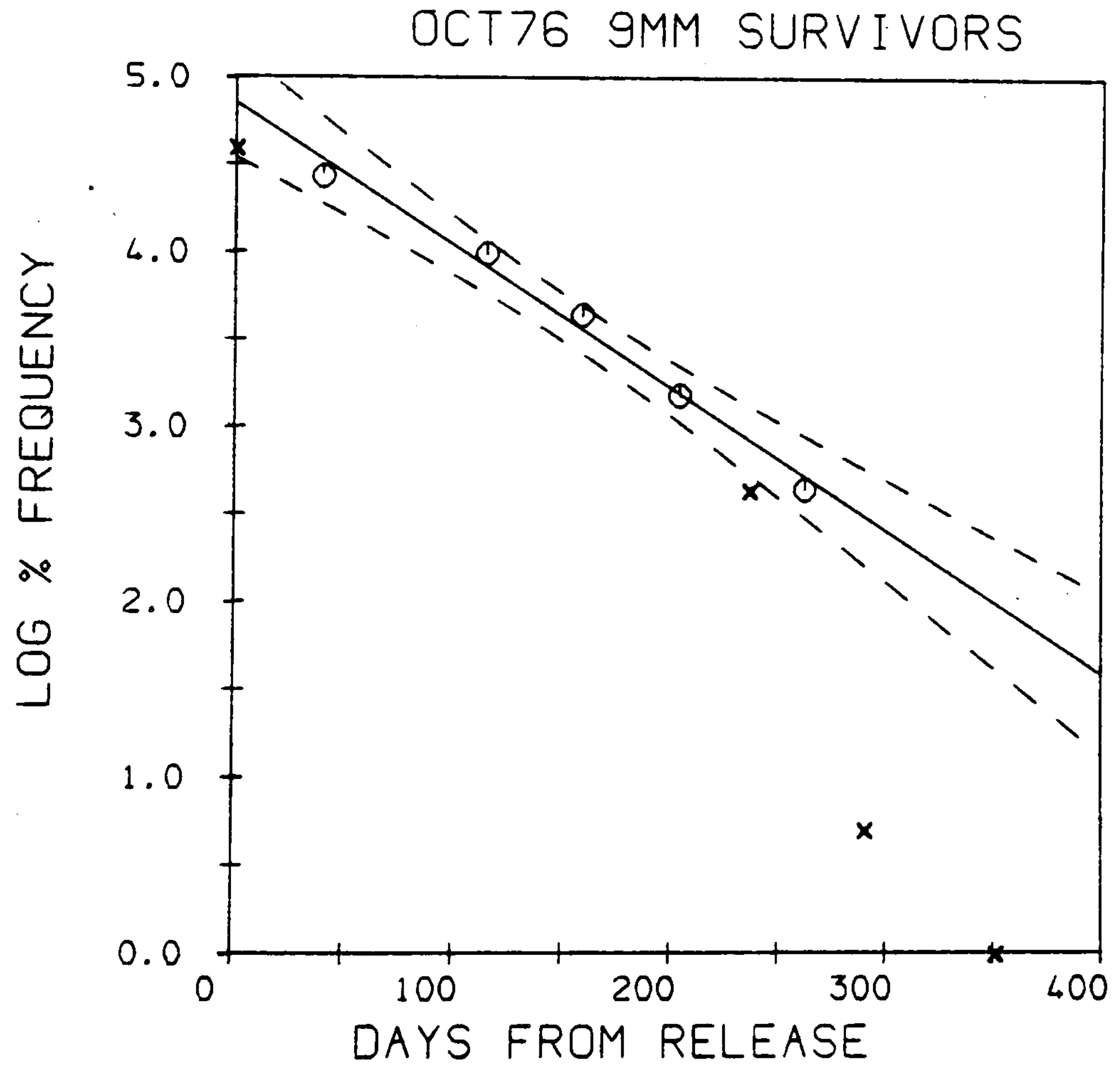
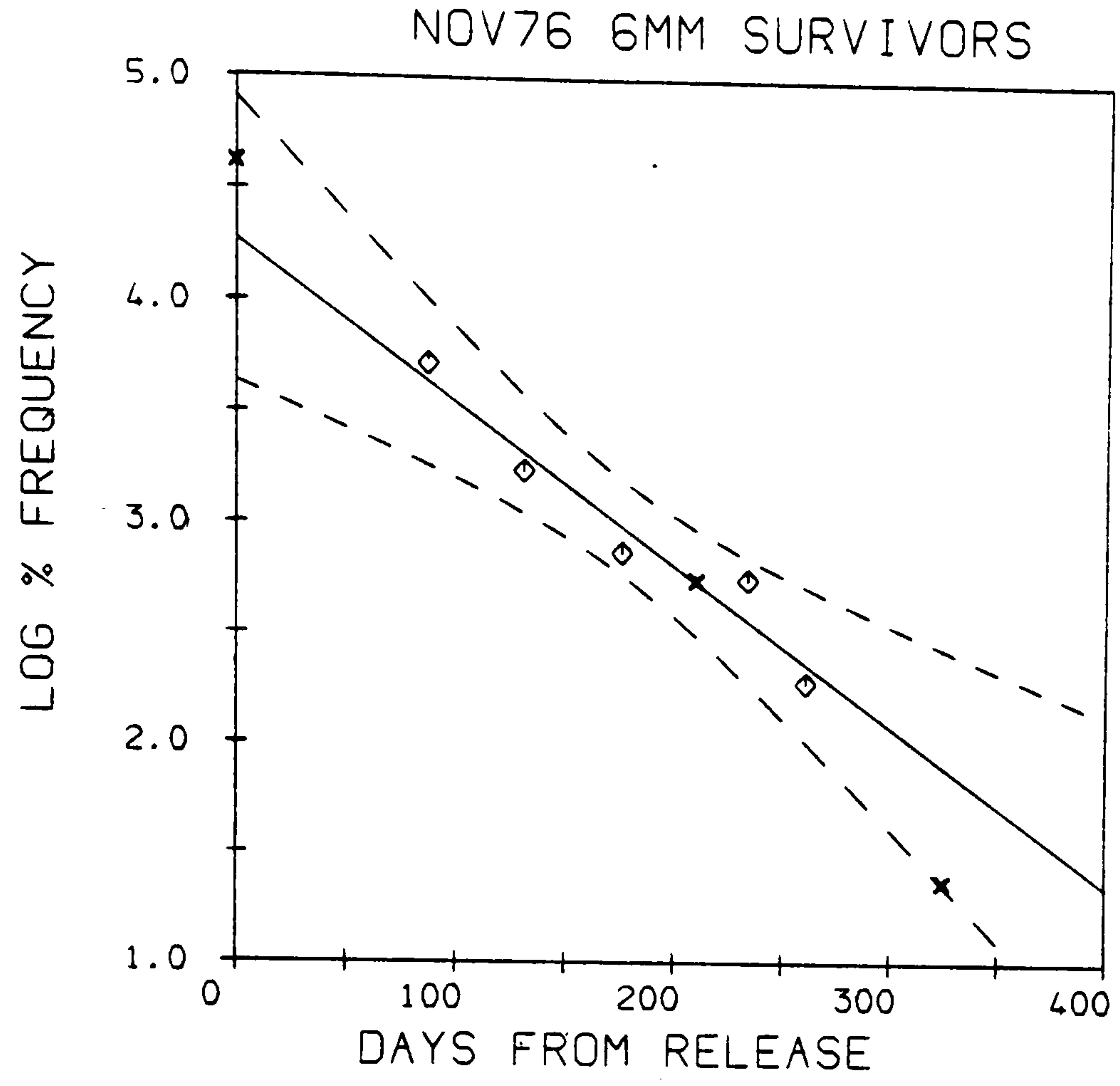


Figure 35. Survivorship of 6 mm and 9 mm cohorts released 22 October 1976. Conventions as in Figure 29.



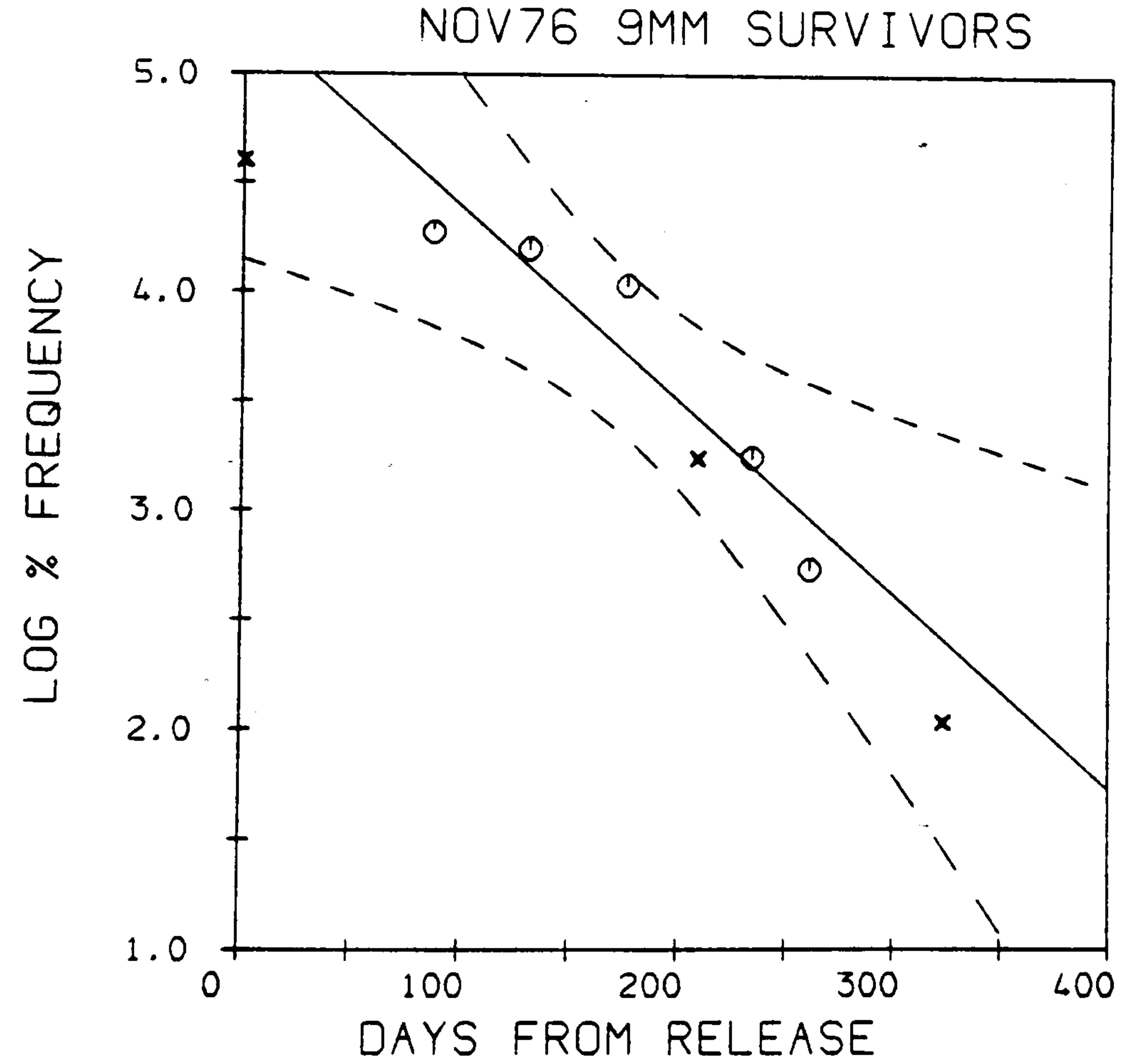
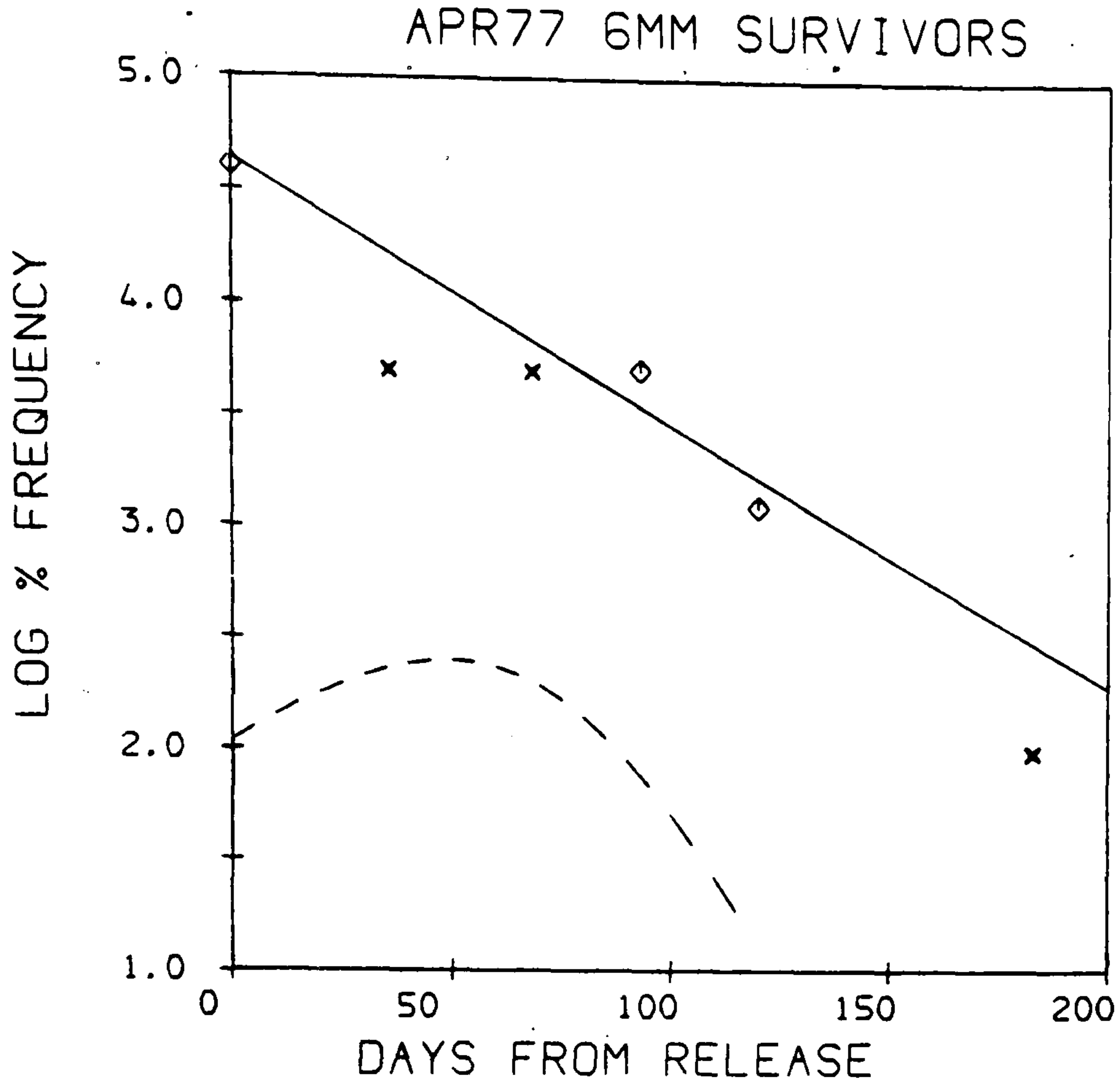


Figure 36. Survivorship of 6 mm and 9 mm cohorts released 19 November 1976. Conventions as in Figure 29. Note Y-axis rescaling.



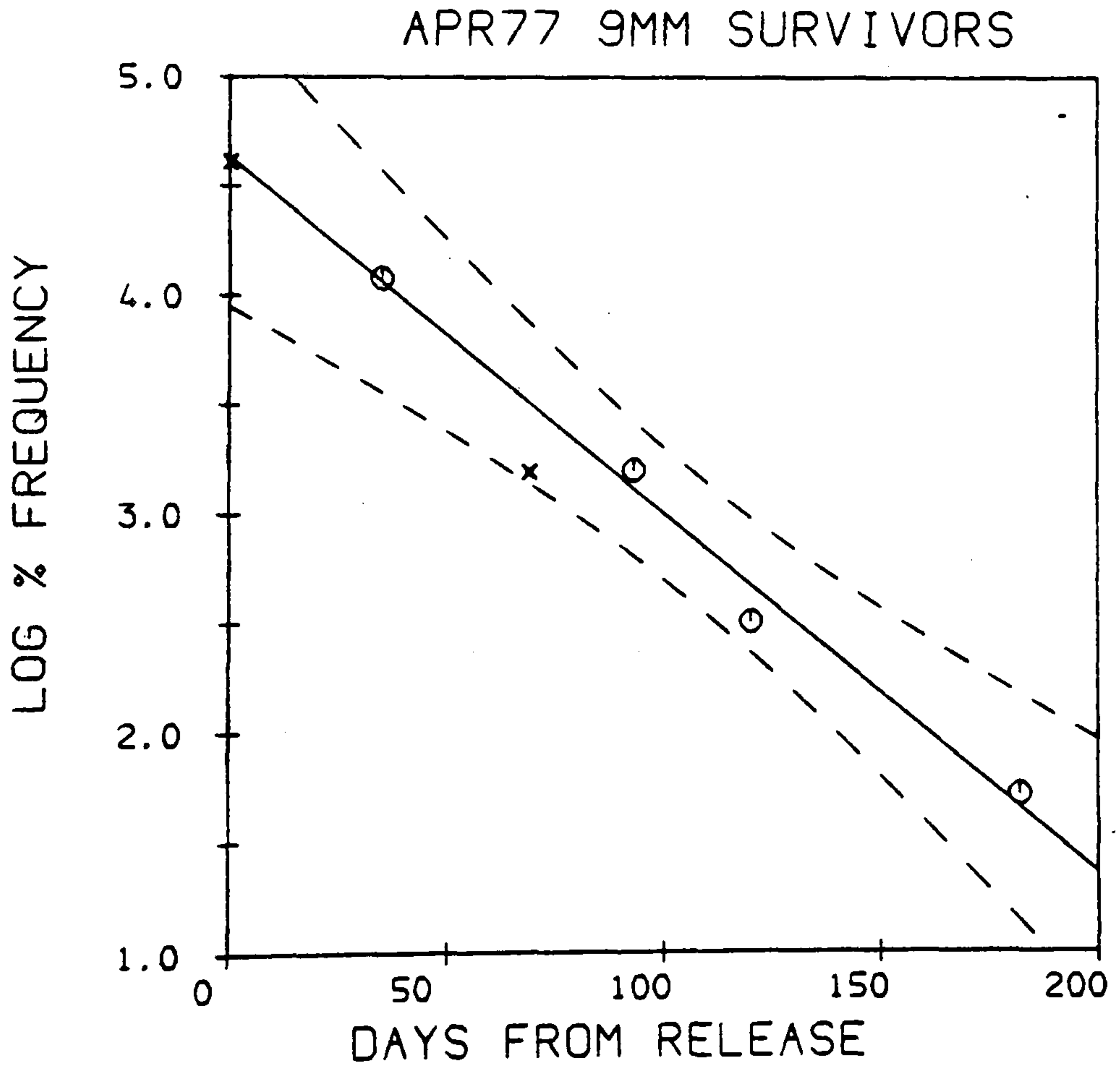
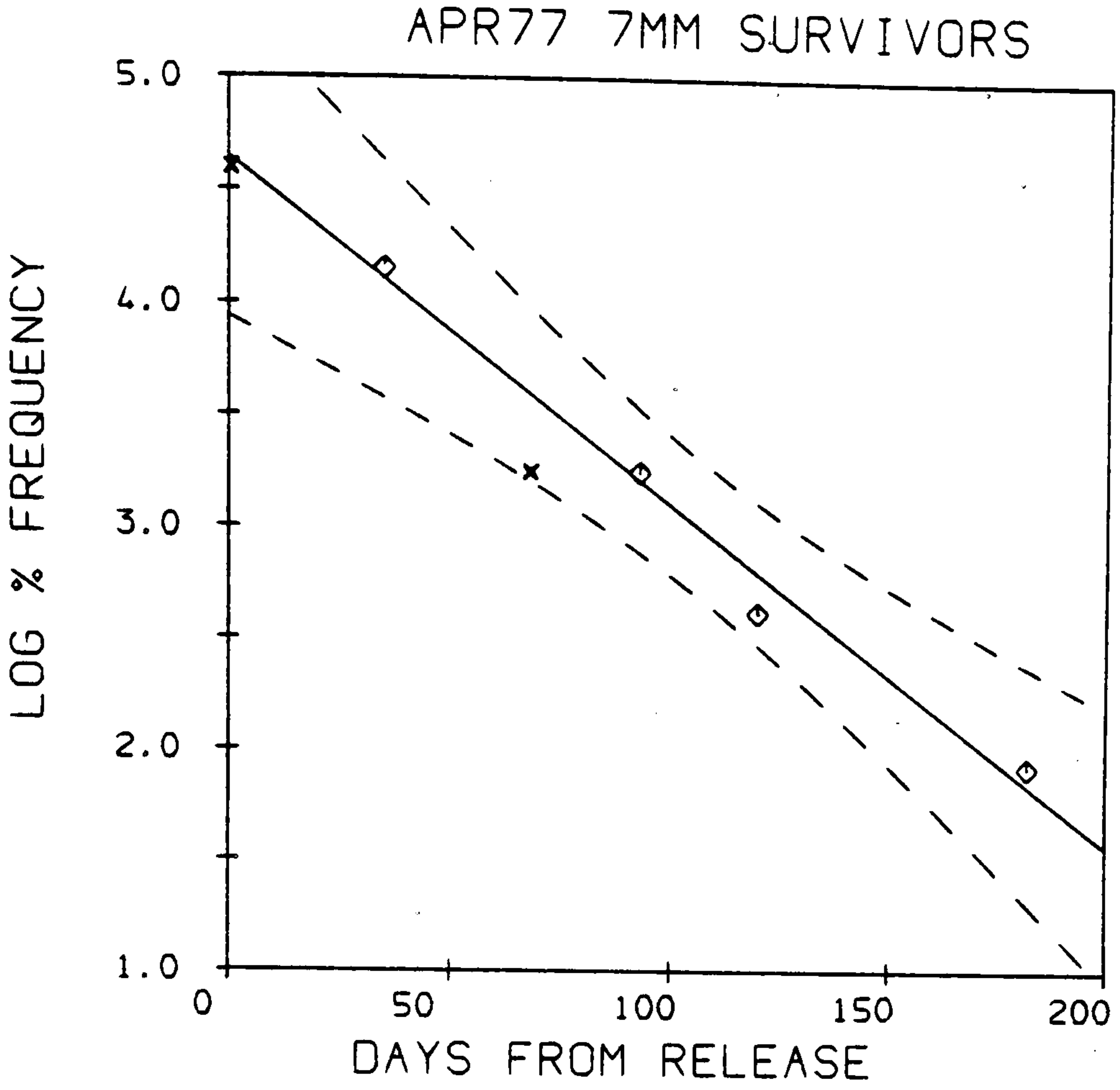


Figure 37. Page 1 of 2. Survivorship of 6 mm and 9 mm cohorts released 9 April 1977. Conventions as in Figure 29. 6 mm regression as explained in text.



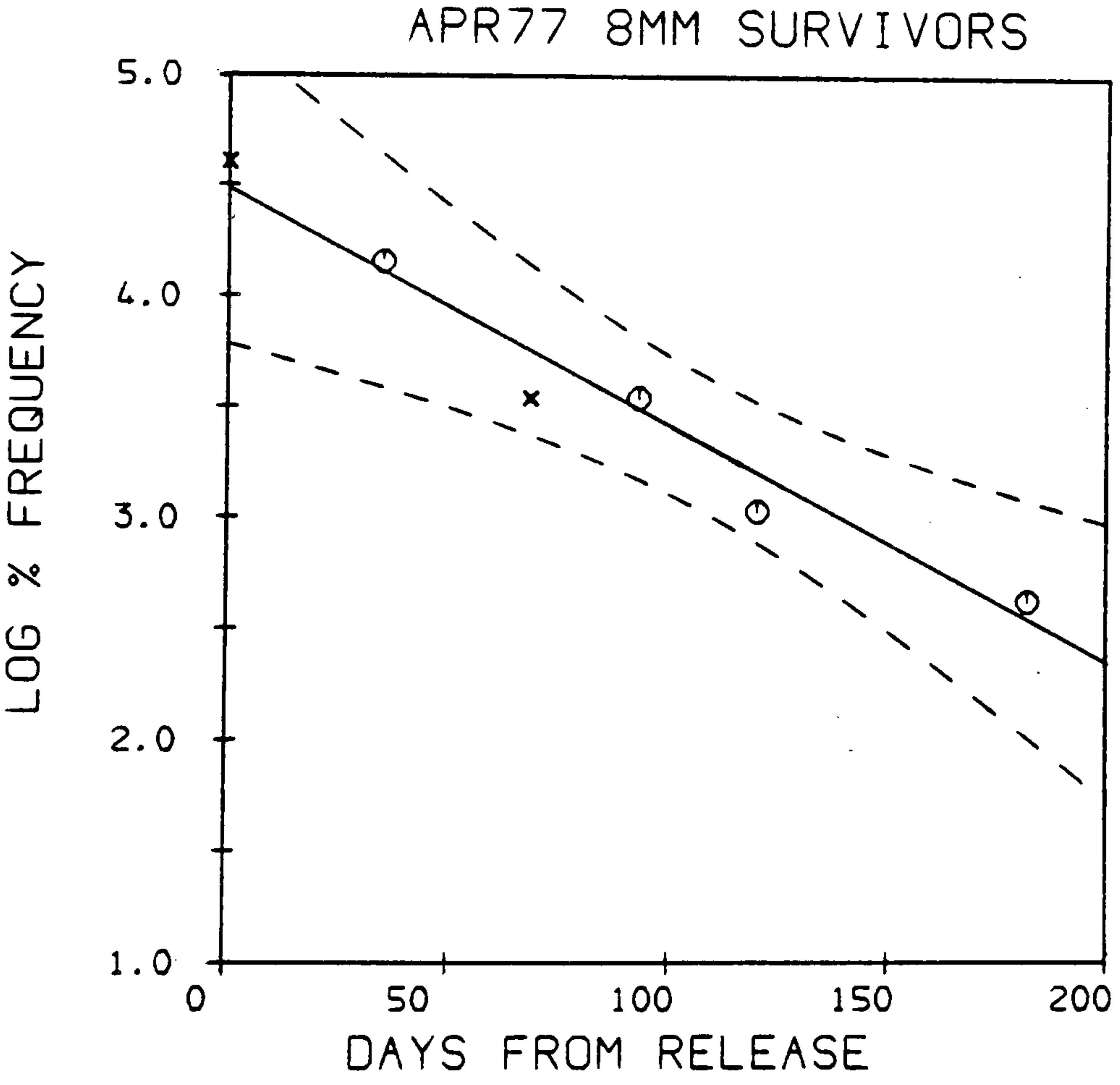
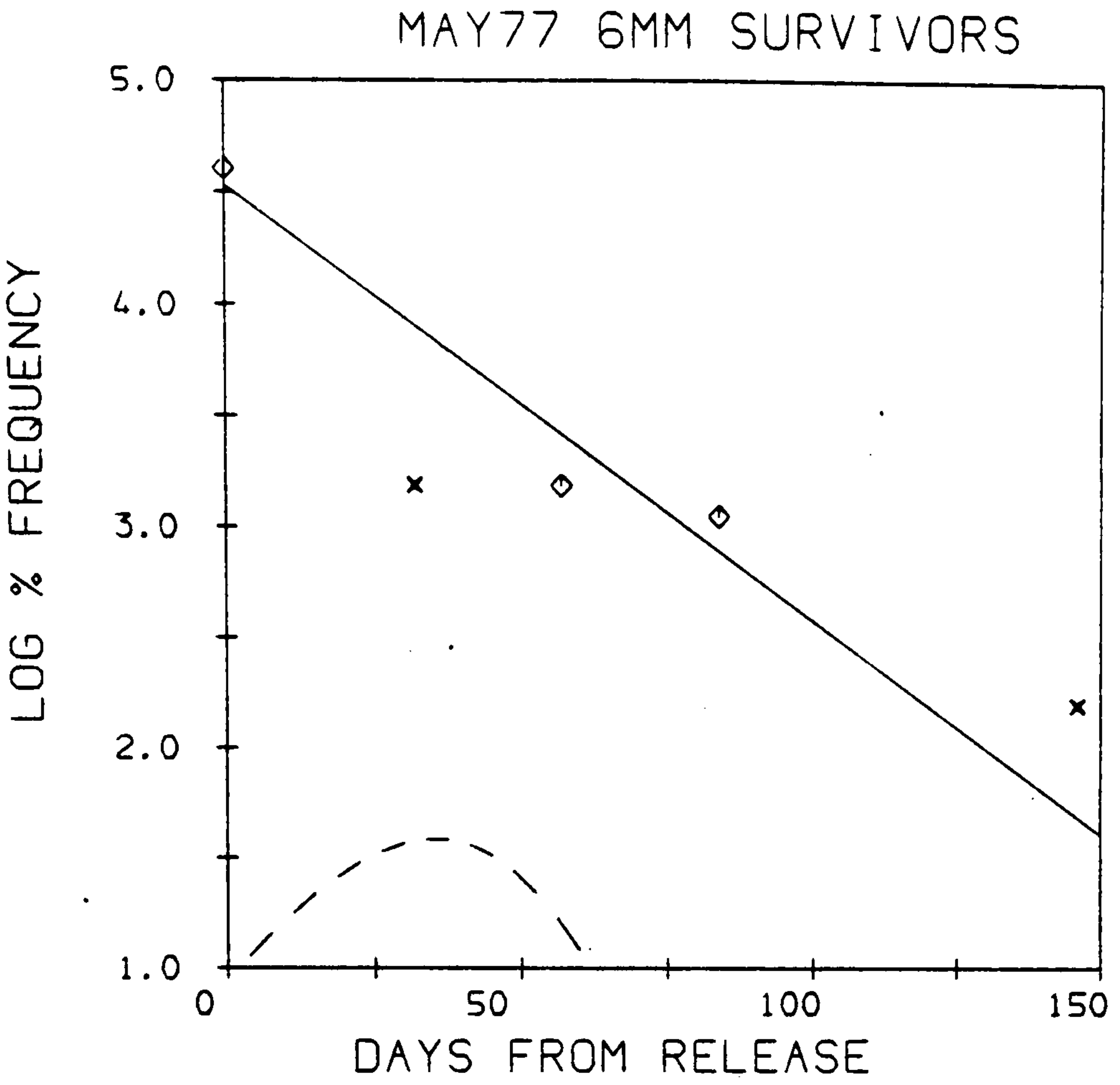


Figure 37. Page 2 of 2. Survivorship of supplementary 7 mm and 8 mm cohorts released 9 April 1977. Conventions as in Figure 29.



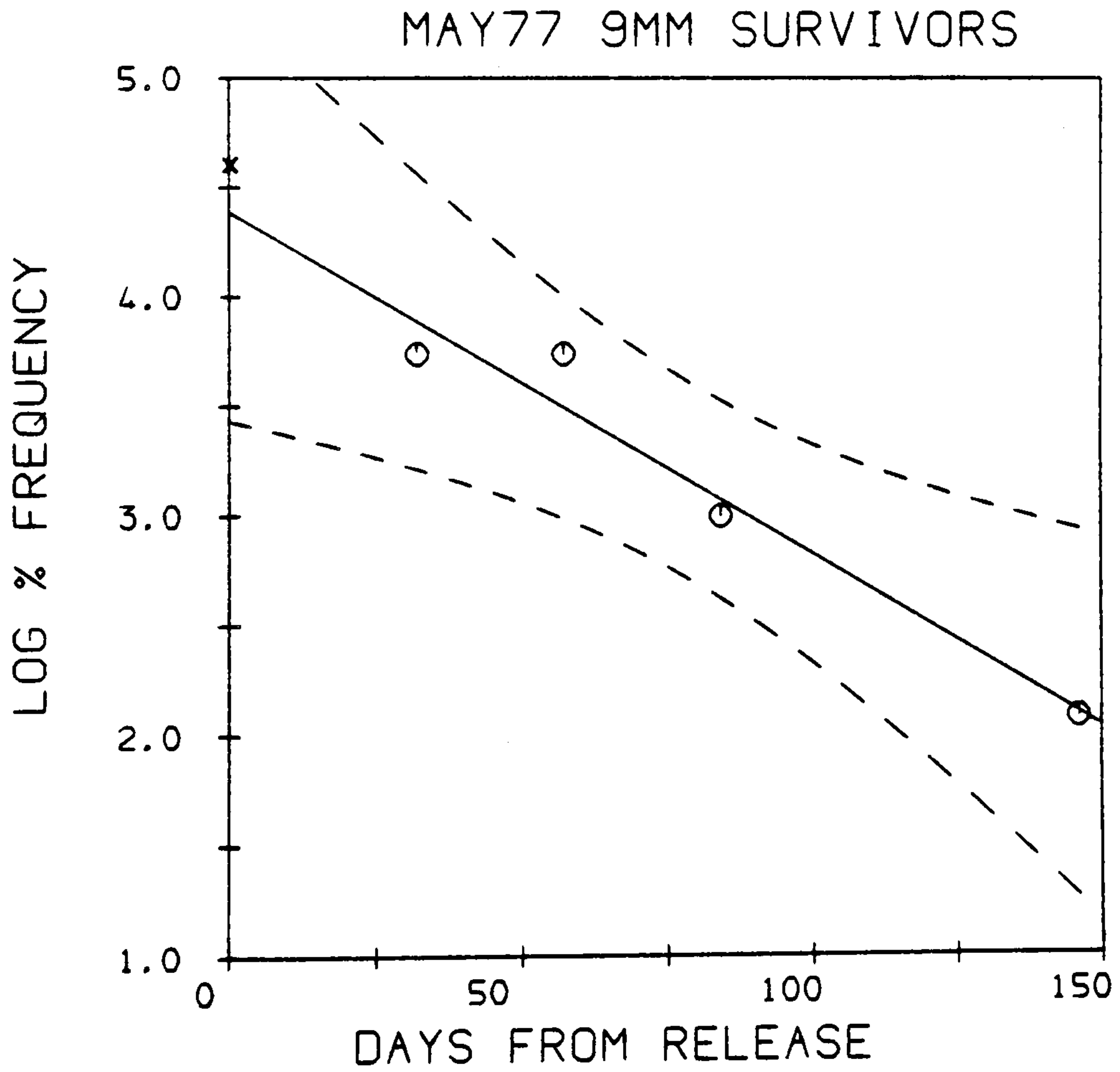
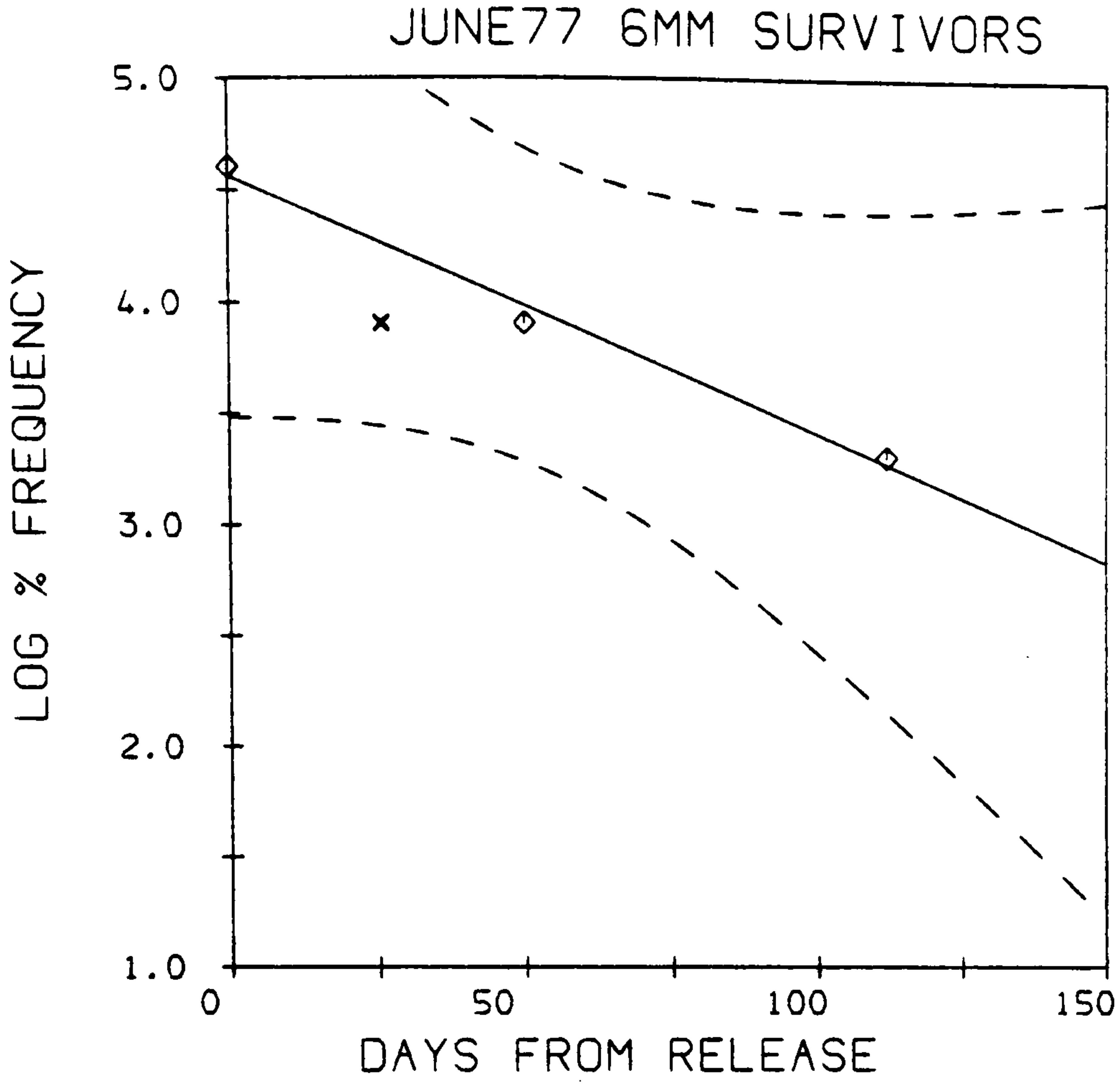


Figure 38. Survivorship of 6 mm and 9 mm cohorts released 15 May 1977. Conventions as in Figure 29. 6 mm regression as explained in text.



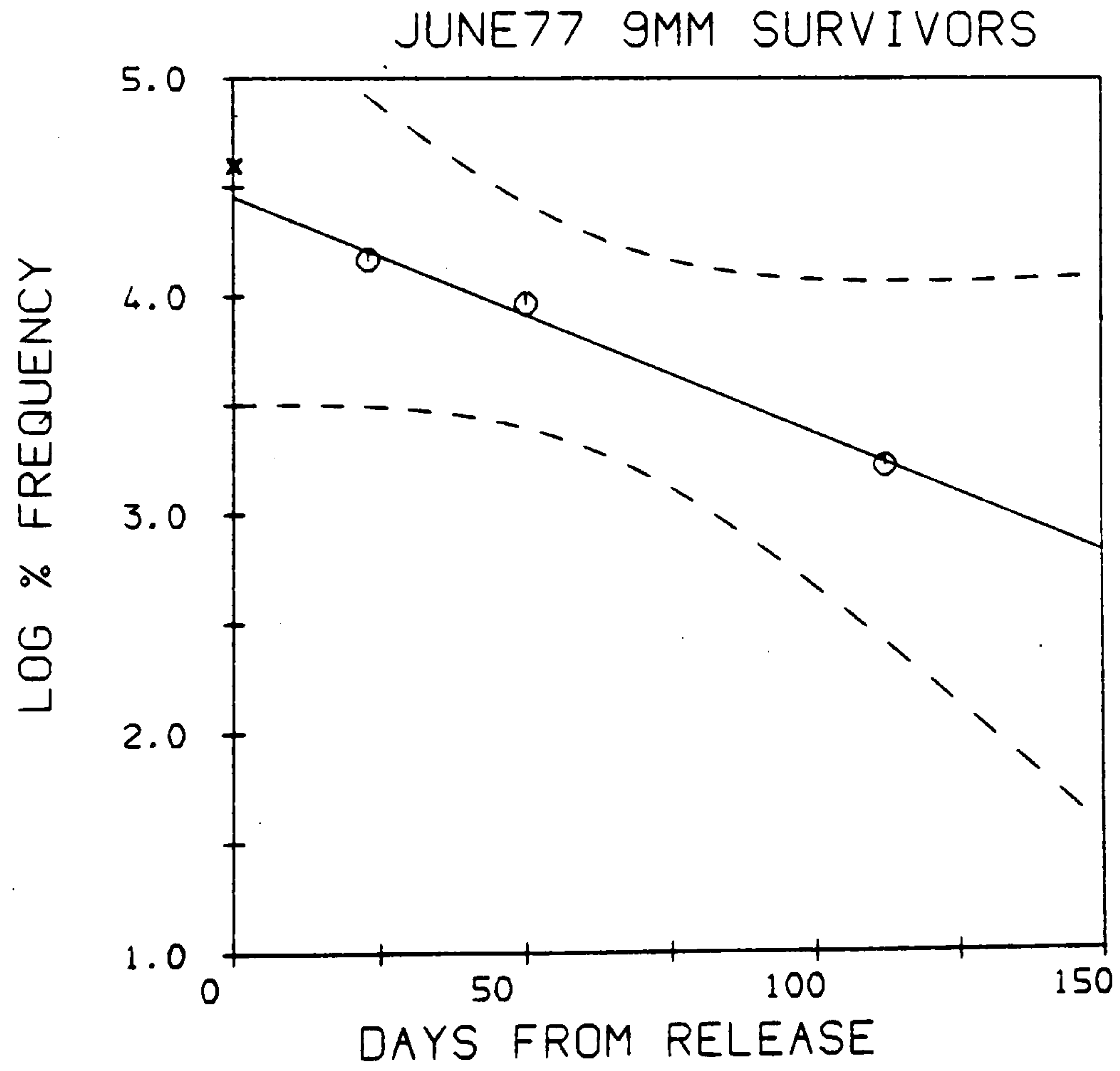
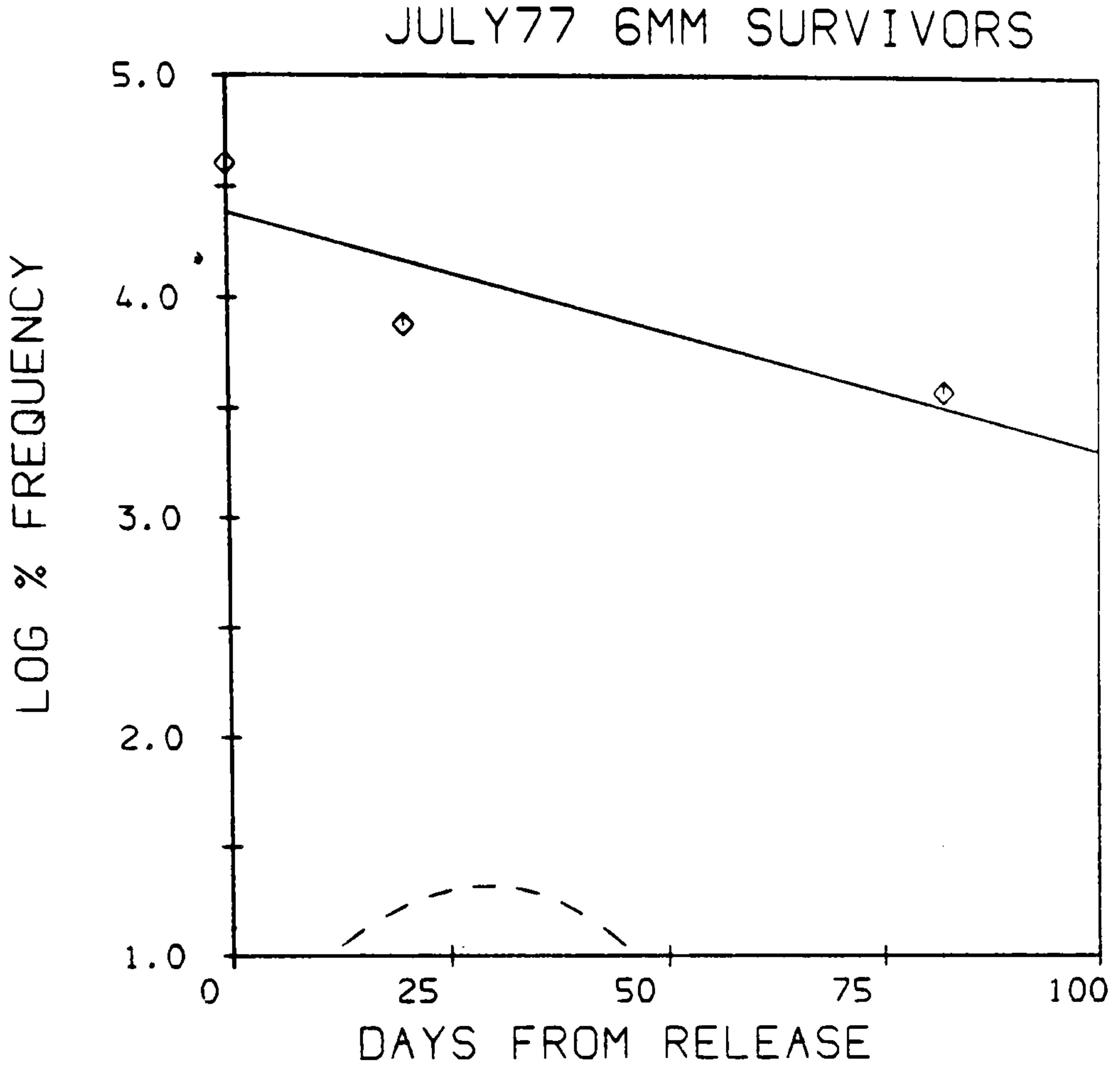


Figure 39. Survivorship of 6 mm and 9 mm cohorts released 18 June 1977. Conventions as in Figure 29. 6 mm regression as explained in text.



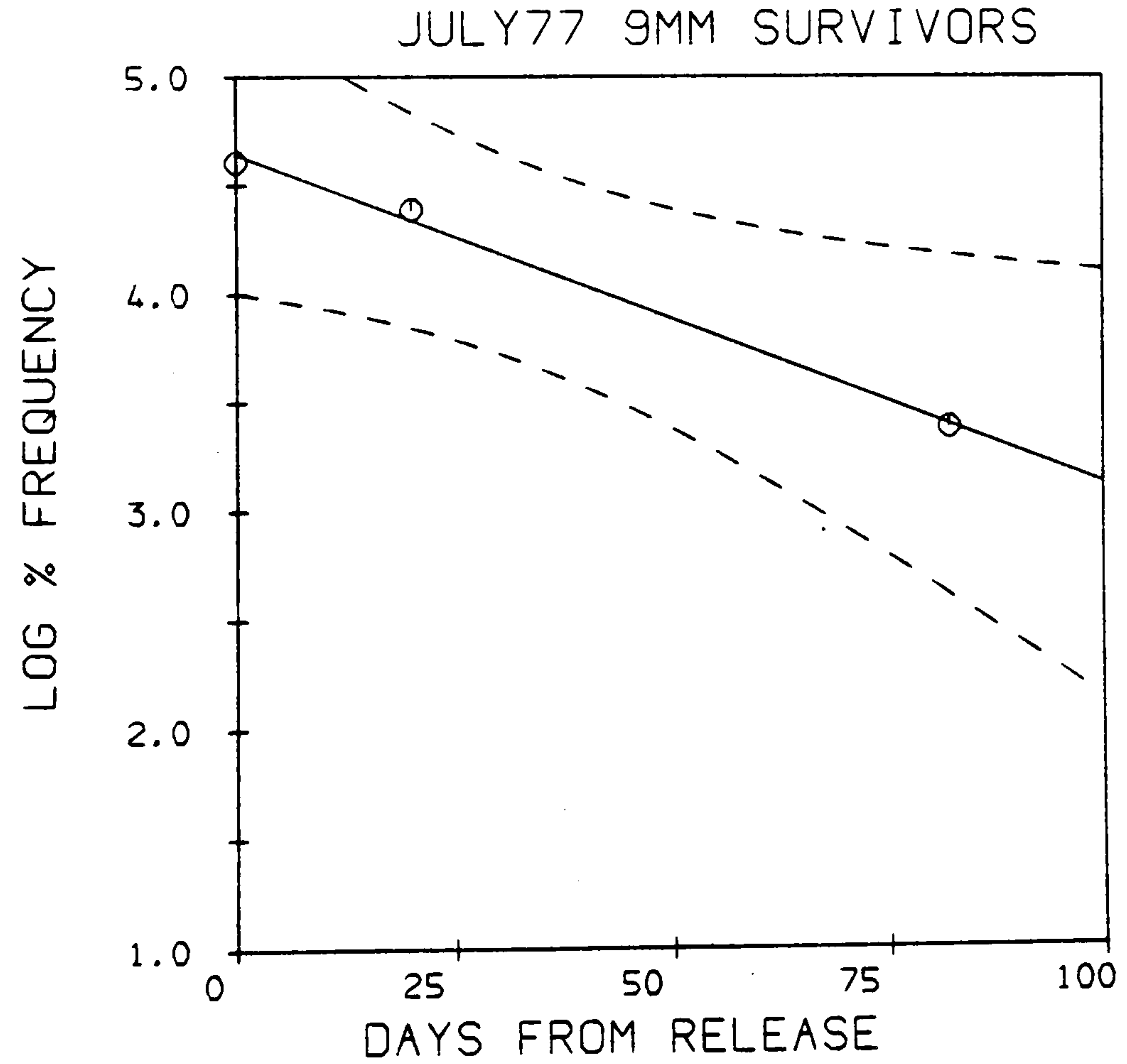
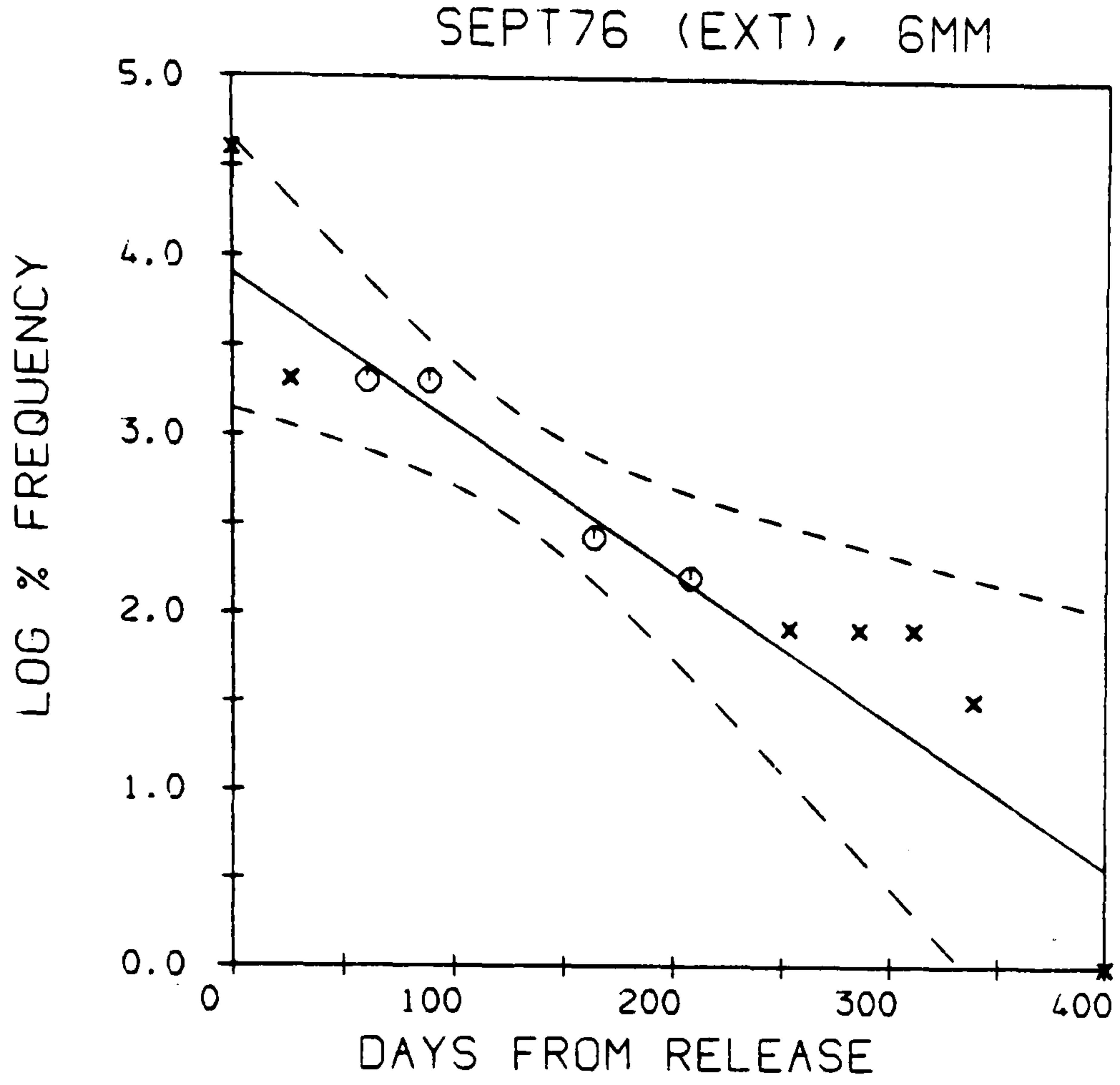


Figure 40. Survivorship of 6 mm and 9 mm cohorts released 18 July 1977. Conventions as in Figure 29. Regressions as explained in text.



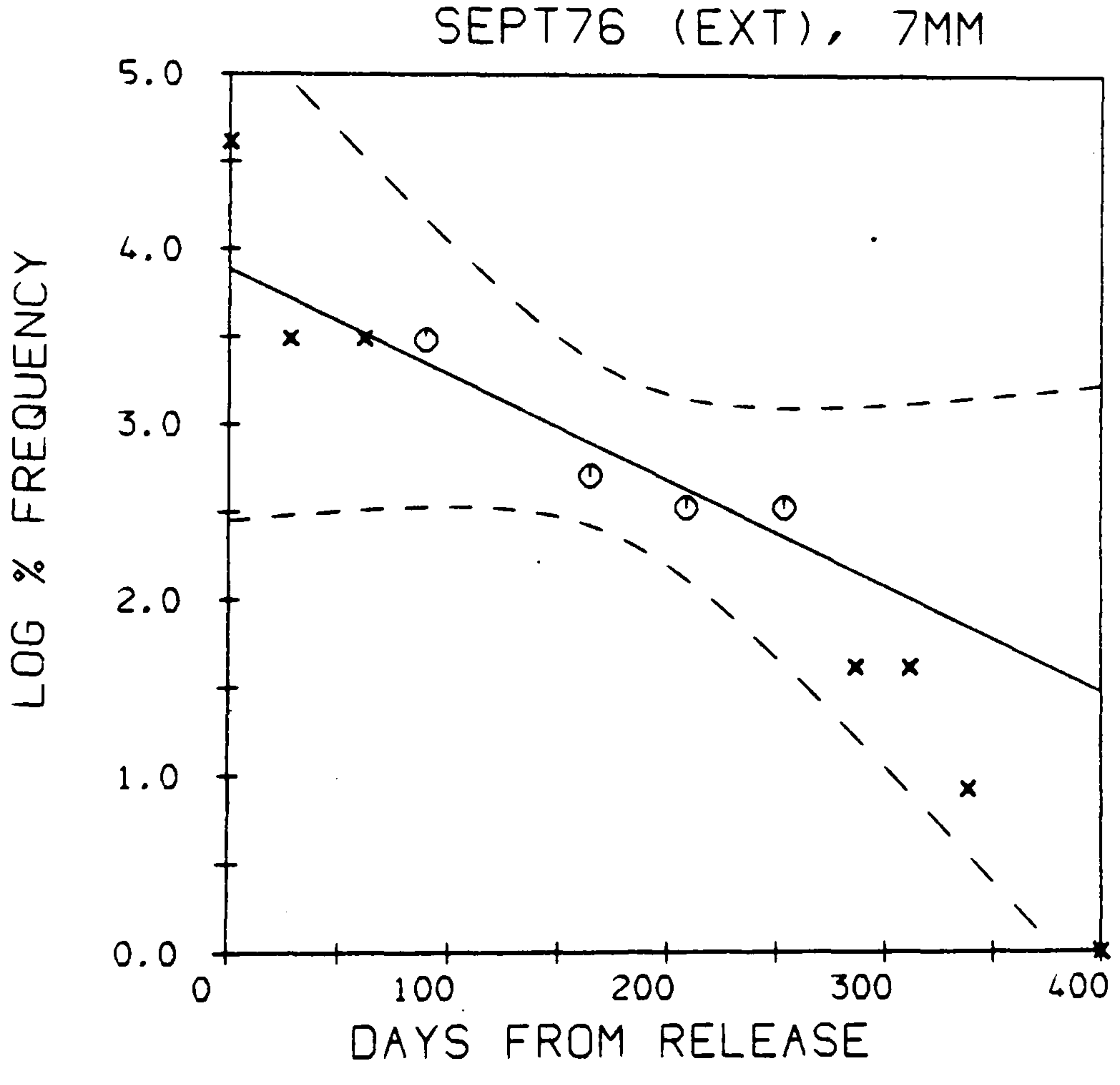
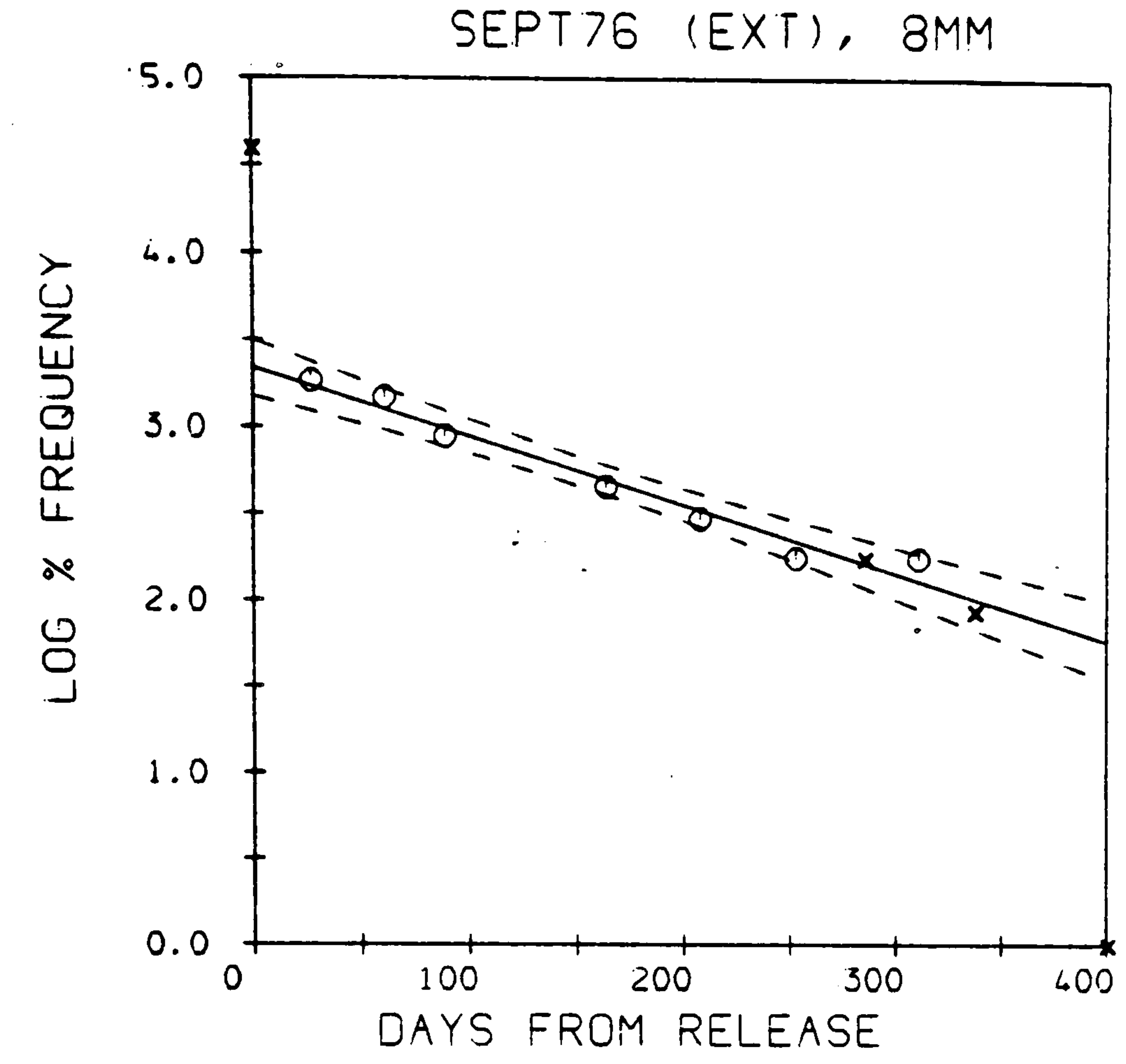


Figure 43. Page 1 of 4. Survivorship of 6 mm (upper) and 7 mm (lower) components of the extended cohort released 3 September 1976. Conventions as in Figure 29. Dates, starting numbers and regressions are in Appendix Tables 6 and 11.



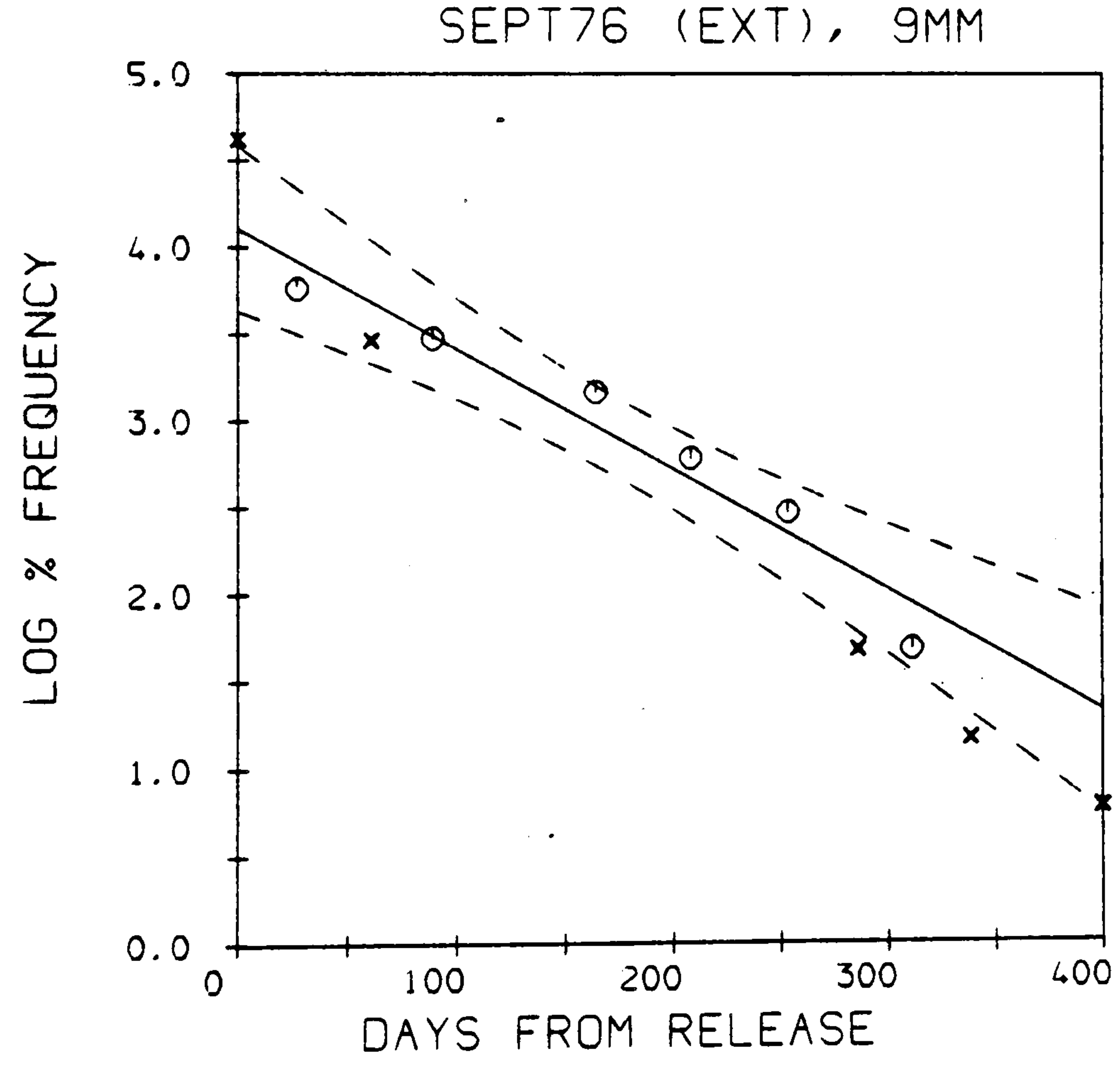
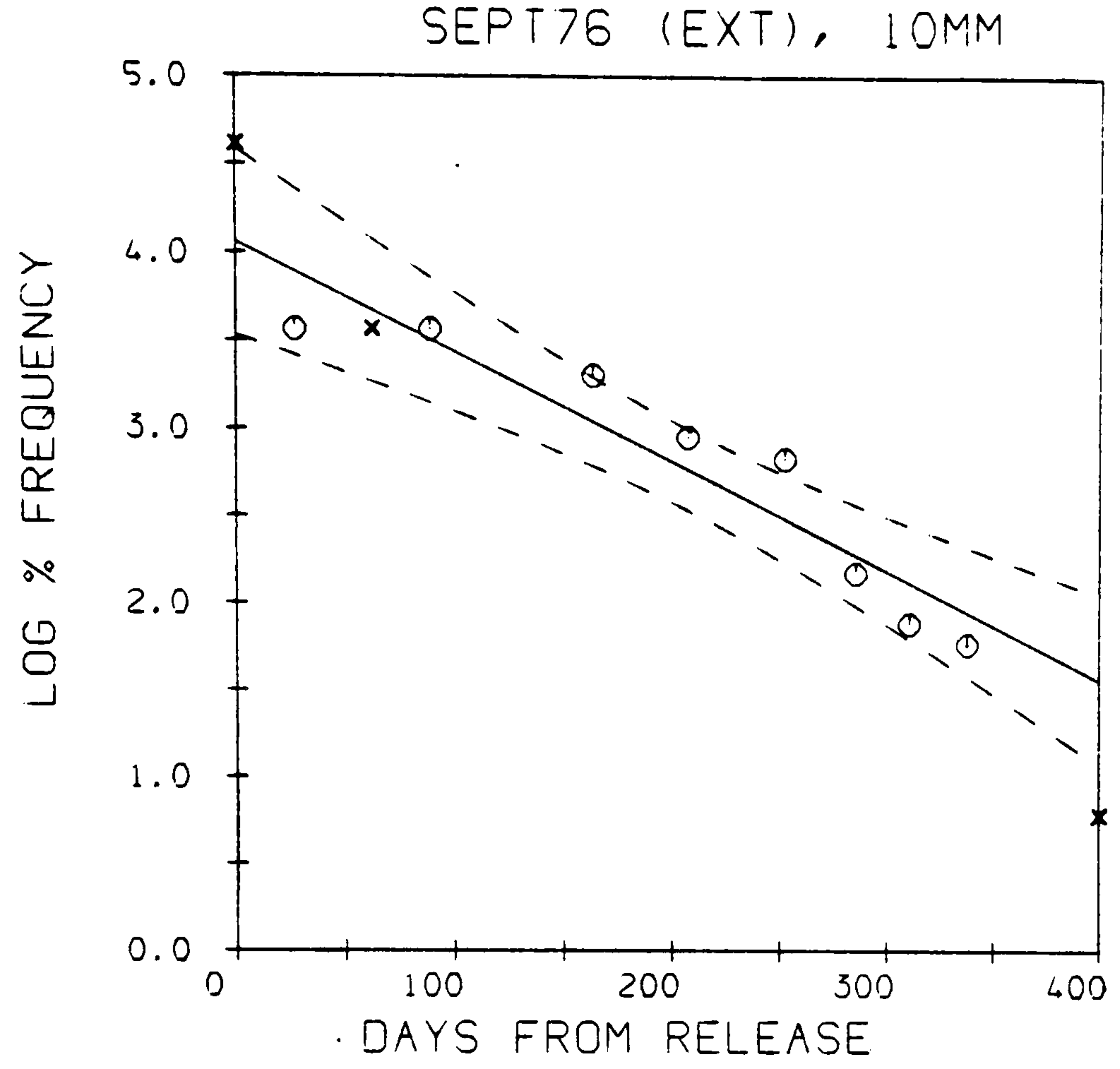


Figure 43, continued. Survivorship of 8 mm and 9 mm components of the extended cohort released 3 September 1976.



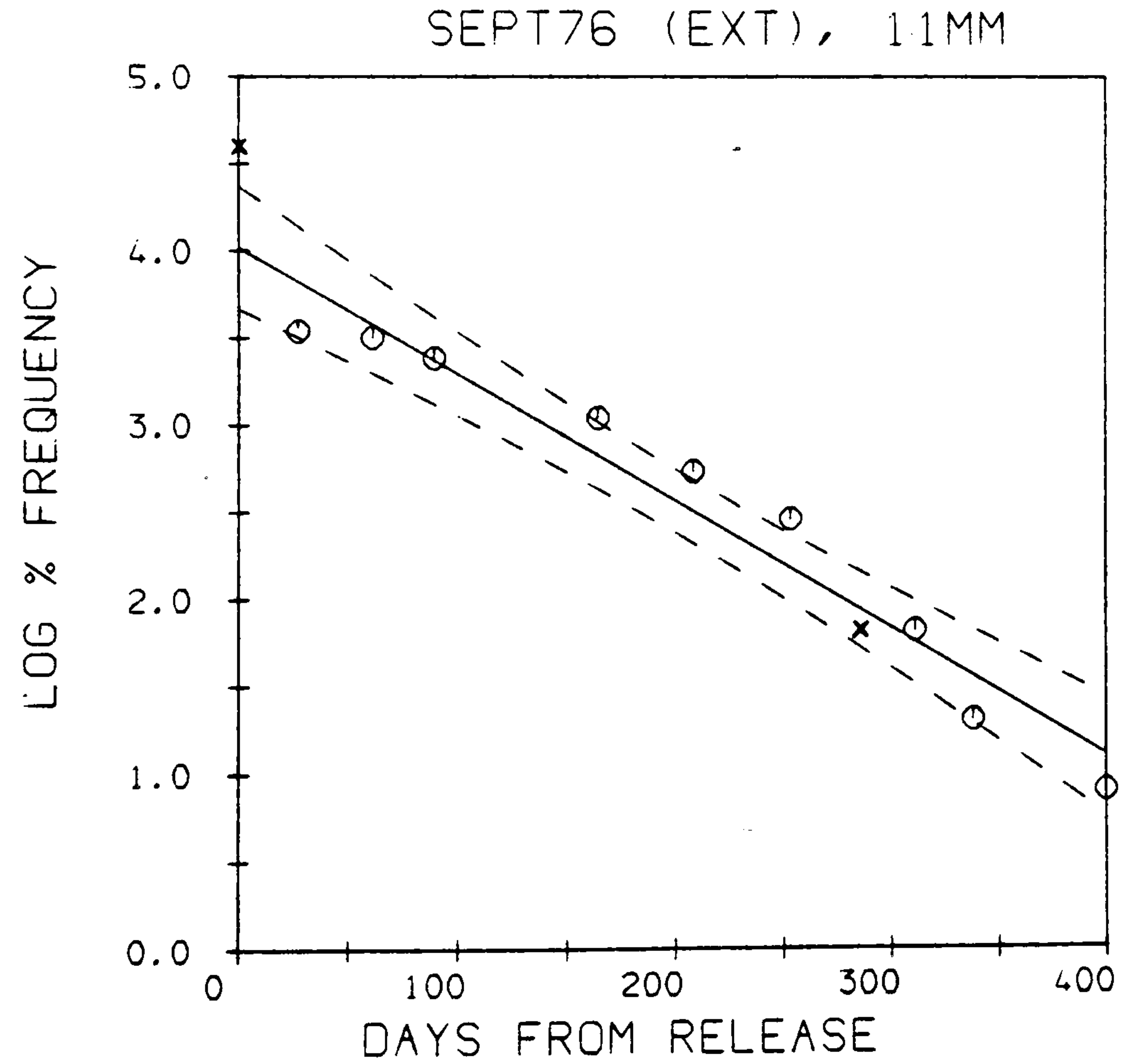


Figure 43, continued. Survivorship of 10 mm and 11 mm components of the extended cohort released 3 September 1976.

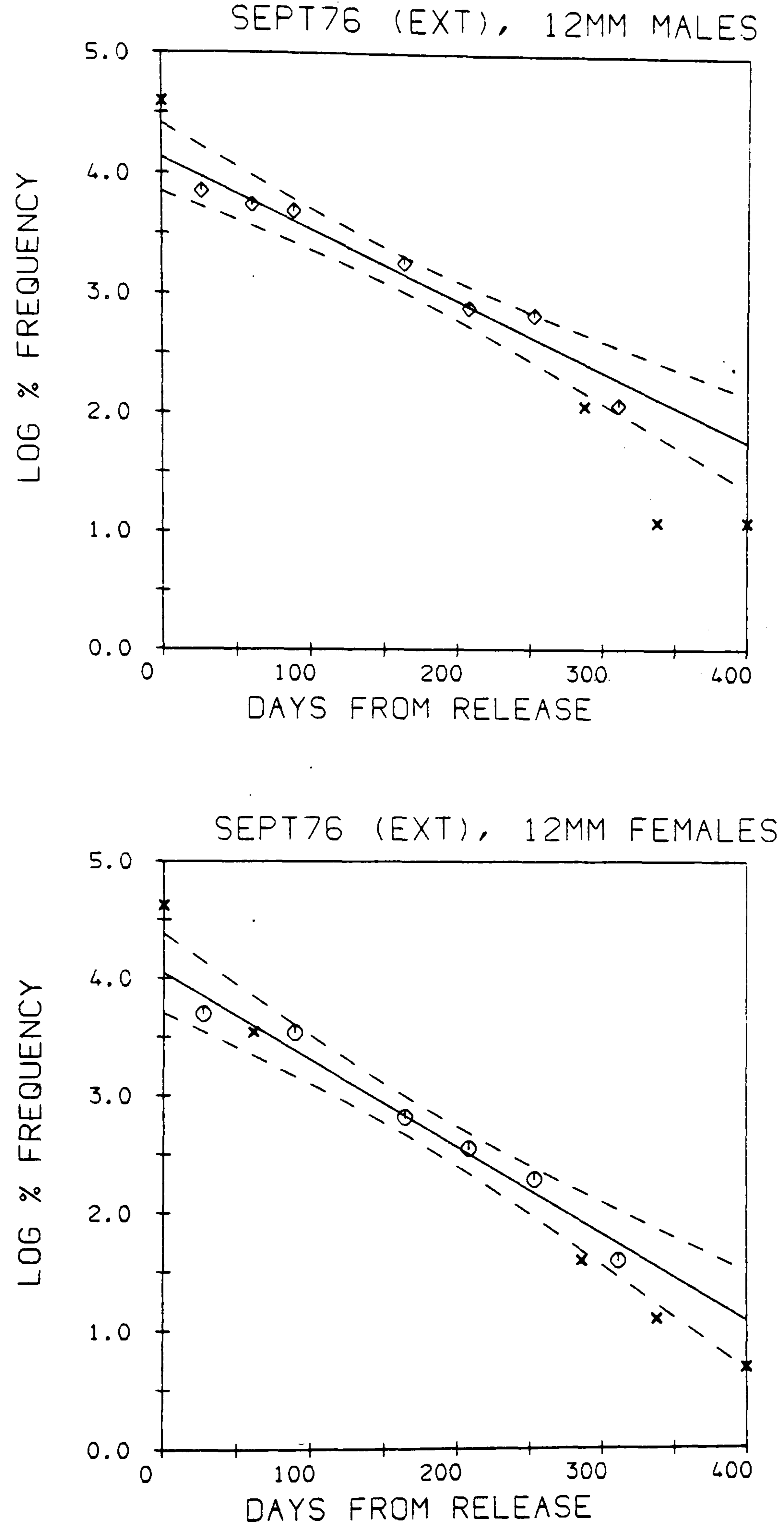
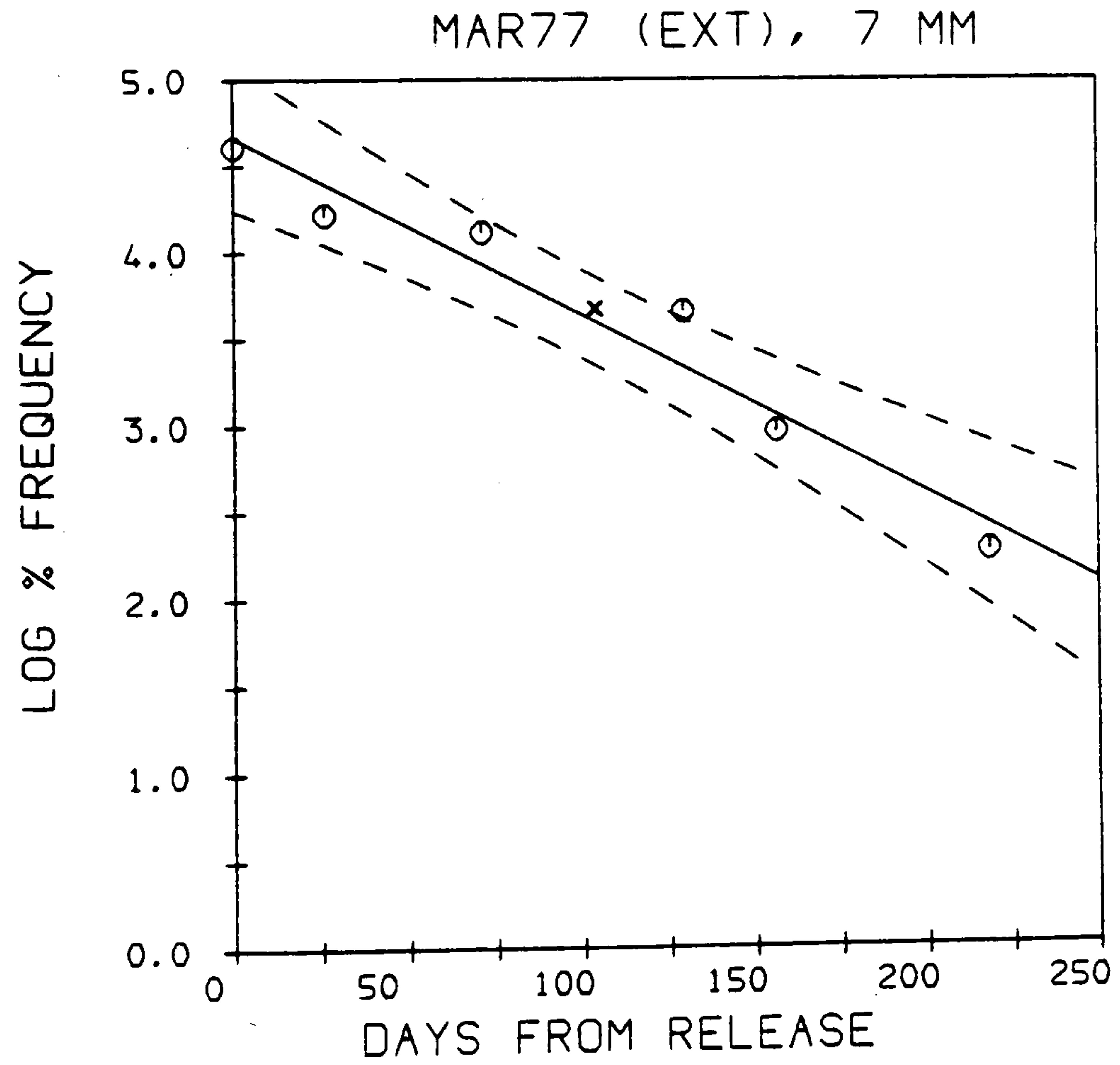
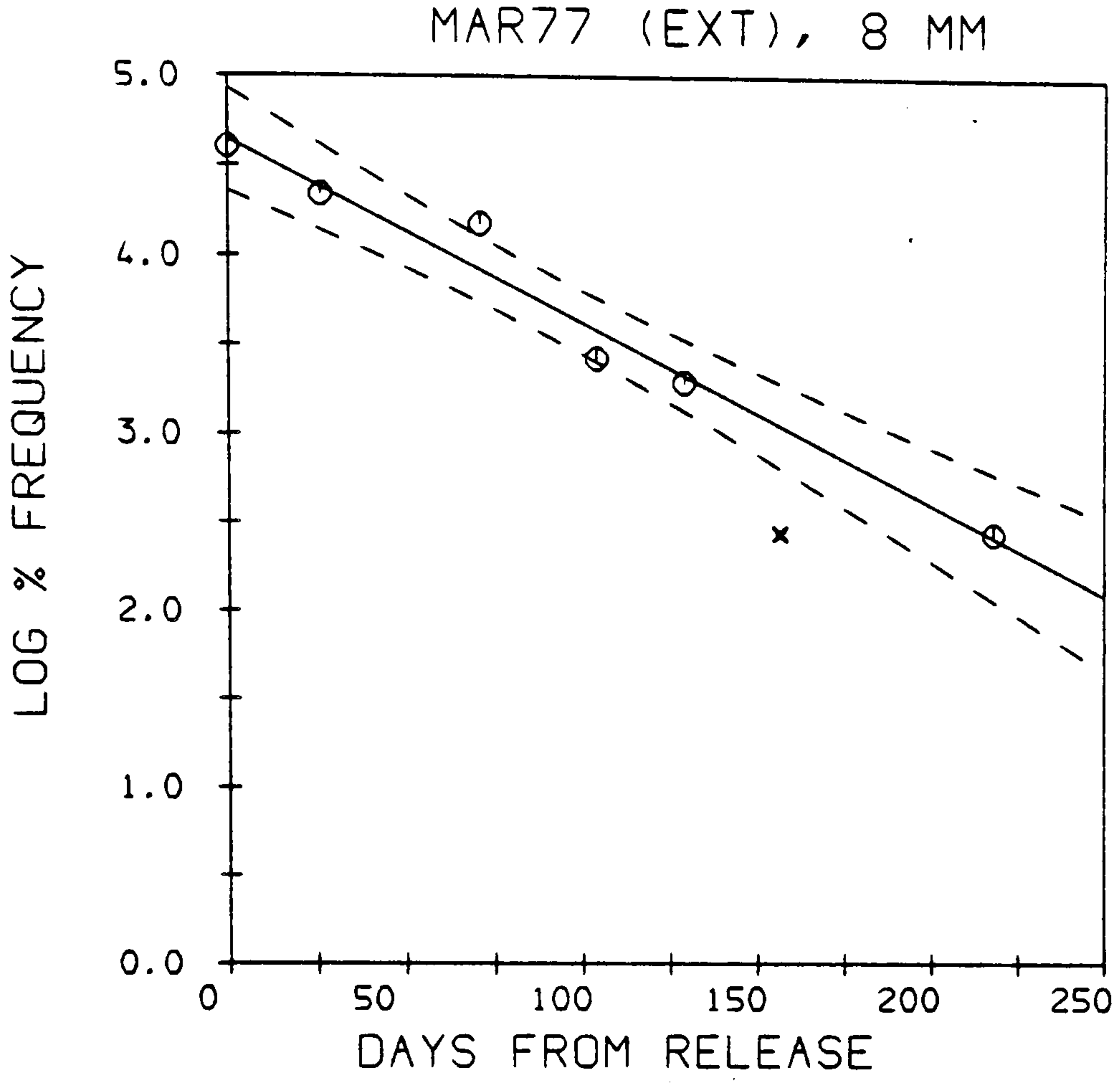


Figure 43, concluded. Survivorship of 12 mm male and female components of the extended cohort released 3 September 1976.

Figure 44. Survivorship curves for eleven component cohorts of the extended cohort released 4 March 1977. 6 mm not presented - see text. Conventions as in Figure 29. Dates, starting numbers and regressions are in Appendix Tables 7 and 12. Regressions illustrated for 7 mm to 10 mm cohorts are improved alternatives discussed in text. This figure extends over six pages.





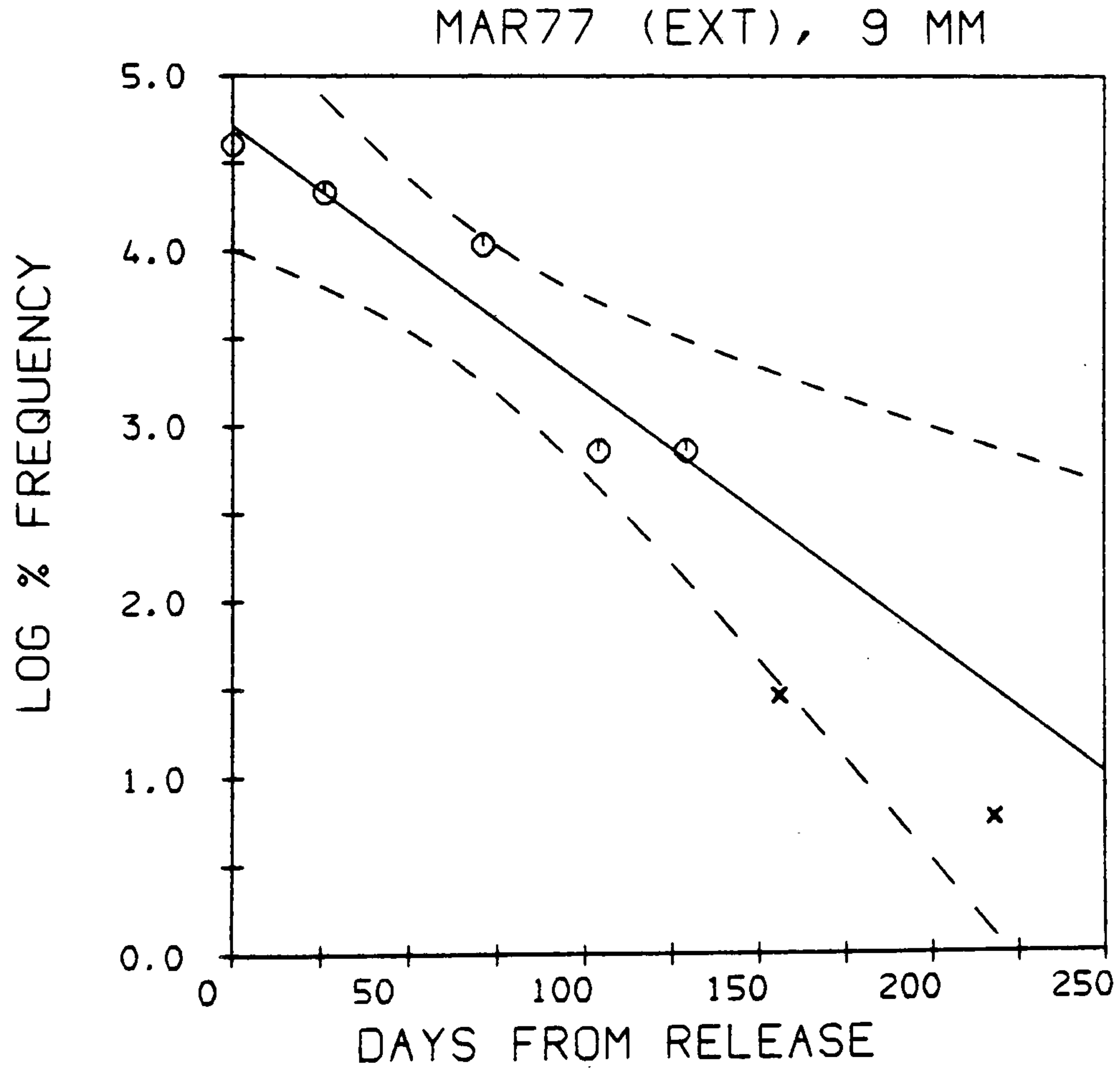
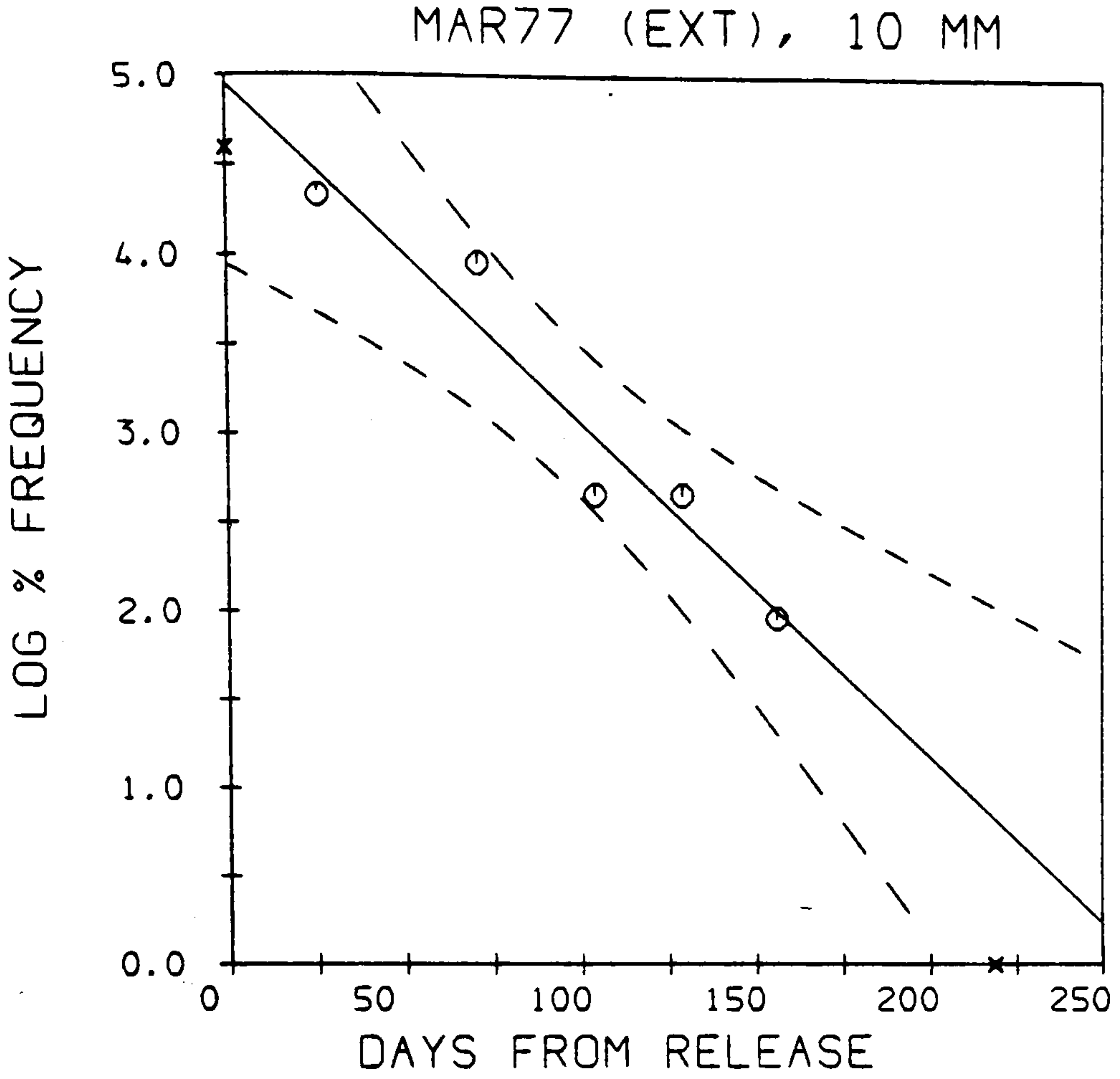


Figure 44, continued. Survivorship of 8 mm (upper) and 9 mm (lower) components of the extended cohort released 4 March 1977.



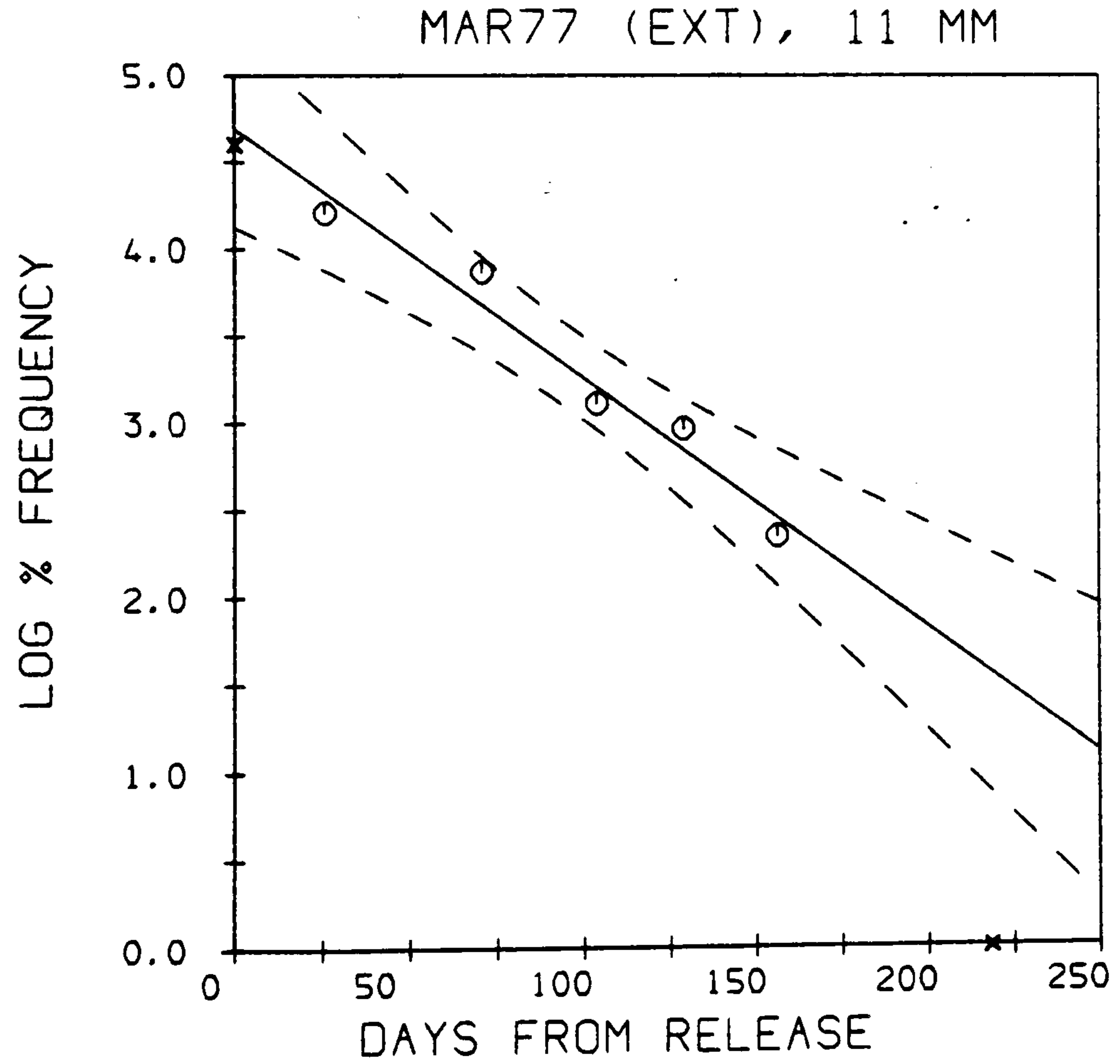
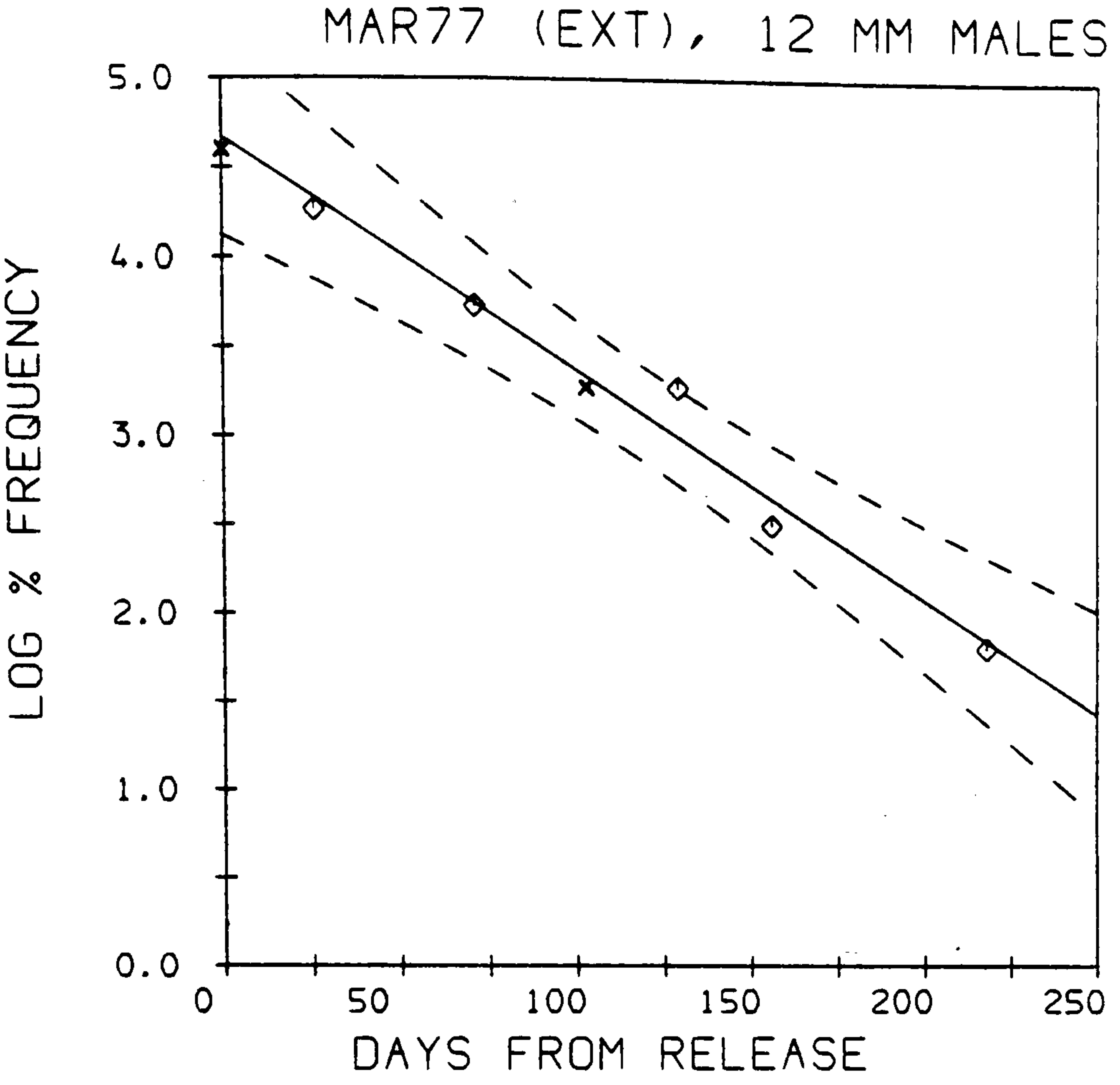


Figure 44, continued. Survivorship of 10 mm and 11 mm components of the extended cohort released 4 March 1977.



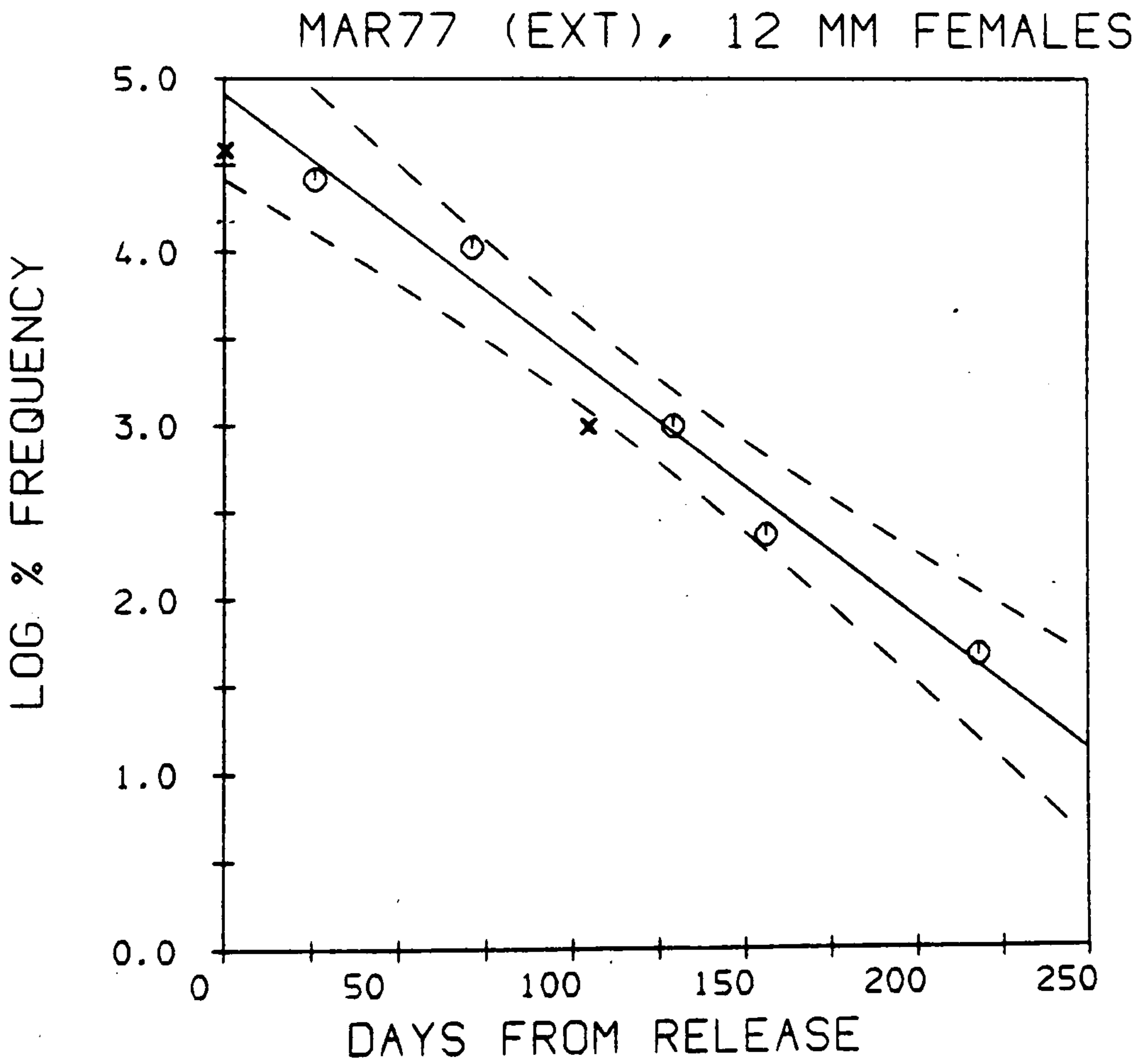
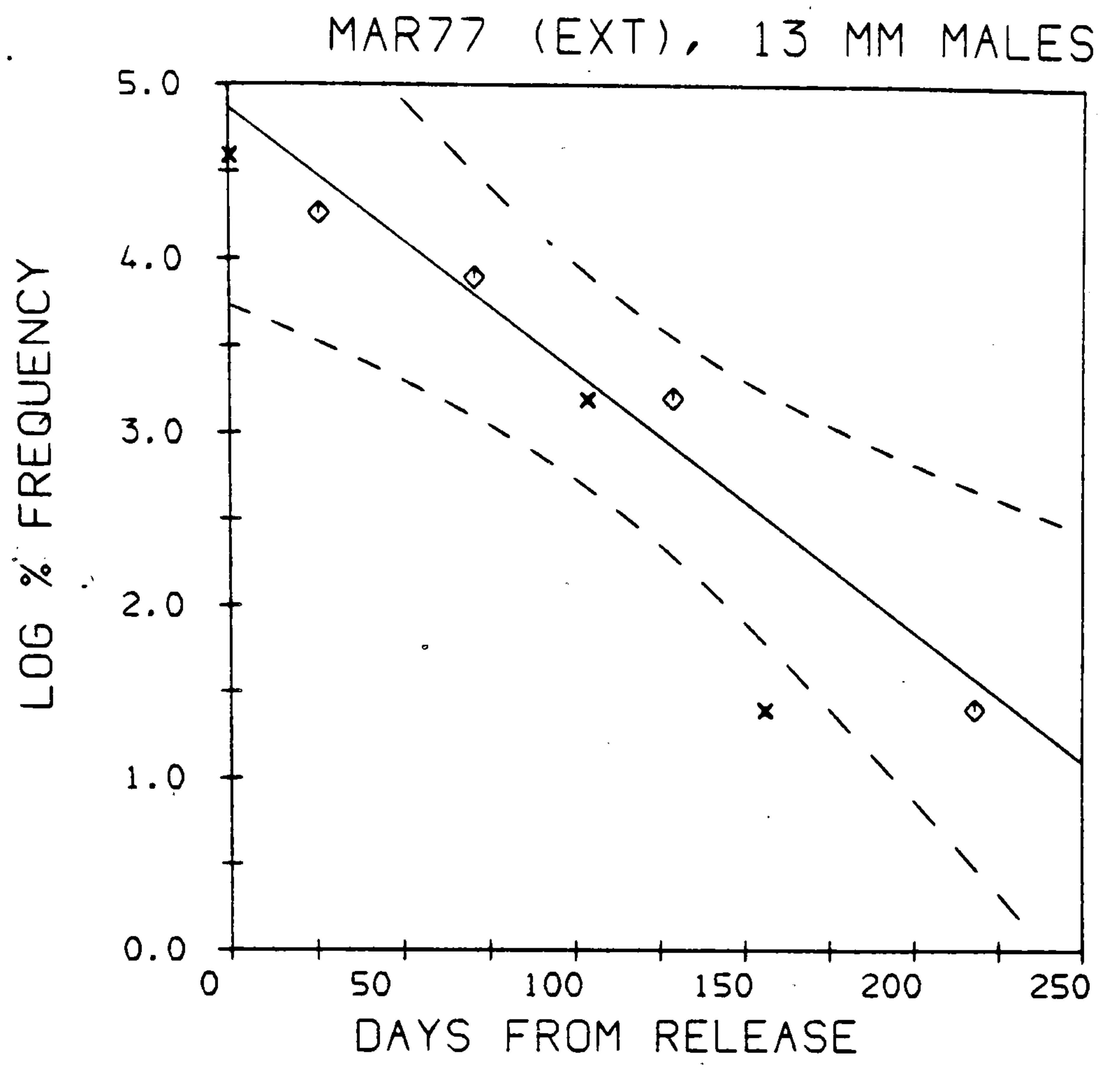


Figure 44, continued. Survivorship of 12 mm male and female components of the extended cohort released 4 March 1977.



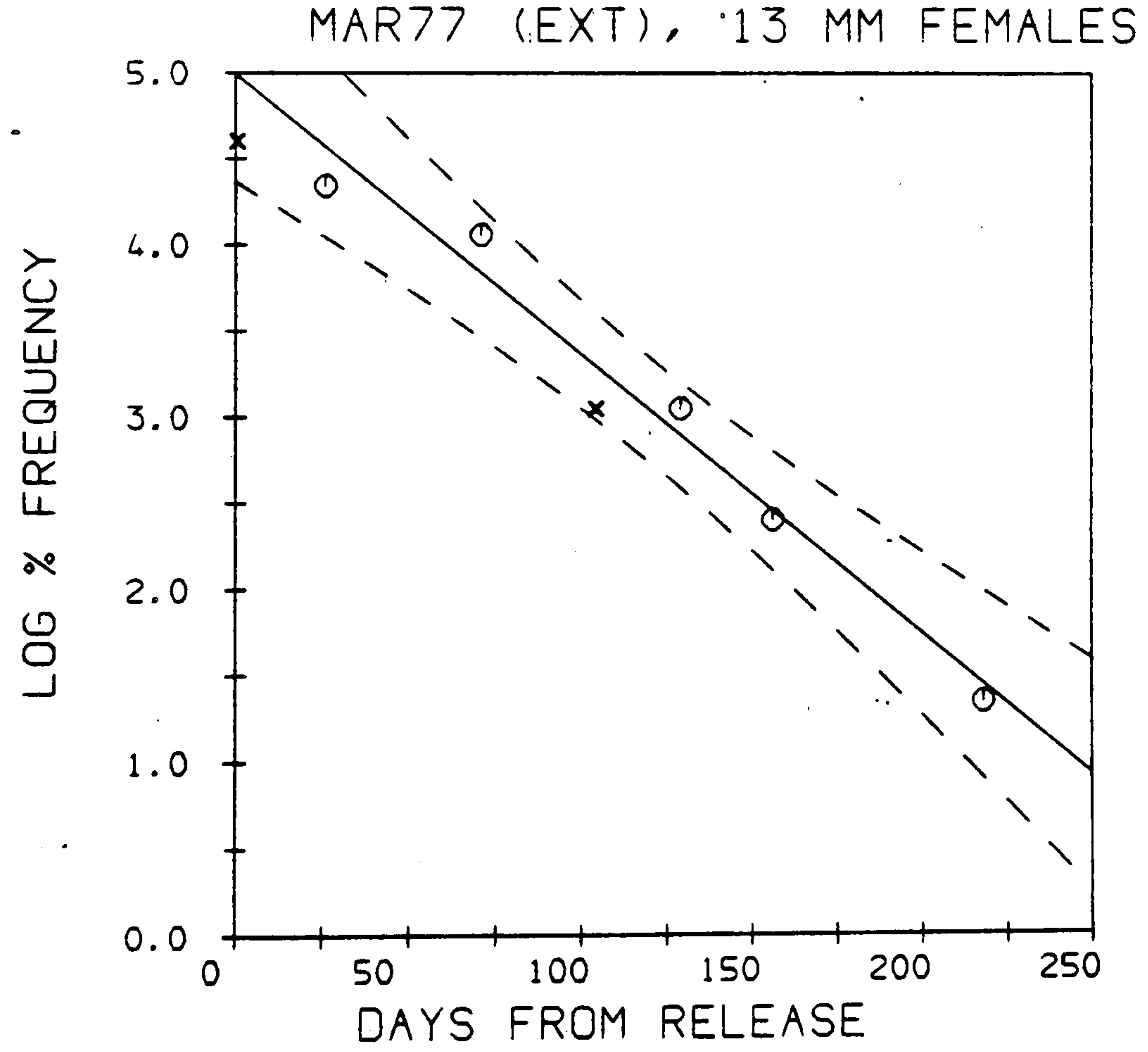
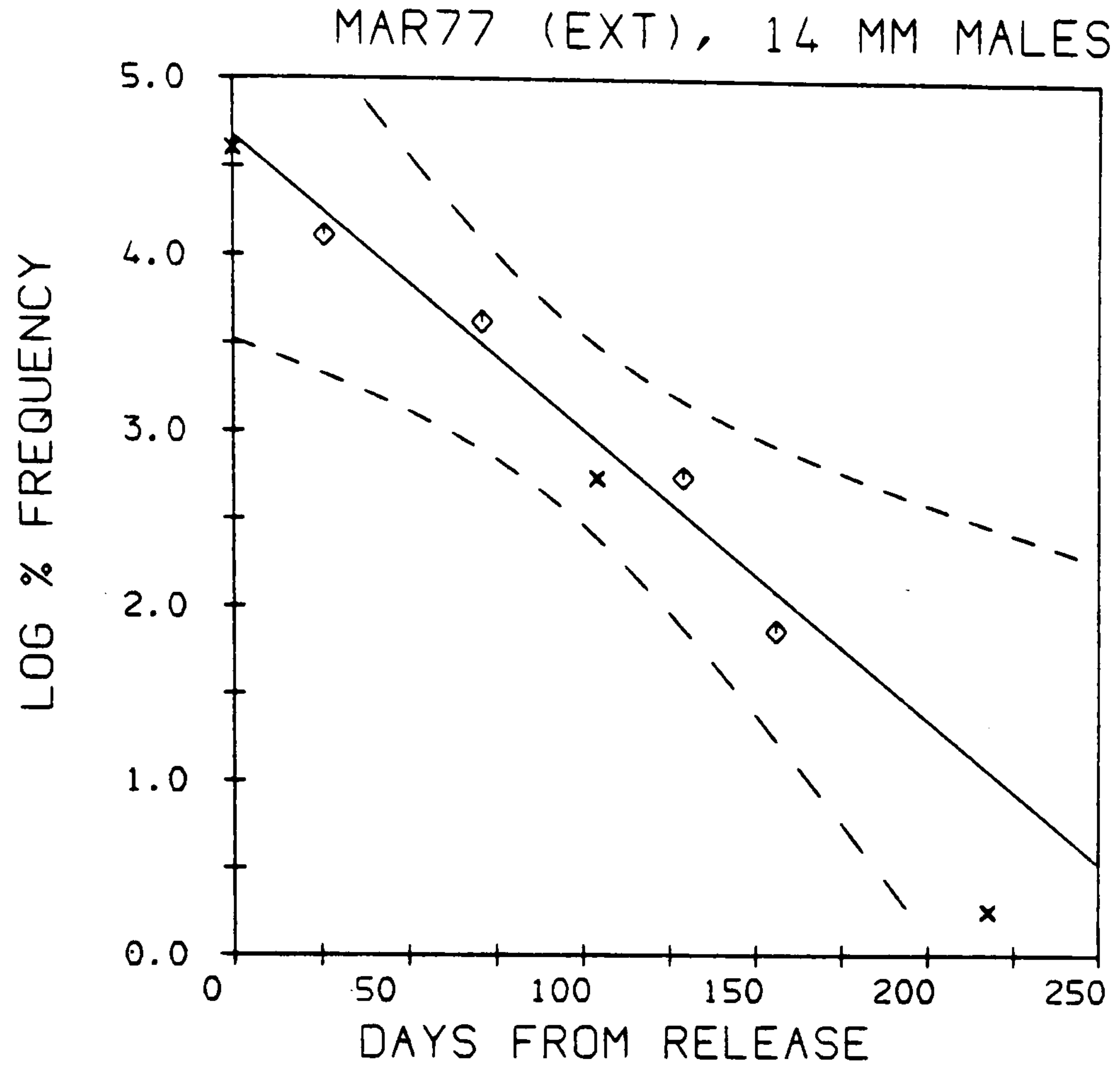


Figure 44, continued. Survivorship of 13 mm male and female components of the extended cohort released 4 March 1977.



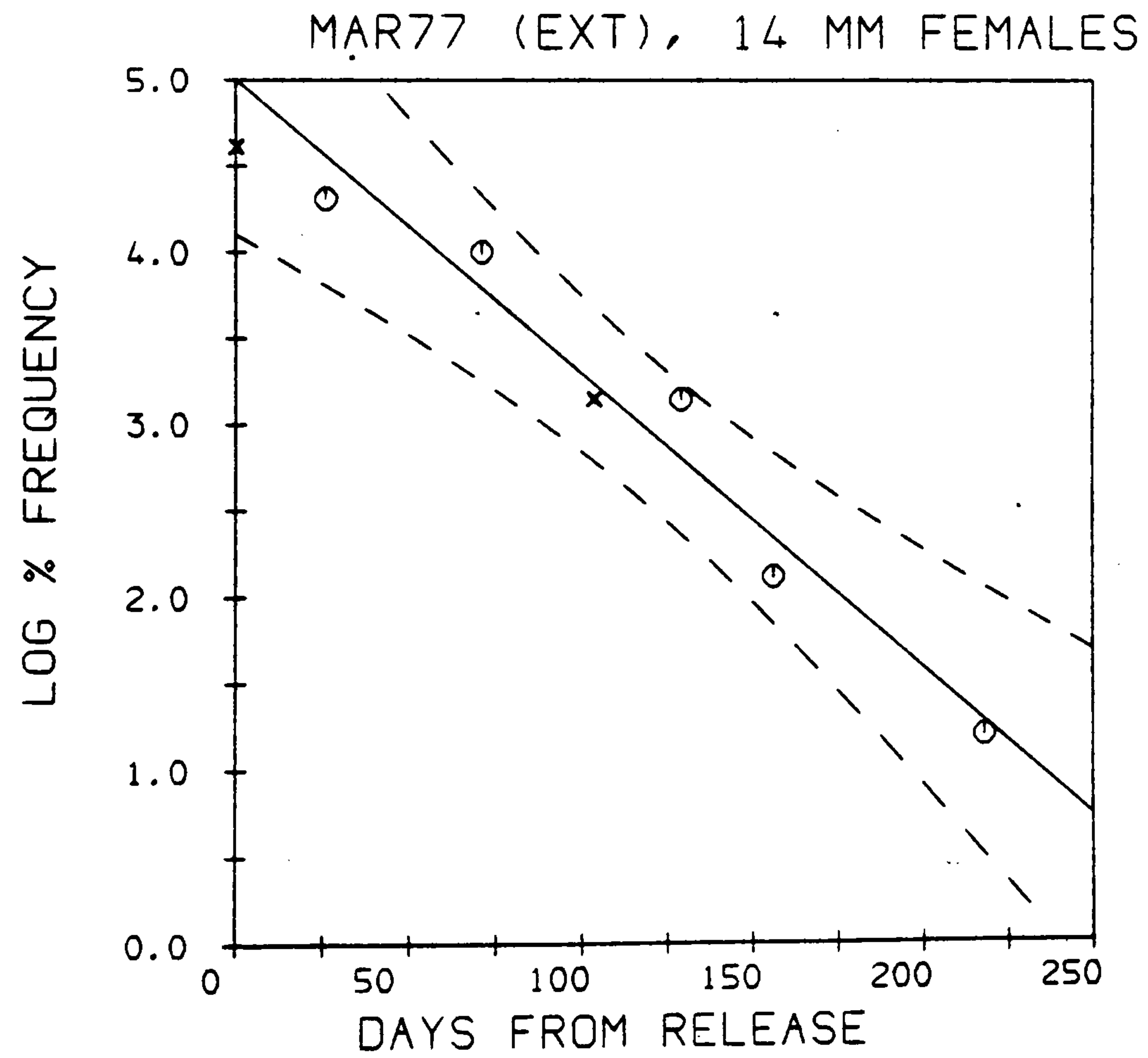


Figure 44, concluded. Survivorship of 14 mm male and female components of the extended cohort released 4 March 1977.

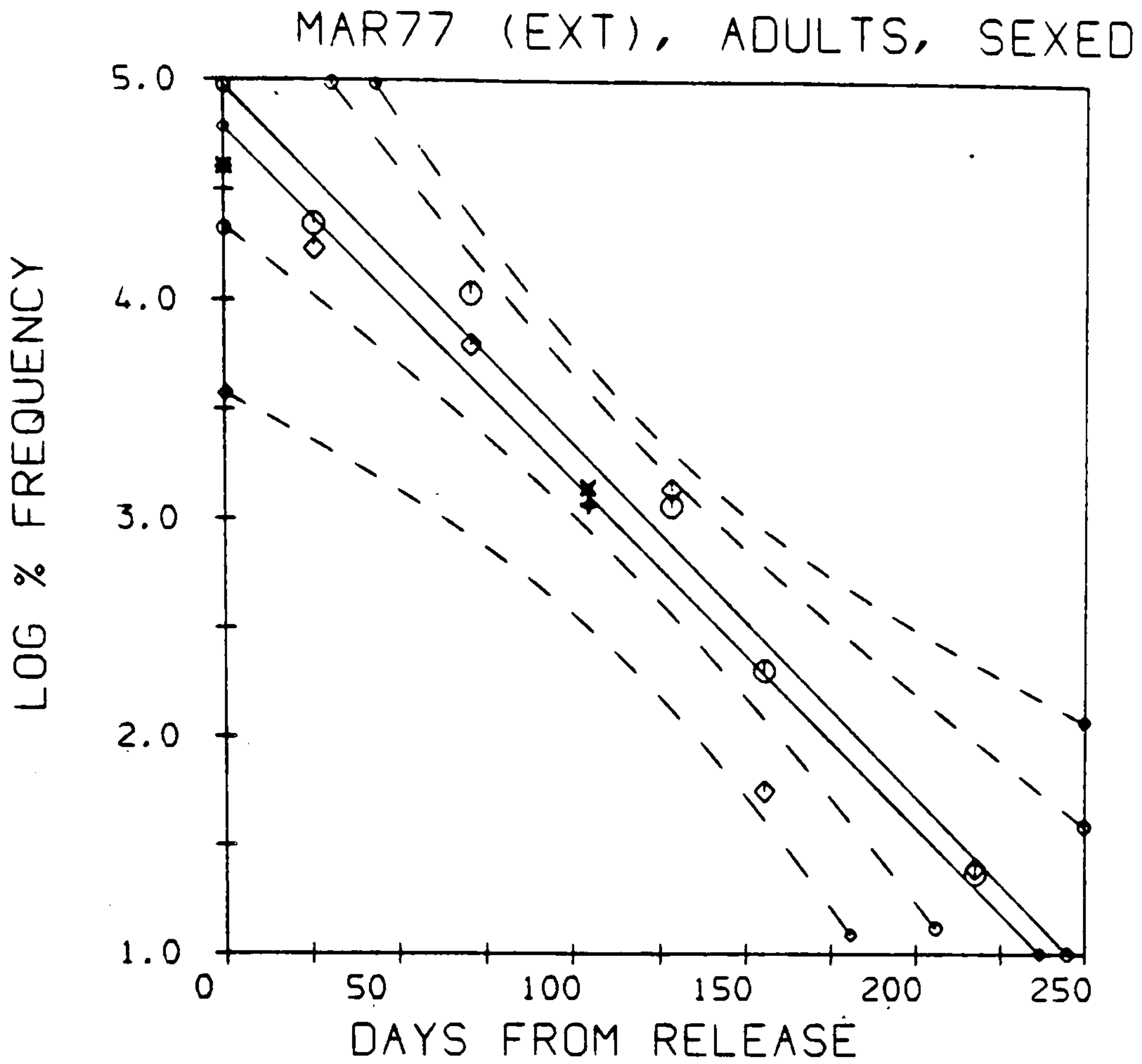


Figure 45. Survivorship of pooled 12 to 14 mm adult male (diamonds) and female (circles) component cohorts of the extended cohort released 4 March 1977. Conventions as in Figure 29. Upper regression line and inner 95% confidence limits are for females. Excluded male points shown as usual, females as crosses. Tiny identification symbols are not data points. 12, 13 and 14 mm data are shown separately in Figure 44. Regressions are in Table 35.

SECTION 10

INDIVIDUAL TAGGING

Introduction

Previous chapters have described growth and survivorship determined from population size-frequency distributions and cohort tagging. Individual variability may be important, particularly in adults, and is best examined by individual tagging. Accordingly, two such programmes were undertaken.

It was desired firstly to evaluate the relationship between shell lip condition and growth activity. Cohort growth results are more meaningful if non-growing snails are eliminated, and shell lip fragility was believed a useful guide.

Second, it was appreciated that the arbitrary final size of 18.0 mm was larger than the usual apparently fully-grown adult at Gorad; much larger adults are known from elsewhere. Sacchi (1969) found size varied predictably with exposure. Some winkles are believed to be long-lived: Hughes & Roberts (1980) have shown that individual L. neritoides may not grow for a year or more and may live perhaps seven years. It was hoped to determine whether L. obtusata grew increasingly slowly with increasing size as in the usual growth equation. If not, predictions of age at given size could be inappropriate.

Further, if individual growth patterns differed markedly, the largest snails would not necessarily be the oldest. Sainsbury (1980) has argued that in molluscs individual variability in the von Bertalanffy growth parameter k is widespread; variability in 1^{∞} did not affect standard equations as seriously as that of k (Section 8).

Various workers have accounted for differing male and female mean sizes by postulating differing growth rates, survival, parasitic infection rates, etc. (reviews in Sections 4, 7, 8). Live-sexing permitted an experimental comparison.

Individual results could be pooled and treated as cohorts, supplementing results already presented, and the accuracy of cohort tagging could be evaluated. Cohort tagging is considerably less labour-intensive and in particular avoids extended release periods if large numbers or scarce sizes must be tagged (see paint methods).

This Section is organised unusually. Methods, results and summaries of the two tagging programmes are presented separately. A grand summary is followed by the discussion as usual, in which an attempt is made to synthesise Sections 6 to 10.

Resin: Methods

The first individual tagging programme commenced in October 1975, before cohort tagging. Freshly collected <u>L. obtusata</u> 13.0 mm and larger were sexed live, then blotted (shell only) and set on dry sandpaper to inhibit movement. Snails for tagging were not selected according to lip condition. Size classes tagged were 13, 14, and 16^+ mm, the last consisting of 16 mm snails and a few 17 mm, both these size classes being scarce. The lower limit of 13 mm was set by shell curvature. An oval patch approximately 5 by 8 mm was sanded from the body whorl, well behind the lip. This removed algae without seriously damaging the shell and aided recognition in case of tag loss.

Commercial 3/16 inch (approx. 5 mm) plastic fish tags proved too rigid and thick, producing a bulge possibly large enough to interfere with normal movement through tangled seaweed, although some winkles bore barnacles Elminius modestus Darwin up to 7 - 9 mm maximum diameter. Tiny flexible numbered plastic tags were prepared by engraving dark green lettering tape with a dental drill. Tags were secured to prepared shells with "Rapid Araldite" quick-setting translucent epoxy resin (Ciba-Geigy (UK) Ltd., Duxford, Cambridge CB2 4QA, England). Resin had to overlap tag edges.

Individual shell dimensions, sex, colour morph, distinguishing markings etc. were recorded. The snails were replaced on sandpaper and left to set in the cool constant-temperature room. After refreshment in ambient sea water and removal of any not behaving normally, snails were released at site A. Abnormality evaluation, release technique, transportation and handling on recapture were as described in Section 8. Snails were released on 13 and 16 October 1975.

Individual records were maintained on recapture, including observations on operculum and shell lip condition and any fresh injuries. Many tags accumulated detritus and had to be dabbed clean, but numbers remained well-defined and easy to read. The green tape blended well with most shells and the background A. nodosum, and the translucent resin was inconspicuous. Silted tags were even less obvious. The tags did not assist recapture, most being noticed upon handling. Tag loss was negligible.

Recapture dates were site A sampling dates (Appendix Table 1; full calendar in Appendix Table 38). Survivorship was analysed in the usual way (Section 9), "cohorts" being the separate and pooled size classes. Sexes were not pooled. For group analysis, certain dates were grouped and arbitrary standard dates were assigned as follows: (release) 16 October 1975

(13 and 16th), 29 October (28 and 29th), 30 November (27, 28 and 30th), 22 February 1976 (20 to 22nd), 24 March (24, 25th), 17 April (13, 17 and 18th). Number found was adjusted to number known to be alive, thus correcting for oversight or temporary emigration. For instance, one 14 mm male was not caught between 12 January 1976 and 14 February 1977. Snails disappearing and found dead after several samples, were considered to have died immediately after release - i.e., date last found alive was last date known to be alive. Survivorship was therefore slightly underestimated. As usual, number alive was analysed in preference to number known to be dead because of the difficulty of establishing death date.

Because snails were not selected for current growth when tagged, changes in mean shell length would seriously have underestimated growth even if corrected for size-specific mortality. Individual growth curves were constructed for those that grew, but numbers did not justify mean curves.

Resin: Condition at release

Numbers and mean shell proportions are given in Table 37. Numbers tagged reflected availability: it was originally planned to tag in the ratio 50:100:50. 150 males and 150 females were released.

Because females had greater mean H than corresponding males - i.e., were more globular - mean H was compared between sexes with the unequal-variances t-test explained in Section 5. Males and females did not differ significantly in any size class.

Seven males and four females had damaged opercula. Typically, a deep notch was torn or cut out of the abapical margin. A 16.4 mm male lacked an operculum altogether.

Table 37

Resin shape

Table 37. Mean shell measurements at release of snails bearing numbered plastic tags. Entries are means with standard deviations in parentheses. M, males; F, females. N, number measured and released. Param., shell parameter

		Size class, mm		
		13	14	16^+
Sex		M	M	M
N		30	100	20
Param.	L	13.62 (0.21)	14.48 (0.29)	16.34 (0.32)
	H	9.17 (0.30)	9.45 (0.34)	10.43 (0.26)
	W	12.95 (0.30)	13.69 (0.60)	15.34 (0.73)
	T	0.60 (0.08)	0.69 (0.09)	0.77 (0.13)
Sex		F	F	F
N		26	100	24
Param.	L	13.57 (0.28)	14.51 (0.26)	16.40 (0.29)
	H	9.31 (0.24)	9.63 (0.30)	10.71 (0.40)
	W	12.91 (0.39)	13.68 (0.41)	15.75 (0.67)
	T	0.63 (0.07)	0.65 (0.08)	0.80 (0.14)

Resin: Opercula

Of 7 males and 4 females with damaged opercula at release, one male effected a partial repair by 5 August 1976. The male lacking an operculum was only recovered once, as was a 14.8 mm female damaged on 27 November.

A 13.3 mm male lost its operculum after 29 October and before 27 November 1975. This operculum remained missing on the next four recaptures, through 24 March 1976. A long rectangular replacement was begun by 18 April and enlarged on 24 May to near completion by 23 June 1976, 91 days after repair presumably began, and more than 210 days after loss.

Resin: Individual growth

Snails were not selected by lip condition when tagged. Indeed, only one had grown by 1 January (day 88, 142 winkles known to be alive; calendar in Appendix Table 38). Numbers growing for the first time in the next few intervals were respectively 2, 8, 8, 7, 4, and 1. That is, snails resumed growth variously between 12 January and 19 August 1976 (308 days from release). Of these 31 however, half merely formed small thickish lip bands but added no measurable increment: 4 on 25 March, and thereafter 2, 5, 4, and 1. So, fifteen snails resumed growth well after tagging, usually during March and April. (Three credited to April had in fact begun to grow in March - i.e., had extended the body whorl spirally - but had not increased L, so seven of fifteen began in March.)

These fifteen growth curves appear in Figure 46, together with that of the long-lived female. Only two snails kept growing for several months (curves F, G) although of course others might have done so had they been caught again (e.g., curves A, C, D). Some added length in one step and then remained at the new size (curves J, K). Curve L incorporates a brief pause in otherwise sustained growth.

Growth as increase in snail length L requires more effort than these curves suggest. For example, the 1.2 mm added by snail H between 22 February and 17 April advanced the body whorl by 6.2 mm.

Individual k and growth rate dl/dt were computed only for periods of sustained growth, and hence for only three snails (Table 38). k could not be computed assuming that the final size seen was l^{∞}, because this would have involved division by zero (Section 8, equation 4, $l^{\infty} - L_2$). Assigning a slightly larger value to avoid this - say, 15.11 mm for curve F - increased k by an order of magnitude for similar reasons.

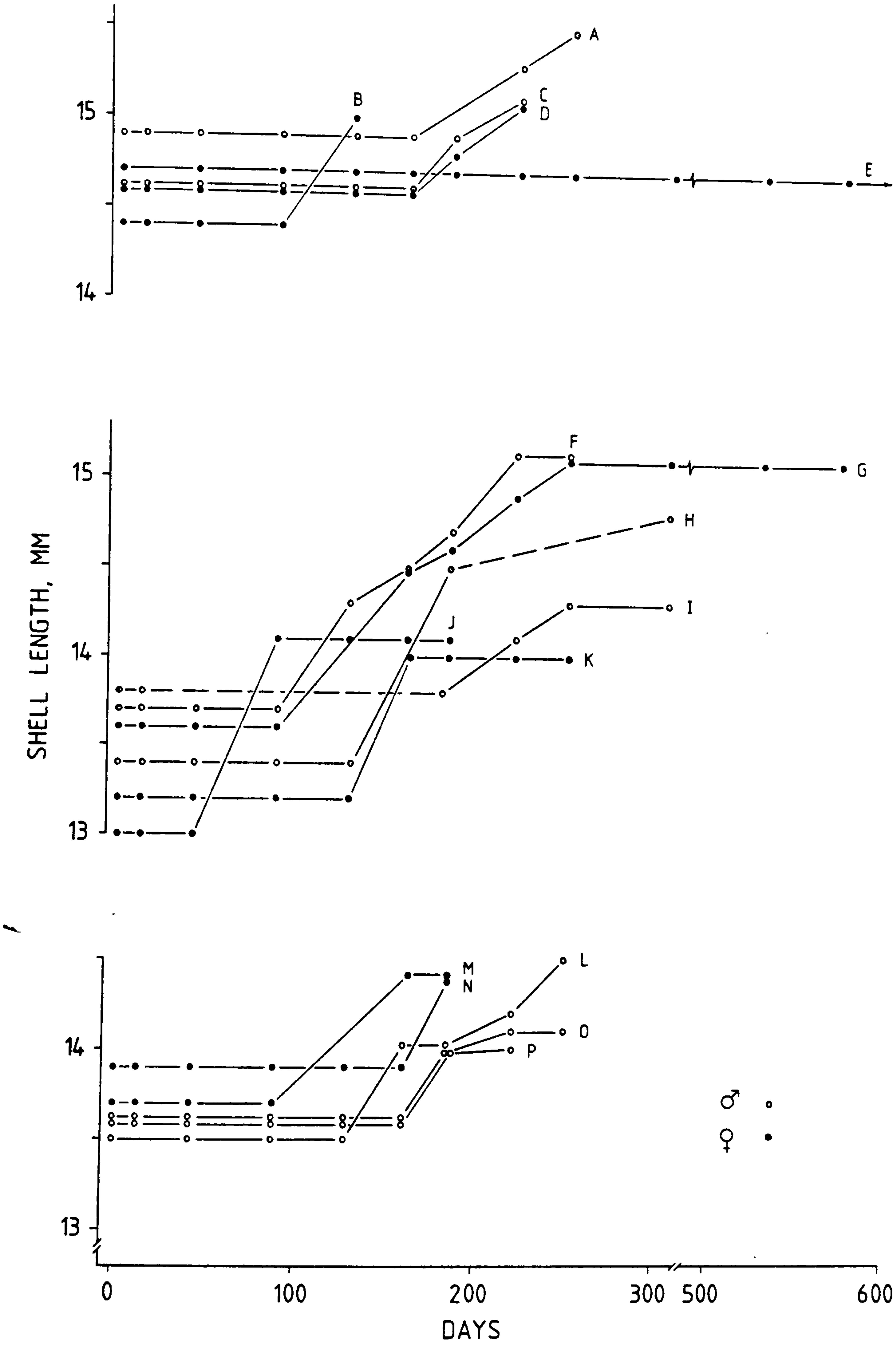
k values for the interval in which all three were growing agreed with the longer-term values. The lower values for snail L in each interval were caused by the three-week growth pause. If the last two line segments were shifted 24 days towards release, recalculated k agreed with that of the other snails.

Mean k incorporating the corrected snail L values was 0.0027 days^{-1} for the longer, and 0.0025 days^{-1} for the shorter, intervals.

Figure 46

Resin intermittent growth curves

Figure 46. Individual growth curves of 15 adult *L. obtusata* bearing tiny numbered plastic tags secured with translucent epoxy resin, released 16 October 1975, showing intermittent growth, and one (curve E) maintaining 14.7 mm for 723 days. All snails appeared to have reached final size when tagged - none had fragile shell lip. All records shown; dashes signify interval in which snail was not seen.


SHELL LENGTH, MM
DAYS
A
B
C
D
E
F
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K
L
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N
O
P
15
14
13
0
100
200
300
500
600
♂ ○
♀ ●

Table 38

Resin individual growth

Table 38. Individual k (days^{-1}) and growth rate dl/dt (mm per day) calculated for those portions of growth curves where growth continued for several recaptures. Curve, labels from Figure 46. Go, initial length, mm. Stop, final length, mm. T, time interval, days. l^{∞} is assumed to be 18.0 mm. Lower set of figures, values for days 129 to 221 when all were growing.

Curve	Go	Stop	T	k	dl/dt
L	13.5	14.5	122	0.0021	0.0082
L	13.5	14.5	98[a]	0.0026[a]	0.0102[a]
G	13.6	15.1	163	0.0026	0.0092
F	13.7	15.1	133	0.0030	0.0105
L	13.5	14.2	92	0.0019	0.0076
L	13.5	14.4	92[a]	0.0024[a]	0.0098[a]
G	14.1[b]	14.9	92	0.0025	0.0087
F	14.3	15.1	92	0.0027	0.0087

[a] 24-day growth pause removed as explained in text

[b] interpolated missing record

Resin: Survivorship

The 16^+ mm snails only maintained satisfactory numbers for about four months, declining steadily (Figure 47 A,B). The very similar male and female regressions (Table 39) were respectively highly and very highly significant (Appendix Table 38). A few individuals persisted until day 308, 19 August 1976.

The 13 mm snails declined less regularly. Male numbers were adequate until day 251, and females lasted until day 184. However, each regression was extended to day 308 to cancel out distorting effects of brief levelling-out. The resulting regressions more properly reflected the overall pattern of decline and were very highly significant. Females declined faster than males, although one female persisted to day 576. (The female day 0 to 184 regression resembled the males more closely: Y-intercept 4.56, slope -0.00865.)

The much more numerous 14 mm snails declined regularly, maintaining satisfactory numbers until day 308. Male and female decay rates were similar. Both regressions were very highly significant. One male survived from day 308 to day 531 with two females, one of which continued to be caught until field work ended 723 days from release.

When all three size classes were pooled within sexes, total numbers remained sufficient through day 308. Male and female decay patterns and regressions were remarkably similar, with identical slopes (Figure 47, C). Regressions were very highly significant.

13 and 14 mm and pooled slopes were lower than corresponding adult March 1977 extended cohort values (Tables 34 and 35, Section 9), in keeping with the general trend seen in 6 and 9 mm cohorts (Table 32).

Table 39

Resin survivorship

Table 39. Survivorship regressions for adults bearing individually-numbered plastic tags secured with epoxy resin, released 16 October 1975. Data are extracted from Appendix Table 38. Late points based on very few snails were rejected as explained in text. First-interval survivorship did not necessitate rejection of day 0 - see Figure 47. M, males; F, females. N, number released. Span, time interval over which regression was calculated. A, Y-intercept. b, negative slope. Note that regressions pooling all sizes are dominated by the 14 mm snails.

Sex	Cohort, mm	N	Span, days	A	b, x 10^{-3}
M	13	30	308	4.57	7.06
	14	100	308	4.61	9.53
	16^+	20	129	4.48	15.16
	Pooled	150	308	4.57	9.04
F	13	26	308	4.67	10.51
	14	100	308	4.70	9.00
	16^+	24	129	4.58	15.89
	Pooled	150	308	4.63	9.04

Figure 47

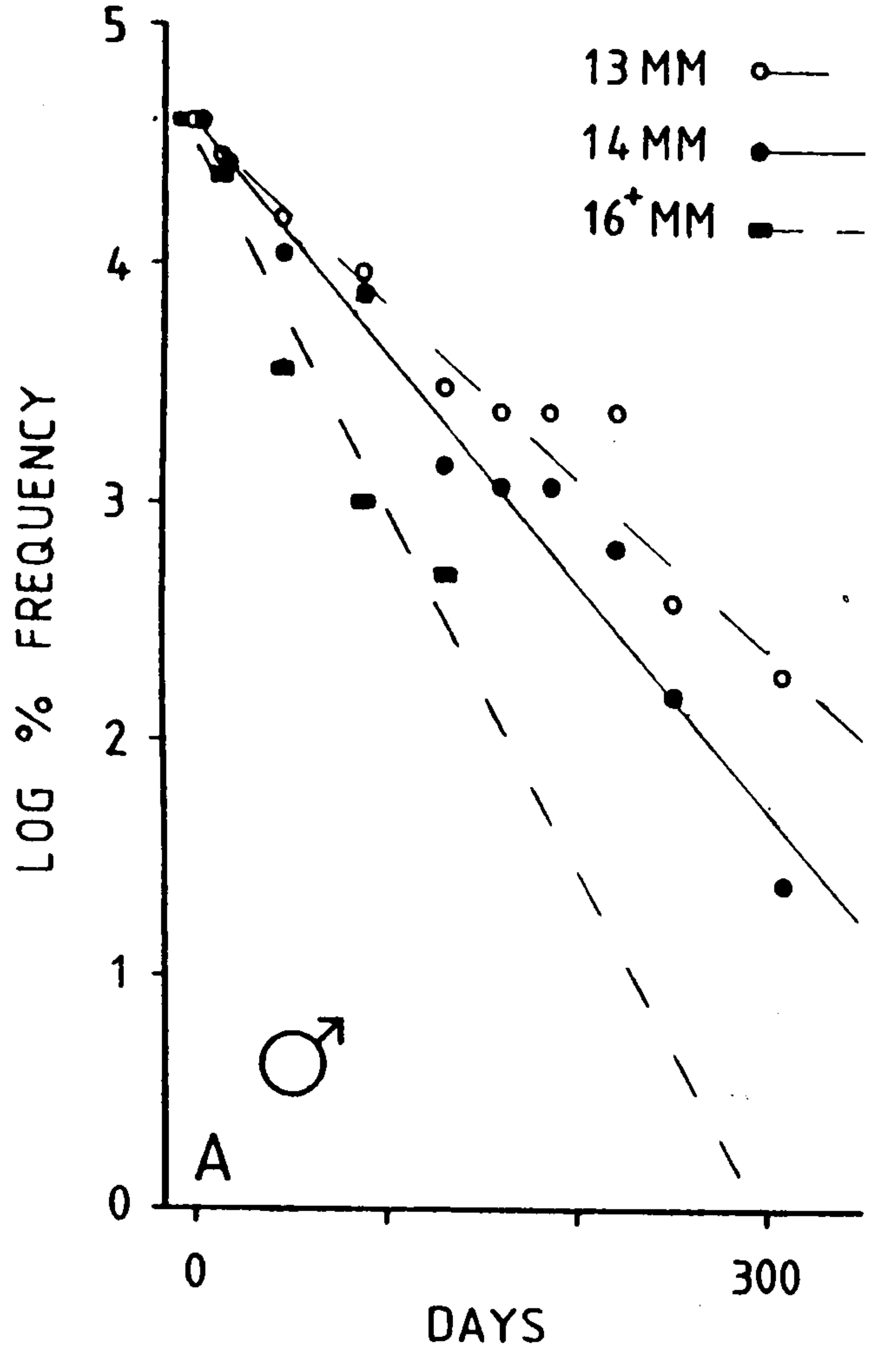
Resin survivorship

Figure 47. Survivorship plots for individually-tagged adults released 16 October 1975. Plots truncated at day 308 (19 August 1976) or earlier as explained in text. Regression lines drawn from equations in Table 39.

A, males. Survivorship of 13, 14 and 16^+ mm cohorts shown separately; numbers released were 30, 100 and 20 respectively.

B, females. Survivorship of 13, 14 and 16^+ mm cohorts shown separately; numbers released were 26, 100 and 24 respectively. Note reversal of 13, 14 mm compared to males.

C, totals. Curves shown in A, B summed within sexes. Note that 14 mm snails dominate each owing to unequal numbers.


A
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DAYS
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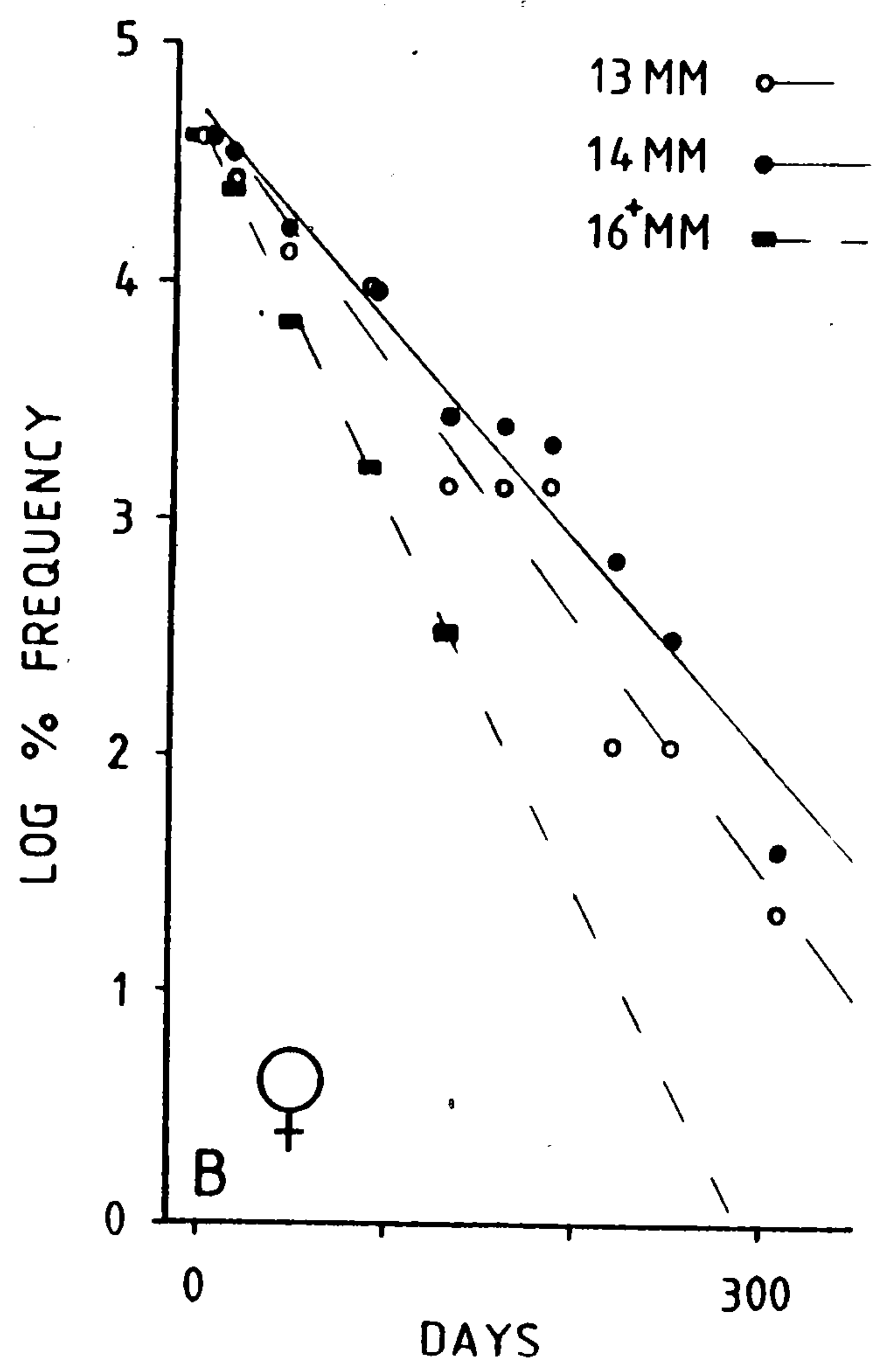
2
3
4
5
0
300
13 MM
14 MM
16⁺MM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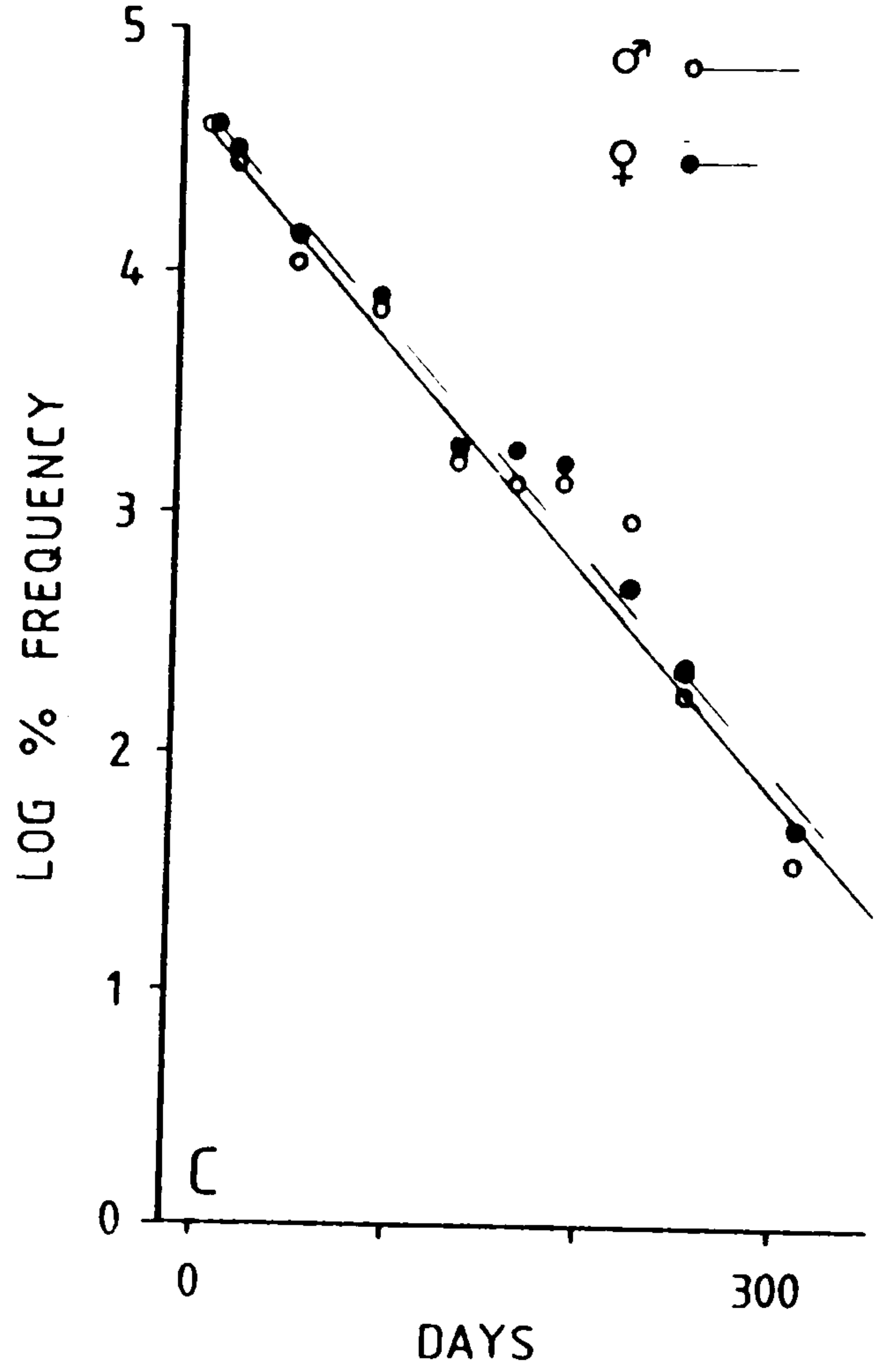
14 MM
16⁺MM


C
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DAYS
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3
4
5
0
300

Resin: Summary of results

1. Inconspicuous tiny numbered tags made by engraving green plastic lettering tape with a dental drill were glued with quick-setting translucent epoxy resin to 13, 14, and 16^+ mm live-sexed adult <u>L. obtusata</u>.

2. 150 males and 150 females, consisting of 100 each 14 mm and approximately equal numbers of the other classes, were released at site A on 13 and 16 October 1975. Individual records were maintained. Shell or operculum damage, shell lip condition, and shell shape parameters were recorded on each recapture.

3. The slightly more globular female shape did not differ significantly from that of males.

4. Damaged opercula were not usually repaired. One male that lost its operculum only began to replace it four months later and took three months.

5. Snails were not selected for growing state when tagged, and none grew before January 1976. Fifteen eventually resumed growth, beginning chiefly in March.

6. Individual growth patterns varied from single brief bursts to more sustained growth. Individual k of three 13 mm snails growing for several months agreed closely and averaged approximately 0.0026 days^{-1}.

7. Survivorship was expressed (as usual) as the natural logarithm of percent alive at a particular elapsed time. Individual records allowed corrections to be made for snails overlooked or temporarily emigrated. Tag loss was negligible and easily recognised.

8. The 16^+ mm males and females declined steadily and lasted about four months. 13 mm winkles declined less regularly over six to eight months, the males surviving longer. Male and female 14 mm winkles declined regu-

larly for about ten months at similar rates. All regressions were significant at the 1% level or better. Slopes for pooled males and pooled females over ten months, dominated by the more numerous 14 mm snails, were identical and the regressions were very highly significant.

9. 13 and 14 mm and pooled slopes were lower than corresponding values for the March 1977 extended cohort.

Paint: Methods

The 12 mm size class was selected for the second individual tagging programme, beginning in February 1976. These small adults were, however, scarce (Figure 7, Section 6). Snails were sorted in the field with a perspex tablet constructed with a deep groove, straight on one side and accurately stepped at 1 mm intervals on the other. Snails were held aperture-down, against the smooth side with the lip facing the stepped side, and slid along the smooth side. Those that came to rest in the 11, 12 or 13 mm steps were taken to the laboratory for careful measurement and selection. If only those stopped in the 12 mm step were taken, lengths 12.0, 12.1 and 12.9 mm were slightly undersampled. This simple cheap device proved effective in reducing field and laboratory time.

Resin tags, while inconspicuous, were bulky. Also, shell curvature set a lower limit of about 13 mm for this technique. Resin tagging demonstrated the need to select actively-growing snails to maximise useful results while numbers remained high. It was believed that snails with a fragile, chisel-edged aperture lip would be growing. The validity of this assumption was subsequently tested.

12.0 to 12.9 mm snails were sexed live and individually recorded for sex, colour morph, shell measurements L H W and T (Figure 2, Section 4), presence and extent of growing lip, barnacles, scars, distortions and distinguishing markings, etc. Markings were entered directly onto three profile drawings on the individual record sheets. Shell measurements were means of three or five readings taken with dial vernier calipers (Section 4).

Shells were blotted, a small oval patch was sanded on the body whorl well behind the lip (Section 8), and painted code numbers were applied as follows.

Ten colours of "Humbrol" enamel paint (Section 8) represented digits 0 through 9. Three-figure serial numbers could be encoded by three small paint dots. Treatment during and after tagging was as usual (Section 8). Snails judged abnormal when refreshed were not released, nor were their numbers reassigned. These constituted only 15 of 337 tagged males (4.45%) and 7 of 281 tagged females (2.49%). Tag loss was slight. Very occasionally tags were partially lost by shell damage. Snails were identified by elimination and re-tagged. Abrasion or flaking did occur, but never all three dots at once. Snails were easily recognised by the sanded area. Missing dot traces visible under the microscope were occasionally ambiguous: maroon/red and orange/khaki required care. Ambiguous snails were identified by distinguishing markings and by elimination, and then re-labelled. Clear partial losses were not fixed, but the record sheets were annotated.

Growing 12 mm shells were uncommon in winter and the detailed individual descriptions restricted the number that could conveniently be tagged at one time. Consequently tagging extended from 9 to 22 February and 9 to 22 March 1976. Even so, not all shells had fragile lips when tagged.

survivorship and growth:

The extended release period complicated analyses that combined individual results - e.g., survivorship - as did occasional recaptures on non-sampling dates or at sites other than A. Some dates were grouped and assigned an arbitrary sample date. For instance, sightings between 16 and 31 March were coded occasion 2 and assigned to 24 March. These arbitrary dates were used for survivorship and mean growth curves. All records were converted from calendar date to days from 1 January 1976, from which release date could be subtracted when necessary to yield days from release (Table 40). All records were transferred to computer files. Full details of dates, coding etc. accompany the raw data, copies of which will be deposited in due course. Address for queries: page 7.

Snails deemed abnormal when examined on recapture - i.e., those that would not attach to or feed on the fresh weed after being measured - were considered moribund, killed, and coded alive on that date but dead the next day.

Survivorship was expressed as usual in terms of number known to be alive at a given elapsed time. Corrections could readily be made for temporary disappearances. Snails that vanished and were later found dead, usually as empty shells, required special treatment. If no growth had occurred, they were assumed (as usual) to have died immediately after the last time seen alive.

If, however, the shell was undoubtedly larger than when last seen, death was arbitrarily taken to have occurred after the standard date closest to the interval's midpoint. For example, a 12.1 mm male released on day 45 was next seen on day 272 as a 13.7 mm empty shell. The midpoint was day 227. The nearest standard date was day 232 (Table 40). This snail was therefore scored alive up to and including that date. When the midpoint fell halfway between two standard dates, the earlier was used as a conservative estimate.

For purposes of growth using grouped data, when a missing snail later appeared alive but no larger, shell measurements were assigned throughout the interval. However, when growth had occurred, no measurements were interpolated. Likewise no effort was made to assign any portion of observed growth to the first half of an interval in which a snail was presumed alive as explained in the previous paragraph.

Table 40

Paint calendar

Table 40. Simplified capture calendar for individually paint-numbered snails released in February and March 1976.

Date		Day	Standard date		Day	Code
01 January	1976	001				
01 February		032				
01 March		061	24 March	1976	084	2
01 April		092	17 April		108	3
01 May		122	24 May		145	4
01 June		153	23 June		175	5
01 July		183				
01 August		214	19 August		232	6
01 September		245	30 September		274	7
01 October		275				
01 November		306	03 November		308	8
01 December		336	01 December		336	9
01 January	1977	367				
01 February		398	14 February	1977	411	10
01 March		426	30 March		455	11
01 April		457				
01 May		487	14 May		500	12
01 June		518	16 June		533	13
01 July		548	11 July		558	14
01 August		579	07 August		585	15
01 September		610				
01 October		640	08 October		647	16

Analysis of individual growth was restricted to snails known to be growing actively. Individual, mean, and composite growth curves were constructed. Individual and group growth increments and parameters k and l^{∞} were calculated. Results were compared between sexes and with cohort results (Section 8). Individual variability of k and l^{∞} was evaluated. Details accompany the results.

Paint: Condition at release

Shell length L was approximately evenly distributed from 12.0 to 12.9 mm in each sex; columellar length W, shell height H, and shell lip thickness T were approximately normally distributed.

To determine whether size and shape of the 322 males and 274 females were similar, mean L, W, H and T were compared by one-way analysis of variance (Table 41).

Females were more globular than males: although mean L did not differ between sexes, female mean H was very highly significantly greater than male mean H. Mean individual H/L ratios were compared as a check; females were highly significantly more globular than males ($P = 0.0096$).

Although male mean lip thickness T was very highly significantly the greater, the 0.03 mm difference between sexes was within the increment of measurement, 0.05 mm. Modal thicknesses were 0.50 mm for males and 0.45 mm for females; ranges were identical (0.35 to 0.75 mm).

Table 41

Shape comparison

Table 41. Mean shell measurements at release, with standard deviations in parentheses, of 322 male and 274 female 12 mm individually paint numbered L. obtusata, with results of ANOVA comparisons between sexes. Param., shell parameter, mm. P(F), significance of stated variance ratio.

Param.	Males	Females	F(d.f.)	P(F)	
L^a	12.52 (0.29)	12.53 (0.28)	0.11 (1, 594)	0.74	NS
W	12.17 (0.41)	12.21 (0.45)	1.90 $(1, 575)^b$	0.17	NS
H	8.55 (0.24)	8.67 (0.25)	33.05 $(1, 592)^b$	0.0000	***
T	0.52 (0.07)	0.49 (0.07)	20.47 (1, 594)	0.0000	***

[a] values not normally distributed - see text

[b] number measured reduced by barnacle encrustation

Outer whorl scarring differed significantly between the sexes (Chi-square 3.93, 1 d.f., $P < 0.05$). Males were more damaged (83 of 322) than females (52 of 274). Proportions having 1, 2 or 3 such scars did not differ significantly between sexes or between shell colour morphs.

Six males (1.86%) had "peckmarks" - a small irregular outer whorl hole with radiating fractures - as did five females (1.82%).

One male had been unsuccessfully drilled, presumably by the dog-whelk Nucella lapillus. Nucella frequently attacks at the operculum, leaving no mark, so shell marks do not necessarily reflect attack intensity

(Pettit 1975). One 13.3 mm male was successfully drilled, near the apex where the shell is at its thinnest, between 23 June and 19 August.

At release, four males and four females had notches or torn opercula. One of each sex lacked an operculum entirely, bringing proportions damaged to 1.55% males and 1.82% females.

Sex ratio at release was 1.175.

Male and female morph ratios at release did not differ (males 269 olivacea : 46 reticulata : 7 citrina, females 231 : 33 : 10, Chi-square 1.70, 2 d.f., P = 0.43).

Tagging stress, if present, may contribute to first-interval disappearances (64 of 596, 10.74%). Disappearance in the first interval was independent of sex or colour. The proportion vanishing (not later found dead) did not differ significantly among morphs (Chi-square 2.35, 2 d.f., P >0.3), between sexes (corrected Chi-square 2.47, 1 d.f., P >0.1), among morphs within sexes (male Chi-square 1.28, 2 d.f., P >0.5; female Chi-square 0.96, 2 d.f., P >0.6), or between sexes within morphs (olivacea corrected Chi-square 1.65, 1 d.f., P = 0.20; fused reticulatas plus citrina corrected Chi-square 0.22, 1 d.f., P >0.5, fused because no citrinas vanished).

Growing status was evaluated independently of lip thickness, according to lip edge sharpness. Not all shells could be classified confidently. This indicator is examined in detail later. Males and females did not differ significantly in proportions considered growing, not growing or unclear (Chi-square 5.65, 2 d.f., P >0.05). Elimination of unclear cases highlighted the similarity (Chi-square 0.04, 1 d.f., P >0.5).

Synopsis: 322 male and 274 female L. obtusata measuring 12 mm in shell length were released. At release, the sexes did not differ significantly in colour morph ratios, proportion considered growing, mean shell length or mean columellar length. A difference in mean shell lip thickness fell within the measurement increment. Males had more outer-whorl damage than females, except for "peckmarks". Females were more globular than males. The proportion vanishing unaccountably before the first recapture was independent of sex or colour morph.

Opercula

Of four males and four females with damaged opercula at release, one female began a repair during June and another in August, respectively at least 92 and 134 days from damage. Others died or disappeared by then, without starting by mid-April.

The male lacking an operculum still did so when last seen on 23 June, 135 days from release. The female was not recovered alive.

A 13.8 mm female suffered one large and three small tears between 19 August and 30 September. No repairs were begun on the seven subsequent recaptures through 10 July 1977, at least 283 days after injury.

A 12.5 mm male lost its operculum between 18 February and 24 March, and had not begun to replace it when last seen on 23 June at least 91 days after loss.

A 14.0 mm male lost its operculum some time in 1977 between 22 February and 16 June, but was not seen alive again.

Three other snails were damaged by 23 June 1976, and another by 19 August, but none was recaptured.

Growing lip condition evaluation

Shells were tentatively classified as growing or not according to shell lip edge condition. Young growing shells characteristically have a delicate chisel-edged lip margin, while large old shells may have smooth rounded lip edges. Many shells cannot be classified with confidence: at release, 125 males and 81 females (38.8 and 29.6% respectively) were scored "unclear".

One might expect "growing" shell lips to be thinner on average than "thickened" ones. This was so at release (Table 42), by about 0.09 mm. The difference applied within sexes as well. Although "growing" males were very highly significantly thicker than "growing" females, the 0.02 mm difference was within the 0.05 mm measurement increment.

The relative proportions of "growing" and "thickened" shells in recaptured survivors were compared. Numbers for standard dates through 19 August 1976, and all later records pooled, were used: Chi-square 949.18, 6 d.f., $P < 0.001$. The proportion "growing" declined very highly significantly with time. Ratios were unchanged through standard date 24 May, then proportion "growing" dropped substantially to 23 June and 19 August. It is unsafe, however, to conclude that growth stops in early summer. Growth also depends on size. Seasonal conclusions require repeated independent groups of similar initial shell size (Section 8).

Table 42

"Growing" lip thicknesses tested

Table 42. Relationship between growth condition estimated from shell lip delicacy and measured lip thicknesses, with results of pairwise ANOVA comparisons. M, males; F, females. N, number measured. T, mean lip thickness with standard deviation in parentheses. Comp., rows compared. P(F), significance of stated variance ratio.

Row	Sex	Estimated condition	N	T
1	M + F	growing	373	0.49 (0.07)
2	M + F	not growing	17	0.58 (0.06)
3	M	growing	188	0.50 (0.07)
4	M	not growing	9	0.58 (0.06)
5	F	growing	185	0.48 (0.06)
6	F	not growing	8	0.59 (0.05)

Comp.	F (d.f.)	P(F)	
1, 2	30.54 (1, 388)	<0.001	***
3, 4	9.19 (1, 195)	<0.01	**
5, 6	26.26 (1, 191)	<0.001	***
3, 5	17.81 (1, 371)	<0.001	***
4, 6	0.12 (1, 15)	0.73	NS

The raw data revealed that some "growing" snails did not increase in L. Accordingly, snails considered "growing" at release and measured at least two months later were examined. Growth was defined as at least 0.2 mm shell length increase because L was recorded to the nearest 0.1 mm. Almost all "growing" snails had grown. 188 males were "growing" at release, 83 were available after two months, and of them 81 had grown; 185 females "growing" at release yielded 94 after two months, of which 92 had grown.

Simple comparisons of mean lengths of "growing" and "thickened" snails over time would be fallacious. Both would necessarily increase: "thickened" shells would appear to grow with the regular addition of increasingly large ex-"growing" shells. Individual records are necessary (see subsection Paint: Mean growth).

Lip thickness in snails confidently considered thickened could subsequently decrease. This phenomenon was associated with renewed growth: 14 males and 20 females resumed growing during the study period. Lip thickness decreases of 0.2 mm or more were rare, and renewed growth did not normally involve a reduction to juvenile values of approximately 0.35 mm.

Synopsis and evaluation: Shells considered from lip margin delicacy to be growing did indeed grow. Most considered thickened grew no further, but enough later resumed growth to question the validity of that classification. Shells at Gorad rarely exceed 0.8 mm shell lip thickness; at other sites, thickened shell lips may indicate final size more reliably. Accordingly, shell lip condition usefully identifies snails actively growing, but does not distinguish intermittently growing snails from those having achieved final size.

Paint: Mean growth

Mean shell lengths of all survivors at various dates proved an unsatisfactory general measure of growth. For instance, female mean L on ten occasions from release to 14 February 1977 was 12.53, 12.64, 12.88, 13.38, 13.64, 13.70, 13.52, 13.38, 13.37, and 13.30 mm. The apparent decline from occasion six is spurious.

In the previous subsection it was shown that classification of shells as "growing" based on shell lip condition is accurate, but classification as "thickened" may introduce errors of unknown magnitude. Mean values for comparison with cohort results (Section 8) were therefore derived from individual records as follows.

On each standard sampling occasion (Table 40), only the lengths of snails known to have survived and grown by the next occasion were used. By eliminating even individuals that grew soon thereafter, snails actively growing when measured were rigorously selected.

The first interval used extended from release to code 2 or 3 depending on release date: code 3 was used for snails released soon before standard day 84 (see Table 40 for codes etc.). Consequently the next interval, to synchronise all snails, was 3 to 4, then 4 to 5, and 5 to 6. Insufficient growing snails remained after occasion 6.

Proportions growing or not were compared between sexes by Chi-square. Mean shell lengths (and standard deviations) were calculated separately for growing males and females on each occasion. The mean sizes to which they grew by the next occasion were also calculated, and these data were combined to form the first of two composite growth curves. k was computed for various intervals of this curve.

(Individual growth increments, k, etc. are treated in the next subsection.)

Proportions growing: The sexes did not differ significantly in proportion of survivors growing in each interval (Table 43). Proportion growing changed with time. 95% grew between occasions 3 and 4 (April to May), but fewer than 40% grew between June and August. Only five snails grew at any time thereafter, and none after May 1977.

Table 43

Proportions growing

Table 43. Numbers surviving from one standard occasion to another and measured, with comparisons between sexes of the proportion growing. Interval, standard sample codes as in Table 40. First interval extends from individual release (R) to code 2 or 3 depending on release date, as explained in text. M, males; F, females. N, measured survivors: this figure excludes snails known to have survived but for which measurements were unavailable. G(%), number and percentage of N that grew during the interval. DNG, number that did not grow. Test, Chi-square (1 d.f.) comparing sexes.

Interval	Sex	N	G	(%)	DNG	Test	P	
R - 2/3	M	203	125	(62)	78			
	F	218	153	(70)	65	3.45	>0.05	NS
3 - 4	M	117	111	(95)	6			
	F	127	121	(95)	6	0.01	>0.9	NS
4 - 5	M	96	69	(72)	27			
	F	96	72	(75)	24	0.002	>0.9	NS
5 - 6	M	59	18	(31)	41			
	F	60	22	(37)	38	0.51	>0.1	NS

Mean lengths: Growing female mean size increased steadily (Table 44). Growing male mean size was unchanged on standard sample date 5 even though 69 males were known to have grown from 13.5 mm on occasion 4 to 13.7 mm on occasion 5.

Table 44

Mean lengths

Table 44. Starting and finishing mean sizes of snails known to be growing actively at release (R) or on each standard sampling date. Stop, snails growing to stated coded date. Start, snails growing from it. Intervals are as in Table 43. N, number measured. L, mean shell length (mm) with standard deviation in parentheses. M, males; F, females.

Date	Sex	Stop		Start	
		N	L	N	L
R	M			125	12.47 (0.29)
	F			153	12.50 (0.28)
2/3	M	125	12.78 (0.30)		
	F	153	12.78 (0.29)		
3	M			111	12.87 (0.33)
	F			121	12.89 (0.34)
4	M	111	13.38 (0.41)	69	13.51 (0.41)
	F	121	13.36 (0.43)	72	13.43 (0.45)
5	M	69	13.74 (0.40)	18	13.52 (0.44)
	F	72	13.73 (0.51)	22	13.72 (0.48)
6	M	18	13.76 (0.44)		
	F	22	13.94 (0.51)		

<u>Composite growth curve</u>: The mean lengths in Table 44 may be combined to form a composite growth curve running from 12.5 to nearly 14 mm. This part of the overall growth curve is of particular interest because some adults seem to stop growing rather than continue to 18.0 mm, the theoretical asymptotic final size. If snails known to be actively growing also tended to level out, the validity of that figure might be open to question.

This region of the previous composite growth curve (Figure 27) was derived from simultaneous growth from 12.5 and 13.5 mm (Table 30, Section 8), while here seasonal effects could only be reduced by rejecting any snails that did not grow.

Where final and starting sizes at one date did not correspond, the line segment representing the previous interval was extrapolated until it reached the new size, and the starting date (as days from 0 at 12.5 mm) was corrected. For example, the 37 days between occasions 3 and 4 had to be extended to 44 days for males to reach 13.5 mm.

The spread of release dates presented another problem. Intervals from release to code 2 (or 3 depending on release date as explained previously) ranged from 15 to 45 days. The male mean interval was 36 days, and the weighted mean (according to number released on each date) was 35 ± 6 days; corresponding female figures were 35 and 34 ± 7. 35 days from code 3 was selected, corresponding to an arbitrary uniform release date of 13 March 1976. So, the increase from 12.5 to 12.8 mm was considered to have taken 35 days, the line segment was extended to the new starting size of 12.9 mm, and the male and female curves were built up from there. Males took 7 days to grow from 13.51 mm on date code 4 to the code 5 starting size 13.52 mm; at this point the male curve adopted the final line segment so as to be more strictly comparable to the female curve. The final schedule is given in Table 45.

The male and female curves were gently sigmoidal, and coincident until code 4, after about 90 predicted elapsed days. Females then grew a bit larger than males by code 5 before changing to a slower rate running approximately parallel to the males. The curves are not illustrated because they are of similar shape to the improved curves based on growth increments presented later.

Table 45

Composite growth data from graphs

Table 45. Times to grow from Table 44 sizes "start" to "stop", corrected for variable initial release date and lack of correspondence on any date between sizes "stop" and "start", as explained in text. Date, standard sample code (Table 40): R, release. T, interval from previous code, days. Tadj, corrected interval, days. Tcum, corrected cumulative days from release.

Date	T	Males		Females	
		Tadj	Tcum	Tadj	Tcum
R	0		0		0
2/3	35		35		35
3		48	48	47	47
4	37	44	92	41	88
5	30	7	99	29	117
6	57	-	156	-	174

k was calculated for the intervals release to 3, 3 to 5, 5 to 6, and release to 6. k is supposed to be independent of starting size, values of which are given in Table 44. Male k for these intervals was respectively 0.0012, 0.0031, 0.0006, and overall 0.0017 days^{-1}. Female k was 0.0016, 0.0025, 0.0009, and overall 0.0017 days^{-1}.

Growth increments and growth rate dl/dt are reported in the next subsection.

Synopsis: Individual records were used to select only those snails actively growing on a particular date. The proportion doing so varied between dates but not between sexes. Satisfactory data were available from release until August. Females grew steadily but the mean size of males growing from 23 June was much lower than that of males reaching it. Male and female composite growth curves, compiled from mean sizes arriving at and leaving each standard date, were gently sigmoidal and similar. Overall k ignoring the inflections was the same in each sex, 0.0017 days^{-1}.

Paint: Individual growth

In a previous subsection, resin-tagged individuals in the 13 mm size class released in October 1975 did not grow until approximately March 1976, and steady growth was not then maintained month after month. The paint-tagged 12 mm adults released in February and March overlapped with them.

Individual growth curves were obtained for many paint-tagged snails. From these were selected long-term curves (snails repeatedly recaptured until at least November) regardless of growth pattern, tall curves (snails gaining at least 2.0 mm regardless of time interval), and segments of all curves where single-interval growth increment could be computed individually.

The increment data formed the basis of the second set of composite growth curves, in a format easier to understand than those in the previous subsection. The long-term and tall curves allowed individual variation in growth parameters k and 1^{∞} to be evaluated.

Increments: The same snails were used as in Tables 43 and 44, i.e., those in which growth was clearly under way. Except from codes 3 to 4 (April to May, Table 40), increments were not quite normally distributed but were gently positively skewed. Skewness was strongest in the first interval (release to code 2 or 3 as appropriate) because of non-uniform release dates. Standard deviations reported are therefore inexact.

Growth rate dl/dt is supposed to decrease with increasing starting size L_1 (compare Figure 26, far end). Mean growth rate did so in each sex from occasions 3 to 6 (Table 46); the low values for the first interval are probably an artefact of using the arbitrary mean interval 35 days.

Table 46

Composite growth data from increments

Table 46. Composite growth data constructed from mean increments and real intervals between standard dates (Table 45, "T"). Data are not extrapolated as in Table 45 ("Tadj"). Results are expressed in cumulative days from arbitrary day 0 and do not correspond to calendar days in Table 40. Go, mean length (mm) at start of interval. M, males; F, females. Inc, mean increment (mm), with standard deviation in parentheses. T, length of interval. Stop, mean size at end of interval (mm), Inc x T. Inc/T, mean growth rate (mm/day x 10^{-3}), with standard deviation in parentheses. Tcum, cumulative days from 0.

Sex	Go	Inc	T	Stop	Inc/T	Tcum
M	12.47	0.30 (0.15)	35	12.77	8.57 (4.26)	35
	12.77	0.52 (0.24)	37	13.29	14.05 (6.49)	72
	13.29	0.24 (0.13)	30	13.53	8.00 (4.23)	102
	13.53	0.23 (0.12)	57	13.76	4.04 (2.09)	159
F	12.50	0.29 (0.15)	35	12.79	8.29 (4.27)	35
	12.79	0.48 (0.22)	37	13.27	12.97 (5.95)	72
	13.27	0.30 (0.18)	30	13.57	10.00 (5.83)	102
	13.57	0.22 (0.13)	57	13.79	3.86 (2.23)	159

Individual increments in the first interval ranged from 0.1 to 0.7 mm. Taking an arbitrary mean interval of 35 days, this corresponded to growth rates 2.86 x 10^{-3} to 20 x 10^{-3} mm per day. The minimum actual interval was 15 days; six females undoubtedly grew, with increments ranging from 0.1 to 0.3 mm, corresponding to growth rates 6.67 x 10^{-3} to 20 x 10^{-3} mm per day. Insufficient snails from the maximum actual interval of 45 days grew, but over the 44 day interval increments ranged from 0.1 to 0.6 mm, equivalent to growth rates 2.27×10^{-3} to 13.64×10^{-3} mm per day. The mean interval gave satisfactory approximations to the true range of growth rates.

In the next interval, increments ranged from 0.1 to 1.0 mm, and growth rates from 2.70×10^{-3} to 2.70×10^{-2} mm per day. Starting size ranged from 12.1 to 13.7 mm and there was no clear relationship between increment and starting size.

In the 30 day interval, increments ranged from 0.1 to 0.8 mm, equivalent to 3.33×10^{-3} to 2.67×10^{-2} mm per day. Starting size ranged from 12.3 to 14.5 mm and again increment did not necessarily increase or decrease with starting size.

In the final 57 day interval, increments ranged from 0.1 to only 0.5 mm, and growth rates from 1.75×10^{-3} to 8.77×10^{-3} mm per day. Increment did not depend on starting size, which ranged from 12.3 to 14.6 mm, and as in the other intervals no difference was apparent between males and females.

Thus over the time period for which suitable data were available, individual growth rate ranged from approximately 2×10^{-3} to 3×10^{-2} mm per day: some snails could be growing an order of magnitude faster than others of similar size. This is a conservative estimate because snails taking more than one interval to achieve measurable increase in shell length L were excluded.

<u>Composite growth curve</u>: The mean increment for each interval, when multiplied by its length, yields a mean increase in shell length. Synchronous male and female composite growth curves, avoiding the complications in the previous set caused by lack of agreement between stopping and starting mean

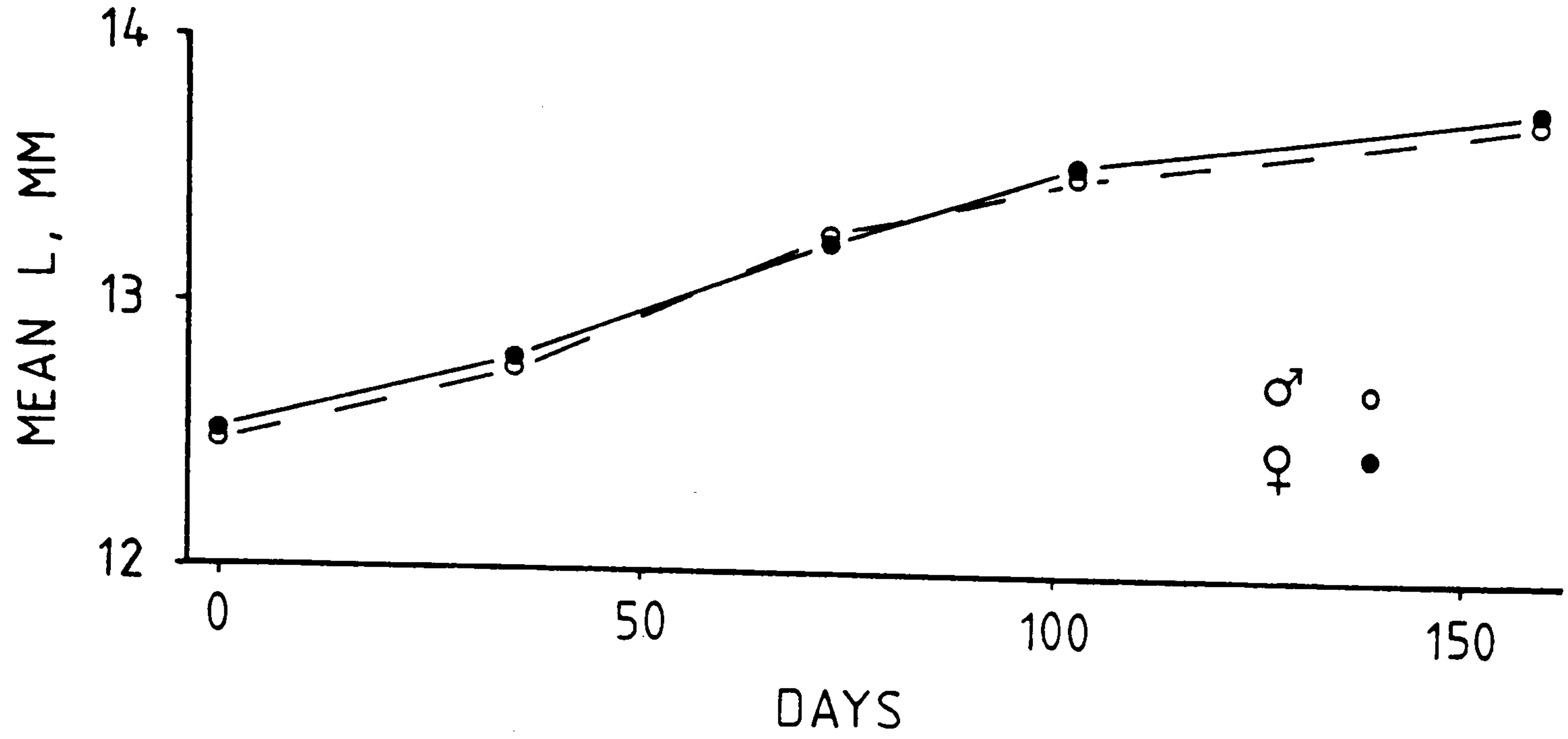


Figure 48. 12.5 mm male and female composite growth curves, constructed from mean increments as explained in text. (Data, Table 46.)

sizes on the same date, may be constructed from initial mean size approximately 12.5 mm. The first interval mean increase is applied, yielding a predicted mean size that becomes the starting size for the next interval. The next mean increase is added, and so on. Results are shown in Table 46 "Stop" and as Figure 48.

These curves are very much the same shape as the previous ones, but are much clearer because intervals coincide. The similarity between males and females is evident. If entries were rounded to 0.1 mm, the curves would be superimposed except that the female point would be the higher at day 72: this irregularity is unimportant.

Day zero is in this case the arbitrarily-chosen (weighted mean as explained previously) 13 March 1976. Other points are located at 17 April, 24 May, 23 June and 19 August. Conventionally k is regarded as unchanging with increasing size, while growth rate dl/dt decreases. The shallower slope of the final segment in both males and females might result from environmental stress, the warm sunny summer of 1976 perhaps being less suitable on average for grazing than the damp spring. The proportion growing dropped from 95% in April to fewer than 40% in June. Accordingly, k was calculated for comparable intervals to the previous composite curves: days 0 - 35, 35 - 102, 102 - 159, and 0 - 159. Male k for these intervals was respectively 0.0016, 0.0023, 0.0009, and overall 0.0017 days^{-1}. Female k was 0.0015, 0.0024, 0.0009, and overall 0.0017 days^{-1}. These values should be compared with those for 6 and 9 mm cohorts growing concurrently (Tables 18 and 19, Section 8).

Long-term curves: Twelve males and thirteen females were recaptured regularly until at least November 1976 (code 8, Table 40). Eleven and seven respectively survived at least a further hundred days to 14 February 1977. Nine and four persisted another hundred days to 14 May, and one male was regularly recaptured through to the end of field work 150 days later, 596 days from release.

Selected growth curves are presented in Figure 49, showing the full range of growth patterns exhibited by these long-recaptured adults.

Perhaps the most striking feature is that only one (curve B) shows any sign of steady growth towards a final size in the order of 18 mm. The rest level out at sizes between 12.9 and 14.7 mm, although a later resumption of growth is not precluded (curve I; resin results).

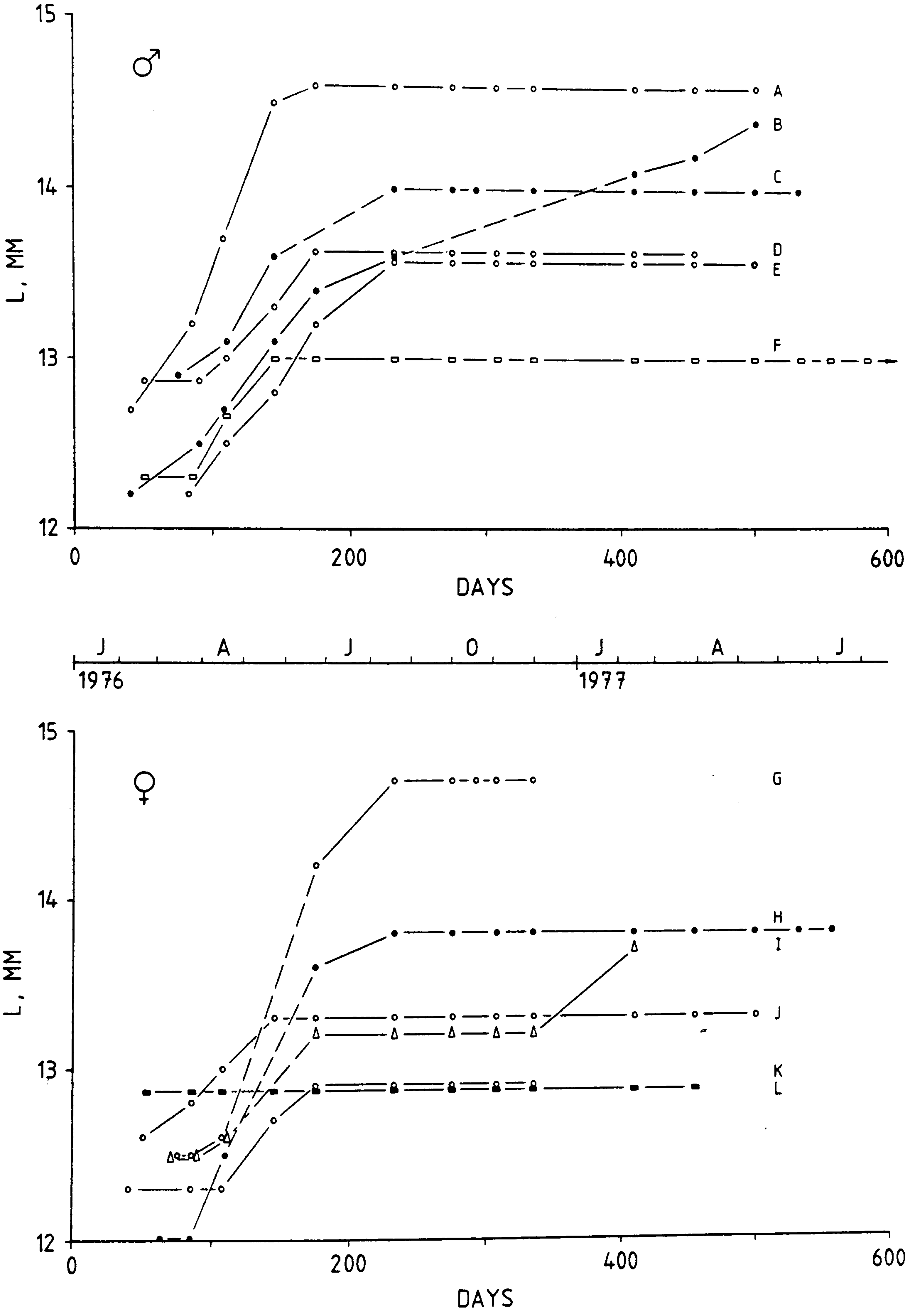
The von Bertalanffy equation calls for asymptotic growth towards final size, not unlike curve E. Another noteworthy feature of several of these curves is the suddenness with which growth stops (curves A, D) or starts (curves F, H).

Figure 49

12 mm long-term growth curves

Figure 49. Selected long-term growth plots of individually paint-numbered males (upper) and females (lower). Plots begin at release and show all records (curve F continued to end of field work on day 647). Long dashes signify missing record(s) (e.g., curve C day 175).

Snails could grow sigmoidally (curves B, G), asymptotically (E, H), stepwise (F, K), intermittently (I), or not at all (L).



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Individual k was computed for periods of sustained growth (Table 47, Appendix Table 39), with corresponding growth rates. Females grew slightly faster and had slightly higher mean k, but ranges were similar. Individual k varied by a factor of three.

Table 47

Long-term mean growth

Table 47. Mean growth data for individually paint-numbered snails recaptured regularly for at least eight months. Data, Appendix Table 39. M, males; F, females. N, number. Go, mean initial size (mm). Inc, mean increment (mm). T, mean duration of sustained growth (days). Inc/T, mean growth rate dl/dt (mm per day, x 10^{-3}) with standard deviation in parentheses. k, mean growth parameter (days^{-1}), with standard deviation in parentheses.

Sex	N	Go	Inc	T	Inc/T	k
M	8	12.54	1.24	159	8.97 (2.85)	0.0019 (0.0007)
F	10	12.47	1.15	106	11.11 (4.59)	0.0021 (0.0008)

Tall curves: The composite growth curves and long-term curves made it seem unlikely that very many L. obtusata would grow to 18 mm at Gorad. However, individual growth patterns could evidently vary as could rates. The composite curves were based on all suitable entries, and so included snails growing at a wide range of rates. The individual records were therefore searched for snails having gained at least 2.0 mm - i.e. having grown into the 14 mm size class - regardless of how long they took to do so.

It was believed that, since few snails grew after mid-summer, these snails would represent the higher range of growth rates. Eight males and twelve females grew more than 2 mm. Selected curves are illustrated in Figure 50.

As expected, growth patterns differed between individuals, but at least a few did not appear to be levelling out. There were some interesting similarities in corresponding segments of different curves (e.g., B, C, D).

It had not been appropriate to compute mean long-term curves, but the tall curves were sufficiently synchronous. The only problem, as usual, was the variety of release dates. Arbitrary release day 50 (19 February 1976, Table 40) was defined for the earliest ones, and sizes on day 50 were interpolated. Some were released after day 50, increasing the number contributing to mean size on and after standard day 84 (24 March). Results are shown in Table 48 and Figure 50. Had the starting sizes agreed more closely, the curves would superimpose nicely: on average, rapidly-growing males and females followed the same pattern with time.

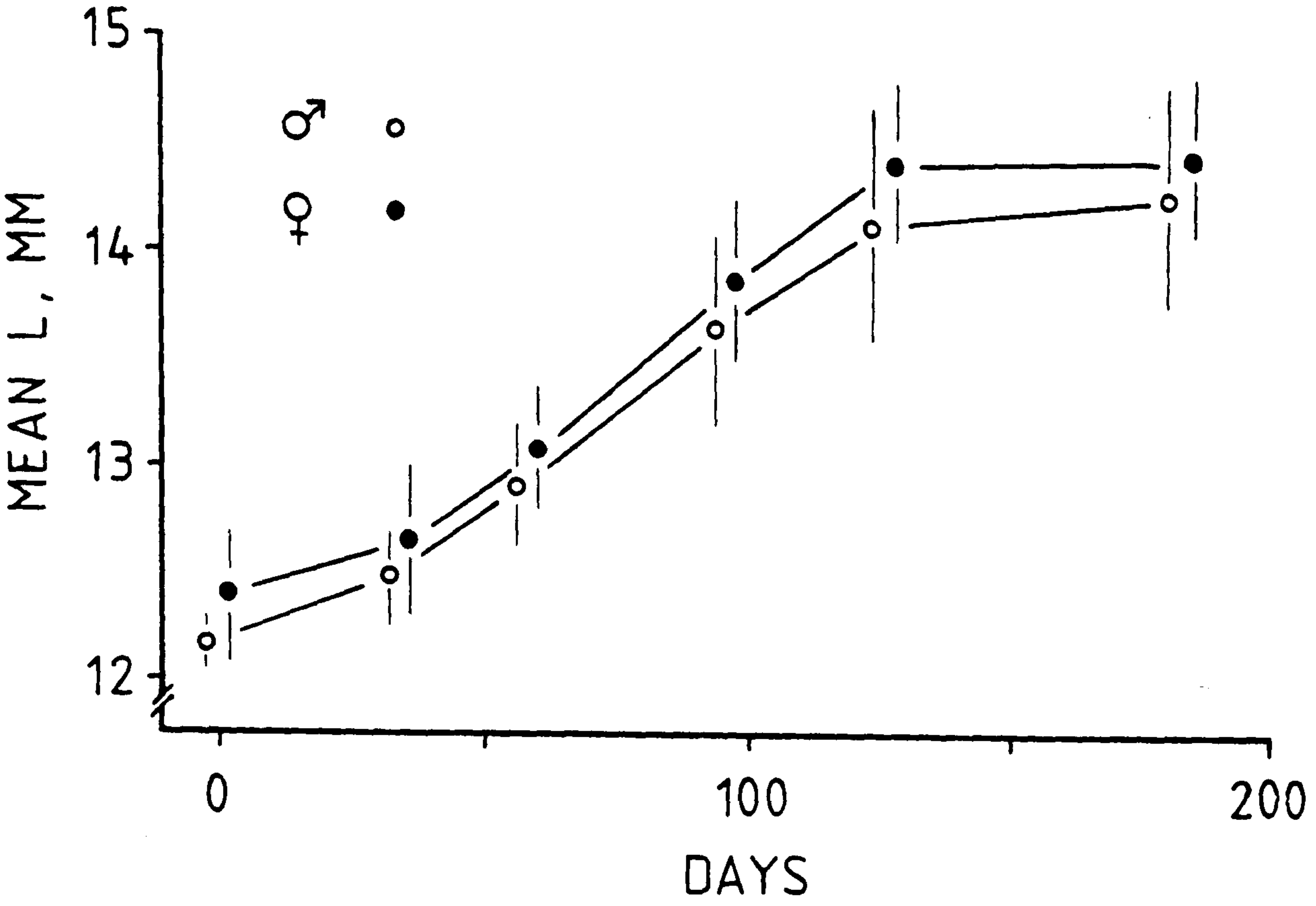
Figure 50

Rapid growth

Figure 50.

Upper: Mean size of male (circles) and female (dots) individually paint-numbered 12 mm adults growing 2 mm or more. Data are in Table 48. Points are laterally displaced for clarity and shown plus and minus one standard deviation.

Lower: Details showing variety of individual curves including approximately linear (curve G), sigmoid (C), intermittent (K), and asymptotic (D). Origins are displaced for clarity: horizontal axis interval is 50 days. Each curve is shown in full; dashes signify missing records.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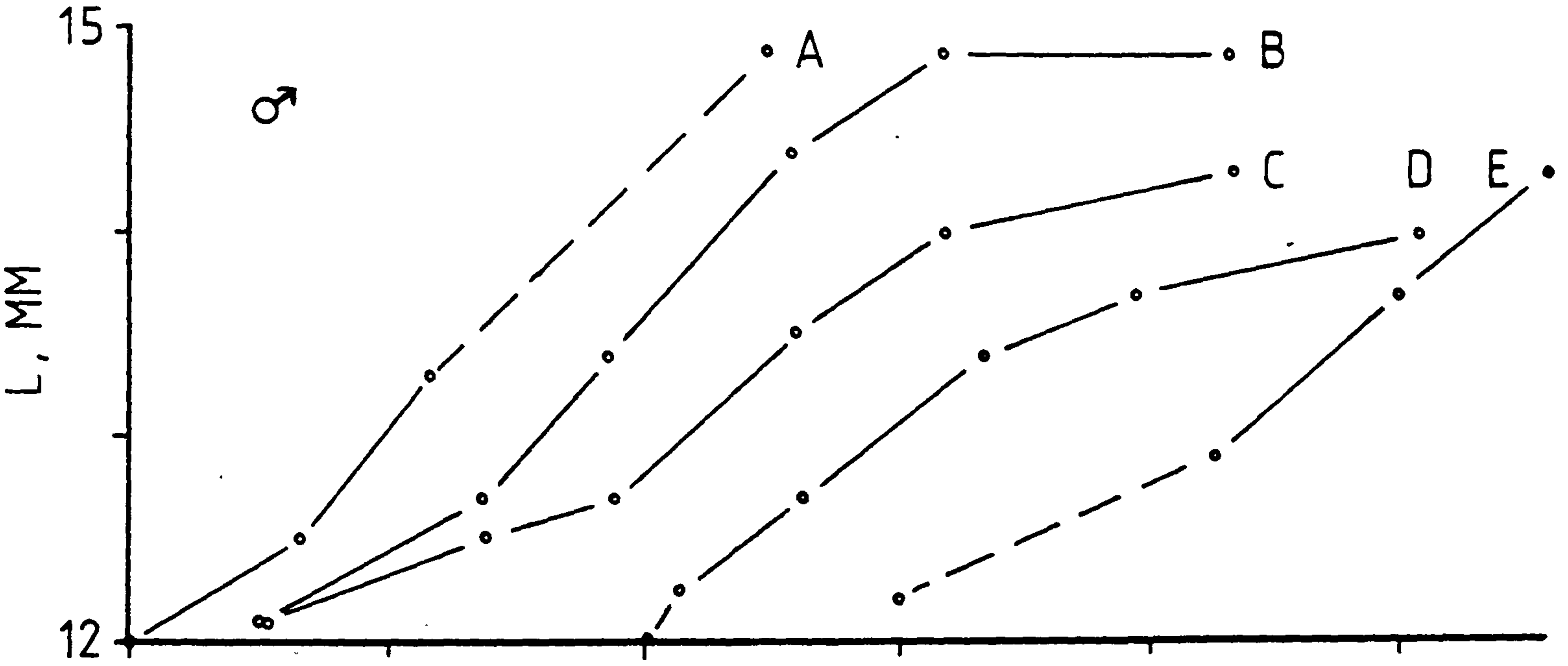
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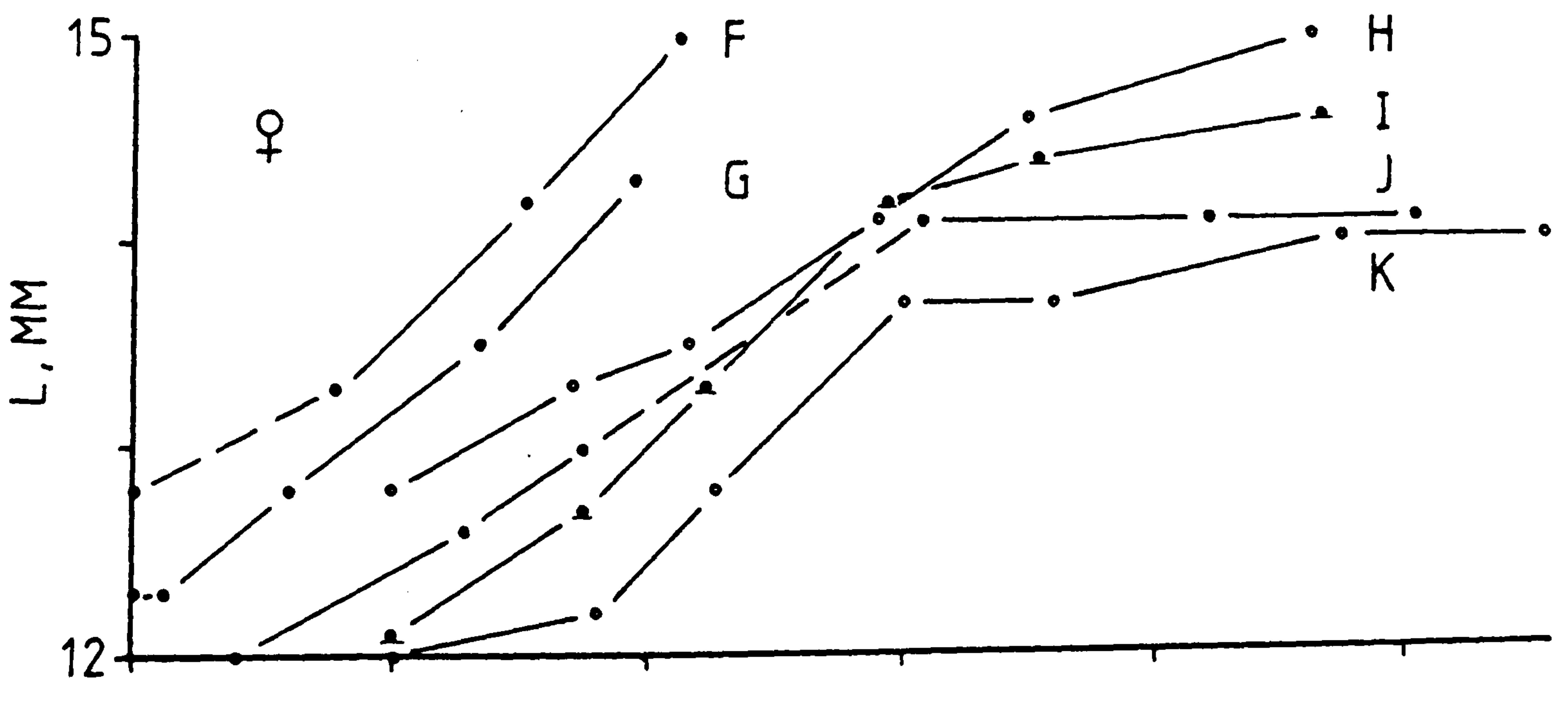
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Table 48

Fast growth curves

Table 48. Mean sizes of rapidly-growing individually paint-numbered snails. Origin of curves is real day 50. Later releases brought number to maximum by real day 84 (calendar, Table 40): see text. (In Figure 50, time axis is days from arbitrary day 50 and not real days - i.e., Elap below.) Day, real day. Elap, days from real day 50. N, number. L, mean shell length (mm), with standard deviation in parentheses. M, males; F, females.

Sex	Day	Elap	N	L	Range
M	50	0	7	12.17 (0.12)	12.0 - 12.3
	84	34	8	12.47 (0.22)	12.1 - 12.7
	108	58	8	12.91 (0.29)	12.7 - 13.4
	145	95	8	13.64 (0.44)	13.1 - 14.4
	175	125	8	14.13 (0.54)	13.4 - 14.9
	232	182	5	14.28 (0.51)	13.6 - 14.9
F	50	0	7	12.39 (0.31)	12.0 - 12.8
	84	34	12	12.64 (0.35)	12.2 - 13.3
	108	58	12	13.08 (0.29)	12.6 - 13.5
	145	95	12	13.87 (0.39)	13.5 - 14.5
	175	125	12	14.43 (0.37)	13.7 - 15.0
	232	182	6	14.48 (0.38)	14.0 - 15.0

k was computed for the central period of steady growth, days 84 to 175 (days 34 to 125 in Figure 50, which shows growth from arbitrary release: origin is real day 50), assuming as usual that $l^{\infty} = 18.0$ mm. Male k was approximately 0.0039, and female 0.0045 days^{-1}, in contrast to the value 0.0017 derived from the composite growth curves.

Individual k computed for periods of steady growth and assuming 18 mm final size, ranged in males from 0.0021 to 0.0063, and in females from 0.0036 to 0.0071 (but normally 0.0056) $days^{-1}$ (Appendix Table 40). Male and female means were respectively 0.0041 and 0.0047 $days^{-1}$ (Table 49).

Variability in k and l^{∞}: To recapitulate results presented so far, three resin-tagged 13 mm adults released in October 1975 showed sustained growth from approximately February to May 1976, with closely similar k of about 0.0026 $days^{-1}$. Composite growth curves constructed from single-interval changes in mean length of 12 mm paint-tagged snails known to be growing - but not selected for life span or growth rate - yielded identical male and female mean k of 0.0017 $days^{-1}$ for a period of five or six months respectively ending in mid-August. k during more active growth between April and June was 0.0031 (males) and 0.0025 (females) $days^{-1}$, agreeing with the concurrent resin results. Composite growth curves constructed from mean growth increments again yielded male and female mean k 0.0017 $days^{-1}$ for the whole curve, or approximately 0.0024 $days^{-1}$ for the central portion.

Table 49

Fast mean growth

Table 49. Mean growth data for individually paint-numbered snails that grew at least 2 mm. Data, Appendix Table 40. Conventions as in Table 47.

Sex	N	Go	Inc	T	Inc/T	k
M	8	12.48	1.68	97	1.75 (0.60)	0.0041 (0.0014)
F	12	12.63	1.80	87	2.11 (0.45)	0.0047 (0.0010)

Eight long-surviving males and ten females had mean k 0.0019 and 0.0021 days^{-1} respectively, much of the steady growth again taking place between March and June; male values ranged from 0.0010 to 0.0033, and female from 0.0011 to 0.0035 days^{-1}. Eight males and twelve females selected for large - not necessarily rapid - size increases generally grew steadily and rapidly between March and June: male and female means were 0.0041 and 0.0047 days^{-1} respectively, with ranges 0.0021 to 0.0063 (males) and 0.0036 to 0.0071 (or more typically 0.0056) days^{-1} (females).

During the spring period favourable for growth, individual k varied approximately sevenfold. This was in keeping with the observation that individual growth rates varied by an order of magnitude. There did not appear to be any important differences between males and females.

All these calculations assumed a uniform asymptotic size of 18.0 mm, the vanishingly scarce maximum size observed at Gorad. Although growth may resume after long intervals of inactivity, many individuals evidently stop growing well before achieving that size. Long-term snails were as small as 12.8 mm, and most were clustered between 13 and 14 mm. Tall curves did not normally extend late enough for confident predictions of final size but several looked likely to clear 15 mm at least.

The general similarity among tall curves if superimposed - most rose very steeply between days 80 and 160 approximately - together with the uncertain terminal shape suggested an experiment. Mean k was substituted into the growth equation which was then solved for l^{∞}. Rearrangement of Section 8 equation (3) yields

$$l^{\infty} - L_1 = (l^{\infty} - L_2) \cdot e^{k(T_2 - T_1)}$$

from which $$l^{\infty} = \frac{L_2 . e^{k(T_2 - T_1)} - L_1}{e^{k(T_2 - T_1)} - 1}$$

Male l^{∞} derived from this equation, using mean k 0.0041 days^{-1}, ranged from 15.6 to 20.2 mm, averaging 17.8 mm. Female values, using mean k 0.0047 days^{-1}, ranged from 16.5 to 20.5 mm, averaging 18.0 mm. The averages are a consequence of assuming l^{∞} to be 18 mm when computing k.

When, however, males were re-calculated using mean long-term k 0.0019 days^{-1}, results were rather less plausible: l^{∞} ranged from 18.6 to 27.6 mm, averaging 22.9 mm. That k had also been calculated on the assumption that l^{∞} was 18 mm.

The large final sizes predicted from applying long-term k to increments seen in snails that grew more than 2 mm - they had not been selected for growth rate - assume in effect that these increments are under the individual's control. Crudely put, these snails might be non-breeders, rapid feeders, more efficient assimilators, etc. If however the large increments resulted, say, from particularly favourable conditions where these individuals resided, then they might not be expected to maintain such rapid growth in the long term. The suddenness with which some individuals start or stop growing was remarked in a previous subsection. k was normally computed for those portions of the growth curves showing steady growth: level end portions were disregarded. To this extent k is something of a fiction: the von Bertalanffy equations assume asymptotic growth, and k is constant throughout life (Section 8).

Nevertheless, it seems clear that growth rate, final size, and k do vary among individuals growing concurrently, from similar sizes (though not necessarily ages - Section 8), in a restricted area of pure A. nodosum. Individual results are related to cohort results in the discussion.

Synopsis: Individual records identified actively-growing snails on each date (as in "Paint: Mean growth" subsection), and individual growth curves were obtained for snails recaptured over long periods or growing substantially. Male and female composite growth curves derived from the increment data were gently sigmoidal and similar; overall k ignoring the inflections was the same in each sex, 0.0017 days^{-1}. Long-term growth curves varied in shape. Individual k computed over periods of sustained growth varied by a factor of three and was slightly higher on average in females, as was growth rate dl/dt, but ranges overlapped substantially. Growth curves of individuals gaining at least 2 mm varied in shape but generally included rapid growth in late spring and were sufficiently similar to permit mean curves, which did not differ between males and females. Individual k again varied approximately two- to threefold, and again females had slightly higher mean k and dl/dt. These mean values were approximately twice the long-term equivalents. Overall, when most snails grew in spring, individual k varied approximately sevenfold and individual growth rates by an order of magnitude. Substitution of their own mean k into individual growth equations for those gaining 2 mm yielded individual l^{∞} varying from 15.6 to 20.5 mm; absurd values were obtained using the lower long-term mean k.

Paint: Survivorship

The wide range of release dates complicated analysis. Accordingly, standard day 84 (24 March 1976) was taken as day 0 and all subsequent days were adjusted. It was therefore unnecessary to reject the new first interval - days 84 to 108 - from regressions as in Section 9.

Survivorship was computed as usual for each sex. Males began with 224 individuals set as 100%, and females with 222. Numbers remained workable for at least 400 days. Numbers initially declined steadily, but both males and females dropped abruptly after 150 days (Figure 51). This drop was attributed to the September gales that reduced many cohorts (Section 9). Female numbers then declined steadily, but males levelled-out through the winter and resumed declining after day 371 (30 March 1977). Four females remained on day 416 when their curve was truncated, and five males on day 474.

It was clear that regressions using all dates would misrepresent the data scatter even if statistically significant. Lines were fitted separately through different portions of the distribution (Appendix Table 41). For the males, a regression using the first five and last four points - in effect, discarding the September drop and winter plateau - gave by far the best fit. The slope was identical to that using all points, and the Y-intercept was closer to the theoretical 4.605 (Table 50). Except for the Y-intercept, which reflected the sudden September drop, female regressions for the first five or last six points agreed closely, so the first was taken as representative. No effort was made to raise the second segment to some extrapolation from the first.

Male and female survivorship did not differ. Regressions were closely similar and very highly significant.

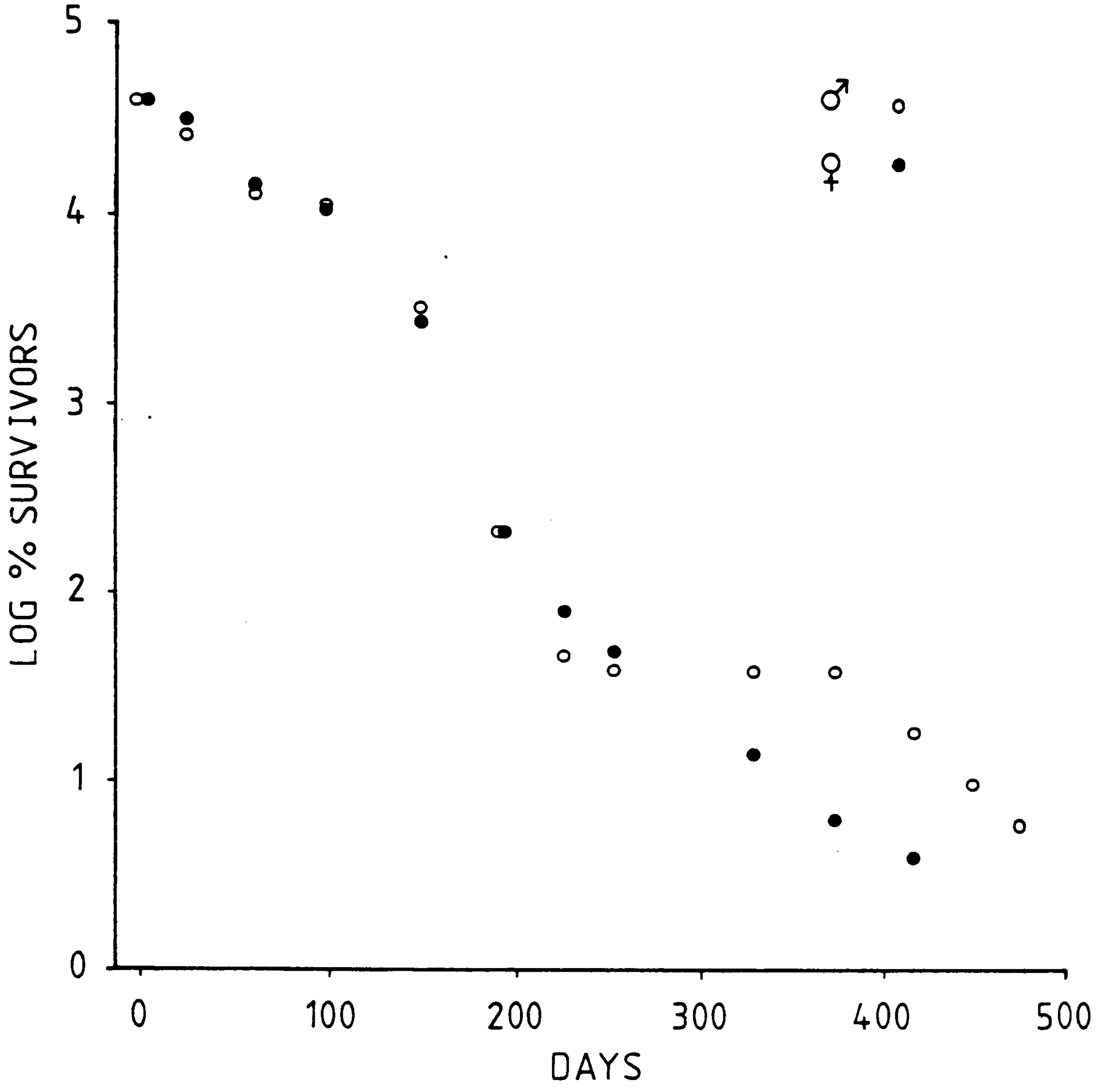

Figure 51. Survivorship of male (circles) and female (dots) individually paint-numbered 12 mm adults released in February and March 1976. Origin is 24 March 1976 as explained in text. Curves end when number drops below 4. See text for regressions.

Table 50

Paint survivorship

Table 50. Survivorship regressions for 12 mm individually paint-numbered adults released in February and March 1976. Data extracted from Appendix Table 41. Late points based on very few snails rejected as usual. First interval not rejected as explained in text; see also Figure 51. M, males; F, females. N, number on 24 March: see text. Span, time interval over which regression was calculated: regressions considered valid for at least 400 days as explained in text. A, Y-intercept. b, negative slope.

Sex	N	Span, days	A	b, x 10^{-3}
M	224	148 + 103	4.66	8.16
F	222	148	4.66	7.90

Location: Most snails were recaptured at site A. Seven were found at site D, and 30 at site L. It was not possible to draw conclusions from the remote recaptures.

Fate: Of 596 snails released, 329 (55.2%) disappeared after one or more sightings and were not seen again dead or alive. 231 (38.8%) were found dead or as empty shells, the latter being usual. 31 (5.2%) were moribund when found or when ready to release, and were killed. Five (0.8%) were accidentally killed. Thus the fates of 267, or 44.8%, of those released were determined. Survivorship was expressed in terms of numbers known alive, rather than numbers known dead, because date of death could not be established as accurately. It was therefore not considered appropriate to estimate emigration by subtracting number known to be dead from number missing.

Paint: Summary of results

1. Three-digit serial numbers encoded as three coloured enamel paint dots were applied to 12 mm live-sexed adult <u>L. obtusata</u>.

2. 322 males and 274 females were released at site A between 9 February and 22 March 1976. Individual records were maintained, including sex, colour, shell measurements L H W and T, presence and extent of growing lip, etc. Distinguishing markings such as shell scars and barnacles were entered onto profile drawings to assist with identification in case of tag loss. Tag damage proved to be slight and easily recognised.

3. At release, males had significantly more outer-whorl scarring than females. Number of scars per shell did not differ between sexes or colour morphs.

4. At release, males and females did not differ significantly in mean shell length or mean columellar length; a difference in mean lip thickness was less than the measurement increment. Females were very highly significantly more globular than males. The proportion considered growing did not differ between sexes.

5. Shell colour morph ratios did not differ between the sexes; 84% were morph olivacea, 13% reticulata, and 3% citrina.

6. Sex ratio at release was 1.175.

7. The proportion vanishing unaccountably in the first interval was independent of sex or colour morph.

8. Damaged opercula were not always repaired, even after several months. Missing opercula were not replaced after as much as three or four months.

9. Actively-growing snails could reliably be identified by their fragile, chisel-edged aperture lips. Shell lip thickness was not as reliable a

guide. Thickened shells lacking growing lips could resume growth after substantial intervals, without decreasing much in thickness.

10. Growth analysis was confined to snails known from individual records to have been actively growing when measured.

11. Satisfactory numbers of such snails remained until August. Proportions growing declined from 95% in May to fewer than 40% in July. Male and female proportions growing did not differ in any interval. Mean sizes were used to construct male and female composite growth curves that did not differ, with identical mean k of 0.0017 days^{-1}.

12. Individual growth increments varied between 0.1 and 1.0 mm, and individual growth rates between 1.75 x 10^{-3} and 2.7 x 10^{-2} mm per day. There was no clear relationship between increment and sex or starting size, which ranged from 12.0 to 14.6 mm.

13. Mean increments were used to construct synchronous male and female composite growth curves that proved identical, with mean k 0.0017 days^{-1}. The curves were gently sigmoidal and may have incorporated seasonal effects excluded from those in Section 8. Segmental k values were approximately 0.0016 (mid-March to mid-April), 0.0024 (mid-April to late June), and 0.0009 days^{-1} (late June to mid-August, after which few snails grew).

14. Individual growth patterns of males and females recaptured for at least eight months varied from no growth through stepwise, intermittent, sigmoidal and asymptotic. Most levelled out below 15 mm; only one grew steadily. Growth could stop or start suddenly. Individual k computed only for periods of steady growth varied by a factor of three. Male and female ranges were similar, but females had slightly higher mean k and mean growth rate. Mean k was approximately 0.0020 days^{-1}, and mean growth rate 0.01 mm per day.

15. Individual growth patterns of males and females growing at least 2 mm varied from approximately linear through intermittent, sigmoidal and asymptotic. Most included rapid growth in April, May and June, and were synchronous enough to permit mean curves. Male and female curves were closely similar: both increased gently in March, rose more steeply and at a constant rate until late June, then effectively levelled out. Mean k for the steep section, approximately 0.0039 (males) and 0.0045 days^{-1} (females), was nearly twice that in the composite curves (0.0024 days^{-1}).

16. Individual k for these snails ranged in males from 0.0021 to 0.0063, and in females from 0.0036 to 0.0071 (but normally 0.0056) days^{-1}. Mean k was approximately 0.0041 and 0.0047 days^{-1} respectively, and mean growth increment 0.02 mm per day. These values were double the long-term snails'.

17. Individual k could vary at least sevenfold, and growth rate by an order of magnitude, for similar-sized snails growing concurrently in a small patch of pure Ascophyllum nodosum. These are conservative range estimates because snails growing very slowly were excluded from analysis. There were no striking differences between males and females.

18. Asymptotic maximum size was assumed throughout to be 18.0 mm, the largest size ever seen at Gorad. Many snails level out well short of that size, some below 13 mm.

19. Survivorship was expressed (as usual) as the natural logarithm of percent surviving against elapsed time. Individual records allowed corrections to be made for snails overlooked or temporarily absent. Analysis began at 24 March to avoid complications from multiple release dates. Curves were interrupted by the September 1976 gales; regressions minimised this distortion. Male and female survivorship did not differ over more than a year.

20. The fates of 267 snails (45%) were established; the rest disappeared. Emigration rates could not be estimated confidently.

Individual tagging results: Grand summary

Detailed resin summary, page 211.

Detailed paint summary, page 247.

Tag loss: Negligible with either technique.

Shell damage: Significantly more paint-tagged males than females had body-whorl scars caused by crab attack or shifting rocks.

Operculum damage or loss: Damage was characteristically a V-shaped notch cut or torn from the abapical margin, consistent with attack by shore crabs *Carcinus maenas*. Damaged or missing opercula could go unrepaired for months.

Sexual dimorphism: 12 mm females were very highly significantly more globular than males but 13, 14 and 16^+ mm snails did not differ.

Morph ratios: Identical in males and females: mostly olivacea.

Lip status: Fragile, chisel-edged aperture margins accurately identify actively-growing snails. Snails with thicker, blunter shell lips have not necessarily finished growing: shell size may remain constant for seven months or more before growth resumes.

Individual growth patterns: Asymptotic growth is not the norm, at least from 12 mm. Adults may remain small, or grow steadily, in one or more brief steps separated by months of inactivity, sigmoidally, or even asymptotically. Abrupt changes in growth rate were common. Large size tended to be achieved in a rapid burst rather than by steady growth over many months: size did not necessarily indicate age.

Individual growth increments and rates: Snails could gain 1 mm in shell length L between samples. The body whorl had to be advanced several mm to increase L so much. Higher increments were observed in spring, and few snails grew in late summer. Neither increment nor growth rate varied predictably with shell size, and the sexes did not differ. Individual growth rates ranged approximately between 0.002 and 0.03 mm/day. The minimum is an underestimate because very slow-growing snails were eliminated from analysis.

Individual k: All computations of k assumed l^{∞} was 18.0 mm, the maximum size encountered at Gorad. k was always computed over periods of sustained growth. Individual k varied between 0.0010 and 0.0071 days^{-1}. Male and female ranges did not differ appreciably.

Mean growth increments and rates: Individual records identified those individuals actively growing when measured: all means were based on them. The proportion growing never differed between males and females, but declined from 95% in spring to almost nil in late summer. Mean growth rate declined with increasing mean starting size. Males and females did not differ. Male and female composite growth curves constructed from mean increments did not differ. The gently sigmoidal shape may well have included seasonal effects. Segmental mean growth rates ranged approximately from 0.014 mm per day in late spring to 0.004 mm per day in summer. Snails recaptured for long periods increased on average by 0.01 mm per day, while those gaining at least 2 mm grew twice as fast.

Mean k: In the composite growth curves, segmental k ranged from 0.0016 (early spring) through 0.0024 (late spring) to 0.0009 (summer) days^{-1}, and mean k for the whole curve was 0.0017 days^{-1}. Mean k for long-recaptured snails was 0.0020 days^{-1}. Males gaining at least 2 mm had mean k 0.0041, and females 0.0047 days^{-1}. The few growing resin-tagged snails had mean k 0.0026 days^{-1} in spring, agreeing with the corresponding segmental k.

Survivorship: Males and females did not differ in decay rates of $\log_e$ percent surviving vs. elapsed time curves. All regression equations accounted for at least 93% of the variance and were significant at the 1% or 0.1% level. The fates of 45% of those released were known. Unaccountable first-interval disappearances of paint-tagged snails were independent of sex or colour morph. It was not possible to establish accurately what proportion of the decay rates were caused by emigration.

Discussion

Paint tagging is a faster and more versatile technique than affixing plastic tags with epoxy resin. Resin tags are no more cumbersome than barnacles, but any extra weight or impediment is undesirable. Tag loss is negligible in either case, but paint traces facilitate recognition. L. obtusata has too thin a shell, at Gorad at least, for paint dots to be sunk into pits made with a dental drill (e.g., Hughes 1980).

The great virtue of individual tagging lies in the far greater accuracy of growth and survivorship estimates. Results can be corrected retrospectively for individuals overlooked or temporarily absent, and in particular variability in individual growth rates and patterns is revealed.

Its greatest limitation lies in the record-keeping. Even when analysis will be performed on a computer, vastly simplifying record-searching especially if a programme such as SPSS is available, initial tagging is slowed and release dates may have to be extended. In the present study, nearly 4,000 cohort-tagged snails were released; that many individually-tagged winkles would have been impracticable.

Although the habitat allows winkles to be effectively lost for ever should they stray only a few metres from the study area, they are sedentary enough for reasonably long-term results to be obtained from repeated clearance of quite a small weed area.

Numbers of tagged snails at site A were always substantially below the naturally-occurring densities: 2,045 untagged snails (net) were removed from site A in February 1976 after clearance of 1,233 in January (Figure 7). Accordingly crowding is not considered to have contributed to losses of tagged snails. Regrettably no data are available to distinguish active from passive movements. N.W. Runham suggested that, to avoid inaccuracies in weighting empty shells, living snails could be encouraged to retract, the opercula sealed with cyanoacrylate glue and the shells sprayed with fluorescent paint. Searches could be made in daylight and then at night using portable UV lamps. This ingenious proposal was not followed-up but might well repay the effort. It would be far cheaper than the radioisotope scheme (Section 9) but has the disadvantage of killing the snails.

Gibson (1970) concluded from desiccation and crab Carcinus maenas predation experiments with Nucella lapillus that the operculum is primarily defensive. Many notched opercula were seen at Gorad, consistent with C. maenas attack by chipping away the body whorl. Many so-damaged shells were found, but usually impact damage could not be discounted. The few tagged snails with damaged or missing opercula seemed little affected and did not repair them urgently as might be expected if the operculum was essential in preventing water loss. On the other hand, shell lip notches were always repaired promptly, whether or not the snail was growing.

Although 12 mm paint-tagged females were significantly more globular than males, no such difference was observed in larger snails or in other samples. L. obtusata cannot be sexed by shell characters (review, Section 4). Male-female differences in mean shell lip thickness and shell injury frequency were found in shape test samples as well (Section 4). Experiments are required before relating male fragility to advanced reproductive development (Section 7). Whatever the cause, a meaningful difference in shell strength could be important where crushing predators abounded (review, Section 4).

The rest of this discussion concerns sex ratio, growth, survivorship and lifespan. Material is drawn from Sections 6 through 10 and supporting literature is not repeated.

Sex ratio: The 12 mm sex ratio 1.175 corresponded exactly to the overall site A 12 mm value (Table 16), so proportions tagged were unbiased. The male excess might be caused in several ways, of which differential growth was thought most likely *a priori* (Section 7 discussion). Certainly males normally grew larger than 12 mm. 12 mm females did not decline faster (Table 50), and first-interval disappearance was independent of sex.

However, male and female composite growth curves were similar (Figure 48), as were mean curves for snails growing substantially (Figure 50) and mean growth rates of long-term survivors (Table 47).

All growth data were solely for actively-growing snails. If fewer males grew than females, then males would tend to dominate the lower end of the adult distribution even if growth and survivorship rates were similar. However, the proportion growing at a given time never differed between the sexes (Table 43).

It is not therefore prudent to attribute the high sex ratio to differential growth or survivorship at about 12 mm. 12 mm males and females grow and decay at similar rates, as do their 14 mm counterparts (Tables 34, 39).

Although the present data are insufficient for a definite conclusion, one result is suggestive. 69 males known to be growing on 24 May 1976 and averaging 13.5 mm reached 13.7 mm on 23 June (Table 44); females performed similarly. However, the mean size of males growing into the next interval was only 13.5 mm, while females averaged 13.7 mm. Unfortunately numbers soon became inadequate. Extended cohort data had suggested that males might stop growing at a smaller average size than females (Section 8).

Until 23 June at least this was untrue: while the proportion growing decreased, the mean size doing so did not.

Growth: Three different growth estimates were obtained using size-frequency analysis, cohort tagging, and individual tagging.

Growth rates estimated from size-frequency distributions, although quick and cheap, are subject to errors of unknown magnitude (Section 6) and do not merit analysis with von Bertalanffy equations etc. The present estimate of approximately 0.12 mm per week, or 0.017 mm per day, agreed with cohort results.

Cohort tagging is to be preferred, especially where actively-growing snails can be identified. Results are similar to those from individual tagging, which gives by far the highest-grade information but often at prohibitive cost.

In particular, individual tagging points up the strikingly erratic growth patterns of at least some individuals, and the variety of general shapes. Differences between curves classed as sigmoidal and asymptotic are unimportant in the long term, but intermittent growth departs from the assumptions of the von Bertalanffy equations sufficiently dramatically to be crucial except over very long periods (see also Hughes & Roberts 1980).

Whether or not individual growth patterns are invariably asymptotic, mean and composite curves are sufficiently so for k computed over periods of steady growth to have heuristic value. One can pretend that the rest of the growth curve would conform - indeed, one must, because k is defined as unchanging throughout life.

Sainsbury (1980) warns that the von Bertalanffy equations devised for individuals may not apply to group means, not so much if l^{∞} varies among individuals, but especially if k does so (Section 8). Gorad *L. obtusata* k varies at least sevenfold among individuals of much the same size living together and growing concurrently.

The question is, how worthwhile is group mean k given this individual variability? If the mean is derived from known individual k, then appropriate means can be used for different analyses. For instance, mean k for snails growing at least 2 mm, twice that for long-term snails growing amongst them, would be the more appropriate value for comparison with small juveniles: most juveniles grow rapidly, especially in spring (Section 8). These adults might perhaps be assumed not to be reproducing, and would be suitable to estimate minimum age at say 15 mm - always assuming that k is unchanged throughout life. In fact their mean k approximately 0.0045 days^{-1} agrees with those of concurrent 6 and 9 mm cohorts (Tables 18, 19).

Similarly, mean long-term individual k is more appropriate for comparison with long-term cohort k values that suppress seasonal variations (Table 20), and the figures agree. Likewise, grand mean k or k computed from composite growth curves agree with comparable cohort data, the main distorting factor being seasonal variation. k for composite growth curves based on September 1976 and March 1977 extended cohorts (Tables 23 to 26, Figure 27) were respectively c. 0.0019 and 0.0024 days^{-1}, agreeing closely with their 6.5 mm components: 0.0015 and 0.0026 days^{-1} respectively. k for the entire increment-based 12 mm composite growth curve (Figure 48) was 0.0017 days^{-1}, and for long-lived individuals 0.0019 days^{-1}. Very approximately, overall mean k for Gorad *L. obtusata* is of the order of 0.0015 to 0.0025 days^{-1}.

Similar k estimates are obtained by various techniques. Ordinary juvenile mean-size k is a reasonable estimate of fast-growing adult k. Extended cohort composite growth curves adequately indicate long-term growth from one size in a fraction of the time and without as much opportunity for unwanted seasonal distortions. Individual tagging has the great virtue of revealing individual variation in k and perhaps l^{∞}.

The von Bertalanffy equation assumes that dl/dt is unaffected by season. Growth rates showed a clear seasonal cycle, with accelerated spring growth and minima in late summer and autumn. Individual, cohort, and extended cohort results conform to this pattern. Many March 1977 adults, or new adults from September 1976 10 to 12 mm cohorts, stopped growing by June to August 1977 at about 14 mm, and few individually-tagged snails grew after August 1976.

Some L. obtusata at Gorad remain at one size for many months before resuming growth. Individually-tagged adult L. irrorata grows on average 0.4 mm per year from mean 18.5 mm (Hamilton 1978). L. neritoides may not grow for two years if weather is unfavourable: Hughes & Roberts (1980) report mean k only 0.00019 days^{-1}, maximum 0.00082. The maximum conforms to the final, late summer, segments of Figure 48. Seasonal differences are also known for L. rudis (0.0003 to 0.0023 days^{-1}, Roberts & Hughes 1980) and L. nigrolineata (Hughes 1980). The predatory Nucella lapillus grows most from June to November, forming non-feeding winter aggregations (Feare 1970).

The seasonal growth pattern must be established before k is calculated, and must be held in mind when that k is used. Infrequent size measurements may prove greatly misleading, especially where growth is intermittent. k computed over a spring burst misrepresents long-term growth, but on the other hand k calculated over too long a period disguises the nature of growth unhelpfully. It would be pointless to compute k for Figure 49 line F over days 50 to 500, yet quite in order for line B.

Figure 27, devised from the extended cohorts, predicts smooth asymptotic growth. September 1976 males growing from 12.43 to 13.5 mm take 175 days (about six months), females from 12.48 to 13.5 require 152 days, and March 1977 (sexes pooled) take 80 days from 12.53 to 13.45 mm and a further 172 days to 15.0 mm, 252 days in all (Table 30). Snails growing at the male rates in Table 46 would need only 95 days, and females 96, to cover the September intervals. Using the Table 46 female rate 0.00829 mm/day they would take 86 and 187 days to cover the two March intervals, 273 days in all. This estimate derived from individual growth increments agrees satisfactorily with the March estimate derived less laboriously from cohort plots. In other words, cohorts using only snails carefully classified as growing provide an adequate estimate of true growth, provided that the appropriate seasons are compared.

Survivorship: Survivorship is reviewed in Section 9. Of interest here is how the resin and paint results relate to the others. Resin-tagged 13 and 14 mm snails survived more successfully than March 1977 extended cohort equivalents (Table 34). Paint-tagged 12 mm snails similarly had lower slopes than March 1977 equivalents, and slightly steeper slopes than corresponding September 1976 extended cohort components (Table 33). Paint slopes were very similar to those in (concurrent) March and April 1976 6 and 9 mm regular cohorts (Table 32).

The general pattern remained as before: between approximately 6 and 14 mm, survivorship is independent of sex and shell size, and shows no clear seasonal trend in contrast to growth.

Lifespan: Several lines of evidence indicate that L. obtusata may live for several years. Sacchi & Rastelli (1966) interpret the multiple rows of penial glands as indicating long adult life. The large and stable adult component of size-frequency distributions - at site A, 50 ± 13% centred on 14 mm (Section 6) - is evidently accumulated from several generations, and there is no evidence for the massive adult seasonal mortality found in L. mariae by Sacchi & Rastelli (1966). Survivorship shows no clear trend with size, although varying individual growth patterns and rates, and seasonally-differing growth rates, make size an unreliable guide to age.

Size-frequency analyses predict a minimum adult age of 18 to 24 months. Composite growth curves from extended cohorts (Figure 27) suggest that 18 months may be too soon if growth rates are indeed overestimated by polymodal analysis, and predict 300 to 400 days to grow from 6.5 to 12.5 mm. 12.5 mm snails take another 150 to 250 days to reach 14 mm (Figures 23, 24, 48, 49), or perhaps 125 days if growing particularly rapidly (Figure 50). Tagged adults may survive as long as 700 days from tagging, so three to four years seems a reasonable estimate. This accords with estimates for L. obtusata elsewhere in Wales (Goodwin 1978; Reimchen 1974) and for other British winkles L. neritoides, L. nigrolineata, and L. rudis (Hughes & Roberts 1980; Hughes 1980; Roberts & Hughes 1980; review, Goodwin 1978).

SECTION 11

GENERAL DISCUSSION

There are relatively few papers on L. obtusata and especially L. obtusata sensu stricto. Work cited here is but a fraction of the extensive littorinid literature (Pettitt 1974).

Predation is clearly an important influence in L. obtusata's life. Emphasis has so far been concentrated on visual predation (e.g., Reimchen 1974, 1979). Pettitt (review, 1975) credits crabs with colour vision, readily detecting prey that contrast with the background, particularly if the prey are striped. The shore crab Carcinus maenas is however a tactile predator, attacking everything encountered but desisting rapidly (Hughes & Elner 1979), so L. obtusata's imitation of seaweed air bladders may involve an element of tactile crypsis in Hughes' (1979) broad sense of resemblance to something inedible.

Although Reimchen (1974) managed to rear hatchlings from spawn of controlled matings (Section 5), the genetics of L. obtusata are poorly known. There is no planktonic dispersal, and adults may live several years. If they breed each year, then after two years they may inbreed with their descendants. Giesel (1971) argues that higher inbreeding between generations leads to a greater likelihood of offspring from different matings having common descent. This would have important consequences for a small isolated population of sedentary, polymorphic snails whose colours are thought to be genetically controlled and strongly adaptive.

British winkle taxonomy has recently been revised with the recognition of the L. saxatilis species complex (e.g., Heller 1975a) and of

L. mariae. The speciation mechanism is uncertain: Heller (1975a) rejects current sympatric speciation, arguing that big differences in penis shape may be responsible. Soans *et al*. (1974) show how disruptive selection may promote rapid sympatric reproductive isolation and speciation, a view endorsed by Scudder (1974). Reimchen (1974) suspects that *L. mariae* has a "dwarf" subspecies at certain shores in response to very localised habitat conditions.

Certainly *L. obtusata* and *L. mariae* are valid sibling species *sensu* Ayala (1972). They may overlap substantially, seemingly sharing similar diets, and on parts of some shores they may be very difficult to distinguish by shell characters. How much they compete is uncertain. Carter *et al*. (1979) demonstrate subtle differences in diet between *Cepaea hortensis* and *C. nemoralis*, underlining the danger of assuming, without careful investigation, that food is not limiting. Goodwin & Fish (1977) suggest characters to separate *L. obtusata* and *L. mariae* radulae, but found considerable within-species variation (SEM's: Bandel 1974; Reimchen 1974).

Although some populations overgraze the fucoids (Section 9), little information on grazing rate is available. Guiterman (1971) found 100 g of *L. obtusata* would eat from 0.8 (February-March) to 3.6 (August) grams of *Fucus vesiculosus* per day. *Ascophyllum nodosum* may double in weight within 5 to 10 days, with fresh weight to 32 kg/m^2 and productivity approximately 640 - 840 gC/m^2/year (Mann 1973), growing at up to 35 mm/month in April in New England (review, Mathieson *et al*. 1976) or 5 - 10 mm/month in Scotland (Schonbeck & Norton 1980b). Seasonal changes in growth rates would affect winkles despite high algal standing stock if snails preferred fresh tissue. Winkles may in turn affect algal diversity and density (e.g., Lubchenco 1978).

The diets, and resource partitioning (Schoener 1974), of sympatric winkles are still little known. Fucoid algae may excrete large quantities of soluble organic matter much of which may be taken up by bacteria eaten by snails (Mann 1973), but may also release objectionable - e.g., phenolic - substances presumably affecting palatability (review, Moebus et al. 1974). Heavy metals are also transferred directly to grazers (e.g., Young 1975).

Lubchenco (1978), in a study of the effect of L. littorea grazing on algal diversity, considered Ascophyllum and Fucus to be unpalatable owing to toughness or chemical defences. Schonbeck & Norton (1980b) cite unpublished evidence that A. nodosum is distasteful to grazing molluscs. Fucus spiralis is considered distasteful to L. obtusata and L. saxatilis (pers. comm. below). Norton's student D.C. Watson is conducting Ph.D. research into food palatability and selective grazing in intertidal gastropods. Preliminary results point to noxious allelochemics effective in repulsing even starved L. littorea but worthless against L. obtusata. As sporelings are similarly repulsive, taste seems to be more important than texture (Watson, pers. comm. 10 August 1981). This may account for the virtual absence from A. nodosum of L. rudis and L. littorea so abundant immediately beneath it.

Littorina obtusata seems a suitable subject for the experiments on genetics and predation now required to supplement the largely descriptive and inferential studies published hitherto. L. obtusata offers many of the features of the celebrated land snail Cepaea nemoralis, including a sympatric sibling, and has the added advantages of being widely distributed, abundant and active all year. Egg capsules may be obtained from controlled matings and cultured in the laboratory (Reimchen 1974). Important predators such as blennies and crabs are readily available and maintained. As an experimental subject, L. obtusata has been strangely overlooked; this unassuming creature may well repay attention.

> It is, I find, in zoology as it is in botany: all nature is so full, that that district produces the greatest variety which is the most examined.
>
> Gilbert White
>
> 8 October 1768

Appendix 1

SIZE FREQUENCY ANALYSIS TESTS

Cassie's (1954) method for probability-paper analysis of polymodal size-frequency distributions was tested using his own data and artificial data consisting of normal distributions having various numbers, means and standard deviations, overlapping to various degrees. The basic method was found to work satisfactorily provided either that the component standard deviations differed when means were similar, or that means of peaks with similar standard deviations were substantially apart. For instance, modes of 13.5 ± 1.5 mm and 14.2 ± 1.3 mm, with numbers 250 and 1000 respectively, were not resolved. Nor were they if the lower mean was changed to 12.5 mm, the peaks now being 1.7 mm apart. These two distributions were separated when the lower mean was changed to 11.5 mm, 2.7 mm from the upper: the histogram looked negatively-skewed and centered on 14 mm, but the inflection was clear on the probability plot. Accordingly, when performing the analyses reported in Section 6, apparently-skewed distributions were treated as overlapping components.

Cassie's overlap correction generally worked well, but care was necessary when one or more classes were missing altogether. More realistic results were obtained for overlap between juveniles and adults, when the latter ended steeply rather than trailing out to 17 mm or so, by fitting the adults from the far end of the curve and subtracting overlap from the juveniles, as explained in Section 6. Difficult inflections could be assigned by computing the juveniles from below, and the adults from above, and setting the inflection arbitrarily at the intersection of the computed straight lines.

The truncation correction proved to contain a flaw in certain circumstances. The remainder of this appendix is a worked example.

Table I

Test data

Length, mm	Number	Cumulative Number	Cumulative %
9 - 9.99	1	1	0.1
10	6	7	0.7
11	38	45	4.5
12	134	179	17.9
13	261	440	44.0
14	281	721	72.1
15	195	916	91.6
16	68	984	98.4
17	16	1000	"99.99"

Artificial data consisting of 1000 snails in nine size classes having mean 14.2 ± 1.3 mm were constructed from statistical tables (Ferguson 1966, and Rohlf & Sokal 1969) by building outwards from the desired mean (Table I).

Simple truncation of large classes, as for instance caused by size-specific sampling error (a phenomenon widely known in net fishing and lobster trapping, but considered unlikely in the present investigation), was simulated by dropping classes 15 to 17 inclusive. This left 721 snails (27.9% truncation) with mean size 13.6 mm. Following Cassie's (1954) method, in which degree of truncation is estimated and then adjusted by trial and error, truncation was determined to be approximately 27%, the mean of the untruncated distribution 14.2 ± 1.3 mm, and the original number 988. Computed values were used to reconstruct the original distribution. When this reconstruction was compared with the original (corrected to 989 to allow for the error in estimated percent truncation), the two distributions agreed well (Table II): Chi-square 2.07, 8 d.f., P >0.98. The original and reconstructed means did not differ significantly (t-test for uniform sample means, Sokal & Rohlf 1969): t (1719 d.f.) 0, 5% critical value 1.98, NS.

Table II

Reconstructed data: simple truncation

Table II. Original distribution from Table I, adjusted to total 989, compared with reconstruction after simple truncation as explained in text. Entries are frequencies rounded to nearest integer.

Length, mm	Original	Reconstruction
9 - 9.99	1	1
10	6	7
11	38	38
12	132	132
13	258	256
14	278	286
15	193	178
16	67	71
17	16	18
	989	987

A more complex form of truncation, more likely in the present investigation although not necessarily indicating sampling error, was simulated by reducing classes 15 to 17 without eliminating them altogether. Class 15 (Table I) was reduced from 195 to 10, and classes 16 and 17 to 1 each. This left 733 snails (26.7% truncation) with mean size 13.6 mm.

The resulting probability-paper plot had the points for classes 9 through 13 lying on a straight line, the 14 mm point about 4% from it, the 15 mm point far away at 14.4%, 16 mm at only 3.5%, and the 17 mm point was close to the line. Truncation is corrected by working outwards, in this case beginning with 14 mm. A 7% truncation correction was necessary to return the 14 mm point to the line. This moved the 15 mm point closer, but shifted the others to the other side. Taking N = 733, numbers from the 17 mm class were 52, 1, 10, 261, 243, 124, 36, 5 and 1. When the 15 mm point was next adjusted, using an 18% correction determined as usual by trial and error, the new line predicted mean size 14.1 ± 1.3 mm, and the fit from 9 through 14 mm was good, but numbers thereafter were ridiculous (Table III).

Table III

Reconstructed data: complex truncation

Table III. Initial and corrected reconstructions of data having numbers in extreme classes severely reduced but not eliminated (see text). Large number of 17 mm snails in initial set is preposterous. Second set reconstructs numbers in extreme classes by extrapolation from others as explained in text. (Numbers not adjusted to untruncated totals.)

Length, mm	Initial set	Corrected set
9 - 9.99	1	1
10	4	5
11	29	31
12	107	102
13	200	198
14	214	213
15	8	132
16	0	42
17	175	9
	738	733

The grotesque value for 17 mm snails arose from the way the distribution is reconstructed once the line is selected. Numbers are assigned beginning at that end of the distribution, so if that point is badly misplaced while preparing the line from the other end, values for extreme cases become nonsensical. The conservative way to correct this artefact is to read values from the fitted line and not from such points. Such a correction is shown in Table III and conforms more properly to field observations, as well as to the original artificial distribution.

The new estimate of mean size was 14.1 ± 1.3 mm, with estimated 26% truncation (1.18 x 1.07) yielding estimated untruncated number 991, which agreed with the original 1000. The original distribution, when corrected to 991, did not differ from the reconstruction: Chi-square 5.11, 8 d.f., P >0.7. The mean sizes also agreed: t (1731 d.f.) 1.58, 5% critical value 1.98, NS.

Appendix 2

APPENDIX TABLES 1 TO 41

Appendix Table 1

Sampling dates

Appendix Table 1. Dates of field samples, tagged snail recapture etc. Some samples took more than one tide to complete; arbitrary "standard dates" were assigned for certain analyses. Informal, preliminary or supplemental samples are omitted. Individually-numbered snails required special treatment as described later. This Table extends over 7 pages.

Date	Standard date	Sample code	Remarks
1975			
April, 1, 3, 5, 8, 11, 15, 22	-	APR75A	Site A repeatedly cleared to determine standing stock, speed and extent of recolonisation, suitability for detailed sampling, etc.
May 20	-	MAY75A	
July 2, 3	-	JULY75A	Many used for shell shape measurements.
August 3	-	AUG75A	
August 31	-	SEP75D	First downshore comparison sample.
Sept. 1	-	SEP75A	
Sept. 29	-	OCT75D	
Sept. 30, Oct. 1	-	OCT75A	
Oct. 29	-	NOV75A	
Nov. 4	-	NOV75L	First lateral comparison sample.
Nov. 7	-	NOV75D	
Nov. 27, 28	-	DEC75A	

continued

Appendix Table 1, continued, page 2 of 7

Date	Standard date	Sample code	Remarks
Dec. 2	-	DEC75L	
Dec. 8	-	DEC75D	
1976			
Jan. 12	-	JAN76A	Very severe gale throughout UK on weekend of 02 January, with high winds and heavy rain. Samples delayed accordingly.
Jan. 14	-	JAN76L	
Jan. 14	-	JAN76D	
Feb. 9	-	FEB76D	
Feb. 10	-	FEB76L	
Feb. 20-22	-	FEB76A	6, 9 and 12 mm snails used for tagging experiments hereafter were often taken in whole or in part from regular samples.
	Feb. 25		Release of first set of 6, 9 mm cohorts.
March 18	-	MAR76L	Many egg cases, particularly near bases of A. nodosum.
March 22	-	MAR76D	Many egg cases, especially on A. nodosum stems near bases.
March 24, 25	March 25	MAR76A	
April 13	-	APR76L	
April 15	-	APR76D	Many egg cases, especially in dense fucoid clumps.

continued

Appendix Table 1, continued, page 3 of 7

Date	Standard date	Sample code	Remarks
April 17, 18	April 18	APR76A	Egg cases less abundant than at site D.
	April 21		Release of 6, 9 mm cohorts.
May 24	May 24	MAY76A	
May 31	-	MAY76L	
June 3	-	MAY76D	Surface silt.
	May 31		Release of 6, 9 mm cohorts.
June 22, 23	June 23	JUNE76A	Numerous tagged snails were moribund or dead when measured. Warm and sunny.
July 1	-	JUNE76L	Hot and sunny.
July 2	-	JUNE76D	Hot and sunny.
August 5	-	AUG76L	Abundant mud on surface. Few egg cases. Weed greatly branched with much fresh growth.
August 9	-	AUG76D	Abundant surface mud. Very few egg cases. Weed almost 2 m long. Most snails below 5 mm diameter sheltering in damaged air bladders. Warm, sunny.
August 17 to 19	August 19	AUG76A	Mud between adjoining rocks. Egg cases frequent (10-20/m^2) but not abundant. Most small snails in damp refuges, damaged air bladders. Many crabs Carcinus maenas, carapace width 2 to 3 cm. Sunny and warm.

continued

Appendix Table 1, continued, page 4 of 7

Date	Standard date	Sample code	Remarks
	August 16		Release of 6, 9 mm cohorts.
	Sept. 3		Release of extended cohort.
Sept. 21	-	SEP76D	Surface water from prolonged rain. Egg cases scarce. Many *L. littorea*.
Sept. 22	-	SEP76L	Prolonged intermittent rain. No egg cases. Many *L. littorea*. Broken air bladders crammed with small *L. obtusata*.
Sept. 28 to 30	Sept. 30	SEP76A	One egg case. Many tagged snails dispersed, ? by gales, especially to dense weed nearby. Release of 6, 9 mm cohorts.
Oct. 19	-	OCT76L	Careful search for dispersed winkles. No egg cases.
Oct. 21	-	OCT76D	No egg cases. *L. littorea* unusually frequent.
Nov. 2, 3	Nov. 3	OCT76A	One egg case. Several *Nucella lapillus* and several patches *N. lapillus* egg cases.
	Oct. 22		Release of 6, 9 mm cohorts.
Nov. 16	-	NOV76D	Much silt. No egg cases.
Nov. 18	-	NOV76L	Few egg cases. Many small *C. maenas*, carapace width 1.5 cm.
Nov. 30, Dec. 1	Dec. 1	NOV76A	Several egg cases. *N. lapillus* 1 to 3 cm long and many eggs.
	Nov. 19		Release of 6, 9 mm cohorts.

continued

Appendix Table 1, continued, page 5 of 7

Date	Standard date	Sample code	Remarks
1977			
Feb. 13, 14	Feb. 14	FEB77A	Many egg cases. Many L. littorea. N. lapillus with several egg cases. A. nodosum much grown, fruiting profusely.
Feb. 16	-	FEB77L	A. nodosum as at site A.
	March 4		Release of extended cohort.
March 29, 30	March 30	APR77A	Cold, snow, hail. Several egg cases. Fifteen N. lapillus with several patches egg cases. Many L. littorea.
April 7	-	APR77D	A. nodosum very long and tangled, fruiting heavily. Many egg cases, especially in dense weed.
	April 9		Release of 6, 7, 8, 9 mm cohorts.
May 10	-	MAY77L	Much surface silt in some areas - avoided for sample.
May 10	-	MAY77D	Much silt. No egg cases. C. maenas to 8 cm carapace width.
May 13, 14	May 14	MAY77A	Much fine sediment, often bonded by sudden bloom of Enteromorpha sp., near to outcrop. 25 C. maenas, mostly 3 cm across. Few egg cases.
	May 15		Release of 6, 9 mm cohorts.
June 12	-	JUNE77L	Few egg cases. Much new fucoid growth; few frustules.

continued

Appendix Table 1, continued, page 6 of 7

Date	Standard date	Sample code	Remarks
June 12	-	JUNE77D	Few egg cases. Weed much grown; few fruiting bodies, if any.
June 15, 16	June 16	JUNE77A	Many egg cases, especially in dampest parts near bases etc. Very numerous C. maenas, 0.5 to 4 cm wide. Weed much grown and not fruiting.
	June 18		Release of 6, 9 mm cohorts.
	July 11		Release of extended cohort.
July 11	July 11	JULY77A	Few egg cases. Ten N. lapillus and two patches egg cases. Many C. maenas. Warm and sunny.
July 14	-	JULY77L	Sample taken near to site A because many dead/empty tagged snails noticed when releasing tagged snails from July 11.
July 21	-	JULY77D	
	July 18		Release of final 6, 9 mm cohorts.
August 6, 7	August 7	AUG77A	Much surface silt. Many C. maenas to 7 cm. Few egg cases. (All silt removed from site A to the laboratory, to screen for buried shells.)
August 23	-	AUG77D	Little silt. Few egg cases, only in wet crevices among bases and dense fucoid stalks.
August 26	-	AUG77L	No silt. No crabs.

continued

Appendix Table 1, concluded, page 7 of 7

Date	Standard date	Sample code	Remarks
Oct. 7, 8	Oct. 8	OCT77A	Much fine sediment between rocks. Egg cases present chiefly at bases of dense fucoids.
Oct. 17	-	OCT77L	One egg case. (At site A, sediment now reduced to a thin layer.)
Oct. 18	-	OCT77D	Few egg cases, deposited as usual. Many large <u>L. littorea</u>; no crabs.

<u>Summary of standard sample dates:</u>

Date	Days from 01 January 1976	Interval, days
25 March 1976	085	-
18 April	109	24
24 May	145	36
23 June	175	30
19 August	232	57
30 September	274	42
03 November	308	34
01 December	336	28
14 February 1977	411	75
30 March	455	44
14 May	500	45
16 June	533	33
11 July	558	25
07 August	585	27
08 October	647	62

Appendix Table 2

Site A size frequency distributions

Appendix Table 2. Raw frequencies, both sexes, in 1 mm size classes, for 25 samples from site A. Size measurement is shell length in mm (Section 4). Histograms are shown in Section 6. For exact dates, see Appendix Table 1. This Table extends over 3 pages.

Sample			Size class			
	3	4	5	6	7	8
APR75A	6	12	25	46	90	159
MAY75A		3	6	3	10	15
JULY75A	41	33	28	34	40	43
AUG75A	2	25	22	21	29	11
SEP75A	2	24	69	45	28	23
OCT75A	9	57	109	96	56	25
NOV75A	6	30	70	87	55	41
DEC75A	27	72	135	176	129	69
JAN76A	16	28	54	115	131	115
FEB76A	8	32	68	145	194	147
MAR76A	6	15	27	64	113	97
APR76A	21	16	22	51	67	72
MAY76A	10	9	11	18	34	52
JUNE76A	31	21	17	24	27	22
AUG76A	72	110	110	50	35	23
SEP76A	45	67	78	43	31	34
OCT76A	17	23	39	28	20	12
NOV76A	8	8	18	17	15	8
FEB77A	14	21	33	56	63	48
APR77A	19	13	21	20	40	33
MAY77A	40	15	15	17	21	24
JUNE77A	138	55	30	17	19	20
JULY77A	95	75	40	32	13	5
AUG77A	112	140	91	45	24	14
OCT77A	65	114	102	96	65	50

continued

Appendix Table 2, continued, page 2 of 3

Sample	Size class					
	9	10	11	12	13	14
APR75A	141	138	91	52	88	269
MAY75A	22	15	21	21	25	107
JULY75A	46	59	96	104	135	487
AUG75A	19	34	33	42	85	181
SEP75A	18	15	10	25	48	94
OCT75A	22	19	10	25	55	113
NOV75A	20	24	31	42	106	161
DEC75A	40	34	46	84	150	232
JAN76A	77	46	33	73	149	263
FEB76A	148	80	85	172	356	432
MAR76A	69	54	59	101	169	228
APR76A	74	44	36	42	95	109
MAY76A	54	60	50	48	164	206
JUNE76A	14	19	23	23	60	75
AUG76A	40	25	47	59	178	217
SEP76A	43	60	95	153	231	187
OCT76A	20	27	33	53	121	95
NOV76A	9	4	13	18	44	28
FEB77A	40	39	48	88	211	152
APR77A	47	31	44	79	200	158
MAY77A	22	24	19	23	82	95
JUNE77A	28	31	28	26	88	199
JULY77A	20	15	13	18	35	87
AUG77A	10	11	7	17	30	54
OCT77A	24	28	19	25	81	180

continued

Appendix Table 2, concluded, page 3 of 3

Sample	Size class 15	16	17	Total
APR75A	208	43	2	1,370
MAY75A	89	15		352
JULY75A	412	97	13	1,670
AUG75A	162	41	4	711
SEP75A	82	10	3	496
OCT75A	87	9		692
NOV75A	88	18	1	780
DEC75A	109	14		1,317
JAN76A	115	17	1	1,233
FEB76A	158	19	1	2,045
MAR76A	81	4		1,087
APR76A	34			683
MAY76A	70	7		793
JUNE76A	27	3		386
AUG76A	43	3		1,012
SEP76A	32	3		1,102
OCT76A	13			501
NOV76A	2			192
FEB77A	22			835
APR77A	30	2		737
MAY77A	27	1		425
JUNE77A	78	7	1	765
JULY77A	28	2		478
AUG77A	28	3		586
OCT77A	83	11	1	944
				21,190

Appendix Table 3

Site L size frequency distributions

Appendix Table 3. Raw frequencies, both sexes, in 1 mm size classes for 18 samples from site L. Size measurement is shell length in mm (Section 4). Histograms are shown in Section 6. For exact dates, see Appendix Table 1. This Table extends over 3 pages.

Sample	Size class 3	4	5	6	7	8
NOV75L	11	12	31	29	18	13
DEC75L	7	12	28	39	37	12
JAN76L	1	3	17	24	35	29
FEB76L	1	5	7	16	31	32
MAR76L	1	2	7	22	29	40
APR76L	6	2	9	30	40	66
MAY76L	5	7	5	12	14	17
JUNE76L	9	6	5	10	16	14
AUG76L	12	27	18	10	6	12
SEP76L	8	10	7	7	14	14
OCT76L	16	30	26	24	13	17
NOV76L	5	16	41	27	23	12
FEB77L		13	14	23	28	18
MAY77L	23	5	2	3	7	17
JUNE77L	22	19	10	11	4	9
JULY77L	50	49	33	24	19	22
AUG77L	53	62	60	47	22	23
OCT77L	25	38	51	48	39	41

continued

Appendix Table 3, continued, page 2 of 3

Sample	Size class					
	9	10	11	12	13	14
NOV75L	10	16	20	30	76	147
DEC75L	10	11	19	26	87	126
JAN76L	28	19	23	37	78	132
FEB76L	27	21	24	34	79	124
MAR76L	45	31	22	61	100	127
APR76L	63	36	42	48	61	86
MAY76L	18	35	40	43	90	149
JUNE76L	23	26	35	52	93	183
AUG76L	21	20	46	60	112	113
SEP76L	13	30	43	102	177	128
OCT76L	25	28	45	68	129	111
NOV76L	16	25	27	51	88	71
FEB77L	18	14	28	71	157	110
MAY77L	11	21	29	23	121	201
JUNE77L	29	34	27	36	93	188
JULY77L	16	14	20	35	88	196
AUG77L	13	19	18	25	64	116
OCT77L	18	12	16	23	42	125

continued

Appendix Table 3, concluded, page 3 of 3

Sample	Size class 15	16	17	Total
NOV75L	89	23	1	526
DEC75L	95	19	1	529
JAN76L	68	7	1	502
FEB76L	105	15	1	522
MAR76L	50	4		541
APR76L	36	2	1	528
MAY76L	84	13		532
JUNE76L	75	12		559
AUG76L	26	3		486
SEP76L	26	3		582
OCT76L	16	1		549
NOV76L	7			409
FEB77L	10	1		505
MAY77L	47			510
JUNE77L	45	5		532
JULY77L	65	14		645
AUG77L	57	8		587
OCT77L	59	4		541
				9,585

Appendix Table 4

Site D size frequency distributions

Appendix Table 4. Raw frequencies, both sexes, in 1 mm size classes for 20 samples from site D. Size measurement is shell length in mm (Section 4). Histograms are shown in Section 6. For exact dates, see Appendix Table 1. This Table extends over 3 pages.

Sample	Size class					
	3	4	5	6	7	8
SEP75D			10	3	8	3
OCT75D	1	5	24	17	16	15
NOV75D	11	10	19	14	17	12
DEC75D	9	10	25	20	14	14
JAN76D	4	6	9	23	19	29
FEB76D	3	10	26	46	31	19
MAR76D	5	2	8	23	44	39
APR76D	1	1	9	19	26	38
MAY76D	11	8	12	14	14	20
JUNE76D	13	9	14	11	19	29
AUG76D		18	6	7	6	7
SEP76D		14	27	11	14	15
OCT76D	13	12	22	17	14	14
NOV76D	4	10	26	24	16	15
APR77D	7	5	5	7	18	25
MAY77D	22	6	8	13	10	9
JUNE77D	42	36	22	12	6	11
JULY77D	18	43	48	39	17	12
AUG77D	20	37	66	74	50	38
OCT77D	67	54	52	67	65	59

continued

Appendix Table 4, continued, page 2 of 3

Sample	Size class					
	9	10	11	12	13	14
SEP75D	12	17	37	54	90	186
OCT75D	11	18	19	61	95	160
NOV75D	11	16	26	70	99	165
DEC75D	15	16	35	58	136	133
JAN76D	14	19	25	76	112	136
FEB76D	23	15	43	56	125	94
MAR76D	18	20	32	74	125	109
APR76D	42	25	25	64	164	90
MAY76D	45	48	56	50	87	132
JUNE76D	36	41	58	57	115	116
AUG76D	20	25	53	71	135	120
SEP76D	14	22	46	67	140	112
OCT76D	25	32	56	74	122	82
NOV76D	23	47	55	75	121	75
APR77D	43	37	38	72	165	86
MAY77D	17	34	39	46	140	151
JUNE77D	19	20	33	38	89	145
JULY77D	15	13	32	34	72	154
AUG77D	12	17	14	15	53	89
OCT77D	36	17	9	19	33	100

continued

Appendix Table 4, concluded, page 3 of 3

Sample	Size class 15	 16	 17	Total
SEP75D	77	13	1	511
OCT75D	77	14		533
NOV75D	56	5		531
DEC75D	44	4		533
JAN76D	43	2		517
FEB76D	20	3		514
MAR76D	28			527
APR76D	16			520
MAY76D	20	2		519
JUNE76D	20			538
AUG76D	23	1		492
SEP76D	9			491
OCT76D	8			491
NOV76D	9			500
APR77D	10			518
MAY77D	26			521
JUNE77D	43	4		520
JULY77D	53	11		561
AUG77D	43	4		532
OCT77D	37	5		620
				10,489

Appendix Table 5

Cohort growth: 6.5 and 9.5 mm

Appendix Table 5. Growth data for routine cohorts. GO, release date, day/month/year. T, days elapsed from release: calendar dates are given in Appendix Table 1. N, number captured and released: all growing unless marked G or A - G, number deemed to be growing; A, total number. Parentheses emphasise that a higher N was recaptured subsequently. L, mean shell length in mm, plus or minus S, standard deviation. Note that L and S are based on N measured, not N subsequently found to be alive, and that S may be misleading if based on a very small N. This Table extends over 5 pages.

GO	T	N	L	S	N	L	S
25/02/76	0	127	6.53	0.26	122	9.43	0.30
	29	(35)	6.89	0.32	35	9.82	0.35
	53	(39)	7.23	0.48	25	10.33	0.46
	89	(27)	8.50	0.54	25	11.51	0.57
	119	40	9.56	0.60	25	12.19	0.57
	176	33	11.22	0.72	16	13.29	0.50
	218	10	10.99	0.72	7	13.19	0.63
	252	(7)	11.30	0.45	6	13.35	0.56
	280	(8)	12.15	0.32	6	13.65	0.62
	355	(6)	12.78	0.29	4	14.00	0.65
	399	10	13.26	0.62	3 G	14.57	0.42
					4 A	14.30	0.63
	444	7	13.71	0.41	2	14.45	0.78
	477	(3)	14.20	0.72	(1)	13.50	-
	502	6	14.30	0.45	(1 A)	14.90	-
	529	2 A	14.25	0.50	1 G	13.60	-
					2 A	14.35	1.06
	591	0	-	-	1 G	13.70	-
					2 A	13.85	0.21

continued

Appendix Table 5, continued, page 2 of 5

GO	T	N	L	S	N	L	S
25/03/76	0	65	6.50	0.26	118	9.40	0.27
	24	33	6.99	0.31	53	10.09	0.41
	60	22	8.19	0.47	(39)	11.35	0.48
	90	21	9.29	0.52	41	12.00	0.59
	147	21	10.69	0.83	26	13.09	0.72
	189	(3)	10.93	0.71	10	13.00	0.56
	223	(3)	11.07	0.64	8	13.08	0.53
	251	4	11.50	0.43	7	13.34	0.61
	326	(2)	12.40	0.28	5	13.44	0.48
	370	(2)	13.10	0.28	4	13.60	0.45
	415	4	13.70	0.50	2 G	14.10	0.28
					3 A	13.77	0.61
	448	2	13.45	0.49	1	14.10	-
	473	2	14.15	0.21	1 G	14.20	-
					2 A	14.45	0.35
	500	1	14.10	-	2 A	14.65	0.35
	562	0	-	-	2 A	14.45	0.35
21/04/76	0	91	6.56	0.27	162	9.45	0.29
	33	(30)	7.58	0.47	(80)	10.77	0.44
	63	51	8.73	0.59	97	11.71	0.53
	120	37	10.23	0.84	82	12.85	0.62
	162	(7)	10.30	0.60	17	12.69	0.58
	196	(12)	10.93	0.67	(13)	12.81	0.60
	225	13	11.35	0.69	15	13.20	0.58
	300	8	12.51	0.55	8 G	13.51	0.69
					9 A	13.52	0.64
	344	6	13.18	0.49	(6)	13.80	0.19
	389	4	13.65	0.77	7	14.16	0.37
	422	(1)	14.80	-	(2)	14.45	0.21
	447	2	15.05	0.35	1 G	14.30	-
					3 A	14.13	0.67

continued

Appendix Table 5, continued, page 3 of 5

GO	T	N	L	S	N	L	S
	474	1 A	15.20	-	2 A	15.00	0.14
	536	1 A	15.00	-	1 A	15.30	-
31/05/76	0	44	6.41	0.31	117	9.52	0.29
	23	(16)	7.33	0.61	86	10.37	0.42
	80	18	8.53	0.70	70	11.72	0.63
	122	6	8.60	0.77	14	11.39	0.83
	156	(2)	9.20	-	(10)	11.88	0.75
	184	3	9.90	0.52	11	12.04	0.99
	259	1	11.70	-	6	12.35	0.88
	303	1	11.40	-	5	13.00	0.72
	348	1	11.70	-	4	13.63	0.79
	381	0	-	-	2	13.95	1.20
	406	0	-	-	2	14.05	1.34
	433	0	-	-	0	-	-
16/08/76	0	51	6.40	0.33	64	9.52	0.27
	45	7	6.59	0.44	5	9.66	0.50
	79	7	7.36	0.55	(2)	10.00	0.85
	107	6	8.28	0.17	3	10.97	0.59
	182	4	9.65	0.26	(2)	12.30	0.28
	226	4	10.68	0.28	3	12.40	0.75
	271	3	12.00	0.36	1	13.60	-
	304	(1)	12.60	-	(0)	-	-
	332	2	12.95	0.21	1	14.60 A	-
	356	0	-	-	1	14.70 A	-
	417	0	-	-	0	-	-
30/09/76	0	61	6.48	0.31	70	9.47	0.25
	34	(22)	7.06	0.29	(37)	9.91	0.38
	62	25	7.68	0.37	39	10.42	0.48
	137	21	8.97	0.55	23	11.57	0.45
	181	(12)	9.98	0.78	18	12.11	0.50
	226	13	11.00	0.71	17	12.79	0.67

continued

Appendix Table 5, continued, page 4 of 5

GO	T	N	L	S	N	L	S
	259	2	11.90	0.57	11	13.16	0.62
	284	2	12.25	0.64	8 G	13.25	0.67
					9 A	13.36	0.70
	311	(0)	-	-	3	13.83	0.83
	373	1	12.50	-	0	-	-
22/10/76	0	41	6.48	0.28	50	9.51	0.28
	40	25	7.14	0.30	42	10.20	0.37
	115	14	8.36	0.33	27	11.07	0.52
	159	12	9.13	0.98	19	11.75	0.69
	204	11	10.23	1.25	12	12.41	0.92
	237	6	10.47	0.51	(5)	12.58	0.88
	262	6	11.07	0.67	7	13.11	0.84
	290	3	12.27	0.64	1	14.10	-
	351	2	12.75	0.49	0	-	-
19/11/76	0	51	6.43	0.28	39	9.62	0.29
	87	21	7.89	0.35	28	10.86	0.36
	131	13	8.88	0.44	26	11.72	0.51
	176	9	9.86	0.28	22	12.46	0.57
	209	(5)	11.28	0.66	(8)	12.84	0.48
	234	8	11.69	0.73	10	13.20	0.58
	261	5	12.32	0.92	6	13.80	0.55
	323	2 G	12.70	1.27	3 A	13.93	0.67
09/04/77	0	27	6.53	0.26	90	9.51	0.26
	35	(8)	7.74	0.55	53	10.92	0.41
	68	(8)	8.84	0.56	(19)	11.66	0.64
	93	11	9.49	0.68	22	12.24	0.76
	120	6	10.45	0.83	11	12.77	0.77
	182	2	11.65	0.64	5	13.70	0.64

continued

Appendix Table 5, concluded, page 5 of 5

GO	T	N	L	S	N	L	S
15/05/77	0	33	6.46	0.33	50	9.47	0.27
	32	(6)	7.02	0.39	21	10.36	0.42
	57	8	7.91	0.61	21	11.07	0.55
	84	7	8.33	0.72	10	11.73	0.55
	146	3	10.23	0.83	4	12.98	0.87
18/06/77	0	40	6.42	0.32	76	9.50	0.30
	23	(17)	6.95	0.44	49	10.26	0.39
	50	20	7.72	0.59	40	11.01	0.43
	112	11	8.84	0.57	19	12.13	0.55
18/07/77	0	95	6.32	0.31	51	9.48	0.31
	20	46	6.76	0.42	41	10.01	0.38
	82	34	8.00	0.57	15	11.46	0.53

Appendix Table 6

September 1976 extended cohort growth

Appendix Table 6. Growth data for extended cohort released 3 September 1976. Conventions as in Appendix Table 5. 12.5 mm data are shown for males (M), females (F), and totals (MF). Note that sex ratio may bias MF. Recapture dates in the calendar are routine sample dates as in Appendix Table 1. This Table extends over 3 pages.

Calendar

release	03 September 1976	day	0
capture	30 September		27
	03 November		61
	01 December		89
	14 February 1977		164
	30 March		208
	14 May		253
	16 June		286
	11 July		311
	07 August		338
	08 October		400

T	N	L	S	N	L	S
0	44	6.47	0.29	40	7.54	0.25
27	(8)	6.59	0.30	(11)	7.56	0.25
61	12	7.17	0.43	(10)	8.24	0.48
89	12	7.95	0.48	13	8.64	0.58
164	5	8.70	0.37	6	9.42	0.80
208	4	9.45	0.17	5	10.28	1.10
253	(2)	9.85	0.64	5	11.08	1.62
286	(2)	11.10	0.00	2	13.25	0.64
311	3	11.53	0.25	2	13.15	1.20
338	2	12.00	0.28	1	12.90	-

continued

Appendix Table 6, continued, page 2 of 3

T	N	L	S	N	L	S
400	0	-	-	0	-	-
0	42	8.48	0.28	93	9.46	0.31
27	11	8.38	0.34	40	9.41	0.32
61	10	9.03	0.36	(29)	10.01	0.35
89	8	9.60	0.46	30	10.48	0.41
164	6	10.40	0.58	22	11.28	0.47
208	5	10.92	0.58	15	12.05	0.52
253	4	11.33	0.92	11	12.85	0.53
286	(2)	11.80	0.00	4	13.18	0.41
311	3 G	12.67	0.90	5	13.26	0.37
	4 A	13.05	1.06			
338	2 G	13.05	1.34	3	13.40	0.87
	3 A	13.57	1.31			
400	0	-	-	2 A	13.65	0.92
0	136	10.48	0.29	163	11.47	0.26
27	48	10.46	0.29	56	11.54	0.25
61	(45)	10.88	0.38	54	11.84	0.36
89	48	11.25	0.46	48	12.21	0.44
164	37	12.05	0.60	34	12.65	0.52
208	26	12.64	0.68	25	13.13	0.56
253	23	13.32	0.87	19	13.56	0.62
286	11 G	13.36	0.59	(6 G)	13.85	0.59
	12 A	13.23	0.72	(7 A)	13.76	0.59
311	7 G	13.76	0.63	8 G	14.00	0.56
	9 A	13.66	0.65	10 A	13.99	0.49
338	4 G	14.10	0.54	4 G	14.10	0.29
	8 A	13.66	0.90	6 A	14.15	0.24
400	3 A	13.30	1.18	4 A	14.08	0.25

continued

Appendix Table 6, concluded, page 3 of 3

T	N	L	S	N	L	S
0	100	12.47M	0.26	102	12.46F	0.31
27	47	12.43	0.26	41	12.48	0.33
61	42	12.63	0.28	(33)	12.74	0.36
89	40	12.87	0.34	35	13.04	0.41
164	24 G	13.13	0.45	17	13.42	0.34
	26 A	13.07	0.46			
208	18	13.57	0.46	13	13.68	0.31
253	17	14.15	0.60	10	14.07	0.31
286	5 G	13.94	0.35	(3)	13.87	0.59
	(6 A)	13.98	0.33			
311	4 G	14.03	0.90	2 G	14.15	0.21
	8 A	13.95	0.66	5 A	13.92	0.48
338	(1 G)	14.90	-	3 A	14.30	0.26
	3 A	14.00	0.90			
400	2 G	14.75	0.07	2 A	14.15	0.07
	3 A	14.47	0.49			
0	202	12.47MF	0.28			
27	88	12.45	0.29			
61	75	12.68	0.32			
89	75	12.95	0.38			
164	41 G	13.25	0.43			
	43 A	13.21	0.45			
208	31	13.61	0.40			
253	27	14.12	0.51			
286	8 G	13.91	0.41			
	(9 A)	13.94	0.40			
311	6 G	14.07	0.71			
	13 A	13.94	0.58			
338	(1 G)	14.90	-			
	6 A	14.15	0.62			
400	2 G	14.75	0.07			
	5 A	14.34	0.39			

Appendix Table 7

March 1977 extended cohort growth

Appendix Table 7. Growth data for extended cohort released 4 March 1977. Conventions as in Appendix Table 5. Adult data are shown for males (M), females (F), and totals (MF). Note that sex ratio may bias MF. Recapture dates in the calendar are routine sample dates as in Appendix Table 1. This Table extends over 4 pages.

Calendar

release	04 March 1977	day	0
capture	30 March		26
	14 May		71
	16 June		104
	11 July		129
	07 August		156
	08 October		218

T	N	L	S	N	L	S
0	18	6.40	0.32	31	7.47	0.27
26	(5)	6.72	0.35	21	8.02	0.35
71	6	8.02	0.35	19	9.49	0.61
104	(4)	9.08	0.49	(8)	10.33	0.69
129	(4)	9.68	0.69	12	10.94	0.76
156	5	10.32	0.95	6	11.35	1.03
218	2	10.90	0.85	3	12.90	1.01
0	26	8.42	0.28	46	9.51	0.27
26	20	9.07	0.36	35	10.13	0.34
71	17	10.23	0.46	26	11.47	0.64
104	8	11.14	0.48	8	11.90	0.59
129	7	11.77	0.62	8	12.64	0.40
156	(2)	12.45	0.64	2	13.35	0.07

continued

Appendix Table 7, continued, page 2 of 4

T	N	L	S	N	L	S
218	2 G	12.80	0.28	1 A	13.30	-
	3 A	12.77	0.21			
0	42	10.45	0.25	67	11.46	0.27
26	32	11.02	0.33	45	11.90	0.33
71	22	12.00	0.35	32	12.79	0.45
104	6	12.55	0.52	15	13.09	0.59
129	6	13.03	0.69	13	13.55	0.48
156	3	13.90	0.46	7 A	14.27	0.44
218	0	-	-	0	-	-
0	98	12.52M	0.30	75	12.54F	0.26
26	70	12.81	0.28	62	12.80	0.27
71	41	13.46	0.44	42	13.33	0.39
104	19 G	13.68	0.42	(11)	13.53	0.33
	(23 A)	13.56	0.49			
129	15 G	13.85	0.51	14 G	13.75	0.40
	26 A	13.77	0.48	15 A	13.71	0.42
156	4 G	14.33	0.38	6 G	14.17	0.39
	12 A	14.08	0.48	8 A	14.18	0.35
218	1 G	13.00	-			
	6 A	14.10	0.68	4 A	13.70	0.54
0	173	12.53MF	0.28			
26	132	12.81	0.28			
71	83	13.40	0.42			
104	30 G	13.63	0.39			
	34 A	13.55	0.44			
129	29 G	13.80	0.45			
	41 A	13.74	0.46			
156	10 G	14.23	0.37			
	20 A	14.12	0.43			
218	1 G	13.00	-			
	10 A	13.94	0.63			

continued -

Appendix Table 7, continued, page 3 of 4

T	N	L	S	N	L	S
0	170	13.40M	0.27	209	13.47F	0.28
26	81 G	13.64	0.29	112 G	13.65	0.28
	121 A	13.64	0.28	161 A	13.65	0.28
71	56 G	14.14	0.36	75 G	14.13	0.35
	84 A	13.99	0.38	121 A	13.97	0.39
104	17 G	14.10	0.45	29 G	14.18	0.41
	(32 A)	13.94	0.43	(43 A)	14.00	0.49
129	13 G	14.59	0.36	17 G	14.54	0.41
	42 A	14.08	0.50	44 A	14.10	0.53
156	2 G	14.05	0.35	5 G	14.52	0.63
	(3 A)	13.87	0.40	23 A	14.19	0.56
218	1 G	14.50	-			
	7 A	13.83	0.46	8 A	13.88	0.63
0	379	13.44MF	0.28	198	14.36MF	0.28
26	193 G	13.64	0.29	74 G	14.54	0.28
	282 A	13.65	0.28	137 A	14.49	0.28
71	131 G	14.13	0.35	47 G	14.95	0.36
	205 A	13.98	0.38	95 A	14.64	0.45
104	46 G	14.15	0.42	18 G	14.86	0.54
	(75 A)	13.98	0.46	(32 A)	14.58	0.53
129	30 G	14.56	0.38	9 G	15.16	0.50
	86 A	14.09	0.51	40 A	14.52	0.49
156	7 G	14.39	0.58	3 G	15.03	0.81
	26 A	14.15	0.55	15 A	14.68	0.48
218	1 G	14.50	-			
	15 A	13.85	0.54	5 A	14.44	0.59
0	77	14.33M	0.26	121	14.39F	0.28
26	21 G	14.46	0.23	53 G	14.56	0.29
	47 A	14.46	0.25	90 A	14.50	0.30
71	13 G	14.80	0.32	34 G	15.01	0.37
	29 A	14.55	0.36	66 A	14.68	0.48

continued

Appendix Table 7, concluded, page 4 of 4

T	N	L	S	N	L	S
104	3 G	14.80	0.53	15 G	14.87	0.56
	(9 A)	14.38	0.42	(23 A)	14.66	0.56
129	(0 G)	-	-	9 G	15.16	0.50
	12 A	14.30	0.25	28 A	14.61	0.54
156	1 G	15.90	-	2 G	14.60	0.42
	5 A	14.66	0.71	10 A	14.69	0.37
218	1 A	14.10	-	4 A	14.53	0.64

Appendix Table 8

April 1977 extended cohort growth

Appendix Table 8. Growth data for supplementary cohorts released 9 April 1977: see also Appendix Table 5. Conventions as in Appendix Table 5. Recapture dates in the calendar are routine sample dates as in Appendix Table 1. All snails were growing.

Calendar

release	09 April 1977	day 0
capture	14 May	35
	16 June	68
	11 July	93
	07 August	120
	08 October	182

T	N	L	S	N	L	S
0	58	7.50	0.29	58	8.52	0.27
35	37	9.06	0.42	37	10.01	0.44
68	(12)	9.88	0.39	(17)	10.71	0.59
93	15	10.67	0.53	20	11.38	0.58
120	8	11.29	0.61	12	12.21	0.36
182	4	12.20	0.42	8	13.21	0.35

Appendix Table 9

July 1977 extended cohort growth

Appendix Table 9. Growth data for extended cohort released 11 July 1977. Conventions as in Appendix Tables 5 and 6. Recapture dates: day 27 is 7 August, and day 89 is 8 October, when field work ended. This Table extends over 2 pages.

T	N	L	S	N	L	S
0	27	6.36	0.30	33	7.44	0.30
27	6	6.92	0.28	12	8.07	0.37
89	4	7.88	0.19	4	9.33	0.58
0	37	8.46	0.33	22	9.43	0.30
27	17	8.98	0.38	6	10.30	0.24
89	10	10.16	0.59	3	11.47	0.31
0	25	10.36	0.30	37	11.42	0.30
27	11	10.93	0.48	18	11.77	0.39
89	4	11.55	0.17	11	12.71	0.63
0	19	12.40M	0.27	24	12.43F	0.29
27	11	12.80	0.33	8	12.69	0.43
89	5	13.54	0.68	4	13.25	0.30
0	43	12.41MF	0.28			
27	19	12.75	0.37			
89	9	13.41	0.54			
0	30	13.50M	0.32	31	13.54F	0.26
27	9 G	13.54	0.32	8 G	13.88	0.29
	11 A	13.58	0.30	10 A	13.78	0.38
89	2 G	13.75	0.07	4 G	13.75	0.13
	4 A	13.58	0.21	7 A	13.87	0.24

continued

Appendix Table 9, concluded, page 2 of 2

T	N	L	S	N	L	S
0	61	13.52MF	0.29			
27	17 G	13.70	0.34			
	21 A	13.68	0.35			
89	6 G	13.75	0.10			
	11 A	13.76	0.27			
0	42	14.46M	0.27	43	14.52F	0.31
27	2 G	14.30	0.14	3 G	14.77	0.15
	3 A	14.30	0.10	5 A	14.62	0.36
89	0	-	-	0 G	-	-
				3 A	14.77	0.15
0	85	14.49MF	0.29			
27	5 G	14.58	0.29			
	8 A	14.50	0.33			
89	0 G	-	-			
	3 A	14.77	0.15			
0	17	15.31M	0.30	24	15.36F	0.35
27	0 G	-	-	2	15.50	0.28
	1 A	15.30	-			
89	0	-	-	1	15.50	-
0	41	15.34MF	0.32			
27	2 G	15.50	0.28			
	3 A	15.43	0.23			
89	1	15.50	-			

Appendix Table 10

6 and 9 mm cohort survivorship regressions

Appendix Table 10. Survivorship summary for 6 and 9 mm tagged cohorts. See Appendix Tables 5 and 8 for full recapture histories. Equations are for natural logarithm of percent surviving vs. elapsed time. N, starting number. A, Y-intercept, with standard error in parentheses. Slope, negative slope with standard error in parentheses - both must be multiplied by 10^{-3}. SE(EST), standard error of the estimate. R^2, squared correlation coefficient. F, variance ratio with degrees of freedom in parentheses. P(F), significance of relationship. X denotes non-standard data selection (see text). This Table extends over 3 pages.

Released	Cohort (mm)	N	A	Slope, x 10^{-3}	SE(EST)
02/76	6	127	3.754 (0.392)	4.54 (1.15)	0.406
	9	122	3.509 (0.142)	6.50 (0.62)	0.233
03/76	6	65	3.972 (0.271)	5.88 (1.28)	0.418
	9	118	4.030 (0.201)	8.21 (0.88)	0.269
04/76	6	91	4.553 (0.077)	7.90 (0.29)	0.082
	9	162	4.412 (0.445)	8.50 (1.88)	0.506
05/76	6 X	44	4.674 (0.209)	15.15 (1.78)	0.238
	9	117	4.331 (0.327)	9.77 (1.49)	0.441
08/76	6 X	51	2.908 (0.074)	4.34 (0.37)	0.095
	9 X	64	2.267 (0.287)	5.32 (1.15)	0.319
09/76	6	61	4.008 (0.137)	4.03 (0.88)	0.102
	9	70	4.403 (0.124)	6.23 (0.60)	0.111
10/76	6	41	4.358 (0.151)	6.36 (0.81)	0.151
	9	50	4.849 (0.097)	8.17 (0.56)	0.095
11/76	6	51	4.269 (0.200)	7.29 (1.06)	0.152
	9	39	5.275 (0.353)	8.88 (1.87)	0.268

continued: R^2 to P(F) overleaf, 1977 cohorts thereafter

Appendix Table 10, continued, page 2 of 3

Released	Cohort (mm)	R^2	F (d.f.)	P(F)	
02/76	6	0.797	15.677 (1,4)	0.017	*
	9	0.933	111.310 (1,8)	<0.001	***
03/76	6	0.841	21.133 (1,4)	0.01	**
	9	0.936	87.565 (1,6)	<0.001	***
04/76	6	0.995	762.488 (1,4)	<0.001	***
	9	0.836	20.454 (1,4)	0.011	*
05/76	6 X	0.973	72.443 (1,2)	0.014	*
	9	0.896	42.858 (1,5)	<0.005	**
08/76	6 X	0.966	141.318 (1,5)	<0.001	***
	9 X	0.843	21.463 (1,4)	<0.01	**
09/76	6	0.955	21.177 (1,1)	0.136	NS
	9	0.964	106.830 (1,4)	<0.001	***
10/76	6	0.939	61.067 (1,4)	<0.005	**
	9	0.986	211.213 (1,3)	<0.001	***
11/76	6	0.941	47.538 (1,3)	0.006	**
	9	0.883	22.544 (1,3)	0.018	*

continued: 1977 cohorts

Appendix Table 10, concluded, page 3 of 3

Released	Cohort (mm)	N	A	Slope, x 10^{-3}	SE(EST)
04/77	6 X	27	4.642 (0.205)	11.79 (2.34)	0.208
	7	58	4.644 (0.164)	15.38 (1.37)	0.145
	8	58	4.485 (0.163)	10.67 (1.36)	0.144
	9	90	4.631 (0.158)	16.36 (1.32)	0.139
05/77	6 X	33	4.530 (0.282)	19.45 (4.81)	0.292
	9	50	4.389 (0.222)	15.69 (2.46)	0.209
06/77	6 X	40	4.562 (0.085)	11.45 (1.20)	0.095
	9	76	4.454 (0.075)	10.88 (1.04)	0.067
07/77	6 X	95	4.385 (0.299)	10.71 (6.15)	0.372
	9 X	51	4.642 (0.051)	15.23 (1.04)	0.063

Released	Cohort (mm)	R^2	F (d.f.)	P(F)	
04/77	6 X	0.962	25.387 (1,1)	0.125	NS
	7	0.984	126.351 (1,2)	0.008	**
	8	0.968	61.461 (1,2)	0.016	*
	9	0.987	154.620 (1,2)	0.006	**
05/77	6 X	0.942	16.346 (1,1)	0.154	NS
	9	0.953	40.587 (1,2)	0.024	*
06/77	6 X	0.989	91.120 (1,1)	0.066	NS
	9	0.991	109.017 (1,1)	0.061	NS
07/77	6 X	0.752	3.038 (1,1)	0.332	NS
	9 X	0.995	214.944 (1,1)	0.043	*

Appendix Table 11

September 1976 extended cohort survivorship regressions

Appendix Table 11. Survivorship summary for extended cohort released 3 September 1976. See Appendix Table 6 for full recapture histories. 12 mm values are pooled data of separate-sex cohorts (M, males; F, females). Conventions are otherwise as in Appendix Table 10.

Cohort, mm	N	A	Slope, x 10^{-3}	SE(EST)
6	44	3.904 (0.176)	8.37 (1.23)	0.144
7	40	3.885 (0.334)	6.02 (1.77)	0.214
8	42	3.339 (0.063)	3.91 (0.34)	0.087
9	93	4.107 (0.171)	6.95 (0.86)	0.201
10	136	4.059 (0.215)	6.22 (0.92)	0.268
11	163	4.019 (0.150)	7.30 (0.62)	0.231
M 12	100	4.132 (0.111)	5.92 (0.59)	0.153
F 12	102	4.045 (0.122)	7.42 (0.61)	0.144
12	202	4.246 (0.172)	8.07 (0.72)	0.266

	R^2	F (d.f.)	P(F)	
6	0.959	46.320 (1,2)	0.021	*
7	0.853	11.578 (1,2)	0.077	NS
8	0.964	133.076 (1,5)	<0.001	***
9	0.943	65.586 (1,4)	<0.005	**
10	0.883	45.392 (1,6)	<0.001	***
11	0.951	136.770 (1,7)	<0.001	***
M 12	0.952	99.428 (1,5)	<0.001	***
F 12	0.973	146.793 (1,4)	<0.001	***
12	0.948	126.503 (1,7)	<0.001	***

Appendix Table 12

March 1977 extended cohort survivorship regressions

Appendix Table 12. Survivorship summary for extended cohort released 4 March 1977. See Appendix Table 7 for full recapture histories. OR, alternative regression explained in text. 12, 13 and 14 mm values are pooled data of separate-sex cohorts (M, males; F, females); slopes of 13, 14 mm exceed those of either sex. Conventions are otherwise as in Appendix Table 10. This Table extends over 2 pages.

Cohort, mm	N	A	Slope, x 10^{-3}	SE(EST)
7	31	4.599 (0.271)	9.02 (2.69)	0.272
		OR 4.666 (0.153)	10.29 (1.22)	0.225
8	26	4.735 (0.249)	11.20 (2.73)	0.211
		OR 4.646 (0.103)	10.18 (0.89)	0.156
9	46	4.864 (0.397)	16.30 (4.36)	0.336
		OR 4.713 (0.222)	14.80 (2.73)	0.291
10	42	4.921 (0.429)	18.41 (4.71)	0.363
		OR 4.951 (0.316)	18.89 (2.94)	0.298
11	67	4.694 (0.178)	14.35 (1.66)	0.168
12	173	4.781 (0.142)	13.89 (1.04)	0.155
13	379	4.934 (0.328)	16.58 (2.39)	0.356
14	198	4.958 (0.273)	17.88 (1.99)	0.296
M 12	98	4.669 (0.172)	12.92 (1.25)	0.186
F 12	75	4.910 (0.155)	15.12 (1.13)	0.168
M 13	170	4.864 (0.263)	15.02 (1.99)	0.286
F 13	209	4.993 (0.197)	16.29 (1.43)	0.214
M 14	77	4.674 (0.269)	16.59 (2.49)	0.251
F 14	121	5.001 (0.282)	17.08 (2.05)	0.306

continued

Appendix Table 12, concluded, page 2 of 2

Cohort, mm	R^2	F (d.f.)	P(F)
7	0.849	11.228 (1,2)	0.079 NS
	OR 0.947	71.245 (1,4)	0.001 **
8	0.894	16.839 (1,2)	0.055 NS
	OR 0.970	131.048 (1,4)	<0.001 ***
9	0.875	13.974 (1,2)	0.065 NS
	OR 0.908	29.454 (1,3)	0.012 *
10	0.884	15.277 (1,2)	0.060 NS
	OR 0.932	41.138 (1,3)	0.008 **
11	0.961	74.684 (1,3)	0.003 **
12	0.984	179.013 (1,3)	<0.001 ***
13	0.941	48.234 (1,3)	0.006 **
14	0.964	81.006 (1,3)	0.003 **
M 12	0.973	106.621 (1,3)	0.002 **
F 12	0.984	179.494 (1,3)	<0.001 ***
M 13	0.966	56.992 (1,2)	0.017 *
F 13	0.977	129.083 (1,3)	<0.005 **
M 14	0.957	44.577 (1,2)	0.022 *
F 14	0.958	69.175 (1,3)	0.004 **

Appendix Table 13

July 1977 extended cohort survivorship regressions

Appendix Table 13. Survivorship summary for extended cohort released 11 July 1977. See Appendix Table 9 for full recapture histories. Adult data could not be pooled within size classes (M, males, F, females). NA, not applicable: regression could not be calculated from available data. Conventions are otherwise as in Appendix Table 10. This Table extends over 2 pages.

Cohort, mm	N	A	Slope, x 10^{-3}	SE(EST)
6	27	4.197 (0.613)	18.86 (11.41)	0.736
7	33	4.441 (0.246)	22.67 (4.58)	0.296
8	37	4.437 (0.252)	13.63 (4.70)	0.303
9	22	4.298 (0.460)	20.44 (8.57)	0.553
10	25	4.488 (0.176)	19.85 (3.27)	0.211
11	37	4.449 (0.234)	12.64 (4.35)	0.281
M 12	19	4.543 (0.094)	14.60 (1.75)	0.113
F 12	24	4.360 (0.368)	18.58 (6.85)	0.442
M 13	30	4.432 (0.260)	21.54 (4.84)	0.312
F 13	31	4.305 (0.450)	14.82 (8.39)	0.541
M 14	42 NA			
F 14	43	4.012 (0.890)	26.15 (16.58)	1.070
M 15	17 NA			
F 15	24	3.934 (1.008)	31.45 (18.76)	1.211

Continued

Appendix Table 13, concluded, page 2 of 2

Cohort, mm	R^2	F (d.f.)	P(F)	
6	0.732	2.734 (1,1)	0.346	NS
7	0.961	24.471 (1,1)	0.127	NS
8	0.894	8.421 (1,1)	0.211	NS
9	0.850	5.685 (1,1)	0.253	NS
10	0.974	36.844 (1,1)	0.104	NS
11	0.894	8.447 (1,1)	0.211	NS
M 12	0.986	69.926 (1,1)	0.076	NS
F 12	0.880	7.359 (1,1)	0.225	NS
M 13	0.952	19.833 (1,1)	0.141	NS
F 13	0.757	3.118 (1,1)	0.328	NS
M 14	NA			
F 14	0.713	2.487 (1,1)	0.360	NS
M 15	NA			
F 15	0.737	2.809 (1,1)	0.342	NS

Appendix Table 14

Shell shape regressions

Appendix Table 14. Details of regressions given in Table 1. Parameters are illustrated in Figure 2. M, 735 males; F, 888 females; MF, sexes pooled. SE, standard error. INT, intercept, mm. R, correlation coefficient. SE(EST), standard error of the estimate. F(d.f.), F-ratio with associated degrees of freedom; P(F), significance of F-ratio. All slopes are significant to P <0.0001, all intercepts are significant to P <0.005, all R are significant to P <0.0001.

Parameters	Sex	Slope	± SE	INT	± SE	R
H vs L	M	0.566	0.004	1.303	0.059	0.979
	F	0.604	0.003	0.864	0.043	0.988
	MF	0.589	0.003	1.030	0.036	0.984
W vs L	M	0.971	0.005	-0.207	0.068	0.991
	F	0.967	0.004	-0.243	0.055	0.993
	MF	0.969	0.003	-0.225	0.043	0.992
T vs L	M	0.044	0.001	0.054	0.018	0.782
	F	0.046	0.001	0.040	0.016	0.807
	MF	0.046	0.001	0.044	0.012	0.796

		R^2	SE(EST)	F(d.f.)	P(F)
H vs L	M	0.959	0.309	17049 (1, 733)	<0.0001
	F	0.976	0.285	36541 (1, 886)	<0.0001
	MF	0.969	0.302	50232 (1, 1621)	<0.0001
W vs L	M	0.981	0.354	38302 (1, 733)	<0.0001
	F	0.985	0.361	58442 (1, 886)	<0.0001
	MF	0.983	0.361	95263 (1, 1621)	<0.0001
T vs L	M	0.612	0.093	1154 (1, 733)	<0.0001
	F	0.651	0.103	1650 (1, 886)	<0.0001
	MF	0.634	0.099	2807 (1, 1621)	<0.0001

Appendix Table 15

Supplementary shell shape regressions

Appendix Table 15. Details of regressions given in Table 2, together with results of pooling the two Gorad replicates (145 snails). Parameters as in Figure 2. Conventions as in Appendix Table 14. This Table extends over 2 pages.

Sample	Parameters	Slope	± SE	INT	± SE
Gorad <u>obtusata</u>	H vs L	0.798	0.017	-0.030	0.020
	W vs L	0.978	0.019	-0.179	0.022
Gorad <u>obtusata</u>	H vs L	0.834	0.013	-0.054	0.011
	W vs L	0.905	0.014	-0.110	0.011
Llanddwyn <u>obtusata</u>	H vs L	0.618	0.009	0.293	0.092
	W vs L	0.930	0.013	-0.224	0.133
Llanddwyn <u>mariae</u>	H vs L	0.598	0.011	0.377	0.080
	W vs L	0.903	0.015	0.066	0.113
Pooled Gorad <u>obtusata</u>	H vs L	0.807	0.010	-0.036	0.010
	W vs L	0.946	0.011	-0.143	0.011

Continued

Appendix Table 15, concluded, page 2 of 2

R	R^2	SE(EST)	F(d.f.)	P(F)
0.984	0.969	0.050	2126 (1,69)	<0.0001
0.987	0.974	0.055	2631 (1,69)	<0.0001
0.991	0.982	0.033	3924 (1,72)	<0.0001
0.992	0.984	0.034	4421 (1,72)	<0.0001
0.995	0.989	0.249	4975 (1,55)	<0.0001
0.995	0.990	0.361	5365 (1,55)	<0.0001
0.985	0.971	0.197	3026 (1,91)	<0.0001
0.987	0.975	0.276	3527 (1,91)	<0.0001
0.989	0.979	0.042	6688 (1,143)	<0.0001
0.991	0.982	0.047	7649 (1,143)	<0.0001

Appendix Table 16

July lip thickness

Appendix Table 16. July 1975 test sample lip thickness distributions. Male and female data are illustrated in Figure 4. Note that sex ratio may affect pooled values. L, 1 mm shell length classes 4.0-4.99 etc. N, number. T, mean lip thickness, mm, with standard deviation in parentheses when numbers permit.

L	Males		Females		Males and Females	
	N	T	N	T	N	T
4	3	0.35	30	0.30 (0.05)	33	0.31 (0.05)
5	10	0.30 (0.05)	18	0.31 (0.05)	28	0.31 (0.05)
6	14	0.34 (0.05)	20	0.36 (0.06)	34	0.35 (0.06)
7	18	0.39 (0.06)	22	0.37 (0.04)	40	0.38 (0.05)
8	20	0.42 (0.05)	23	0.45 (0.06)	43	0.43 (0.05)
9	26	0.48 (0.07)	20	0.49 (0.05)	46	0.49 (0.06)
10	32	0.53 (0.06)	27	0.52 (0.06)	59	0.53 (0.06)
11	57	0.58 (0.08)	40	0.54 (0.07)	97	0.56 (0.08)
12	54	0.56 (0.07)	50	0.58 (0.07)	104	0.57 (0.07)
13	59	0.62 (0.07)	76	0.63 (0.10)	135	0.63 (0.09)
14	212	0.70 (0.10)	275	0.71 (0.10)	487	0.70 (0.10)
15	183	0.74 (0.11)	230	0.76 (0.12)	413	0.75 (0.12)
16	44	0.81 (0.14)	53	0.86 (0.15)	97	0.83 (0.14)
17	5	0.83 (0.10)	8	0.86 (0.17)	13	0.85 (0.14)
	737		892		1629	

Appendix Table 17

March/April lip thickness

Appendix Table 17. Lip thickness distributions in eleven pooled samples taken between 24 March and 22 April, 1975. See also Figure 5. Conventions as in Appendix Table 16. Note that upper and lower limits of range were sometimes set arbitrarily as explained in text.

L	Males		Females	
	N	T	N	T
3	1	0.35	0	
4	2	0.35	4	0.35
5	14	0.36 (0.03)	9	0.35 (0.00)
6	26	0.36 (0.03)	30	0.36 (0.03)
7	59	0.37 (0.05)	56	0.38 (0.05)
8	111	0.40 (0.07)	137	0.39 (0.07)
9	155	0.45 (0.08)	160	0.43 (0.08)
10	161	0.49 (0.09)	167	0.47 (0.09)
11	92	0.49 (0.09)	109	0.48 (0.09)
12	66	0.49 (0.09)	70	0.50 (0.10)
13	161	0.57 (0.11)	154	0.58 (0.10)
14	405	0.66 (0.12)	386	0.66 (0.11)
15	227	0.74 (0.14)	236	0.72 (0.11)
16	34	0.80 (0.14)	51	0.79 (0.15)
17	2	0.78	4	0.98
	1516		1573	

Appendix Table 18

Llanddwyn lip thickness

Appendix Table 18. Lip thickness distributions for Littorina obtusata and L. mariae in Llanddwyn Island sample of 23 August 1974. See Figure 6. Conventions as in Appendix Table 16. Sexes pooled owing to small numbers. Range, thinnest and thickest shell lips observed.

L	L. obtusata			L. mariae		
	N	T	Range	N	T	Range
2	1	0.25				
3	3	0.30	0.25 - 0.35	3	0.32	0.25 - 0.40
4	3	0.40	0.35 - 0.45	10	0.40 (0.04)	0.35 - 0.45
5	5	0.38	0.35 - 0.45	18	0.41 (0.07)	0.35 - 0.60
6	3	0.45	0.40 - 0.50	11	0.50 (0.10)	0.35 - 0.70
7	5	0.50	0.45 - 0.55	15	0.60 (0.05)	0.50 - 0.70
8	7	0.56 (0.08)	0.50 - 0.70	20	0.74 (0.13)	0.60 - 1.00
9	4	0.71	0.55 - 0.85	8	0.89 (0.12)	0.70 - 1.10
10	3	0.80	0.70 - 0.90	7	0.93 (0.08)	0.80 - 1.00
11	4	0.78	0.65 - 1.05	1	1.40	
12	1	1.10				
13	6	1.21 (0.22)	1.00 - 1.60			
14	9	1.39 (0.18)	1.15 - 1.60			
15	3	1.62	1.50 - 1.70			
	57			93		

Appendix Table 19

Morph frequencies

Appendix Table 19. Numbers of each morph in 27 samples coded as in Appendix Table 1. Morphs: R, reticulata (light and dark); C, citrina; O, olivacea. N, total classified.[1] This Table extends over 2 pages.

Sample		Morph		N
	R	C	O	
AUG76A	198	82	673	953
SEP76A	160	53	803	1016
OCT76A	108	29	364	501
NOV76A	37	11	144	192
MAY77A	59	20	307	386
JUNE77A	95	73	552	720
JULY77A	62	46	318	426
AUG77A	82	65	439	586
OCT77A	193	41	710	944
Sum	994	420	4310	5724
AUG76L	95	26	336	457
SEP76L	100	12	450	562
OCT76L	95	26	379	500
NOV76L	66	24	276	366
MAY77L	92	22	382	496
JUNE77L	80	26	386	492
JULY77L	102	46	416	564
AUG77L	95	56	436	587
OCT77L	126	30	385	541
Sum	851	268	3446	4565

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[1] When N differs from sample size shown in Appendix Table 1, snails were removed for tagging before morphs were scored.

Continued

Appendix Table 19, concluded, page 2 of 2

Sample	Morph R	C	O	N
AUG76D	132	11	322	465
SEP76D	94	15	357	466
OCT76D	112	25	312	449
NOV76D	126	6	321	453
MAY77D	119	10	362	491
JUNE77D	101	21	367	489
JULY77D	135	18	354	507
AUG77D	82	30	420	532
OCT77D	136	26	458	620
Sum	1037	162	3273	4472

[1] When N differs from sample size shown in Appendix Table 1, snails were removed for tagging before morphs were scored.

Appendix Table 20

Juvenile morph frequencies

Appendix Table 20. Distribution of morphs among representative juveniles from Appendix Table 19. Conventions as in Appendix Table 19. Samples AUG76D and SEP76D lacked 3 mm snails. This Table extends over 2 pages.

Sample		Morph		N
	R	C	O	
AUG76A	18	69	205	292
SEP76A	15	40	135	190
OCT76A	3	18	58	79
NOV76A	1	7	26	34
MAY77A	4	16	50	70
JUNE77A	9	64	150	223
JULY77A	21	42	147	210
AUG77A	19	58	266	343
OCT77A	33	28	220	281
Sum	123	342	1257	1722
AUG76L	2	23	32	57
SEP76L	0	5	20	25
OCT76L	1	16	55	72
NOV76L	6	9	47	62
MAY77L	3	13	14	30
JUNE77L	2	17	32	51
JULY77L	6	41	85	132
AUG77L	6	44	125	175
OCT77L	12	14	88	114
Sum	38	182	498	718

Continued

Appendix Table 20, concluded, page 2 of 2

Sample	Morph R	 C	 O	N
AUG76D	2	3	19	24
SEP76D	0	7	34	41
OCT76D	2	15	30	47
NOV76D	7	3	30	40
MAY77D	2	4	30	36
JUNE77D	8	19	73	100
JULY77D	11	18	80	109
AUG77D	6	17	100	123
OCT77D	21	19	133	173
Sum	59	105	529	693

Appendix Table 21

Adult morph frequencies

Appendix Table 21. Distribution of morphs among representative adults from Appendix Table 19. Conventions as in Appendix Table 19. This Table extends over 2 pages.

Sample		Morph			N
		R	C	O	
AUG76A		129	7	302	438
SEP76A		80	3	367	450
OCT76A		60	8	161	229
NOV76A		23	3	48	74
MAY77A		39	3	162	204
JUNE77A		67	7	291	365
JULY77A		34	3	113	150
AUG77A		32	4	76	112
OCT77A		93	4	247	344
	Sum	557	42	1767	2366
AUG76L		57	3	191	251
SEP76L		69	1	261	331
OCT76L		55	5	196	256
NOV76L		38	11	117	166
MAY77L		72	6	291	369
JUNE77L		65	9	252	326
JULY77L		83	4	262	349
AUG77L		62	4	171	237
OCT77L		67	9	150	226
	Sum	568	52	1891	2511

Continued

Appendix Table 21, concluded, page 2 of 2

Sample		Morph		N
	R	C	O	
AUG76D	85	5	188	278
SEP76D	54	5	202	261
OCT76D	57	4	151	212
NOV76D	64	2	139	205
MAY77D	95	3	219	317
JUNE77D	57	1	219	277
JULY77D	93	0	186	279
AUG77D	40	5	140	185
OCT77D	52	1	117	170
Sum	597	26	1561	2184

Appendix Table 22

Juvenile morph percentages

Appendix Table 22. Data of Appendix Table 20 expressed as percentages. S, standard deviation. S^2, variance.

Morph	Site	Range, %	Mean, %	± S	S^2
R	A	2.9 - 11.7	6.4	2.9	8.66
	L	0 - 10.5	5.2	3.9	15.14
	D	0 - 17.5	7.9	5.1	25.67
C	A	10.0 - 28.7	20.7	5.2	26.49
	L	12.3 - 43.3	26.9	10.9	118.64
	D	7.5 - 31.9	15.6	7.1	50.06
O	A	67.3 - 78.3	72.9	3.8	14.59
	L	46.7 - 80.0	67.9	11.2	125.96
	D	63.8 - 83.3	76.5	6.2	37.87

Appendix Table 23

Adult morph percentages

Appendix Table 23. Data of Appendix Table 21 expressed as percentages. Conventions as in Appendix Table 22.

Morph	Site	Range, %	Mean, %	± s	s^2
R	A	17.8 - 31.1	24.5	5.1	26.10
	L	19.5 - 29.7	23.0	3.2	10.42
	D	20.6 - 33.3	27.3	5.0	25.22
C	A	0.7 - 4.1	2.2	1.2	1.43
	L	0.3 - 6.6	2.4	1.9	3.65
	D	0 - 2.7	1.2	0.9	0.78
O	A	64.9 - 81.6	73.3	5.9	35.25
	L	66.4 - 78.9	74.6	4.2	17.56
	D	66.7 - 79.1	71.5	4.7	21.80

Appendix Table 24

Monthly comparisons, juveniles, sites L v D

Appendix Table 24. Contingency tables and associated Chi-square values for monthly comparisons of juvenile morph frequencies at sites L versus D. Data are raw frequencies from Appendix Table 20. See text for September 1976, omitted from calculations at foot of table. P, significance.

Month	Site	Morph R	Morph C	Morph O	Chi-square	P	
AUG76	L	2	23	32			
	D	2	3	19	7.36	<0.05	*
SEP76	L	0	5	20			
	D	0	7	34	0.00	<1.0	NS
OCT76	L	1	16	55			
	D	2	15	30	3.50	<0.2	NS
NOV76	L	6	9	47			
	D	7	3	30	2.67	<0.3	NS
MAY77	L	3	13	14			
	D	2	4	30	10.04	<0.01	**
JUNE77	L	2	17	32			
	D	8	19	73	4.26	<0.2	NS
JULY77	L	6	41	85			
	D	11	18	80	8.55	<0.02	*
AUG77	L	6	44	125			
	D	6	17	100	5.58	<0.1	NS
OCT77	L	12	14	88			
	D	21	19	133	0.26	<0.9	NS

Total Chi-square (16 df)	42.22	P <0.001	***
Pooled Chi-square (2 df)	25.96	P <0.001	***
Heterogeneity Chi-square (14 df)	16.26	P >0.3	NS

Appendix Table 25

Monthly comparisons, adults, sites L v D

Appendix Table 25. Contingency tables and associated Chi-square values for monthly comparisons of adult morph frequencies at sites L versus D. Data are raw frequencies from Appendix Table 21.

Month	Site	Morph			Chi-square	P
		R	C	O		
AUG76	L	57	3	191		
	D	85	5	188	4.60	0.1 NS
SEP76	L	69	1	261		
	D	54	5	202	2.70	>0.2 NS
OCT76	L	55	5	196		
	D	57	4	151	1.72	>0.3 NS
NOV76	L	38	11	117		
	D	64	2	139	10.41	<0.01 **
MAY77	L	72	6	291		
	D	95	3	219	10.53	<0.01 **
JUNE77	L	65	9	252		
	D	57	1	219	6.52	<0.05 *
JULY77	L	83	4	262		
	D	93	0	186	10.71	<0.01 **
AUG77	L	62	4	171		
	D	40	5	140	1.66	>0.3 NS
OCT77	L	67	9	150		
	D	52	1	117	3.84	>0.1 NS

Total Chi-square (18 df)	52.69	P <0.001 ***
Pooled Chi-square (2 df)	17.96	Inappropriate
Heterogeneity Chi-square (16 df)	34.73	P <0.01 **

Appendix Table 26

Comparisons of juvenile and adult morph frequencies

Appendix Table 26. Totals from Appendix Tables 20 and 21 compared within sites by Chi-square (two degrees of freedom). J, juveniles. A, adults. All tests very highly significant (P <0.001).

Site	Age	Morph R	 C	 0	Chi-square
A	J	123	342	1257	
	A	557	42	1767	506.68
L	J	38	182	498	
	A	568	52	1891	510.18
D	J	59	105	529	
	A	597	26	1561	303.84

worked example:

Marginal totals for site A:

Juveniles, 1722 Adults, 2366 R, 680 C, 384 0, 3024 Sum, 4088

Expected frequencies from these totals:

Juveniles:	R, 286	C, 162	0, 1274	
Adults:	R, 394	C, 222	0, 1750	Sum, 4088

Cell values of Chi-square (***, P <0.001):

Juveniles:	R, 92.90 ***	C, 200.00 ***	0, 0.23 NS
Adults:	R, 67.43 ***	C, 145.95 ***	0, 0.17 NS

Sum of cell values, 506.68

Check: Total Chi-square = $\sum \frac{(\text{observed})^2}{\text{expected}} - n = 4594.68 - 4088 = 506.68$

Appendix Table 27

Polymodal size-frequency analysis, site A

Appendix Table 27. Results of probability paper analysis of the histograms shown in Figure 7, left column. See text for explanation of treatment of doubtful modes. x denotes month not common with sites L and D. Prop, estimated percentage in mode, with corresponding number in parentheses. Mean, estimated mean shell length (mm). S, estimated standard deviation (mm). Arbitrary values are underlined. OR, alternative solution; choice between alternatives was arbitrary - see text. These results are shown as Figure 8. This Table extends over 4 pages.

Sample		Prop		Mean	S
x APR75A		9	(123)	6.6	1.5
		46	(630)	9.8	1.5
	OR	55	(754)	9.4	1.7
		45	(617)	14.8	0.8
x MAY75A		3.4	(12)	5.6	0.4
		15.6	(55)	9.0	1.0
		15	(53)	11.9	0.9
		66	(232)	14.9	0.7
x JULY75A		6.5	(109)	4.5	1.1
		9.5	(159)	8.3	1.4
		16	(267)	11.8	1.1
		68	(1135)	14.9	1.0
x AUG75A		7	(50)	4.9	0.5
		9	(64)	7.5	1.0
	OR	16	(114)	6.3	1.8
		14	(99)	11.0	1.1
		70	(498)	14.8	1.0

continued

Appendix Table 27, continued, page 2 of 4

Sample	Prop		Mean	S
x SEP75A	30	(149)	5.8	0.8
	16	(79)	9.0	1.4
	54	(268)	14.5	1.2
x OCT75A	50	(346)	6.1	1.2
	8	(55)	10.0	1.0
	42	(291)	14.5	0.9
NOV75A	40	(312)	6.7	1.6
	18	(140)	12.5	1.4
	42	(328)	14.6	0.9
DEC75A	48	(632)	6.5	1.5
	18	(237)	12.5	1.8
	34	(448)	14.4	0.8
JAN76A	48	(592)	7.7	1.8
	16.6	(205)	13.3	1.2
	35.4	(436)	14.6	0.8
FEB76A	42	(859)	8.1	1.8
	58	(1186)	14.0	1.1
MAR76A	38	(413)	7.9	1.5
	62	(674)	13.8	1.1
APR76A	6	(41)	4.0	0.8
	50	(342)	8.5	1.7
	44	(300)	13.8	1.1
MAY76A	3	(24)	4.2	1.0
	34	(270)	9.4	1.8
	63	(499)	14.1	0.9

Appendix Table 27, continued, page 3 of 4

Sample		Prop		Mean	S
JUNE76A		18	(69)	4.2	1.2
		22	(85)	7.7	1.2
		10	(39)	11.0	0.8
	OR	24	(93)	12.1	1.5
		50	(193)	14.1	1.0
	OR	36	(139)	14.4	0.8
AUG76A		38	(385)	5.1	1.5
		6	(61)	9.3	0.5
		8	(81)	11.4	0.6
	OR	18	(182)	12.4	1.2
		48	(485)	14.1	0.8
	OR	38	(384)	14.3	0.7
SEP76A		24	(264)	5.3	1.3
		10	(110)	9.5	1.0
		66	(728)	13.4	1.4
OCT76A		28	(140)	5.9	1.6
		12	(60)	10.5	0.8
		60	(301)	13.6	0.9
NOV76A		40	(77)	6.3	1.7
		16	(31)	11.2	1.4
		44	(84)	13.7	0.6
x FEB77A		35	(292)	7.3	1.9
		23	(192)	12.5	1.4
		42	(351)	13.9	0.7
x APR77A		5	(37)	4.0	0.9
		30	(221)	9.0	2.1
		65	(479)	13.7	0.9

continued

Appendix Table 27, concluded, page 4 of 4

Sample	Prop		Mean	S
MAY77A	13	(55)	3.7	0.5
	17	(72)	7.0	1.3
	18	(77)	10.5	1.2
	52	(221)	14.1	0.8
JUNE77A	32	(245)	3.7	1.7
	8	(61)	8.8	0.9
	9	(69)	11.1	0.8
	OR 17	(130)	10.1	1.8
	51	(390)	14.4	0.8
JULY77A	54	(258)	4.6	1.6
	8	(38)	9.9	0.6
	6	(29)	12.1	0.5
	32	(153)	14.6	0.7
AUG77A	73	(428)	4.6	1.8
	5	(29)	10.5	1.2
	22	(129)	14.3	0.9
OCT77A	55	(519)	5.8	2.1
	5	(47)	10.8	0.8
	40	(378)	14.4	0.9

Appendix Table 28

Polymodal size-frequency analysis, site L

Appendix Table 28. Results of probability paper analysis of the histograms shown in Figure 7, centre column. See text for explanation of treatment of doubtful modes. x denotes month not common with sites A and D. Conventions as for Appendix Table 27. These results are shown as Figure 9. This Table extends over 3 pages.

Sample		Prop		Mean	S
NOV75L		22	(116)	6.2	1.6
		18	(95)	12.1	1.6
		60	(315)	14.7	0.9
DEC75L		26	(138)	6.5	1.4
		20	(106)	12.8	1.9
		54	(285)	14.7	0.8
JAN76L		25	(126)	7.5	1.4
		15	(75)	11.2	1.5
		60	(301)	14.4	0.8
	OR	27	(135)	7.7	1.6
		17.5	(88)	12.0	1.5
		55.5	(279)	14.5	0.8
FEB76L		23	(120)	8.0	1.4
		9	(47)	11.1	0.7
		68	(355)	14.6	0.9
MAR76L		40	(216)	9.2	2.0
		60	(325)	14.1	0.9
APR76L		49	(259)	8.7	1.7
		12	(63)	11.7	0.8
		39	(206)	14.2	0.9

continued

Appendix Table 28, continued, page 2 of 3

Sample	Prop		Mean	S
MAY76L	3.5	(19)	4.7	1.0
	11.5	(61)	8.4	1.4
	18	(96)	11.4	0.9
	67	(356)	14.4	0.9
JUNE76L	4	(22)	4.4	1.3
	7	(39)	7.8	1.0
	22	(123)	11.4	1.5
	67	(375)	14.5	0.8
AUG76L	15	(73)	4.9	1.5
	9	(44)	9.5	0.8
	14	(68)	11.6	0.5
	62	(301)	13.9	0.9
SEP76L	4.5	(26)	4.6	0.9
	6.5	(38)	8.0	0.9
	9	(52)	10.7	0.8
	80	(466)	13.5	1.0
OCT76L	19	(104)	5.3	1.3
	18	(99)	10.1	1.3
	63	(346)	13.6	1.0
NOV76L	31	(127)	6.3	1.3
	19	(78)	11.0	1.0
	50	(204)	13.7	0.8
x FEB77L	21	(106)	7.1	1.5
	23	(116)	12.2	1.4
	56	(283)	13.8	0.7

continued

Appendix Table 28, concluded, page 3 of 3

Sample	Prop		Mean	S
MAY77L	6	(31)	3.6	0.7
	6	(31)	8.3	0.6
	13	(66)	11.2	1.0
	75	(382)	14.3	0.9
JUNE77L	12	(64)	4.5	1.3
	17	(90)	10.2	1.1
	71	(378)	14.2	0.8
JULY77L	26	(168)	4.8	1.5
	8	(52)	8.8	1.0
	9	(58)	12.1	1.0
	57	(367)	14.5	0.8
AUG77L	44	(258)	5.2	1.7
	13	(76)	10.9	1.5
	43	(253)	14.4	0.8
OCT77L	49	(265)	6.5	1.9
	OR 34	(184)	5.6	1.4
	15	(81)	8.5	1.0
	8	(43)	11.9	1.0
	43	(233)	14.6	0.7

Appendix Table 29

Polymodal size-frequency analysis, site D

Appendix Table 29. Results of probability paper analysis of the histograms shown in Figure 7, right column. See text for explanation of treatment of doubtful modes. x denotes month not common with sites A and L. Conventions as for Appendix Table 27. These results are shown as Figure 10. This Table extends over 3 pages.

Sample		Prop		Mean	S
x SEP75D		4.5	(23)	6.9	0.8
		23.5	(120)	11.7	1.1
		72	(368)	14.5	0.8
x OCT75D		17	(91)	6.9	2.1
		13	(69)	12.1	1.4
		70	(373)	14.4	0.9
NOV75D		16.6	(88)	6.4	1.9
		18.4	(98)	12.2	1.6
		65	(345)	14.1	0.9
DEC75D		16	(85)	6.0	1.5
		20	(107)	11.8	2.0
		64	(341)	14.1	0.9
JAN76D		12	(62)	6.5	1.0
		8	(41)	8.7	0.5
	OR	20	(103)	7.5	1.8
		23	(119)	12.6	1.8
		57	(295)	14.1	0.8
FEB76D		26	(134)	6.7	1.3
		6	(31)	9.5	0.6
		18	(93)	11.9	0.7
		50	(256)	14.0	0.7

Appendix Table 29, continued, page 2 of 3

Sample	Prop		Mean	S
MAR76D	1.5	(8)	3.8	1.0
	25	(132)	7.8	1.1
	6.5	(34)	10.9	0.7
	67	(353)	13.7	1.0
APR76D	33	(172)	8.8	1.9
	67	(348)	13.6	0.9
MAY76D	4	(21)	4.0	0.8
	8	(41)	6.8	1.1
	28	(145)	10.3	1.0
	60	(312)	13.7	0.9
JUNE76D	4	(22)	3.9	0.3
	4.7	(25)	5.9	0.4
	15.3	(82)	8.7	0.6
	18	(97)	11.1	0.6
	58	(312)	13.8	0.9
AUG76D	4	(20)	4.4	0.4
	4	(20)	6.8	1.0
	8	(39)	9.8	0.7
	24	(118)	11.9	0.7
	60	(295)	14.0	0.7
SEP76D	11	(54)	5.1	1.3
	8	(39)	8.6	1.0
	22	(108)	11.8	1.0
	59	(290)	13.8	0.7
OCT76D	17	(83)	5.8	1.6
	33	(162)	11.1	1.4
	50	(246)	13.7	0.7

continued

Appendix Table 29, concluded, page 3 of 3

Sample	Prop		Mean	S
NOV76D	18	(90)	6.4	1.4
	22	(110)	10.6	1.0
	60	(300)	13.4	0.9
x APR77D	3	(15)	4.2	1.1
	25	(166)	9.7	1.6
	72	(337)	13.5	0.9
MAY77D	5.5	(29)	3.5	0.8
	6.5	(34)	6.8	1.0
	22.9	(119)	11.1	1.3
	65.1	(339)	14.0	0.7
JUNE77D	22	(114)	4.5	1.3
	9	(47)	9.5	1.1
	14	(73)	12.0	1.0
	55	(286)	14.2	0.8
JULY77D	30	(168)	5.5	1.2
	6	(34)	9.5	0.9
	9	(50)	11.8	0.6
	55	(309)	14.4	0.8
AUG77D	54	(287)	6.3	1.5
	7	(37)	10.5	1.0
	39	(208)	14.3	0.9
OCT77D	35	(217)	4.8	1.6
	33	(205)	8.2	1.4
	OR 68	(422)	6.5	2.3
	32	(198)	14.3	0.9

Appendix Table 30

Sex ratios at site A

Appendix Table 30. Numbers (N) and sex ratios (SR) in 1 mm size classes in 25 samples from site A. Sample codes as in Appendix Table 1. Blank, no snails. Dash, one sex only. T, snails used in tagging and not sexed. (T), N depleted by tagging. SRT, sex ratio of totals. This Table extends over 6 pages.

Sample	Size class, mm					
	3		4		5	
	N	SR	N	SR	N	SR
APR75A	6	0.20	12	0.20	25	1.08
MAY75A			3	0.50	6	0.50
JULY75A			33	0.10	28	0.56
AUG75A	2	-	25	-	22	0.16
SEP75A	2	-	24	-	69	0.35
OCT75A	9	0.13	57	0.12	109	0.58
NOV75A	6	0.20	30	0.58	70	0.89
DEC75A	27	-	72	0.38	135	0.67
JAN76A	16	0.23	28	0.56	54	1.00
FEB76A	8	0.33	32	0.52	68	0.94
MAR76A	6	-	15	0.88	27	0.69
APR76A	21	0.31	16	0.45	22	0.69
MAY76A	10	0.11	9	0.80	11	1.20
JUNE76A	31	0.11	21	0.11	17	0.55
AUG76A	72	0.18	110	0.36	110	0.64
SEP76A	45	0.07	67	0.18	78	0.37
OCT76A	17	0.42	23	0.64	39	0.63
NOV76A	8	0.14	8	0.60	18	0.64

continued

Appendix Table 30, continued, page 2 of 6

Sample	Size class, mm					
	3		4		5	
	N	SR	N	SR	N	SR
FEB77A	14	0.17	21	0.62	33	0.83
APR77A	19	0.58	13	0.63	21	1.10
MAY77A	40	0.38	15	0.88	15	0.50
JUNE77A	138	0.25	55	0.72	30	1.14
JULY77A	95	0.34	75	0.56	40	1.00
AUG77A	112	0.08	140	0.56	91	0.86
OCT77A	65	1.17	114	1.04	102	0.92
Sum	769		1,018		1,240	
Males	152		311		509	
Females	617		707		731	
SRT		0.25		0.44		0.70

continued

Appendix Table 30, continued, page 3 of 6

Sample	Size class, mm					
	6		7		8	
	N	SR	N	SR	N	SR
APR75A	46	0.84	90	1.09	159	1.01
MAY75A	3	0.50	10	1.00	15	0.67
JULY75A	34	0.70	40	0.82	43	0.87
AUG75A	21	0.62	29	0.93	11	2.67
SEP75A	45	0.73	28	1.33	23	1.09
OCT75A	96	0.75	56	0.51	25	1.08
NOV75A	87	0.61	55	0.83	41	0.86
DEC75A	176	0.89	129	1.19	69	0.82
JAN76A	115	0.80	131	1.02	115	0.80
FEB76A	18(T)	0.50	194	0.78	147	0.88
MAR76A	40(T)	1.00	113	1.17	97	1.20
APR76A	T		67	1.39	72	0.89
MAY76A	T		34	0.70	52	1.00
JUNE76A	24	2.00	27	0.59	22	0.69
AUG76A	16(T)	0.23	35	0.75	23	0.64
SEP76A	T		31	0.82	34	0.89
OCT76A	28	0.56	20	0.67	12	5.00
NOV76A	17	2.40	15	0.50	8	0.60
FEB77A	56	0.93	63	1.33	48	0.66
APR77A	T		T		T	
MAY77A	T		21	0.91	24	1.18
JUNE77A	T		19	1.38	20	1.50
JULY77A	T		13	1.17	5	0.67
AUG77A	45	0.73	24	0.71	14	1.33
OCT77A	96	0.71	65	1.03	50	0.85
Sum	963		1,309		1,129	
Males	424		638		546	
Females	539		671		583	
SRT		0.79		0.95		0.94

continued

Appendix Table 30, continued, page 4 of 6

Sample	Size class, mm					
	9		10		11	
	N	SR	N	SR	N	SR
APR75A	141	1.24	138	1.06	91	0.63
MAY75A	22	0.38	15	0.50	21	0.62
JULY75A	46	1.30	59	1.19	96	1.40
AUG75A	19	0.90	34	0.70	33	2.00
SEP75A	18	1.57	15	0.88	10	1.00
OCT75A	22	0.47	19	0.58	10	0.67
NOV75A	20	0.67	24	1.00	31	0.94
DEC75A	40	0.60	34	0.70	46	0.77
JAN76A	77	0.83	46	1.19	33	1.36
FEB76A	26(T)	1.00	80	1.05	85	1.13
MAR76A	10(T)	0.25	54	1.45	59	0.97
APR76A	T		44	0.91	36	0.71
MAY76A	T		60	0.76	50	1.08
JUNE76A	14	1.80	19	0.90	23	0.77
AUG76A	15(T)	0.88	25	1.50	47	1.35
SEP76A	T		60	0.76	95	1.07
OCT76A	20	1.22	27	1.25	33	1.75
NOV76A	9	1.25	4	0.33	13	0.30
FEB77A	40	0.67	39	2.00	48	1.18
APR77A	T		31	0.94	44	1.44
MAY77A	T		24	1.00	19	1.71
JUNE77A	T		31	0.94	28	0.65
JULY77A	T		15	0.50	13	1.60
AUG77A	10	2.33	11	1.20	7	1.33
OCT77A	24	1.40	28	0.87	19	1.11
Sum	573		936		990	
Males	279		465		506	
Females	294		471		484	
SRT		0.95		0.99		1.05

continued

Appendix Table 30, continued, page 5 of 6

Sample	Size class, mm					
	12		13		14	
	N	SR	N	SR	N	SR
APR75A	52	0.93	88	1.26	269	1.19
MAY75A	21	0.75	25	0.92	107	0.98
JULY75A	104	1.08	135	0.78	487	0.77
AUG75A	42	1.10	85	0.70	181	0.76
SEP75A	25	0.79	48	1.40	94	0.88
OCT75A	25	1.78	55	0.83	113	1.22
NOV75A	42	1.63	106	1.12	161	1.04
DEC75A	84	1.15	150	1.17	232	0.95
JAN76A	73	1.15	149	1.22	263	1.01
FEB76A	172	1.29	356	0.98	432	0.76
MAR76A	101	1.35	169	1.11	228	0.90
APR76A	42	2.00	95	0.94	109	0.91
MAY76A	48	0.92	164	0.91	206	0.75
JUNE76A	23	0.35	60	0.71	75	0.97
AUG76A	59	1.19	178	0.98	217	1.01
SEP76A	153	1.01	231	0.94	187	0.83
OCT76A	53	1.65	121	0.92	95	0.67
NOV76A	18	1.00	44	0.83	28	0.75
FEB77A	88	1.26	211	0.87	152	0.90
APR77A	79	1.63	200	0.85	158	0.76
MAY77A	23	1.30	82	1.34	95	1.02
JUNE77A	26	1.36	88	1.10	199	0.91
JULY77A	18	0.80	35	0.75	87	0.85
AUG77A	17	0.70	30	2.33	54	1.00
OCT77A	25	0.92	81	1.31	180	0.88
Sum	1,413		2,986		4,409	
Males	763		1,484		2,072	
Females	650		1,502		2,337	
SRT		1.17		0.99		0.89

continued

Appendix Table 30, concluded, page 6 of 6

Sample	Size class, mm			
	15		16^{+}	
	N	SR	N	SR
APR75A	208	0.82	45	0.45
MAY75A	89	0.89	15	0.67
JULY75A	412	0.79	110	0.80
AUG75A	162	0.91	45	0.96
SEP75A	82	1.22	13	2.25
OCT75A	87	0.89	9	0.29
NOV75A	88	0.69	19	0.73
DEC75A	109	1.02	14	0.75
JAN76A	115	1.30	18	0.64
FEB76A	158	0.98	20	0.67
MAR76A	81	1.03	4	3.00
APR76A	34	1.83		
MAY76A	70	1.33	7	0.75
JUNE76A	27	0.93	3	-
AUG76A	43	1.53	3	0.50
SEP76A	32	0.78	3	0.50
OCT76A	13	0.44		
NOV76A	2	-		
FEB77A	22	0.69		
APR77A	30	0.30	2	1.00
MAY77A	27	0.42	1	-
JUNE77A	78	0.56	8	0.14
JULY77A	28	0.65	2	1.00
AUG77A	28	0.87	3	0.50
OCT77A	83	0.60	12	0.50
Sum	2,108		356	
Males	984		150	
Females	1,124		206	
SRT		0.88		0.73

Appendix Table 31

Mean sex ratios at site A

Appendix Table 31. Data of Appendix Table 30 expressed as means. N, number of months used in calculation. MSR, mean sex ratio. S, standard deviation. Upper rows, all months used. Lower rows, only months having at least 40 snails used, to reduce distortion by small numbers (e.g., October 1976 8 mm, 5.00 - excluded from both rows).

Size class, mm	N	MSR	S	Range
3	19	0.28	0.25	0.07 - 1.17
	7	0.35	0.38	0.08 - 1.17
4	23	0.52	0.26	0.10 - 1.04
	8	0.49	0.30	0.12 - 1.04
5	25	0.74	0.27	0.16 - 1.20
	11	0.75	0.24	0.35 - 1.00
6	18	0.86	0.52	0.23 - 2.40
	10	0.80	0.12	0.61 - 1.00
7	24	0.94	0.27	0.50 - 1.39
	11	1.02	0.26	0.51 - 1.39
8	23	0.99	0.43	0.60 - 2.67
	11	0.90	0.44	0.66 - 1.20
9	18	1.04	0.53	0.25 - 2.33
	5	0.93	0.65	0.60 - 1.30
10	25	0.97	0.36	0.33 - 2.00
	8	1.05	0.24	0.76 - 1.45
11	25	1.10	0.42	0.30 - 2.00
	10	1.10	0.79	0.63 - 1.44
12	25	1.16	0.38	0.35 - 2.00
	15	1.29	0.31	0.92 - 2.00
13	25	1.05	0.33	0.70 - 2.33
	22	1.01	0.21	0.70 - 1.40
14	25	0.91	0.14	0.67 - 1.22
	24	0.91	0.14	0.67 - 1.22
15	24	0.90	0.36	0.30 - 1.83
	15	0.97	0.28	0.56 - 1.53
16^+	19	0.85	0.68	0.14 - 3.00

Appendix Table 32

Site A adult sex ratios

Appendix Table 32. 12.0 mm and larger snails in 25 samples from site A. Data condensed from Appendix Table 30. N, number. M, males; F, females. SR, sex ratio. Chi-square, Chi-square values (4 degrees of freedom unless subscript indicates otherwise) with significance. x denotes month lacking samples from both sites L and D, excluded from bottom line.

Month	N	M	F	SR	Chi-square	
x Apr75	662	328	334	0.98	10.98	$P < 0.05$ *
x May75	257	122	135	0.90	0.70	NS
x July75	1,248	556	692	0.80	2.77	NS
x Aug75	515	234	281	0.83	2.56	NS
x Sep75	262	137	125	1.10	3.89	NS
x Oct75	289	146	143	1.02	6.52	NS
Nov75	416	208	208	1.00	6.56	NS
Dec75	589	300	289	1.04	1.63	NS
Jan76	618	325	293	1.11	3.64	NS
Feb76	1,138	546	592	0.92	10.14	$P < 0.05$ *
Mar76	583	299	284	1.05	3.97	NS
Apr76	280	148	132	1.12	7.04_3	NS
May76	495	232	263	0.88	4.49	NS
June76	188	84	104	0.81	7.94	NS
Aug76	500	256	244	1.05	2.38	NS
Sep76	606	289	317	0.91	1.31	NS
Oct76	282	133	149	0.89	8.24_3	$P < 0.05$ *
Nov76	92	43	49	0.88	2.56_3	NS
x Feb77	473	228	245	0.93	2.74_3	NS
x Apr77	469	217	252	0.86	14.51	$P < 0.01$ **
May77	228	116	112	1.04	7.57	NS
June77	399	185	214	0.86	10.51	$P < 0.05$ *
July77	170	75	95	0.79	0.44	NS
Aug77	132	69	63	1.10	5.54	NS
Oct77	381	177	204	0.87	5.89	NS
Sum	11,272	5,453	5,819			
Less x	7,097	3,485	3,612			

Appendix Table 33

Site L adult sex ratios

Appendix Table 33. 12.0 mm and larger snails in 18 samples from site L. Format as in Appendix Table 32. x denotes month not common with sites A and D, excluded from bottom line.

Month	N	M	F	SR	Chi-square	
Nov75	366	192	174	1.10	3.36	NS
Dec75	354	182	172	1.06	3.67	NS
Jan76	323	157	166	0.95	2.08	NS
Feb76	358	182	176	1.03	3.00	NS
Mar76	342	176	166	1.06	7.76	NS
Apr76	234	135	99	1.36	6.46	NS
May76	379	177	202	0.88	6.02	NS
June76	415	194	221	0.88	8.05	NS
Aug76	314	162	152	1.07	10.31	$P < 0.05$ *
Sep76	436	211	225	0.94	9.38	NS
Oct76	325	164	161	1.02	6.97	NS
Nov76	217	105	112	0.94	13.79_3	$P < 0.01$ **
x Feb77	349	150	199	0.75	3.26	NS
May77	392	225	167	1.35	7.50_3	NS
June77	367	183	184	0.99	0.57	NS
July77	398	185	213	0.87	2.79	NS
Aug77	270	122	148	0.82	3.63	NS
Oct77	253	128	125	1.02	3.17	NS
Sum	6,092	3,030	3,062			
Less x	5,743	2,880	2,863			

Appendix Table 34

Site D adult sex ratios

Appendix Table 34. 12.0 mm and larger snails in 20 samples from site D. Format as in Appendix Table 32. x denotes month not common with sites A and L, excluded from bottom line.

Month	N	M	F	SR	Chi-square	
x Sep75	421	195	226	0.86	1.91	NS
x Oct75	407	192	215	0.89	3.54	NS
Nov75	395	202	193	1.05	1.89	NS
Dec75	375	178	197	0.90	5.04	NS
Jan76	369	175	194	0.90	1.00	NS
Feb76	298	135	163	0.83	9.95	P <0.05 *
Mar76	336	173	163	1.06	4.59_3	NS
Apr76	334	169	165	1.02	0.62_3	NS
May76	291	138	153	0.90	1.74	NS
June 76	308	154	154	1.00	0.80_3	NS
Aug76	350	169	181	0.93	0.93	NS
Sep76	328	147	181	0.81	0.87_3	NS
Oct76	286	124	162	0.77	3.00_3	NS
Nov76	280	133	147	0.90	3.39_3	NS
x Apr77	333	182	151	1.21	9.34_3	P <0.05 *
May77	363	183	180	1.02	0.41_3	NS
June77	319	163	156	1.04	1.81	NS
July77	324	169	155	1.09	4.92	NS
Aug77	204	108	96	1.13	8.13	NS
Oct77	194	91	103	0.88	6.34	NS
Sum	6,515	3,180	3,335			
Less x	5,354	2,611	2,743			

Appendix Table 35

Mean adult sex ratios, all samples

Appendix Table 35. Sex ratios of Appendix Tables 32 to 34 expressed as means. N, number of months. MSR, mean sex ratio. S, standard deviation.

Site	N	MSR	S	Range
A	25	0.95	0.11	0.79 - 1.12
L	18	1.01	0.16	0.75 - 1.36
D	20	0.96	0.11	0.77 - 1.21

Appendix Table 36

t-tests for Appendix Table 35

Appendix Table 36. Mean sex ratios shown in Appendix Table 35 compared pairwise by t-tests (equal variances assumed). DF, degrees of freedom. Significance, result of test with probability; N.T., not tested.

Sites	t	DF	Significance			
			2 tails		1 tail	
A v L	1.50	41	A = L	P >0.10	A = L	P >0.05
A v D	0.33	43	A = D	P >0.20	N.T.	
L v D	1.25	36	L = D	P >0.20	L = D	P >0.10

Appendix Table 37

Monthly comparisons of total adult frequencies

Appendix Table 37. Results of Chi-square tests, comparing the relative numbers of adult males and females in sites A, L and D in the 17 months having samples from all three sites, and results of similar tests comparing sites L and D only. Tests have two and one degree of freedom respectively. All tests are non-significant (P >0.05).

Month	A v L v D		L v D	
Nov75	0.51		0.19	
Dec75	1.51		1.07	
Jan76	2.85		0.09	
Feb76	2.00		2.00	
Mar76	0		0	
Apr76	2.72		2.93	
May76	0.03		0.03	
June76	1.46		0.82	
Aug76	1.05		0.60	
Sep76	1.07		1.05	
Oct76	3.19		3.19	
Nov76	0.14		0.04	
May77	4.37		3.61	
June77	1.71		0.09	
July77	3.61		2.24	
Aug77	3.25		2.79	
Oct77	1.12		0.58	
Total Chi-square (d.f.)	30.59 (34)	P >0.5	21.32 (34)	P >0.9
Pooled	2.39 (2)	P >0.3	2.09 (1)	P >0.1
Heterogeneity	28.20 (32)	P >0.5	19.23 (33)	P >0.9

Appendix Table 38

Resin survivorship

Appendix Table 38. Survivorship summary for resin-tagged adults released 16 October 1975. Conventions as in Appendix Table 10. This Table extends over 2 pages.

Sex	Cohort (mm)	N	A	Slope, x 10^{-3}	SE(EST)
M	13	30	4.572 (0.097)	7.06 (0.57)	0.177
	14	100	4.611 (0.110)	9.53 (0.64)	0.200
	16^+	20	4.483 (0.147)	15.16 (2.02)	0.216
	Pooled	150	4.573 (0.110)	9.04 (0.64)	0.201
F	13	26	4.669 (0.122)	10.51 (0.71)	0.222
	14	100	4.702 (0.098)	9.00 (0.57)	0.178
	16^+	24	4.583 (0.024)	15.89 (0.32)	0.035
	Pooled	150	4.626 (0.072)	9.04 (0.42)	0.131

		R^2	F (d.f.)	P(F)	
M	13	0.944	153.678 (1, 8)	<0.001	***
	14	0.961	220.787 (1, 8)	<0.001	***
	16^+	0.932	56.167 (1, 3)	<0.005	**
	Pooled	0.956	196.525 (1, 8)	<0.001	***
F	13	0.960	217.056 (1, 8)	<0.001	***
	14	0.965	248.956 (1, 8)	<0.001	***
	16^+	0.998	2425.189 (1, 3)	<0.001	***
	Pooled	0.981	465.720 (1, 8)	<0.001	***

continued

Appendix Table 38, concluded, page 2 of 2

Resin Calendar

release	16 October 1975	day 0
capture	29 October	13
	30 November	45
	12 January 1976	88
	22 February	129
	24 March	160
	17 April	184
	24 May	221
	23 June	251
	19 August	308
	30 September	350
	3 November	384
	1 December	412
	14 February 1977	487
	30 March	531
	14 May	576
	16 June	609
	11 July	634
	7 August	661
	8 October	723

Appendix Table 39

Long-life individual growth data

Appendix Table 39. Individual growth increments, growth rates, and k for individually paint-numbered snails recaptured regularly for at least eight months. Data calculated for periods of sustained growth. M, males; F, females. Go, initial size (mm). Inc, length increase (mm). T, time span of growth (days). Inc/T, growth rate (mm per day, x 10^{-3}). k, growth parameter (days^{-1}, x 10^{-3}) assuming l^{∞} = 18.0 mm. Curve, illustrated in Figure 49.

Sex	Go	Inc	T	Inc/T	k	Curve
M	12.2	1.4	150	9.33	1.84	E
	12.2	2.2	460	4.78	1.04	B
	12.3	0.7	61	11.48	2.15	F
	12.4	1.1	123	8.94	1.78	
	12.7	0.8	96	8.33	1.70	
	12.7	1.9	134	14.18	3.31	A
	12.9	0.7	91	7.69	1.62	D
	12.9	1.1	156	7.05	1.56	C
F	12.0	1.6	106	15.09	2.93	
	12.0	1.8	148	18.92	2.41	H
	12.3	0.6	67	8.96	1.66	K
	12.5	0.7	91	7.69	1.50	I[a]
	12.5	1.4	91	15.38	3.23	
	12.5	1.4	135	10.37	2.18	
	12.5	2.2	147	14.97	3.48	G
	12.6	0.6	104	5.77	1.13	
	12.6	0.7	96	7.29	1.45	J
	13.2	0.5	75	6.67	1.47	I[b]

[a] initial rise

[b] renewed growth

Appendix Table 40

Rapid growth data

Appendix Table 40. Individual growth increments, growth rates, and k for individually paint-numbered snails growing at least 2 mm after tagging. Data calculated for periods of sustained growth, normally days 84 - 175 (approximately). Conventions as in Appendix Table 39. Curve, illustrated in Figure 50. ±, excluded when computing means.

Sex	Go (mm)	Inc (mm)	T (days)	Inc/T (mm/day, x 10^{-2})	k (days^{-1}, x 10^{-3})	Curve
M	12.1	1.9	91	2.09	4.28	
	12.2	1.5	90	1.67	3.32	D
	12.2	2.1	130	1.62	3.46	E[a] ±
	12.5	0.9	84	1.07	2.13	b
	12.5	1.5	91	1.65	3.50	C
	12.5	2.4	91	2.64	6.30	A
	12.6	1.1	91	1.21	4.15	E[c]
	12.7	1.1	91	1.21	2.56	d ±
	12.7	1.9	148	1.28	3.00	e
	12.7	2.2	91	2.42	5.89	B
F	12.2	1.5	60	2.50	4.98	K[f]
	12.2	2.3	91	2.53	5.55	
	12.3	2.0	91	2.20	4.75	G
	12.4	1.8	91	1.98	4.26	
	12.5	1.7	90	1.89	4.10	
	12.6	1.5	90	1.67	3.57	J
	12.6	1.9	61	3.12	7.11	
	12.7	1.7	90	1.89	4.30	I
	12.8	2.2	106	2.08	5.19	F[g]
	12.9	1.7	91	1.87	4.45	
	13.0	2.0	91	2.20	5.62	
	13.0	2.0	91	2.20	5.62	h ±
	13.3	1.3	90	1.44	3.59	H

[a] release to 175; [b] Fig. 49 curve B; [c] day 84 value interpolated: compare [d] day 175 value estimated: compare (f); [e] days 84-232; [f] level end segment disregarded: days 85-145; [g] days 69-175: compare (h); [h] curve F with ~~day 84 value interp~~olated.

Appendix Table 41

Paint survivorship

Appendix Table 41. Survivorship summary for paint-numbered adults released in February and March 1976, with 24 March taken as origin. Conventions as in Appendix Table 38. Points, days included in regression, recalculated as shown in Figure 51. N, number on 24 March.

Sex	Points	N	A	Slope, x 10^{-3}	SE(EST)
M	0 - 148	224	4.598 (0.041)	7.01 (0.49)	0.057
	0 - 252		4.871 (0.199)	12.78 (1.31)	0.326
	0 - 474		4.414 (0.227)	8.20 (0.81)	0.458
	371 - 474		4.470 (0.101)	7.73 (0.24)	0.018
	0 - 148 + 371 - 474		4.662 (0.035)	8.16 (0.12)	0.066
F	0 - 148	222	4.659 (0.052)	7.90 (0.62)	0.072
	0 - 416		4.702 (0.147)	10.69 (0.63)	0.281
	190 - 416		3.662 (0.133)	7.58 (0.43)	0.086

Sex	Points	R^2	F(d.f.)	P(F)	
M	0 - 148	0.985	201.182 (1, 3)	<0.001	***
	0 - 252	0.941	95.207 (1, 6)	<0.001	***
	0 - 474	0.895	103.512 (1, 11)	<0.001	***
	371 - 474	0.998	1076.176 (1, 2)	<0.001	***
	0 - 148 + 371 - 474	0.999	4755.849 (1, 7)	<0.001	***
F	0 - 148	0.982	160.940 (1, 3)	<0.001	***
	0 - 416	0.970	289.869 (1, 9)	<0.001	***
	190 - 416	0.987	304.885 (1, 4)	<0.001	***

LITERATURE CITED

Abbreviations generally follow the World List of Scientific Periodicals, 4th Ed., 1960. Titles in foreign languages are given in full.

Studies published before 1966, and many thereafter, may confound L. obtusata s.s. and L. mariae. X denotes work known or thought likely to be based on a mixture of these species.

For comprehensive bibliography see Pettitt 1974.

Alifierakis, N.S. & A.J. Berry 1980 Rhythmic egg-release in Littorina littorea (Mollusca: Gastropoda). J. Zool., Lond. 190 (3): 297 - 307

Ayala, F.J. 1972 Competition between species. Am. Scient. 60 (3): 348 - 357

X Bakker, K. 1960 Feeding habits and zonation in some intertidal snails. Archives Néerlandaises de Zoologie 13 (2): 230 - 257

Ballantine, W.J. 1961 A biologically-defined exposure scale for the comparative description of rocky shores. Fld. Stud. 1 (3): 1 - 19

X Bandel, K. 1974 Studies on Littorinidae from the Atlantic. Veliger 17 (2): 92 - 114

X Barkman, J.J. 1955 On the distribution and ecology of Littorina obtusata (L.) and its subspecific units. Archives Néerlandaises de Zoologie 11 (1): 22 - 86

Baudoin, M. 1975 Host castration as a parasitic strategy. Evolution, Lancaster, Pa. 29 (2): 335 - 352

Bengtson, S.-A., A. Nilsson, S. Nordström & S. Rundgren 1976
Polymorphism in relation to habitat in the snail *Cepaea hortensis* in Iceland.
J. Zool., Lond. 178 (2): 173 - 188

Bequaert, J.C. 1943 The genus *Littorina* in the western Atlantic.
Johnsonia 1 (7): 1 - 27

X Berger, E.M. 1973 Gene-enzyme variation in three sympatric species of *Littorina*.
Biol. Bull. Mar. Biol. Lab., Woods Hole 145 (1): 83 - 90

X Berger, E.M. 1977 Gene-enzyme variation in three sympatric species of *Littorina*. II. The Roscoff population, with a note on the origin of North American *L. littorea*.
Biol. Bull. Mar. Biol. Lab., Woods Hole 153 (2): 255 - 264

Berry, R.J. & J.H. Crothers 1974 Visible variation in the dog-whelk, *Nucella lapillus*.
J. Zool., Lond. 174 (1): 123 - 148

Bertness, M.D. 1977 Behavioral and ecological aspects of shore-level size gradients in *Thais lamellosa* and *Thais emarginata*.
Ecology 58 (1): 86 - 97

Borkowski, T.V. 1974 Growth, mortality, and productivity of South Floridian Littorinidae (Gastropoda: Prosobranchia).
Bull. mar. Sci. 24 (2): 409 - 438

X Bray, C.J. 1974 A study of the mobility of *Littorina obtusata* (L.)
M.Sc. thesis, Univ. Wales viii + 81 pp.

Bryant, E.H. 1976 A Comment on the Role of Environmental Variation in Maintaining Polymorphisms in Natural Populations.
Evolution, Lancaster, Pa. 30 (1): 188 - 190

Cain, A.J. & P.M. Sheppard 1950 Selection in the polymorphic land snail Cepaea nemoralis.
Heredity, Lond. 4 (3): 275 - 294

Cameron, R.A.D. & P. Williamson 1977 Estimating migration and the effects of disturbance in mark-recapture studies on the snail Cepaea nemoralis L.
J. Anim. Ecol. 46 (1): 173 - 179

Carter, M.A., R.C.V. Jeffery, & P. Williamson 1979 Food overlap in co-existing populations of the land snails Cepaea nemoralis (L.) and Cepaea hortensis (Müll).
Biol. J. Linn. Soc. 11 (2): 169 - 176

Cassie, R.M. 1954 Some uses of probability paper in the analysis of size-frequency distributions.
Aust. J. Mar. Freshwater Res. 5 (3): 513 - 522

Clarke, B. 1962 Natural selection in mixed populations of two polymorphic snails.
Heredity, Lond. 17 (3): 319 - 345

Clarke, B. 1975 The causes of biological diversity.
Scient. Am. 233 (2): 50 - 60

Clarke, B. 1979 The evolution of genetic diversity.
Proc. R. Soc. B 205 (1161): 453 - 474

Cloern, J.E. & F.H. Nichols 1978 A von Bertalanffy Growth Model with a Seasonally Varying Coefficient.
J. Fish. Res. Bd. Can. 35 (11): 1479 - 1482

Creese, R.G. & A.J. Underwood 1976 Observations on the biology of the trochid gastropod Austrocochlea constricta (Lamarck) (Prosobranchia).
I. Factors affecting shell-banding pattern.
J. exp. mar. Biol. Ecol. 23 (3): 211 - 228

Crothers, J.H. 1975 On variation in Nucella lapillus (L.): shell shape in populations from the south coast of England.
Proc. malac. Soc. Lond. 41 (6): 489 - 498

X Daguzan, J. 1976a Contribution à l'étude de la croissance et de la longévité de quelques Littorinidae (Mollusques Gastéropodes Prosobranches).
Archives de Zoologie expérimentale et génerale 117 (1): 57 - 80
(In French, with brief prefaces in French and English but no true abstract or summary. Title, studies on the growth and longevity of several Littorinidae (Mollusca, Gastropoda, Prosobranchia).)

Daguzan, J. 1976b Contribution à l'écologie des Littorinidae (Mollusques Gastéropodes Prosobranches). I. Littorina neritoides (L.) et Littorina saxatilis (Olivi).
Cahiers de Biologie Marine 17 (2): 213 - 236
(In French, with very brief summaries in English and Italian. Title, studies on the ecology of Littorinidae (Mollusca, Gastropoda, Prosobranchia), etc.)

X Daguzan, J. 1976c Contribution à l'écologie des Littorinidae (Mollusques Gastéropodes Prosobranches). II. Littorina littorea (L.) et Littorina littoralis (L.).
Cahiers de Biologie Marine 17 (3): 275 - 293
(In French, with telegraphic English summary. Title, same as 1976b.)

Dalby, D.H., E.B. Cowell, W.J. Syratt, & J.H. Crothers 1978 An exposure scale for marine shores in western Norway.
J. mar. biol. Ass. U.K. 58 (4): 975 - 996

Ebert, T.A. 1980 Estimating parameters in a flexible growth equation, the Richards function.
Can. J. Fish. Aquat. Sci. 37 (4): 687 - 692

Elner, R.W. 1980 The Influence of Temperature, Sex and Chela Size in the Foraging Strategy of the Shore Crab, Carcinus maenas (L.). Mar. Behav. & Physiol. 7: 15 - 24

Elner, R.W. & R.N. Hughes 1978 Energy maximization in the diet of the shore crab, Carcinus maenas. J. Anim. Ecol. 47 (1): 103 - 116

Elner, R.W. & D.G. Raffaelli 1980 Interactions between two marine snails, Littorina rudis Maton and Littorina nigrolineata Gray, a predator, Carcinus maenas (L.), and a parasite, Microphallus similis Jägerskiold. J. exp. mar. Biol. Ecol. 43 (2): 151 - 160

Emson, R.H. & R.J. Faller-Fritsch 1976 An experimental investigation into the effect of crevice availability on abundance and size-structure in a population of Littorina rudis (Maton): Gastropoda: Prosobranchia. J. exp. mar. Biol. Ecol. 23 (3): 285 - 297

Falk, J.H. 1974 Estimating experimentor-induced bias in field studies: a cautionary tale. Oikos 25 (3): 374 - 378

Feare, C.J. 1970 Aspects of the ecology of an exposed shore population of dogwhelks Nucella lapillus (L.). Oecologia 5 (1): 1 - 18

Ferguson, G.A. 1966 Statistical Analysis in Psychology and Education. 2nd ed. Toronto, McGraw-Hill, x + 446 pp.

Gendron, R.P. 1977 Habitat selection and migratory behaviour of the intertidal gastropod Littorina littorea (L.). J. Anim. Ecol. 46 (1): 79 - 92

Gibson, J.S. 1970 The function of the operculum of Thais lapillus (L.) in resisting desiccation and predation.
J. Anim. Ecol. 39 (1): 159 - 168

Giesel, J.T. 1970 On the maintenance of a shell pattern and behavior polymorphism in Acmaea digitalis, a limpet.
Evolution, Lancaster, Pa. 24 (1): 98 - 119

Giesel, J.T. 1971 The relations between population structure and rate of inbreeding.
Evolution, Lancaster, Pa., 25 (3): 491 - 496

Gillespie, J.H. 1975 The role of migration in the genetic structure of populations in temporarily (sic) and spatially varying environments. I. Conditions for polymorphism
Am. Nat. 109 (966): 127 - 135

Goodhart, C.B. 1977 Symposium on polymorphism in Gastropoda: concluding remarks.
Malacologia 16 (1): 47

Goodwin, B.J. 1978 The growth and breeding cycle of Littorina obtusata (Gastropoda: Prosobranchiata) from Cardigan Bay.
J. molluscan Stud. 44 (2): 231 - 242

Goodwin, B.J. 1979 The egg mass of Littorina obtusata and Lacuna pallidula (Gastropoda: Prosobranchia).
J. molluscan Stud. 45 (1): 1 - 11

Goodwin, B.J. & J.D. Fish 1977 Inter- and intraspecific variation in Littorina obtusata and L. mariae (Gastropoda: Prosobranchia).
J. molluscan Stud. 43 (3): 241 - 254

Grahame, J. 1969 Shedding of the Penis in Littorina littorea.
Nature, Lond. 221 (5184): 976

Gromko, M.H. 1977 What is frequency-dependent selection? Evolution, Lancaster, Pa. 31 (2): 438 - 442

Grüneberg, H. 1979 A search for causes of polymorphism in Clithon oualaniensis (Lesson) (Gastropoda; Prosobranchia). Proc. R. Soc. B 203 (1153): 379 - 386

Guiterman, J.D. 1971 The Population Biology of Littorina obtusata (L.) (Gastropoda: Prosobranchiata). unpub. Ph.D. thesis, Univ. Wales vii + 167 pp.

Hamilton, P.V. 1976 Predation on Littorina irrorata (Mollusca: Gastropoda) by Callinectes sapidus (Crustacea: Portunidae). Bull. mar. Sci. 26 (3): 403 - 409

Hamilton, P.V. 1978 Intertidal Distribution and Long-Term Movements of Littorina irrorata (Mollusca: Gastropoda). Mar. Biol. 46 (1): 49 - 58

Harvey, P.H., N. Birley & T.H. Blackstock 1975 The effect of experience on the selective behaviour of song thrushes feeding on artificial populations of Cepaea (Held). Genetica 45 (2): 211 - 216

Heath, D.J. 1975 Colour, Sunlight and Internal Temperatures in the Land-Snail Cepaea nemoralis (L.). Oecologia 19 (1): 29 - 38

Heller, J. 1975a The taxonomy of some British Littorina species, with notes on their reproduction. Zool. J. Linn. Soc. 56 (2): 131 - 151

Heller, J. 1975b Visual selection of shell colour in two littoral prosobranchs. Zool. J. Linn. Soc. 56 (2): 153 - 170

Heller, J. 1976 The effects of exposure and predation on the shell of two British winkles.
J. Zool. 179 (2): 201 - 213

Heppell, D. 1974 The naming of winkles: an historical synopsis. Paper to symposium "Taxonomic Trends in the Littorinidae", 19 March 1974, abstracted in:
C.W. Pettitt, ed., Littorinid Tidings 1: 2 - 3 (mimeo, avail. Pettitt, The Museum, Univ. Manchester, Manchester M13 9PL, England.

Hilborn, R. & C.J. Krebs 1976. Fates of disappearing individuals in flucturating populations of *Microtus townsendii*.
Can. J. Zool. 54 (9): 1507 - 1518

Hoagland, K.E. 1977 A gastropod color polymorphism: one adaptive strategy of phenotypic variation.
Biol. Bull. mar. biol. Lab., Woods Hole 152 (3): 360 - 372

X Holland, D.L., R. Tantanasiriwong, & P.J. Hannant 1975 Biochemical Composition and Energy Reserves in the Larvae and Adults of the Four British Periwinkles *Littorina littorea*, *L. littoralis*, *L. saxatilis*, and *L. neritoides*.
Mar. Biol. 33 (3): 235 - 239

Hughes, R.N. mimeo Von Bertalanffy growth equation: algebraic manipulations plus notes on the Gompertzian growth function.
(author is at School of Animal Biology, UCNW, Bangor, Gwynedd LL57 2UW, Wales).

Hughes, R.N. 1979 Optimal diets under the energy maximization premise: the effects of recognition time and learning.
Am. Nat. 113 (2): 209 - 221

Hughes, R.N. 1980 Population dynamics, growth and reproductive rates of Littorina nigrolineata Gray from a moderately sheltered locality in North Wales.
J. exp. mar. Biol. Ecol. 44 (2/3): 211 - 228

Hughes, R.N. & R.W. Elner 1979 Tactics of a predator, Carcinus maenas, and morphological responses of the prey, Nucella lapillus.
J. Anim. Ecol. 48 (1): 65 - 78

Hughes, R.N. & D.J. Roberts 1980 Growth and reproductive rates of Littorina neritoides (L.) in North Wales.
J. mar. biol. Ass. U.K. 60 (3): 591 - 599

Hughes, R.N. & D.J. Roberts 1981 Comparative demography of Littorina rudis, L. nigrolineata and L. neritoides on three contrasted shores in North Wales.
J. Anim. Ecol. 50 (1): 251 - 268

X Janssen, C.R. 1960 The influence of temperature on geotaxis and phototaxis in Littorina obtusata (L.).
Archives Néerlandaises de Zoologie 13 (4): 500 - 510

Johnson, G.B. 1971 Metabolic Implications of Polymorphism as an Adaptive Strategy.
Nature, Lond. 232 (5309): 347 - 348

Jones, W.E. & A. Demetropoulos 1968 Exposure to wave action: measurements of an important ecological parameter on rocky shores on Anglesey.
J. exp. mar. Biol. Ecol. 2 (1): 46 - 63

Kitching, J.A. & J. Lockwood 1974 Observations on Shell Form and its Ecological Significance in Thaisid Gastropods of the Genus Lepsiella in New Zealand.
Mar. Biol. 28 (2): 131 - 144

Kitching, J.A., L. Muntz, & F.J. Ebling 1966 The ecology of Lough Ine. XV. The ecological significance of shell and body forms in Nucella.
J. Anim. Ecol. 35 (1): 113 - 126

Knight, W. 1968 Asymptotic Growth: An Example of Nonsense Disguised as Mathematics.
J. Fish. Res. Bd. Can. 25 (6): 1303 - 1307

X Knudsen, J. 1949 Geographical Variation of Littorina obtusata (L.) in the North-Atlantic.
Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kobenhavn 111: 247 - 255

Kuris, A.M. 1974 Trophic interactions: similarity of parasitic castrators to parasitoids.
Q. Rev. Biol. 49 (2): 129 - 148

Laver, J., Co. Ltd. 1980 Laver's Liverpool Tide Table
leaflet, 16 pp.

Lubchenco, J. 1978 Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities.
Am. Nat. 112 (983): 23 - 39

Macdonald, P.D.M. & T.J. Pitcher 1979 Age-groups from size-frequency data: a versatile and efficient method of analysing distribution mixtures.
J. Fish. Res. Bd. Can. 36 (8): 987 - 1001

Manchester, University of, Regional Computer Centre: see UMRCC.

Manly, B.J.F. 1971 Estimates of a marking effect with capture-recapture sampling.
J. appl. Ecol. 8 (1): 181 - 189

Mann, K.H. 1973 Seaweeds: Their Productivity and Strategy for Growth. Science, N.Y. 182 (4116): 975 - 981

Mathieson, A.C., J.W. Shipman, J.R. O'Shea, & R.C. Hasevlat 1976 Seasonal growth and reproduction of estuarine fucoid algae in New England.
J. exp. mar. Biol. Ecol. 25 (3): 273 - 284

Maynard Smith, J. 1962 Disruptive selection, polymorphism and sympatric speciation.
Nature, Lond. 195 (4836): 60 - 62

Maynard Smith, J. 1966 Sympatric speciation.
Am. Nat. 100 (916): 637 - 650

McDonald, J.F. & F.J. Ayala 1974 Genetic response to environmental heterogeneity.
Nature, Lond. 250 (5467): 572 - 574

X McMahon, R.F. & W.D. Russell-Hunter 1974 Responses to low oxygen stress in relation to the ecology of littoral and sublittoral snails.
Biol. Bull. mar. biol. Lab., Woods Hole 147 (2): 490

X McMahon, R.F. & W.D. Russell-Hunter 1977 Temperature relations of aerial and aquatic respiration in six littoral snails in relation to their vertical zonation.
Biol. Bull. mar. biol. Lab., Woods Hole 152 (2): 182 - 198

Miller, S.L. 1974 Adaptive design of locomotion and foot form in prosobranch gastropods.
J. exp. mar. Biol. Ecol. 14 (2): 99 - 156

Moebus, K., K.M. Johnson, & J. McN. Sieburth 1974 Rehydration of Desiccated Intertidal Brown Algae: Release of Dissolved Organic Carbon and Water Uptake.
Mar. Biol. 26 (2): 127 - 134

Murray, J. & B. Clarke 1978 Changes of gene frequency in *Cepaea nemoralis* over fifty years.
Malacologia 17 (2): 317 - 330

Newkirk, G.F. & R.W. Doyle 1975 Genetic Analysis of Shell-Shape Variation in *Littorina saxatilis* on an Environmental Cline.
Mar. Biol. 30 (3): 227 - 237

Nie, N.H., C.H. Hull, J.G. Jenkins, K. Steinbrenner, & D.H. Bent 1975 *SPSS: statistical package for the social sciences*. 2nd Ed.
New York, McGraw-Hill, xxiv + 675 pp.

Palmer, A.R. 1980 Locomotion rates and shell form in the Gastropoda: a re-evaluation.
Malacologia 19 (2): 289 - 296

Pettitt, C.W. 1974 An Indexed Bibliography of the Family Littorinidae (Gastropoda: Mollusca) 1758 - 1973.
Manchester Museum Publications NS 4.74 36 pp
(Subsequent additions available from author, Manchester Museum, University of Manchester, Manchester M13 9PL, England.)

Pettitt, C.W. 1975 A review of the predators of *Littorina*, especially those of *L. saxatilis* (Olivi) (Gastropoda: Prosobranchia).
J. Conch., Lond. 28 (6): 343 - 357

Pinder, J.E. III, J.G. Wiener, & M.H. Smith 1978 The Weibull distribution: a new method of summarizing survivorship data.
Ecology 59 (1): 175 - 179

X Pohley, W.J. 1976 Relationships among Three Species of *Littorina* and Their Larval Digenea.
Mar. Biol. 37 (2): 179 - 186

Raffaelli, D.G. 1978a The relationship between shell injuries, shell thickness and habitat characteristics of the intertidal snail Littorina rudis Maton.
J. molluscan Stud. 44 (2): 166 - 170

Raffaelli, D.G. 1978b Factors affecting the population structure of Littorina neglecta Bean.
J. molluscan Stud. 44 (2): 223 - 230

Raffaelli, D.G. 1979 Colour polymorphism in the intertidal snail Littorina rudis Maton.
Zool. J. Linn. Soc. 67 (1): 65 - 73

Raffaelli, D.G. & R.N. Hughes 1978 The effects of crevice size and availability on populations of Littorina rudis and Littorina neritoides.
J. Anim. Ecol. 47 (1): 71 - 83

Reimchen, T.E. 1974 Studies on the biology and colour polymorphism of two sibling species of marine gastropod (Littorina).
Ph.D. thesis, Univ. Liverpool v + 389 pp.

Reimchen, T.E. 1979 Substratum heterogeneity, crypsis, and colour polymorphism in an intertidal snail (Littorina mariae).
Can. J. Zool. 57 (5): 1070 - 1085

Richardson, A.M.M. 1975 Winter predation by thrushes, Turdus ericetorum (Turton), on a sand dune population of Cepaea nemoralis (L.).
Proc. malac. Soc. Lond. 41 (6): 481 - 488

Roberts, D.J. & R.N. Hughes 1980 Growth and Reproductive Rates of Littorina rudis from Three Contrasted Shores in North Wales, UK.
Mar. Biol. 58 (1): 47 - 54

Rohlf, F.J. & R.R. Sokal 1969 Statistical Tables
San Francisco, Freeman xi + 253 pp.

X Russell-Hunter, W.D. & R.F. McMahon 1974 Patterns of aerial and aquatic respiration in relation to vertical zonation in four littoral snails.
Biol. Bull. mar. biol. Lab., Woods Hole 147 (2): 496 - 497

Sacchi, C.F. 1967 Sur les variations du rapport des sexes au cours de l'année chez Littorina obtusata L. (Gastropoda, Prosobranchia).
Comptes Rendus Hebdomadaires des Séances de L'Académie des Sciences, Paris 264 (Série D: Sciences Naturelles): 1504 - 1506
(In French, with French abstract. Title, seasonal variations in sex ratio of, etc.)

Sacchi, C.F. 1969 Recherches sur l'écologie comparée de Littorina obtusata (L.) et de Littorina mariae Sacchi et Rast. (Gastropoda, Prosobranchia) en Galice et en Bretagne.
Investigacion Pesquera, consejo superior de investigaciones cientificas (Barcelona) 33 (1): 381 - 413
(In French, with English summary (p. 412). Title, studies on the comparative ecology of ...... in Galicia and Brittany.)

Sacchi, C.F. & M. Rastelli 1966 Littorina mariae, nov. sp.; les différences morphologiques et écologiques entre "nains" et "normaux" chez l'"espèce" L. obtusata (L.) (Gastr., Prosobr.) et leur signification adaptive et évolutive.
Atti Della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano 105 (4): 351 - 369
(In French, with Italian and English summaries, and Latin and French diagnoses. Title, L. mariae, nov. sp., the adaptive and evolutionary meaning of morphological and ecological differences between "dwarf" and "normal" forms of the "species" L. obtusata (L.) (Gastropoda, Prosobranchia).)

Sainsbury, K.J. 1980 Effect of individual variability on the von Bertalanffy growth equation.
Can. J. Fish. Aquat. Sci. 37 (2): 241 - 247

Schoener, T.W. 1974 Resource Partitioning in Ecological Communities.
Science, N.Y. 185 (4145): 27 - 39

Schonbeck, M.W. & T.A. Norton 1978 Factors controlling the upper limits of fucoid algae on the shore.
J. exp. mar. Biol. Ecol. 31 (3): 303 - 313

Schonbeck, M.W. & T.A. Norton 1979 An Investigation of Drought Avoidance in Intertidal Fucoid Algae.
Botanica mar. 22 (3): 133 - 144

Schonbeck, M.W. & T.A. Norton 1980a The Effects on Intertidal Fucoid Algae of Exposure to Air under Various Conditions.
Botanica mar. 23 (3): 141 - 147

Schonbeck, M.W. & T.A. Norton 1980b Factors controlling the lower limits of fucoid algae on the shore.
J. exp. mar. Biol. Ecol. 43 (2): 131 - 150

Scudder, G.G.E. 1974 Species concepts and speciation.
Can. J. Zool. 52 (9): 1121 - 1134

Seed, R. 1978 Observations on the adaptive significance of shell shape and body form in dogwhelks (Nucella lapillus (L.)) from N. Wales.
Nature in Wales 16 (2): 111 - 122

Smith, D.A.S. 1975 Polymorphism and selective predation in Donax faba Gmelin (Bivalvia: Tellinacea).
J. exp. mar. Biol. Ecol. 17 (2): 205 - 219

Smith, D.A.S. 1976 Disruptive selection and morph-ratio clines in the polymorphic snail Littorina obtusata (L.) (Gastropoda: Prosobranchia).
J. molluscan Stud. 42 (1): 114 - 135

SMITH, J.E. & G.E. NEWELL 1955 THE DYNAMICS OF THE ZONATION OF THE COMMON PERIWINKLE (LITTORINA LITTOREA (L.)) ON A STONY BEACH.
J. ANIM. ECOL. 24 (1): 35-56.

Soans, A.B., D. Pimentel, & J.S. Soans 1974 Evolution of reproductive isolation in allopatric and sympatric populations.
Am. Nat. 108 (959): 117 - 124

Sokal, R.R. & F.J. Rohlf 1969 Biometry. The Principles and Practice of Statistics in Biological Research.
San Francisco, Freeman xxi + 776 pp.

Spight, T.M. 1973 Ontogeny, environment, and shape of a marine snail *Thais lamellosa* Gmelin.
J. exp. mar. Biol. Ecol. 13 (3): 215 - 228

Spight, T.M. 1976 Colors and patterns of an intertidal snail, *Thais lamellosa*.
Res. Popul. Ecol. Kyoto Univ. 17 (2): 176 - 190

Struhsaker, J.W. 1968 Selection Mechanisms Associated with Intraspecific Shell Variation in *Littorina picta* (Prosobranchia: Mesogastropoda).
Evolution, Lancaster, Pa. 22 (3): 459 - 480

Taylor, L.R. & R.A.J. Taylor 1977 Aggregation, migration and population mechanics.
Nature, Lond. 265 (5593): 415 - 421

Thomas, J.S. 1974 The Effect of the Rediae of *Cryptocotyle lingua* (Creplin, 1825) (Digenea: Heterophyidae) and *Himasthla leptosoma* (Creplin, 1829) (Digenea: Echinostomatidae) on the Glycogen and Free Sugar Levels of the Digestive Gland and Gonad of *Littorina littorea* (Linnaeus, 1758) (Gastropoda: Prosobranchia).
Veliger 17 (2): 207 - 210

Thompson, W.A. & I. Vertinsky 1975 Bird flocking revisited: the case with polymorphic prey.
J. Anim. Ecol. 44 (3): 755 - 765

UMRCC (University of Manchester Regional Computer Centre) 1980a
SPSS at UMRCC.
Manchester, UMRCC, iv + 51 pp.

UMRCC 1980b SPSS Version 7 Procedures Volume1 - Regression.
Manchester, UMRCC, vii + 67 pp.

X Underwood, A.J. 1972 Tide-model analysis of the zonation of intertidal Prosobranchs. I. Four species of *Littorina* (L.).
J. exp. mar. Biol. Ecol. 9 (3): 239 - 255

X Underwood, A.J. 1973 Studies on zonation of intertidal prosobranch molluscs in the Plymouth region.
J. Anim. Ecol. 42 (2): 353 - 372

Underwood, A.J. & R.G. Creese 1976 Observations on the biology of the trochid gastropod *Austrocochlea constricta* (Lamarck) (Prosobranchia). II. The effects of available food on shell-banding pattern.
J. exp. mar. Biol. Ecol. 23 (3): 229 - 240

X Van Dongen, A. 1956 The preference of *Littorina obtusata* for Fucaceae.
Archives Néerlandaises de Zoologie 11 (3): 373 - 386

Vermeij, G.J. 1972 Intraspecific shore-level size gradients in intertidal molluscs.
Ecology 53 (4): 693 - 700

Vermeij, G.J. 1973a Coral Reef Project - Papers in Memory of Dr. Thomas F. Goreau. 15. West Indian molluscan communities in the rocky intertidal zone: a morphological approach.
Bull. mar. Sci. 23 (2): 351 - 386

Vermeij, G.J. 1973b Morphological Patterns in High Intertidal Gastropods: Adaptive Strategies and their Limitations.
Mar. Biol. 20 (4): 319 - 346

Vermeij, G.J. 1974 Marine faunal dominance and molluscan shell form. Evolution, Lancaster, Pa. 28 (4): 656 - 664

Vermeij, G.J. 1979 Shell Architecture and Causes of Death of Micronesian Reef Snails. Evolution, Lancaster, Pa. 33 (2): 686 - 696

Vermeij, G.J. & J.D. Currey 1980 Geographical variation in the strength of thaidid snail shells. Biol. Bull. mar. biol. Lab., Woods Hole 158 (3): 383 - 389

von Bertalanffy, L. 1960 Principles and theory of growth. Ch. 2, pages 137 - 259, in: W.W. Nowinski, ed., Fundamental aspects of normal and malignant growth. Amsterdam, Elsevier.

X Walton, C.L. 1915 The Distribution of some Littoral Trochidae and Littorinidae in Cardigan Bay. J. mar. biol. Ass. U.K. 10 (1): 114 - 122

Wilkins, N.P. & D. O'Regan 1980 Genetic Variation in Sympatric Sibling Species of Littorina. Veliger 22 (4): 355 - 359

Williams, I.C. & C. Ellis 1975 Movements of the common periwinkle, Littorina littorea (L.), on the Yorkshire coast in winter and the influence of infection with larval Digenea. J. exp. mar. Biol. Ecol. 17 (1): 47 - 58

Williamson, P., R.A.D. Cameron, & M.A. Carter 1977 Population dynamics of the landsnail Cepaea nemoralis L.: a six-year study. J. Anim. Ecol. 46 (1): 181 - 194

X Young, M.L. 1975 The transfer of ^{65}Zn and ^{59}Fe along a Fucus serratus (L.) → Littorina obtusata (L.) food chain.
J. mar. biol. Ass. U.K. 55 (3): 583 - 610

Zipser, E. & G.J. Vermeij 1978 Crushing behavior of tropical and temperate crabs.
J. exp. mar. Biol. Ecol. 31 (2): 155 - 172